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Interaction of seed dispersal and environmental filtering affects woody encroachment patterns in coastal grassland

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Abstract. Encroachment of woody plants into grasslands has occurred worldwide and includes coastal ecosystems. This conversion process is mediated by seed dispersal patterns, environmental filtering, and biotic interactions. As spatiotemporally heterogeneous, harsh environments, barrier islands present a unique set of challenges for dispersal and establishment. Environmental conditions act as filters on dispersed seeds, thereby influencing encroachment and distribution patterns. Seldom have patterns of propagule dispersal been considered in the context of woody encroachment. We quantified dispersal and post-dispersal processes of an encroaching woody population of *Morella cerifera* relative to directional rate of encroachment and observed distribution patterns on an Atlantic coastal barrier island with strong environmental filtering. We analyzed historic foredune elevation as a proxy for reduced interior environmental stress. The dispersal kernel was leptokurtic, a common characteristic of expanding populations, but rate of encroachment has slowed since 2005. Expansion pattern was related to foredune elevation, which limits encroachment below a threshold elevation. This difference between dispersal kernel behavior and encroachment rate is due to limited availability of suitable habitat for *Morella* and temporal variability in chlorides during the time of germination. Our results demonstrate that processes mediating seeds and seedling success must be accounted for to better understand establishment patterns of encroaching woody plants.

Key words: biogeomorphic; biotic interactions; environmental filtering; post-dispersal; shrub expansion.

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INTRODUCTION

Woody encroachment into grassland communities has occurred on nearly every continent throughout the Americas, Australia, and Africa, within the past 150 yr (Hagenah et al. 2009, Brantley and Young 2010, D'Odorico et al. 2012, Anadón et al. 2014). Mechanisms of woody encroachment are multi-faceted and can include factors that operate at global (i.e., climate warming), regional (i.e., rainfall, CO_2, and temperature), or landscape scale, as well as shifts in disturbance regimes (i.e., fire frequency, introduction or removal of grazing and dispersing animals), or intrinsic properties of the system (Van Auken 2000, Knapp et al. 2008, D'Odorico et al. 2012, Munson et al. 2016). Woody encroachment may be favored when constraints for woody species growth are reduced, which vary by ecosystem (D'Odorico et al. 2012, Archer et al. 2017). Seldom has propagule dispersal been considered when investigating woody encroachment. Propagule expansion can occur independently or in combination with other drivers resulting in a change of species distribution across a landscape (McConkey et al. 2012). We examined seed dispersal of an encroaching woody species into a coastal environment where it is unclear if woody species encroachment is facilitated by seed dispersal and if environmental heterogeneity limits establishment.

Woody encroachment in coastal systems is unique as vegetative communities are closely coupled to both atmospheric and oceanic drivers (Arkema et al. 2013). Along the Mid-Atlantic Coast, woody encroachment has occurred on barrier islands that are losing island area due to sea-level rise (Young et al. 2007, Zinnert et al. 2016). Over the last 30 yr, Virginia barrier islands have experienced dramatic shifts in plant species dominance, with over 40% of land cover changing from grassland to shrub thicket on most islands (Young et al. 2007, Zinnert et al. 2016; Fig. 1). This abrupt shift in species composition has been attributed to climate warming and sustained microenvironmental modification by the expanding species, *Morella cerifera* L. (Myricaceae; Zinnert et al. 2011, D'Odorico et al. 2012, Thompson et al. 2017, Huang et al. 2018), and may affect sediment mobility as islands respond to sea level (J. C. Zinnert, et al. *unpublished manuscript*; Zinnert et al. 2017). Understanding dispersal and post-dispersal establishment is essential for predicting future encroachment in this rapidly changing landscape where islands are disconnected from the mainland and one another.

A series of drivers affect plant community dynamics, including seed dispersal and post-dispersal processes (Lambers et al. 2008). Seed arrival is the first important ecological step when considering expanding populations (Kot et al. 1996, Turchin 1998, Dennis et al. 2007, Schupp et al. 2010, Prather et al. 2017). In coastal barrier systems, dispersal is limited by geographic isolation, making specialized dispersal mechanisms particularly important in shaping communities (Zinnert et al. 2017). Seed arrives to barrier islands through wind, ocean, and birds, with birds dispersing most woody species to barrier islands (Ehrenfeld 1990, Shiflett and Young 2010). For bird-dispersed seeds, presence of woody vegetation provides perches, increasing seed rain into the system (Joy and Young 2002, Prather et al. 2017). Recent studies focusing on long-distance avian dispersal show that propagules may disperse hundreds of kilometers from source populations (Nathan 2006, Viana et al. 2016). In this study, we quantify dispersal in a spatially disconnected system, where long-distance events contribute to woody encroachment. As islands become reduced in size, inter-island distance is increasing (Zinnert et al. 2016, Deaton et al. 2017).

Post-dispersal processes influence the fate of the dispersed seed. The post-dispersal process includes abiotic heterogeneity (e.g., soil salinity, soil moisture) and biotic interactions (e.g., competition, facilitation). Post-dispersal processes may contribute to the expansion or reduction of species through strongly influencing seed survival, seedling establishment, and resulting distribution patterns of plants (Wang et al. 2002, Amodeo et al. 2017). A broad spatial distribution of propagules increases the chance that woody species will arrive in locations optimal for their establishment. Species that arrive at a particular location must have suitable physiological traits to survive local environmental conditions (Tilman and Lehman 2001). Species arriving in systems with high environmental heterogeneity, such as are present in coastal ecosystems, may lack necessary traits to overcome a given stress. In addition, seed recruitment may be low in communities with strong environmental filters that may include heterogeneous resources, frequent disturbances, or limited perches for avian long-distance dispersal (Sales et al. 2013, Prather et al. 2017). In coastal systems, environmental filtering is based on position relative to shoreline, elevation above the freshwater lens, and spatial heterogeneity of salinity due to storm overwash (Young et al. 2011).

