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Immediate effects of microclimate modification enhance native shrub encroachment

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Abstract. Shrubs have become more dense and expanded beyond their range all over the world for a variety of reasons including increased temperatures, overgrazing, and alteration of historical fire regime. Native shrubs have been encroaching on Virginia barrier island grasslands for over half a century for unknown reasons. Species composition, soil nutrients, leaf area index (LAI), and ground and air temperature were recorded across the shrub to grass transition and at free-standing shrubs in a coastal grassland in order to determine the effect of shrub encroachment on plant community and microclimate. Species richness was significantly lower inside shrub thickets. Soil water content, organic matter, nitrogen (N), carbon (C), and LAI were higher in shrub thickets and free-standing shrubs compared to grasslands. Summer and fall maximum temperatures were lower and more moderate where shrubs were present. Fall and winter minimum temperatures were highest inside shrub thickets. Native shrubs impact microclimate and species composition immediately upon encroachment. These shrubs lower overall species composition, increase soil nutrients and moisture, moderate summer temperature, and increase winter temperature, which has consequences on a larger scale. As barrier islands are critical for protecting marsh and mainland habitats, understanding this mechanism for shrub expansion is important to predict future encroachment of shrubs and displacement of grassland habitat.

Key words: barrier island; coastal; grassland; *Morella cerifera;* Virginia Coast Reserve; woody expansion.

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INTRODUCTION

Shrub encroachment into grassland habitat has occurred globally for decades (Archer et al. 1995, Rundel et al. 2014). The northern advance of woody species around the Arctic Circle has been attributed to an increase in global temperature averages (Tape et al. 2006, Sistla et al. 2013). Shifts in precipitation regimes and atmospheric CO_2 drive the encroachment of shrubs into African savannas (Sankaran et al. 2005, Higgins and Scheiter 2012). Overgrazing by cattle, often with a subsequent change in fire regime, is linked to shrub expansion in the American west and southwest, especially in the Chihuahuan Desert (Grover and Musick 1990, Archer et al. 1995, Brown and Archer 1999, Goslee et al. 2003, Ansley and Rasmussen 2005, Briggs et al. 2005, Van Auken 2009, Bestelmeyer et al. 2013). Due to the dense growth form that shrubs exhibit, many species reinforce a microclimate which ameliorates abiotic conditions and enhances plant growth. This positive feedback mechanism plays an important role for many encroaching shrub communities (D'Odorico et al. 2010).

Recent shrub encroachment is generally recognized as a response to anthropogenic disturbance and often a threat to ecosystems, although historically, shrubs represent a shift in successional states after a natural disturbance (Connell and

Slatyer 1977). Shrub encroachment differs from successional shrub recruitment in that it is an abrupt response to a disturbance event such as overgrazing or climate change, which does not precede succession by trees (Bestelmeyer 2011). Negative effects associated with recent shrub expansion include decreased species diversity (Crawford and Young 1998, Briggs et al. 2002, Isermann et al. 2007, Knapp et al. 2008), extreme alteration in community structure (Huxman et al. 2005, Rundel et al. 2014), the creation of alternate stable states (D'Odorico et al. 2012), nutrient cycling shifts (Brantley and Young 2010), and increased susceptibility of shrubland to disturbance compared to previous ecosystems (Parizek et al. 2002, Knapp et al. 2008).

Native shrub encroachment may have positive interactions with the community (Battaglia et al. 2007, Vallés et al. 2011). These interactions include increased soil nutrients and biomass with minimal effects on diversity. Effects of shrub encroachment cannot universally be described as ecologically negative, but some ecosystems may be more susceptible to degradation upon encroachment (Eldridge et al. 2011, Zinnert et al. 2016). On barrier islands, aeolian and hydrological transport of sediment are land-moving forces that grasslands tolerate, even in overwash events caused by hurricanes (Miller et al. 2010). However, the stability of shrubland habitat and the effect it has on fine-scale abiotic and biotic conditions are yet to be determined. If shrublands are not stable in such disturbance events, then islands will be at higher risk of erosion upon shrub encroachment (Zinnert et al. 2016). Given the importance of the barrier islands, it is critical to gain a better understanding of shrub encroachment for coastal resource management.

