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Key Points:
- The Mid-Atlantic coastal forests in Virginia are episodically stressed by disturbance from extreme storm events
- The decline in radial growth shows a statistically significant correlation with the magnitude of the extreme storm (storm surge height and wind speed)
- The decline in radial growth is observed for up to 4 years after extreme storm events

Supporting Information:
- Supporting Information S1
- Data Set S1
- Table S1
- Table S5

Correspondence to:
A. Fernandes,
arnold26@bu.edu

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Declining Radial Growth Response of Coastal Forests to Hurricanes and Nor'easters

Arnold Fernandes[1], Christine R. Rollinson[2], William S. Kearney[1], Michael C. Dietze[1], and Sergio Fagherazzi[1]

[1]Department of Earth and Environment, Boston University, Boston, MA, USA, [2]Morton Arboretum, Lisle, IL, USA

Abstract The Mid-Atlantic coastal forests in Virginia are stressed by episodic disturbance from hurricanes and nor'easters. Using annual tree ring data, we adopt a dendroclimatic and statistical modeling approach to understand the response and resilience of a coastal pine forest to extreme storm events, over the past few decades. Results indicate that radial growth of trees in the study area is influenced by age, regional climate trends, and individual tree effects but dominated periodically by growth disturbance due to storms. We evaluated seven local extreme storm events to understand the effect of nor'easters and hurricanes on radial growth. A general decline in radial growth was observed in the year of the extreme storm and 3 years following it, after which the radial growth started recovering. The decline in radial growth showed a statistically significant correlation with the magnitude of the extreme storm (storm surge height and wind speed). This study contributes to understanding declining tree growth response and resilience of coastal forests to past disturbances. Given the potential increase in hurricanes and storm surge severity in the region, this can help predict vegetation response patterns to similar disturbances in the future.

Plain Language Summary Every few years the hurricane season makes the news highlight for its devastating impacts and 2017 has been such a year. Although hurricanes and nor'easters occur every year in the Atlantic Ocean, it is only the extreme events making landfall that leave a major mark on the society, as well as natural ecosystems. It is therefore important to understand the impacts of such extreme events using historical proxy records. Here we use annual tree ring growth as a proxy to understand how past extreme storm events affected the Mid-Atlantic coastal forests in Virginia. Our results show a general decline in radial growth for up to 4 years after the extreme storm event, after which the radial growth starts recovering. A statistically significant correlation is observed between the magnitude of growth decline and the storm characteristics (wind speed and storm surge height). Given the potential increase in hurricanes and storm surge severity in the region, such studies can help predict vegetation response patterns to similar disturbances in the future.

1. Introduction

Coastal and estuarine landscapes host some of the most valuable and vulnerable ecosystems globally (Barbier et al., 2011; Lotze et al., 2006; Parker & Crichton, 2011). The Mid-Atlantic coastal region of the United States, which covers Delaware and parts of New Jersey, Maryland, Virginia, and North Carolina, boasts complex ecosystems composed of wetland forests, saltwater marshes, freshwater marshes, bays, and estuaries (Najjar et al., 2000). Forests account for about 70% of the land cover in this region (Jones et al., 1997). Climate projections indicate that sea level, temperature, storminess, and streamflow will increase in this region in response to global warming (Najjar et al., 2000; Rogers & McCarty, 2000). Furthermore, recent studies show that Atlantic hurricane activity is projected to increase due to a rise in sea surface temperature (Goldenberg et al., 2001; Saunders & Lea, 2008; Wang et al., 2017). However, this relationship is equivocal due to large variations between different modeling methods (Knutson et al., 2010). A median 25-fold and 40-fold increase in the annual number of local 100 year floods is expected along the contiguous U.S. coastline by 2050, under probabilistic relative sea level projections for Representative Concentration Pathway 4.5 and 8.5, respectively (Buchanan et al., 2017). Damage from storm surges and wind associated with these storms can influence the structure, development, species composition, and diversity of forests (Lugo, 2008).

Forests in this region can also be dramatically affected by other environmental drivers such as variation in temperature and precipitation, extreme drought, or flooding events (Mickler et al., 2012). Sea level rise can lead to a progressive landward shoreline displacement along the coast and cause the forest-marsh boundary to migrate inland (Kirwan et al., 2016; Robichaud & Bégin, 1997). These stressors have been reported to cause reduced forest growth, failure in regeneration, or dieback events (Kirwan et al., 2016; Mickler et al., 2012). Coastal forests of South Carolina suffered increased mortality in response to saltwater infiltration from storm surges and extreme wind damage that accompanied the 1989 Hurricane Hugo (Hook et al., 1991). On the west coast of Florida, regeneration failure is observed in coastal forests due to sea level rise (Williams et al., 1999). Therefore, understanding the response and resilience of coastal forests to past environmental changes can help predict their response patterns and manage these forests appropriately in the future.

Dendrochronological and statistical techniques have been an effective tool to reconstruct the response of forests to changing environmental conditions over time, including changes in sea level (Kirwan et al., 2007; Robichaud & Bégin, 1997), temperature, and precipitation (e.g., Byun et al., 2013; Harley et al., 2011; Panayotov et al., 2010; Schofield et al., 2016; Tipton et al., 2016). Annual tree ring widths are influenced by several factors including the age and species of the tree, competition from neighboring trees, soil conditions, climate, local or stand-wide disturbance pulses and annual variability among individual trees (Cook et al., 1990; Fritts, 1976; Speer, 2010). In coastal environments, tree rings have also been observed to respond to tropical storms and hurricanes (Conner & Inabinette, 2003; Johnson & Young, 1992; Miller et al., 2006; Rodgers III et al., 2006). The effects of these disturbance episodes on tree growth can be studied by analyzing their resilience, that is, the capacity of the trees to recover after disturbance and regain their pre-disturbance structure and function (Folke et al., 2004; Scheffer et al., 2001).

We postulate that low-lying trees in the Mid-Atlantic coastal forest in Virginia are episodically damaged through the direct influence of flooding and strong winds during extreme storm events. By adopting a dendroclimatic and statistical modeling approach, this paper aims to (a) identify periods of declining tree ring growth following extreme storm events and (b) understand the response and resilience of vegetation to extreme storm events in the Mid-Atlantic coastal region, on the Eastern Shore of Virginia National Wildlife Refuge.

2. Materials and Methods

2.1. Study Area

2.1.1. Geographic Setting

The study site is a stand of *Pinus taeda (L.)* (loblolly pine), located on the Eastern Shore of Virginia National Wildlife Refuge, Virginia, USA. It is a secondary growth stand that is predominantly populated by *Pinus taeda* with a tree density of approximately 318 trees per hectare. Some other species found in the study area include *Ilex vomitoria* (yaupon holly), *Iva frutescens* (marsh elder), *Baccharis halimifolia* (groundsel tree), *Myrica cerifera* (bayberry), and *Smilax* spp. (greenbrier). Topographic changes due to compaction, erosion, and autogenic succession can lead to changes in the elevation of trees relative to each other and to mean sea level. The soil at the study site is, however, very sandy, and therefore, compaction is expected to be negligible. Wave and tidal energy are minimal at this location, so erosion within the forest boundary is unlikely. However, the sea level itself rose on the order of 50 cm between 1904 and 2015 (extrapolated from the Sewells Point tide gauge, Virginia; National Oceanic and Atmospheric Administration (NOAA), 2016). While historical topographic data are not available at a high enough resolution to determine the extent of elevation changes, historical maps and aerial imagery do not show significant changes of the forest boundary, so we assume that the relative distance of the trees to the forest-marsh boundary did not change over the course of the study period.

The refuge lies on the southern tip of the Delmarva Peninsula, Virginia, USA, and is bordered by the Atlantic Ocean on the East and the Chesapeake Bay on the West (Figure 1a). This site is adjacent to the Virginia Coast Reserve (VCR), which is designated by the National Science Foundation as a Long-Term Ecological Research site. The Delmarva Peninsula formed when rising sea levels during the late Pleistocene and Holocene filled the lower Susquehanna river valley, creating the Chesapeake Bay and isolating the area from the mainland (Colman et al., 1990; Hobbs, 2004; Rice, 2004). Sea level fluctuations, climate, tidal energy, and sand supply control the present-day morphology of the barrier islands and marsh-lagoonal systems along the eastern side of the Delmarva Peninsula (Demarest & Leatherman, 1985). The average rate of sea level rise at VCR is approximately 4 mm/yr (National Oceanic and Atmospheric Administration (NOAA), 2010), which is about twice the global rate.

