Climate-driven regime shifts in a mangrove–salt marsh ecotone over the past 250 years

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Climate change is driving the tropicalization of temperate ecosystems by shifting the range edges of numerous species poleward. Over the past few decades, mangroves have rapidly displaced salt marshes near multiple poleward mangrove range limits, including in northeast Florida. It is uncertain whether such mangrove expansions are due to anthropogenic climate change or natural climate variability. We combined historical accounts from books, personal journals, scientific articles, logbooks, photographs, and maps with climate data to show that the current ecotone between mangroves and salt marshes in northeast Florida has shifted between mangrove and salt marsh dominance at least 6 times between the late 1700s and 2017 due to decadal-scale fluctuations in the frequency and intensity of extreme cold events. Model projections of daily minimum temperature from 2000 through 2100 indicate an increase in annual minimum temperature by 0.5 °C/decade. Thus, although recent mangrove range expansion should indeed be placed into a broader historical context of an oscillating system, climate projections suggest that the recent trend may represent a more permanent regime shift due to the effects of climate change.

mangroves | climate change | regime shift | historical ecology

Numerous studies have linked increases in atmospheric and oceanic temperatures to changes in the abundance, distribution, phenology, and community composition of terrestrial and marine taxa (1, 2). These changes have been particularly pronounced at zones of transition, that is, ecotones, between temperate and tropical ecosystems, as range expansion of tropical species has led to a "tropicalization" of temperate ecosystems (3, 4). While much attention has focused on the impacts of changing mean temperatures, there is an increasing understanding that discrete events such as heat waves or hard freezes can drive ecological change at these ecotones (5, 6). Furthermore, over the past few decades annual minimum and maximum temperatures have increased faster than mean temperatures (7). However, most studies that have documented the ecological impacts of climate extremes have been based on a single episode, as it is difficult to obtain long-term time series of events that are, by definition, rare. As a result, it can be difficult to identify the thresholds associated with ecosystem response and to determine the degree to which climate change has impacted the frequency and intensity of these events.

The transition zone between mangrove- and salt marsh–dominated coastal wetlands provides an ideal case study to examine tropicalization of ecosystems. The global distribution of these 2 ecosystems is largely determined by climate. Mangroves are limited to tropical, subtropical, and some temperate regions, while salt marshes dominate higher latitudes (8). However, some mangrove range limits are associated with rainfall rather than temperature gradients (9). In recent decades, there have been observations of mangroves expanding into salt marshes in tropical–temperate transition zones around the world (10). Some mangrove expansions have been linked to changes in climatic factors thought to set the poleward range limits of mangroves, namely increases in air temperature, decreases in the frequency and intensity of freezes, and changes in rainfall patterns (6, 11).

Rapid, large-scale conversion of herbaceous salt marsh to woody mangroves, or vice versa, is an ecological regime shift as these changes will have considerable impacts on physical and biological processes. For example, increases in mangrove cover may increase carbon storage and facilitate higher rates of sediment accretion in response to sea level rise (12). On the other hand, mangrove expansion may lead to a loss of habitat for certain fauna, including some species of migratory birds that require open vegetation structure (12). These habitat changes are also likely to impact the community structure of fish, invertebrates, and other species that inhabit these coastal wetlands.

The Atlantic coast of northeast Florida is an example of a mangrove–salt marsh transition zone that has seen significant changes over the past few decades. We define this ecotone as the coastal wetlands between the most northern population of mangroves at present, Fort George Inlet, 30.41°N, and the southern end of Merritt Island at 28.00°N (Fig. 1 and *SI Appendix*). In this region, wetlands typically consist of mangroves interspersed with salt marsh vegetation. Three species of mangroves are found in Florida: *Avicennia germinans*, *Rhizophora mangle*, and

Significance

In recent years, tropical species have expanded poleward into temperate regions. For example, along the east coast of North America, mangroves have expanded into salt marshes in response to decreases in the frequency of extreme freezes. But questions remain about how mangrove abundance has changed over longer timescales and the role of anthropogenic climate change. We used a mixed methods approach to document a series of climate-driven shifts in mangrove abundance over the past 250 y. However, climate model projections suggest warming may push this fluctuating system toward a persistent state of mangrove dominance. This historical approach can be applied to a variety of ecosystems to place the effects of climate change in the context of long-term natural climate variability.

