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Principal Factors Influencing Tree Growth in Low-Lying Mid Atlantic Coastal Forests

LeeAnn Haaf [1,2,*], Salli F. Dymond [3] and Danielle A. Kreeger [1,2]

1 Department of Biodiversity, Earth and Environmental Sciences, Drexel University, Philadelphia, PA 19104, USA; dkreeger@delawareestuary.org
2 Partnership for the Delaware Estuary, Wilmington, DE 19801, USA
3 Department of Earth and Environmental Sciences, University of Minnesota Duluth, Duluth, MN 55812, USA; sdymond@d.umn.edu
* Correspondence: lhaaf@delawareestuary.org

Abstract: Flood frequencies in coastal forests are increasing as sea level rise accelerates from 3–4 mm year^{-1} to possibly more than 10 mm year^{-1} by the end of this century. As flooding increases, coastal forests retreat, ghost forests form, and coastal marshes migrate inland. The existence of ghost forests makes the mechanism of forest retreat clear: low-lying trees become more exposed to coastal flooding until they ultimately die. Variability in these retreat rates, however, makes it difficult to predict where and when retreat will continue to occur. Understanding tree growth responses to tidal water levels relative to other environmental factors is a critical step in elucidating the factors that influence retreat variability. Here, dendrochronology was used to study factors that contribute to variations in growth patterns in four coastal forests fringing the Delaware and Barnegat Bays. Species chosen for study included loblolly pine (*Pinus taeda*), pitch pine (*Pinus rigida*), and American holly (*Ilex opaca*). Pearson's and partial correlation tests showed that growth relationships with monthly environmental conditions varied across sites and were moderate in strength (generally $R < 0.5$), but each site had at least one significant growth-water level correlation. As coastal flooding exposure is spatially dependent, tree chronologies were also separated into high and low elevation groups. Pearson's and partial correlation tests of the mean differences between elevation groups showed that at some sites, low elevation trees grew less than high elevation trees when water levels were high, as might be expected. At one site, however, lower elevation trees grew more when water levels were higher, which suggests that other interacting factors—regardless of current flood exposure—potentially have positive, yet likely temporary, influence over tree growth in these low-lying areas.

Keywords: coastal flooding; sea level rise; dendrochronology; *Pinus taeda*; *Pinus rigida*; *Ilex opaca*

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1. Introduction

Low-lying coastal forests adjacent to intertidal areas are being transformed by rapidly rising tidal water levels. In the Mid Atlantic, sea level is rising 3–4 mm year^{-1} and will likely surpass 10 mm year^{-1} within the 21st century [1,2]. Mean high water has risen even faster over the last 19 years, exceeding 8 mm·year^{-1} in some Mid Atlantic locations [3]. Higher water levels lead to higher flood frequencies and/or durations in these low-lying forests. As flood heights reach critical thresholds, trees die, and the forest retreats. Ghost forests, or the remnants of forests that have succumbed to rising sea levels, have expanded over the last several decades in Florida, North Carolina, Virginia, Maryland, and New Jersey [4–10]. As ghost forests develop, forest biodiversity is lost [9] and carbon is liberated through aboveground biomass losses [10]. In turn, as coastal forests retreat, tidal marshes—a highly valued habitat at risk of loss through rapidly rising sea levels—can migrate upslope [7]. Thus, the expansion of ghost forests as sea levels rise has implications for low-lying forests as well as for adjacent coastal habitats.

Although some coastal forests already flood during high water episodes (which are caused by astronomical or meteorological events), accelerated sea level rise will also lead to increased flooding. More frequent and longer duration tidal exposure leads to soil salinization and waterlogging beyond what is typically tolerated by most non-halophytic terrestrial species [11,12]. As a result, increased flooding leads to tree stress and death in forests adjacent to the intertidal zone, thereby precipitating forest retreat [8,13,14]. In early stages of retreat, forests with the closest proximity to the salt marsh are usually the first to show signs of reduced regeneration [13–15] and to experience death of mature trees [16–18]. Areas with gentle slopes are most likely to have expansive retreat patterns, yet they also have the most retreat rate variability [6,7]. Variability in forest retreat rates make it difficult to predict where or when future forest recession may occur [19]. This ultimately hinders coastal adaptation and management, where protecting assets (e.g., agricultural fields, roads, or buildings), adjusting to climate change, and accommodating increased flood risks are principal challenges.

Mechanisms driving the variability in low-lying coastal forest retreat have not yet been fully explored in the Mid Atlantic, although several mechanisms have been proposed. For instance, in southern New England, rather than suffering from increased coastal flood exposure, trees along the marsh-forest ecotone had greater growth, likely due to edge effects (e.g., light availability) [20]. This suggests that ecological factors, even those that are transitory, along the marsh-forest ecotone can contribute to variability in retreat rates. Interactions with local environmental conditions (e.g., drought) may also exacerbate or attenuate the effects of saltwater floods at the site- or species-specific level [4,21]. Storm surge has also been specifically implicated as a major factor mitigating forest retreat [5,18,22,23]. The effects of incrementally rising water levels on growth over time, however, is likely more subtle than the effects of large, intense, but rare events. On a basic level, these proposed mechanisms largely revolve around how tree growth, and therefore stress, is influenced by coastal flooding. Yet, only one previous study in the Mid Atlantic, which used one species at one site, has attempted to find correlations between tree growth and water level [5]. More information on the growth responses of multiple species to coastal flooding across several sites across the Mid Atlantic is needed to help deduce mechanisms that are of broad relevance to forest retreat as sea levels rise.

Environmental factors that influence tree growth can be studied through dendrochronology or the annual patterns of tree ring widths [24–26]. Suboptimal growth conditions produce thin annual rings, and these patterns can be compared to existing environmental records such as temperature, precipitation, and drought [24–26]. In low-lying coastal forests, coastal flooding is likely an additional exogenous influence over variability [5,18,20]. Here, dendrochronology was used to study factors that contribute to variations in growth patterns of different tree species (i.e., *Pinus taeda*, *Pinus rigida*, *Ilex opaca*) of coastal forests within two different estuarine settings (i.e., Delaware Bay and Barnegat Bay). Correlation and partial correlation tests were used to find relationships between tree growth and temperature, precipitation, drought, and tidal water levels. These tests were run on ring width chronologies, as well as chronologies built to represent the growth differences between high and low elevation trees. The effects of incrementally rising sea level on species-specific susceptibility to mortality requires more thorough investigation and understanding how current exogenous factors, including tidal water levels, influence annual ring growth is a critical first step.

2. Materials and Methods

2.1. Study Sites and Species

Trees were sampled at two sites in the Delaware Bay and two sites in Barnegat Bay (Figure 1). Located in the U.S. Mid Atlantic, Delaware Bay is situated between the states of Delaware and New Jersey; whereas, Barnegat Bay, a shallow lagoon in New Jersey is bordered by the mainland to the west and a thin barrier island to the east. Forested sites were chosen based on having an abundance of large, low-lying trees, which can be difficult

to find along bays with extensive coastal land use (i.e., agriculture, as in the Delaware Bay, or development, as in the Barnegat Bay). Sites were further refined based on slope and proximity to intertidal marshes, and where the sites have a 50% likelihood of being fully inundated with 1.2 m (4 ft) of sea level rise by 2050 [2,27,28].