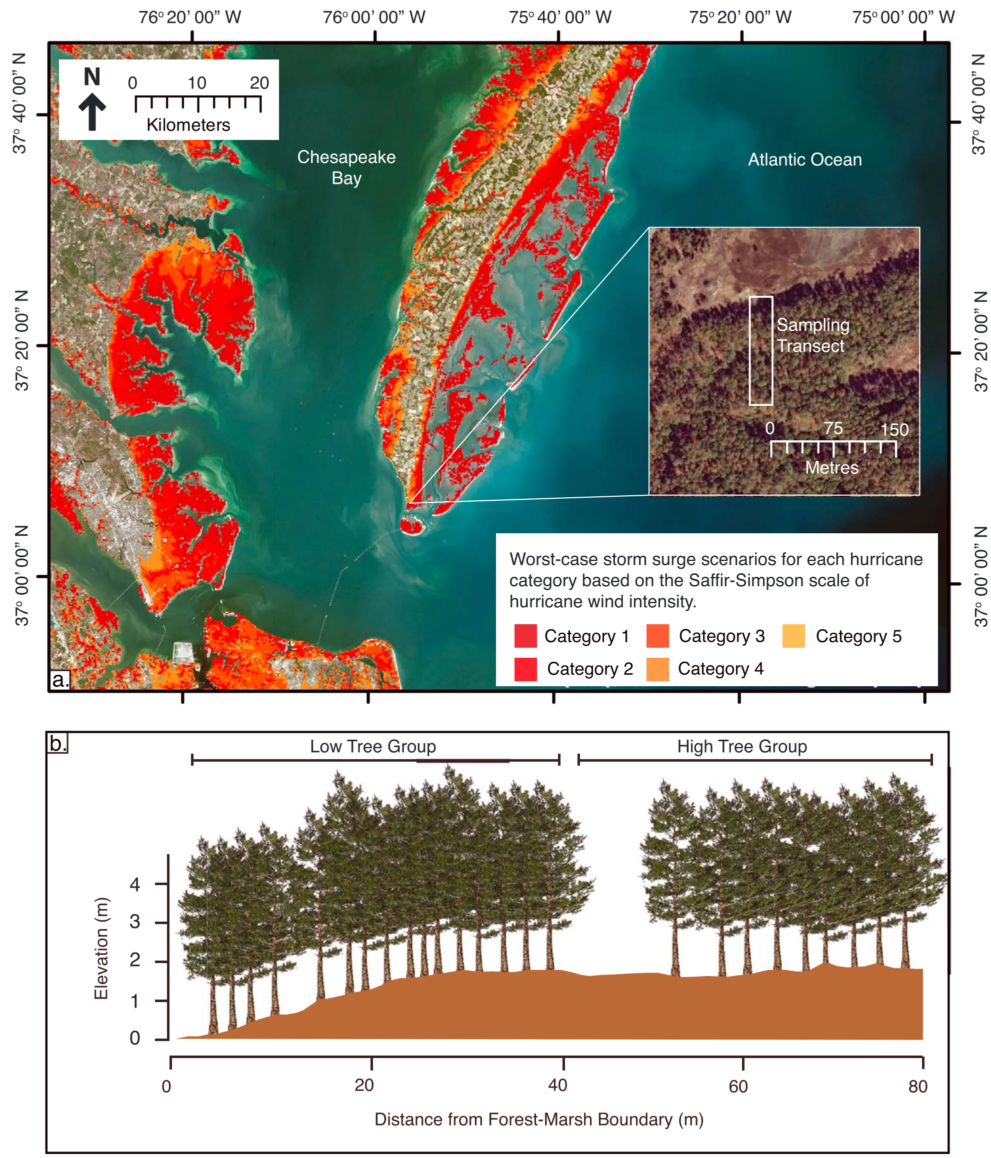

Figure 1. Geographic setting and geomorphology of the study area illustrating (a) satellite imagery displaying areas affected by storm surges during hurricanes (Jelesnianski et al., 1992). Categories 1 through 5 refer to the Saffir-Simpson scale of hurricane wind intensity. The inset shows the study site where *Pinus taeda* trees were sampled. (b) Schematic displaying elevation change along the sampling transect. The distance between trees is not to scale, for illustrative purposes only.

2.1.2. Climate and Storm Activity

The mean temperature at the study site during April, July, October, and January are approximately 14°C, 25°C, 17°C, and 5°C, respectively, with mean total precipitation of 91 mm per month (1,095 mm/yr), distributed evenly throughout a year. The climate data set used in this study is 4 km resolution monthly Parameter-elevation Regressions on Independent Slopes Model (PRISM) AN81m time series data set (PRISM Climate Group, 2015). This data set is modeled using climatologically aided interpolation in which the long-term average data sets serve as the predictor grids. It uses all of the station networks and data sources used by the PRISM Climate Group to provide the best possible climate data estimates at a given time. From PRISM data, we used mean monthly temperature and total monthly precipitation for a single centrally located point at 37.1280°N, 75.9611°W for the period ranging 1903 to 2015.

A storm surge can be defined as an abnormal rise of water generated by a storm, higher than the predicted astronomical tides (National Oceanic and Atmospheric Administration (NOAA), 2016). The study site is subject

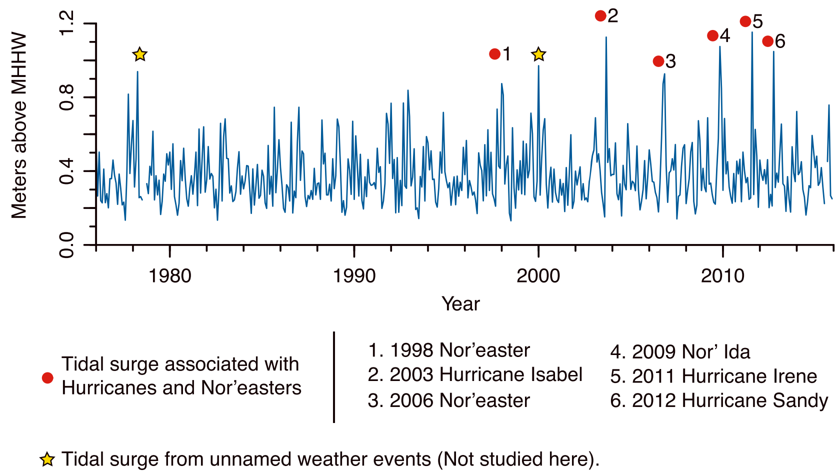

Figure 2. Monthly highest water levels relative to the monthly mean higher high water (MHHW) recorded at the Chesapeake Bay Bridge Tunnel water level station near the study site (National Oceanic and Atmospheric Administration (NOAA), 2016). Demarcated extreme spikes in water levels (red circles) correspond to storm surges associated with hurricanes and nor'easters. Yellow stars indicate high water levels from unnamed meteorological events.

to two such major storm types—hurricanes and nor'easters (Parker & Crichton, 2011) (Figures 1a and 2). The peak hurricane season in Virginia spans across the summer months of August and September, but notable events have also been reported into the fall season. The hurricane events are generally of short duration, characterized by high wind speeds and large storm surges (Parker & Crichton, 2011). Unlike hurricanes, nor'easters generally occur during the fall, winter, and early spring, are comparatively slower, have a longer duration, and can produce equally large storm surges (Dolan & Davis, 1992). In this study, water level data of monthly and hourly resolution were retrieved from the nearest tidal station—8638863 Chesapeake Bay Bridge Tunnel, Virginia (National Oceanic and Atmospheric Administration (NOAA), 2016). The water level measurements made at the Chesapeake Bay Bridge Tunnel tidal station have also been used as a proxy for those at the present site in another previous study by Paquier et al. (2017). Wherever necessary, additional water level data were also retrieved from the 8638610 Sewells Point tidal station, Virginia (National Oceanic and Atmospheric Administration (NOAA), 2016), which has a longer record but is further away. Based on a combination of storm surge magnitude and duration recorded at the Chesapeake Bay Bridge Tunnel tidal station, events with extremely high water levels ($\geq$1 m above mean higher high water (MHHW)) (see Ezer & Atkinson, 2014) or long flooding duration ($\geq$30 h above 1 m NAVD88) obtained from tidal records were identified as extreme storm events. Since the continuous water level records are only available from 1975, extreme storm events prior to 1975 were identified based on the description from historical reports that display maximum impact on Virginia. Only seven storms were identified that met these criteria between 1904 and 2015, namely, 1933 Chesapeake-Potomac Hurricane, 1962 Ash Wednesday Nor'easter, 1998 Nor'easter, 2003 Hurricane Isabel, 2009 Nor'Ida, 2011 Hurricane Irene, and 2012 Hurricane Sandy. Strong tidal surges from unnamed meteorological events marked in Figure 2, which did not meet our study criteria, may also have left some disturbance imprint in the tree ring record. We do not explore these events in detail.

2.2. Sampling and Chronology Preparation

We sampled 43 *Pinus taeda* trees along a transect representing an increasing distance from the forest-marsh boundary and elevation above sea level. On average, two cores per tree were collected at breast height (1.4 m) with a 5 mm increment borer using standard procedures outlined in Stokes and Smiley (1968). To understand the response of trees to extreme storm events as a function of increasing distance from the forest-marsh boundary, the sampled trees that correlated well as described ahead were divided into two groups: trees closer to the marsh (<40 m from the forest-marsh boundary, $n = 16$) and those further inland ($\geq$40 m from the forest-marsh boundary, $n = 9$), hereby referred to as low and high tree groups, respectively (Figure 1b).

The ring width series were cross-dated visually using skeleton plots and marker rings. Ring widths were then measured using WinDENDRO software (Regent Instruments, 2012). The computer program COFECHA (Holmes, 1983) was used to statistically confirm cross dating. Cores with a correlation coefficient less than 0.235, which represents a 95% level of confidence when testing 50 year segments, were discarded. Thus, only

25 trees (46 cores) were used in this study. These trees were evenly distributed within the low and high tree groups. The average mean sensitivity, a measure of year-to-year variability in ring width, and series intercorrelation, a measure of the strength of the common signal between all trees, obtained from COFECHA were 0.342 and 0.394, respectively. The series intercorrelation was within the 0.35–0.6 range, while the mean sensitivity value was slightly higher than the 0.15–0.3 range reported for similar *Pinus taeda* chronologies (Cook et al., 1998), indicating that the trees are highly sensitive to yearly changes in growth-limiting factors. For all the core samples that did not hit the pith, the pith year was estimated following the method developed by Duncan (1989), which assumes concentric ring growth such that the ring boundaries can be considered arcs of circumferences with the pith in the center. The oldest tree was 113 years old with the sample mean age being 89 years in 2015. The raw ring width data and details on the sampling location, elevation, and tree age are provided in supporting information Data Set S1 and Table S1, respectively.

Using the Dendrochronology Program Library in R (dplR) package (Bunn, 2008), we compiled chronologies for the whole site (stand-level) and the site stratified by distance from the forest-marsh boundary (group-level) as well as retained average detrended ring width indices (RWI) for each tree for analysis. Cores were detrended with a cubic smoothing spline, having a wavelength equal to 2/3 the length of individual ring width series and a frequency response of 50% to minimize any age-related trend (Cook & Peters, 1981). The RWI of multiple cores of each tree were then averaged to obtain a single time series for each tree. The RWI of individual trees were then averaged together using a Tukey's biweight robust mean (Cook et al., 1990) to build the mean chronology for 25 trees (stand-level) (supporting information Figure S1). Group-level mean chronologies for low and high tree groups were created using the above procedure, and the RWI of individual trees were also retained for analysis. The stand-level mean chronology in this study spans the period from 1904 to 2015.

2.3. Identification and Impact Analysis of Extreme Storm Events

The impact of extreme storm events on radial growth of the trees was studied using two methods: (1) event year analysis: to identify low-growth episodes (if any) following the extreme storm events and (2) superposed epoch analysis (SEA): to isolate growth response signals to key events (in this case, extreme storms), which may be difficult to detect in the presence of noise from other competing influences operating at similar time scales. A summary of the extreme storm events analyzed using these methods is provided in supporting information Table S3.

2.3.1. Event Year Analysis

The year-to-year variation in tree ring widths contains information about the relationship of the tree with its environment. Event years are defined as years with a remarkable increase or decrease in radial growth (Schweingruber et al., 1990). Event years were calculated using radial growth data to determine if there were low-growth episodes following the extreme storm events. The analysis was performed using the relative growth change method (Schweingruber et al., 1990) using the pointRes package in R (van der Maaten-Theunissen et al., 2015). In this method, the ratio of radial growth in the current year and the average growth in four preceding years was calculated. The percentage relative growth changes were then used to identify event years for the trees. A positive event year was defined as the year with at least 60% increase in growth, whereas a negative event year was defined as the year with at least 40% decrease in growth as compared to the average growth in the preceding 4 years, following Schweingruber et al. (1990).