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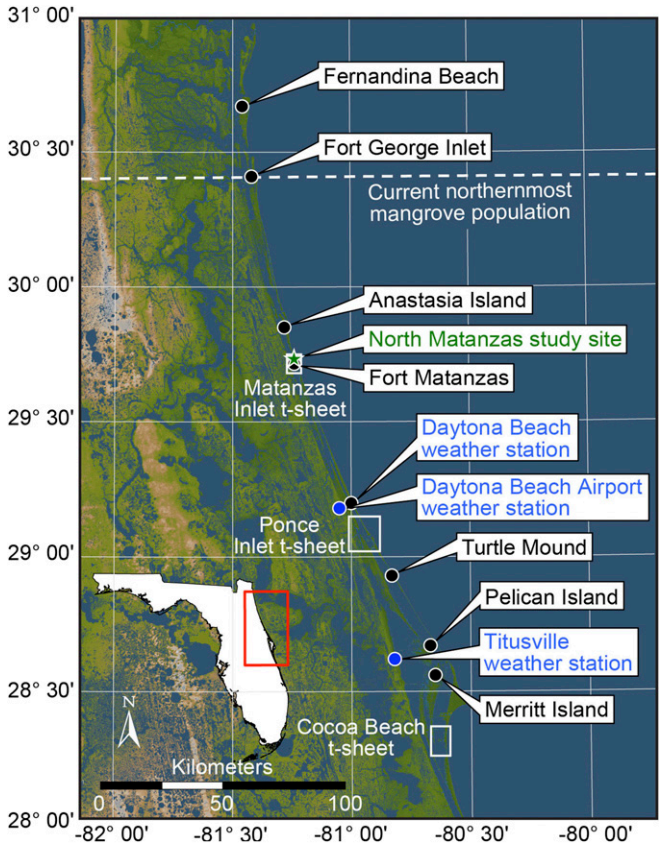

Fig. 1. Map of the mangrove–salt marsh ecotone region on the northeast coast of Florida. The North Matanzas study site is labeled in green, locations of t-sheets are identified by white boxes, weather stations used to reconstruct T_{min} and FDD are labeled in blue, and other landmarks mentioned in historical data are labeled in black.

Laguncularia racemosa. *Avicennia germinans* is considered to be the most tolerant to cold temperatures (13, 14) and forms the northernmost population at Fort George Inlet (*SI Appendix*). The northernmost populations of *R. mangle* and *L. racemosa* are found about 40 km south of Fort George Inlet. Mangrove distributions in this region appear to be strongly regulated by temperature (9, 15), and since the early 1990s, a decrease in the frequency of extreme cold events has led to a doubling of mangrove area (6). While these changes are consistent with expectations of warming due to anthropogenic climate change, there were a series of hard freezes throughout the 1980s that caused widespread mortality of mangroves across the southeast United States (16), and recent mangrove expansion may simply represent a recovery from those events associated with natural climate oscillations (17, 18).

In this study we used a mixed methods approach to document variability in mangrove abundance in northeastern Florida from the late 1700s to 2016. We combined remote sensing, climate data, and historical data to extend previous decadal-scale studies of mangrove dynamics in this region (e.g., refs. 6 and 18) to over 250 y. We developed a temperature-based model of mangrove suitability by comparing aerial surveys of mangroves to climate station data. This model was used to hindcast mangrove suitability in the Florida mangrove–salt marsh ecotone. We then validated the hindcast model with a variety of historical datasets dating from the late 1700s. Finally, climate model simulations were used to examine how future increases in temperature may impact mangrove suitability in this region.

Extreme Freezes Lead to Decreases in Mangrove Abundance

Previous laboratory experiments identified a temperature threshold of −3.2 °C that was associated with mangrove mortality in northeast Florida (13, 14). This threshold was used to create a metric called freezing degree-days (FDD) that integrates frequency and severity of mangrove-damaging freeze events. FDD are the cumulative degree-days below −3.2 °C calculated using daily minimum temperatures (see *Methods* for details). We combined daily minimum temperature from climate stations located in Daytona Beach and Titusville, Florida, and National Oceanic and Atmospheric Administration (NOAA) 20th Century Reanalysis data to calculate annual T_{min} (the coldest day of the year) and annual FDD at Daytona Beach from 1850 to 2017. This station was selected because of the length and continuity of its climate record. However, Daytona Beach is in the southern part of the ecotone (Fig. 1), so the northern portions likely experienced slightly colder minimum temperatures than are reported here. Between 1850 and 2016, mean annual T_{min} was −1.7 °C, and the mean annual FDD was 2.6. Both of these metrics were highly variable (SD = 2.8 °C and 5.9, respectively; Fig. 2*A*). Especially severe freezes occurred in the winters of 1894/1895, 1904/1905, 1939/1940, 1980/1981, 1984/1985, and 1989/1990 (FDD = 22.2, 14.3, 44.4, 16.1, 21.1, and 16.7, respectively; Fig. 2*B*).

