



OPEN

Decreased temperature variance associated with biotic composition enhances coastal shrub encroachment

Lauren K. Wood^{1,2}, Spencer Hays³ & Julie C. Zinnert¹ ✉

Regime shift from grasslands to shrub-dominated landscapes occur worldwide driven by altered land-use and climate change, affecting landscape function, biodiversity, and productivity. Warming winter temperatures are a main driver of expansion of the native, evergreen shrub, *Morella cerifera*, in coastal landscapes. Shrub establishment in these habitats alters microclimate, but little is known about seasonal differences and microclimate variance. We assessed influence of shrubs on microclimate variance, community composition, and community physiological functioning across three vegetation zones: grass, transitional, and shrub in a coastal grassland. Using a novel application of a time-series analysis, we interpret microclimatic variance modification and elucidate mechanisms of shrub encroachment at the Virginia Coast Reserve, Long-Term Ecological Research site. As shrub thickets form, diversity is reduced with little grass/forb cover, while transpiration and annual productivity increase. Shrub thickets significantly reduced temperature variance with a positive influence of one day on the next in maximum air, minimum air, and maximum ground temperature. We also show that microclimatic temperature moderation reduces summer extreme temperatures in transition areas, even before coalescence into full thickets. Encroachment of *Morella cerifera* on the Virginia barrier islands is driven by reduced local exposure to cold temperatures and enhanced by abiotic microclimatic modification and biotic physiological functioning. This shift in plant community composition from grassland to shrub thicket alters the role of barrier islands in productivity and can have impacts on the natural resilience of the islands.

Woody vegetation is rapidly encroaching into grassland globally as a result of altered environmental drivers^{1–3}. The abrupt conversion to shrub-dominated habitats includes drivers such as altered fire or grazing pressures, increased atmospheric CO₂, and altered temperature ranges^{3–6}. Warming temperatures associated with macroclimatic change, particularly in winter minima, can expand the range limits of cold-intolerant shrub species^{3,6–8} while microclimatic variance in precipitation enhances success of woody vegetation, particularly in the transition ecotones^{9,10}. Thus, no single factor provides dominant influence on woody encroachment.

Increased annual temperatures may improve physiological functioning of encroaching species, possibly as a feedback between abiotic microclimatic conditions and shrub success to promote range expansion for woody shrubs^{3,7}. On smaller scales, encroaching woody vegetation frequently modifies microclimatic conditions resulting in intra- and interspecific facilitation^{11–14}. Changes in microclimatic temperatures within shrub thickets include temperature moderation with diminished instances of extreme temperatures that can decrease productivity and cause physiological damage of xylem structures^{3,6}. In areas with warming winter temperatures, thicket-forming species that are vulnerable to cold-associated damage, such as freezing-induced embolism, are able to take advantage of fewer cold temperature extremes^{1,6,15}. Multiple encroaching species are cold intolerant, thus a warming climate and self-reinforcing microclimatic modification allow aggressive expansion of shrubs in to historical grassland^{3,8,11,13,16–18}.

¹Department of Biology, Virginia Commonwealth University, 1000 West Cary St, Richmond, VA, 23225, USA.

²Integrative Life Sciences Doctoral Program, Virginia Commonwealth University, 1000 West Cary St, Richmond, VA, 23225, USA. ³Department of Statistics, Indiana University, 919 E. 10th St, Bloomington, IN, 47408, USA. ✉e-mail: jczinnert@vcu.edu

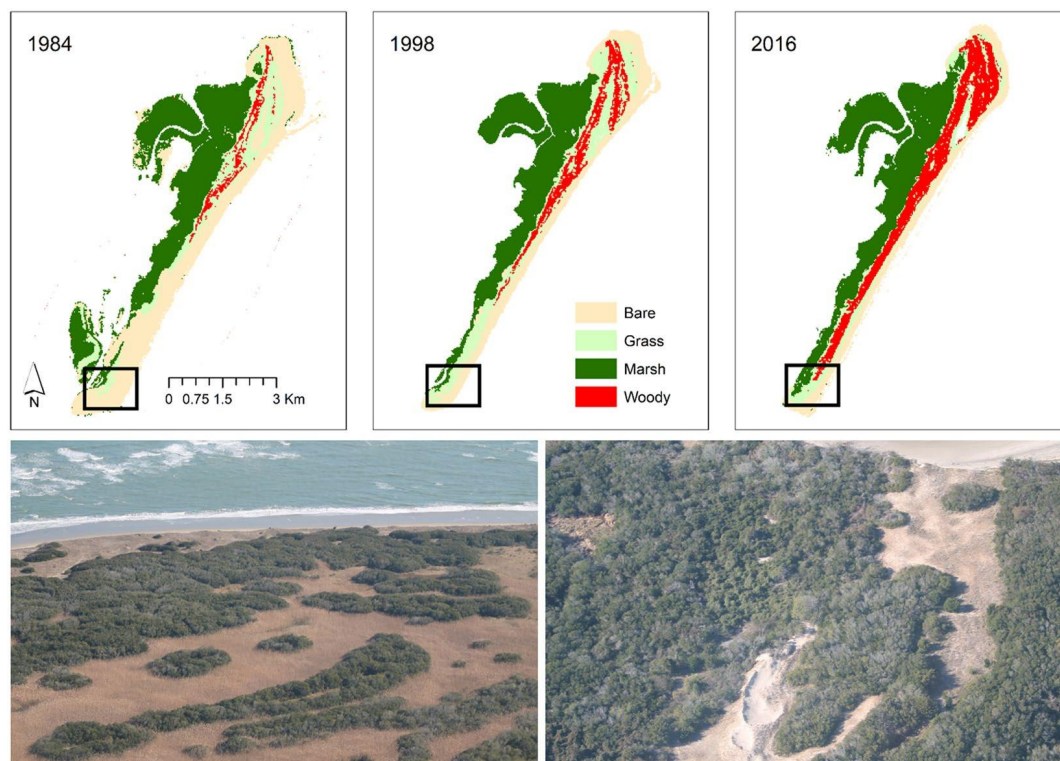


Figure 1. Shrub cover has expanded on Hog Island, Virginia since 1984 represented in red. Data are from Zinnert *et al.*³³. The black box denotes the study area. Photos of shrub cover on the southern portion of the island from November 2017 provided by Julie C. Zinnert.

