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Shrub expansion in maritime forest responding to sea level rise

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Abstract

Expansion of shrubs has been observed in a number of biomes and in response to diverse global change drivers. Noting shrub expansion in coastal forests affected by sea level rise, we began to monitor shrub populations in a transgressing loblolly pine forest in coastal Virginia. Forest study plots spanned a gradient of salinity and progression towards a ghost forest state, from high forest with a relatively closed canopy, to mid and low forest, where there were few remaining live canopy trees. Shrubs of the species *Morella cerifera* were censused for three years from 2019 to 2021. Shrub distributions were compared to distributions of the invasive grass *Phragmites australis* to test if competition with this invasive species played a role in the observed shrub distribution. Shrubs were most abundant in the mid forest, whereas *P. australis* was most abundant in the low forest, but we did not detect a negative correlation between changes in occupancy of *P. australis* and shrubs. Rapid growth of shrubs in the mid and high forest radically changed the forest understory structure during the study period. Basal area of shrubs in the mid and high forest tripled, and shrub occupancy increased from 45 to 66% in the high forest, with high patchiness between plots. A flooding event salinized the site in late 2019, during the study. Following the flood, soil porewater salinities in the low forest remained above levels known to cause mortality in *M. cerifera* for several months. We postulate that high salinity, rather than competition with *P. australis*, filters *M. cerifera* from the low forest, whereas moderate salinity in the mid and high forest favors *M. cerifera* growth and expansion. The increase in shrubs appears to be a hallmark of salt-affected maritime forest, with the shrub front occurring in advance of other indicators of transgression such as *P. australis* invasion.

1 Introduction

Shrub growth forms are responsive to a variety of global changes in a diversity of ecosystems, from Arctic tundra (Mod and Luoto, 2016; Mekonnen *et al.*, 2021) to dryland grasslands (Van Auken, 2000, 2009) to barrier-island swale communities (Zinnert *et al.*, 2011, 2016; Wood, Hays and Zinnert, 2020). The significant increase in abundance and dominance of shrubs, or shrubification, in these ecosystems occurs for a wide variety of reasons. In Arctic tundra and barrier-island swale communities, shrubification is a result of warmer temperatures that favor shrubs over grasses and herbs (Thompson, Zinnert and Young, 2017; Wood, Hays and Zinnert, 2020). Whereas, in dryland ecosystems, shrubs are increasing due to their resistance to ongoing grazing pressure and an associated reduction in fires as grazers reduce natural fuel loads (Archer *et al.*, 2017). These increases in shrubs have had cascading effects for flora and fauna, as well as ecosystem cycling of carbon and nutrients (Kaarlejärvi *et al.*, 2012), evidence that shrubification can fundamentally change ecosystems.

As a growth form, shrubs are severely understudied relative to trees and grasses (Götmark, Götmark and Jensen, 2016). In changing ecosystems, the shrub growth form has unique advantages that enable expansion. Specifically, relative to trees, shrubs invest less resources in structural growth of stems and branches, and can, therefore, allocate greater biomass to roots that can access deeper pools of water and allow persistence through periods of drought or stress (Whittaker and Woodwell, 1969). The shrub growth strategy has been described as production of many relatively small, low investment or "throwaway" stems that can be sacrificed in high stress periods or environments (Götmark, Götmark and Jensen, 2016). Shrubs can also engineer a microclimate favorable to the germination and growth of conspecifics (Wood, Hays and Zinnert, 2020). Most shrub seedlings quickly establish relatively high leaf area and biomass. Furthermore, multiple stems of shrubs allow for rapid horizontal growth, and adventitious roots can emerge from stems close to the ground allowing new vertical shoots to develop (Götmark, Götmark and Jensen, 2016). Production of multiple stems is generally recognized as a persistence strategy in woody plants (Bond and Midgley, 2001). For these reasons, shrubs may be better positioned than other growth forms to persist in a highly variable environment, such as maritime forest ecosystems periodically salinized by storm events and, increasingly, by rising sea level.