Aerial photos collected between 1942 and 2013 of North Matanzas (29.73°N, 81.24°W; Fig. 1), a coastal wetland near the mangrove range limit in Florida, show a series of transitions between mangrove and salt marsh dominance (Fig. 2*C* and ref. 19). In 1942, 2 y after extreme freezes during the winter of 1939/1940, North Matanzas was dominated by salt marsh. Over the next decade, mangroves expanded across the site. Moderate freezes in the late 1960s corresponded to a slight reduction in mangrove area in 1971. Then a series of hard freezes during the 1980s preceded a return of salt marsh dominance by the early 1990s. Over the past 2 decades, relatively mild winters with few hard freeze events have facilitated mangrove expansion. Changes in mangrove area at North Matanzas corresponded negatively to cumulative FDD during the 10 y prior to each observation ($y = 18.69e^{-0.03x}$; R^2 = 0.48, *SI Appendix*, Fig. S1). This relationship supports the hypothesis that mangrove distribution and abundance in this ecotonal region are controlled by winter temperature extremes (9,

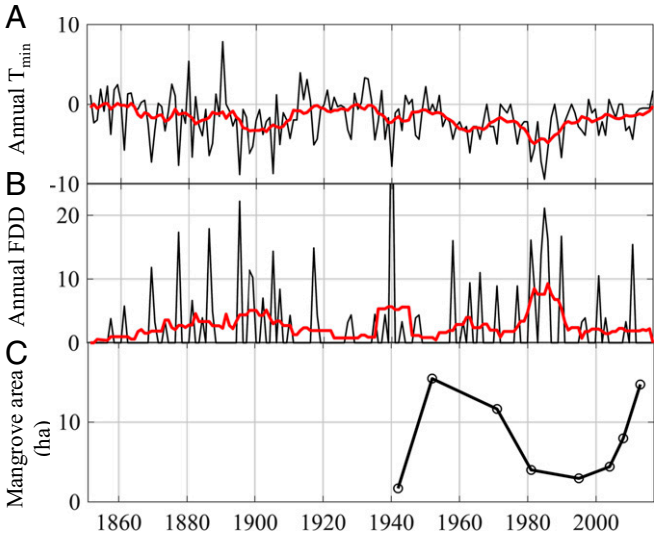

Fig. 2. Time series of (*A*) annual T_{min}, that is, the coldest day of the year at Daytona Beach, (*B*) annual cumulative FDD at Daytona Beach, and (*C*) mangrove area at the North Matanzas study site. Red lines in *A* and *B* represent 10-y moving average.

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15). We summed FDD during the 10 y prior to each observation in order to account for the cumulative effect of multiple cold winters and potential lags in mangrove recovery. There is still relatively high uncertainty in this relationship due to the low number of sample points, variability in the resistance of different mangrove life stages and phenotypes to freezing temperatures (13, 20), and/or processes that control the dispersal and recruitment of mangroves (21), which would lead to variability in recovery rates in between freezes.

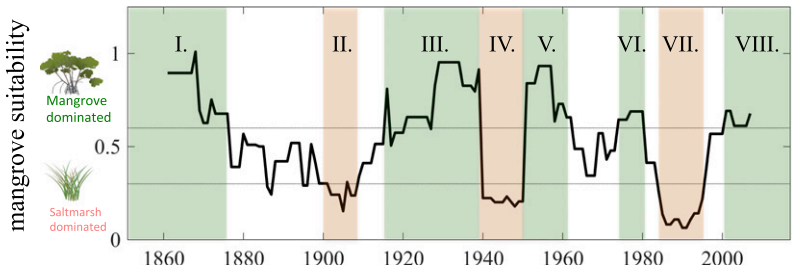
Previous Regime Shifts

The severe freezes in 1940 and the 1980s were large-scale events that had major impacts throughout Florida (19, 22–24). Therefore, mangrove responses to these events at the North Matanzas site likely reflect responses throughout the mangrove–salt marsh ecotone in northeastern Florida. As such, we used the relationship between mangrove cover at North Matanzas and FDD (*SI Appendix*, Fig. S1) along with our daily temperature record to estimate mangrove suitability in coastal wetlands across the Florida ecotone between 1850 and 2016 (Fig. 3). While this model is a somewhat qualitative estimate of mangrove suitability, it still enables us to identify a series of temperature-driven regime shifts.

