

Sea-level driven acceleration in coastal forest retreat

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Ghost forests consisting of dead trees adjacent to marshes are a striking feature of low-lying coastal and estuarine landscapes, and represent the migration of coastal ecosystems with relative sea level rise (RSLR). Although ghost forests have been observed along many coastal margins, rates of ecosystem change and their dependence on RSLR remain poorly constrained. Here, we reconstruct forest retreat rates with sediment coring and historical imagery at five sites along the mid-Atlantic U.S. coast, a hotspot for accelerated RSLR. We find that the elevation of the marsh-forest boundary generally increased with RSLR over the last 2,000 years, and that retreat accelerated concurrently with the late 19th century acceleration in global sea level. Lateral retreat rates increased through time for most sampling intervals over the last 150 years, and modern lateral retreat rates are two to fourteen times faster than pre-industrial rates at all sites. Substantial deviations between RSLR and forest response are consistent with previous observations that episodic disturbance facilitates the mortality of adult trees. Nevertheless, our work suggests that RSLR is the primary determinant of coastal forest extent, and that ghost forests represent a direct and prominent visual indicator of climate change.

INTRODUCTION

Global sea level has been rising at accelerating rates since the end of the 19th century and threatens coastal communities, infrastructure, and ecosystems (Church and White, 2006; Kemp et al., 2009; Kemp et al., 2011; Kemp et al., 2013). Perhaps in response, forests are retreating to higher elevations along the North American Atlantic coast, leaving behind “ghost forests” of dead trees and stumps now surrounded by marshland (Clark, 1986; Ross et al., 1994; Young, 1995; Williams et al., 1999; Conner et al., 2007; Kirwan et al., 2007; Smith, 2013; Raabe and Stumpf, 2016; Kirwan et al., 2016; Langston et al., 2017; Schieder et al., 2018; Fagherazzi et al., 2019; Kirwan and Gedan, 2019). Observations of ghost forests across the Atlantic and Gulf Coasts of North America indicate that forest retreat is widespread in gently sloping, coastal

plain environments (Smith, 2013; Raabe and Stumpf, 2016; Schieder et al., 2018). Reconstructions based on 19th century maps indicate that recent upland submergence formed about 1/3 of all marshes in the Chesapeake region, and that marsh migration into retreating uplands compensated for marsh erosion along the Chesapeake Bay and Florida Gulf Coast (Raabe and Stumpf, 2016; Schieder et al., 2018). Coastal forest retreat is ecologically important, as the transition of uplands to wetlands reorganizes plant communities (Langston et al., 2017), enhances carbon burial (Quirk et al., 2011), contributes to the expansion of invasive species (Smith, 2013), and influences endangered bird species habitat (Field et al., 2017).

Although ghost forests are a prominent feature of many coastal landscapes, coastal change research typically focuses on more seaward portions of the landscape, such as barrier islands, intertidal wetlands, and subtidal ecosystems (FitzGerald et al., 2008). Coastal evolution models, for example, include complex feedbacks between marsh vegetation growth, inundation, and sediment accumulation (Fagherazzi et al., 2012), but assume that forest retreat is driven by simple topographic inundation (Feagin et al., 2010; Schile et al., 2014; Kirwan et al., 2016a, Kirwan et al., 2016b; Schuerch et al., 2018). Other work suggests a lag between RSLR and forest retreat, where increases in inundation frequency and soil salinity prevent the survival of seedlings rather than adult trees, so that coastal forests retreat landward only following episodic mortality of adult trees (Clark, 1986; Williams et al., 1999; Kirwan et al., 2007). Coastal evolution models predict that marsh migration into continuously retreating uplands is a primary and globally relevant mechanism for marsh survival in the face of RSLR at the expense of upland ecosystems (Kirwan et al., 2016a; Schuerch et al., 2018), but there are concerns that actual ecosystem change could be too slow to compensate for rapid marsh loss (Smith, 2013; Field et al., 2016). Therefore, coastal transgression potentially depends on the poorly understood interplay between RSLR and episodic disturbance. Here, we explore the impact of late-Holocene sea level rise (i.e., the last 2,000 years) on coastal forest retreat to better understand the pace of ecosystem change along the rapidly transgressing mid-Atlantic coast.