Shrubs are an important component of maritime forest understory communities, where they provide climate control, soil stabilization, water balance, and carbon uptake (Götmark, Götmark and Jensen, 2016). Maritime forests are being greatly affected by sea level rise and associated saltwater intrusion into groundwater (Taillie *et al.*, 2019; Tully *et al.*, 2019; Conner *et al.*, 2022). Marsh migration and dead trees at the edge of maritime forests are visible indicators of plant community change resulting from sea level rise (Kirwan and Gedan, 2019; Ury *et al.*, 2021). Tree regeneration is suppressed by flooding and salinity (Fagherazzi *et al.*, 2019; Ury *et al.*, 2020; Woods, Swall and Zinnert, 2020). As maritime forest tree canopies open due to tree stress and mortality, species that were previously shaded out, such as marsh grasses and opportunistic invasive species like the invasive common reed, *Phragmites australis*, establish and spread (Fagherazzi *et al.*, 2019; Taillie *et al.*, 2019; Shaw, Jobe and Gedan, 2022). Shrubs are among the growth forms that have been observed to increase in response to tree mortality and light availability. For example, in dying tree islands in the Florida Gulf Coast, the halophytic shrubs *Lycium carolinianum* and *Iva frutescens* increased in abundance over two decades and across a gradient of impact (Langston, Kaplan and Putz, 2017).

In maritime forests located on the eastern shore of Virginia, the wax myrtle shrub *Morella cerifera* (L.) Small (synonymous, Myrica cerifera, ITIS, 2022) frequently dominates the understory, but is somewhat limited to the forest edge (Brinson, Christian and Blum, 1995; Duberstein *et al.*, 2020). Its geographic range extends to the North Atlantic Coastal Plain of the United States (Shao and Halpin, 1995) and the Caribbean basin, and it is introduced in Hawaii ('GBIF Backbone Taxonomy', no date). *M. cerifera* is an important component of the maritime forest community and increasing in recent decades on barrier islands (Huang *et al.*, 2018; Woods, Tuley and Zinnert, 2021). *M. cerifera* is an actinorhizal, moderately salt-tolerant evergreen shrub (Young, Erickson and

Semones, 1994; Tolliver, Martin and Young, 1997; Naumann, Young and Anderson, 2007; Woods, Swall and Zinnert, 2020; i.e. more salt tolerant than co-existing glycophytes but less so than several other woody species in the same system; Anderson *et al.*, 2022) and an early successional species that can form dense thickets (Kurten *et al.*, 2008).

We investigated whether sea level rise presents yet another global change factor causing shrubification, in this case, within the herbaceous and relatively open understory communities of maritime pine forest. If shrubs are indeed increasing in abundance or dominance in maritime forest, there may be cascading effects to the ecosystem due to the identity of the shrub, here, an N-fixing and ecosystem engineering species, or due to associated changes in ecosystem stature and structure. Additionally, understanding shrub dynamics is essential to inventories of ecosystem carbon, models of vegetation change at the terrestrial-aquatic interface, and remote sensing interpretation of coastal change. Prior to the study period, we anecdotally observed an increasing number of shrubs in forests that are rapidly transgressing. Therefore, we predicted that shrubs would increase in number, size, and basal area over time in forested areas affected by sea level rise, and that these changes would be correlated with one of two abiotic changes: 1) increasing salinity, or 2) increasing light availability, which results from tree canopy decline. Lastly, we expected to see a decrease in shrub presence where the invasive common reed *P. australis* has increased, due to competition between *M. cerifera* and *P. australis* for light resources.

2 Materials and Methods

2.1 Study site

We tested these hypotheses in a well-characterized Mid-Atlantic maritime forest using three years of shrub census data in plots that span a gradient of salinity stress and state of transition to marsh. The Brownsville Forest, located in Nassawadox, Virginia within the Virginia Coast Reserve Long-Term Ecological Research site, is typical of a Mid-Atlantic maritime forest, with dominant tree cover of mature loblolly pine (*Pinus taeda*) making up 50 to 75% of basal area (34 ± 13 m^2 ha^{-1}). Other common tree species at the site include *Nyssa sylvatica*, *Acer rubrum*, and *Ilex opaca*. Nearer to the coastal forest edge, eastern redcedar trees, *Juniperus virginiana*, are also common, as are *Baccharis halimifolia* and *Iva frutescens* shrubs. However, in the forest understory, where our plots were located, *Morella cerifera* was the only common shrub species. The site is owned and managed by The Nature Conservancy. Annually, Nassawadox receives an average of 1200 mm of rainfall and 25.5 mm of snowfall, and annual temperature ranges from summer highs averaging around 31° C and winter lows of -0.5° C. Coastal land slope, an important predictor of the rate of forest retreat and marsh migration, is exceedingly low at the site (Molino *et al.*, 2021). Based on hydrologic monitoring on-site, the forest has been subjected to salinity stress from flood events and saltwater intrusion. During the study period, saltwater flooding affected the site in October 2019 and May 2021 (Fagherazzi and Nordio, 2022; Nordio *et al.*, 2022). At the coastal forest edge where groundwater salinities are highest, a dying, ghost forest borders the marsh, while further inland where groundwater salinities are lower, a healthier forest, with a comparatively closed canopy, resides.