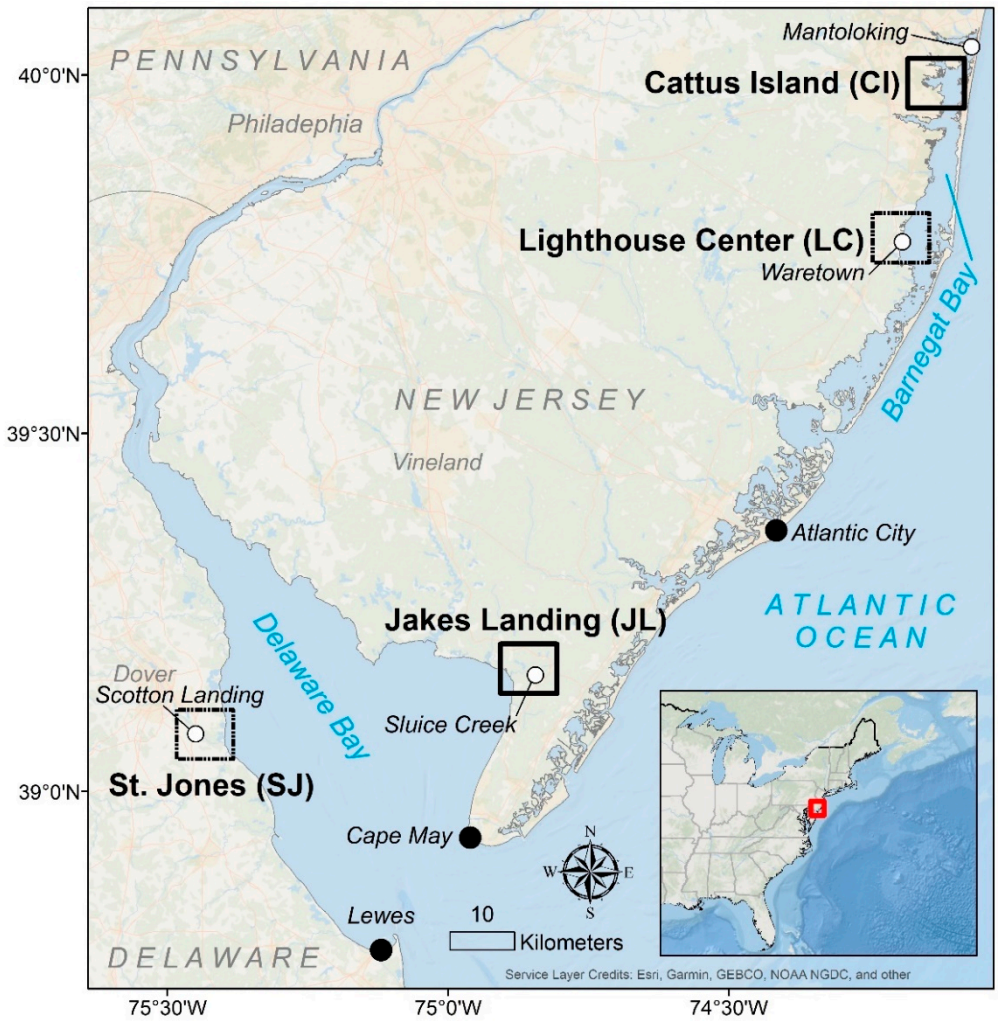

Figure 1. Map of study sites (bold labels), with box colors indicating study tree genera: solid lines are *Pinus* and broken lines is *Ilex*. Inset shows position of sites (red box) in the Mid Atlantic, along the eastern coast of the U.S. NOAA tide gauges (black circles) and local gages (white circles) are also depicted in this map. St. Jones and Jakes Landing are in the Delaware Bay, where tides range from 1.6 to 1.8 m. Cattus Island and Lighthouse Center are in Barnegat Bay, a shallow lagoon, where tide ranges are approximately 0.4 m or less.

Temperature and precipitation data for the study areas were obtained from the National Centers for Environmental Information (NCEI) regional climate datasets (available range from 1895–2020) (Table 1). The Standardized Precipitation Evapotranspiration Index (SPEI) was used as a metric for regional drought; these data were obtained from the Climate Engine [29] (Table 1). Mean winter temperatures were ~0.8 °C warmer in Delaware Bay compared to Barnegat Bay. Barnegat Bay received slightly more precipitation (~10–20 mm) than Delaware Bay on average. Seasonal winds varied more across sites. Across sites, autumn and winter winds had higher wind speeds on average compared to spring and summer (Supplemental material—Table S1). Overall, Barnegat Bay generally had higher wind speeds than Delaware Bay. Winds also came from more south-westerly directions (218–236°) in autumn and winter, but southern directions in the spring and summer (180–195°) (Supplemental Materials—Table S1). Climate variables (temperature, precipita-

tion, drought) were averaged by month and then summarized by season (spring—April, May, June; summer—July, August, September; autumn—October, November, December; winter—January, February, March) for comparison (Table 1).

Table 1. Description and means of seasonal climatic variables from 1980–2019. Temperature and precipitation data were derived from NOAA's NCEI database, whereas drought index (SPEI) were sourced from the Climate Engine. Standard deviations are in parenthesis. Seasons are the mean (temperature, drought) or sum (precipitation) of three-month intervals as follows: January, February, March—winter; April, May, June—spring; July, August, September—summer; and October, November, December—autumn.

Site	Climate Division	Coordinates (Latitude, Longitude)	Season	Mean Temperature (°C)	Mean Precipitation (mm)	Mean Drought Index (SPEI)
JL	New Jersey Southern	39.39, −75.29	Spring	16.3 (4.4)	280 (42)	0.0257 (0.78)
			Summer	22.7 (2.1)	317 (49)	0.0702 (0.78)
			Autumn	8.83 (4.6)	284 (47)	0.142 (0.94)
			Winter	3.00 (2.9)	281 (42)	0.253 (0.77)
SJ	Delaware Southern	39.08, −75.44	Spring	17.3 (4.4)	297 (45)	−0.0241 (0.87)
			Summer	23.0 (2.3)	324 (49)	0.112 (0.92)
			Autumn	8.68 (4.7)	267 (46)	0.160 (0.95)
			Winter	3.26 (3.3)	265 (42)	0.0594 (0.78)
CI	New Jersey Coastal	40.02, −74.07	Spring	16.0 (4.5)	303 (44)	0.149 (0.75)
			Summer	22.3 (2.3)	332 (52)	0.00515 (0.82)
			Autumn	8.03 (4.6)	291 (50)	0.189 (0.95)
			Winter	2.28 (3.1)	286 (46)	0.313 (0.74)
LC	New Jersey Coastal	39.78, −74.11	Spring	16.0 (4.5)	303 (44)	−0.0665 (0.82)
			Summer	22.3 (2.3)	332 (52)	0.0170 (0.79)
			Autumn	8.03 (4.6)	291 (50)	0.218 (0.79)
			Winter	2.28 (3.1)	286 (46)	0.299 (0.84)

Tree species were selected at each site based on their prevalence, large relative size, and distribution close to the marsh edge at each site. In Delaware Bay, loblolly pine (*Pinus taeda* [30]; Supplemental material—Table S2) was sampled at Jakes Landing and American holly (*Ilex opaca* [31]; Supplemental material—Table S2) was sampled at the Saint Jones River. Jakes Landing (JL) is located along Dennis Creek, a tributary of the Delaware Bay, in Cape May County, New Jersey. The Saint Jones (St. Jones) Delaware National Estuarine Research Reserve (SJ) is located along the St. Jones River, in Kitts Hummock, Kent County, Delaware. In Barnegat Bay, pitch pine (*Pinus rigida* [30]; Supplemental material—Table S2) was sampled at Cattus Island and American holly (*Ilex opaca*; Supplemental material—Table S2) was sampled at the Lighthouse Center. Cattus Island County Park (CI) is in Toms River, Ocean County, New Jersey. Lastly, the Lighthouse Center (LC) is a natural resource education camp located on Barnegat Bay in Ocean County, New Jersey.