2.3.2. Superposed Epoch Analysis

SEA was performed using the dplR package (Bunn, 2008) to isolate growth response signals to key events (in this case, extreme storm events), which may be difficult to detect in the presence of noise from other competing influences operating at similar time scales. SEA was conducted on RWI of individual trees, and group and stand-level mean chronologies. Individual RWI were normalized by subtracting the mean and dividing it by the standard deviation for the entire time record to minimize the chance that a single anomaly may disproportionately influence the composite analysis and ensure internal consistency. The scaled mean RWI were then averaged at 13 temporal lags centered on the key dates thereby creating a composite of the tree ring response in the year of disturbance (lag year 0), and in each of the 6 years preceding and following the disturbance. Our study involves five key dates representing a combination of highest storm surge magnitude and duration: 1933 Chesapeake-Potomac Hurricane, 1962 Ash Wednesday Nor'easter, 1998 Nor'easter, 2003 Hurricane Isabel, and 2009 Nor'Ida. Ten thousand bootstrap samples were used to compute 95% confidence intervals for the scaled RWI for each year in the superposed epoch. The 2011 Hurricane Irene and 2012 Hurricane Sandy could not be included as a key date in the SEA as ring width data for 6 years post-storm were not available. Furthermore, no fire scars or any reported evidence of non-storm key events (e.g., insect outbreaks) that occurred in the same year as the extreme storm event was found. The mean RWI during the disturbance period showed no significant correlation (p-value <0.05) with Palmer Drought Severity Index either, at our study site. This precludes the likelihood of any non-storm key events complicating the growth response signal to extreme storms detected by SEA, thereby increasing the accuracy of the results.

2.4. Nonlinear Growth Response Model

Having identified periods of declining tree ring growth following extreme storm events (see section 3.1), a generalized additive mixed model (GAMM) was built to characterize the growth response of trees to other factors like climate, age, individual tree variability, and distance from the forest-marsh boundary (tree group), along with disturbance due to extreme storm events. The advantage of GAMM is its ability to model potentially nonlinear relationships between response and predictor variables and to incorporate both fixed and random effects to account for repeated measures (e.g., individual trees) (Wood, 2006; Zuur, 2012; Zuur et al., 2009). The model was constructed using the mgcv package in R (Wood, 2007) using the following equation:

$$\ln(\mathrm{RW}) = \mathrm{I} + \mathrm{s(temp)} + \mathrm{s(precip)} + \mathrm{tree\ group} + \mathrm{s(age,\ by = tree\ group)} + \mathrm{storm\ disturbance} + \mathrm{treeID_{re}}, \quad (1)$$

where (I) is the parametric estimate of the intercept and (s) represents the inclusion of a cubic regression spline that detects and allows the nonlinear response of raw ring width series of individual tree cores (RW) to each predictor variable. The climate was characterized using mean seasonal temperature (temp) and total annual precipitation (precip) using data retrieved from PRISM (PRISM Climate Group, 2015). For each year, the monthly temperature was averaged across the following seasons: spring (April to June), summer (July to September), fall (October to December), and winter (January to March) (see Kirwan et al., 2007). Precipitation was summed across the whole year. A fixed categorical variable (tree group) was included in the model to determine the contribution of tree groups (low and high tree groups) to variance in ring width. The (age) predictor represents the age of the trees estimated by the method developed by Duncan (1989). As the mean age of low (81 years) and high (103 years) tree groups in 2015 differed by 22 years, a (by = tree group) argument was included in the age predictor to model potentially different trends over time in low and high tree groups. The categorical predictor (storm disturbance) was included as a logical class variable to represent an observed disturbance in tree ring growth following extreme storm events (see section 3.1). As continuous water level records at the nearest tidal station were available post-1975 (about 36.6% of the temporal span of our tree ring record), using storm disturbance as a categorical predictor over storm surge height as discrete values was preferred to account for disturbance in growth due to extreme storm events prior to 1975 as well. The climate variables (temp and precip), tree age (age), tree group and storm occurrence (storm disturbance) were included in the model as fixed effects. The variation among individual trees was incorporated as a random effect ($\mathrm{treeID_{re}}$) so that the model produces a random coefficient for each tree core, which is modeled as a Gaussian random effect. Smoothing parameters of the spline, knots, and rigidity were decided using the generalized cross-validation method such that two knots were equally spaced per 3°C change in seasonal temperature, 400 mm change in precipitation, and 15 years increase in age. We did not account for the effects of error in the interpolation and any nonclimatic variations due to station factors introduced in the PRISM AN81m time series data set, and additional work on evaluating the sources of uncertainty could increase the accuracy of the climate-tree growth relationship modeled by the GAMM. Although artifacts have been observed in PRISM climate data (Beier et al., 2012), they do not appear to vary systematically with geographical factors like elevation or distance to coast, in the U.S. Northeast (Bishop & Beier, 2013). To ensure that the grouping of trees does not reduce the variability explained by the model, an alternate GAMM was tested using tree distance from the forest-marsh boundary as a numeric variable instead of a categorical tree group variable. Results are, however, not appreciably altered (refer to supporting information Table S4).

2.5. Forest Resilience to Discrete Disturbance Events

From the results of the SEA and event year analysis (section 3.1), a 4 year low-growth (disturbance) period was identified beginning at the year of the extreme storm events and 3 years following it. The characteristics of each extreme storm event differ in terms of proximity to the site, wind speeds, storm surge height, and duration of flooding and may thereby affect tree growth differently. To characterize this effect, we computed Kendall's tau (τ), a rank-based correlation coefficient, between mean RWI across the seven disturbance events, and storm-specific factors like storm surge height and wind speed. Storm surge height was obtained from the monthly highest water level recorded at the 8638610 Sewells Point tidal station, Virginia (National Oceanic and Atmospheric Administration (NOAA), 2016), which has continuous water level data from 1927 onward. Considering that the highest water level recorded at the Sewells point and Chesapeake Bay Bridge Tunnel tidal stations is highly correlated during their common temporal span (Pearson's correlation coefficient = 0.987, p-value <0.05), they would rank similarly for Kendall's correlation. Highest sustained wind speeds were obtained from the hourly observations recorded at the Norfolk NAS local climatological data station in Virginia (supporting information Table S2) (National Oceanic and Atmospheric Administration (NOAA), 2017).

Furthermore, to characterize the difference in growth between tree groups across different extreme storm events, a two-way, two-tailed analysis of variance (ANOVA) was performed on RWI as a function of tree group, storm effect, and their interaction. The tree group factor was categorized into two classes: low tree group and high tree group. The storm effect factor was categorized into seven classes: disturbance period associated with the 1933, 1962, 1998, 2003, 2009, and 2011 extreme storms and no storm (the remaining years during the 1904–2015 period when no extreme storm events affected the study site). In order to meet the assumptions of normality and homogeneity of variances, the RWI of individual trees were log-transformed. The two-way ANOVA was followed by Tukey's honest significant difference (HSD) post hoc test to localize the significant differences among tree groups and extreme storms and view the pairwise comparisons at p-value <0.05.

Having concentrated solely on ring width growth in the method mentioned above, we analyzed the resilience of the stand during disturbance periods associated with four extreme storm events: 1933 Chesapeake-Potomac Hurricane, 1962 Ash Wednesday Nor'easter, 1998 Nor'easter, and 2003 Hurricane Isabel. Resilience is the capacity of forests to reorganize while undergoing changes so as to retain their original function, structure, identity, and feedbacks (Folke et al., 2004). We computed three metrics: resistance, recovery, and resilience, according to the definitions described in Lloret et al. (2011) to characterize how the trees respond to and recover from disturbance due to the extreme storms. These metrics were compared between trees belonging to the low and high tree groups to determine if the resilience of the trees varied as a function of distance from the forest-marsh boundary. The mean RWI values for each tree were computed for the low-growth (disturbance) period (*Dr*) and the 4 years before (*PreDr*) and after (*PostDr*) the disturbance period. Resistance can be defined as the inverse of radial growth reduction during the disturbance and was estimated as the ratio between *Dr* and *PreDr*. Recovery corresponds to the ability of the trees to recover relative to the damage experienced by them during the disturbance and was estimated as the ratio between *PostDr* and *Dr*. Resilience corresponds to the capacity of the trees to reach their pre-disturbance growth levels and was estimated as the ratio between *PostDr* and *PreDr*. The selected low-growth periods (*Dr*) were 1933–1936, 1962–1965, 1998–2001, 2003–2006. Hereafter, we refer to each of these according to the first year: 1933, 1962, 1998, and 2003, respectively. Since the tree ring record used in this study is only until 2015, the *PostDr* period corresponding to the 2009 Nor'Ida, 2011 Hurricane Irene, and 2012 Hurricane Sandy could not be defined and were therefore not used in this analysis. One sample t-test were then performed to determine if the resistance, recovery, and resilience of low and high tree groups were significantly different from the base value 1 indicating a significant change in growth patterns at a 95% confidence level.

3. Results

3.1. Identification and Impact Analysis of Extreme Storm Events

A relationship between the decline in radial growth and extreme storm events was observed at an individual tree level. Almost all trees show a negative event year (≥40% decline in growth compared to average growth in preceding 4 years) following the extreme storm events of 1933, 1962, 1998, 2003, 2009, 2011, and 2012 in Virginia (Figure 3a). A relatively higher number of low group trees exhibit a decline in growth as compared to high group trees, following the 1933, 1962, and 1998 storms (Figures 3b and 4).

An increase in the number of trees showing a negative event year was observed for up to 3 years following the extreme storm events. Following the 1933 storm event, about 60% of the low tree group and 50% of the high tree group showed a negative event year by 1936 (Figure 4). After the 1962 storm event, about 70% of the low tree group and only 10% of the high tree group showed a negative event year by 1965 (Figure 4). After the 1998 storm event, about 55% of the low tree group showed a negative event year by 2001 (Figure 4). For the 2003, 2009, 2011, and 2012 extreme storm events, the percentage of trees showing negative event years in 3 years post-storm is variable. Growth suppressions were also observed between 1955–1957 and 1978–1980 (Figure 4).