In 2019, twenty-four 20 x 20 m plots were established at three levels spanning the gradient, which were termed "high" (apparently healthy forest, furthest inland, approx. 300 m from the marsh edge), "mid" (stressed forest, approx. 200 m from the marsh edge), and "low" (incipient ghost forest, closest to marsh, 100 m from the marsh edge). The forest levels were designated based on tree species composition and tree condition. In high forest, the canopy was nearly closed and deciduous tree species were present. In the mid forest, there were gaps in the canopy where branches or individual trees had died, and deciduous species were absent from the canopy, and in low forest, canopy cover was lower still, many tree snags were present, and eastern redcedars were more common. In each level, eight plots were marked with T-posts at the plot corners and a PVC pole at the plot center.

2.2 Shrub census

Within each forest plot, a circular plot with a radius of 2 m around the center pole was designated for the shrub census. All shrubs with woody stems (i.e. excluding seedlings) within the circular plot were tagged and included in the shrub census. Annual data was collected during the first half of each summer growing season (mid-June to early-July). To quantify shrub growth over the span of three years (2019-2021), the following characteristics of each shrub (i.e. "individual shrub metrics") were measured annually: height, canopy area, and stem diameter. In 2021, new shrubs were added to the census if they met the woody stem criteria. No new shrubs were added to the census in 2020 due to COVID-19 restrictions and limited data collection capacity, however, the census was otherwise conducted normally in 2020.

Shrub metrics were measured according to standard protocols (Kauffman *et al.*, 2016). Height was measured from the ground to the highest point of the shrub. Canopy area was estimated as an ellipse by measuring the longest and widest sections of each individual's canopy and multiplying the two canopy radii by pi. A caliper was used to measure stem diameter of the largest stem of each shrub at 2 cm above the soil surface. Stem diameter was used to estimate cross-sectional stem area, and the cross-sectional area of all stems within a plot was summed and divided by the plot area to estimate plot-scale shrub basal area. Plot-scale shrub density was calculated as the number of shrub individuals in each plot divided by plot area.

2.3 Landscape occupancy of shrubs and *Phragmites australis*

To document shrub cover at the landscape scale, the 20 x 20 m plots were systematically surveyed for shrub presence or absence. Every 5 m, on five parallel transects spaced 5 m apart, the presence (≥ 1 shrub stem) or absence of shrubs within a 1 m radius was observed and recorded in early July of each year. The first and last transects aligned with plot edges. A compass was used to maintain the same orientation of all the transects, and a handheld GPS (Garmin eTrex 22) was used to mark the coordinates of the starting point and to map sample locations within GIS.

Using the same survey design, we described the presence and stem density of *Phragmites australis* within the forest plots. The same density scale described in Shaw et al. (2022) was used. Specifically, a zero denoted *P. australis* absence, a 1 that one to three stems were present, a 2 that there was a small group of stems, a 3 that there was a sparse stand, and a 4 that there was a fully developed stand. To track landscape occupancy of shrubs and *P. australis* density through time, we calculated the proportion of points with shrubs present and the average density of *P. australis* in each plot in each year. We also used ArcMap to visualize shrub occupancy and *P. australis* density.

We expected to see shrub occupancy decrease in locations where *P. australis* increased, which would suggest a competitive relationship between the two species in which *P. australis* can outcompete shrubs for limiting light resources in the understory. We expected this pattern to be most apparent in the low forest where *P. australis* was predicted to be more abundant. We mapped distribution changes to compare sample locations that experienced an increase, no change, or a decrease for both shrubs and *P. australis*.