We used historical accounts from books, personal journals, scientific journal articles, logbooks, photographs, and historical maps collected between the mid-1700s and 2018 to test whether these rare and disparate observational records supported our mangrove suitability reconstructions. See *Methods* and *SI Appendix* for more details about these historical records. Below, we identify 6 regime shifts in our reconstructed mangrove suitability time series and describe the historical evidence that supports or contradicts the existence of these transitions (Fig. 3).

Mangrove Dominance in 1700s and 1800s. There is evidence that mangroves were widespread across the ecotone between the late 1700s and the early 1800s (prior to the start of our reconstructed time series of mangrove suitability). In 1766, botanist William Bartram documented black mangroves (*A. germinans*) on Anastasia Island (29.8°N, 81.2°W), near the current mangrove range limit (25). Between the late 1700s and early 1800s there were other reports of mangroves on Anastasia Island (29.71°N to 29.91°N, 81.23°W to 81.29°W; ref. 26), Turtle Mound (28.93°N, 80.83°W; ref. 26), and Pelican Island (29.159°N; ref. 27). In addition, written descriptions from the late 1700s of Fort Matanzas, a site near the current mangrove range limit, describe the region as a mix of marsh and mangroves (28).

In February 1835, a freeze occurred that damaged citrus farms across the southeast (24). Following that winter, Jacob Motte documented islands of dead mangroves in Mosquito Lagoon (29.03°N, 80.92°W), which, based on his description, were *R. mangle* islands (29). Some mangroves recovered after this freeze, with J. L. Williams (30) reporting the occurrence of live mangroves in 1839 at the same location where Motte documented dead *R. mangle* mangroves. This freeze may have facilitated localized salt marsh expansion, although it is unclear if this led to a regional regime shift back to marsh dominance. If so, any period of salt marsh dominance was likely short-lived. No other significant freeze events were reported between 1835 and 1867, when John Muir described "clumps of mangrove and forests of moss-dressed, strange trees appearing low in the distance" near Fernandina Beach (30.67°N), which is ~25 km north of the current northernmost mangrove population (31). This is the only record we found of mangroves farther north than their current range limit (Fig. 1). Moreover, other records also include references to mangroves along the northeastern coast of Florida between 1839 and 1887 (30, 32). Our temperature records start in 1850 and show a pronounced lack of extreme cold events between 1850 and 1867 (mean and SD of annual T_{min} = −0.16 and 2.3 °C, mean and SD of annual FDD = 0.56 and 1.6). Our model estimates that mangrove suitability in the ecotonal region was especially high at this time (Fig. 3).



Date	Dominance	Evidence
mid 1800s	I. mangroves	• Mangroves listed in description of Fort Matanzas from late 1700s (28) • Observations of mangroves across ecotone (27, 30, 32) • Mangroves near Fernandina Beach, north of current range limit (31)
1900-1910	II. saltmarsh	• Decline in mangrove cover at Matanzas Inlet between 1867 and 1872 • Photos of Fort Matanzas between 1900-1915 show lack of mangroves • Freezes in 1894/1895 devastated citrus industry in Florida (24)
1920s-1930s	III. mangroves	• Observations of mangroves on Merritt Island (36) • Mangrove present in photos of Fort Matanzas from late 1920s • Increase in mangrove cover at Ponce de Leon Inlet between 1874 and 1928
1940s	IV. saltmarsh	• Low mangrove cover at North Matanzas (19) • Decline in mangrove cover at Cocoa Beach between 1928 and 1949
1950-1960 & late 1970s	V. & VI. mangroves	• Increases in mangrove cover at Ponce de Leon Inlet between 1928 and 1957 • Mangroves abundant on map of Matanzas Inlet from 1957 • Increases in mangrove cover at North Matanzas (19)
mid-1980s	VII. saltmarsh	• Decreases in mangrove cover at North Matanzas (19) • Freezes during the 1980s devastated citrus industry in central Florida (23) • Declines in mangrove cover across southeast USA (18, 22, 37)
2000- 2016	VIII. mangroves	• Increases in mangrove cover at North Matanzas (19) • Mangrove expansion across southeast USA (6, 38, 37, 39)

Fig. 3. Modeled time series of mangrove suitability and evidence for regime shifts.

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Transition to Salt Marsh Dominance in Late 1800s. During winter 1894/1895, severe freezes destroyed citrus crops across Florida (24) and caused large-scale mortality of mangroves. A study of Florida manatees in the Indian River, ∼60 km south of the ecotone (33), noted that after the winter of 1894/1895 "nearly every [mangrove] tree along the whole stretch of the Indian River was killed to the ground." Prior to the 1894/1895 freeze, *A. germinans* in northeastern Florida were an important source of honey, and there are reports of how the freezes destroyed entire stands of honey-producing trees (34, 35). In addition, photos taken of Fort Matanzas between 1900 and 1915 show that this site was dominated by salt marsh, with no mangroves visible near the fort (Fig. 4*A* and *SI Appendix*, Fig. S2*A*). After these severe freezes, we found no written records of mangroves occurring in northeastern Florida until 1927, when (36) reported seaside sparrows nesting in mangroves on Merritt Island (28.3°N, 80.7°W), considerably farther south than earlier records.