On the Atlantic coast of North America, *Morella cerifera* (L.) Small (Myricaceae) shrub thickets clearly represent a different community structure compared to grasslands, and decreased plant diversity as well as increased soil nitrogen has been observed with the shift to shrubland (Crawford and Young 1998, Brantley and Young 2010). *Morella cerifera* is an evergreen nitrogen fixer, which is native to the southeastern United States. It exhibits a vigorous physiology and remarkable resource-use efficiency in a variety of conditions (Naumann et al. 2007, 2008, Vick 2011, Shiflett et al. 2013, 2014). Sudden expansion in recent decades is unprecedented and could be a divergence from successional trends, although historical records of the barrier islands are limited (Young et al. 2007, Zinnert et al. 2016). Encroachment has been associated with an increase in air temperature and atmospheric CO_2 concentration (Zinnert et al. 2011), but mechanisms promoting expansion have not been identified and underlying causes are not well understood.

Shrub microclimates can create a positive feedback with plant growth as a mechanism for expansion. Distinct microclimates under shrub canopies have been documented in desert, arctic, and other more moderate climates (Sturm et al. 2005, Kennedy and Sousa 2006, D'Odorico et al. 2010, Vallés et al. 2011, D'Odorico et al. 2013). Shrub microclimates are conducive to growth because temperatures are moderated; winter temperatures are warmer and summer temperatures are cooler (Ramírez et al. 2015). Dense canopies can protect from harsh external conditions (Vallés et al. 2011). Enhanced hydraulic conductivity (Shiflett et al. 2014) and fog precipitation (Kennedy and Sousa 2006) of shrub thickets can increase water availability, while leaf litter and root leachate can increase soil nutrient composition (Brantley and Young 2010). Decomposition of leaf litter and retention of ground-emitted thermal radiation are sources of warmth under the canopy (He et al. 2010, D'Odorico et al. 2013). Canopy cover also reduces convectional heat loss by decreasing exposure to wind. The conditions of shrub microclimates suggest an environment that favors growth and reproduction creating feedbacks that further expansion.

Our objective was to identify fine-scale microclimate characteristics of *M. cerifera*, a thicket forming shrub which is encroaching on Virginia barrier islands, and to quantify the effect on neighboring plant and soil composition in order to better understand a potential mechanism of expansion. Based on previous studies, we do not expect natural heterogeneity to contribute a significant amount to the soil properties and temperature along transects (Brantley and Young 2010; D. R. Young, *unpublished data*). Several studies have shown microclimate effects at the patch scale on non-thicket-forming shrubs, but shrub thickets may cause greater effects than single shrubs alone (Vallés et al. 2011, Ramírez et al. 2015). We predicted that shrub thicket-induced biofeedback with microclimate promotes shrub encroachment and thicket stability. Thus, shrub thickets would have lower species richness than adjacent grasslands and free-standing shrubs, but have increased soil nitrogen, carbon, organic matter, and water availability due to the redistribution of organic matter in leaf litter. We also hypothesized that *M. cerifera* thickets would impact microclimate with increased minimum temperature during winter months and moderate summer temperatures relative to grassland and free-standing shrubs.

METHODS

Study site

Our study was conducted on Hog Island, a barrier island within the Virginia Coast Reserve (VCR; Fig. 1). The VCR includes about 18 islands and is the longest stretch of undeveloped coastline on the eastern United States (Badger 1993). Hog Island lies near the center of the VCR, from about "37°27′54.1″ N, 75°39′51.4″ S to 37°22′00.8″ N, 75°43′20.1″ W." The islands are dynamic in their response to the physically dominated environment, being in a constant state of change as a result of powerful wind and water effects on sediment budgets and geomorphology (Ehrenfeld 1990, Hayden et al. 1991). There are beaches and dunes on the ocean side of Hog Island and tidal salt marshes on the lagoon side (Fig. 1). In the interior of the island, the dune-swale community is composed of mixed grass–shrubland, with small trees occurring sparsely. Over the last 30 yr, a 40% increase in shrub encroachment into grassland has been documented across the VCR (Zinnert et al. 2016).