2.4 Abiotic conditions

Abiotic measurements of porewater salinity and canopy gap fraction were made throughout the study period. Porewater samples were collected opportunistically following rain events from the top 20 cm of soil using a pushpoint sampler (MHE Products). Salinity of the porewater sample was measured with a handheld conductivity and salinity meter (Hach, accuracy +/- 0.1 ppt). On each sampling occasion, three porewater samples from each plot were collected. Each sample was measured individually and the mean of the three values was used as an estimate of plot porewater salinity. The proportion of the canopy composed of light gaps was estimated for each plot using photos collected with a fisheye lens attached to a smartphone. The smartphone was placed on top of the center pole of each plot, with the camera pointed upwards toward the sky. Low hanging vegetation was pushed out of the frame in order to get a clear photo of the tree canopy. Photos were checked for quality and corrected for overexposure. Photos were analyzed in ImageJ software by binarizing the image and recording the proportion of dark pixels (canopy) relative to dark and light pixels (canopy plus sky). Canopy gap portion was calculated as 1 - [canopy proportion]. This process was inspired by the canopy cover index developed by Tichý (2016).

2.5 Statistical analysis

As 97% of shrubs in the census were *Morella cerifera* (n = 324 of 334 shrubs), the remaining n=10 individuals, which were tree seedlings of species *Ilex opaca* (n=9) and *Juniperus virginiana* (n=1), were excluded from the data analysis to focus on *M. cerifera* dynamics. For individual shrub metrics (canopy area, height, and stem diameter), mean and standard error values of all individuals within each forest level were plotted for each year. For plot-scale metrics (shrub density, basal area, occupancy of shrubs and *P. australis*, and abiotic variables), mean and standard error values of all plots in a forest level (n=8 per level) were plotted for each year. Annual changes in metrics were calculated relative to the 2019 baseline census to visualize change through time. The effects of forest level (low, mid, and high) and year (2019, 2020, and 2021) and their interaction on individual shrub and plot-scale response variables were tested using two-way repeated measures ANOVA (RM-ANOVA). For individual shrub metrics, only shrubs encountered in all years were included, to accurately quantify shrub growth and to avoid potential bias from missing data. Whereas, in analyses at the plot scale, we included all shrubs found in one or more years to account for recruitment and mortality between censuses.

Prior to RM-ANOVA, normality was checked using Quantile-Quantile plots, and when required, response variables were transformed using square root or cube root transformations. The assumption of sphericity was checked using Mauchly's test of sphericity and corrected with the Greenhouse-Geisser correction within the *rstatix* package (Kassambara, 2022). When RM-ANOVAs indicated significant effects (p-value <0.05), pairwise t-tests with Bonferroni corrected p-values were used to identify differences between levels or years.

To understand the relationship between the abiotic measures and shrub metrics, we tested for Spearman rank correlations between each plot-scale response variable and the plot-scale abiotic variables of canopy cover, peak salinity in 2019, and the increase in salinity resulting from the flooding event (calculated as the early summer salinity subtracted from the post-event peak salinity in 2019). We investigated lag effects by testing correlations between the shrub metrics from each year and the abiotic conditions of all other years, with the expectation, for example, that the salinity associated with the flooding event of 2019 might be observed only in the shrub response of subsequent years.

We used a contingency table of observed distribution changes of *M. cerifera* and *P. australis* and a chi-square test of data from each forest level to distinguish if there was a statistically significant relationship between the increase, decrease, or no change in *M. cerifera* and *P. australis* presence between 2019 and 2021, with each survey point as an observation (n = 200 points per forest level). All statistical analysis and data visualization were done in R statistical software (R version 3.6.1, CRAN), and the following packages were used in data manipulation and visualization: *tidyr* (Wickham and Henry, 2020), *ggplot2* (Wickham, 2016), *stringr* (Wickham and Wickham, 2019), and *lubridate* (Spinu *et al.*, 2018).

3 Results

3.1 Shrub Census

Between 2019 and 2021, there was a rapid increase in all individual shrub metrics (canopy area, height, and stem diameter, Fig. 1a-c) reflecting high growth of shrubs at this site (significant main effect of Year for all individual metrics in Table 1, Fig. S1). Shrub height was the only individual metric to exhibit a significant interactive effect of forest level and year, which was a result of the increasing height of shrubs through time in the mid and high forest but not in the low forest, as well as the initially greater height of shrubs in the mid forest relative to high forest, a difference which disappeared in later years (Fig. 1b).