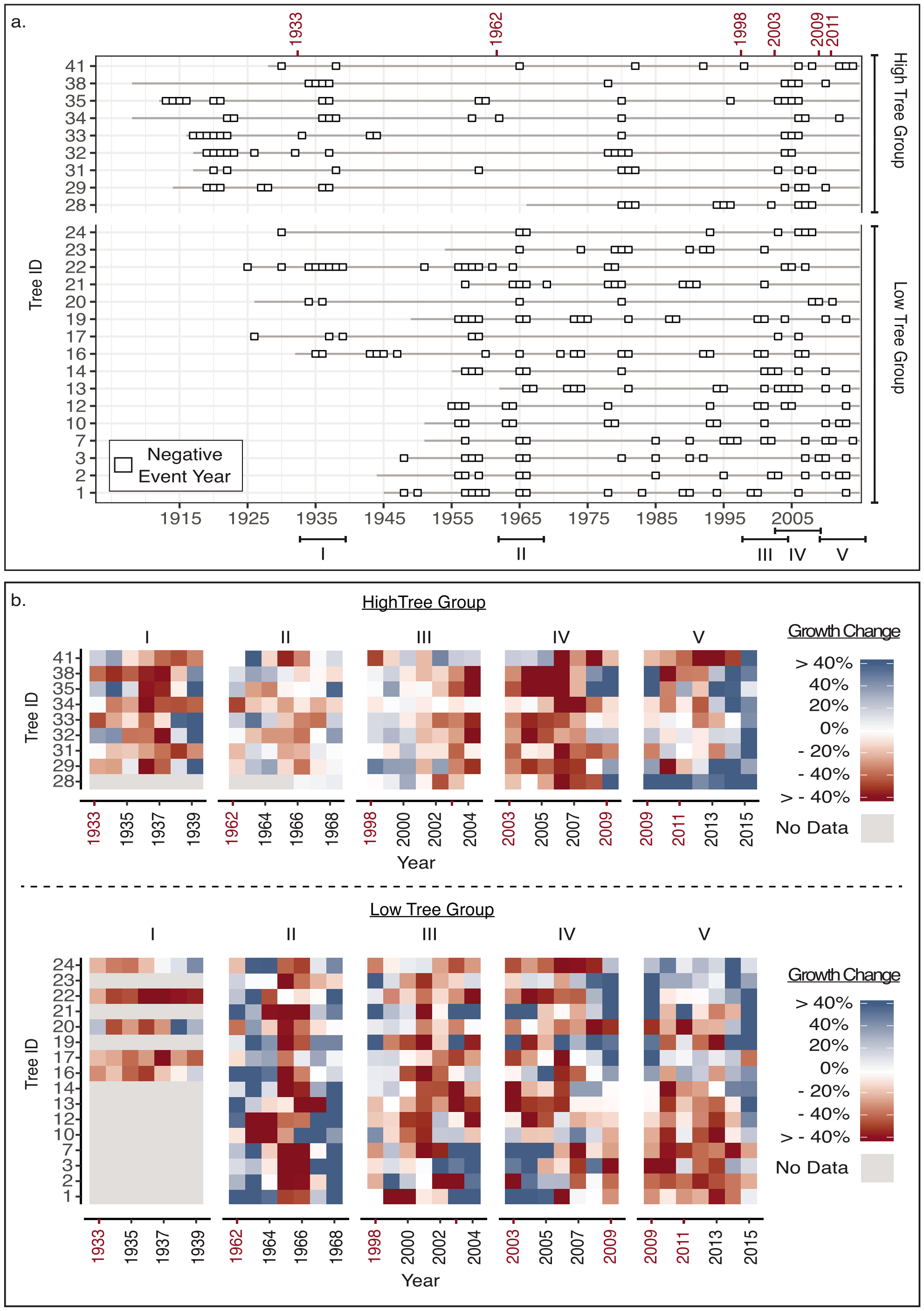

Figure 3. Relative growth change and event years for individual trees with the extreme storm event years marked in red. (a) Dot plot showing negative event years for individual trees at the study site. (b) Panels I–V show gradual relative growth change post-1933, 1962, 1998, 2003, and 2009 extreme storm events, for time windows, marked I-V in Figure 3a. The relative growth change was calculated as the ratio of radial growth in the current year and the average growth in four preceding years, of individual trees. The majority of the trees show a negative event year (≥40% decline in growth), 3 years post-storm.

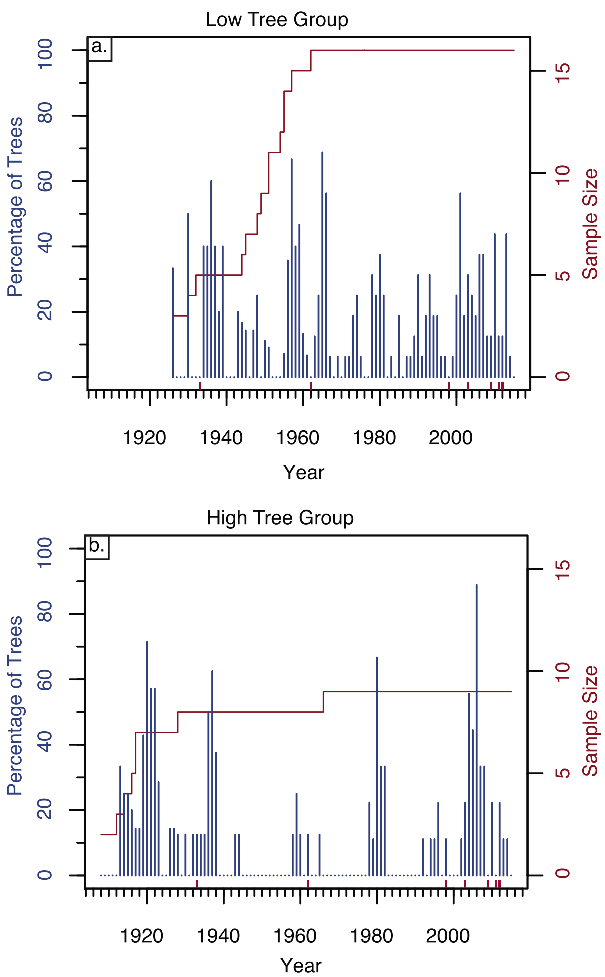

Figure 4. Percentage of trees showing negative event years among the (a) low tree group and (b) high tree group at the study site. Red line indicates the sample size and red markers on the *x*-axis represent the seven extreme storm events considered in this study.

SEA revealed a common growth response signal of declining RWI to the five extreme storm events analyzed (Figure 5). The decline in RWI starts in the year of the storm, and a relatively large decrease in RWI is observed 3–4 years after the storm. At a stand-level (i.e., using the mean chronology of all trees), a declining trend in RWI is observed for up to 3 years following the extreme storm event, after which the RWI start recovering. A similar response is observed in the high tree group. However, the low tree group shows a decline in RWI for up to 4 years after the extreme storm event, after which it begins to recover (Figure 5). Because of the occurrence of extreme storms associated with the 1998 Nor'easter, 2003 Hurricane Isabel, and 2009 Nor'Ida, within short intervals (<13 years) there is a bias introduced in the pre-storm lag years (−6 to −1) (Figure 5).

3.2. Nonlinear Growth Response Model

Variations in radial growth of the trees were modeled by climate, age, storm disturbance, and individual tree variations, with the final GAMM explaining 49.80% of deviance in radial growth. Spring, summer, fall, and winter temperature, total precipitation, tree age, storm disturbance, and variation among individual trees were found to be significant predictors of radial growth (*p*-value <0.05) (Table 1). Tree group based on distance from the forest-marsh boundary was found to be a nonsignificant predictor at a 95% confidence level. Overall, variation among individual trees explained the highest proportion of deviance in radial growth (18.96%) followed by tree age (14.54%). Total annual precipitation (1.65%) explained slightly more deviance in radial growth as compared to the mean temperatures in spring (0.45%), summer (0.38%), fall (0.35%), and winter (0.16%). Total annual precipitation and mean seasonal temperature show variable influences on radial growth. High precipitation influenced radial growth negatively (Figure 6). High radial growth was observed in both low and high tree groups at a young age (<20 years old), and a decline in radial growth was observed as the trees grow older (>90 years old) (Figure 6).

3.3. Forest Resilience to Discrete Disturbance Events

The mean RWI across the disturbance periods associated with the seven extreme storm events showed a significant inverse relationship with both storm surge height ($\tau = -0.809$) and wind speed ($\tau = -0.975$) at *p*-value <0.05 from the results of Kendall's correlation analysis. Furthermore, the two-way ANOVA indicated a statistically significant effect of extreme storm events and the interaction between tree groups and extreme storm events on RWI. Pairwise comparison using Tukey's HSD post hoc test indicated that mean growth of the high tree group was significantly lower (*p*-value <0.05) during the disturbance period associated with the 1933, 2003, and 2009 extreme storm events than that during the 1962 and 1998 extreme storms. In addition, the mean growth of the high tree group during the disturbance period associated with the 2011 extreme storm event was significantly lower (*p*-value <0.05) than that during the 1998 extreme storm only. No significant differences in mean growth of the low tree group were observed between the analyzed extreme storm events at 95% confidence level. In addition, no significant, consistent difference was observed between low and high tree groups during all the disturbance periods. Additional information on the results of ANOVA and Tukey's HSD post hoc test are provided in supporting information Table S5.

The radial growth of low and high tree groups showed a mixed response to extreme storm events in terms of resistance, recovery, and resilience (Figure 7). The low tree group showed a significantly low resistance and resilience toward the 1933 extreme storm event (mean <1, *p*-value <0.05). During the 1962 extreme storm event, the high tree group showed a significantly low mean recovery and resilience (mean <1, *p*-value <0.05). Both tree groups had high mean resistance to this extreme storm event (mean ≈1 or higher). Both tree groups also had high mean resistance and resilience toward the 1998 extreme storm event (mean ≈1 or higher). A significantly low mean resistance and resilience toward the 2003 extreme storm was observed in the high tree group (mean <1, *p*-value <0.05).

