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Edge effects of an expanding shrub in a coastal grassland

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Abstract

Shrub expansion into grassland systems is a global phenomenon. Changing land uses and climate change are the main drivers, with common outcomes including reduced species richness and loss of historical grasslands. Coastal systems are no exception, and along the mid-Atlantic coast, *Morella cerifera* (southern wax myrtle) is rapidly expanding into grassland communities. *Morella* shrubs form dense monospecific thickets. It has been documented that established thickets modify the microclimate resulting in higher soil moisture, low light availability, and moderated temperatures within. It is unknown how *M. cerifera* affects plant communities that thrive on the edge of these thickets. We assessed these communities for differences in microclimate, vegetation composition, and nutrient availability to quantify effects of living along the shrub edge. Plots were identified in the swale (low-elevation habitat behind dunes) on Hog Island, Virginia, USA, along the edge of shrub thickets and paired with an adjacent open grassland plot. Trait-based comparisons were completed on species that overlapped between both communities (i.e., *Spartina patens*, *Solidago sempervirens*, *Andropogon virginicus*, and *Panicum amarum*). Along the shrub edge, we found reduced species richness, but increased cover, stem density, and height of grasses relative to open grasslands, with morphological traits indicative of competition along the thicket edge. The microclimate of the shrub edge was highly shaded, had higher soil moisture at lower depths, and cooler summer temperatures relative to the open grassland. *Spartina patens* was the most dominant species in both communities; however, the relative importance of the species was 250% higher in the shrub edge. As the shrub thicket continues to expand, we expect increased dominance of *Spartina patens* around the thicket. Shrubs and the modified shrub edge community may impact resilience to sea-level rise and storms with future climate change.

KEYWORDS
community composition, grass-shrub ecotone, leaf functional traits, microclimate, shrub expansion

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INTRODUCTION

Shrub expansion into previously grassland-dominated communities is a global phenomenon driven by climate and land-use change (van Auken, 2000; reviewed in: Naito & Cairns, 2011). Many shrub species may form monospecific thickets that are so dense that other vegetation is limited by the restricted light availability (Knapp et al., 2008; Shiflett et al., 2017). Historically, many woody species were latitudinally restricted in their range due to low winter temperatures, but warming minimum temperatures are contributing to expanding ranges for certain species (D'Odorico et al., 2013; Huang et al., 2018; Stuart et al., 2007). Additionally, highly disturbed sites, such as coastal systems, are experiencing increased woody expansion globally (Archer et al., 1995; Huang et al., 2020; Williamson et al., 2011). On barrier islands, the woody expansion can deplete limited freshwater resources (Peguero-Pina et al., 2020; Winkler et al., 2019) as the source of freshwater comes from precipitation input to the freshwater lens (Aguilar et al., 2012; Kiflai et al., 2020; Wood et al., 2024) and woody species generally require more water than herbaceous species due to higher leaf area (Wood, 2021). This can impact the surrounding edge community through altered light and water resources.

Along the US mid-Atlantic and Gulf coasts, *Morella cerifera* (southern wax myrtle; previously *Myrica cerifera*; hereafter referred to as "*Morella*") is a native, evergreen, nitrogen-fixing shrub, with an expanding range due to warming winter temperatures and associated decrease in frost damage (Huang et al., 2021). On barrier islands, *Morella* displaces grassland species in protected inland areas behind prominent foredunes because of salt sensitivity (Tolliver et al., 1997; Woods & Zinnert, 2024), reducing species and functional diversity (i.e., graminoids, forbs; Brown & Zinnert, 2020; Standish et al., 2014; Thompson et al., 2017). Within the thickets, *Morella* draws up the groundwater (Wood et al., 2020) and increases transpiration due to high hydraulic conductivity and leaf area (Shiflett et al., 2017; Wood, 2021). Light levels within the thickets are reduced to levels that exclude other species (Brantley & Young, 2008). At the seedling stage, young shrubs are facilitated by the presence of grass (Sinclair et al., 2020), further enhancing shrub expansion into grassland. High leaf litterfall of *Morella* inputs nitrogen into otherwise nitrogen deficient sandy soils (Brantley & Young, 2008, 2010) similar to related species *Myrica faya*, which has expanded in Hawai'i through altering soil chemistry (Vitousek & Walker, 1989). Although we know how shrub expansion alters microclimate, soil nutrients, and carbon content in the displaced grassland habitat (Brantley & Young, 2008; Thompson et al., 2017), a knowledge gap remains regarding how the unique microclimate of *Morella* impacts the plant communities and traits along the grassland–shrubland ecotone.

Intermediary communities occur along the grass-shrub ecotone (i.e., where the grassland community meets the shrub community; Duniway et al., 2010; Lett & Knapp, 2003). The grass-shrub ecotone experiences differences in light, water, and nutrient availability relative to grasslands (Duniway et al., 2010; Lett & Knapp, 2003; Matlack, 1993; Murcia, 1995), similar to those observed along forest edges (Fischer et al., 2021; Groeneveld et al., 2009; Saunders et al., 1991). Plant species take advantage of these moderated light environments, similarly to the high competition for light in the shaded understory (Goldblum & Beatty, 1999; Matlack, 1994). These moderated environments can lead to more competitive traits among the plant communities (Alba et al., 2019). Moderated abiotic conditions can be ideal for further seedling establishment of woody species (D'Odorico et al., 2013; Jackson et al., 2002), further expanding the shrub thickets.

Shrub encroachment can have long-term impacts on functional traits of the plant community, driven by input of resources by shrubs or decreased resource access due to shrub use. In stressful environments, surrounding species invest in acquisitive traits (Utaile et al., 2020) or resource conservation traits (Geissler et al., 2019). Limited light and increased nutrients can contribute to increased grassland species height and biomass initially (Saixiyala et al., 2017) before the shrubs outcompete grassland species (Dahl et al., 2020; Randle et al., 2018). Previous research focused on the mechanisms of *Morella* expansion and plant physiological and ecosystem level consequences (Battaglia et al., 2007; Brantley & Young, 2008; Huang et al., 2018; Paudel & Battaglia, 2021; Wood et al., 2024), but the impacts on the edge plant communities and species traits remain unknown. As shrubs continue to expand, the shrub edge community also increases in area (Huang et al., 2021).