Leading up to the winter of 1894/1895, our model shows a relativity gradual decline in mangrove suitability starting in the late 1860s that is not well supported by historical evidence (Fig. 3). During this time, our historical climate reconstruction identified particularly cold winters in 1868/1869, 1876/1877, and 1885/1886 (FDD = 11.8, 17.3, and 17.9, respectively). However, Florida citrus growers documented no major impact of freezes during this period, and we did not find other written evidence of mangrove mortality events. Our reconstructed time series of daily temperature prior to 1900 is based on NOAA 20th Century Reanalysis data rather than climate station observations, so there is more uncertainty in the pre-1900 FDD record.

Transition to Mangrove Dominance Between 1920 and 1930. Our model indicates that a lack of hard freezes over the next few decades led to increases in mangrove suitability by the early 1920s. Photos of Fort Matanzas show that by the late 1920s mangroves had colonized marshy areas around the fort (Fig. 4*B* and *SI Appendix*, Fig. S2*B*). We also observed an increase in mangrove area between 1874 and 1928 on historical t-sheet maps of Ponce Inlet (*SI Appendix*, Table S1 and Fig. S3).

Transition to Salt Marsh Dominance Following 1940 Freeze. The winter of 1940 was exceptionally cold. The annual minimum temperature during this winter was −7.8 °C, and there was an especially high frequency of freezing events, resulting in a total of 44.4 FDD, which is by far the highest winter total recorded during our time series (Fig. 2*B*). Vegetation maps at Cocoa Beach show a large decline in mangrove cover between 1928 and 1949 (*SI Appendix*, Table S1 and Fig. S4). Additionally, our aerial imagery time series of the North Matanzas site begins in 1942, and this first image exhibited the lowest amount of mangrove cover of all 8 image dates (Fig. 2*C*).

Transition to Mangrove Dominance in 1950s. As described above, Rodriguez et al.'s (19) time series of aerial imagery at North Matanzas shows an increase in mangrove area at this site between 1942 and 1952. Winters between 1942 and 1952 were particularly warm; the mean annual T_{min} during this 10-y time period was −0.94 °C, and the mean FDD was only 0.89. Also, there were at least 3 hurricanes during the 1940s that traveled up the east coast of Florida, which could have acted to promote long-distance dispersal of mangrove propagules from southern Florida into the northern Florida ecotone (21). The lack of extreme freezes during this period likely facilitated the recovery of plants that survived the 1940 freeze and enabled the recruitment of new mangrove seedlings.

NOAA t-sheet vegetation maps of Matanzas Inlet and Ponce Inlet also show mangrove expansion during this period. Mangrove area increased from 9 to 48 ha between 1872 and 1957 at Matanzas Inlet (*SI Appendix*, Table S1 and Fig. S5) and from 450 to 1,400 ha between 1928 and 1957 at Ponce Inlet (*SI Appendix*, Table S1 and Fig. S3).

Transition to Salt Marsh Dominance in 1980s. The aerial imagery time series from (19) shows mangrove area declining from 1952 through 1995. The decline was gradual at first but increased rapidly during the 1980s, a decade with particularly frequent extreme cold events. The period from 1980 to 1989 had the highest mean FDD of any 10-y period during the temperature time series (9.3). Winter 1984/1985 had the coldest minimum