METHODS

We reconstructed the historical marsh-forest boundary (“coastal treeline”) at five U.S. mid-Atlantic study sites (Fig. 1) over the last 2,000 years with a combination of sediment coring, map and aerial photograph analysis. The U.S. mid-Atlantic is an ideal study region because local RSLR rates are three to four times faster than the global average (Sallenger et al., 2012), and forest retreat is prominent in its gently sloping coastal plain estuaries (Kirwan and Gedan, 2019). We chose five undeveloped sites where widespread forest retreat had been previously observed: Cedar Creek, MD; Hell Hook, MD; Goodwin Island, VA; Long Shoal River, NC; Cedar Island, NC (Fig. 1). Each site is adjacent to a microtidal estuary with irregularly flooded marshes dominated by *Phragmites australis*, *Spartina patens*, *Distichlis spicata*, and *Juncus roemerianus*, and low elevation upland forests dominated by *Pinus taeda* and *Juniperus virginiana*. Previous work estimated lateral retreat rates at the MD and NC sites based on stratigraphy (Young, 1995; Hussein, 2009). We supplemented those measurements by analyzing historical maps and photographs at each site, developing a full reconstruction of forest retreat at an additional site (Goodwin Island), and determining the underlying topography of the submerged forest at each site. This approach allows us to calculate changes in both the elevation and lateral position of the coastal treeline to enable cross-site synthesis focused on changes in forest retreat rates through time.

We mapped the marsh-forest boundary through time with about ten historical maps and photographs per site from the years 1848 to 2014 (Schieder, 2018). We manually delineated the marsh-forest boundary in each map or photograph following previously established methods (Raabe and Stumpf, 2015; Schieder et al., 2018). Lateral forest retreat rates were determined along an individual transect at each site by dividing the change in distance from the modern marsh-forest boundary by the number of years between images. Spatially averaged rates were determined by dividing the area of forest retreat by the number of years between images and the length of the marsh-forest boundary. We then calculated changes in the elevation of the coastal treeline through time (i.e. vertical retreat rates) by estimating the elevation of the buried marsh-forest boundary on each image from stratigraphic cross-sections developed for each site (described below, Suppl. Fig. 1-5). This elevation-based

approach normalizes for the effects of topographic variability and allows us to more properly isolate the effects of sea level rise.

To reconstruct forest retreat rates on centennial-millennial timescales, we collected sediment cores along a transect at Goodwin Island, and reinterpreted stratigraphic data from earlier work at the Cedar Creek and Hell Hook sites (Hussein, 2009) and the Long Shoal River and Cedar Island sites (Young, 1995). At Goodwin Island, we determined the depth of the marsh-forest boundary in each core based on visual sediment characteristics, organic content, and bulk density (Suppl. Fig. 6). The visual interpretation of the marsh-forest boundary was based on changes in color, density, and amount of organic material, where surficial marsh sediments were dark brown, soft, fine grained, organic rich, including rhizomes of high marsh plant species (e.g., *Spartina patens* and *Distichlis spicata*). We interpreted the underlying gray, dense, coarse grained, inorganic sediment as the antecedent terrestrial sediment. We considered the transition from terrestrial to marsh sediment as the depth where organic matter content increased to > 10 % and bulk density decreased to < 0.5 g cm⁻³, based on observations from a variety of salt marshes, and on sediment core profiles taken in the modern forest at the Goodwin Island study site. The timing of marsh-forest transition was determined via radiocarbon dating in the three oldest cores (i.e., cores G17, G13, and G20), and by extrapolating a ¹³⁷Cs derived accretion rate in the youngest core (i.e., core G4) following previous methods (Kemp et al., 2013; Schieder, 2018). We used the CALIB Radiocarbon Calibration 7.0.4 program to convert uncalibrated radiocarbon ages and uncertainties to calendar years at all sites (Suppl. Table 1-3).

We compiled stratigraphic, map, and photo-based reconstructions of the marsh-forest boundary through time to develop a single chronology of forest retreat. Towards this effort, we developed a stratigraphic-cross section at all sites (Suppl. Fig. 1-5), where elevations of the underlying terrestrial surface were calculated by subtracting the thickness of organic rich sediment from modern marsh elevations. Modern marsh elevations were determined from existing data at the Maryland sites, and by newly collected RTK surveys at the other 3 sites. Elevations at all sites were converted to a common vertical datum (MHHW) using Vdatum (<https://vdatum.noaa.gov/>).