Sampled pitch pines at Cattus Island were distributed over a larger area and were further from the marsh-forest edge compared to loblolly pines at Jakes Landing because the topography at Cattus Island sloped more gently by comparison (0.023 at Jakes Landing vs. 0.012 at Cattus Island; Supplemental material—Table S3). Holly trees at St. Jones were situated most narrowly along the marsh-upland edge, whereas holly trees at the Lighthouse Center were dispersed more widely away from the marsh (Supplemental material—Table S3).

2.2. Water Level Data

Maximum monthly water level reports were obtained for each National Oceanic and Atmospheric Administration (NOAA) real-time gage in closest proximity to each study site (Cape May, Lewes, and Atlantic City; NOAA, 2020) (Supplemental material—Table S4) [32]. Local water levels were obtained from either United States Geologic Survey (USGS) gages (Mantoloking, Waretown, and Sluice Creek) or from the National Estuarine Research Reserve System Wide Monitoring Program (Scotton Landing) (Supplemental material—Table S4). Both NOAA and local water level datasets were used as proxies for forest flooding as there were no data that could corroborate that water level height at tide gauges translated directly to surficial flooding in forests. NOAA tide gages had the longest datasets but were often far from each site (see Figure 1). USGS maintains tide gages located closer to three New Jersey sites, but records are short (~2000s–present). The Scotton Landing tide gage on the St. Jones River was also short (ca. 2008). NOAA monthly water level records before 1980 were inconsistent for the study areas, frequently with consecutive missing values for more than 3-month increments. Water level datasets were therefore truncated to 1979, where periods of missing data did not exceed two consecutive months. Remaining missing values were resolved by time series interpolation within each time series using the "forecast" package in R [33]. Monthly mean higher high water (MHHW) for each site was calculated for local tide gauge data using the R package "vulntoolkit" [34].

Flood heights likely attenuate across the distance from the nearest gauges to the forest study sites, especially as land elevations increase and meteorological exposures (e.g., positioning relative to predominate wind directions) vary. Therefore, representativeness of NOAA tide gages as a proxy for local flood heights was discerned by comparing monthly NOAA MHHW levels with the monthly local gage MHHW for each site. Partial least square regression (PLS), using the "mdatools" package in R [35], was also used to identify what factors drove local water levels variations relative to NOAA records. PLS analyses were run on the residuals of the linear relationship between local and NOAA gauge seasonal MHHW using wind speed, wind direction, precipitation anomalies, temperature anomalies, and year as predictors. Precipitation and temperature data were obtained from NOAA National Centers for Environmental Information, as described above, and wind data were obtained from the Climate Engine [29]. Kendall's concordance (W), or the degree of similarity between datasets relative to a 1:1 relationship, was also calculated using the "synchrony" package in R [36].

2.3. Field, Laboratory, and Analysis Protocols

Trees were sampled along the marsh-forest ecotone (<3.0 m North American Vertical Datum 1988 (NAVD88) in elevation and <300 m distances from the marsh edge) along a gradient of elevations from the salt marsh edge upslope to forest interiors (Figure 2). Individual tree selection was based on size (>15 cm diameter at breast height) and overall condition (e.g., free of obvious damage, rot, or disease). Diameter at breast height and coordinates were recorded for each tree. One core was extracted from each tree with a 5 mm Haglöf increment borer and placed into labeled plastic straws for transport back to the laboratory for preparation and analysis. A minimum of 51 trees were sampled at each site to produce a robust sample set, but more cores were extracted if year to year variability was high.

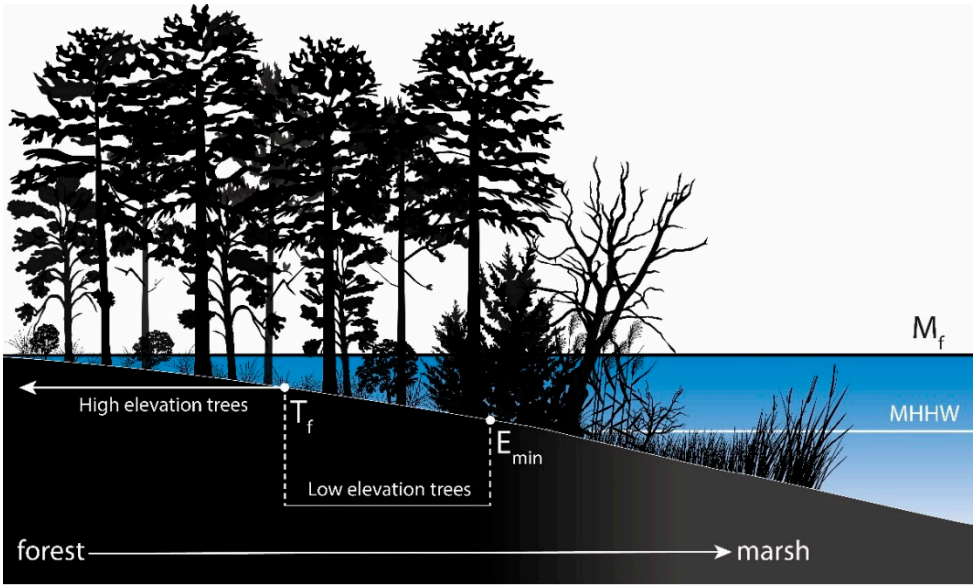

Figure 2. Diagram of elevation gradient from marsh to forest, where high and low elevation trees were sampled above mean higher high water (MHHW). High and low elevation trees were separate by a flood level threshold (T_f), which is a function of site-specific metrics such as the maximum recorded flood elevation (M_f) and the lowest sampled tree elevation (E_{min}).

Cores were mounted, dried, and sanded with a series of progressively finer sandpaper (220 to 5000 grit). After sanding, tree ring widths were measured to a precision of ±0.001 mm using a Velmex® unislide measuring table coupled with Tellervo® measurement software. Cross-dating verification was performed in COFECHA [37]. Chronologies were constructed from 51 loblolly pines from Jakes Landing (JL), 60 American hollies from St. Jones (SJ), 51 pitch pines from Cattus Island (CI), and 51 American hollies from the Lighthouse Center (LC). Individual tree chronologies were detrended using cubic smoothing splines and converted to ring width indices (RWI). Mean chronologies were developed via biweight robust means. Chronologies were built and prewhitened in R statistical software with the "dplR" package [38,39].