Overwash occurs when foredunes are destroyed resulting in salt intrusion to inland communities, which reduces germination of salt intolerant species (Middleton 2016). Foredunes may offer protection to interior communities, depending on variations in elevation and length (Zarnetske et al. 2015, Zinnert et al. 2017). As a result, communities with high-elevation foredunes may experience less salt intrusion and less

Fig. 1. Shrub expansion on the north end of Hog Island, Virginia, in 2013. Expansion occurs into low-lying elevation swales and has occurred at an unprecedented rate across the landscape. Photograph credit: John Porter.

stress. *Morella cerifera* occupies low-elevation swales at a minimum distance from the shoreline (Young et al. 2011). Biogeomorphic interactions between topography and vegetation are important drivers in barrier islands (Duran Vinent and Moore 2015, Goldstein et al. 2017, Zinnert et al. 2017, Stallins and Corenblit 2018) and may affect suitability of germination and seedling growth based on access and amount of freshwater (Young et al. 2011).

Post-dispersal processes are important in structuring spatial composition of the resulting community. Successful establishment of woody plants can lead to an alteration of competitive relationships in favor of woody plants over grasses as they surpass the grass canopy. Established plants may ameliorate microenvironmental conditions (e.g., reduced soil temperature, increased soil moisture and nutrients; Stinca et al. 2015, Barron-Gafford et al. 2017). Thus, encroaching species may have a favorable impact on their own establishment through these microenvironmental modifications (D'Odorico et al. 2012, Huang et al. 2018). In coastal ecosystems, encroaching shrubs may reduce wind effects including sea spray, provide perches to facilitate bird dispersal of seeds, and moderate local microclimate including temperatures, humidity, and light (Thompson et al. 2017). Expansion occurs in plant communities because of the reduction in environmental constraint, which allows a species to proliferate at an increased rate (Archer et al. 2017).

To bridge a knowledge gap between seed dispersal and environmental heterogeneity on woody encroachment in coastal grasslands, we quantify dispersal distribution of *Morella cerifera* and relate it to the rate of encroachment and observed distribution patterns on an Atlantic coastal barrier island with strong environmental filtering. As *Morella* is known to survive in areas with >1 m tall dunes (Miller et al. 2008), we include analysis of foredune elevation over two time frames as a proxy for environmental filtering (Young et al. 2011). We hypothesized that the pattern and distribution of seed dispersal of *Morella* would be like that of an expanding population (i.e., leptokurtic), and that encroachment is related to foredune development. We conducted an analysis that would be informative of whether encroachment rate was dispersal limited or establishment limited by environmental conditions.

METHODS

Study site and system

Among systems that have experienced woody encroachment are the barrier islands of the Virginia Coast Reserve (VCR), a Long Term Ecological Research site owned by The Nature Conservancy (Hayden et al. 1991) and left in a natural state. This offers an opportunity to examine woody encroachment in the absence of introductions or human-altered dispersal patterns. Warming temperatures, especially in winter, have been identified as a driver of woody expansion on the VCR in recent decades (Huang et al. 2018). However, endogenic processes, such as seed dispersal, have not been studied in this system. The dominant shrub of the VCR is *Morella cerifera* L. (Myricaceae), an evergreen shrub that occurs along the Atlantic coast of North America from New Jersey to Florida and along the Gulf of Mexico. Adults can reach up to 6 m in height and often coalesce into monospecific thickets (Young et al. 1994, Silberhorn 1999). Flowers bloom April through June, and drupes (3–5 mm diameter), containing one seed (2–3 mm in diameter) ripen in the following autumn, August through November (Young and Young 1992). Upwards of 10,000 fruits may be produced by an individual shrub each year (Kwit et al. 2004). Birds consume the berries and disperse seeds by defecation (Levey et al. 2005). A variety of birds forage *Morella* berries, primarily the Yellow-rumped myrtle warbler (*Dendroica coronata coronata*) which overwinter in the region (Borgmann et al. 2004). A congener, *M. pensylvanica* L., overlaps in range with *M. cerifera* from New Jersey to North Carolina (Young and Young 1992, Silberhorn 1999). Both species occur throughout the VCR and will be collectively referred to as *Morella* (Shiflett and Young 2010). The distribution of *Morella* is constrained to a narrow range of elevation within grassy swale on barrier islands (Young et al. 2011), and this area was the focus of our study (Fig. 2).

Field research was conducted between 2012 and 2013 on Hog Island, Virginia (37°40′ N, 75°40′ W), a barrier island that is part of the VCR. The Island is 11 km long, and the width ranges from 2.5 km at the widest point to 0.5 km at the most narrow (Fig. 2). The island has a southwest–northeast orientation and lies 8 km from the mainland of the Eastern Shore peninsula of Virginia. The eastern shoreline of the island is in direct interface with the Atlantic Ocean, whereas the western edge of the upland transitions into tidal saltmarsh. Despite land loss on other Virginia barrier islands, Hog Island has remained relatively stable over the last >30 yr (Zinnert et al. 2016).