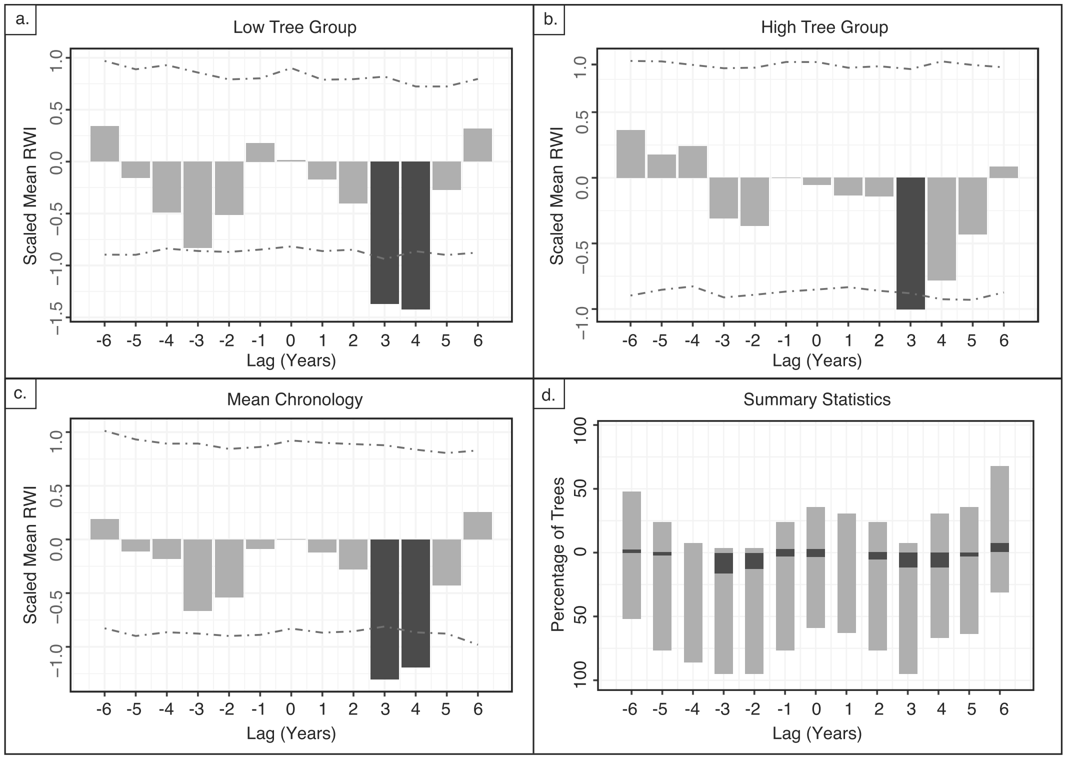

Figure 5. Results of superposed epoch analysis conducted on the mean chronology of (a) low tree group, (b) high tree group, and (c) all trees, indicating the response of radial tree growth for a 13 year window centered on dates of five extreme storms recorded in Virginia. (Refer to section 2.3.2.) Individual ring width indices (RWI) were normalized to minimize the chance that a single anomaly may disproportionately influence the composite analysis. Bars above and below the *x*-axis indicate above and below average RWI, respectively, for the 13 year window. Declining RWI trend across years is indicative of low-growth periods, whereas a growing trend across years indicates radial growth recovery. Dark gray shading shows statistically significant (at a 95% sample confidence) growth anomalies. (d) Summary of superposed epoch analysis conducted on individual trees. Dark gray shading shows the percentage of trees with statistically significant (at a 95% sample confidence) growth anomalies.

Table 1
Model Statistics of Radial Growth in Pinus taeda

Predictors	*F*-statistic	Deviance explained (%)	*p*-value
Winter temperature	3.117	0.16	0.020
Fall temperature	12.468	0.35	<0.001
Summer temperature	14.533	0.38	<0.001
Spring temperature	10.715	0.45	<0.001
Precipitation	32.270	1.65	<0.001
Tree age (high)	128.828	14.54	<0.001
Tree age (low)	70.002		< 0.001
Individual tree effects	31.215	18.96	<0.001
Storm disturbance	58.701	NA	<0.001
Tree group (low or high trees)	0.098	NA	0.754

Note. The approximate deviance explained by individual predictors and their corresponding *F*-statistic and *p*-values are listed. Predictors with *p*-value <0.05 are considered statistically significant. Mean seasonal temperatures, total annual precipitation, and tree age were modeled as fixed effects using cubic regression splines. Storm disturbance and tree group were included as fixed categorical variables and variations among individual trees was modeled as a random effect. Total deviance explained: 49.80%, adjusted R^2: 0.489.

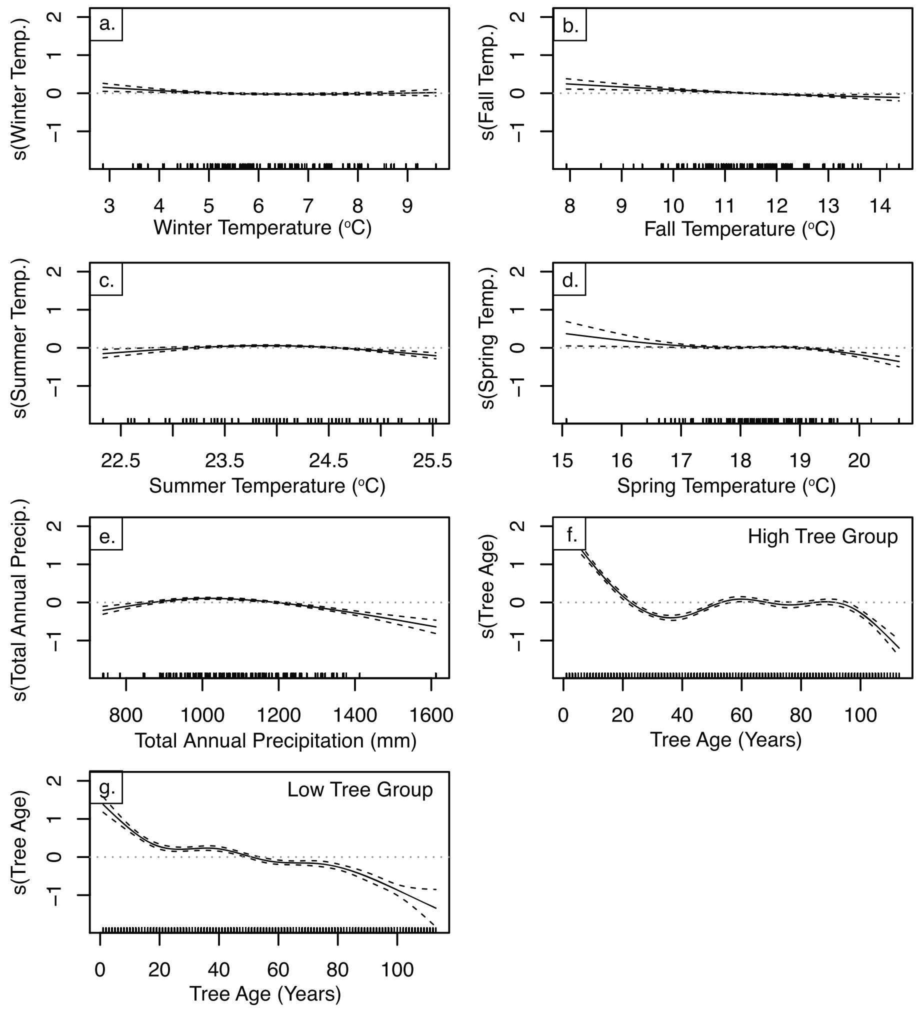

Figure 6. (a–g) Standardized partial predictors of radial growth in *Pinus taeda* estimated using cubic regression splines in generalized additive mixed model. Dashed lines represent 95% confidence intervals. The *x*-axis represents the measured values of each variable.

4. Discussion

4.1. Influence of Climate and Extreme Storm Events on Tree Ring Growth Patterns

An association is observed between the decline in radial growth and extreme storm events on the Eastern Shore of Virginia National Wildlife Refuge. This decline in radial growth of *Pinus taeda* was observed for up to 4 years following the seven extreme storm events analyzed in this study (Figures 3 and 5). Growth suppression observed in both low and high tree groups during the 1978–1980 period (Figure 4) may be associated with the 1978 Northeastern United States blizzard or due to a storm surge from an unnamed meteorological event (Figure 2). While the cause of a strong growth suppression during the 1955–1957 period (Figure 3a) could not be analyzed as no local tidal records are available for that period, we hypothesize this low-growth period to be associated with the 1954 Hurricane Hazel and 1955 tropical storms Connie and Diane. The growth suppression following storms observed from our study is in accord with several other works. Johnson and Young (1992) observed a similar association between decline in ring width of *Pinus taeda* and occurrence of hurricanes and nor'easters on the Delmarva barrier islands. Samuelson et al. (2013) and Robichaud and Bégin (1997) also reported a similar 3 to 4 year growth decline in ring width following storm events.

We associate the growth reduction observed in *Pinus taeda* with flooding and storm wind effects. Flooding affects the soil structure and salinity, decreases or eliminates soil O_2, accumulates CO_2, produces potentially toxic compounds, reduces Fe and Mn, and induces anaerobic decomposition of organic matter (Kozlowski, 1997; Ponnamperuma, 1984). These changes in soil properties can affect the physiological functions of

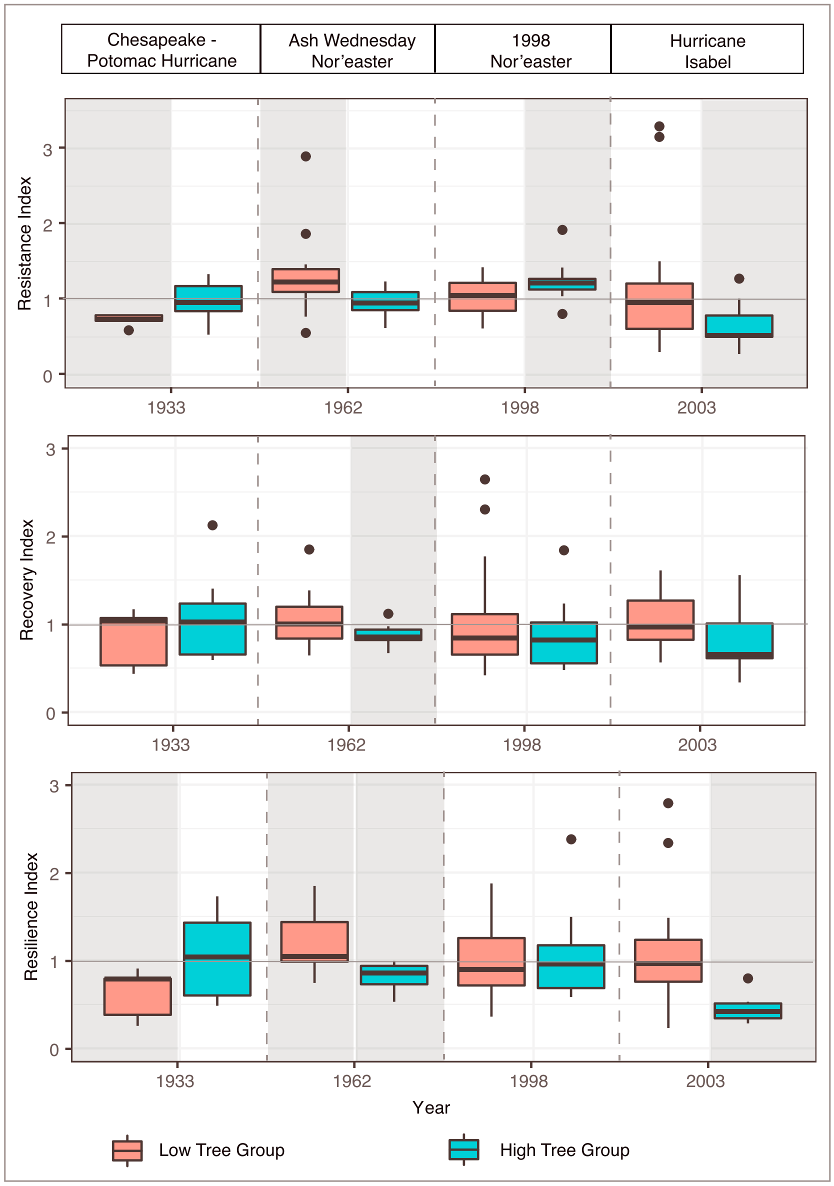

Figure 7. Resistance, recovery, and resilience of low and high tree groups for the 1933, 1962, 1998, and 2003 low-growth periods. The band inside each box represents the corresponding median value. Gray regions represent indices that are significantly different (p-value <0.05) from the base value one as indicated by one-sample t-test.