COASTAL TREELINE ELEVATION

We found that the elevation of the coastal treeline increased at all five sites through time, with forests retreating from elevations ~ 1.7 m below modern sea level to elevations ~ 0.2 m above mean sea level today over the last 2,000 years (Fig. 2). Relative sea level in the mid-Atlantic region rose between ~ 2.5 (North Carolina) and ~ 3.5 m (New Jersey) during the same time period (Kemp et al., 2011; Kemp et al., 2013), suggesting that coastal treeline elevations increased more slowly than RSLR, and that the position of the forest-marsh boundary relative to sea level has become lower through time.

Millennial timescale reconstruction also reveals an abrupt increase in coastal treeline elevations in the late 19th century that is coincident with global acceleration in RSLR rates (Fig. 2). Treeline elevations at all sites increased gradually between 65 BCE and the late 19th century, and then increased at more rapid rates thereafter. Piecewise linear shape language modeling (SLM) identified a late 19th century breakpoint (1872 CE) at which forest retreat rates started to accelerate (Suppl. Fig. 7). These analyses suggest that the onset of recent acceleration in forest retreat (~ 1872 CE) is closely tied to the onset of rapid RSLR observed in North Carolina (1865 – 1915 CE) (Kemp et al., 2009; Kemp et al., 2011), New Jersey (1830 – 1873 CE) (Kemp et al., 2013), and globally (late 18th century – 1900 CE) (Church and White, 2006). The average rate of change in coastal treeline elevation approximately tripled at all sites, from 0.8 mm yr^{-1} prior to 1872 AD to 2.6 mm yr^{-1} afterward (Fig. 2; Suppl. Fig. 8). RSLR rates in the mid-Atlantic also roughly tripled in the late 19th century (1 mm yr^{-1} to $2.1 - 3.3 \text{ mm yr}^{-1}$ CE in NC (Kemp et al., 2009; Kemp et al., 2011); 1.68 to 4.5 mm yr^{-1} in NJ (Kemp et al., 2013)), suggesting a tight connection between sea level and the elevation of the coastal treeline over century to millennial timescales.

ACCELERATING RATES OF LATERAL FOREST RETREAT

We reconstructed rates of lateral forest retreat through time as the change in distance between the historical and modern marsh-forest boundary in each time interval based on aerial

images and sediment coring. Unlike treeline elevation reconstructions, lateral retreat rates depend on the slope of the submerged topography, where RSLR leads to faster lateral retreat for more gently sloping uplands, and is sensitive to changes in slope along individual transects and between transects. Despite this potential complication, our reconstructions of lateral forest retreat indicate that modern retreat rates (1872 – 2015 CE) are two to fourteen times faster than historic rates (65 BCE – 1872 CE) (Table 1). Lateral forest retreat rates increased from 0.26 - 0.68 m yr⁻¹ to 1.65 - 4.61 m yr⁻¹ after the onset of accelerated RSLR.

Although transect-based analyses allow long-term reconstructions of forest retreat, the approach is sensitive to changes in underlying slope along the transects and localized disturbance events (e.g., fire, insect invasion, storms, etc.) that could be particularly influential at small spatial and temporal scales. To minimize these effects, we also measured changes in forest area on maps and photographs across larger spatial scales at each site (0.6 – 9.4 km² of retreat) (Fig. 1). Modern retreat rates were positive in each time step and location, and generally increased in each time interval throughout the 20th and 21st centuries, suggesting that encroaching marshland continuously replaced retreating coastal forests in parallel with accelerating RSLR (Fig. 3). Spatially averaged retreat rates are two to ten times higher than pre-1872 CE rates, and the most recent forest retreat rates (< 35 years) are about two to four times higher than early 20th century rates (Fig. 3; Table 1). Forest retreat at the Long Shoal River site, for example, increased from 0.37 m yr⁻¹ before 1872 CE to 1.5 m yr⁻¹ in the mid-1900s and to 3.7 m yr⁻¹ during the early 21st century.