Pearson's correlation tests were run among RWI, temperature anomalies (1901–2000 base period), precipitation anomalies (1901–2000 base period), drought (SPEI), and maximum tidal water level values from long term NOAA gages from 1980–2019. These tests were run using the "dcc" function in the "treeclim" R package [40]. Correlation tests were performed monthly from the antecedent June to the concurrent September. Partial correlation tests of these variables were carried out using the "seascorr" function in the "treeclim" package in R [40,41] using 95% or 90% confidence intervals to determine the significance of each test. Partial correlation tests were performed monthly from the antecedent August to the concurrent September.

Flooding exposure is spatially dependent, so low elevation trees experience more frequent and longer duration flood events in comparison to trees at higher elevations. Elevation of each sampled tree was extracted from USGS Coastal National Elevation Database (CoNED) Delaware Bay and Barnegat Bay topobathy digital elevation model (DEM) [42,43]. Accuracy of digital elevation models in forests is typically <0.5 m [44]. For forestry applications this is generally regarded as accurate [44], but this error is rather large for coastal applications where centimeter-scale differences in flood heights determine whether trees are flooded or not. Regardless, CoNED DEM elevations are still suitable to separate trees into high and low elevation groups. For this, threshold values were

developed using flood heights and the DEM-based range of tree elevations at each site to group trees into high and low flood exposure groups (Figure 2):

$$T_f = (M_f - E_{min})/2 + E_{min} \quad (1)$$

where T_f is the flood elevation threshold, M_f is the maximum flood tide level on record, and E_{min} is the minimum tree elevation. M_f determination excluded extreme water level events that were >500% larger than MHHW datum (e.g., Hurricane Sandy in Barnegat Bay) (Supplemental material—Table S5). This exclusion removes potential bias associated with very extreme events and ensures that low elevation trees are more regularly flooded over time compared to high elevation trees. Differences between high and low group chronology lengths and tree sizes were compared using Student's *T*-test ($\alpha < 0.05$). Variation in tree growth along an elevation gradient was determined by comparing whether separating the chronologies into high or low elevation groups improved (via Akaike Information Criterion) heterogeneous variance-covariance models across all chronologies using the "dendro.varcov" function in the "DendroSync" R package [45].

To isolate the effect of the elevation gradient (a proxy for flood exposure) at each study site, trees were separated into high and low elevation groups using T_f. A chronology of differences was then created by subtracting annual means of the high elevation (low flood exposure) group from the low elevation (high flood exposure) group:

$$C_d = H - L \quad (2)$$

where C_d is the chronology of differences, L is the low elevation (high flood frequency) chronology and H is the high elevation (low flood frequency) chronology. Negative C_d values indicate that, during that year on average, low elevation ring widths were larger than high elevation ring widths. Pearson's and partial correlations tests were run among the chronology of differences and monthly temperature, precipitation, drought, and water levels, similar to the process described above.

3. Results

3.1. Water Levels

From the early 2000s to 2019, MHHW levels at local tide gauges and NOAA tide gauges were reasonably correlated (Supplemental material—Table S6). Relationships between the NOAA Atlantic City gauge and Mantoloking, the local USGS gage used for Cattus Island, had the lowest correlation coefficient ($R = 0.560$) but the highest concordance coefficient ($W = 0.75$). Mantoloking water level heights are likely not as well represented by those observed at Atlantic City due to the large variance between the two gauges (based on *R*), but the relationship was still reasonably synchronous (based on *W*). Thus, NOAA records were used as a proxy for water level heights to test for relationships between water level and tree growth at each site (Supplemental material—Table S6). However, it is important to note that NOAA water levels were on average 0.4 to 1 m higher than local water levels, relative to NAVD88 (see Supplemental material—Table S4).

From PLS analysis, wind direction primarily explained the variance between local and NOAA gauges followed by wind speed at Jakes Landing (where linear regression coefficients (*m*) were $m = -0.39$ for windspeed and $m = -0.24$ for wind direction; $p < 0.01$) and Cattus Island ($m = -0.51$ for windspeed and $m = -0.20$ for wind direction; $p < 0.01$) (Supplemental material—Table S7). At St. Jones, wind direction was more influential than wind speed ($m = -0.26$ for windspeed and $m = -0.51$ for wind direction; $p < 0.05$) (Supplemental material—Table S8). At the Lighthouse Center, wind speed and direction had similar influence ($m = -0.24$ for windspeed and $m = -0.26$ for wind direction; $p < 0.001$) (Supplemental material—Table S8). Generally, precipitation and temperature were not significant predictors of the variance between local and NOAA gauges, except for temperature at Sluice Creek ($m = -0.20$, $t = -2.13$, $p < 0.05$) and precipitation at Waretown ($m = +0.12$, $t = +2.17$, $p < 0.05$) (Supplemental material—Table S7).

3.2. Tree Ring Analysis

The oldest trees on average in the study were American hollies at the Lighthouse Center (LC) (112 years) and the youngest trees on average were loblolly pines at Jakes Landing (JL) (58 years) (Table 2; Figure 3). Trees sampled in the Delaware Bay were, on average, ~40–80 years younger than those in the Barnegat Bay. Loblolly pines at Jakes Landing were ~10 cm larger in diameter than pitch pines at Cattus Island (CI) (Table 2). American hollies at the Lighthouse Center were ~7 cm larger in diameter than hollies at St. Jones (SJ). Generally, American hollies were smaller in diameter than pine trees. Jakes Landing loblolly pines had the largest average ring widths (2.89 ± 1.6 mm), followed by pitch pines at Cattus Island (1.77 ± 1.0 mm). American hollies ring widths were smaller than pines; ring widths at St. Jones (1.41 ± 0.88 mm) were larger on average than those at Lighthouse Center (1.26 ± 0.62 mm) (Table 2). Interseries correlations were modest, ranging from 0.504 to 0.571 (Table 2). Marker years across chronologies included 1961–1966 (droughts) and 1978–1979 (blizzards), although the magnitude and precise year of these markers were not necessarily consistent across sites or species (see Figure 3).

Table 2. Summaries of chronologies developed for each site, including site, species, number of cores (*n*), mean diameter at breast height (DBH, in cm ± standard deviation (sd)), mean chronology length (in years ± sd), interseries correlation, and sensitivity.