Pinus taeda. Storms can exert multiple stresses on forests. Storm surges bring salt water to flood forests, while heavy precipitation can result in freshwater flooding. Precipitation can also lower the salt stress associated with a storm surge by flushing salt from soil (Ponnamperuma, 1984). Defoliation and structural damage from wind can stress trees or lead to mortality (Brokaw & Walker, 1991; Cooper-Ellis et al., 1999). Each storm brings a different amount of surge, precipitation, and wind, and the relative strength of each of these processes can vary over the course of a storm. The present data are unable to distinguish between these different mechanisms for forest decline. However, further analysis might model the effects of storms with different ratios of storm surge, precipitation, and wind on forest health or look at the effects of storms on forests in different edaphic or topographic settings. These analysis might magnify the importance of one stressor over another, to identify the processes responsible for specific episodes of forest decline. Soil salinization due to flooding has been reported to cause browning and loss of needles or leaves in *Pinus taeda* along with a decrease in nutrient use efficiency, nitrogen retention, and physiochemical retention mechanisms (Blood et al., 1991). Soil inundation can also reduce root growth of *Pinus taeda* (DeBell et al., 1984). The reduced supply of oxygen to tree roots and sedimentation during flooding can further damage or injure the roots (Bratkovich et al., 1993; Kozlowski, 1985). Wind associated with hurricanes and nor'easters have been reported to affect the growth of *Pinus taeda* by increased salt spray (Levy, 1983), damage, or loss of branches and defoliation (Brokaw & Walker, 1991; Gresham et al., 1991; Negrón-Juárez et al., 2010).

Major losses in leaf surface area due to the storm would result in reduced radial growth of *Pinus taeda* until the leaf surface is replaced (Kuprionis, 1970). Wiley and Zeide (1991) observed a reduction in diameter growth of *Pinus taeda* for 8 years after the 1974 ice storm in southeast Arkansas that caused severe crown damage, bending and breakage of stems; the following 6 years, however, showed similar or increased diameter growth of broken trees relative to undamaged trees (see also Bragg & Shelton, 2010). Belanger et al. (1996) also reported a lack of recovery in diameter growth of *Pinus taeda* with severe crown damage for a 5 year period following the 1983 storm in central Georgia. Similar effects may have resulted in reduced radial growth of *Pinus taeda* observed in our study for up to 4 years following the extreme storms. The decline in radial growth during the disturbance period can be further explained by the allocation of carbohydrates to dormant buds, branch formation, and to add roots, thereby giving precedence to the demands for restoring crown components and roots in damaged trees over lower stem growth (Belanger et al., 1996; Bragg & Shelton, 2010; Shelburne et al., 1993; Waring & Pitman, 1985).

Radial growth usually begins to recover after the disturbance period depending on the frequency of storms in the immediate future. High frequency of disturbances is expected to accelerate environmental change and deplete individual tree reserves needed to withstand and overcome stressful episodes, thereby reducing their resilience (Lloret et al., 2011). One disturbance can increase the susceptibility of the forest to another disturbance (Oliver & Larson, 1996). The combined effect of successive disturbances of different nature can lead to negative responses and slow forest-canopy recovery (Díaz-Delgado et al., 2002; Payette & Delwaide, 2003). The low tree group, which lies closer to the marsh, is subject to frequent low-magnitude storm surges (Figure 1b). The increased exposure of the low tree group to storm surges could be the reason for the relatively higher number of low group trees exhibiting a decline in growth as compared to high group trees, following the 1933, 1962, and 1998 extreme storms as seen in the results of event year analysis (Figures 3 and 4). However, considering that decline in growth of both low and high tree groups was variable following the 2009, 2011, and 2012 extreme storm events, no definite conclusion about the impact of extreme storm events as a function of distance from the forest-marsh boundary can be made.

In addition, tree age was found to be an important variable that influences radial growth (Table 1). Initially, the low and high tree groups show a reverse-J growth pattern, typical of trees growing in an increasingly competitive environment. Both tree groups display high radial growth prior to age 20 and lower radial growth after 90 years (Figure 6). A possible scenario is that rapid radial growth occurred until canopy closure at the age of 20 years, after which growth begins to decline due to increasing competition, structural changes, and shifts in carbon allocation associated with canopy closure and maximum foliage (Smith & Long, 2001). This is consistent with the growth pattern observed by Reams (1996) in *Pinus taeda* from the Virginia Coastal Plain. Bendtsen and Senft (1986) also observed a decline in radial growth of *Pinus taeda* from North Carolina until the age of 12 years after which the ring width remained relatively constant till the age of 30 years. The drop in radial growth of both low and high group trees post-90 years may be associated with the beginning of senescence.

Furthermore, variations among individual trees was found to be a significant predictor that explained the highest proportion of deviance in radial growth (18.96%) (Table 1). This could be attributed to microsite variability, competition, and variations in tree vigor (Amateis & Burkhart, 2016; Bullock & Burkhart, 2005; Ryu et al., 2013). Microsite effects include the heterogeneity in soil moisture levels and nutrient availability across relatively small distances within the study site, which can affect the competition among trees (Amateis & Burkhart, 2016; Bullock & Burkhart, 2005; Fajardo & McIntire, 2007). The competition involves the struggle between individual trees to acquire limiting resources like light, water, and nutrients that together determine rates of carbon acquisition (Grime, 2001).

Radial growth was also found to be influenced by mean seasonal temperature and total annual precipitation, although the deviance explained by these predictors was relatively low as compared to tree age and individual tree variability (Table 1). Radial growth was found to be negatively associated with high precipitation (Figure 6). A plausible explanation to this could be water stress associated with an increase in saturation of the soil and associated low aeration (Fowells, 1965; Schultz, 1997).

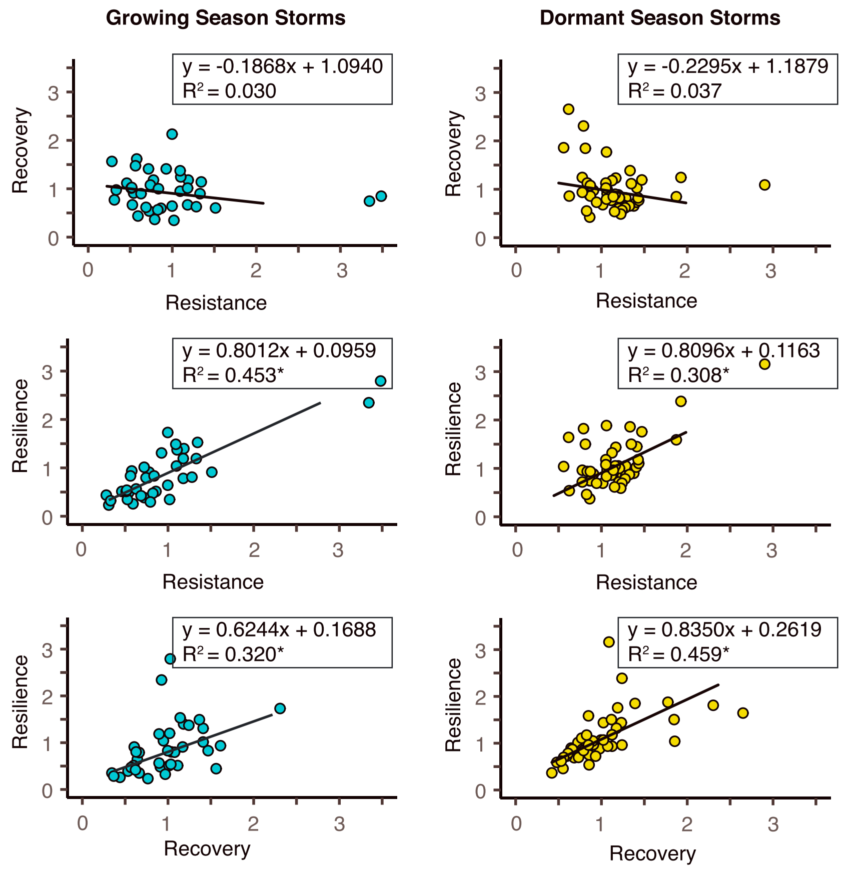

Figure 8. The relationship between resistance, recovery, and resilience of 25 *Pinus taeda* trees during low-growth periods associated with extreme storm events occurring during the growing (1933 and 2003) and dormant (1962 and 1998) seasons. The solid lines represent linear regression lines. Asterisk indicates significant linear relationship at p-value <0.05. High leverage points were not included in the regression analysis.

4.2. Forest Resilience to Discrete Disturbance Events

The resistance, recovery, and resilience to extreme storm events varied between low and high tree groups (Figure 7). The forest resilience toward extreme storm events was found to be partially related to the timing of the storm, that is, whether the storm occurred during the growing season or the dormancy period. Flooding during the growing season, especially in late spring, is found to be more detrimental to the immediate tree growth than flooding during the dormant season (Bratkovich et al., 1993). This is consistent with the results of two-way ANOVA on RWI as a function of tree group and disturbance period associated with extreme storms. The results indicated a significantly lower (p-value <0.05) mean growth in high tree group during the disturbance period associated with extreme storms occurring in the growing season (1933 Chesapeake-Potomac Hurricane and 2003 Hurricane Isabel) than those occurring in the dormancy period (1962 Ash-Wednesday Nor'easter and 1998 Nor'easter).

