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Roles of seed dispersal and environmental filters in establishment of the dominant shrubs: *Morella cerifera* and *M. pensylvanica*, on an Atlantic barrier island

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Roles of seed dispersal and environmental filters in establishment of the dominant shrubs: *Morella cerifera* and *M. pensylvanica*, on an Atlantic barrier island

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

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Abstract

ROLES OF SEED DISPERSAL AND ENVIRONMENTAL FILTERS IN ESTABLISHMENT OF THE DOMINANT SHRUBS: MORELLA CERIFERA AND M. PENSYLVANICA, ON AN ATLANTIC BARRIER ISLAND

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A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science at Virginia Commonwealth University.

Virginia Commonwealth University, 2014

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Patterns of the expansion of woody cover into grasslands on barrier islands of the Virginia coast were investigated. Seed dispersal of the dominant shrub *Morella* spp., was sampled deploying seed traps (n = 82) throughout a landscape under shrub encroachment pressure on Hog Island, VA. Traps were placed underneath: fruiting *Morella*, non-fruiting *Morella*, co-occurring species (*Iva frutescens* and *Baccharis halimifolia*) and in grass land, (no shrub cover). Environmental filters that act upon dispersed seeds and subsequently determine establishment patterns were also investigated. Dispersal distribution throughout the encroachment zone was leptokurtic

and dispersal among cover types suggest co-occurring shrub species facilitate dispersal by functioning as bird perches. Interaction of biotic and abiotic factors mediate a complex process of establishment by influencing dispersal, germination and seedling survival to ultimately determine distribution patterns of woody plants in coastal environments.

Introduction and Background

Expansion of woody species into grasslands has been observed in many ecosystems including Atlantic coast barrier islands and attributed to a variety of factors such as shifts in fire regime, grazing, increase in atmospheric CO₂ and climate change, (Knapp et al. 2008). Conversion of grasslands to shrub communities is a successional process common to coastal environments (Young et al. 1995); however, expansion of shrub cover in recent decades has been attributed to processes other than autogenic succession (Knapp et al. 2008, Zinnert et al. 2011). Thus understanding biotic and abiotic factors that affect the patterns spread of woody species will aid in predicting ecosystem responses to global change.

On Virginia barrier islands, Landsat imagery analysis has shown a transition from grassland to woody cover over three decades (Zinnert et al. 2011). On Hog Island, VA woody cover increased from 7.7% of total upland area in 1984 to 30.8% in 2010, while 41% of grassland area was replaced by woody species during the same interval (Zinnert et al. 2011). The dominant woody species on Hog Island is the shrub *Morella cerifera*, also *Myrica cerifera* L. (Myricaceae) (Young et al. 1995). Underlying mechanisms that allow *M. cerifera* to encroach into grasslands and dominate plant communities of coastal environments are not fully understood. Thicket expansion was related to coinciding climate change (increased atmospheric CO₂, decreases in mean precipitation of the hydrologic year, and increased storm frequency) during the same period (Zinnert et al. 2011). Evaluation of change in shrub cover on Hog Island from Zinnert et al. (2011) and Google Earth imagery indicate an apparent directionality of thicket expansion on Hog Island. Grasslands immediately southward of established

thickets are 'under colonization pressure' and this area was identified as the shrub 'encroachment zone'.

Morella cerifera is an evergreen shrub that grows up to about 6 m tall, commonly referred to as southern bayberry or wax myrtle (Silberhorn 1999). It is most common in mesic environments of North America along the Atlantic coast from New Jersey to Florida and along the Gulf of Mexico (Silberhorn 1999). Flowers bloom in April through June and fruit ripen in the following autumn, August through November (Young and Young 1992). The fruit are drupes with a bluish-grey, waxy coating, each containing one seed (Silberhorn 1999) and are consumed by birds which, disperse the seeds by defecation (Levy et al. 2005). Seeds are typically 2-3 mm in diameter (Martin and Barkley 1961). More than 10,000 fruits may be produced by an individual shrub in one year (Kwit et al. 2004).