The study was conducted on Hog Island from May 2015 to March 2016. In order to quantify the effect of the shrub thicket on microclimate, transects were established that traverse the edge of three shrub thickets (n = 3) and monitored from May 2015 to March 2016. Each transect began 10 m inside the shrub thicket, crossed perpendicularly through the thicket edge, and ended in the open canopy grassland, 10 m away from the thicket edge. Along these 20-m transects were sampling points every 5 m, with an additional point ~500 m south at a free-standing shrub. The midpoint of each transect that coincided with the edge of the thicket was defined as the location where cover transitions from grass to shrubs. The thickets were chosen because they were at least 20 m wide, roughly level elevation, of similar age, and the adjacent grassland was free of shrubs that may influence the grassland plots. The points located within free-standing shrubs in the grassland were intended to capture microclimate effects of shrubs that did not grow inside a thicket.

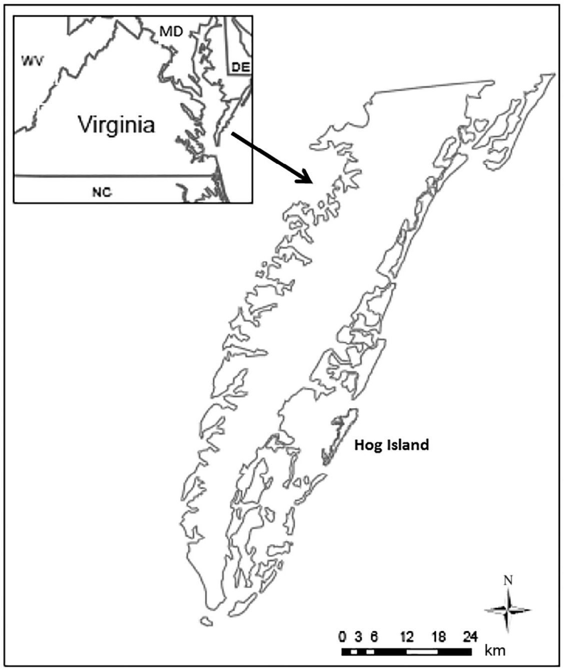

Fig. 1. The Eastern Shore of Virginia showing the barrier islands that compose the Virginia Coast Reserve. Field work for this study was conducted on Hog Island.

Species composition and soil attributes

In order to determine the relationship between plant composition and soil nutrient content, species cover was measured and soil sampled once from all plots between July and August 2015. All transects were sampled on the same day, with different measurements taken during the 2-month timeframe. Species cover was measured in 2-m^2 plots at each plot using the Daubenmire cover classes method (Daubenmire 1959, Weakley et al. 2012). Percent (%) cover of three functional groups, forbs, graminoids, and shrubs, is reported. Leaf litter depth was measured in the summer at all points along each transect from

Table 1. Mean (±SE) of richness and % cover for all functional groups and plots sampled on Hog Island, Virginia, United States.

Composition	10 m inside thicket	5 m inside thicket	Thicket edge	5 m outside thicket	10 m outside thicket	Free-standing shrub
Richness						
Forbs	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	5.0 ± 1.2^{a}	4.0 ± 1.2^{ab}	3.7 ± 1.7^{ab}	3.3 ± 0.9^{b}
Graminoids	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	2.0 ± 0.0^{a}	2.3 ± 0.0^{a}	2.3 ± 0.7^{a}	3.0 ± 0.6^{a}
Shrubs	1.0 ± 0.0^{a}	1.3 ± 0.3^{a}	1.0 ± 0.0^{a}	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	1.7 ± 0.3^{a}
% Cover						
Forbs	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	26.7 ± 5.0^{a}	15.6 ± 7.5^{ab}	16.3 ± 10.7^{ab}	9.7 ± 3.6^{ab}
Graminoids	0.0 ± 0.0^{b}	0.0 ± 0.0^{b}	38.5 ± 7.5^{a}	56.3 ± 6.4^{a}	46.5 ± 7.9^{a}	50.8 ± 13.5^{a}
Shrubs	97.5 ± 0.0^{a}	97.6 ± 0.1^{a}	33.3 ± 2.9^{b}	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}	38.0 ± 10.4^{b}

Note: Letter codes denote significant differences.

ground level. Leaf area index (LAI) was measured in the growing season of 2015 in constant sunlight between 11:00 and 14:00 hours using a plant canopy analyzer (Model LI-3100C; LI-COR, Lincoln, Nebraska, USA).