Regime shifts in vegetation and the resulting modified microclimate beget community changes, often leading to increased diversity with sparse canopy shrubs and decreased diversity in densely leaved canopies^{13,18,19}. These altered plant communities tend to have higher productivity and carbon assimilation and may support different faunal species. Changes in productivity increase soil nutrient assimilation and alters soil microbial communities²⁰. While the drivers and stresses differ among various habitats undergoing woody encroachment, resulting community change and ecosystem consequences are similar.

Among landscapes that have experienced regime shift from grass to woody vegetation are low elevation swale/slack communities along the United States mid-Atlantic and Gulf coasts^{21–26}. Coastal ecosystems in this region have reduced diversity relative to inland communities²⁷ with unique environmental stressors. On a large scale, wind, waves, tides, and storms result in dynamic sediment movement, sea spray, low canopy cover, and highly reflective sandy sediment, which increase irradiance. Regionally, atmospheric and oceanic climate change drivers are altering temperatures, storm regime, and sea level^{25,28}. Species diversity is restricted as a result of these environmental filters^{27,29}. For island landscapes, species diversity is additionally filtered by dispersal^{26,27,30}. The vegetation on barrier islands is further limited by the availability of freshwater and precipitation regime; barrier islands have a freshwater lens that is entirely precipitation-fed^{21,31,32}. Coastal habitats are understudied environments where vegetation dynamics present an unique opportunity to understand shrub encroachment mechanisms.

Over the past 32 years, shrub cover has increased on the Virginia barrier islands by ~40% despite an overall decrease in island area due to sea level rise and erosion (Fig. 1)^{28,33}. *Morella cerifera* (wax myrtle), a native, evergreen shrub forms thickets up to 7 m tall with increased leaf area index (LAI), increasing community productivity and nitrogen input into the system^{34,35}. High productivity of shrubs, along with formation of monospecific thickets, influences carbon assimilation and nutrient input into the system. Evidence suggests *M. cerifera* has been expanding due to decreased exposure to extreme winter temperatures, which impair shrub physiological functioning^{6,13,28}. Warmer temperatures in the winter and cooler temperatures in the summer likely enhance shrub survival and productivity. Further, experimental and modeling results demonstrate that a small increase in minimum temperature cause a shift from grassland to *M. cerifera* dominated alternative stable state⁶.

Although mean temperature modification occurs between grass and shrub regime shift, temperature extremes and variance have yet to be quantified across zones including areas in transition. In order to understand the mechanism of shrub encroachment into coastal grassland, our objective was to quantify microclimate variance, community physiology, and community composition in three vegetation zones: grassland, transition areas, and shrub thickets. We hypothesize that shrub encroachment immediately impacts the community (including transition areas) by reducing species diversity, but increases productivity and transpiration. We further hypothesize that shrub canopy creates self-reinforcing microclimate modification. We use a time-series analysis as a novel way to interpret microclimatic modification to better understand the mechanisms of shrub encroachment.

Variable	Grass zone	Transition zone	Shrub zone
Graminoid cover	86.1 ± 2.2 ^a	32.4 ± 2.2 ^b	0.9 ± 2.2 ^c
Forb cover	13.9 ± 2.4 ^a	6.7 ± 2.4 ^{ab}	1.0 ± 2.4 ^b
Woody cover	— ^a	60.9 ± 2.3 ^b	98.1 ± 2.3 ^c
H' Diversity	1.7 ± 0.1 ^a	1.6 ± 0.1 ^a	0.1 ± 0.1 ^b

Table 1. Plant functional type % cover using the Daubenmire method and Shannon-Wiener biodiversity across zones on Hog Island, VA. Values represent mean ± SE. Letters represent differences among zones according to the Tukey post-hoc test.

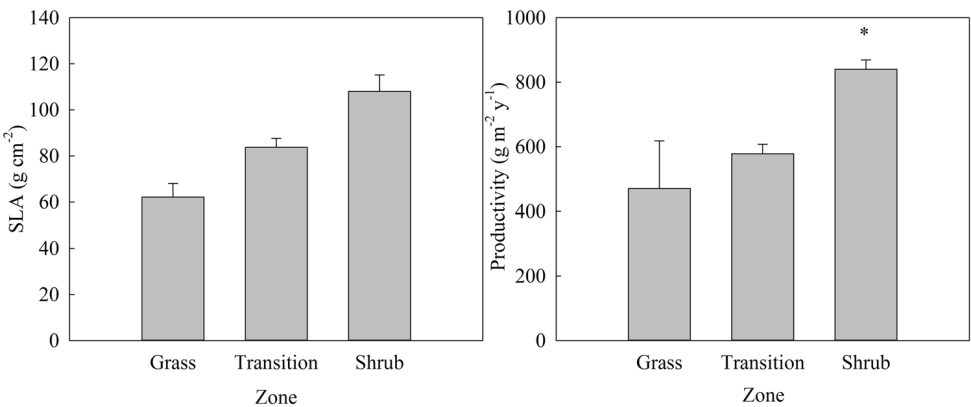


Figure 2. Specific leaf area (SLA; left) and annual net primary productivity (ANPP; right) across the three vegetation zones. Values represent mean ± SE. The asterisk represents significant differences using a post-hoc Tukey Test.

Results

Species composition and physiology. Species richness was highest in grassland (6 ± 0) and transition plots (5 ± 0) (Table s.1). Grassland had highest cover of graminoid species (86 ± 2%), which was significantly higher than transition and shrub plots (F = 84.65, P < 0.0001, Table 1). Forb cover differed between grass (14 ± 2%) and shrub plots (1 ± 2%) only. Transition areas decreased grass cover (32 ± 2%) with increased shrub cover (61 ± 2%) compared to grassland plots. Shrub plots effectively excluded all other plant functional types, reducing species richness to 2 ± 0 and exhibiting 98 ± 2% woody cover (Table s.1, Table 1). Percent cover for species composition shifted from dominant grass, *Spartina patens*, in grasslands to shrub monoculture of *Morella cerifera* with *Baccharis halimifolia* found along the edge (Table s.1). Coastal communities tend to have low vegetation diversity. Establishment of shrubs reduced Shannon-Weiner diversity from 1.7 ± 0.1 in grassland to 0.1 ± 0.1 in fully thicketed shrubs (F = 68.98 P < 0.0001, Table 1). Transition plots did not differ in diversity from grassland.