Seed dispersal, grass cover, and soil salinity

In August of 2012, transects (*n* = 7) oriented south from the edge of the southernmost thicket were established in low-lying grassy swale with plots ~50 m apart up to 300 m (Fig. 2). This area was fronted by dunes >2 m tall. At each plot, seed traps were deployed. Due to landscape heterogeneity and irregularity of the upland–marsh interface (Fig. 2), positions along transects that would have been in saltmarsh or dune were not included because *Morella* is confined to upland portions of the island (Hayden et al. 1991, Young et al. 1994, 2011). Thus, not all plots along transects were exactly 50 m apart. Distinction between dune, marsh, and grassy swale was determined based on known and distinct species composition within each community type (McCaffery and Dueser 1990*a*, *b*).

Seed traps were constructed of a screen mesh attached to a square wooden frame (0.46 × 0.46 m), each covering an area of 0.21 m^2. They were placed at ground level and staked in place with a 0.3 m long galvanized spike that was flush with the ground surface. This design was developed so that traps could collect at ground level near the shrub edge as fruiting *Morella* branches often grow close to ground, and to minimize disturbance by high winds. Traps were sampled in fall 2012 and fall 2013. Some traps were disturbed by flooding or other perturbations and were excluded from analysis.

Adjacent to each plot, percent cover of *Morella* and grasses (all graminoids, including sedges) were surveyed using a 1 × 1 m quadrat were measured in spring 2013. From the center of each sampling site, soil samples were collected to assess salinity in March and April of 2013, when *Morella* seeds germinate in this system. Two time points were chosen to assess the spatial variation

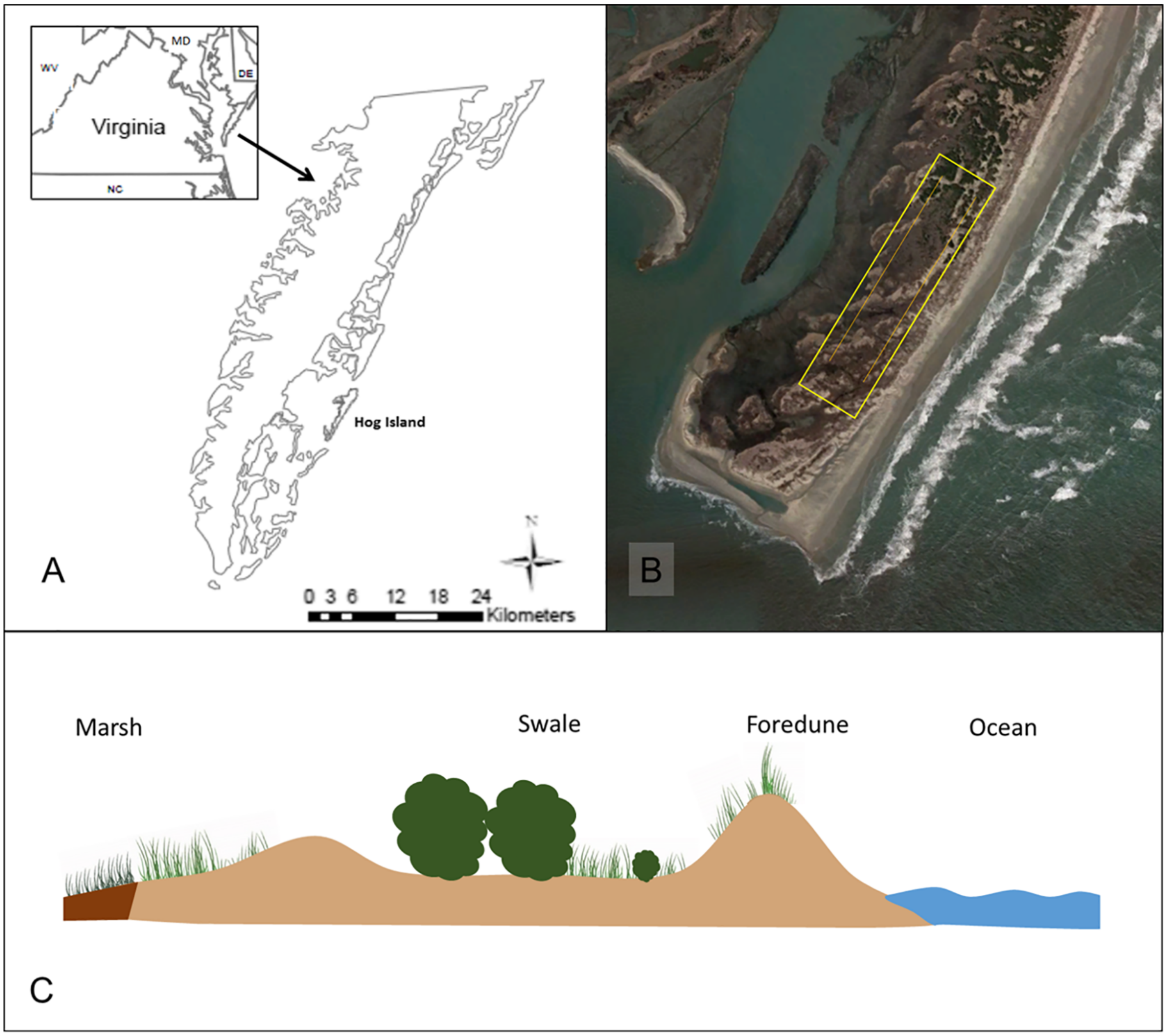

Fig. 2. Study site of Hog Island, Virginia (A). South end of Hog Island with yellow box delineating the approximate location of the encroachment zone; two transects are shown in gold. Plots occurred along transects ~50 m apart beginning at thicket edge (B). Cross-shore transect of a barrier island. *Morella* is found in the low-lying elevation swales (C).

in soil salinity within the swale during the time of germination. Salinity of soil samples was measured using the water extraction method for total chlorides in dry soil (Young et al. 1994).