INTERPLAY BETWEEN SEA LEVEL RISE AND EPISODIC DISTURBANCE

Our work is among the first to explore how RSLR is affecting terrestrial landscapes over timescales long enough to discern their response to the interaction between episodic disturbance and long-term RSLR. Previous work identified rapid conversion of forest to marsh (Clark, 1986; Young, 1995; Hussein, 2009; Smith, 2013; Raabe and Stumpf, 2016; Kirwan et al., 2016a; Schieder et al., 2018), but demonstrated that disturbance events (e.g. storms, fire) are necessary to drive ecological transitions (Clark, 1986; Young, 1995). These observations likely explain significant deviations between RSLR and our reconstructions of forest retreat. For

example, the magnitude of treeline elevation change averaged across all 5 sites (~ 2 m) is less than the magnitude of sea level rise (~ 2.5 - 3.5 m) over the last 2,000 years (Fig. 2). This suggests that forests are surviving progressively lower elevations relative to sea level than in the past, and underscores previous observations that adult trees are resistant to flooding (Clark, 1986; Young, 1995; Williams et al., 1999; Kirwan et al., 2007). Twentieth century lateral forest retreat rates vary between about 1 and 5 m yr^{-1} across sites, but are not easily predicted by local RSLR and topographic slope (Table 1). For example, the migration rate at the site with the lowest slope is far less (2 - 4 m yr^{-1}) than would be predicted by simple topographic inundation (9 - 11 m yr^{-1}) (i.e. predicted migration = RSLR/slope) (Table 1). These deviations between RSLR and rates of forest retreat are consistent with the paradigm that salt tolerant trees are generally resilient to RSLR, so that habitat change significantly lags behind RSLR (Clark, 1986; Young, 1995; Williams et al., 1999; Kirwan et al., 2007).

Together, these observations suggest that the interplay between long-term RSLR and episodic disturbance control the position of the coastal treeline. Deviations between RSLR and forest retreat confirm that local disturbance events influence the pace of ecosystem change, and create lags between RSLR and forest retreat along individual transects. However, coastal forests at all five sites retreated roughly in parallel with RSLR over the last 2,000 years. Vertical and lateral rates of forest retreat began accelerating at about the same time as the late 19th century global sea level acceleration (Fig. 2), and spatially averaged retreat rates increased during most sampling intervals over the 20th and 21st centuries (Fig. 3). Our work therefore identifies RSLR as the primary driver of forest retreat along the U.S. mid-Atlantic coast, where ghost forests represent a direct indicator of climate change.

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TABLES

Table 1 | Site characteristics and lateral forest retreat rates before and after 1872 CE. Topographic slope represents the slope of the underlying, submerged topography along transects used in Figure 2, and is reported directly from Hussein (2009) for the Maryland sites. RSLR rates are derived from linear regression of monthly NOAA data at the Cambridge (MD), Gloucester Point (VA), Oregon Inlet Marina (NC) and Beaufort (NC) tide gauges, over a consistent time period at each site (1994-2003). Transect retreat rates are based on the transects used in Figure 2, while total loss and spatially averaged rates are for the spatial domains used in Figure 3. SLM analysis of treeline elevation data identified a breakpoint year of 1872, and lateral retreat rates after 1872 CE are two to fourteen times faster than rates before 1872 CE.

Site	Topographic slope	RSLR (1994 – 2003) (mm yr ⁻¹)	Transect retreat rate (m yr ⁻¹) < 1872	Transect retreat rate (m yr ⁻¹) > 1872	Total loss (km ²)	Length of m-f boundary (km)	Spatial averaged retreat rate (m yr ⁻¹)
Hell Hook, MD	0.0026	2.84	0.27	2.18	4.9	34	0.85
Cedar Creek, MD	0.0003	2.84	0.68	1.87	6.4	27	4.34
Goodwin Island, VA	0.0019	3.22	0.26	3.3	0.6	3	1.25
Long Shoal River, NC	0.0024	3.44	0.37	4.61	9.4	23	2.9
Cedar Island, NC	0.0019	1.62	0.32	1.65	3.9	21	1.3