Soil samples were collected in order to measure nitrogen, carbon, organic matter, and relative water content. Leaf litter was removed and soil was sampled from the top 15 cm of the mineral layer. Soil samples were sent to the Cornell Isotope Laboratory for determining total nitrogen and carbon contents. Organic matter was measured by loss through ignition in a muffle furnace, as outlined in Crawford et al. (2007). Relative water content was calculated by dividing the fresh weight of the soil from the oven (80°C) dry weight.

Temperature data

Three temperature sensors (iButtons, Thermodata) set at ground level, 20 cm, and 100 cm, recorded bihourly measurements at each of the six plots along each transect, including the free-standing shrubs. Temperature will be discussed as mean daily maximum and mean daily minimum during summer (1 June–31 August), autumn (1 September–30 November), and winter (1 December–29 February). Meteorological data were gathered from a station on Hog Island 10 km north of our field site (Porter and Spitler 2016).

Analyses

One-way ANOVA ($\alpha = 0.05$) was used to determine differences among treatments in soil composition, leaf litter, and LAI between all plots. Two-way ANOVA was performed to test height × plot interaction for temperature data for all seasons. If two-way interactions were significant, one-way ANOVA was performed across plots at each given height to test interactions across transects. All data were visually inspected for normality. Bartlett's test was used to test equality of variances (Snedecor and Cochran 1989). Post hoc Tukey's tests were conducted if significant differences were detected in order to determine what factors differed (Tukey 1949).

RESULTS

Species composition, LAI, and litter depth

Richness of forbs, graminoids, and shrubs was significantly different along transects ($F = 4.4$, $P = 0.016$; $F = 11.2$, $P < 0.001$; $F = 12.9$, $P < 0.001$, respectively). Thicket plots had nearly 100% coverage by *M. cerifera* and had significantly higher cover than other locations ($F = 101.1$, $P < 0.001$; Table 1). Thicket plots had no forb ($F = 3.7$, $P = 0.03$) or graminoid cover ($F = 12.4$, $P = 0.002$). Grassland plots had highest cover of graminoids, but with comparable species richness to thicket edge and free-standing shrub plots (Table 1). Leaf area index was highest in the thicket, decreasing significantly in the free-standing shrub and the thicket edge, with the lowest values in the grassland ($F = 142$, $P < 0.001$; Fig. 2). Leaf litter depth was deepest 10 m inside the thicket (11.7 ± 0.9 SE cm) and was significantly deeper than all other plots except for the plot 5 m inside the thicket ($F = 33.38$, $P < 0.001$; Fig. 2). Leaf litter 5 m inside the thicket was significantly deeper than the thicket edge and grassland plots, but was not deeper than the litter under the free-standing shrubs.

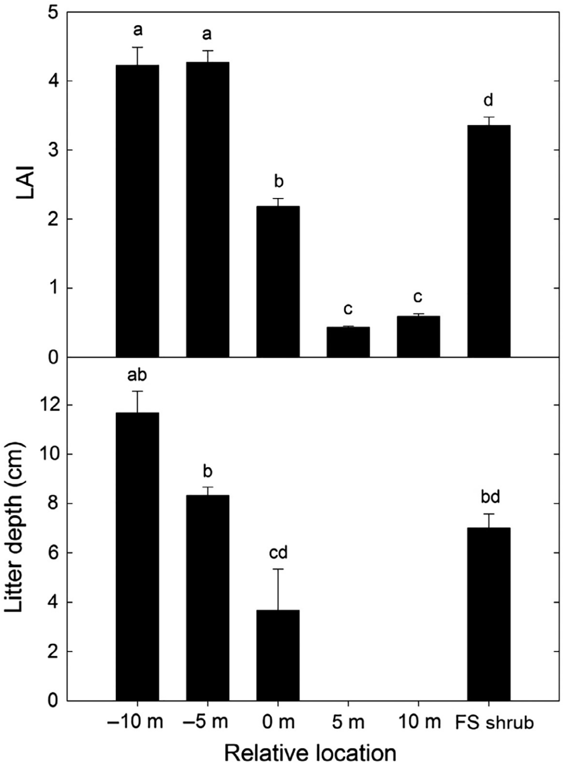

Fig. 2. Leaf area index and leaf litter depth across transects on Hog Island, Virginia. Relative location refers to plot distance to thicket edge where −10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Values are means ± 1 SE. Letters denote significant ($\alpha = 0.05$) differences among locations.