A congener of *M. cerifera*, *Morella pensylvanica* Loisel (Myricaceae), commonly called northern bayberry or simply, bayberry, has a more northerly distribution extending from maritime provinces in Canada south to North Carolina. The *Morella* congeners overlap in range from New Jersey to North Carolina (Young and Young 1992, Silberhorn 1999). The biology *Morella pensylvanica* is similar to that of *M. cerifera* with the few exceptions that it is deciduous, has slightly wider leaf blades, and larger seeds and fruit; seeds are typically 3-5 mm in diameter (Martin and Barkley 1961, Silberhorn 1999). Both species occur on Hog Island, VA and throughout the Virginia Coastal Reserve thus, this study includes both species and hereafter will be collectively referred to as *Morella* (Shiflett and Young 2010).

A variety of birds forage *Morella* fruit: Downy Woodpecker (*Picoides pubescens*), Red-bellied Woodpecker (*Melanerpes carolinus*), Carolina Chickadee (*Parus carolinensis*), Northern Cardinal (*Cardinalis cardinalis*), Rubycrowned Kinglet (*Regulus calendula*), Tufted Titmouse (*Baeolophus bicolor*), Pine Warbler (*Dendroica pinus*), Gray Catbird (*Dumetella carolinensis*) and White-eyed Vireo (*Vireo griseus*) and especially the Yellow-rumped Warbler (*Dendroica coronata*) (Borgmann et al. 2004). While seed dispersal by birds to and among barrier islands has been studied (Ehrenfeld 1990, Shiflett and Young 2010), seed dispersal within a barrier island landscape has received less attention. Seeds dispersed by birds that consume the fruit and defecate the seeds, as well as fruit that fall directly from shrubs will both contribute to seed dispersal patterns of *Morella* across the landscape.

Nathan and Muller-Landau (2000) classify the combined affects of agents that move seeds from their parent plant to a substrate as Phase I dispersal and any secondary movement of seeds thereafter as Phase II dispersal. The extent of the collective seed shadow of individuals of a plants population throughout the colonization front of *Morella* will determine the seed dispersion pattern which will serve as an initial template for the colonization process (Nathan and Muller-Landau 2000). Dispersal distributions of propagules of invading populations, in this case seeds of *Morella*, are typically leptokurtic (Turchin 1998, Kot et al. 1996). The behavior of the “tail” of propagule dispersal distribution is of particular importance to quantifying the rate of advancement of spreading populations (Turchin 1998). Propagules dispersed by a variety of vectors typically result in leptokurtic, ‘fat tailed’ distributions with long distance

dispersal events of particular importance to species invasion and range expansion (Nathan and Muller-Landau 2000).

Once seeds are dispersed, the microenvironmental conditions determine seed survivability, seedling establishment and distribution patterns (Nathan and Muller-Landau 2000). Barrier islands are spatio-temporally heterogeneous landscapes with soils varying in salinity, moisture, flood frequency and nutrient availability among others (Young et al. 1995). Two of the most important environmental factors that determine plant species distribution on barrier islands are soil salinity and moisture availability (Ehrenfeld 1990, Young et al. 1994). Soil chlorides collected from the rooting zone of *M. cerifera* shrubs were $< 500 \mu\text{g/g}$ with 88% $< 50 \mu\text{g/g}$ (Young et al. 1994). However, germination experiments showed that *M. cerifera* seeds germinate poorly in conditions of salinity above $10 \text{ g} \cdot \text{L}^{-1}$, and were totally inhibited at higher salinity (Young et al. 1994). Therefore, a second template that acts on establishment by determining seed germination and seedling survival are the abiotic factors of soil salinity and moisture present where seeds are dispersed.

This two-step process acts as a filter that influences the distribution patterns of *Morella* as invasion of grasslands occurs. The goals of my study were to quantify the spatial distribution and patterns of *Morella* seed dispersal and investigate environmental filters that determine invasion patterns of this shrub into grasslands on a coastal barrier island. I primarily focused on the extent and distribution of *Morella* seeds dispersed into a landscape of apparent colonization. I hypothesized that the spatial distribution of *Morella* seeds dispersed into a landscape under encroachment pressure will have leptokurtic qualities. My second objective was to evaluate the distribution of established

shrubs and seedlings in relation to microenvironmental conditions within the *Morella* encroachment zone. I hypothesized that the establishment pattern of *Morella* in a landscape under encroachment pressure will be a subset of areas determined by commonality to both characteristics of seed dispersal patterns and suitable soil conditions. Linking distribution patterns to underlying processes that influence dispersal and seedling establishment of *Morella* will provide insight to the invasion process of this and other woody plants into grasslands.