Recovery of the trees is a function of the impact of the event inducing the disturbance (Lloret et al., 2011). In our case, this impact, which can be defined by the magnitude of decline in ring width during the disturbance period, would be a function of storm characteristics (proximity to the site, wind speeds, storm surge height, and duration of flooding) as well as resistance of individual trees and overall stand dynamics. Comparison of resistance versus recovery points toward an inverse relationship as expected (Figure 8). Strong resistance would indicate a very low decline in ring width during the disturbance period. This can be interpreted as a low damage and a fast recovery. This trade-off between resistance and recovery after extreme storm events could occur if both these components at least partially depend on the amount of stored carbon reserves needed to withstand and overcome the stress (Galiano et al., 2011). More resilient trees showed higher recovery (Figure 8) that could be attributed to either high amount of stored reserves or increased availability of resources due to a decrease in competition. In addition, we observe a very gentle but positive linear trend between resistance and resilience (Figure 8). This indicates that if the impact during the extreme storm events was large (low resistance), the trees do not return to their original pre-disturbance state (low resilience). These could be signs of a progressive decrease in resilience over time on account of constant exposure to coastal inundation due to the proximity to the forest-marsh boundary.

Although multiple factors (tree age, competition, microsite factors, and to some extent macroclimate) provide an explanation for variation in growth of *Pinus taeda* over time, the focus of our study points toward how discrete occurrences like extreme storm events could influence the growth pattern periodically. Carefully controlled experimental data would be necessary to derive the cause and effect relationship with storms.

This study was an exploratory data analysis to understand how extreme storm events disrupt the regular annual tree growth patterns in coastal forests. While this study is purely based on classical statistical approach, a tidal simulation modeling approach would serve as a confirmatory analysis to support the findings in this work. Currently, this research is constricted by the availability of a variety of data and research design. First, the limited continuous tidal data at approximately 22 km from the study site cover only about 36.6% of the temporal span of our tree ring record. The remaining records are present only for extreme storm events and are not at the same temporal resolution. Second, continuous records of hourly maximum sustained wind speed obtained from the Norfolk Weather station span only 63.4% of our tree ring record and are located approximately 35 km away. Third, lack of tree mortality data hinders the possibility of understanding if the observed reduced growth in the years following hurricanes and nor'easters could also lead to tree mortality. No high-resolution data on changes in canopy cover post-hurricanes and nor'easters are available, which could have helped provide better ecological interpretations. Lastly, data collection is always limited by the research design and primary scope of the project. Having similar sampling conducted across multiple transects in surrounding regions would provide further verification on the dominant geomorphological and climatic controls. Coastal forests are constantly subject to flooding, and these may overlap with years of climate-limited growth; this further complicates the signal between the impact of storms versus the low growth from unfavorable climatic conditions. Although we use statistical methods like SEA (section 2.3.2) to try and isolate the common signal across different storms, sampling trees from adjacent local regions that were not flooded could help run better and more complicated signal processing analysis.

5. Conclusion

The projected increase in frequency and intensity of storm surges is likely to affect the Mid-Atlantic coastal forests in the foreseeable future. This study aimed at identifying periods of declining tree ring growth following hurricanes and nor'easters and understanding the response and resilience of vegetation in this region following these disturbances. Results indicated episodic suppressions in radial growth for up to 4 years after the extreme storm events, following which the radial growth started recovering. The timing, intensity, and frequency of the storms were found to partially influence tree growth response. We observed a statistically significant correlation between the decline in radial growth and the storm intensity (storm surge height and wind speed). An inverse relationship was also observed between the resistance of trees to extreme storm events and their recovery. Although the growth at our site was found to be influenced by age, regional climate trends, and individual tree effects, however, episodic disturbances due to extreme storms appear to control radial growth trend from time to time. Carefully controlled experimental data are required to identify concrete thresholds for storm impact parameters, which in turn would help in better managing storm affected coastal forests.

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References

Amateis, R. L., & Burkhart, H. E. (2016). Simulating the effects of site index variation within loblolly pine plantations using an individual tree growth and yield model. In *Proceedings of the 18th biennial southern silvicultural research conference. e-Gen. Tech. Rep. SRS-212* (pp. 614). US Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Anderson, B., Schumacher, A., Guikema, S., Quiring, S., Ferreri, J., Staid, A., … Zhu, L. (2017). The stormwindmodel package. Retrieved from https://www.r-project.org

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169–193.

Beier, C. M., Signell, S. A., Luttman, A., & DeGaetano, A. T. (2012). High-resolution climate change mapping with gridded historical climate products. *Landscape Ecology*, *27*(3), 327–342.

Belanger, R., Godbee, J., Anderson, R., & Paul, J. (1996). Ice damage in thinned and nonthinned loblolly pine plantations infected with fusiform rust. *Southern Journal of Applied Forestry*, *20*(3), 136–142.

Bendtsen, B., & Senft, J. (1986). Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood and fiber science*, *18*(1), 23–38.

Bishop, D. A., & Beier, C. M. (2013). Assessing uncertainty in high-resolution spatial climate data across the US Northeast. *PloS one*, *8*(8), e70260.

Blood, E., Anderson, P., Smith, P., Nybro, C., & Ginsberg, K. (1991). Effects of Hurricane Hugo on coastal soil solution chemistry in South Carolina. *Biotropica*, *23*(4A), 348–355.

Bragg, D. C., & Shelton, M. G. (2010). Recovery of planted loblolly pine 5 years after severe ice storms in Arkansas. *Southern Journal of Applied Forestry*, *34*(1), 13–20.

Bratkovich, S., Burban, L., Katovich, S., Locey, C., Pokorny, J., & Wiest, R. (1993). Flooding and its effect on trees, *Miscellaneous Publication*. Newtown Square, PA: U.S. Dept. of Agriculture, Forest Service, Northern Area State and Private Forestry.

Brokaw, N. V. L., & Walker, L. R. (1991). Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica*, *23*(4), 442–447.

Buchanan, M. K., Oppenheimer, M., & Kopp, R. E. (2017). Amplification of flood frequencies with local sea level rise and emerging flood regimes. *Environmental Research Letters*, *12*(6), 064009.

Bullock, B. P., & Burkhart, H. E. (2005). An evaluation of spatial dependency in juvenile loblolly pine stands using stem diameter. *Forest Science*, *51*(2), 102–108.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*(2), 115–124.

Byun, J. G., Lee, W. K., Kim, M., Kwak, D. A., Kwak, H., Park, T., … Jung, J. H. (2013). Radial growth response of *Pinus densiflora* and *Quercus* spp. to topographic and climatic factors in South Korea. *Journal of Plant Ecology*, *6*(5), 380–392.

Colman, S. M., Halka, J. P., Hobbs, C., Mixon, R. B., & Foster, D. S. (1990). Ancient channels of the Susquehanna River beneath Chesapeake Bay and the Delmarva Peninsula. *Geological Society of America Bulletin*, *102*(9), 1268–1279.

Conner, W. H., & Inabinette, L. W. (2003). Tree growth in three South Carolina (USA) swamps after Hurricane Hugo: 1991–2001. *Forest Ecology and Management*, *182*(1), 371–380.

Cook, E., Briffa, K., Shiyatov, S., Mazepa, V., & Jones, P. (1990). Data analysis. In E. R. Cook & L. A. Kairiukstis (Eds.), *Methods of dendrochronology* (pp. 97–162). Dordrecht, Netherlands: Springer Science.

Cook, E. R., & Peters, K. (1981). The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-ring bulletin*, *41*, 45–53.

Cook, E. R., Nance, W. L., Krusic, P. J., & Grissom, J. (1998). Modeling the differential sensitivity of loblolly pine to climatic change using tree rings. In R. A. Mickler, & S. Fox (Eds.), *The productivity and sustainability of southern forest ecosystems in a changing environment* (pp. 717–739). New York, NY: Springer.

Cooper-Ellis, S., Foster, D. R., Carlton, G., & Lezberg, A. (1999). Forest response to catastrophic wind: Results from an experimental hurricane. *Ecology*, *80*(8), 2683–2696.

DeBell, D., Hook, D., McKee, W., & Askew, J. (1984). Growth and physiology of loblolly pine roots under various water table level and phosphorus treatments. *Forest Science*, *30*(3), 705–714.

Demarest, J. M., & Leatherman, S. P. (1985). Mainland influence on coastal transgression: Delmarva Peninsula. *Marine Geology*, *63*(1-4), 19–33.

Díaz-Delgado, R., Lloret, F., Pons, X., & Terradas, J. (2002). Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. *Ecology*, *83*(8), 2293–2303.

Dolan, R., & Davis, R. E. (1992). An intensity scale for Atlantic coast northeast storms. *Journal of Coastal Research*, *8*(4), 840–853.

Duncan, R. (1989). An evaluation of errors in tree age estimates based on increment cores in Kahikatea (*Dacrycarpus dacrydioides*). *New Zealand Natural Sciences*, *16*, 31–37.

Ezer, T., & Atkinson, L. P. (2014). Accelerated flooding along the US East Coast: On the impact of sea-level rise, tides, storms, the Gulf Stream, and the North Atlantic Oscillations. *Earth's Future*, *2*, 362–382. https://doi.org/10.1002/2014EF000252

Fajardo, A., & McIntire, E. J. (2007). Distinguishing microsite and competition processes in tree growth dynamics: An a priori spatial modeling approach. *The American Naturalist*, *169*(5), 647–661.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C. S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 557–581.

Fowells, H. A. (1965). *Silvics of forest trees of the United States*. Washington, DC: Agric. Handb. US Dep. Agric. 271.

Fritts, H. C. (1976). *Tree rings and climate*. London: Academic Press.

Galiano, L., Martínez-Vilalta, J., & Lloret, F. (2011). Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytologist*, *190*(3), 750–759.

Goldenberg, S. B., Landsea, C. W., Mestas-Nuñez, A. M., & Gray, W. M. (2001). The recent increase in Atlantic hurricane activity: Causes and implications. *Science*, *293*(5529), 474–479.

Gresham, C. A., Williams, T. M., & Lipscomb, D. J. (1991). Hurricane Hugo wind damage to southeastern US coastal forest tree species. *Biotropica*, *23*, 420–426.

Grime, J. P. (2001). *Plant strategies, vegetation processes, and ecosystem properties*. Chichester, UK: John Wiley & Sons.