Site	Species	*n*	Mean DBH (cm ± sd)	Mean Chronology Length (Years ± sd)	Interseries Correlation	Sensitivity
JL	*Pinus taeda*	51	55 ± 15	58 ± 16	0.571	0.294
SJ	*Ilex opaca*	60	22 ± 5	70 ± 21	0.504	0.532
CI	*Pinus rigida*	51	44 ± 8	90 ± 40	0.522	0.362
LC	*Ilex opaca*	51	29 ± 5	112 ± 25	0.512	0.384

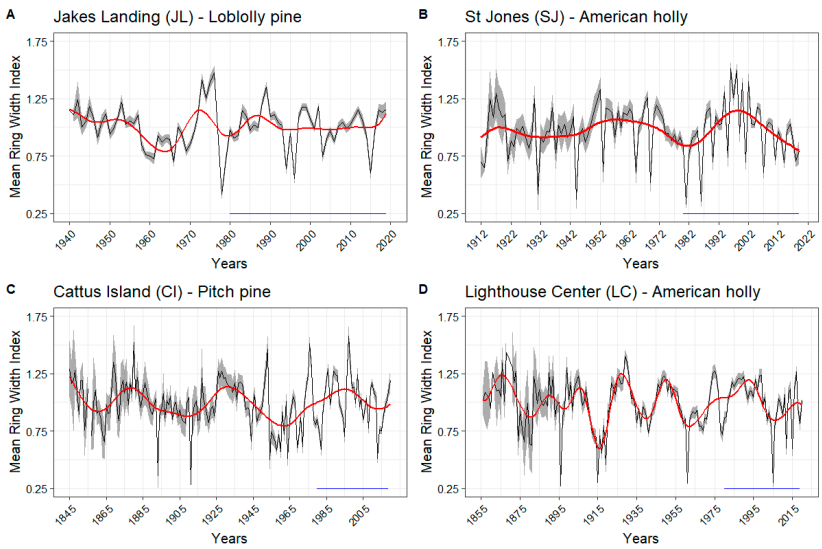

Figure 3. Mean chronologies for (**A**) Jakes Landing loblolly pines, (**B**) St. Jones American hollies, (**C**) Cattus Island pitch pines, and (**D**) Lighthouse Center American hollies. Mean chronologies (black line) with splines (red line) are bounded by standard error (light grey). The blue horizontal line in the bottom right of each graph shows the extent of the water level records (and therefore, the extent of the climatic data used in correlations), which was 1980–2019.

3.3. Factors Influencing Tree Growth in Low-Lying Forests

Tree responses to temperature, precipitation, drought, and water levels varied across species and sites. Significant correlation coefficients (R) were < 0.5, which is moderate to weak correlation strength. At Jakes Landing, loblolly pine growth was significantly ($\alpha = 0.05$) negatively correlated with antecedent December water levels ($R = -0.304$) and July drought index ($R = -0.295$), but positively correlated with February temperatures ($R = +0.399$), as well as May and antecedent September drought indices ($R = +0.368$ and +0.209, respectively). At St. Jones, American holly growth was significantly ($\alpha = 0.05$) positively correlated with antecedent December precipitation ($R = +0.275$), January water levels ($R = +0.235$) and March precipitation ($R = +0.281$). Cattus Island pitch pine growth was positively significantly correlated with September drought index ($R = +0.325$; $\alpha = 0.05$), but negatively correlated with June water levels ($R = -0.215$; $\alpha = 0.1$). At the Lighthouse Center, American holly growth was positively significantly ($\alpha = 0.05$) correlated with August drought index ($R = +0.288$). All other relationships from antecedent June to concurrent September were not significant.

Partial correlation tests for growth with water level and temperature, precipitation, or drought showed that accounting for variability between these variables changed several correlation test outcomes (Figure 4; Supplemental material—Tables S8 and S9). For instance, at Jakes Landing, accounting for temperature, precipitation, and drought indices reduced the significance (i.e., was no longer significant at $\alpha = 0.05$) of the negative relationship between growth and antecedent December water levels. Yet, accounting for variation in precipitation improved (i.e., became significant at $\alpha = 0.05$) negative growth-water level correlations for March (Figure 4A). Accounting for variability in temperature, precipitation, and drought improved negative growth-water level correlations for antecedent September for American hollies at St. Jones (Figure 4B). Accounting for variability in water levels for Cattus Island pitch pine also improved the growth correlations with antecedent October drought indices and February-March temperatures (Figure 4C). Cattus Island pitch pine growth-water level relationships for antecedent October-November and March became significantly negative after accounting for variation in drought indices and precipitation, respectively. Additionally, accounting for variability in precipitation also improved growth-water level correlations in March. Conversely, June growth-water level significance for Cattus Island pitch pines declined after accounting for variability in temperature and drought indices. By accounting for variability water levels, the significance of precipitation and drought indices in antecedent August and June, respectively, improved (i.e., became significant at $\alpha = 0.1$) for American hollies at the Lighthouse Center (Figure 4D). Lastly, after accounting for variation in June precipitation and water levels, these variables had significant negative correlations with American holly growth at the Lighthouse Center.

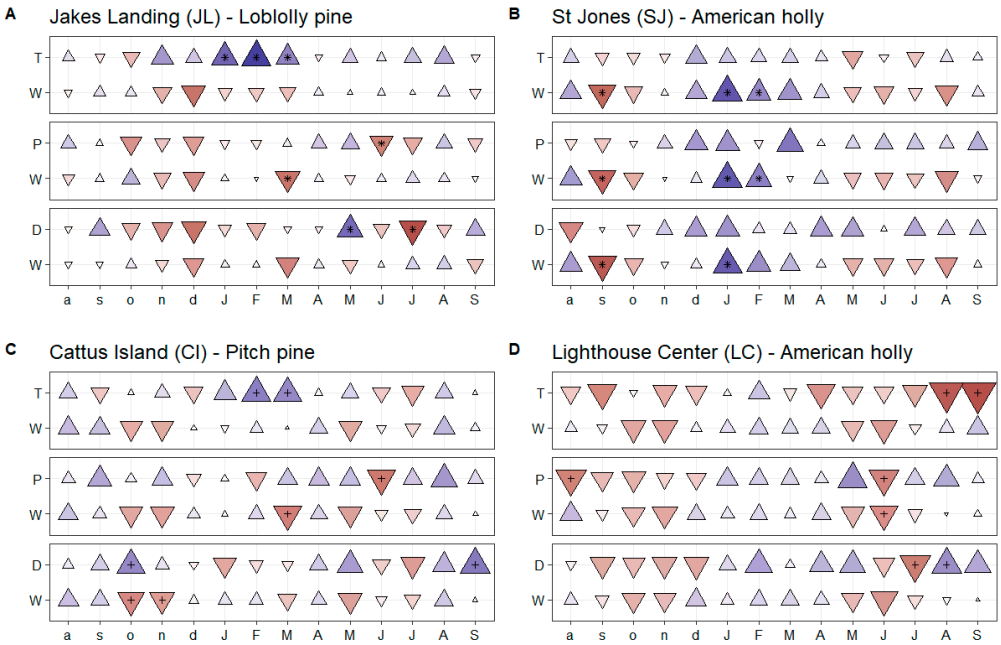

Figure 4. Partial correlation results for (**A**) Jakes Landing loblolly pine, (**B**) St. Jones American holly, (**C**) Cattus Island pitch pine, and (**D**) Lighthouse Center American holly. Pairwise tests were temperature (T), precipitation (P), and drought (D) as primary variables and water levels (W) as secondary variables. Positive correlations are represented by upwards, blue triangles, whereas negative correlations are downwards, red triangles. Saturation and size of symbols reflect the strength of the correlation (i.e., *R*), ranging from +0.5 to −0.5. Significant correlations are noted with a symbol depending on α-level (asterisk for α = 0.05 in (**A**,**B**), or plus sign for α = 0.1 in (**C**,**D**)). Antecedent months are given using all lower-case letters, whereas concurrent months are given in capital letters.