Methods

Field site

My study was conducted on Hog Island, VA (37° 40'N, 75° 40' W) of the Virginia Coastal Reserve (VCR), an LTER site managed by The Nature Conservancy. Hog 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. 1). The island has a Southwest – Northeast orientation and is 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 saltmarsh. The area currently under pressure of encroachment and colonization by *Morella* was within 1 km of the south end as of 2012 (Fig. 1). This study focused on this encroachment zone.

Study design

Seven, box-transects oriented parallel to the edge of the southern-most thicket, where placed 50 m apart, covered the encroachment zone, 300 m southward and 200

m wide (Figure 1). Transects were oriented approximately East-West, from the base of the primary dune, extending to the marsh-side of the island, thus transecting the island. The location of each transect in relation to the southern-most thicket allowed for sampling of seeds dispersed with respect to distance from thicket edge, from 0 m – 300 m away. At 50 m intervals along each transect, seed traps were deployed and samples were collected as described below. Due to heterogeneity of the landscape and irregularity of the shape of the upland-marsh interface, positions along transects that would extended into the saltmarsh were not included because sampling from the saltmarsh was not germane to the study as *Morella* is not associated with the saltmarsh and confined to the upland portion of the island (Hayden et al. 1991, Young et al. 1994). Thus, not all transects extended equal lengths across the island. There were 30 plots in all; transect 1 (0 m from thicket edge) n = 5, transect 2 (50 m) n = 5, transect 3 (100 m) n = 5, transect 4 (150 m) n = 4, transect 5 (200 m) n = 4, transect 6 (250 m) n = 4, transect 7 (300 m) n = 3.

Seed Dispersal

Seed traps (n = 82) were constructed of a screen mesh attached to a square wooden frame (0.46 x 0.46 m), each covering an area of 0.21 m² for a total sampling area of 17.22 m². They were placed at ground level and staked in place with a 0.3 m long galvanized spike. This design was developed so that traps could collect at ground level as fruiting *Morella* branches may grow close to the ground, and to minimize disturbance by high winds. At 50 m intervals along each transect seed traps were placed under 5 cover types as encountered: fruiting *Morella* (deployment scheme

explained below), non-fruiting *Morella* (n = 11), co-occurring shrub species: *Iva frutescens* (n = 11) and *Baccharis halimifolia* (n = 8), and no-cover (grassland where there was no shrub cover) (n = 9). For the cover types: non-fruiting *Morella*, *B. halimifolia*, *I. frutescens* and no-cover, a single trap was installed for each cover type depending on presence or absence per site.

At sites with fruiting *Morella*, several traps were installed and oriented so that continuous coverage extended from the edge of fruiting *Morella* cover to 1.37 m (3 traps) or 1.83 m (4 traps), per site conditions. The decision to place 3 or 4 traps was based on proximity of other cover types in order to avoid placing any traps under multiple cover types. These traps were placed so that the closest side of each box was: 0 m, 0.46 m, 0.91 m, and 1.37 m from the edge of fruiting shrub cover, effectively covering an immediate area 0.46 m wide and 1.37 or 1.83 m long that extended away from cover edge (see Figure 2). Traps placed under these conditions were used for estimation of the seed shadow of fruiting *Morella* and will be collectively referred to as the 'seed shadow' group. The seed shadow group was comprised of the following: 0 m - 'frt.morella.1' (n = 12), 0.46 m - 'frt.morella.2' (n=12), 0.91 m - 'frt.morella.3' (n = 11), 1.37 - 'frt.morella.4' (n= 7).

Trapped seeds were collected monthly, from August 2012 to March 2013 and identified as *Morella* spp. (Martin and Barkley 1961). Due to the overlap in seed size and a lack of other distinguishing characteristics between *Morella* congeners, seeds were simply identified as *Morella*.

Establishment patterns

Establishment patterns of *Morella* in relation to grasses was investigated by surveying percent cover throughout the encroachment zone using the same box-transects described above. Relationships between established *Morella* and soil conditions were investigated by comparing soil salinity with establishment patterns throughout the encroachment zone.