Despite differences in plant functional type and species composition, SLA did not differ among zones (F = 1.80, P = 0.208, Fig. 2) although there was a trend towards higher SLA in shrub plots. ANPP was highest in full shrub thickets (χ = 9.0, P = 0.0111) and 1.4–1.8 x greater than transition and grass plots (Fig. 2). Establishment of shrubs increased transpiration (E) during spring and summer (season x zone interaction, F = 9.16, P < 0.0001, Fig. 3). In spring, E was 2.5–9.5 x higher than transition and grass plots. In summer, shrub E was highest, with a 3–11 fold increase relative to transition and grass plots respectively. Transition E trended toward being higher than grass zones by 12 and 14 mg H₂O m⁻² s⁻¹ in spring and summer respectively but was not statistically different in either season (Fig. 3).

Microclimate. Shrub plots exhibited lower variance in both ground and air temperatures relative to grass and transition plots, most notably in in maximum air temperature. Shrub variance was 13.4 °C and 18.2 °C lower than transition and grass, respectively (shrub σ² = 11.9, transition σ² = 25.3, and grass σ² = 30.1) (Fig. 4). Grass and transition plot maximum air temperatures were not normally distributed (K-S = 0.0073, P < 0.001 and K-S = 0.056, P = 0.013, respectively) where shrub plots were normally distributed (K-S = 0.041, P = 0.167). Annual temperatures in grass plots exhibited a wider range and higher variance (Fig. 4). Shrub plots had the lowest mean maximum air temperature throughout all of the seasons (P ≤ 0.0125) (Fig. 5). Minimum ground temperatures were altered throughout all seasons as well; transition plots had consistently higher temperatures than shrub and grass. All three vegetation zones were different in summer for maximum air and ground temperature and minimum ground temperature (P ≤ 0.0125).

Auto-regressive conditional heteroscedasticity (ARCH) showed that shrub zones exhibited a local effect of variance across maximum and minimum air temperatures as well as maximum ground temperature (P = 0.0022, P = 0.0021, P = 0.0109, respectively; Table 2). Grass zones had a marginal local effect of the temperature variance in minimum ground temperature only (t = 2.03, P = 0.04). Transition zones had a local effect in minimum air temperature only (P = 0.03).

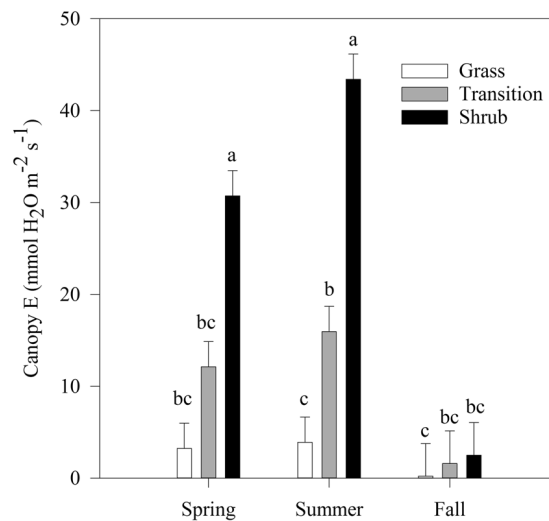


Figure 3. Two-way ANOVA of seasonal transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) across zones. Values represent mean $\pm$ SE. Letters indicate differences among season and zone based on Tukey post-hoc test.

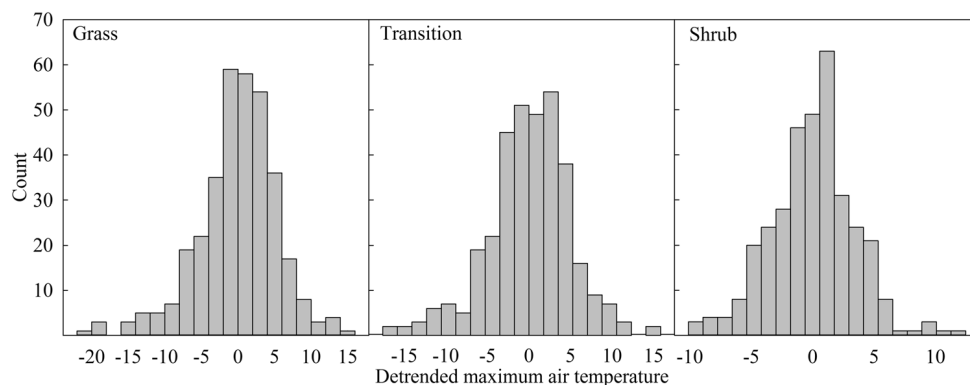


Figure 4. Frequency distribution of detrended maximum air temperature for grass, transition and shrub zones from Hog Island, Virginia.

Extreme warm temperatures in summer were higher in grassland plots relative to transition and shrub plots (Fig. 6). Shrub plots were cooler than grass in the summer by 18.4°C and the warmer in the winter by 2.5°C ($P=0.0013$ and $P=0.021$ respectively, Fig. 6). Winter and summer extreme temperatures did not differ between shrub and transition plots ($P=0.058$, Fig. 6). Shrub zones exhibited cooler mean and maximum temperatures than transition and grass zones ($P<0.001$ for both) (Table s.2). Annual minimum temperatures did not differ statistically ($P=0.07$) (Table s.2).

Discussion

Encroachment of *Morella cerifera* in coastal systems has consequences for landscape function by creating new ecological scenarios with increased shrub cover and loss of other species³³. *Morella cerifera* rapidly expands across the landscape, creating full monospecific thickets within ~ 15 years after seedlings establish, and arrests succession preventing establishment of maritime forest³⁶. We show that shrub presence decreases extreme temperatures and temperature variance, even in transition areas with freestanding shrubs that have not coalesced into thickets. Annual maximum temperature is lower within shrub thickets. The immediate effect of shrub presence impacts evapotranspiration, potentially creating a positive feedback with shrub growth³⁷. Once shrubs coalesce into expansive thickets, they reduce biodiversity but increase productivity, a notable departure from expected biodiversity-productivity relationships^{38–40}.

Macroclimatic warming has been documented along the VCR over the last 32 years and associated with *M. cerifera* success^{6,28}. Here we show that microclimatic temperature moderation reduces summer extreme temperatures with shrub presence, even before coalescence into full thickets (i.e. 8.7 and 18.4°C cooler in transition and shrub zones, respectively). The transition zone is similar to both grass and shrubs with respect to extreme winter temperatures. This expands on our previous understanding of microclimate modification by highlighting the gradual change in extreme temperatures^{3,13,41,42}.