3.4. Variation in the Effects of Coastal Flooding along an Elevation Gradient

Flood regularity (i.e., degree of flood frequency and duration) varied among sites (Supplemental material—Table S10). Flood frequencies, derived from local tide gauges, at T_f were greatest at St. Jones at 1.3% (Supplemental material—Table S10). St. Jones also had the lowest elevation trees (Supplemental material—Table S3). Other sites had flood frequencies 0.2% or less. Flood durations were greatest at Cattus Island at 16%, whereas the flood duration at other sites were 0.3% or less (Supplemental material—Table S10). Trees with the lowest elevations in Barnegat Bay sat 20–40 cm lower relative to the NAVD88 compared to those in the Delaware Bay, but Barnegat Bay sat higher relative to local MHHW (Supplemental material—Tables S3 and S10).

Mean chronology lengths were significantly longer in the low elevation loblolly pines than the high elevation pines at Jakes Landing (t = 2.82, p < 0.01), although low elevation pines had significantly smaller diameters (t = 2.08, p = 0.04) (Supplemental material—Table S11). Few cores from Jakes Landing were deep enough to reach pith, however, so chronology length may not adequately represent relative tree age. Mean chronology lengths did not differ between high and low elevation trees at other sites. American holly diameters, however, were significantly larger in high elevations than low elevations at both St. Jones (t = 2.17, p = 0.03) and the Lighthouse Center (t = 2.52, p = 0.02). Diameters between low and high elevation pitch pines at Cattus Island were not significant (Supplemental material—Table S11).

High elevation trees did not consistently grow more than low elevation trees over time (Figure 5). Mean differences (±standard deviation) across chronologies were +0.01 ± 0.1 for Jakes Landing loblolly pine, +0.02 ± 0.3 for St. Jones American holly, +0.009 ± 0.2 for Cattus Island pitch pine, −0.01 ± 0.2 for Lighthouse Center American holly (where positive values indicate higher RWI at higher elevations). Variance-covariance models suggested that for

both sites with pines species (Jakes Landing and Cattus Island) chronologies (high vs. low elevation) had compound symmetry within groups (Supplemental material—Table S12), which indicates group-specific residual variation existed. Conversely, for American hollies, covariance between high and low elevation tree chronologies was not significant at the Lighthouse Center and St. Jones chronology covariances were unstructured (Supplemental material—Table S12).

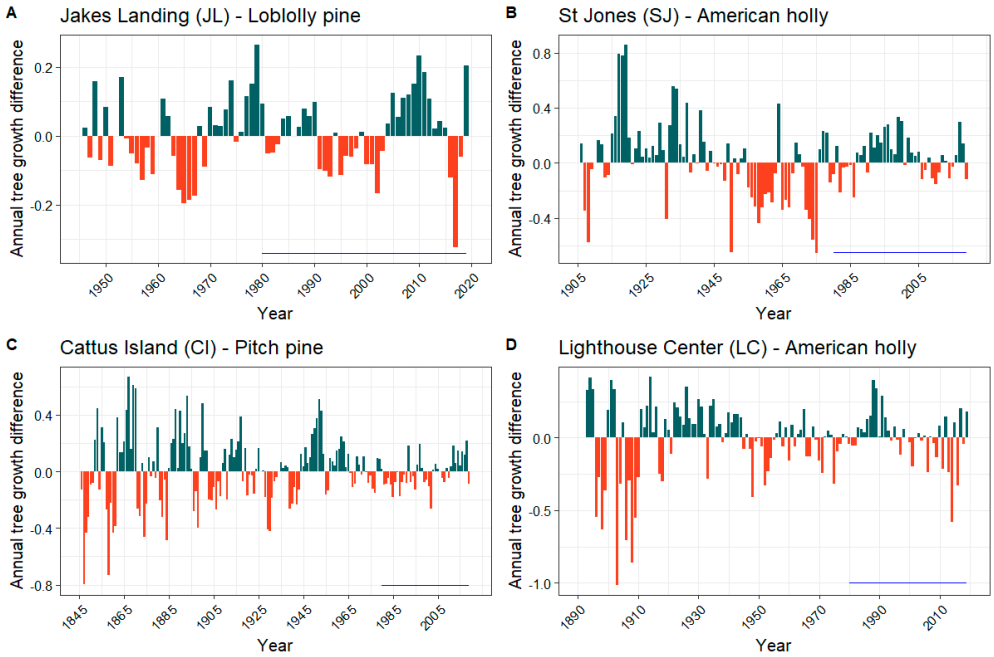

Figure 5. Chronologies of differences between high and low elevation trees for (**A**) Jakes Landing loblolly pines, (**B**) St. Jones American hollies, (**C**) Cattus Island pitch pines, and (**D**) Lighthouse Center American hollies. Chronologies of differences show where, on average, high elevation trees grew more (dark green) or less (light orange) than low elevation trees. The blue horizontal line in the bottom right of each graph shows the extent of the water level records (and therefore, the extent of the climatic data used in correlations), which was 1980–2019.

Correlations of differences between high and low elevation tree growth with temperature, precipitation, drought, and water levels varied across species and sites (Figure 6; Supplemental material—Table S13). At Jakes Landing, differences between high elevation and low elevation loblolly pine growth were positively significant (α = 0.05) with antecedent November precipitation and drought index (R = +0.357 and +0.372, respectively). At St. Jones, differences between high elevation and low elevation American holly growth was positively significantly (α = 0.05) with concurrent September precipitation (R = +0.302), but significantly negative with antecedent June drought index (R = −0.228). At Cattus Island, differences between high elevation and low elevation pitch pine growth was positively significantly (α = 0.05) with September temperature (R = +0.245) and August drought indices (R = +0.350). At the Lighthouse Center, differences between high elevation and low elevation American holly growth was significantly (α = 0.05) negative with antecedent June precipitation (R = −0.399). All other relationships from antecedent June to concurrent September were not significant.