To understand how *Morella* influences the grassland edge community, we quantified microclimate (i.e., temperature, water, and light availability), soil characteristics, and vegetative community composition along the shrub edge and in the adjacent open grassland. Within these habitats, we quantified functional traits differences of dominant co-occurring species. We hypothesized that due to lower light, higher groundwater, and increased soil nutrients, the shrub edge would exhibit differences in community composition with plant traits indicative of resource acquisition (e.g., taller plants, high specific leaf area, low leaf dry matter content [LDMC], high leaf nitrogen). In the open grassland, we expected that plant

traits would be indicative of resource conservation (e.g., shorter plant height, low specific leaf area, high LDMC, low leaf nitrogen).

METHODS

Study site

This research was performed on Hog Island, VA, USA, which is part of the Virginia barrier islands positioned along the Eastern Shore of Virginia (Figure 1). The Virginia Coast Reserve (VCR) Long-Term Ecological Research (LTER) conducts research throughout this island chain, on land and in the adjacent bays. Permitting research on Hog Island is currently managed by The Nature Conservancy (TNC). Hog Island has been uninhabited since the dissolution of the town of Broadwater in the 1930s. On the southern end of the island, there is sediment accretion in front of two dune ridges, with an intermediate swale in between dunes and more swale habitat behind the second dune ridge. This project was completed in the back swale where the majority of the shrubs are encroaching.

Shrub perimeter

Based on imagery used in Huang et al. (2021) we calculated shrub perimeter from 1986, 1994, and 2013. Full methods are described in Huang et al. (2021) but briefly summarized here. Shrub cover was assessed from geo-rectified aerial photography (USGS Earth Explorer) and hyperspectral imagery on 5 July 1986 (color infrared), 20 March 1994 (RGB), and 26 May 2013 (48 band hyperspectral; USACE-TEC & JALBTCX, 2013). Regions of interest (ROI) were selected in each year for shrub cover using the bands available in each image (ENVI 5.5.3, LH3 Harris Geospatial) based on geo-rectified aerial photography, and field-surveyed woody thickets of known age using a Trimble Geo-XT GPS unit. Supervised classifications were performed using the maximum likelihood method. Resulting shrub cover was exported to ArcGIS 10.7 (ESRI) and then exported to FRAGSTATS 4.2 for spatial pattern analysis. Perimeter and area of each shrub patch were calculated.

Microclimate and soil characterization

Plots were selected in the swale on Hog Island, at the edge of separate *M. cerifera* thickets and in nearby, unencroached open grassland ($n = 10$) between 10 and 30 m away from the thicket edge. Plots were 25 × 100 cm to capture the ecotone along the shrub edge. Here, the shrub edge is defined as the area immediately surrounding a shrub thicket that is shaded by the shrubs. Microclimate was assessed by measuring air temperature, light under the canopy, and groundwater depth. In each plot, iButton data loggers (Maxim Integrated, San Jose, CA) were used to collect air temperature (in degrees Celsius) every 2 h; loggers were placed within the grass at each plot. A ceptometer (Decagon Devices, Pullman, WA) was used to assess instantaneous light levels measured as photosynthetically active radiation (PAR) and leaf area index (LAI) which was measured one day each summer during midday for two consecutive years. Wells were installed at a depth of 1 m from the soil surface in the shrub edge and grassland plots ($n = 3$) to measure water table differences using HOBO water level data loggers (Onset Computer Corporation, Bourne, MA).

Soils were collected in summer 2021 at the edge of each plot at multiple depths (0–10, 11–20, 21–30 cm), placed in sealed plastic bags, and kept on ice until they were weighed for fresh soil mass. Soils were dried at 70°C for 72 h to obtain dry mass for relative water content. After drying, soil subsamples were sent to the Cornell Isotope Laboratory (COIL; https://cobsil.cornell.edu) for percentage of nitrogen (N), percentage of carbon (C), $\delta^{13}C$, and $\delta^{15}N$. The nutrient analyses will indicate if the soils are being affected by nutrient additions of *Morella* from leaf litter and the isotope analyses will indicate if nitrogen is taken up by *Morella* through actinorhizal fixation.

Vegetative composition and plant functional traits

Percent cover and maximum height of each species within each plot were assessed at the beginning and end of the growing season, May and August in 2021 and 2022. Percent cover of each species was assessed visually in 5% increments and the stretched height of the tallest plant (in centimeters) was collected for each species. For community analysis community-weighted heights (Lavorel et al., 2008) were calculated as

$$\text{Community} - \text{weighted height} = \sum \text{cover}_{\text{species}} \times \text{height}_{\text{species}} \quad (1)$$

Within each plot, stem density for each species was assessed in a 10 × 10 cm subplot and scaled to square meters for community analysis. Relative importance was calculated for each species present, as a function of