Soil attributes

Soil organic matter was not significantly different, although there was a trend of increased organic matter when inside the thicket ($F = 2.75$, $P = 0.07$; Fig. 3). Thicket plots had significantly higher soil water content than grassland plots ($F = 14.94$, $P < 0.001$; Fig. 3). The free-standing shrub resembled thicket and thicket edge plots, while grassland plots had the lowest soil water content. Soil N and C were not significantly different across plots, but there was a trend of higher N and C inside the shrub thicket and at the free-standing shrub compared to outside the thicket ($F = 2.15$, $P = 0.13$ and $F = 2.01$, $P = 0.15$, respectively; Fig. 3). Variability was higher within thicket plots.

Temperature

Summer mean maximum air temperature was 28.2°C and the mean minimum temperature was 21.3°C during 2015. There was an interaction between height and transect location for mean summer maximum and minimum temperatures ($F = 393.9$, $P < 0.001$, and $F = 6.1$, $P = 0.002$, respectively). Summer ground temperatures were much higher outside the thicket compared to inside the thicket and in free-standing shrubs ($F = 818.2$, $P < 0.001$; Fig. 4). The mean maximum

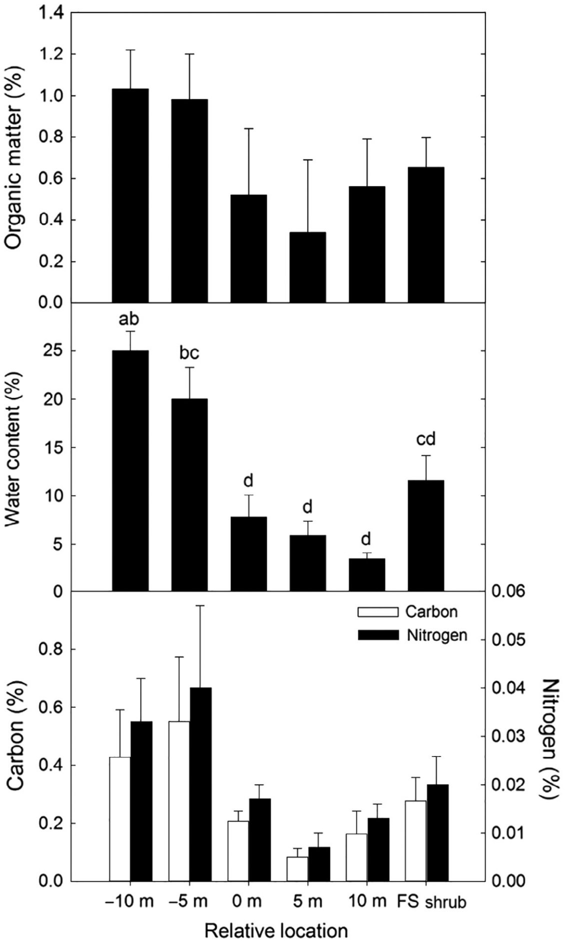

Fig. 3. Soil organic matter (%), water content (%), carbon (%), and nitrogen (%) across transects on Hog Island, Virginia. Relative location refers to plot distance to thicket edge where –10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Values are means ± 1 SE. Letters denote significant ($\alpha = 0.05$) differences among locations.

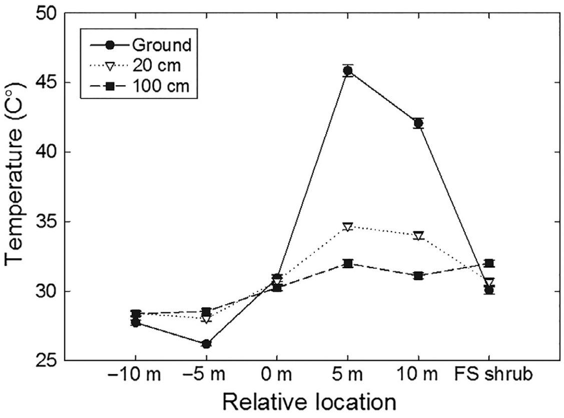

Fig. 4. Mean summer maximum temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean summer maximum temperature according to meteorological station on Hog Island, Virginia. Relative location refers to plot distance to thicket edge where −10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Values are means ± 1 SE.