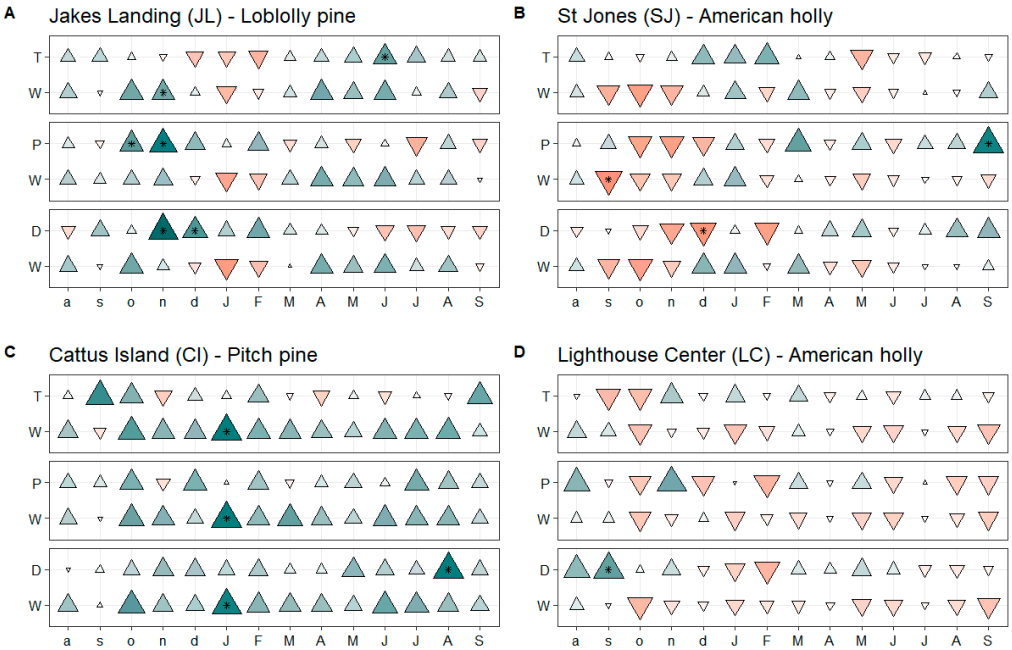

Figure 6. Partial correlation results for chronologies of difference between high and low elevation trees for (**A**) Jakes Landing loblolly pine, (**B**) St. Jones American holly, (**C**) Cattus Island pitch pine, and (**D**) Lighthouse Center American holly. Pairwise tests were temperature (T), precipitation (P), and drought (D) as primary variables and water levels (W) as secondary variables. Positive correlations (upwards, green triangles) represent correlation relationships where high elevation trees grew more, whereas negative correlations (downwards, orange triangles) are where low elevation trees grew more. Saturation and size of symbols reflect the strength of the correlation (i.e., R), ranging from +0.5 to −0.5. Significant correlations are noted with an asterisk ($\alpha = 0.05$). Antecedent months are given using all lower-case letters, whereas concurrent months are given in capital letters.

Different chronology partial correlation tests with water level and temperature, precipitation, or drought showed that accounting for variability between these variables changed several correlation test outcomes (Figure 6). For instance, for Jakes Landing loblolly pine, accounting for antecedent November temperature improved the significance (i.e., became significant at $\alpha = 0.05$) of the positive correlation (i.e., that high elevation trees grew more) between growth differences and water levels (Figure 6A). Similarly, accounting for water levels improved the positive correlations with antecedent December drought indices, antecedent October precipitation, and June temperature. At St. Jones, accounting for precipitation improved the negative correlation (i.e., low elevation trees grew more) with antecedent September water levels (Figure 6B). Similarly, accounting for water levels improved the negative correlation with antecedent December drought indices. Accounting for variability in temperature, precipitation, and drought improved positive difference-water level correlations in January for pitch pines at Cattus Island (Figure 6C). Lastly, accounting for water level variability improved the positive correlation between growth differences and antecedent September drought indices for American holly at the Lighthouse Center (Figure 6D).

4. Discussion

In the context of coastal management, predicting where and when low-lying forests will be lost to accelerated sea level rise will be an important component of adapting to climate change [8,13]. In this study, we analyzed growth relationships with climate and coastal floods, using long term NOAA water level heights as proxies for coastal flooding. Systematic assessment of how tidal water levels affect growth of various species in coastal forest will be a critical step in understanding where, and how quickly, forest retreat will

occur across the Mid-Atlantic and potentially throughout the U.S. East Coast as flood frequencies increase with sea level rise.

4.1. Factors Influencing Tree Growth in Low-Lying Forests

Temperature and precipitation are considered the primary drivers of tree growth [24–26] but as this study suggests, tree growth in low-lying coastal forests can also be significantly influenced by coastal water levels. Growth-water level correlation in the antecedent June was significantly negative ($R = -0.215$) for pitch pines at Cattus Island, which could simply correspond to the negative effects of saltwater exposure during the active growing season, as might be expected. In Delaware Bay, loblolly pine at Jakes Landing ($R = -0.304$ in the antecedent December) and American holly at St. Jones (partial correlations $R = \sim -0.4$ for antecedent September) (Figure 4; Supplemental material—Table S9) had significantly negative growth-water level correlations in the latter part of the previous growing season. It has been shown that summer drought in Mediterranean pines alters latewood morphology, producing wider tracheid lumens with thinner cell walls [46]. If salinity exposure mimics drought by increasing osmotic stress [12], trees exposed to saltwater floods in the latter part of the growing season might be more vulnerable to freeze-induced emboli (i.e., cavitation), thereby reducing growth capacities in the following growing season [12,47,48]. This mechanism may not be true for other sites or species. Late season negative responses were not found at either site in Barnegat Bay, even though hollies were also studied at one of those sites (i.e., Lighthouse Center). This suggests that site-specific conditions play particularly important roles in species-specific responses. Furthermore, contrary to the expectations that higher tidal water levels would incite negative responses, American holly at St. Jones growth had significantly positive correlations ($R = +0.235$) between growth and January water levels (Figure 4). More data from these and other species from low-lying coastal forests in various geographic settings are needed to disentangle site-specific influences and further elucidate possible common mechanisms of tree growth responses to tidal water levels.

If species-specific mechanisms mediate ring production, there will be cross-site consistency in species response to environmental conditions. Dendroclimatological studies often make use of species-specific consistency to reconstruct climate over broad regions (e.g., American Southwest [49,50]). As such, Cattus Island pitch pines responded negatively to wet Julys (positive drought indices) after accounting for variability in water levels ($R = -0.36$; Supplemental material—Table S10), which likely represents a similar negative response to wet summers as found by others [51–53]. After accounting for variability in water levels, pitch pine at Cattus Island also responded positively to warmer February and March temperatures ($R = +0.31$ and $+0.35$, respectively; Supplemental material—Table S10), which was similar to other pitch pine studies [52–54]. At Jakes Landing, loblolly pines had significantly positive growth-temperature correlations for February ($R = +0.399$, 95% CI), which was similar to loblolly pines previously studied in a coastal forest in Maryland [5]. The same study also showed the most negative growth-sea level correlations (1981–2000) were for autumn sea levels (October–December), although this result was not statistically significant [5]. It is, however, still comparable to the negative correlation reported here for antecedent December water levels at Jakes Landing ($R = -0.304$). This consistency is suggestive of loblolly pines being sensitive to tidal water levels in the latter part of the year (e.g., October–December). Currently, there are no studies that report on the response of pitch pine to tidal water levels or American holly responses to climate and/or tidal water levels.

The prevalence of significant partial correlations that account for water level variability suggests that water levels can influence tree responses to other environmental variables indirectly, even if correlations with water levels are not directly significant. Only a few Pearson's correlations were significant across sites (ten in total across sites, or ~4% of tests run), seventeen partial correlations were significant for additional variables after accounting for variations in water level (~3% of partial correlations run; Figure 4; Supplemental material—Tables S9 and S10). American holly at the Lighthouse Center in Barnegat Bay, for

instance, did not have any significant growth-water levels correlations, but by accounting for variability in water levels through partial correlation, July growth-drought relationships became apparent (Figure 4; Supplemental material—Table S10). Although these findings suggest that indirect relationships between coastal water levels and tree growth frequently occur, inconsistencies across sites regarding timing and direction of the effects (positive versus negative correlation) make it difficult to determine broader patterns.