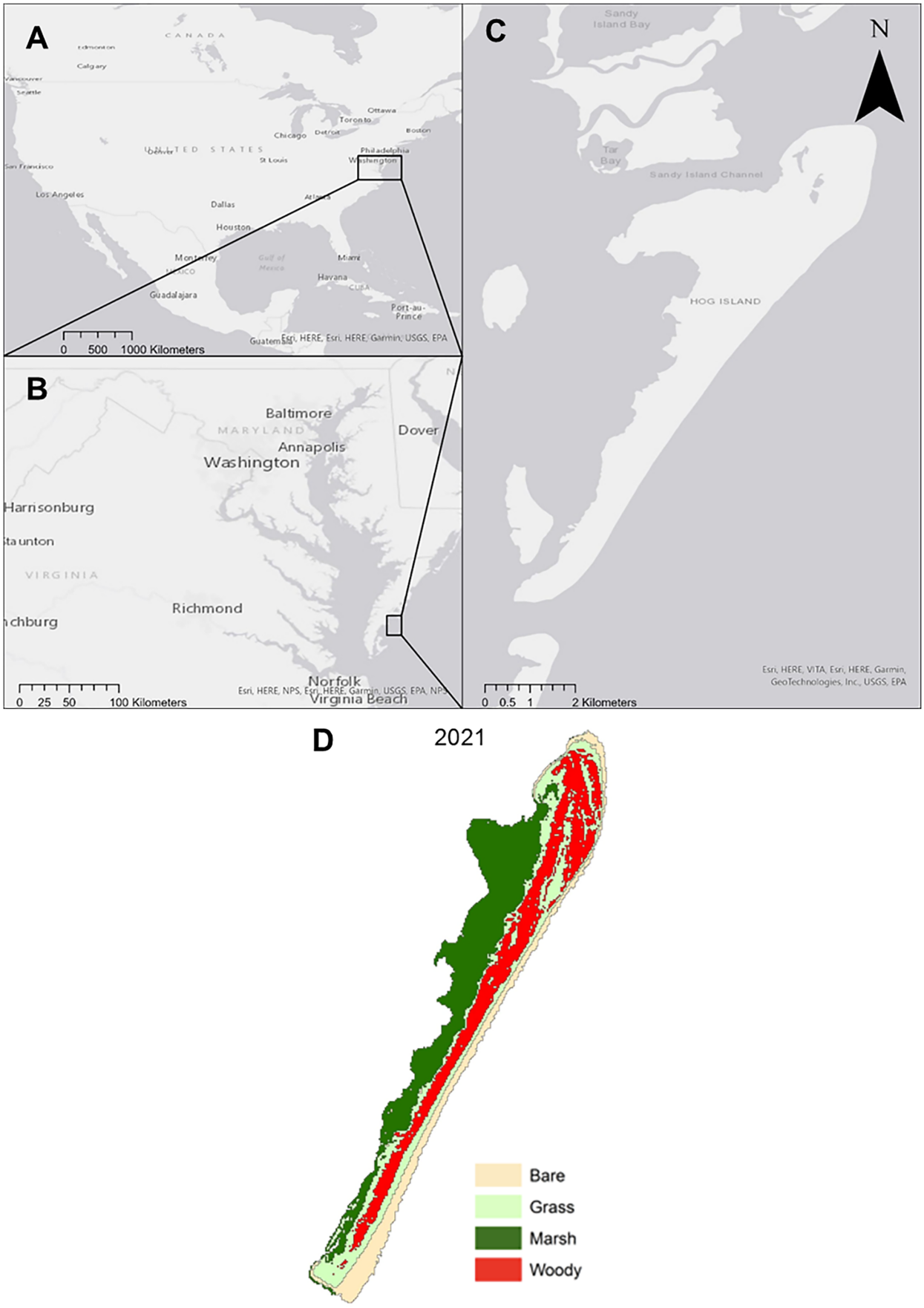


FIGURE 1 (A) Map of the United States with the eastern shore of Virginia delineated; (B) enlarged map of Virginia with Hog Island delineated; (C) map of Hog Island; (D) Hog Island map with vegetation classifications derived from 2021 Landsat imagery.

species frequency, stem density, and cover relative to the total community:

$$\text{Relative importance} = \left(\frac{\text{Frequency}_{\text{species}}}{\text{Frequency}_{\text{total}}} + \frac{\text{Stem density}_{\text{species}}}{\text{Stem density}_{\text{total}}} + \frac{\text{Cover}_{\text{species}}}{\text{Cover}_{\text{total}}}\right) \times 100. \quad (2)$$

This calculation ranges from 0 to 300 with higher numbers equating to dominance at the site.

Spartina patens (also referred to as *Sporobolus pumilis*), *Panicum amarum*, *Andropogon virginicus*, and *Solidago sempervirens* (hereafter referred to by genus) were dominant species that occurred in both shrub edge and grassland sites and, thus, were used for detailed plant trait measurements (Appendix S1: Table S1). From sites adjacent to the sampling plots, plants were harvested aboveground and placed in a cooler until further processing could occur ($n = 20$ per species). Aboveground material was harvested to quantify LDMC, specific leaf area (SLA), leaf percentage of nitrogen (%N), percentage of carbon (%C), $\delta^{13}C$, $\delta^{15}N$, and stem-specific density (SSD), following the protocols from the functional trait handbook (Pérez-Harguindeguy et al., 2013). Fresh leaves were stored in a wet paper towel, on ice, until they were scanned (Epson scanner, Suwa, Japan) to obtain the projected leaf area (WinRhizo, Regent Instruments, Quebec City, Canada). Leaves were dried at 60°C for 72 h and weighed to calculate LDMC and SLA. Stem volume was calculated by measuring the diameter (in millimeters) and length of a stem (in millimeters), then dried at 60°C for 72 h and weighed to calculate SSD. Dried leaves were ground using a Wiley Mill (Thomas Scientific, Chadds Ford Township, PA) and sent to the Cornell Isotope Lab (COIL) for nutrient and stable isotope analysis of carbon and nitrogen. Isotope analyses inform the mechanisms of nutrient uptake and water use (Zinnert et al., 2013).

Statistical analysis

Repeated measures ANOVA was used for temperature and water table depth data to determine monthly differences in grassland and shrub edge microclimates. The Bonferroni adjustment was used for the post hoc analysis. Two-way ANOVAs were completed on trait data using location and species as factors. Percent cover, stem density, height, and aboveground biomass were all log-transformed to meet ANOVA assumptions. When data did not meet assumptions following transformations, two-sample nonparametric tests (Kruskal–Wallis) were analyzed per species with location as the factor. Kruskal–Wallis tests were used to analyze the nutrient differences in the soil, PAR, and LAI. For species trait analysis t tests were run to compare locations with a Bonferroni p-value adjustment for multiple t tests or Wilcoxon signed-rank tests when data did not meet assumptions. Community composition based on species cover was further compared with a permutational multivariate ANOVA (PERMANOVA) using Bray–Curtis as the distance measure with location and year as the response variables and visualized with nonmetric multidimensional scaling (NMS). PERMANOVA was used to compare species leaf traits using a correlation distance matrix of leaf traits, and visualized with principal components analysis (PCA). All statistics were run in R (R 4.1.0) and JMP with graphing carried out in R.

RESULTS

Microclimate

As *Morella* expanded on Hog Island from 1986 to 2013, shrub area increased by 268% and perimeter by 233% (Table 1). The edge community increased ~10 km per year over the 27-year time period. The shrub edge had a moderated microclimate, with greater soil water content and lower PAR levels relative to grassland. Temperatures were less variable throughout the year and on average, 1.5°C cooler at the shrub edge than the grassland (Figure 2). There were significant differences observed between shrub edge and grassland temperatures in all months except December and January ($F_{1,11} = 22.64$, $p < 0.0001$; Figure 2; Appendix S1: Table S2). Maximum summer temperatures occurred in August and were 8°C higher in the grassland (50.3 ± 2.1°C) compared to shrub edge (42.6 ± 1.9°C). The top 10% of daily maximum temperatures were calculated for each location, with grassland temperatures reaching an average of 10°C higher than shrub edge (59 ± 0.4°C and 46 ± 0.5°C, respectively; $t = 170$, $p < 0.0001$). Winter minimum temperatures were coolest in January, on average 1.8°C cooler in the grassland (−5.5 ± 1.1°C) than the shrub edge (−4.5 ± 0.7°C, $t = -9.62$, $p < 0.0001$).