Woody establishment and foredune elevation

Analysis of directionality and patterns of woody encroachment on Hog Island incorporated shapefiles derived from land cover classifications by Zinnert et al. (2011) of years: 1984, 1988, 1993, 1998, and 2010. Additionally, land cover for 2005 and 2015 was classified using similar methods to link to foredune elevations (below) and to allow for inclusion of the most recent interval, between 2010 and 2015. Landsat TM7 images from 22 August 2005 and 1 July 2015 were obtained from the USGS Earth Explorer data portal. These dates were chosen because they coincided with the summer growing season, timing of imagery used by Zinnert et al. (2011), and minimal cloud cover among available dates. Each image was radiometrically corrected by Quick Atmospheric Correction (QUAC). The Normalized Difference Vegetation

Index (NDVI) was derived from the image in ENVI 10.2 (Exelis, Herndon, Virginia, USA) and used to estimate woody cover in 2005 and 2015 based on the difference between grassland and shrubland NDVI (Zinnert et al. 2016). The 2015 data were field confirmed with GPS at the front of woody encroachment. A shapefile of woody cover was exported to ArcGIS 10 (ESRI, Redlands, California, USA) in which direction and rate of thicket encroachment were estimated in m/yr using the simple linear measurement tool.

We used records of maximum foredune elevation (m; NAVD88) for Hog Island derived from Lidar in 1998 and 2005 (Oster and Moore 2009). Foredune elevation was determined by selecting the seaward-most dune crest. The berm was used for locations with no dune crest above 1.5 m. Using ArcGIS 10 (ESRI), the shapefile for woody cover in 1998 and 2005 was used to manually subset the foredune elevation dataset into locations with and without adjacent shrubs.

ANALYSES

To provide a density measure for seed dispersal with respect to distance from thicket edge for dispersal kernel analysis, density of dispersed seeds at each plot was calculated. This was done separately for each year, 2012 and 2013. Non-linear regressions were fit to the dispersal kernel of *Morella* throughout the encroachment zone as seed density (no. of seeds/m^2) ~distance from thicket edge (0–300 m; Turchin 1998, Zar 2010). Regressions were performed with the nlsLM function in R (version 3.0.3; R Development Core Team 2013) and fit by Gaussian, exponential, and power functions as described by Turchin (1998). Model fits were evaluated by Akaike's information criterion for comparison (Burnham and Anderson 2002). The Gaussian model would indicate a mesokurtic distribution, whereas the exponential would indicate a leptokurtic distribution and the power a leptokurtic, extremely fat-tailed distribution.

Frequency histograms for foredune elevation with and without shrubs were compared using the Kolmogorov-Smirnov (KS) test (Zar 2010). Soil salinity was evaluated with a two-factor ANOVA to test interaction between distance from thicket edge and time samples were collected (March and April), and Pearson's correlations were used to determine relationships among field-measured variables. Chlorides and *Morella* cover were log-transformed to meet normality assumptions, but raw data are used in graphs.

RESULTS

Dispersal

A total of 3006 and 2613 seeds were collected during the winters of 2012 and 2013, respectively. For 2012, *Morella* seed dispersal was best fit by the exponential model followed by Gaussian and power models (Table 1), indicating a leptokurtic distribution (Fig. 3). However, the same analysis of the 2013 season yielded little difference between models with the power of the best fit followed closely by the Gaussian and exponential (Table 1; Fig. 3). Visual inspection of plots revealed a spike in dispersal at 200 m from the thicket edge in both years, more so in 2013 than 2012. Conducting the same analyses with dispersal values at the 200 m distance omitted yielded a

Table 1. Dispersal kernel model results from 2012 and 2013 with all data included and data at the 200 m peak omitted.

			All data				200 m omitted			
Year	Model	Equation	*a*	*b*	*c*	AIC	*a*	*b*	*c*	AIC
2012	Gaussian	$y = a^{*}e^{(-x^{*}b)}$	301.00	0.23000		729.46	301.00	0.22000		611.68
	Exponential	$y = (b^{*}(x^2)) - a$	-483.40^{***}	-0.00767^{*}		726.86	-481.40^{***}	-0.00786^{*}		609.26
	Power	$y = a^{*}(x^b) + c$	−6.20	0.83000	629^{***}	730.96	−6.50	0.84000	636^{**}	612.98
2013	Gaussian	$y = a^{*}e^{(-x^{*}b)}$	303.00^{*}	0.00076		716.11	375.50^{***}	0.00966		558.27
	Exponential	$y = (b^{*}(x^2) - a$	-295.00^{**}	−0.00079		716.12	-260.00^{***}	-0.00424^{*}		561.09
	Power	$y = a^{*}(x^b) + c$	−82.00	0.00004	343^{*}	715.95	−7.89	0.70000^{***}	360	561.21

Notes: AIC, Akaike's information criterion.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