At the plot-scale, density differed by forest level, with the mid forest having the highest shrub density (22,978 ± 5,722 shrubs/ha, mean ± s.e. across all years), then the high forest (6,864 ± 2,450 shrubs/ha), followed by the low forest (846 ± 199 shrubs/ha), and there was no change in shrub density over the course of the study (Fig. 1d). In contrast to density, basal area increased dramatically during the study (Fig. 1e), driven by the growth in individual stem diameter. Basal area roughly tripled in the high and mid forest, from 0.6 ± 0.4 and 2.4 ± 0.9 m^2/ha, respectively, in 2019, to 1.7 ± 0.9 and 6.5 ± 2.0 m^2/ha in 2021 (Fig. 1).

Change in the mid and high levels was approximately linear between 2019 and 2021, with both years showing substantial increases in individual shrub growth and basal area (Fig. 1). Contrastingly, the low forest experienced far less change in all metrics, and far greater variability, due to the low density of shrubs and resulting small sample size. There were only seven individuals in the low forest, one of which was not found in 2020 and two others of which were very large and considered statistical outliers.

3.2 Landscape occupancy of shrubs and *Phragmites australis*

Shrub occupancy was consistently highest (> 80%) in the mid forest plots over the three-year period (main effect of Level, Table 1, Fig. 2). The significant interactive effect between forest level and year on shrub occupancy (Table 1) was driven by increasing differences between the mid and low forest levels through time (Fig. 2, S2, S3). Interestingly, while the low and high forest levels never differed significantly in shrub occupancy, they tended toward greater difference through time (2019: low vs. high, t(7) = -0.104, p = 1.000; 2020: t(7) = -2.84, p = 0.076; 2021: t(7) = -2.89, p = 0.070). In 2019, both low and high forest plots had approximately 45% shrub occupancy (44 ± 0.04% in low and 45± 0.12% in high forest), but in 2020, there was a sharp increase in shrub occupancy in the high forest (to 66 ± 0.12%) and a slight decrease in the low forest (to 39 ± 0.05%), both of which persisted into 2021 (Fig. 2a).

As opposed to shrub occupancy, *P. australis* density peaked in the low forest (Fig. 2, main effect of Level). *Phragmites australis* density at the site increased across all forest levels from 2019 to 2020 (2019 vs. 2020, t(23) = -3.03, p = 0.018), but showed a more stagnant trend from 2020 and 2021 (2020 vs. 2021, t(24) = -0.77, p = 1.000). Average *P. australis* density, using the index described, increased in the low forest from an average of 2.6 ± 0.5, or a handful of stems, in 2019 to 3.1 ± 0.3, a sparse stand, in 2021. *P. australis* increased in the mid forest from 1.5 ± 0.4 in 2019 to 1.9 ± 0.5 in 2021 and in the high forest from 0.5 ± 0.2 in 2019 to 0.7 ± 0.4 in 2021 (Fig. 2, S4, S5).

3.3 Relationship between shrubs and *Phragmites australis* occupancy across the landscape

While there were more points in the low forest than mid or high forest levels that exhibited the expected "*P. australis* increase, shrub decrease" relationship (9.5% of points), the strongest pattern across all levels was overwhelmingly "no change, no change" (Figure 2c). Chi-square tests were non-significant for all levels (Table 2), indicating independence between distribution changes of *P. australis* and shrubs.

3.4 Abiotic conditions and their effect on shrub growth

Porewater salinity peaked in October 2019, due to a flooding event caused by Tropical Storm Melissa, which passed offshore during October 11-14, 2019 and elevated the spring tide series by about 1 m (Nordio *et al.*, 2022). Although the coarse temporal coverage of porewater sampling may have missed other smaller flooding and saltwater intrusion events, independent high frequency sampling from several of the same forest plots (Fagherazzi and Nordio, 2022) suggests that the data presented here accurately represent the system. In all time points, porewater salinity was significantly higher in the low forest, where it ranged from 4 to 16 ppt, than in the high forest, where it ranged from 1 to 10 ppt (Level effect, Table 3, Fig. 3). In two of the four collection dates (on 2019-10-29 and 2021-08-08), porewater salinity in the low forest was also significantly higher than in the mid forest (Date:Level effect, Table 3), suggesting that the forest levels represented a consistent gradient in salinity stress, even as salinity stress varied considerably between sampling occasions (Date effect, Table 3). Similarly, canopy gap portion reflected a consistent stress gradient (Level effect, Table 3). There were significantly higher gap portions in the low forest (0.66 ± 0.02) than in the high (0.45 ± 0.03, t(23) = -8.20, p <0.0001) and in the low forest than the mid forest (0.55 ± 0.02, t(23) = 3.03, p = 0.018). Canopy gap portion was not statistically significantly different between time points, though there appeared to be a slight increase in the gap portion in the low forest from 2019 to 2020 (Fig. 3b) that might represent a response of canopy trees to the 2019 flooding event. Relatedly, we observed a significant negative correlation between peak salinity with tree canopy cover and change in salinity with tree canopy cover (Fig. 3c).