TABLE 1 Perimeter and cover of shrubs over 27 years.

Year	Perimeter (km)	Area (ha)
1986	120.1	84.9
1994	308.3	119.9
2013	400.5	313.2

Note: Increased perimeter creates increased edge effects.

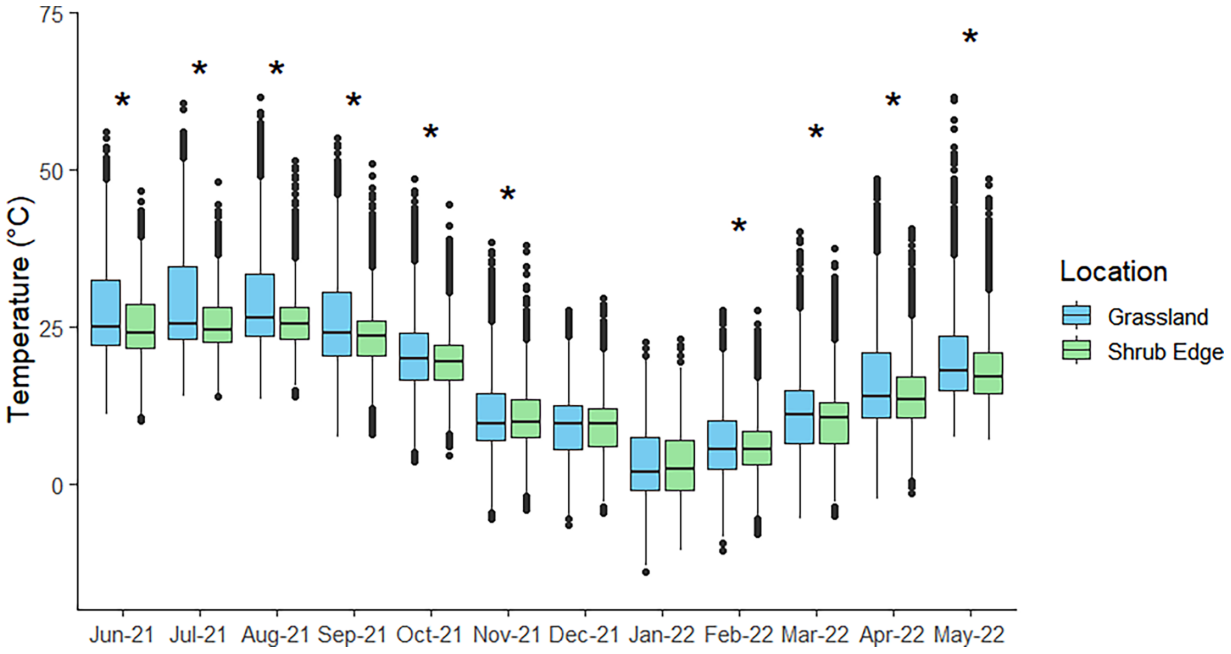


FIGURE 2 Temperature for one year throughout the grassland and shrub edge plots. The bold midline is the median of the data; boxes indicate the middle 50% of data points. The "whiskers" indicate the full spread of data points, with individual points being outliers. Asterisks indicate significant ($p < 0.05$) post hoc differences with Bonferroni adjustment in location during that month (i.e., every month except December and January) following repeated measures ANOVA.

Light (PAR) was reduced by 283% at the shrub edge (533 ± 126 μmol m^{-2} s^{-1}), with more variability than that observed in grassland (1510 ± 55 μmol m^{-2} s^{-1}; $\chi^2 = 14.29$, $p = 0.0001$). Water availability, measured through depth to groundwater and soil water content, was higher at the shrub edge than in the grassland ($F_{1,10} = 1176$, $p < 0.0001$; $F_{1,10} = 10.06$, $p < 0.01$, respectively; Appendix S1: Tables S3 and S4). At the shrub edge, mean annual groundwater was ~21 cm closer to the soil surface (Figure 3). Soils were wetter at the shrub edge than in the grassland at 21–30 cm depth (Figure 4). $\delta^{15}N$ was 13% lower in grassland soils and shrub edge values were significantly closer to zero, which indicated nitrogen from fixation ($\chi^2 = 9.80$, $p = 0.002$; Table 2). Soil $\delta^{13}C$ was slightly lower in the shrub edge ($t = 2.25$, $p = 0.04$; Table 2). There were no differences in percent carbon or nitrogen in the soils (Table 2).

Community composition

The shrub edge had fewer species than open grassland but with four times higher vegetative cover, >500 more stems/m^2, and plants that were ~56 cm taller (Table 2). Seasonal differences were observed for species richness ($F_{1,9} = 4.033$, $p = 0.02$) and height ($F_{1,9} = 6.69$, $p < 0.0001$). Biomass was almost 10 times greater along the shrub edge. The shrub edge was dominated by tall, densely growing grass species, particularly *Spa. patens*, which had double the relative importance value at the shrub edge (Table 2; Appendix S1: Table S1). Species composition included six species that existed only in the grassland and two observed only at the shrub edge plots (Appendix S1: Table S1). The most dominant species in both locations were *Spartina*, *Solidago*, *Andropogon*, and *Panicum*. To better disentangle the community composition between locations and years a PERMANOVA was performed. There was a significant difference between locations ($F_{1,9} = 12.222$, $p = 0.0002$), but not between years ($F_{1,9} = 1.9101$, $p = 0.0882$; Figure 5; Appendix S1: Table S10).