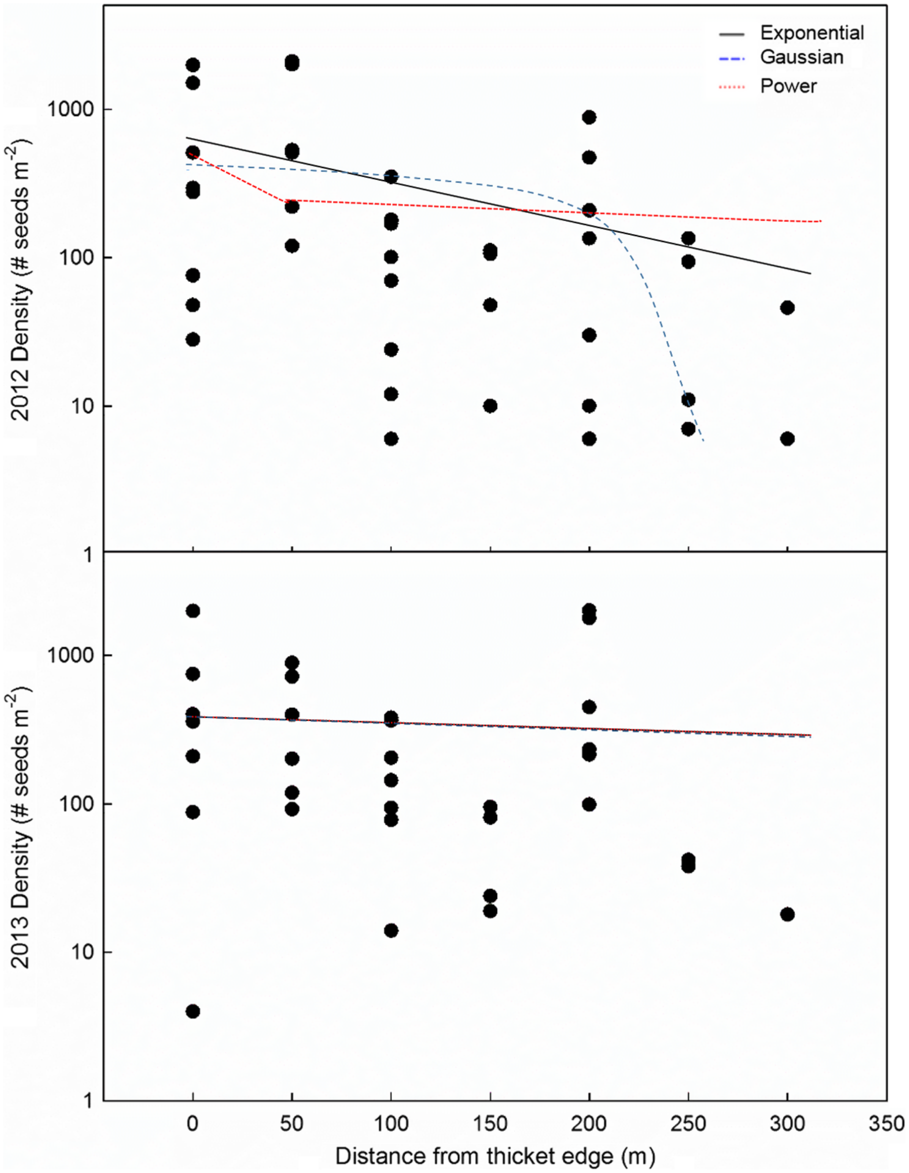

Fig. 3. *Morella* seed dispersal from thicket edge from the 2012–13 winter season. Model fits were exponential function in 2012 (Akaike's information criterion, AIC: 726.86) and the power model in 2013 (AIC: 715.95).

similar result for 2012, but in 2013, the exponential model fit best followed by the power and the Gaussian (Table 1). Thus, *Morella* seed dispersal was leptokurtic in both years.

Vegetation cover and soil salinity

Grass cover was highly variable throughout the encroachment zone (Fig. 4), and there was no correlation between grass and woody cover ($r = -0.17$, $P = 0.50$). The peak in dispersal at 200 m from the thicket edge coincided with a small spike in *Morella* cover (7 ± 11%) and grass cover (80 ± 14%; Fig. 4). The spike in seed dispersal at this distance was assumed due to established, freestanding *Morella* shrubs.

Soil chlorides in March (722 ± 214 μg Cl/g) were higher than in April (286 ± 212 μg Cl/g; $F = 45.32$, $P < 0.001$), and there was a significant difference in distance ($F = 67.55$, $P < 0.001$), with higher chlorides at 100 and 150 m from the