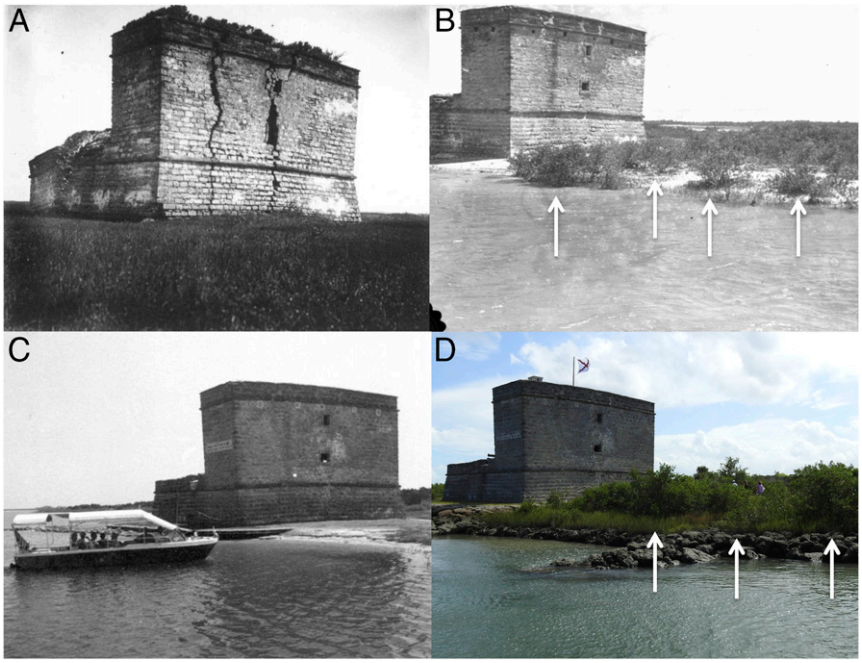

Fig. 4. Photographs of the rear of Fort Matanzas taken in (*A*) 1900 to 1915, (*B*) 1934, (*C*) 1981, and (*D*) 2018. Black mangroves (*Avicennia germinans*) are identified with white arrows on *B* and *D*.

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temperature (−9.4 °C) of any year on record. Other extreme freezes occurred in 1980/1981, 1983/1984, and 1989/1990. The combined effect of multiple freezes during the 1980s was likely especially harmful to mangroves in the ecotone.

These freezes had impacts across the southeastern United States. Other studies have documented significant mangrove mortality along the Atlantic and Gulf of Mexico coasts in response to the cold events of the 1980s (18, 22, 37). In addition to reducing mangrove cover across the ecotone, freezes during the 1980s devastated citrus farming in central Florida (23).

Transition to Mangrove Dominance in 2000s. There was a reduction in the frequency of extreme cold events from the early 1990s to 2016, which corresponded to mangrove expansion across northern Florida (6, 19) as well as the Gulf of Mexico coasts of Florida, Louisiana, and Texas (37–39). Pictures of Fort Matanzas show a substantial expansion of mangroves at this site between 1981 and 2018 (Fig. 4 *C* and *D*) and between 1969 and 2018 (*SI Appendix*, Fig. S6). While moderate freeze events occurred in 2000/2001 and 2010/2011, the freezes were not severe enough to cause large-scale mangrove mortality in the Florida ecotone (minimum temperatures at the Daytona Beach station were −3.9 °C in 2000/2001 and −4.4 °C in 2010/2011). In addition to expansion of mangroves within their range limits, there is also evidence that the location of the northern range limit of mangroves in Florida migrated northward over this period (40). In 2016 we found an established population of mangroves in Fort George Inlet (30.41°N; *SI Appendix*). This is the northernmost mangrove population observed in recent history and is located only slightly south of the northernmost observation in our historical record (recorded on the northern end of Amelia Island in 1867 by John Muir).

In summary, our FDD-based model of mangrove–salt marsh ecotone regime shifts is supported by multiple lines of historical evidence. The cycles we identified generally match modeled estimates of mangrove abundance between 1893 and 2014 in Port Fourchon, Louisiana, a site near the northern range limit of mangroves along the Gulf of Mexico coastline (37). Therefore, it is likely that these regime shifts are regional-scale phenomena, as large-scale mortality events following hard freezes lead to rapid changes in regime state. However, we did not find evidence for hysteresis in this system, and these changes appear to be reversible. In the absence of extreme cold events, dispersal via episodic storms and recolonization of mangroves allow the system to shift back to a mangrove-dominated state.

Climate Change Causing a More Permanent Northward Shift of the Ecotone

Historical oscillations between mangrove and salt marsh dominance on Florida's Atlantic coast in recent centuries appear to be largely driven by natural climate variability. Recent mangrove expansion is at least partially a recovery from a series of extreme freezes in the 1980s. While we found a significant warming trend in annual T_{min} of 0.12 °C/y between 1980 and 2017, there was no significant long-term positive trend in annual T_{min} over our entire observed temperature record (1850 to 2017). However, warming due to anthropogenic climate change may cause the recent expansion of mangroves to be a more permanent shift toward mangrove dominance in this ecotonal region.