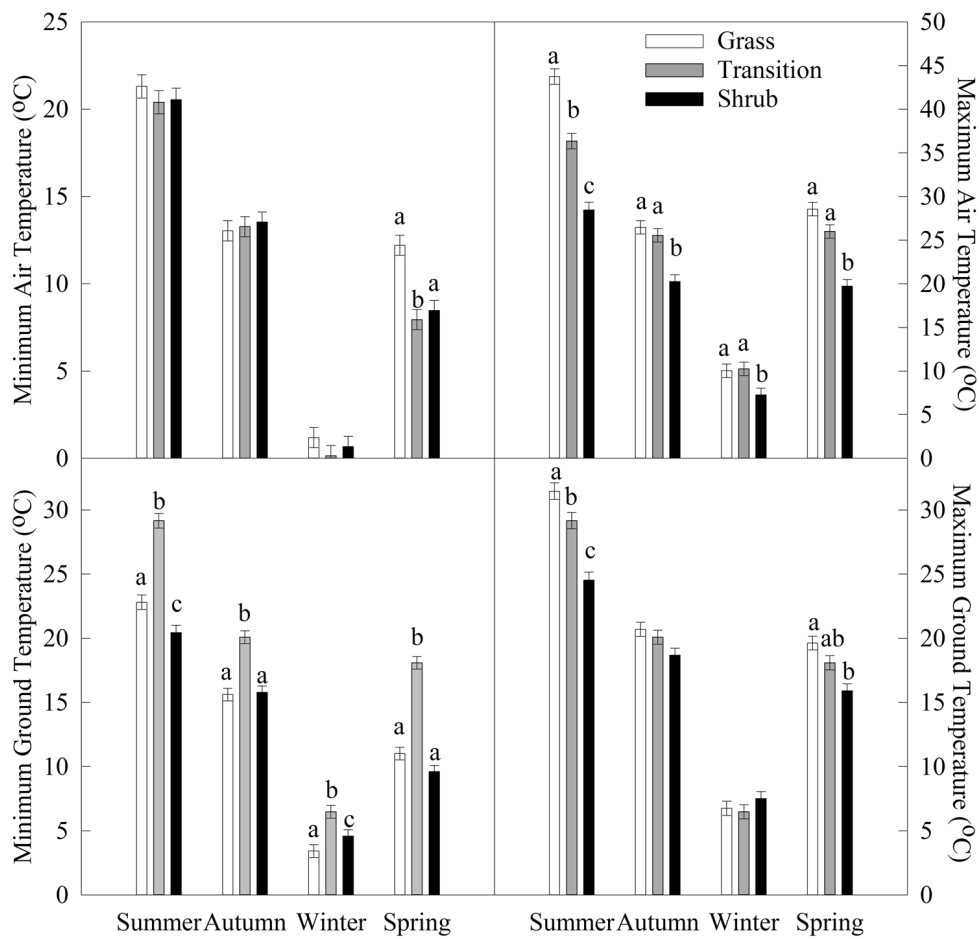


Figure 5. Mean maximum and minimum air and ground temperatures across the grass, transition, and shrub zones divided into season. Bars represent mean $\pm$ SE. Letter codes denote significant differences with Tukey test within each season among zones.

Zone	Max air	Min air	Max ground	Min ground
Grass	$t = 1.04$, $P = 0.2987$	$t = 0.54$, $P = 0.5894$	$t = 0.92$, $P = 0.3570$	$t = 2.03$, $P = 0.0425$
Transition	$t = 0.89$, $P = 0.3733$	$t = 2.24$, $P = 0.0254$	$t = 0.96$, $P = 0.3376$	$t = 2.01$, $P = 0.0448$
Shrub	$t = 2.98$, $P = 0.0029$	$t = 2.30$, $P = 0.0217$	$t = 2.35$, $P = 0.0190$	$t = 1.95$, $P = 0.0511$

Table 2. Autoregressive conditional heteroskedasticity results for maximum and minimum temperatures in grass, transition, and shrub zones on Hog Island, VA. Significant values in bold indicate local control of one day on the next.

Recent literature has demonstrated the importance of climate variance, as mean values may not fully represent climatic influence^{10,43}. Here we document through ARCH analysis that shrubs have a significant impact on temperature variance, creating self-reinforcing microclimate modification observed in both minimum and maximum temperatures. Shrubs also impact transition areas through modifying variance of minimum temperatures. As shrubs exhibit hydraulic failure when temperatures are $< -15^{\circ}\text{C}$, reduced temperature variance in winter months may be critical to the success of shrub growth. In this system, water is typically not limiting, especially in cooler, winter months³¹. Variability in temperature and water availability may have a larger role in shrub encroachment globally^{9,10}.

With the change from grassland to shrubland, we document 3- to 11-fold higher canopy transpiration (E) where shrubs are present (transition and shrub zones) relative to open grassland. This has implications for a system reliant on precipitation input^{44–46}. When precipitation rate is low, shrubs access the freshwater lens, reducing groundwater, and potentially decreasing water availability for the surrounding plant communities in summer months, which can alter diversity and function^{31,47}. Most notably in summer, shrub presence increases transpiration, which may create a positive feedback wherein water evaporation accelerates evaporative cooling and decreases temperature stress, bringing microclimate closer to photosynthetic temperature optimum of 30°C ⁴⁸. Microclimate modification within shrubs likely benefits vegetation function.

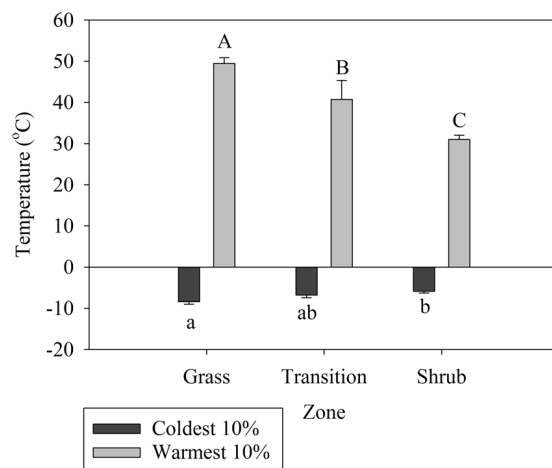


Figure 6. The 10% most extreme temperatures during the winter (black) and summer (white). Values represent mean $\pm$ SE. Letters represent statistical differences.