ground temperature 5 m outside the thicket was 45.9 ± 0.4°C, while 5 m inside the thicket, it was 26.2 ± 0.2°C. At 20 and 100 cm above the soil surface, air temperature was significantly hotter outside the thicket compared to inside the thicket and at the free-standing shrub ($F = 159.5$, $P < 0.001$, and $F = 56.91$, $P < 0.001$, respectively). At 100 cm, the difference in air temperature from 5 m outside the thicket to 5 m inside the thicket was 3.4 ± 0.3°C. Mean maximum summer temperatures at thicket edge and free-standing sensors differed by <2°C.

During autumn of 2015, mean maximum air temperature from the meteorological station on Hog Island was 21.6°C and the mean minimum temperature was 14.8°C. There was a significant interaction across plots and heights for mean autumn maximum temperatures ($F = 48.7$, $P < 0.001$). Mean maximum ground temperature was significantly warmer outside the thicket compared to inside the thicket and at free-standing shrubs ($F = 103.3$, $P < 0.001$; Fig. 5). This difference was also significant at 20 and 100 cm ($F = 29.6$, $P < 0.001$, and $F = 10.9$, $P < 0.001$, respectively). Mean minimum ground temperature and air temperature at 20 cm was significantly warmer inside the thicket and at the free-standing shrub at ground level ($F = 6.3$, $P < 0.001$, and $F = 5.04$, $P < 0.001$, respectively; Fig. 5). Mean minimum air temperature at 100 cm was significantly warmer at the free-standing shrub compared to grasslands, but no other temperatures differed significantly ($F = 3.18$, $P = 0.007$).

Winter 2016 mean maximum air temperature was 11.2°C, while mean minimum temperature was 3.6°C. There were significant interactions across plots and heights for mean winter maximum and minimum temperatures ($F = 14.3$, $P < 0.001$, and $F = 6.2$, $P = 0.002$, respectively). Mean maximum temperature was significantly warmer at the thicket edge and outside the thicket

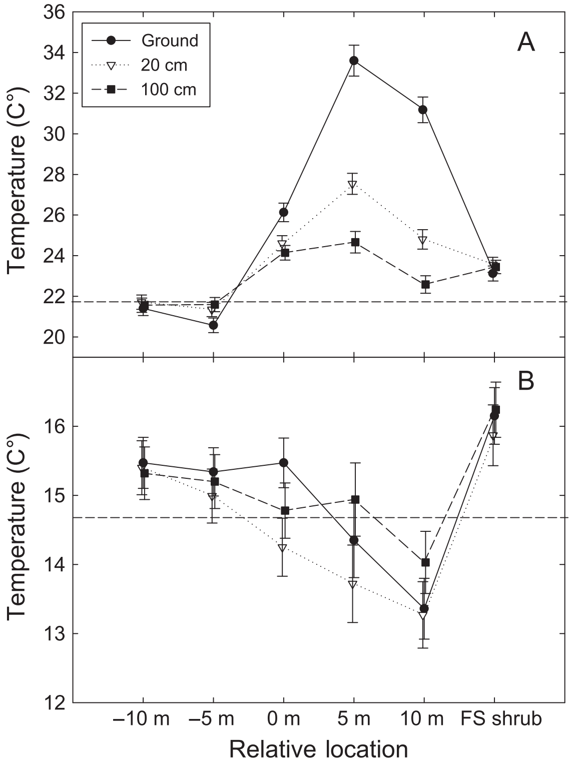

Fig. 5. Mean fall maximum (A) and minimum (B) temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean fall maximum and minimum temperatures, respectively, according to meteorological station on Hog Island, VA. Relative location refers to plot distance to thicket edge where −10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Values are means ± 1 SE.