To examine the impact of climate change on future mangrove–salt marsh dynamics, we used statistically downscaled records of daily minimum temperature from 1850 to 2100 simulated by 18 general circulation models for the Coupled Model Intercomparison Project Phase 5 (CMIP5). We used these simulated climate records to evaluate projected changes in the frequency and intensity of extreme cold events during the rest of the century (Fig. 5). The multimodel mean projection indicates an increase in annual minimum temperature of 0.5 °C/decade and a decrease in FDD of 0.16/decade between 2000 and 2100. By 2100, the multimodel mean annual T_{min} is 2.6 °C, and FDD is 0.01 (compared to −2.01 °C and 2.75 FDD for 1860 to 2010), suggesting that even mild freezes will become increasingly rare in this region over the next century.

If these projected trends are realized, we expect mangroves within the current ecotone to be largely freed from freeze damage, enabling them to more permanently displace salt marsh vegetation. We applied our mangrove suitability model to each of the CMIP5 realizations in order to project mangrove suitability in the ecotone through 2100 (*SI Appendix*, Fig. S7). The multimodel mean projection suggests that mangrove suitability will increase through the end of the century as the probability of freeze event strong enough to induce widespread mangrove mortality steadily declines. After 2060, all 18 modeled climate realizations project consistently suitable conditions for mangroves.

This expansion of mangroves across the current ecotone will likely be accompanied by a northward migration of the range limit of mangroves. Correlative distribution models have indicated that relatively small increases in minimum annual temperatures can lead to large-scale northward movement of mangroves (14, 41). The multimodel mean climate projection suggests a 5 °C increase in annual T_{min} between 2000 and 2100. Based on the mangrove distribution models developed by (41), this 5 °C increase would lead to mangroves expanding into Georgia and South Carolina.

Similar changes may occur near other mangrove range limits that are controlled by cold air temperatures. In recent decades expansion of mangroves has been observed near range limits in the Gulf of Mexico, the United States, southeastern Australia, China, and South America (10). In addition, correlative distribution modeling suggests that mangrove species around the world will shift their distributions poleward in response to future climate change (42). However, variability in the tolerance of different populations and species of mangroves to cold air temperatures will lead to regional differences in the climatic thresholds associated with mangrove expansion (43, 44). It is also important to note that not all poleward mangrove range limits are controlled by air temperature extremes (9). Range limits that are controlled by

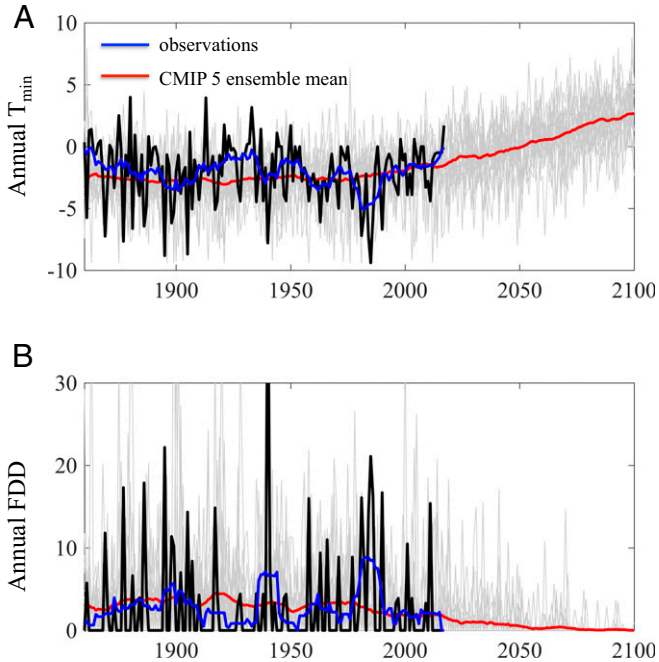

Fig. 5. (*A*) Annual T_{min}, that is, the coldest day of the year, and (*B*) annual cumulative FDD at Daytona Beach. Black and blue lines represent gap-filled observational data (blue line is the 10-y moving average). Gray lines represent individual CMIP5 model realizations, and the red line gives the ensemble mean.

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other processes such as freshwater availability or dispersal limitation may respond differently to future climate change.

Conclusions

Regime shifts between herbaceous salt marsh and woody mangroves provide one example of how climate change can impact ecosystem structure and function, particularly near the boundaries of climatic zones (e.g., temperate–tropical ecotones). Other examples of tropicalization have been documented in kelp forests (3, 4), seagrass meadows (45), and Mediterranean systems (46). However, many ecosystems in these transition zones are highly dynamic, which makes it difficult to separate the effects of anthropogenic climate change from natural climate variability. Creative use of long-term data from disparate historical sources can enable scientists to characterize natural variability in the state of dynamic ecosystems, place recent changes in a broader historical context, and better understand the drivers of abrupt change.