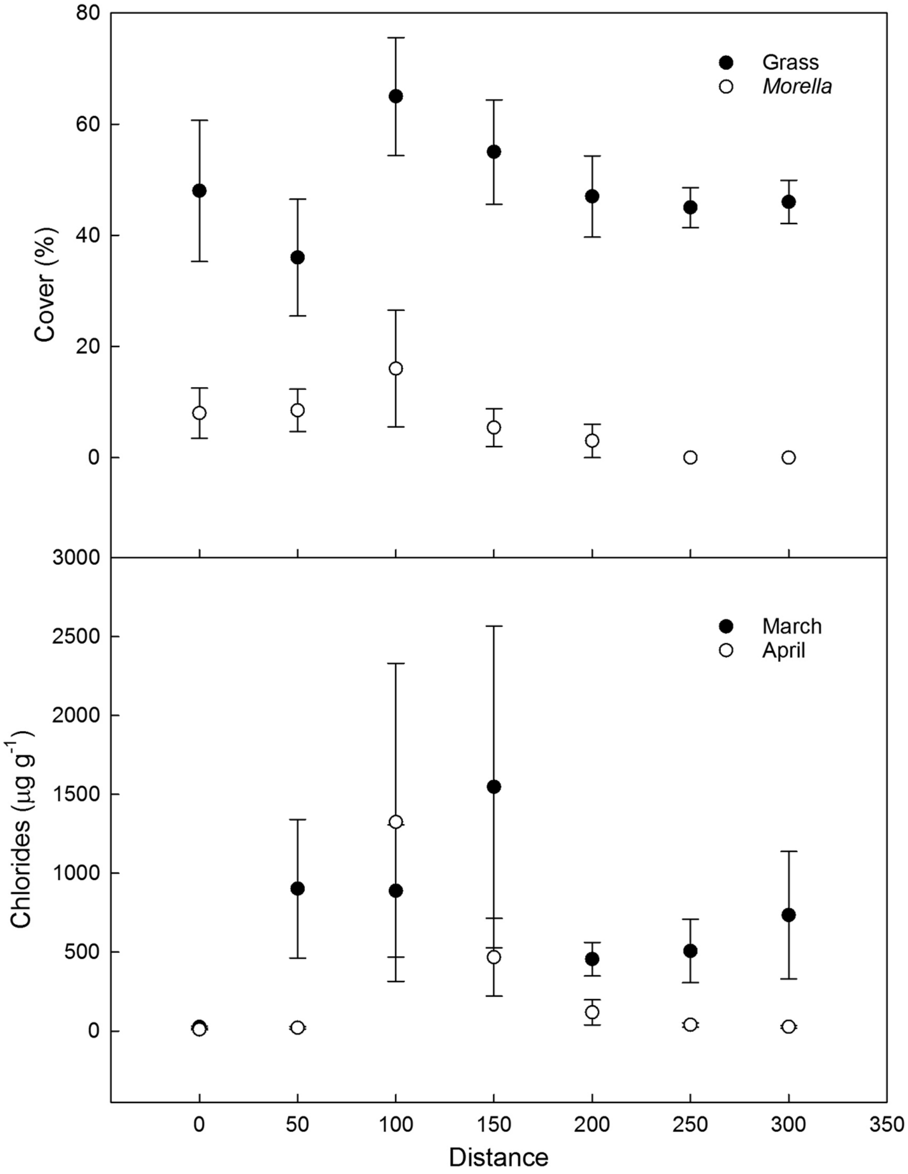

Fig. 4. Percent cover of *Morella* and grasses (top) and soil chlorides (µg/g dry soil) during March (middle) and April (bottom) of 2013.

thicket edge. There was no interaction between time and distance from thicket edge ($F = 16.53$, $P = 0.44$), and there were no correlations between vegetation cover and chlorides ($P > 0.20$).

Woody establishment and foredune elevation

From 1984 to 1993, woody cover expanded southward and parallel to the oceanside shoreline at a rate of nearly 100 m/yr (Table 2, Fig. 5). Between 1993 and 2005, this rate accelerated, covering as much as 300 m/yr. Since 2005, the rate has slowed to <100 m/yr. This indicates that woody expansion on Hog Island occurred rapidly, and is still underway, but has decelerated over the past decade. For both 1998 and 2005, no foredune sites with adjacent shrubs exist when the foredune is lower than 1.75 m, and only few sites have established shrubs with

Table 2. Distance and advancement rates of woody encroachment on Hog Island, Virginia, USA.

Interval	Distance (m)	Rate (m/yr)
1984–1988	150	37.5
1988–1993	474	94.9
1993–1998	1423	284.5
1998–2005	1801	300.1
2004–2010	629	104.9

foredunes of only 2 m (Fig. 6). However, foredunes not backed by shrubs span a range of elevations. For each year, a two-sample Kolmogorov-Smirnov test indicated that foredune elevations for shrub and no-shrub sites come from different distributions (1998: KS = 0.54, $P < 0.0001$; 2005: KS = 0.54, $P < 0.0001$).

Discussion

Our objectives were to investigate dispersal and post-dispersal processes that influence patterns of woody encroachment into barrier island grasslands. Specifically, we calculated seed dispersal kernels of the dominant encroaching shrub (*Morella*) from recent years and considered environmental filters that act on seeds post-dispersal, specifically vegetation cover and salinity. We quantified rate of woody encroachment over several decades and related that to foredune elevation. On Hog Island, direction of woody encroachment was parallel to the shoreline and related to foredune elevation (1.75 m). Dispersal kernels from late fall of 2012 and 2013 were leptokurtic, which is typical of an expanding population (Turchin 1998); however, recent decline in encroachment rate is due to saturation of suitable habitat (Young et al. 2011). Our results highlight the interaction between seed dispersal and environmental filtering post-dispersal processes that determine encroachment rates and influence the resulting establishment patterns that emerge (D'Odorico et al. 2012).