We detected no significant correlation between peak salinity or change in salinity and any of the plot-scale shrub metrics (Fig. 3c). However, there was a significant positive correlation of tree canopy cover with shrub density and shrub basal area in all years (Fig. 3c).

4 Discussion

In this three-year period, we observed rapid growth of shrubs throughout the understory of the Brownsville Forest, particularly in the mid and high levels of forest, where the effects of sea level rise and saltwater intrusion are less visually apparent than in the low forest. Basal area of shrubs in the mid and high forest levels approximately tripled, as existing shrubs grew rapidly in stem diameter. Shrub landscape occupancy in the high forest increased from 45 to 66% between 2019 and

2020. The structure of the forest understory in the high forest plots, which began this short study as relatively open and with low vegetative cover, was transformed by *Morella cerifera* expansion.

Compared to the mid and high forest, the shrub layer of the low forest had few shrubs and changed little over time. While shrubs expanded in mid and high forest plots, the low forest experienced a slight decrease in shrub occupancy. Low forest plots were instead characterized as having a higher density of *P. australis*, which increased gradually through time at all forest levels. Spread of *P. australis* at the trailing edge of retreating forest has now been observed at a number of sites throughout the Mid-Atlantic (Smith, 2013; Shaw, Jobe and Gedan, 2022). We observed that, relative to the dominance of *P. australis* in the low forest, shrub expansion is occurring in deeper areas of coastal forest, where forest dieback in response to salinity is less apparent. The shrub front is advancing ahead of the ghost forest edge.

That neither tree canopy cover nor porewater salinity had the predicted effect on shrub metrics is likely an outcome of the relatively short timescale of our study. Forest canopy gap portion did not significantly change during the study period; a longer time period is necessary to observe directional change across the site. Other studies of coastal vegetation change that spanned decadal timescales have detected effects of tree canopy cover decline and salinity increase on vegetation change (Taillie *et al.*, 2019; Woods, Tuley and Zinnert, 2021; Anderson *et al.*, 2022). Instead, we observed a positive correlation of tree canopy cover with shrub basal area and shrub canopy area that reflects spatial autocorrelation of greater shrub dominance in the deeper forests levels where canopy cover is also greater.

As is typical of the coastal forest ecotone (Brinson, Christian and Blum, 1995; Taillie *et al.*, 2019; Tully *et al.*, 2019; Conner *et al.*, 2022), salinity stress was highly dynamic during this study, with a pulse in soil porewater salinity attributable to a major storm surge event early in the study period (Nordio *et al.*, 2022). The porewater salinity levels reached 16 ppt in the low forest. In comparison, salinities in the mid and high forest levels ranged from 2 to 12 ppt and 1 to 10 ppt, respectively. Tolliver et al. (1997) observed 60% mortality in *M. cerifera* that were experimentally exposed to 10 ppt for 30 days, and 100% mortality in individuals exposed to 20 ppt. Seawater of 10 ppt can reduce germination probability in *M. cerifera* by about 50% relative to a freshwater control, and salinity of 20 ppt prevents germination entirely (Woods, Swall and Zinnert, 2020). Among coastal shrubs, *M. cerifera* was ranked as more sensitive to salinity than *Baccharis halimifolia* and *Iva frutescens* (Young, Erickson and Semones, 1994). But *M. cerifera* is more salt-tolerant than many forest understory species, due to its adaptations to tolerate salinity stress, such as closing its stomata gradually to prevent damage to the photosynthetic apparatus (Naumann, Anderson and Young, 2008) and using its wide canopy to gather scarce freshwater resources from rain (Allen and Conner, 2021). This moderate salinity tolerance of *Morella cerifera* explains why the species appears to be thriving in the lower salinity zones of the mid and high forest, but is less common and exhibits slower rates of growth in the low forest, where salinity levels have breached its tolerance threshold.