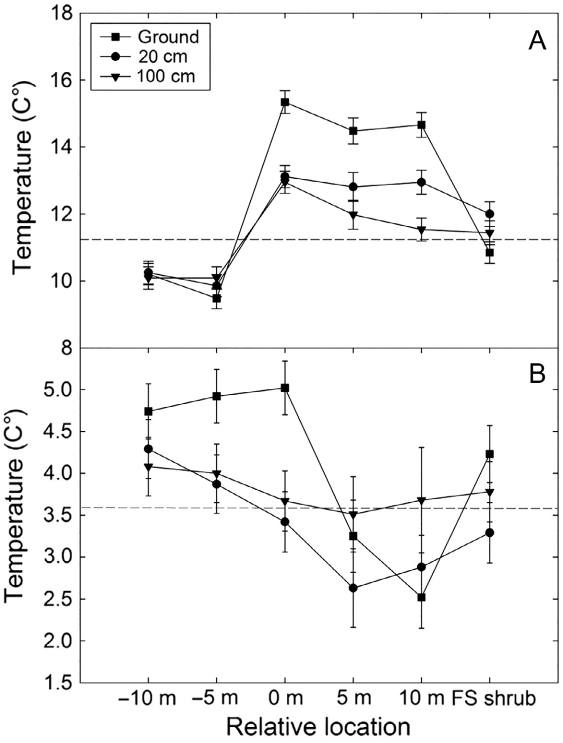

Fig. 6. Mean winter maximum (A) and minimum (B) temperatures of plots across transects at ground level, 20 cm, and 100 cm. Dashed line represents mean winter maximum and minimum temperatures, respectively, according to meteorological station on Hog Island, Virginia. Relative location refers to plot distance to thicket edge where −10 m indicates 10 m inside the shrub thicket and 10 m indicates 10 m outside the thicket; FS shrub stands for free-standing shrub. Values are means ± 1 SE.

compared to inside the thicket and the free-standing shrub at ground level, 20 cm, and 100 cm ($F = 59.5$, $P < 0.001$; $F = 16.5$, $P < 0.001$; and $F = 10.36$, $P < 0.001$, respectively; Fig. 6). For each height, the thicket edge had the warmest mean maximum temperature across plots. Mean minimum ground temperature was significantly warmer inside the thicket, at the thicket edge, and at the free-standing shrub compared to the grassland ($F = 8.68$, $P < 0.001$; Fig. 6). For example, the plot 10 m inside the thicket was 2.2 ± 0.5°C warmer than the plot 10 m outside the thicket. At 20 cm, air temperature was significantly warmer inside the thicket compared to outside the thicket ($F = 2.58$, $P = 0.025$). There was no significant difference in temperature across plots at 100 cm, but thicket and free-standing shrub plots were all warmer than plots outside the thicket. The free-standing shrub also had warmer minimum ground temperatures than grassland plots ($F = 5.95$, $P = 0.003$).

Discussion

Our study evaluated effects of native shrub encroachment on fine-scale abiotic and biotic factors. The expansion of *M. cerifera* in coastal systems has a significant impact on the surrounding environment. We found that *M. cerifera* significantly changed air temperature, soil components, and plant species composition immediately upon encroachment into grassland and continuing through thicket formation. Species richness was lower in the shrub thickets, as expected (Crawford and Young 1998), while species cover and richness were highest at the thicket edge and free-standing shrubs compared to the grassland. The reason for the sudden die-off of species upon entering the thicket is not known, but is likely related to lower light availability and higher litter depth (Brantley and Young 2007).

Our hypotheses concerning soil attributes were partially supported; higher water availability and litter depth occurred in the thicket compared to the grassland. Organic matter, N, and C were similar across plots, with higher variability in the thicket. Soil organic matter content and soil C were higher in the thicket due to litter deposited over the sandy soil. The amount of organic matter inside the thicket was smaller than that found in older thickets (Crawford and Young 1998). More time may be needed to decompose litter (Graziani and Day 2015). Higher soil N was caused by the nitrogen-fixing effects of *Frankia*, the symbiotic bacteria living in root nodules of *M. cerifera* (Young et al. 1992). In the grassland, soil N is very low, sometimes undetectable, and may leach out of the sandy soil quickly.