The homogenization of the landscape with *Morella* expansion is contrary to other extreme habitats, where encroaching species with open canopies provide refugia to more sensitive species⁴⁹. In this system, transition zones reflect an amalgam between grass and shrub zones in microclimate measures and plant cover; however, our hypothesis that diversity would be reduced in these zones was not supported, and we did not find evidence of transition areas providing refugia for other species. In landscapes where encroaching shrub density is high and nitrogen is added via nitrogen fixation³⁴, a sharp decline in species richness is observed^{50,51}. For barrier island systems, the decrease in diversity and homogenization of vegetative communities with fully formed thickets across the landscape has negative consequences by modifying sediment dynamics and reducing island migration in response to sea level rise³³.

Encroachment and altered PFT cover across the zones results in obvious structural complexity change with taller shrubs and more complex branching relative to grassland^{35,37,51}. In many studies a standard functional trait used to assess differences in vegetative community functioning (i.e. SLA) is also observed to differ between woody and herbaceous communities⁵². In this coastal system, SLA was not statistically different among the zones despite the difference in PFT and plant forms (i.e. deciduous herbaceous vs. woody evergreen). There is a trend of lower SLA in grassland and higher SLA in shrubland. *Morella cerifera* has unique functional traits for an evergreen species that are representative of a resource acquisitive species^{37,52,53}.

Identifying mechanisms of shrub encroachment in a vulnerable landscape is an important part of understanding the consequences for landscape change. Feedbacks between microclimate and transpiration alter overall landscape function change with the regime shift from grassland to shrubland. We use a novel time-series analysis to show that microclimate modification is self-reinforcing through temperature variance in plots where shrubs are present (i.e. both transition areas with free-standing shrubs and full monospecific thickets). Variance in abiotic niche constraints may play a bigger role in shrub encroachment in many habitats; ARCH may be used to better illuminate the drivers of woody expansion globally. Enhanced microhabitat and high physiological activity of the encroaching shrub likely accelerates expansion of *M. cerifera*, leading to a shrub monoculture. This expansion has consequences for ecosystem function as seen in high ANPP, but also creates new ecological scenarios that alter response of barrier islands to sea-level rise³⁷.

Methods

Study site. Research was conducted on Hog Island in Northampton County, VA 37°27' N, 75°40' W, part of the Virginia Coast Reserve (VCR), a National Science Foundation funded Long-term Ecological Research site owned and run by the Nature Conservancy. Hog Island is ~8 km from the Eastern Shore of Virginia, ~12 km long and undergoes less rollover and sediment erosion than smaller, lower topography islands. Between 1984 and 2016, shrub cover increased from 7% of upland to 29% on Hog Island³³ (Fig. 1). Shrubs encroachment has been documented on many other islands in the VCR over the same timeframe^{25,33}. Due to heavy encroachment on Hog Island, we focused on the encroachment zone in the southern portion of the island as all suitable habitat, defined by elevation, has been occupied by shrubs north of our study location^{29,30,54}. In 1984, the study area was composed of grassland, marsh, and sandy soils (i.e. bare) that may contain low vegetative cover. By 1998, the area was fully converted to grassland with no interior marsh. Due to dispersal limitations, shrubs reached the southern portion of the island in the last decade, providing an opportunity to study the encroachment process³⁰. Shrubs did not dominate the landscape until the late 1970s to early 1980s and this regime shift has been linked through experiments and models to fewer freezing events through since the 1970s^{6,23,25}. Historical records indicate that maritime forest occurred on Hog Island in the early 1900s, however, since the 1980s, succession has been altered by development of tall monospecific shrub thickets of *M. cerifera* and lack of transition to maritime forest^{29,36}. Forested plots on other nearby islands have transitioned to dominance by *M. cerifera* (Zinnert, unpublished data). Once established, seedlings grow rapidly and shrub thickets persist on the landscape unless lost due to shoreface erosion from sea-level rise^{33,55}.