4.2. Variation in the Effects of Coastal Flooding along an Elevation Gradient

Chronologies of differences between high and low elevation trees in this study suggested that low elevation trees, despite higher likelihoods of saltwater flood exposure, did not consistently grow less than high elevation trees (Figure 5). It is expected that, as sea levels rise, low elevation trees on gentle slopes die first [16,18], which is corroborated by the standing dead trees often observed at the marsh-forest ecotone [5,6,8,13]. Yet, in contrast with these expectations, recent studies suggest a more diminutive role of topographical slope in forest retreat patterns than originally assumed. Across the Chesapeake Bay, for example, slope did not account for as much of the variability in forest retreat as expected, especially at low slopes [7]. Large variation in retreat rates at lower slopes was also documented in New Jersey [6]. Carr et al. [55] suggest that, in a Virginia coastal forest, flood patterns and forest recovery were likely as influential as slope in early stages of modeled forest retreat. In this study, the Lighthouse Center had the gentlest slope (~0.001 $m \cdot m^{-1}$), but growth differences between high and low elevation hollies at this site did not correlate with water levels, perhaps due to the distance of these trees to the marsh edge and their high elevations relative to MHHW (Figure 6; Supplemental material—Tables S3 and S13). Jakes Landing and St. Jones had similar slopes (~0.02 $m \cdot m^{-1}$; Supplemental material—Table S3), but flood frequencies were much greater at St. Jones (Supplemental material—Table S10). As such, it might be expected that low elevations trees at St. Jones would grow less than high elevation trees with higher water levels, but the significantly negative partial correlation (i.e., low elevation trees grew more) between growth differences and antecedent September water levels suggest the opposite (Figure 6B). Yet, even with less flooding compared to St. Jones, differences between high and low elevation trees at Jakes Landing had the anticipated positive correlation with antecedent November water levels (Figure 6A). Further, individual low elevation pine chronologies in this study were more similar to each other than high elevation chronologies (and vice versa). However, this was not the case for American hollies, whose variance-covariance structures did not support differences between the groups (Supplemental material—Table S13). Given this, tree positioning relative to modes of flood exposure and species-specific characteristics likely interact with slope, thereby influencing some of the forest retreat variability across the Mid Atlantic.

Ecological or other site-specific factors likely play important roles in tree growth relationships relative to flooding in coastal forests. Some of these contextual factors may explain the positive tree growth-water level correlations observed in this study. For instance, Field et al. [20] observed higher recent growth rates in trees near the marsh edge compared to trees further inland. Those data, in addition to results for St. Jones in this study (Figure 6B), support the hypothesis that tree positioning closer to the marsh along the marsh-forest ecotone may occasionally have ecological benefits that temporarily outweigh negative effects of saltwater floods at some sites in mature trees. Edge effects result from reduced competition for light or perhaps water resources, but these benefits likely do not extend to saplings or germination that are more sensitive to flooding or saltwater exposure [13,14,56,57]. Overall, beneficial edge effects likely only occur briefly before trees become stressed and die with increased flooding, as the expansion of ghost forests evince.

Precise estimates of flooding are also difficult to hindcast in coastal forests. Even if gauges show water level heights comparable to tree elevations, attenuation of flood height from the gauge to the forest means that the forest might not have experienced a similar level of surficial flooding. Here, local water level heights were lower than the NOAA gauge heights used for correlation tests, where differences could be most attributed to wind speed and direction (Supplemental material—Table S7). Variability in wind exposure

is likely an important component of flooding in coastal forests [55], but as tree growth was investigated at an annual-level and local long-term records are sparse, it is difficult to disentangle how wind exposure influences tree growth-water level relationships. Lastly, even if surficial flooding does not occur, water level effects might be belowground. As groundwater rises with sea level rise [18,58,59], groundwater will likely play an influential role in soil moisture available to trees in coastal forests [13,14].

5. Conclusions

Variability of coastal forest retreat, especially at low slopes, suggests that the process of retreat is rather complex. To begin investigating this complexity, this study used dendrochonological methods to determine whether tree growth patterns correlated with tidal water levels relative to other environmental variables, and to discern whether differences existed between high and low elevation trees. At the coastal forest sites studied, water levels were indeed found to be an influencing factor of tree growth, however this influence was not always negative as might be expected. Site-specificity in responses to water level and other conditions were common, even if similarities were expected—as was the case for the two sites where American holly was studied. These site-specific patterns are likely the result of differences in flood exposure and other location-specific conditions, such as ecological factors (e.g., edge effects). Although results were largely site-specific, these data suggested that water levels directly and indirectly contribute to growth patterns in coastal forests. More data for these and other coastal tree species will be needed for different sites to discern broadly relevant relationships versus context- or site-specific relationships between water levels and tree growth, which explain spatial variation in forest retreat. Nevertheless, water levels and inundation patterns are an important consideration for coastal managers attempting to embrace landscape level changes occurring due to sea level rise.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12101351/s1, Table S1: Description and means of wind variables from 1980–2019 sourced from the Climate Engine. Standard deviations are in parenthesis. Table S2: Descriptions of the study species, with their distribution temperature and precipitation ranges. Table S3: Descriptions of tree sampling sites, including site coordinates, study species, elevation (in meters relative to North American Vertical Datum 1988 (NAVD88) and local mean higher high water (MHHW)), tree distances from the marsh edge, slope (in meters: Δelevation Δdistance-1), and forest types. Table S4: Description and means of seasonal water levels at local and NOAA gauges from 1980–2019. Table S5: Local flood elevations and low-high group elevation cut off values in m NAVD88. Table S6: Descriptions of NOAA and local tide gauges, as well as the statistical results for the relationship between the two gauges for each site. Table S7: Partial least square results for factors driving differences between local and NOAA water level heights. Table S8: Partial correlation results for site-specific mean chronologies for Jakes Landing loblolly pine (JL-PITA) and St Jones American holly (SJ-ILOP). Table S9: Partial correlation results for site-specific mean chronologies for Cattus Island pitch pine (CI-PIRI) and Lighthouse Center American holly (LC-ILOP). Table S10: Flood frequency estimated derived from local gauges from ~2000–2019 using the "vulntoolkit" R package, Table S11: High and low elevation group tree size (from diameter at breast height or DBH) and mean chronology length (outer year-inner year) for each site. Table S12: Variance-covariance model results for the differences between high and low elevation chronologies. Table S13: Partial correlation results for site-specific difference of high versus low elevation tree growth for Jakes Landing loblolly pine (JL-PITA), St Jones American holly (SJ-ILOP), Cattus Island pitch pine (CI-PIRI), and Lighthouse Center American holly (LC-ILOP).

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Data Availability Statement: Publicly available data used in this study can be found at the hyperlinks provided within the references list, which includes data from NOAA and USGS. Tree ring measurements and their metadata will be available on the Partnership for the Delaware Estuary's website at https://delawareestuary.org/science-and-research/, accessed on 20 August 2021.

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