Cooler summer temperatures in the thicket compared to adjacent grassland were likely caused by dense canopies which decreased sunlight inside the thicket (Brantley and Young 2007). The grassland adjacent to the shrub thickets had lower plant cover. Incident solar radiation had a high heating effect on the sand, causing daytime ground temperatures to regularly exceed 50°C during the summer, with mean maximum temperatures at

44.0 ± 0.3°C. Average shrub thicket temperature was 29.3 ± 0.1°C. Considering that the photosynthetic temperature optimum of *M. cerifera* is ~30°C (Young 1992), the shrub thicket and free-standing shrubs benefit from microclimate effects during the summer, where temperatures are moderate and remain close to the 30°C optimum. Additionally, the effect on microclimate (in terms of soil attributes and temperature) is immediate as seen in the free-standing shrubs. This finding was not expected and explains the success of *M. cerifera* across the barrier island landscape.

As predicted, warmer minimum temperatures occurred inside the thicket during the winter time. Ground temperature was 2.1 ± 0.3°C warmer on average inside the thicket and at the thicket edge compared to the adjacent grassland. Air temperature at 20 cm was 1.1 ± 0.4°C warmer inside the thicket compared to outside the thicket. Again, free-standing shrubs unexpectedly had warmer minimum temperatures compared to grassland plots. The Virginia barrier islands are the northern edge of *M. cerifera*'s native range, where freezing temperatures can cause damage and may be a limiting factor for growth (D'Odorico et al. 2010). Warmer winter temperatures and reduced precipitation have been observed on Hog Island and correlated with landscape-scale shrub expansion (Zinnert et al. 2011). The warming caused by shrub thickets and free-standing shrubs should have positive impacts on the shrub thicket, especially in extreme cold temperatures (Young 1992). Warmer temperatures can also extend the active period of soil microbes and invertebrates, leading to more nutrient cycling and possibly more activity by the nitrogen-fixing bacterium, *Frankia*, associated with *M. cerifera*.

Barrier islands are a novel system for studying shrub thicket microclimates as a mechanism for expansion. Most studies have been in arid or arctic environments, where causes of shrub encroachment are better understood and microclimate benefits such as water and warmth retention are more apparent. Overgrazing sparked the encroachment of shrubs in the American southwest, where shrub microclimates offer significant protection from freeze damage and drought (He et al. 2014). Climate warming has allowed shrubs to expand north in the Arctic, while the microclimates they form further increase annual biological activity in the soil and woody vegetation. Our study shows that encroaching shrubs may also benefit from a microclimate in locations where the need for relief from pressures such as freezing temperatures and water availability is not as apparent as in arid or arctic environments. The barrier island shrubs occupy a temperate, mesic environment; however, they have similar effects on the environment around them, including increased soil nutrient content, increased litter depth, increased minimum temperatures, and more moderate summer temperatures.

It is well known that average global temperatures have been rising for thousands of years, with an accelerated rate of increase in recent history (IPCC 2014). It is possible that climate warming in concert with microclimate warming has surpassed a tipping point, or threshold, allowing *M. cerifera* to encroach on neighboring island species that are no longer able to compete with its increasingly robust physiology (Shiflett et al. 2014) as indicated by the expansion in different years (Young et al. 2007, Zinnert et al. 2011, 2016). Increased shrub microclimate temperatures recorded in New Mexico at the landscape scale were comparable to the amount of temperature increase expected over a century under global warming conditions (He et al. 2014). On Hog Island, winter warming caused by shrub thickets at a fine scale is also comparable to about a century of global warming (~2°C). Warmer minimum temperatures could be considered a possible cause of expansion because *M. cerifera* physiology is tightly correlated with temperature (Young 1992, Shiflett et al. 2014), which is a constraining factor for *M. cerifera* survival north of this region. With expected increases in global temperature, winter microclimate warming may further enhance productivity and expansion of this evergreen shrub.

The consequences of shrub encroachment on barrier islands relate to island resilience to coastal storms as well as longer-term resistance to sea-level rise (Zinnert et al. 2017). In areas with shrub encroachment, extensive woody vegetation augments resilience by allowing the system to absorb disturbance while remaining within the same state. Woody vegetation provides stability. However, over longer timeframes (decades), extensive woody cover blocks sediment transfer, causing extensive shoreline erosion (Zinnert et al. 2016).

Conversely, grassland with little to no woody vegetation promotes movement of sediments which is necessary for barrier island migration (Zinnert et al. 2017). Thus, shrub encroachment has particular relevance for coastal management in short-term stabilization and long-term barrier island persistence.

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