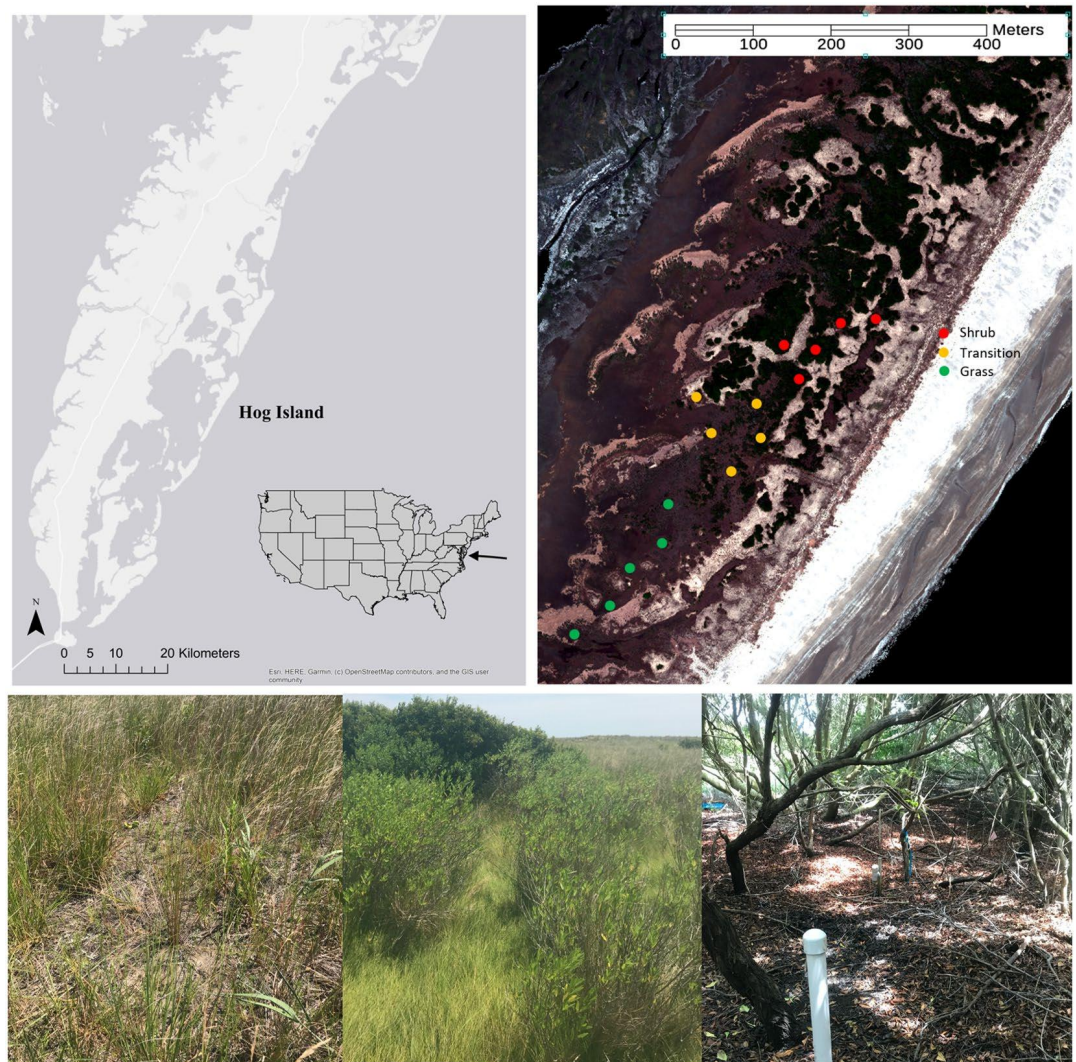


Figure 7. Study location of Hog Island, Virginia. Map produced using © OpenStreetMaps contributors from the ArcGIS basemap, permitted under an open license for academic and commercial use, created by Lauren K. Wood. Approximate plot locations of vegetation types are overlaid on high resolution 2013 imagery⁶¹. Representative images of grass, transition and shrub zones. Photos provided by Lauren K. Wood.

Experimental design. A map of the VCR was created using ArcGIS version 10 imagery (Esri, Redlands, CA) (Fig. 7). Fifteen spatially disparate 5×5 m plots were established during the summer of 2014 and categorized as one of three vegetation zones: grassland, transition, and shrub zones (Fig. 7). Microtopography is variable at small spatial scales and plays an important role in vegetation composition due to access to the freshwater lens³². The range of elevation where *M. cerifera* exists is narrow³² and grassland plots were placed at similar elevations to those of the transition and shrub plots to limit confounding factors. Further, each plot is considered independent as they are separated by geomorphic features such as interior dunes, relic marsh channeling with high salinity, and other topographic features that exclude *M. cerifera* establishment (Fig. 7). These geomorphic features allow for independence of all variables measured in this study. Each shrub plot was placed within thickets separated by the previously mentioned factors. Grass canopy height was ~ 0.7 m maximum, the canopy in the transition zone was ~ 1.5 m, and thicket canopy was >4 m in height. Plot elevation ranged from 0.7 m to 1.6 m above sea level. Within each plot soil, surface and air temperature were measured hourly from July 2014 to September 2017 (HOBO U23-003, Onset Inc. Bourne, MA).

Species composition was quantified using the Daubenmire method at the end of the growing season⁵⁶. Species composition was divided into plant functional type (PFT) and percent cover was normalized within each PFT to total cover. Shannon-Wiener Diversity index was calculated using the following equation:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

where p is the proportion of individuals of i th species.

Specific leaf area (SLA) of the two most predominant species per plot was assessed in 2016 by getting dry weight of 2 cm² leaf area for woody species and a linear portion of leaf for graminoid species of at least 4 cm long. Community-weighted SLA was calculated using up to the two most abundant species, accounting for species that represent >10% in each plot using the following equation:

$$\sum_{i=1}^R p_i t_i$$

where p is the normalized relative contribution of the species and t is the species SLA.

Stomatal conductance (Decagon Devices SC-1, Pullman, WA) was measured on north facing, sun-exposed branches of three to five plants of the two most prevalent species in each zone over three seasons. Stomatal conductance (g_s) was measured during spring, summer, and autumn of 2017 on the same day between 10:00–14:00 in all plots and restricted to sunny days (PPFD > 1300 $\mu\text{mol m}^{-2} \text{s}^{-1}$) to minimize confounding factors. Leaf area index (LAI) (Li-Cor 2200 C) was assessed annually at the end of the 2017 growing season. Leaf-level transpiration (E) was derived from g_s multiplied by daily vapor pressure deficit. Canopy E was calculated using up to the two most abundant species in each plot using the following equation:

$$\sum_{i=1}^R p_i t_i \times \text{LAI}$$

where p is the normalized relative contribution of the species and t is the leaf-level transpiration, multiplied by LAI to get canopy-wide transpiration^{57,58}.

Shrub biomass was collected by randomly selecting and clipping 50 shoots of the current year's growth around the north side of the shrub crowns. Shoots were then dried at 60 °C for 72 hours. Annual net primary productivity (ANPP) was derived using the allometric equation for juvenile *M. cerifera* shrubs⁵⁹:

$$\text{ANPP} = 707 + (31 * g \text{ shoot}^{-1})$$

To estimate ANPP of herbaceous species, aboveground biomass in 10 × 100 cm plots was harvested at peak biomass. Biomass was dried and weighed as described above.

Statistical analysis. One-way analysis of variance (ANOVA) was used to determine differences in extreme temperature events of the 10% warmest temperatures in the summer and coolest temperatures in the winter, PFT, and SLA. ANPP across vegetation zones was analyzed using non-parametric Kruskal Wallance test due to unequal variances. Mean maximum temperature and canopy transpiration (E) were analyzed using two-way ANOVA among seasons and zones. Maximum detrended air temperature was tested for normal distribution using a Kolmogorov-Smirnov (K-S) test. Due to unequal variance and lack of normality, Kruskal Wallance test was used to compare among zones within seasons for maximum, minimum air and ground temperatures. A Bonferonni correction was applied to account for multiple comparisons. To compare across zones, temperature data were detrended to remove seasonal variance. Autoregressive conditional heteroskedasticity (ARCH) test of daily mean temperatures addressed temperature variance relative to local microclimate over time. This test, derived from economics, is a time series analysis to test for variance differences among zones; positive ARCH will exhibit high variance leading to high variance of the next day as described in Seekell *et al.*⁶⁰. This is a novel approach to analyzing microclimate data.

Data availability

Temperature data from this project are available at the Virginia Coast Reserve data portal: Wood, L. and J. Zinnert. 2018. Ground and Air Temperatures on Hog Island, VA in grassland, shrub thicket, and transition, 2014–2018. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication knb-lter-vcv.309.1 (<https://doi.org/10.6073/pasta/51e468eb007b91a9c2905433eb0eb6d9>).