Methods

FDD Time Series. T_{min} data from 1937 to 2017 were acquired from the Daytona Airport station (station ID USC00082150) through the Global Historical Climatology Network (47). This time series was gap filled and extended back to 1901 by calibrating the T_{min} records from the nearby Daytona Beach (5 km; station ID USW00012834) and Titusville (67 km; station ID USC00088942) stations. We then extended this observational record back to 1851 using calibrated daily T_{min} data from NOAA 20th Century Reanalysis (48). FDD was calculated from daily T_{min} data following Eq. 1 from (14):

$$\mathrm{FDD} = \max([0; T_{base} - T_{min}]), \text{ with } T_{base} = -3.2\ ^{\circ}\mathrm{C}.$$

Model of Mangrove Suitability. The FDD time series was used to reconstruct mangrove dynamics in the ecotone using the relationship identified in *SI Appendix*, Fig. S1. We modeled mangrove suitability as a unitless index by scaling the relationship from North Matanzas from 0 to 1, where 1 represents the highest cover of mangrove observed over the 71-y aerial photo time series. We defined mangrove dominance as when the index of mangrove suitability was >0.6 and salt marsh dominance as when the index of mangrove suitability was <0.3. If the index was between 0.3 and 0.6, then we estimated that neither vegetation type dominated. See *SI Appendix*, *Limitations* for the rationale behind our unitless suitability index and the relatively conservative definitions for mangrove and salt marsh dominance.

Historical Data. The historical evidence can be separated into 4 categories: 1) observations of mangroves from across the mangrove–salt marsh ecotone described in written accounts of naturalists, explorers, scientists, and surveyors; 2) a time series of photographs of Fort Matanzas, a fort built by the Spanish in 1740 to guard Matanzas Inlet, which is 1 km from the North Matanzas study site and 14.5 km south of St. Augustine, Florida; 3) maps of shoreline vegetation known as topographic sheets (t-sheets) created by NOAA between the late 1800s and mid-1900s at 3 sites within the mangrove–salt marsh ecotone, Cocoa Beach (surveys conducted in 1928 and 1949), Ponce Inlet (1874, 1928, and 1957), and Matanzas Inlet (1872 and 1957); and 4) records from citrus farmers in Florida describing freezes that significantly impacted citrus production across the state. Citrus crops are sensitive to extreme cold events, so freezes that caused large-scale citrus mortality likely also negatively impacted mangroves (24). We have included a more detailed description of the Fort Matanzas photographs and NOAA historical t-sheets in the *SI Appendix*.

Climate Model Simulations. To characterize future trends in annual minimum temperature and FDD, we used simulated records of daily T_{min} for 1850 to 2100 from an ensemble of 18 general circulation models (GCMs) as part of CMIP5 (49). For 1850 to 2005 we used the CMIP5 "historical" scenario in which all simulations were forced by common historical records of solar radiation, aerosols, land cover, and greenhouse gas concentrations. For 2006 to 2100 we considered the most aggressive emissions scenario (Representative Concentration Pathway 8.5) (50) in order to characterize the upper bound on projected trends. For each scenario, we only considered the first simulation available from each model. From each simulation, we extracted the daily T_{min} record data for the grid cell overlapping with the Daytona Beach climate station, and we bias corrected the CMIP5 data using the gap-filled observational record. For calibration, we used a quantile distribution adjustment such that the simulated records of daily T_{min} had the same temporal distribution (based on the cumulative distribution function) as the observed record during the calibration period of 1921 to 2000.

A limitation of this approach is that simulated daily T_{min} values are not allowed to fall outside of the observed 1921 to 2000 distribution. Therefore, as projected temperatures warm, the maximum possible daily T_{min} value remains capped at the 1921 to 2000 observed maximum, so T_{min} projections for warmer months are almost certainly underestimated. However, we are interested in the coldest days of the year; thus, this limitation does not affect our projections of annual T_{min} or FDD. An additional caveat is that there is relatively high uncertainty in climate model representation of extreme events. The relatively low resolution of GCMs leads to dampening of land–ocean temperature gradients in coastal areas, and models do not yet adequately represent all drivers of regional climate extremes such as the El Niño–Southern Oscillation (51) and stratospheric circulation (52).

Limitations. There are limitations to our historical mixed methods approach that result from challenges inherent in acquiring repeated observations of a given area over long time periods. For example, there is uncertainty in our hindcast model of mangrove suitability resulting from limited availability of data that could be used to parameterize this model. Also, there are limitations associated with the spatial and temporal coverage of our historical datasets. We have included a detailed discussion of these limitations in the *SI Appendix*.

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