Species functional traits

Species differences were observed in most functional traits (Table 3) with all species being significantly taller along the shrub edge. *Spartina* and *Andropogon* had higher stem densities at the shrub edge, while *Solidago* stem density was decreased at the shrub edge (Table 3). Along the shrub edge, *Solidago* exhibited 27% higher LDMC ($p < 0.001$; Table 3) and SLA was higher in *Solidago*, *Andropogon*, and *Panicum* ($p = 0.001$, $p = 0.009$, $p < 0.001$; Table 3). No differences were observed in SSD. *Solidago* had higher leaf percent nitrogen ($p = 0.001$) and lower leaf percent carbon

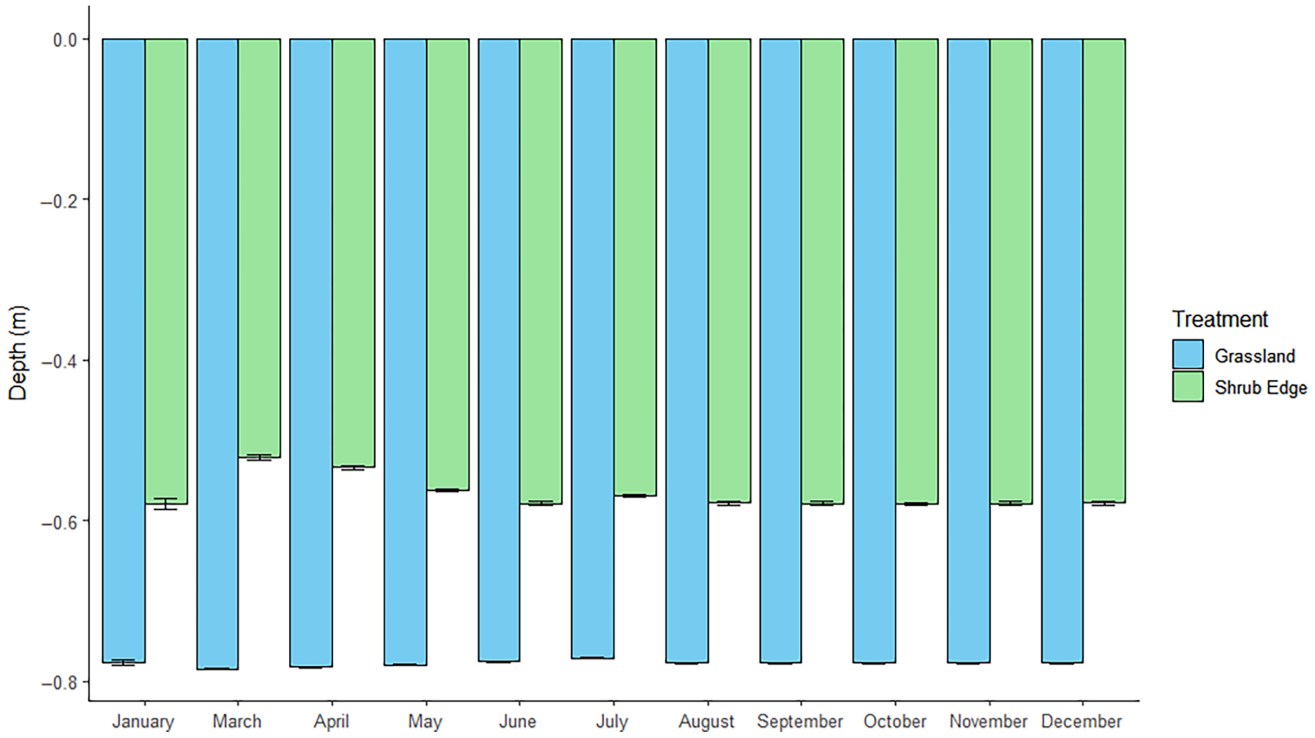


FIGURE 3 Water table depth for grassland and shrub edge as it varied by month. Bars are means and error bars are SE. Treatment was significantly different for all months measured based on repeated measures ANOVA and post hoc tests with Bonferroni adjustment.

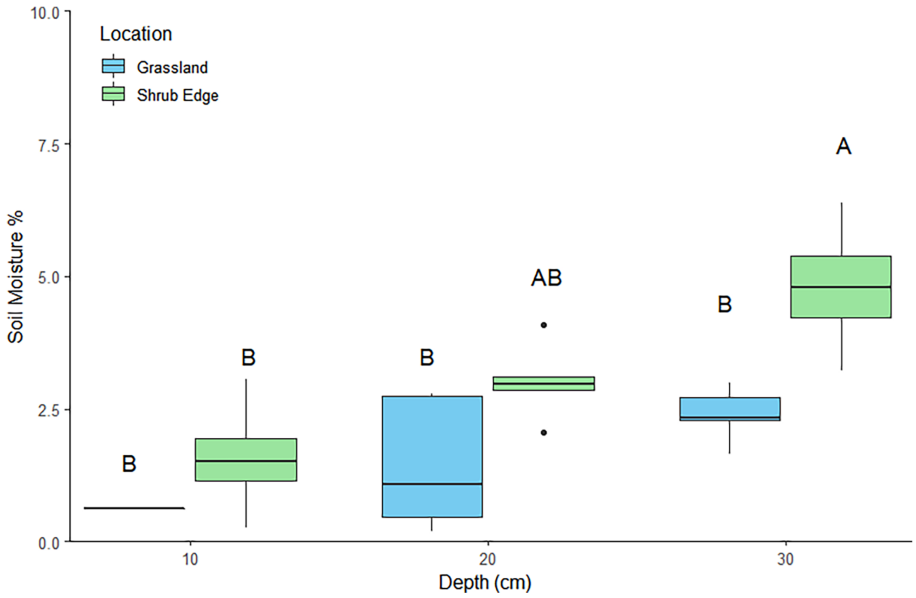


FIGURE 4 Soil water content (in percentage) at three depths (0–10, 11–20, 21–30 cm) and two different location treatments (grassland and shrub edge). The bold midline is the median of the data; boxes indicate the middle 50% of data points. The "whiskers" indicate the full spread of data points, with individual points being outliers. Letter codes indicate significant differences of Tukey post hoc tests following two-way ANOVA.

($p = 0.04$) at the shrub edge (Table 3). Measurements of leaf $\delta^{15}N$ for *Andropogon* were lower along the shrub edge ($p = 0.03$; Table 3). No other differences were observed.

When traits were analyzed with a PERMANOVA, there was a significant difference between location ($F_{1,9} = 170.08$, $p < 0.001$) and species ($F_{3,9} = 1561.1$, $p < 0.001$; Table 4) but no interaction, with all species

TABLE 2 Plot-based metrics between the grassland and shrub edge communities with means (or community-weighted means [CWM] for height) and SEs shown.