Received: 10 December 2019; Accepted: 28 April 2020;

Published online: 19 May 2020

References

1. Tape, K., Sturm, M. & Racine, C. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. *Glob. Change Biol.* **12**, 686–702 (2006).
2. Bestelmeyer, B. T. *et al.* Analysis of abrupt transitions in ecological systems. *Ecosphere* **2**, 1–16 (2011).
3. D'Odorico, P. *et al.* Vegetation-microclimate feedbacks in woodland-grassland ecotones. *Glob. Ecol. Biogeogr.* **22**, 364–379 (2013).
4. Van Auken, O. W. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* **31**, 197–215 (2000).
5. Knapp, A. K. *et al.* Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Glob. Change Biol.* **14**, 615–623 (2008).
6. Huang, H., Zinnert, J. C., Wood, L. K., Young, D. R. & D'Odorico, P. A non-linear shift from grassland to shrubland in temperate barrier islands. *Ecology* **99**, 1671–1681 (2018).
7. He, Y., D'Odorico, P. D., De Wekker, S. F. J., Fuentes, J. D. & Litvak, M. On the impact of shrub encroachment on microclimate conditions in the northern Chihuahuan desert. *J. Geophys. Res.* **115**, D21120, <https://doi.org/10.1029/2009JD013529> (2010).
8. Devaney, J. L., Lehmann, M., Feller, I. C. & Parker, J. D. Mangrove microclimates alter seedling dynamics at range edge. *Ecology* **98**, 2513–2520 (2017).
9. Yu, K., Saha, M. V. & D'Odorico, P. The effects of interannual rainfall variability on tree-grass composition along Kalahari rainfall gradient. *Ecosystems* **20**, 975–988 (2017).
10. Rudgers, J. A. *et al.* Climate sensitivity functions and net primary production: A framework for incorporating climate mean and variability. *Ecology* **99**, 576–582 (2018).

11. D'Odorico, P. *et al.* Positive feedback between microclimate and shrub encroachment in the northern Chihuahuan desert. *Ecosphere* **1**, 1–11 (2010).
12. Ratajczak, Z., Nippert, J. B., Hartman, J. C. & Ocheltree, T. W. Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. *Ecosphere* **2**(11), 121, <https://doi.org/10.1890/ES11-00212.1> (2011).
13. Thompson, J. A., Zinnert, J. C. & Young, D. R. Immediate effects of microclimate modification enhance native shrub encroachment. *Ecosphere* **8**, 2–e01687, <https://doi.org/10.1002/ecs2.1687> (2017).
14. Thomas, A. D. *et al.* The influence of trees, shrubs, and grasses on microclimate, soil carbon, nitrogen, and CO₂ efflux: Potential implication of shrub encroachment for the Kalahari rangelands. *Land Degrad. Dev.* **29**, 1306–1316, <https://doi.org/10.1002/ldr.2918> (2018).
15. Medeiros, J. S. & Pockman, W. T. Drought increases freezing tolerance of both leaves and xylem of *Larrea tridentata*. *Plant Cell Environ.* **34**, 43–51 (2011).
16. Pockman, W. T. & Sperry, J. S. Freezing-induced xylem cavitation and northern limit of *Larrea tridentata*. *Oecologia* **109**, 19–27 (1997).
17. Körner, C. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* **115**, 445–459 (1998).
18. Archer, S., Schimel, D. S. & Holland, E. A. Mechanisms of shrubland expansion: land use, climate or CO₂? *Clim. Chang.* **29**, 91–99 (1995).
19. Bühlmann, T., Hiltbrunner, E. & Körner, C. *Alnus viridis* expansion contributes to excess reactive nitrogen release, reduces biodiversity and constrains forest succession in the Alps. *Alp. Bot.* **124**, 187–191 (2014).
20. Sedghi, N., Adams, E. C. & Day, F. P. Carbon input and accumulation in freshwater to brackish marshes on the barrier islands of Virginia, USA. *Wetlands* **37**, 729–739 (2017).
21. Hayden, B. P., Santos, M. C. F. V., Shao, G. & Kochel, R. C. Geomorphological controls on coastal vegetation at the Virginia Coast Reserve. *Geomorphology* **12**, 283–300 (1995).
22. Battaglia, L. L., Denslow, J. S. & Hargis, T. G. Does woody species establishment alter herbaceous community composition of freshwater floating marshes? *J. Coast. Res.* **23**, 1580–1587 (2007).
23. Young, D. R. *et al.* Cross-scale patterns in shrub thicket dynamics in the Virginia barrier complex. *Ecosystems* **10**, 854–863 (2007).
24. Feagin, R. A. *et al.* Going with the flow or against the grain? The promise of vegetation for protecting beaches, dunes, and barrier islands from erosion. *Front. Ecol. Environ.* **13**, 203–201 (2015).
25. Zinnert, J. C. *et al.* Spatial-temporal dynamics in barrier island upland vegetation: the overlooked coastal landscape. *Ecosystems* **19**, 685–697 (2016).
26. Zinnert, J. C., Stallins, J. A., Brantley, S. T. & Young, D. R. Crossing scales: complexity of barrier island processes for predicting future change. *Bioscience* **67**, 39–52 (2017).
27. Ehrenfeld, J. G. Dynamics and processes of barrier island vegetation. *Aquat. Sci.* **2**, 437–480 (1990).
28. Fenster, M. S. & Hayden, B. P. Ecotone displacement trends on a highly dynamic barrier island: Hog Island. *Virginia. Estuar. Coast.* **30**, 978–988 (2007).
29. Young, D. R., Brantley, S. T., Zinnert, J. C. & Vick, J. K. Landscape position and habitat polygons in a dynamic coastal environment. *Ecosphere* **2**(6), art71 (2011).
30. Woods, N. N. *et al.* Interaction between seed dispersal and environmental filtering affects woody encroachment patterns in coastal grassland. *Ecosphere* **10**(7), e02818 (2019).
31. Aguilar, C., Zinnert, J. C., Polo, M. J. & Young, D. R. NDVI as an indication for changes in water availability to woody vegetation. *Ecol. Indic.* **23**, 290–300 (2012).
32. Masterson, J. P. *et al.* Effects of sea-level rise on barrier island groundwater system dynamics – ecohydrological implication. *Ecolhydrology* **7**, 1064–1071 (2014).
33. Zinnert, J. C. *et al.* Connectivity in coastal systems: Barrier island vegetation influences upland migration in a changing climate. *Glob. Chang. Biol.* **25**, 2419–2430 (2019).
34. Brantley, S. T. & Young, D. R. Shifts in litterfall and dominant nitrogen sources after expansion of shrub thickets. *Oecologia* **155**, 337–345 (2008).
35. Brantley, S. T. & Young, D. R. Linking light attenuation, sunflecks, and canopy architecture in mesic shrub thickets. *Plant Ecol.* **206**, 225–236 (2010).
36. Bissett, S. N., Zinnert, J. C. & Young, D. R. Woody expansion facilitates liana expansion and affects physical structure in temperate coastal communities. *Ecosphere* **7**(6), e01383, <https://doi.org/10.1002/ecs2.1383> (2016).
37. Shiflett, S. A., Zinnert, J. C. & Young, D. R. Coordination of leaf N, anatomy, photosynthetic capacity, and hydraulics enhances evergreen expansive potential. *Trees* **28**, 1635–1644 (2014).
38. Adair, E. C., Hooper, D. U., Paquette, A. & Hungate, B. A. Ecosystem context illuminates conflicting roles of plant diversity in carbon storage. *Ecol. Lett.* **21**, 1604–1619 (2018).
39. Liu, X. *et al.* Tree species richness increases ecosystem carbon storage in subtropical forests. *Proc. R. Soc. Lond.* **285**, 20181240 (2018).
40. Guo, Y. *et al.* Increasing water availability and facilitation weaken biodiversity–biomass relationships in shrublands. *Ecology* **100**(3), e02624, <https://doi.org/10.1002/ecs2.2624> (2019).
41. He, Y., D'Odorico, P. & De Wekker, S. F. J. The role of vegetation–microclimate feedback in promoting shrub encroachment in the northern Chihuahuan desert. *Glob. Chang. Biol.* **21**, 2141–2154 (2015).
42. von Arx, G., Pannatier, E. G., Thimonier, A. & Rebetez, M. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *J. Ecol.* **101**, 1201–1213 (2013).
43. Gremer, J. R. *et al.* Increasing temperature seasonality may overwhelm shifts in soil moisture to favor shrub over grass dominance in Colorado Plateau drylands. *Oecologia* **188**, 1195–1207 (2018).
44. Moreno-de las Herreras, M., Diaz-Sierra, R., Turnbull, L. & Wainwright, J. Assessing vegetation structure and ANPP dynamics in grassland-shrubland Chihuahuan ecotone using NDVI-rainfall relationships. *Biogeosciences* **12**, 2907–2925 (2015).
45. Knapp, A. K., Ciais, P. & Smith, M. D. Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. *New Phytol.* **214**, 41–47 (2016).
46. Petrie, M. D. *et al.* Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. *Glob. Chang. Biol.* **24**, 1935–1951 (2018).
47. Shao, G., Shugart, H. H. & Young, D. R. Simulation of transpiration sensitivity to environmental changes for shrub (*Myrica cerifera*) thickets on a Virginia barrier island. *Ecol. Model.* **78**, 235–248 (1995).
48. Young, D. R. Photosynthetic characteristics and potential moisture stress for the actinorhizal shrub, *Myrica cerifera* (Myricaceae), on a Virginia barrier island. *Am. J. Bot.*, 2–7. (1992).
49. Badano, E. I. *et al.* Facilitation by nurse plants contributes to vegetation recovery in human-disturbed desert ecosystems. *J. Plant Ecol.* **9**, 485–497 (2016).
50. Shackelford, N., Renton, M., Perring, M. P., Brooks, K. & Hobbs, R. J. Biodiversity change in heathland and its relationship with shifting local fire regimes and native species expansion. *J. Plant Ecol.* **8**, 17–29 (2015).
51. Zhou, L. *et al.* Ecological consequences of shrub encroachment in the grasslands of northern China. *Landsc. Ecol.* **34**, 119–130 (2019).