Our hypothesis that the reduced density and growth of shrubs in the low forest might be explained by competition with *P. australis* was not supported, as we were unable to detect a negative correlation between *M. cerifera* and *P. australis* that would have been indicative of competitive exclusion. Instead, the lower density, slower growth, and decline in occupancy of *M. cerifera* in the low forest is better explained by a direct effect of high salinity. However, other indirect interactions may shape the distribution of *M. cerifera* in the coastal forests and possibly even favor *M. cerifera* expansion in the mid and high forest. For example, more negative effects of moderate salinity stress on trees than shrubs could mediate changes in water availability within soils which favor shrub expansion. Bird dispersal of *M. cerifera* (USDA, 2022) may also contribute to *M. cerifera* expansion in the mid and high forest, where perching trees offer habitat to birds, and gradual opening in the tree canopy provides enough sunlight at the forest floor for *M. cerifera* to thrive. Shrub-shrub positive feedbacks have been observed in barrier island swale plant communities, in which shrubs create a microclimate that enhances shrub recruitment (Wood, Hays and Zinnert, 2020). Lastly, *M. cerifera* has a symbiotic relationship with *Frankia* sp*.,* an actinorhizal nitrogen-fixing bacteria (Kurten *et al.*, 2008). Other studies have found that *Frankia* populations flourished in soils high in organic matter (Wijnholds and Young, 2000; Young et al., 1992). If mid and high forest soil provides higher quality resources for *Frankia* populations, this might benefit *M. cerifera*.

4.1 Implications of shrub expansion for forest ecosystems undergoing transgression

N-fixing shrubs in the Myricaceae have been known to radically alter ecosystem nutrient cycling (Vitousek *et al.*, 1987). The effects of the invasion of *Morella faya* (formerly, *Myrica faya*) in the Hawaiian Islands are well-known (Vitousek *et al.*, 1987); it alters successional processes through nitrogen enrichment and significantly increases the resource base for the entire ecosystem. Somewhat lesser known, where *M. cerifera* is introduced in the Hawaiian Islands, it also makes nitrogen more available to surrounding biota (Kurten *et al.*, 2008). Similarly, *M. cerifera* can exert strong ecological effects in the maritime forest. A study on the barrier islands of Virginia's Eastern Shore found that soil nitrogen content was highest in soil under *M. cerifera* thickets (Young et al., 1992). For this reason, we predict that the expansion of *M. cerifera* is likely to increase the supply of biologically available nitrogen in transitioning coastal forest.

Shrubification in other biomes has had many ecosystem-level effects beyond soil nutrient availability. The expansion of shrubs throughout the forest understory can strongly influence biodiversity, through changes in vegetation structure and soil properties (Archer *et al.*, 2017). In other, more arid systems, woody plant encroachment has been shown to alter hydrologic cycles by changing soil infiltration rates, with effects on soil fertility and plant species richness (Archer *et al.*, 2017).

For the case of *M. cerifera* expansion in the maritime forest, we expect that shifts in shrub-tree interactions will be a consequential outcome of shrubification. In *M. cerifera* thickets on barrier islands, recruitment of *Pinus taeda* seedlings was inhibited by shading (Tolliver, Colley and Young, 1995). Lack of forest regeneration has been noted as a shift in *P. taeda*-dominated forests affected by salinity (Kearney, Fernandes and Fagherazzi, 2019). Therefore, shrub expansion and inhibition of tree recruitment may play a critical role in forest transition in this region. Shrub dominance has been suggested to be an intermediate or alternative successional pathway during forest transition (Woods, Tuley and Zinnert, 2021). The enhanced growth and colonization of shrubs that we observed and this alternative trajectory may explain the large increase in scrub-shrub dominated areas during forest transition (Ury *et al.*, 2021).

5 Conclusion

We observed encroachment by shrubs, specifically *Morella cerifera,* in the understory of maritime forest, which we suggest is an indicator of transgression in advance of *Phragmites australis* and the coastal forest treeline. Over the span of our study period, shrub metrics (canopy area, height, stem diameter, basal area, and occupancy) increased most dramatically in the mid and high forest. The dominance of *M. cerifera* in the understory of maritime forest may serve as an important indicator of ecosystem transition from healthy forest to ghost forest and eventually marsh. In this study, we add maritime forest to the list of ecosystems in which shrubification is occurring, and identify the likely driver as salinity stress related to sea level rise and saltwater intrusion.