FIGURES

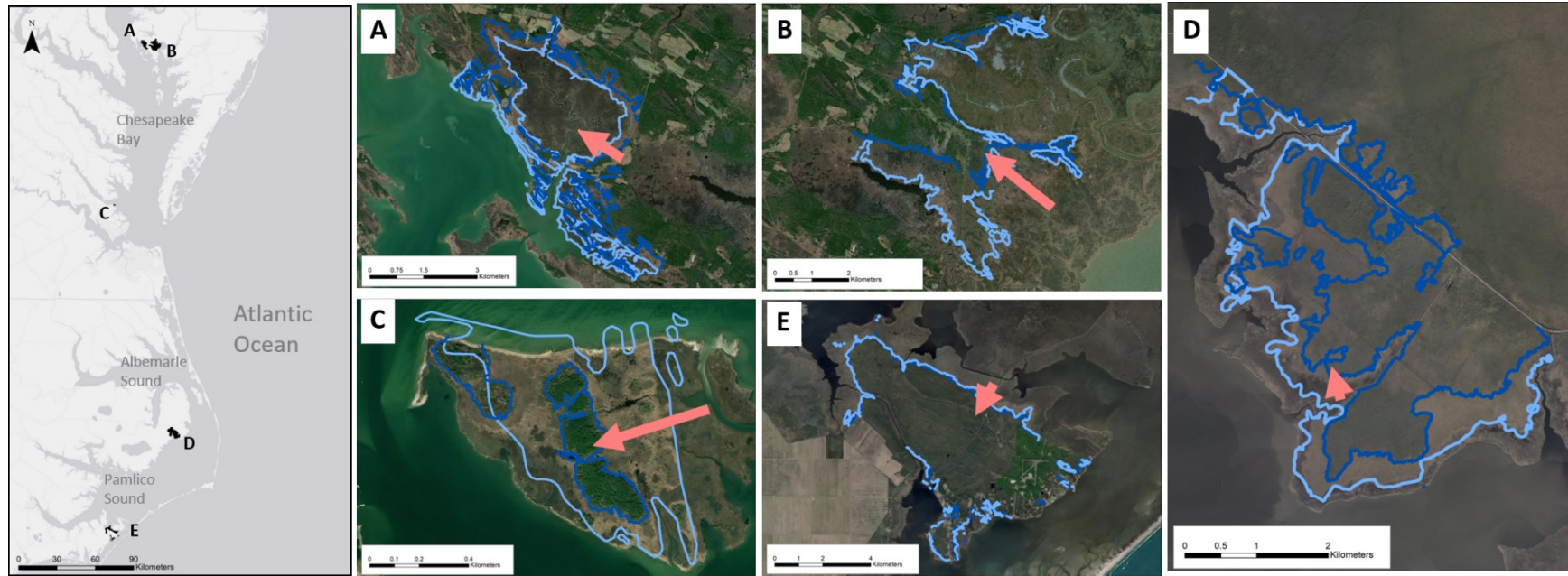


Fig. 1 | Map of study sites along the U.S. Mid-Atlantic coast. From north to south: (A) Hell Hook, MD; (B) Cedar Creek, MD; (C) Goodwin Island, VA; (D) Long Shoal River, NC; (E) Cedar Island, NC. Black areas indicate mapping extent of each site. Drowning of terrestrial forests leads to the creation of ghost forests along the marsh-forest transition zone. Ghost forests were present in all five study sites. Light blue line indicates the marsh-forest boundary from the earliest (i.e. mid-19th Century) map, and dark blue line indicates the boundary on the most recent aerial photograph at each site. These domains were used for all spatially averaged analyses (i.e. Fig. 3, Table 1). The location of sediment core transects, used for all transect-based analyses (i.e. Fig. 2), and direction of forest retreat are shown with the coral arrows.