52. Valencia, E. *et al.* Functional diversity enhances the resistance of ecosystem functionality to aridity in Mediterranean drylands. *New Phytol.* **206**, 660–671 (2015).
53. Ficken, C. D. & Wright, J. P. Nitrogen uptake and biomass resprouting show contrasting relationships with resource acquisitive and conservative plant traits. *J. Veg. Sci.* **30**, 65–74 (2019).
54. Zinnert, J. C., Shiflett, S. A., Vick, J. K. & Young, D. R. Woody vegetative cover dynamics in response to recent climate change on an Atlantic coast barrier island: a remote sensing approach. *Geocarto Int.* **26**, 595–612 (2011).
55. Sinclair, M. N., Woods, N. N. & Zinnert, J. C. Seasonal facilitative and competitive trade-offs between shrub seedlings and coastal grasses. *Ecosphere* **11**(1), e02995 (2020).
56. Daubenmire, R. F. A canopy-coverage method of vegetational analysis. *Northwest Sci.* **33**, 43–66 (1959).
57. Leuning, R., Kelliher, F. M., Depury, D. G. G. & Schulze, E. D. Leaf nitrogen, photosynthesis, conductance and transpiration – scaling from leaves to canopies. *Plant Cell Environ.* **18**, 1183–1200 (1995).
58. Garnier, E. *et al.* Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85**, 2630–2637 (2004).
59. Brantley, S. T. Seasonal and spatial variation in leaf area index, litter production and light levels in *Myrica cerifera* shrub thickets across a barrier island chronosequence. Masters thesis, Department of Biology, Virginia Commonwealth University, Richmond, VA. (2005).
60. Seekell, D. A., Carpenter, S. R., Cline, T. J. & Pace, M. L. Conditional heteroskedasticity forecasts regime shift in a whole ecosystem experiment. *Ecosystems* **15**, 741–747 (2012).
61. USACE-TEC and JALBTCX Hyperspectral imagery for Hog Island, VA, 2013 ver 7. Environmental Data Initiative. <https://doi.org/10.6073/pasta/6a5cc305e93c2baf9283facee688c504>. Accessed 2020-03-31. (2018).

Acknowledgements

This work was supported by the National Science Foundation Long-Term Ecological Research grants DEB-1237733 and DEB-1832221 to JC Zinnert. Thank you to The Nature Conservancy and the Virginia Coast Reserve for site access and support. Thanks to Natasha Woods, Joseph Brown, Michael Sinclair, Eddie Long, and Philip Austin Tuley for field support and assistance in data collection.

Author contributions

L.K.W. assisted with design of experiment, performed experiments, analyzed data, and wrote the manuscript. S.H. analyzed data and assisted with writing. J.C.Z. conceived and designed the experiment and assisted with data analysis and writing. All authors reviewed the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41598-020-65161-3>.

Correspondence and requests for materials should be addressed to J.C.Z.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2020