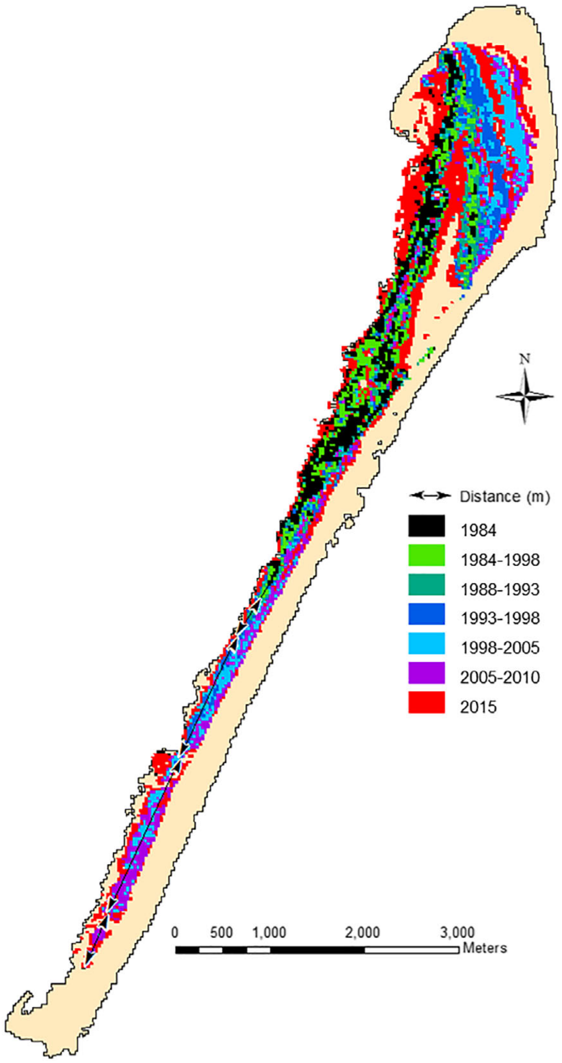

Fig. 5. Expansion of woody cover on Hog Island, Virginia, from 1984 to 2015.

Patterns that we observed agree with previous work in plant invasions and *Morella* seed dispersal (Nathan and Muller-landau 2000, Levey et al. 2008, Herrmann et al. 2016). In particular, establishment of individuals occurs at long distances ahead of an invasion front. Cain et al. (2000) defined long-distance dispersal (LDD) as dispersal events in which seeds are dispersed >100 m from the parent plant and discussed the importance of LDD for estimating and predicting invasion rates. Our results demonstrate that the establishment of fruiting *Morella* 200 m from the thicket edge indicates past LDD events have served to increase dispersal throughout the grassland and influence rate of woody encroachment. This may lead to a positive feedback with expansion and distribution as established *Morella* shrubs create a moderated microclimate to favor *Morella* seedling establishment, even in younger, freestanding shrubs (Thompson et al. 2017).

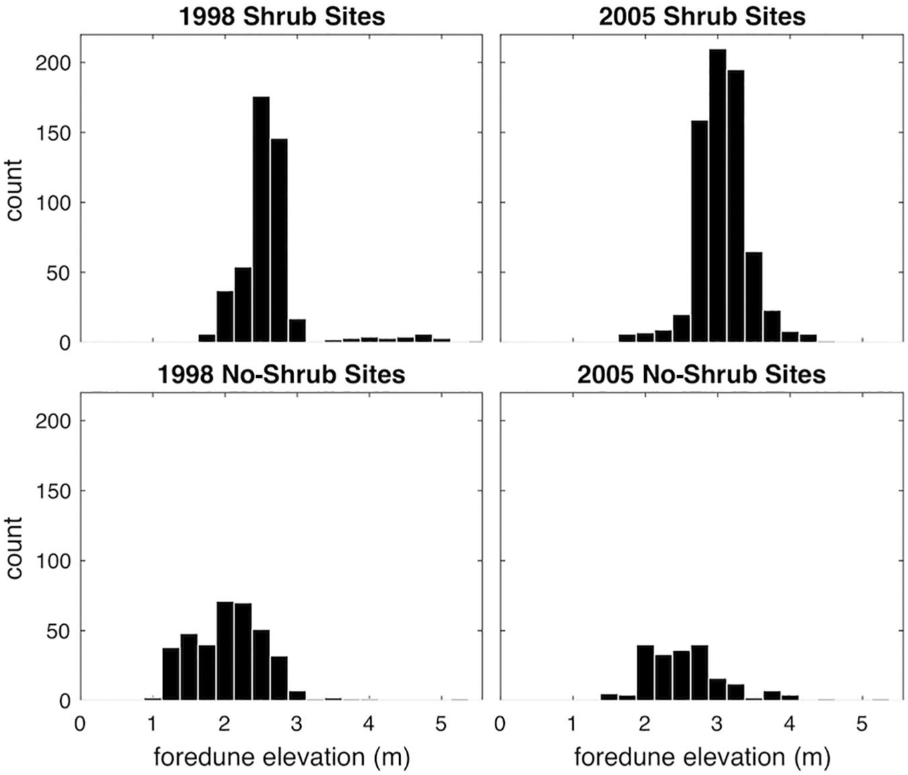

Fig. 6. Histogram of Foredune elevations (m; NAVD88) for sites with (top) and without (bottom) shrubs for 1998 (left) and 2005 (right).

In a heterogeneous environment, such as found on barrier islands, dispersal is particularly difficult to estimate due to the variable influence of plant characteristics and disperser traits and the added challenge of sampling the range of landscape features that are relevant to dispersal. Because of this, most dispersal studies often assume a homogenous landscape (Gosper et al. 2005), but heterogeneity of barrier islands has a strong influence on dispersal patterns. Landscape-scale characteristics such as vegetation patchiness and cover, topographic heterogeneity (which can lead to salinity variability), and fragmentation influence disperser behavior (Levey et al. 2008, Herrmann et al. 2016). Studies show that bird dispersal of *Morella* seeds is controlled by biotic interactions (Moss 1993, Shiflett and Young 2010). Since fruit ripening of *Morella* coincides with the migratory season, seed dispersal may be extensive (Mabey et al. 1993). Zinnert et al. (2011) found that *Morella* occupies only 46% of suitable habitat (based on elevation and distance to shoreline), suggesting that the heterogeneous landscape onto which seeds disperse may not be advantageous for germination or establishment (Menezes et al. 2017).