Metric	Grassland	Shrub edge	Test statistic			p
			χ^2	F	t	
Below-canopy PAR (μmol m^{-2} s^{-1})	**1324 ± 56.4**	**797 ± 88.4**	**19.20**			**<0.0001**
LAI	**0.31 ± 0.05**	**0.58 ± 0.10**	**4.29**			**0.03**
Species richness	**4.6 ± 0.3**	**3.1 ± 0.3**		**19.67**		**<0.0001**
Shannon diversity	**1.17 ± 0.1**	**0.64 ± 0.1**		**23.63**		**<0.0001**
Percent cover (%)	**16.1 ± 1.3**	**69.3 ± 6.1**		**56.69**		**<0.0001**
Stem density (m^2)	**1377 ± 133**	**1944 ± 169**		**27.17**		**<0.0001**
CWM height (cm)	**32.0 ± 1.4**	**88.5 ± 3.8**		**90.47**		**<0.0001**
Biomass (g m^{-2})	**89.6 ± 15.6**	**803.0 ± 120.4**		**84.29**		**<0.0001**
Soil % nitrogen	0.01 ± 0.001	0.01 ± 0.001			−1.00	0.33
Soil % carbon	0.08 ± 0.008	0.10 ± 0.014			−1.04	0.32
Soil C:N	7.70 ± 0.55	8.30 ± 0.51			−0.78	0.45
Soil $\delta^{13}C$	**−21.37 ± 0.29**	**−22.15 ± 0.24**			**2.25**	**0.04**
Soil $\delta^{15}N$	**−1.08 ± 0.12**	**−0.12 ± 0.24**			**−3.43**	**<0.01**

Note: The test statistic is the result of using location as the main effect. The *p* values in boldface are significant. Full two-way ANOVA results including time and site as factors are shown in supplementary tables for species richness (Appendix S1: Table S5), percent cover (Appendix S1: Table S6), stem density (Appendix S1: Table S7), CWM height (Appendix S1: Table S8), and biomass (Appendix S1: Table S9).
Abbreviations: LAI, leaf area index; PAR, photosynthetically active radiation.

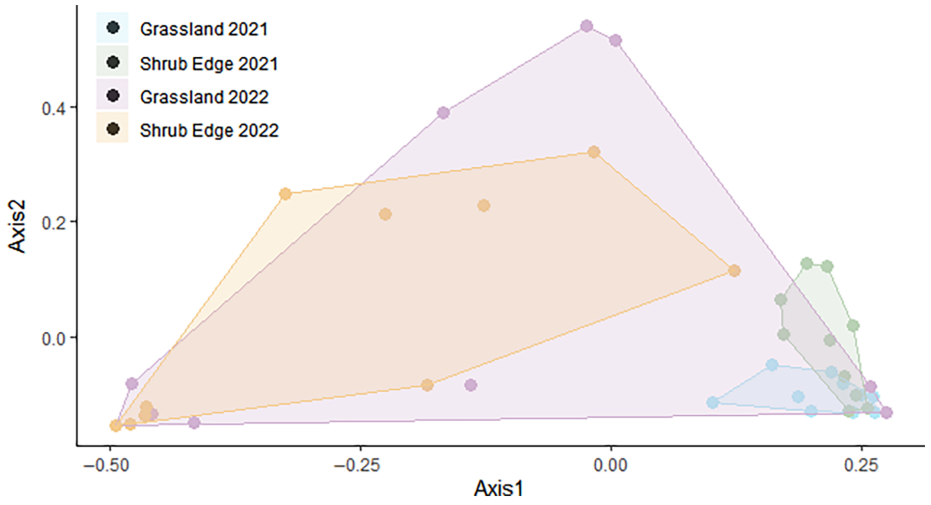


FIGURE 5 Nonmetric multidimensional scaling analysis of community composition based on location and year.

being significantly different from one another. This was visualized with a PCA, in which Axis 1 explained 42.87% of the variation and Axis 2 explained 28.42% of the variation (Figure 5). Nitrogen ($r = 0.88$, $p < 0.0001$), C:N ($r = -0.89$, $p < 0.0001$), SLA ($r = 0.76$, $p < 0.0001$), and $\delta^{15}N$ ($r = 0.39$, $p < 0.0001$) drove separation along axis 1, whereas $\delta^{13}C$ ($r = 0.93$, $p < 0.0001$) and carbon content ($r = -0.67$, $p < 0.0001$) were strongly correlated with axis 2 (Figure 6).

DISCUSSION

Coastal grassland communities on barrier islands are nutrient and freshwater resource limited due to minimal nutrient input and quick leaching through sandy soils (Bolyard et al., 1979). These plant communities are further impacted by expanding shrubs and shrub thickets that modify the microclimate (Thompson et al., 2017). Our study documents shrub expansion modification of

TABLE 3 Species leaf and stem traits between the grassland and shrub edge communities with means and SEs shown for all.