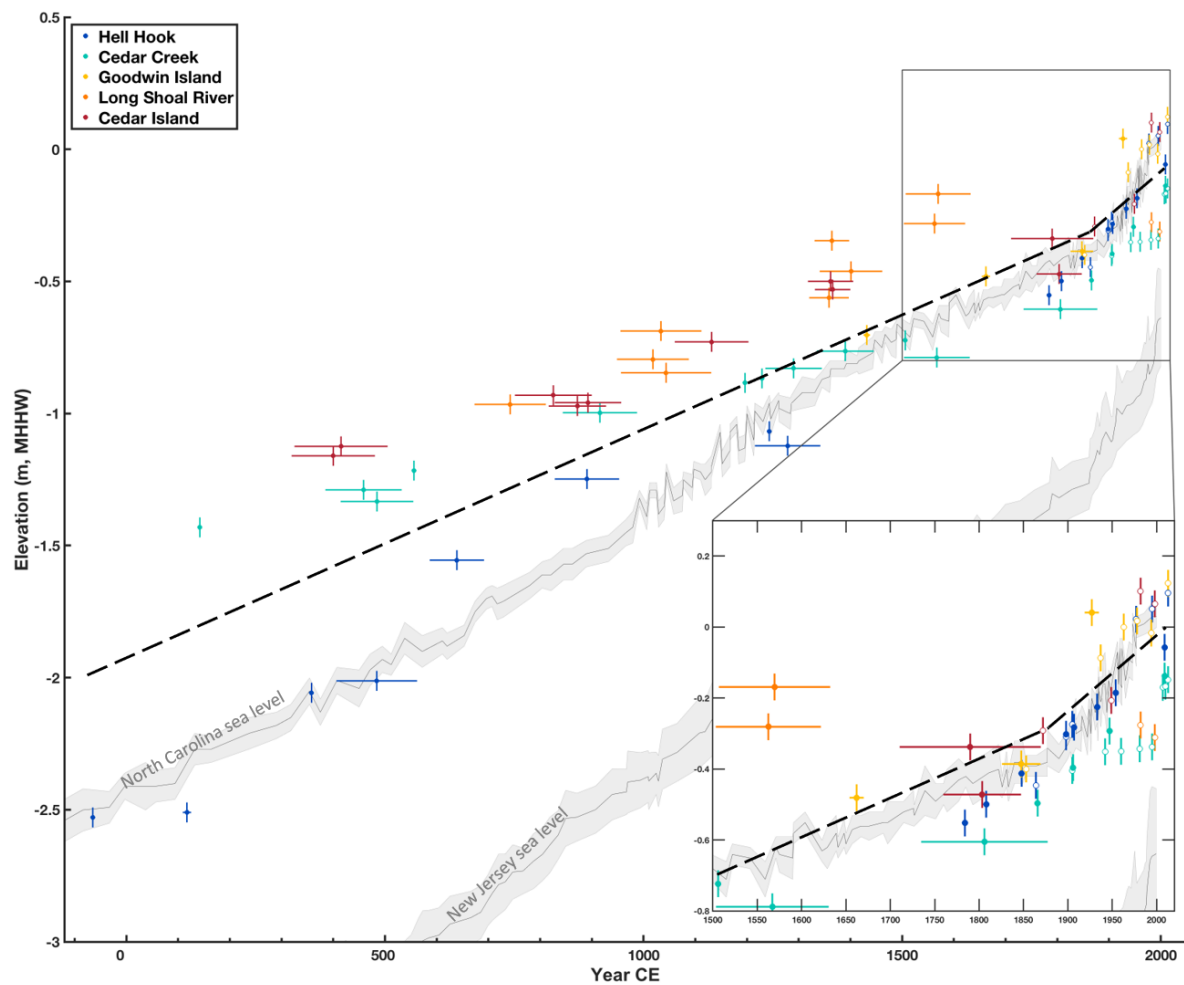


Fig. 2 | Sea-level driven changes in coastal treeline elevation. The elevation of the marsh-forest boundary through time was determined along a transect at each study site, with a combination of stratigraphic (solid circles) and map/photo (open circles) derived sources. Vertical error bars represent uncertainties in identifying the marsh-forest boundary based on visual interpretation, bulk density and organic matter, and horizontal error bars represent uncertainties associated with dating methods. Core-derived elevations at Cedar Island and Long Shoal River, as well as Hell Hook and Cedar Creek sites are based on re-analyses of Young (1995) and Hussein (2009). SLM fit (dashed black line) identifies a breakpoint in elevation change rate around 1872 CE. Long-term relative sea level trend (gray line) is based on paleo-marsh analyses in New Jersey (Kemp et al., 2013) and North Carolina (Kemp et al., 2011).