Once species successfully establish, they may create a range of stress gradients across a single habitat patch, potentially changing the effect from one of stress reduction to stress induction, with both competition and facilitation operating depending on spatiotemporal scale (Jurgens and Gaylord 2016, Dohn et al. 2017). The balance between competition and facilitation is complex and can shift the outcome of biotic interactions. Studies also show that facilitation (aboveground) and competition (belowground) can occur simultaneously and have a net positive interaction for the encroaching species (Maestre et al. 2001, 2003*a*, *b*). Woody seedlings can also respond to small-scale heterogeneity, and woody encroachment may be enhanced by grasses (Maestre et al. 2003*b*, Archer et al. 2017). At our barrier island study site, nearer the thicket edge, *Morella* cover is highest, displacing grasses (Thompson et al. 2017). However, with increased distance from the thicket edge, grass and *Morella* cover decreased, except for a peak at 200 m. At 200 m, an increase in *Morella* seeds and grass cover coincided with freestanding *Morella* which demonstrates the effects of habitat modification as described by Thompson et al. (2017). Our results did not show a correlation between grasses and woody cover, which suggests that the potential of facilitation of shrubs by grasses is complex with multiple factors. Overall, there is high variability in vegetation cover, and it is unknown if there is some minimum amount of grass cover necessary for *Morella* to establish which has been seen in other systems (Maestre et al. 2001, De Dios et al. 2014). In South African grasslands that have recently experienced shrub encroachment, grass cover and herbivory were found to influence shrub seed germination timing and seedling survival (Hagenah et al. 2009). For barrier islands, grass cover may ameliorate environmental stresses faced by germinating seeds and establishing seedlings, by shading or some other biotic interaction (De Dios et al. 2014), but little is known about the potential for facilitation of woody species by grasses in this system.

Our results highlight the importance of biogeomorphic controls on woody vegetation through absence of established shrubs in areas where fronting dunes are <1.75 m, an elevation higher than the 1 m limit observed by Miller et al. (2008). Although this does not account for potential of seedling establishment, we show that shrubs cannot reach full maturity below the threshold elevation of 1.75 m, indicating that foredune height is a limiting factor. Fresh groundwater availability, soil moisture, and soil salinity vary greatly with foredune elevation in the sandy soils of barrier islands (Hayden et al. 1995). Soil salinity, in particular, is a major determinant of plant community distribution patterns and varies spatiotemporally, often fluctuating outside of the tolerable range of *Morella* (>500 μg/g dry soil; Ehrenfeld 1990, Young et al. 1994). In early spring, when *Morella* seeds germinate, soil salinity was more temporally variable in areas where establishment was minimal (i.e., low woody cover) and often above the range of tolerance for *Morella*. Paudel and Battagilia (2013) and Tolliver et al. (1997) show that *Morella* is sensitive to higher salinities at the germination and seedling stages of development, respectively. If suitable habitat is unavailable due to high salinity or other environmental stressors, dispersal will be of little to no importance to encroachment rates. Seeds may not germinate nor seedlings establish in areas without sufficient foredune elevation to limit disturbance in the interior (Miller et al. 2008). However, if dunes are reduced from threshold elevation, encroachment will be inhibited.

Based on our multi-decadal analysis of woody encroachment, we found encroachment of *Morella* to be highly influenced by both dispersal and environmental filtering. We found a deceleration since 2004, with 2010–2015 exhibiting the slowest rate (<6 m/yr), much slower than the peak rate of 300 m/yr before 2005. This deceleration suggests that *Morella* encroachment was driven by dispersal prior to 2005 and may now be establishment limited through post-dispersal environmental filtering, potentially controlled by foredune elevation and soil salinity (Young et al. 2011).

The foredune is highly dynamic and may erode frequently due to changes in wind and wave patterns and storm surge. The increase in frequency and intensity of hurricanes, tropical storms and nor’easters experienced in the Mid-Atlantic region (Davis and Dolan 1993, LaRow et al. 2014) could be the reason for the decrease in woody encroachment and affect dune elevation. As a result, the soil salinity tolerance of *Morella* may have been reached. As the frequency of the number of named storms is expected to increase for the Mid-Atlantic region (LaRow et al. 2014), woody encroachment into grasslands may be adversely impacted.

Sea-level rise and shoreline retreat may also impact the woody encroachment rate, as favorable interior habitat and island area gets smaller. On the Virginia barrier islands, upland area has been reduced over time and *Morella* is expanding into maritime forest habitat (Bissett et al. 2016). The success of *Morella* could be due to advantages at the germination stage of development over tree species when salinity has increased (unpublished data). *Morella* expansion continues in stable portions of the island that are slower to erode, accounting for the increased encroachment as islands decline in size (Zinnert et al. 2019). *Morella* is expanding into grassland and forested habitat in coastal areas throughout the

Mid-Atlantic and Gulf coast regions with undetermined consequences for species richness and coastal stability.

Conclusions

We demonstrate that processes mediating the success of seeds and seedlings must be accounted for to better understand the establishment patterns of encroaching woody plants. Seed dispersal patterns across the landscape were characteristic of invading species. Woody encroachment, whether by a native or an introduced species, may have principles common to other biological invasions. Although the dispersal kernel was indicative of an expanding population, rate of encroachment has slowed in recent years. In our system, strong environmental filtering controlled by dune growth to a threshold elevation (1.75 m) limits successful establishment and growth of *Morella* seeds, resulting in a patchy landscape. Our results show that encroachment rate over a particular period is related to both seed dispersal and post-dispersal processes. Most studies have not considered both biotic (i.e., dispersal, grass cover) and specific abiotic heterogeneity (i.e., soil salinity, foredune elevation) that influence establishment patterns.

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