Harley, G. L., Grissino-Mayer, H. D., & Horn, S. P. (2011). The dendrochronology of *Pinus elliottii* in the lower Florida Keys: Chronology development and climate response. *Tree-Ring Research*, *67*(1), 39–50.

Hobbs, C. H. (2004). Geological history of Chesapeake Bay, USA. *Quaternary Science Reviews*, *23*(5), 641–661.

Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, *43*(1), 69–78.

Hook, D. D., Buford, M. A., & Williams, T. M. (1991). Impact of Hurricane Hugo on the South Carolina coastal plain forest. *Journal of Coastal Research*, *SI 8*, 291–300.

Jelesnianski, C. P., Chen, J., & Shaffer, W. A. (1992). *SLOSH: Sea, lake, and overland surges from hurricanes* (Vol. 48). Silver Springs, MD: US Department of Commerce, National Oceanic and Atmospheric Administration, National Weather Service.

Johnson, S. R., & Young, D. R. (1992). Variation in tree ring width in relation to storm activity for Mid-Atlantic barrier island populations of *Pinus taeda*. *Journal of Coastal Research*, *8*(1), 99–104.

Jones, K. B., Riitters, K. H., Wickham, J. D., Tankersley Jr, R. D., O'Neill, R. V., Chaloud, D. J., … Neale, A. C. (1997). *An ecological assessment of the United States Mid-Atlantic Region: A landscape atlas*. Washington, DC: United States Environmental Protection Agency. Office of Research and Development, 20460, EPA/600/R-97/130.

Kirwan, M. L., Kirwan, J. L., & Copenheaver, C. A. (2007). Dynamics of an estuarine forest and its response to rising sea level. *Journal of Coastal Research*, *23*(2), 457–463.

Kirwan, M. L., Temmerman, S., Skeehan, E. E., Guntenspergen, G. R., & Fagherazzi, S. (2016). Overestimation of marsh vulnerability to sea level rise. *Nature Climate Change*, *6*(3), 253–260.

Knutson, T. R., McBride, J. L., Chan, J., Emanuel, K., Holland, G., Landsea, C., … Sugi, M. (2010). Tropical cyclones and climate change. *Nature Geoscience*, *3*, 157–163.

Kozlowski, T. (1985). Soil aeration, flooding, and tree growth. *Journal of Arboriculture*, *11*(3), 85–96.

Kozlowski, T. (1997). Responses of woody plants to flooding and salinity. *Tree Physiology Monograph*, *1*, 1–29.

Kuprionis, J. (1970). *Recovery of loblolly, slash, and shortleaf pines bent by snowfall and/or ice* (Bulletin No. 4, p. 34). Ruston, LA: Louisiana Polytechnic Institute School of Agriculture and Forestry.

Levy, G. F. (1983). A study of vegetational dynamics on Parramore Island, Virginia. *Castanea*, *48*(1), 32–36.

Lloret, F., Keeling, E. G., & Sala, A. (2011). Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, *120*(12), 1909–1920.

Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., … Jackson, J. B. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science*, *312*(5781), 1806–1809.

Lugo, A. E. (2008). Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral Ecology*, *33*(4), 368–398.

Mickler, R. A., Birdsey, R. A., & Hom, J. (2012). *Responses of northern US forests to environmental change* (Vol. 139). New York, NY: Springer Science & Business Media.

Miller, D. L., Mora, C. I., Grissino-Mayer, H. D., Mock, C. J., Uhle, M. E., & Sharp, Z. (2006). Tree-ring isotope records of tropical cyclone activity. *Proceedings of the National Academy of Sciences*, *103*(39), 14,294–14,297.

Najjar, R. G., Walker, H. A., Anderson, P. J., Barron, E. J., Bord, R. J., Gibson, J. R., … Swanson, R. S. (2000). The potential impacts of climate change on the Mid-Atlantic coastal region. *Climate Research*, *14*(3), 219–233.

Negrón-Juárez, R., Baker, D. B., Zeng, H., Henkel, T. K., & Chambers, J. Q. (2010). Assessing hurricane-induced tree mortality in US Gulf Coast forest ecosystems. *Journal of Geophysical Research*, *115*, G04030. https://doi.org/10.1029/2009JG001221

National Oceanic and Atmospheric Administration (NOAA) (2010). *NOAA tide predictions database, NOAA Center for Operational Oceanographic Products and Services*. Sliver Spring, MD: NOAA. Retrieved from https://www.tidesandcurrents.noaa.gov/

National Oceanic and Atmospheric Administration (NOAA) (2016). National Oceanic and Atmospheric Administration.

National Oceanic and Atmospheric Administration (NOAA) (2017). Local Climatological Data, National Centers for Environmental Information.

Oliver, C. D., & Larson, B. C. (1996). *Forest stand dynamics*. New York, NY: John Wiley & Sons.

Panayotov, M., Bebi, P., Trouet, V., & Yurukov, S. (2010). Climate signal in tree-ring chronologies of *Pinus peuce* and *Pinus heldreichii* from the Pirin Mountains in Bulgaria. *Trees*, *24*(3), 479–490.

Paquier, A.-E., Haddad, J., Lawler, S., & Ferreira, C. M. (2017). Quantification of the attenuation of storm surge components by a coastal wetland of the US Mid Atlantic. *Estuaries and Coasts*, *40*(4), 930–946.

Parker, S., & Crichton, G. (2011). *Effects of global climate change at the Virginia Coast Reserve*. The Nature Conservancy in Virginia: Report from the Virginia Coast Reserve climate change threats workshop.

Payette, S., & Delwaide, A. (2003). Shift of conifer boreal forest to lichen–heath parkland caused by successive stand disturbances. *Ecosystems*, *6*(6), 540–550.

Ponnamperuma, F. N. (1984). Effects of flooding on soils. In T. T. Kozlowski (Ed.), *Flooding and plant growth* (pp. 9–45). Orlando, FL: Academic Press.

PRISM Climate Group (2015). PRISM Climate Data, Oregon State University. Retrieved on September 21, 2015 from http://prism.oregonstate.edu

Reams, G. A. (1996). Radial growth trends of loblolly pine in the Virginia Coastal Plain. *Canadian Journal of Forest Research*, *26*(9), 1660–1669.

Regent Instruments (2012). *Windendro 2012b*. Quebec, Canada: Regent Instruments.

Rice, S. M. (2004). Eastern shore of Virginia and Fisherman Island National Wildlife Refuges: Comprehensive conservation plan (Tech. Rep.). U.S. Fish and Wildlife Service.

Robichaud, A., & Bégin, Y. (1997). The effects of storms and sea-level rise on a coastal forest margin in New Brunswick, eastern Canada. *Journal of Coastal Research*, *13*(2), 429–439.

Rodgers III, J. C., Gamble, D. W., McCay, D. H., & Phipps, S. (2006). Tropical cyclone signals within tree-ring chronologies from Weeks Bay National Estuary and Research Reserve, Alabama. *Journal of Coastal Research*, *22*(6), 1320–1329.

Rogers, C. E., & McCarty, J. P. (2000). Climate change and ecosystems of the Mid-Atlantic Region. *Climate Research*, *14*(3), 235–244.

Ryu, S. R., Wang, G. G., & Walker, J. L. (2013). Factors influencing loblolly pine stand health in Fort Benning, Georgia, USA. *Forest Science and Technology*, *9*(3), 137–146.

Samuelson, L. J., Eberhardt, T. L., Bartkowiak, S. M., & Johnsen, K. H. (2013). Relationships between climate, radial growth and wood properties of mature loblolly pine in Hawaii and a northern and southern site in the southeastern United States. *Forest Ecology and Management*, *310*, 786–795.

Saunders, M. A., & Lea, A. S. (2008). Large contribution of sea surface warming to recent increase in Atlantic hurricane activity. *Nature*, *451*(7178), 557–560.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596.

Schofield, M. R., Barker, R. J., Gelman, A., Cook, E. R., & Briffa, K. R. (2016). A model-based approach to climate reconstruction using tree-ring data. *Journal of the American Statistical Association*, *111*(513), 93–106.

Schultz, R. P. (1997). *Loblolly pine: The ecology and culture of loblolly pine (Pinus taeda L.)*, Agricultural Handbook 713. Washington, DC: US Department of Agriculture, Forest Service.

Schweingruber, F., Eckstein, D., Serre-Bachet, F., & Bräker, O. (1990). Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia*, *8*, 9–38.

Shelburne, V., Hedden, R., & Allen, R. (1993). The effect of site, stand density, and sapwood permeability on the relationship between leaf area and sapwood area in loblolly pine (*Pinus taeda L.*) *Forest Ecology and Management*, *58*(3-4), 193–209.

Smith, F. W., & Long, J. N. (2001). Age-related decline in forest growth: An emergent property. *Forest Ecology and Management*, *144*(1), 175–181.

Speer, J. H. (2010). *Fundamentals of tree-ring research*. Tucson, AZ: University of Arizona Press.

Stokes, M. A., & Smiley, T. L. (1968). *An introduction to tree ring dating*. Chicago, IL: University of Chicago Press.

Tipton, J., Hooten, M., Pederson, N., Tingley, M., & Bishop, D. (2016). Reconstruction of late Holocene climate based on tree growth and mechanistic hierarchical models. *Environmetrics*, *27*(1), 42–54.

van der Maaten-Theunissen, M., van der Maaten, E., & Bouriaud, O. (2015). pointRes: An R package to analyze pointer years and components of resilience. *Dendrochronologia*, *35*, 34–38.

Wang, X., Liu, H., & Foltz, G. R. (2017). Persistent influence of tropical North Atlantic wintertime sea surface temperature on the subsequent Atlantic hurricane season. *Geophysical Research Letters*, *44*, 7927–7935. https://doi.org/10.1002/2017GL074801

Waring, R., & Pitman, G. (1985). Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology*, *66*(3), 889–897.
Wiley, S., & Zeide, B. (1991). Investigation of growth 14 years after glaze damage in a loblolly pine plantation. In *Proc. of Sixth Biennial Southern Silvicultural Research Conference* (pp. 272–281). US For. Serv. Gen. Tech. Rep. Se-70.
Williams, K., Ewel, K. C., Stumpf, R. P., Putz, F. E., & Workman, T. W. (1999). Sea-level rise and coastal forest retreat on the west coast of Florida, USA. *Ecology*, *80*(6), 2045–2063.
Wood, S. (2006). *Generalized additive models: An introduction with R*. Boca Raton: Chapman and Hall/CRC.
Wood, S. (2007). The mgcv package. Retrieved from https://www.r-project.org
Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Science and Business Media.
Zuur, A. F. (2012). *A beginner's guide to generalized additive models with R*. Newburgh, UK: Highland Statistics Ltd.