Trait	Location	*Panicum*	*Spartina*	*Solidago*	*Andropogon*
Height (cm)	Grassland	**24.48 ± 1.77**	**51.82 ± 3.20**	**30.43 ± 2.92**	**28.08 ± 6.64**
	Shrub edge	**47.67 ± 10.58**	**88.84 ± 5.88**	**54.14 ± 6.01**	**74.13 ± 7.85**
Stem density (10 cm^2)	Grassland	1.48 ± 0.14	**8.88 ± 1.68**	**1.95 ± 0.19**	**3.83 ± 0.96**
	Shrub edge	1.17 ± 0.17	**15.64 ± 1.84**	**1.36 ± 0.17**	**5.88 ± 0.99**
Cover (0.25 m^2)	Grassland	**1.70 ± 0.32**	**4.47 ± 0.78**	6.33 ± 0.99	**6.00 ± 1.13**
	Shrub edge	**3.67 ± 0.84**	**57.88 ± 7.65**	6.64 ± 1.45	**25.06 ± 6.92**
Leaf dry matter content (LDMC)	Grassland	0.36 ± 0.01	0.46 ± 0.01	**0.23 ± 0.01**	0.28 ± 0.01
	Shrub edge	0.35 ± 0.02	0.48 ± 0.02	**0.18 ± 0.03**	0.25 ± 0.01
Stem specific density (SSD) (mg mm^{-3})	Grassland	0.71 ± 0.12	1.57 ± 0.19	0.34 ± 0.01	0.18 ± 0.01
	Shrub edge	0.57 ± 0.08	2.27 ± 0.33	0.30 ± 0.02	0.18 ± 0.01
Specific leaf area (SLA) (cm^2 g^{-1})	Grassland	**117.36 ± 2.76**	69.71 ± 2.57	**84.68 ± 2.23**	**185.83 ± 10.84**
	Shrub edge	**154.20 ± 5.32**	73.71 ± 3.97	**127.93 ± 9.11**	**249.16 ± 12.96**
Leaf percent nitrogen	Grassland	0.98 ± 0.04	0.48 ± 0.03	**1.47 ± 0.09**	1.84 ± 0.06
	Shrub edge	1.05 ± 0.06	0.55 ± 0.04	**2.22 ± 0.13**	1.75 ± 0.09
Leaf percent carbon	Grassland	46.02 ± 0.12	45.98 ± 0.21	**47.66 ± 0.57**	44.72 ± 0.20
	Shrub edge	45.57 ± 0.17	46.10 ± 0.31	**45.85 ± 0.23**	44.19 ± 0.22
Leaf C: N	Grassland	47.71 ± 2.04	100 ± 5.39	**33.95 ± 1.80**	24.80 ± 0.80
	Shrub edge	46.33 ± 3.91	88.83 ± 5.53	**21.75 ± 1.40**	26.52 ± 1.47
Leaf $\delta^{15}N$	Grassland	−1.80 ± 0.19	−2.80 ± 0.25	−2.65 ± 0.13	**−1.55 ± 0.10**
	Shrub edge	−1.35 ± 0.28	−2.35 ± 0.34	−1.70 ± 0.68	**−2.01 ± 0.11**
Leaf $\delta^{13}C$	Grassland	−13.24 ± 0.04	−13.90 ± 0.05	−29.01 ± 0.15	−13.11 ± 0.05
	Shrub edge	−13.33 ± 0.07	−14.11 ± 0.09	−29.12 ± 0.22	−13.13 ± 0.11

Note: Boldface indicates significant differences between locations within a species resulting from either *t* tests using a Bonferroni adjustment for multiple tests, or Wilcoxon signed-rank test which was used for height, stem density, and cover.

TABLE 4 Permutational multivariate ANOVA results for trait data by species and location.

Source	df	SS	Mean sum of squares	*F*	*p*
Species	3	0.66003	0.2201	1561.1	<0.001
Location	2	0.02397	0.02397	170.08	<0.001
Interaction	3	−0.0172	−0.00574	−40.751	1.00
Residual	112	0.0158	0.000141		
Total	119	0.68255			

microclimate, community composition, and traits along the shrub edge relative to unencroached grassland. Previous research found that by 2013, shrub thickets on Hog Island covered almost 50% of the island, up from ~10% in the 1970s (Huang et al., 2021). Our results indicate that as shrubs expand, the edge community increases and responds to the moderated environment by exhibiting resource acquisitive traits. Plants were taller and denser when adjacent to shrubs, resulting in higher aboveground biomass and changes in leaf traits. These trait differences could influence resilience to further disturbance (Brown & Zinnert, 2020) anticipated with storms and sea-level rise.

Microclimate modification

The results support our hypothesis that the shrub edge has a moderated microclimate that impacts the grassland community leading to altered plant traits. The shrub edge microclimate was moderated with lower light levels, and cooler summer temperatures relative to open grassland

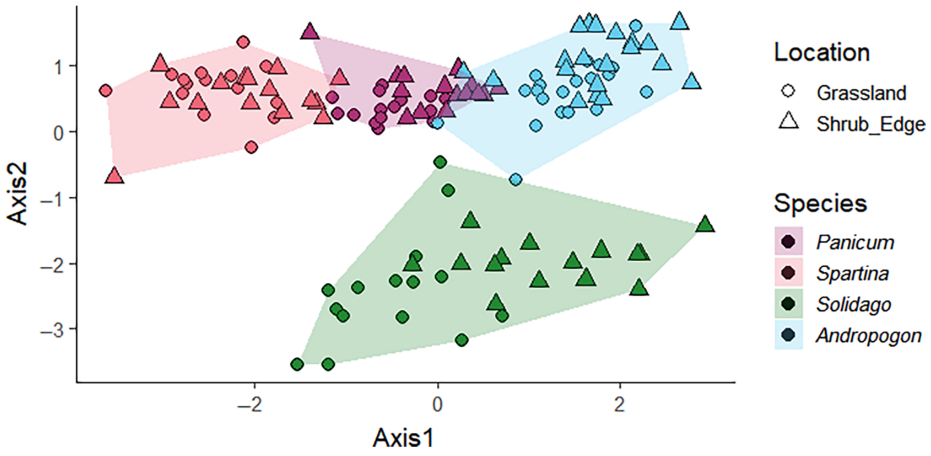


FIGURE 6 Principal components analysis of trait data, color-coded by species, with shapes to differentiate location.

(Thompson et al., 2017; Wood et al., 2020). Seedling establishment benefits from this climate modification (Sinclair et al., 2020; Woods et al., 2019), which may allow for further thicket expansion, but also provides a unique microenvironment that allows for greater abundance and growth of *Spartina*.

Water is a limited resource in barrier island grasslands that is directly related to precipitation inputs (Bolyard et al., 1979) The high canopy cover and LAI across the island (Brantley & Young, 2007; Huang et al., 2021), along with high evapotranspiration rates of *Morella* (Woods et al., 2021), likely result in the water table being elevated closer to the soil surface near shrub thickets. The soil is also significantly wetter at the shrub edge at lower depths due to the high leaf area of *Morella* thickets which reduces ground light levels and increases leaf litter (Brantley & Young, 2007), leading to a slower absorption of rainfall. *Morella* roots are concentrated in the top 20 cm of soil, explaining why soil moisture did not differ from grassland at these depths (Conn & Day, 1993).