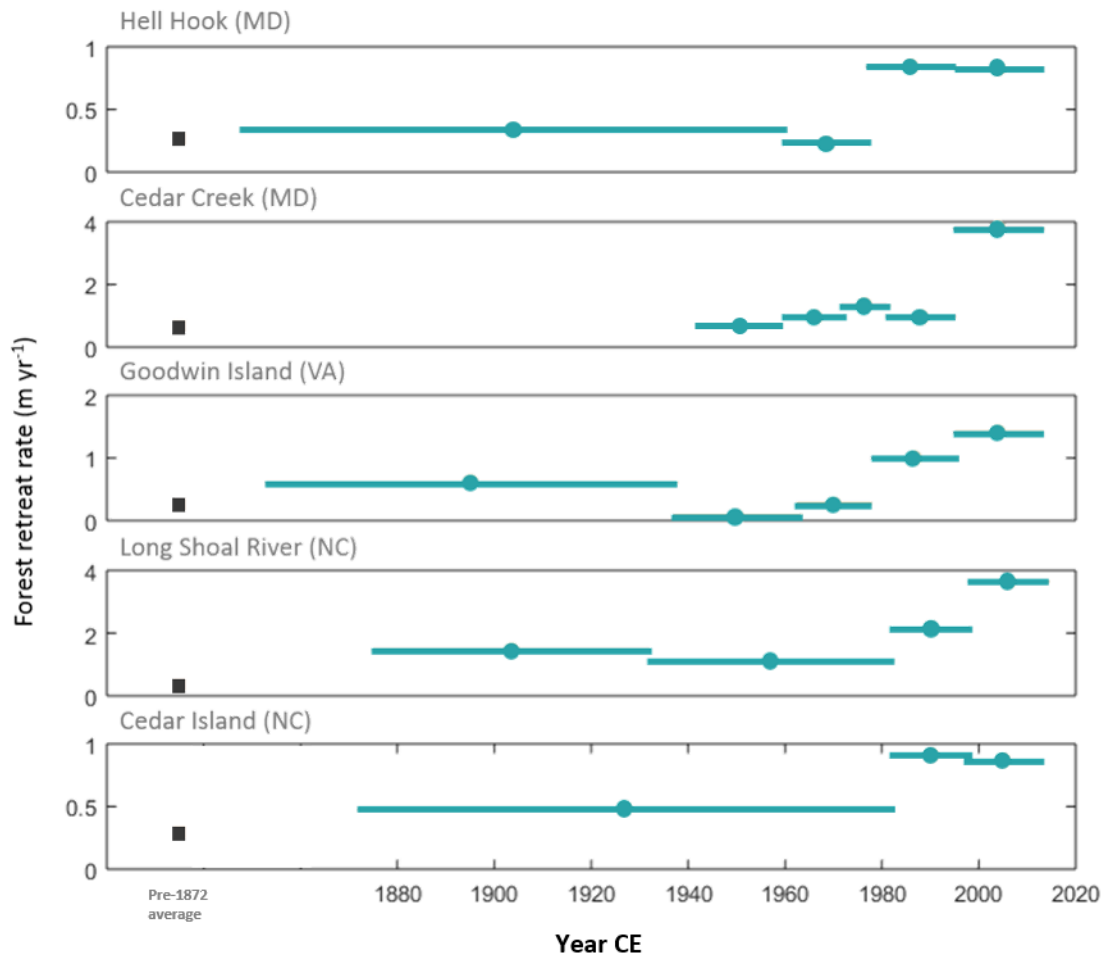


Fig. 3 | Spatially averaged lateral forest retreat rates through time. Green circles indicate 20th century forest retreat rates averaged over km scale spatial domains indicated in Figure 1, where bars indicate the period of time between map or photo sources. Black squares indicate the average lateral retreat rate prior to 1872 CE determined from the same transects used in Figure 2. The pre-1872 CE rates are based on stratigraphy and the earliest map at each site, while the post-1872 CE rates are based entirely on maps and photographs. Modern forest retreat rates exceed historic rates, and generally increase through time.