6 Author Contributions

KG conceived of the study and KG and AP designed the survey protocols. RS, AP, and KG collected data in 2019 and 2021, and CB and JM collected data during the 2020 season when the Covid pandemic made field work difficult. RS analyzed the data and wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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9 Supplementary Material

Supplementary Figures 1-5 contain individual shrub metric and plot change data and maps of shrub occupancy and *Phragmites australis* stem density.

10 Data Availability Statement

The datasets generated and analyzed in this study are published in the Virginia Coast Reserve Data Catalog (http://www.vcrlter.virginia.edu/cgi-bin/browseData.cgi). Shrub and *Phragmites* data can be found within Gedan et al. (2022b, doi:10.6073/pasta/f5d6779021676538649c445dc3a4fbf7) and abiotic data within Gedan et al. (2022a, doi:10.6073/pasta/126bf89e433dd6cb8671c4a4d173b8f3).

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Tables

Table 1. Repeated Measures ANOVA for individual shrub and plot-scale metrics. Significant p-values (<0.05) are bolded. Values are Greenhouse-Geisser corrected for sphericity where necessary.

Response variable	**Factor**	**df**	**F**	**p-value**
Canopy Area	Level	2, 242	0.703	0.496
	Year	1.78, 429.77	32.805	**p<0.0001**
	Year:Level	3.55, 429.77	0.333	0.834
Height	Level	2, 264	0.921	0.400
	Year	1.57, 415.06	26.784	**p<0.0001**
	Year:Level	3.14, 415.06	3.168	**0.0220**
Stem Diameter	Level	2, 259	2.362	0.0960
	Year	1.86, 481.02	22.031	**p<0.0001**
	Year:Level	3.71, 481.02	1.839	0.1250
Density	Level	2, 21	7.981	**0.003**
	Year	1, 21	0.614	0.442
	Year:Level	2, 21	1.663	0.214
Basal Area	Level	2, 21	11.347	**0.0005**
	Year	1.26, 26.43	33.594	**p<0.0001**
	Year:Level	2.52, 26.43	10.613	**0.0002**
Shrub Occupancy	Level	2, 21	8.202	**0.0020**
	Year	1.59, 33.38	5.123	**0.0170**
	Year:Level	3.18, 33.38	6.195	**0.0020**
Phragmites Occupancy	Level	2, 21	10.813	**0.0006**
	Year	1.43, 30.11	8.632	**0.0030**
	Year:Level	2.87, 30.11	1.291	0.2950

Table 2. Statistical summary table for Chi-square tests of the relationship between shrub presence and *Phragmites australis* presence in high, mid, and low forest plots.

Forest level	**Chi-squared**	**df**	**p-value**
High forest	1.8371	4	0.7657
Mid forest	4.4722	4	0.3459
Low forest	6.4939	4	0.1652

Table 3. Repeated Measures ANOVA for abiotic variables. Significant p-values (<0.05) are bolded and values are Greenhouse-Geisser corrected for sphericity.

Response variable	**Factor**	**df**	**F**	**p-value**
Salinity	Level	2, 21	59.611	**p<0.0001**
	Date	1.75, 36.84	416.038	**p<0.0001**
	Date:Level	3.51, 36.84	5.825	**0.0010**
Canopy gap portion	Level	2, 21	7.933	**0.0030**
	Date	1.28, 26.87	3.479	0.0640
	Date:Level	2.56, 26.87	1.997	0.1460

12 Figures

Figure 1. Individual shrub metrics of a) canopy area, b) height, and c) stem diameter and plot-scale shrub metrics of d) shrub density and e) shrub basal area for the study years of 2019-2021. Asterisks denote p-value thresholds of factors of forest level, year, and their interaction in RM-ANOVA.

Figure 2. a) Shrub occupancy, b) *Phragmites australis* occupancy, and c) a contingency table showing the proportion of points with increases, no change, and decreases in *P. australis density* or shrub occupancy in each of the forest levels. In c), warmer colors represent higher proportions, with the highest proportion of points showing no change in both metrics.

Figure 3. Abiotic variables of a) porewater salinity sampled on four occasions, b) canopy gap portion measured annually, and c) correlations between abiotic variables and shrub metrics. In c), only significant correlations are depicted; blank cells indicate non-significant relationships and values are correlation coefficients. Red colors indicate negative correlations and blue colors indicate positive correlations.