Sandy soils are nutrient poor due to leaching (reviewed in: Huang & Hartemink, 2020); thus, measuring soil nutrients can be highly variable based on precipitation and groundwater levels. Nitrogen fixers have an advantage in these environments by supplying nitrogen to the soil and benefiting the adjacent vegetation. *Morella*, a known nitrogen fixer, has low nitrogen resorption rates prior to leaf drop resulting in high amounts of nitrogen input into the soil relative to grassland (Brantley & Young, 2008). There were no differences in soil percent nitrogen between the habitats, which is consistent with previous findings in the shrub interior (Thompson et al., 2017; Wood et al., 2024), indicating high variability of nutrient inputs and may reflect thicket age (Brantley & Young, 2010). The lack of difference in soil nitrogen could also be due to leaching (Wood et al., 2024) or uptake by plants in the form of higher biomass. We expected to observe isotopic differences in nitrogen along the shrub edge to indicate fixed nitrogen in leaves and soils (closer to zero). $\delta^{15}N$, which was significantly enriched, indicates that *Morella* presence is enhancing the soil nutrient composition, either directly in the soil through fixation or from leaf litter nutrient deposition during decomposition (Delwiche et al., 1979). This is consistent with findings from other *Morella* (*Myrica*) species' expansion into grassland communities. This has been observed both in native habitat with *M. pensylvanica* (Rogers et al., 1985) and non-native habitat with *M. faya* (Vitousek & Walker, 1989).

Community composition

The shrub edge community had significantly higher percent cover, stem density, height, and biomass than the grassland community. Increases in plant height at the shrub edge may be a response to light limitations from the shrub canopy (Aarssen, 1995; Yan et al., 2012). Increased vegetation density likely results from the resources available along the shrub edge. This dense graminoid cover has led to decreased species richness in the shrub edge when compared to open grassland. Few species can dominate and crowd out other species along the edge. However, the richness of the shrub edge remains higher than that within the thicket, which is a *Morella* monoculture (Thompson et al., 2017). Due to the light limitations, the shrub edge community was dominated by tall, clonal grass species that can persist in lower light environments, particularly *Spartina* (Kottler & Gedan, 2022). This species is highly adaptable to several landscapes (Burdick & Mendelssohn, 1987; Silander & Antonovics, 1979), and depending on the habitat is referred to as a foundational species (Gedan & Burtness, 2010) or an

ecosystem engineer (Chung, 2006). *Spartina* had the highest relative importance (RI) for both communities; however, it increased from 21% RI in the grassland to 54% in the shrub edge community due to its high stem density (Table 2; Appendix S1: Table S1).

As *Spartina* increased in dominance, species richness decreased by 34% at the shrub edge, with a total of six grassland species missing from the shrub edge. Typically, an increase in biodiversity leads to an increase in biomass (Tilman, 1996). However, in this mesic coastal system, decreased biodiversity due to shrubs is associated with an increase in biomass under shrubs (Wood et al., 2020) and at the shrub edge as reported here. Increased biomass can impact barrier island resilience to sea-level rise by adding resistance to sediment movement (Leonard & Croft, 2006), resulting in higher erosion (Zinnert et al., 2019). However, the dominant shrub edge species, *Spartina*, is also known to tolerate high salinity and burial that occurs with overwash (Wolner et al., 2013). The impact of shrub edge biomass and change in dominance may play an important role in the response of barrier islands to sea-level rise and sediment movement (Reeves et al., 2022).

The shrub edge has a moderated microenvironment (increased nutrients and freshwater, moderated light and temperature), creating a lower stress habitat, with plants exhibiting traits of resource acquisition (Brown & Zinnert, 2020) relative to the higher stress environment in the open grassland. The shrub edge is almost exclusively perennial species, with only two annuals occurring with a relative importance of <10 (Appendix S1: Table S1). Conversely, in the grassland, there was higher richness of annual plants (5) and *Conyza canadensis* was one of the top five dominant species. Perennials outcompeting annuals in a resource-limited environment is an indicator of competition (Ning et al., 2022).

Species intraspecific comparisons

Trait differences between shrub edge and grassland sites mirror their different microclimatic conditions. At the shrub edge, SLA was higher in all species, except *Spartina*. Higher SLA indicates the "shade leaf" response to the low light levels on the shrub edge. Instead of acclimating leaves to the shade, *Spartina* may enhance light capture through increased height relative to the surrounding graminoid and forb species. Along with decreased SLA, grassland *Solidago* was noted to often have insect leaf damage, which was not observed for *Solidago* found at the shrub edge (Riffe, personal observation). This could affect both SLA and LDMC. While no insects were found on our plant samples, *Solidago* is susceptible to goldenrod leaf miner, red goldenrod aphid, and the goldenrod leaf beetle (Sheahan, 2014). No differences in SSD were observed between communities.

Leaf nutrient results indicated several location differences. *Solidago* had higher leaf percent nitrogen and lower C:N (an indicator of lower nutrient use efficiency) at the shrub edge, which is likely due to increased nitrogen availability for plant uptake near *Morella*. Leaf $\delta^{15}N$ was significantly decreased in *Andropogon* leaves at the shrub edge. However, all data were in the possible range to indicate fixation, suggesting that grassland species benefit from rhizosheath fixation (Bergmann et al., 2009) which has been observed in coastal grasslands (Brown & Zinnert, 2021). Nutrient studies have found an increase in *Spartina* after nutrient input with no effects on soil properties (Matzke & Elsey-Quirk, 2018), which could explain how *Spartina* growth has increased through using the nitrogen input from *Morella*, although we did not detect any increases in soil or leaf nitrogen at the shrub edge.

CONCLUSIONS

M. cerifera expansion along the mid-Atlantic and Gulf coasts has arrested the typical successional pathway to maritime forest (Bissett et al., 2016; Ehrenfeld, 1990). This has landscape-level consequences through preventing sediment movement into the island interior as the island responds to sea-level rise by landward migration. Along with these landscape-level changes, *Morella* expansion has also affected the surrounding grassland communities by reducing species richness and enhancing the dominance, growth, and biomass of perennial grasses, most notably *Spartina patens*. Our results show that as shrubs expand, they simultaneously modify the surrounding grassland landscape, leading to loss of biodiversity and creating novel trait profiles across the landscape. We document that co-occurring species in the swale exhibit different leaf traits between open grassland and shrub edge, indicating physiological plasticity in response to different microclimatic conditions. This new grass-shrub ecotone could have further impacts on barrier island response to climate change. Despite the mechanism of enhanced growth and alterations in species composition (e.g., modified temperature, increased water availability, enhanced nitrogen input, or a combination of factors), the resulting shrub edge community exhibits higher biomass production that may result in differential responses to common disturbances (i.e., storm-induced overwash of sediment and salinity, erosion) in this coastal environment.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Riffe & Zinnert, 2025) are available from the Environmental Data Initiative (EDI) Data Portal: https://doi.org/10.6073/pasta/4d4154e8f8784e2eb60afd7aa3061ba3.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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