In May of 2013, a 1 m² square PVC frame was used to estimate percent cover. At the same 50 m intervals along the box transects described above, a plot was designated by disorienting myself (to avoid bias) and throwing a landscaping flag over my left or right shoulder (alternating from one plot to the next). From the point designated by the thrown flag, three more flags were placed 5 m away from the first, demarking a 5 x 5 m quadrat. The PVC frame was then used to distinguish each of the 25 cells (1 x 1 m each) of the quadrat. Percent cover of *Morella* and grasses (including any sedge or rush species) was recorded for each cell. Established *Morella* shrubs or seedlings were defined as individuals that had grown at least as high as adjacent vegetation. One soil sample was collected from near the center of each quadrat in March and April of 2013. Salinity of soil samples were measured using the water extraction method described in Young et al. (1994), for total chlorides in dry soil.

Analysis

Dispersal patterns

Due to the patchiness of shrub cover (*Morella*, *B. halimifolia* and *I. frutescens*) throughout the landscape, sampling of seed dispersal among cover types was not even among transects. Potential distance effects on seed dispersal among each cover type

was not evaluated because patchiness of those cover types lead to sampling that did not allow for an appropriate, meaningful analysis. However, for estimation of the dispersal kernel throughout the encroachment zone, density of dispersed seeds was calculated by pooling all cover types sampled and dividing the total number of seeds collected from each transect by the total trap area of the corresponding transect. This provided a measure of dispersal density with respect to distance from thicket edge for analysis of the dispersal kernel. To evaluate differences in dispersal among cover types the seed count of each trap was totaled for the season, and then grouped by associated cover type for comparison.

Non-linear regressions were used to fit dispersal kernels to *Morella* seed dispersal throughout the encroachment zone (Turchin 1998, Zar 2010). The response variable, density of seeds captured ($\# \text{ seeds/ m}^2$), was plotted on a log scale with respect to distance from thicket edge (0 – 300 m) along with non-linear regression lines (Turchin 1998, Zar 2010). Regressions were performed with the `nlsLM` function in R (R Core Development Team, version 3.0.2) and fit: Power, Exponential and Gaussian formulas as prescribed for evaluating dispersal tail behavior by Turchin (1998) (Table 1). The `AIC` function in R was used to apply Akaike's Information Criteria (AIC) to compare model fits (Burnham and Anderson 2002). The Gaussian model would indicate a mesokurtic distribution of dispersal whereas the Exponential a leptokurtic distribution and the Power, a leptokurtic and extremely 'fat-tailed' distribution.

Distribution of the seed shadow group was estimated by the same procedure for evaluating the dispersal tail throughout the encroachment zone. Density of seeds captured ($\# \text{ seeds/ m}^2$) with respect to distance from the center of traps from shrub

cover were used for this analysis (e.g. for traps that covered 0 – 0.46 m, 0.23 m was used as the distance value).

Differences of *Morella* seed dispersal among each of the five cover types sampled were analyzed by total number of seeds captured throughout the season by each trap. For this portion of the analysis, the closest and furthest traps of the seed shadow group were compared with the other cover types because they represent the extremes of the seed shadow group. The closest and furthest traps of the seed shadow group were treated as separate groups so that a total of six groups were compared: fruiting *Morella* closest (frt.morella.1) and farthest (frt.morella.4), non-fruiting *Morella* (non.frt.morella), *B. halimifolia* (bac), *I. frutescens* (iva) and no-cover (no.cover). One-way ANOVA and Tukey tests were performed to identify differences among groups (Zar 2010). Due to the large number of seeds in the group of traps closest of the seed shadow group (frt.morella.1), separate one-way ANOVA and Tukey tests were conducted that included only the farthest traps of the seed shadow group (frt.morella.4) for comparison with the other cover types in an attempt elucidate relationships among the farthest traps of the shadow group (frt.morella.4) and the four other groups: (non-fruiting *Morella* (non.frt.morella), *B. halimifolia* (bac), *I. frutescens* (iva) and no-cover (no.cover). Statistically significant differences were determined using an alpha level of 0.05.

Morella establishment patterns

Percent cover of each cover class was averaged for each quadrat surveyed. Simple linear regressions between chlorides and percent cover were used to determine if there was a direct relationship between salinity and established *Morella* or grasses.

Results

Dispersal throughout landscape

A total of $n = 4667$ *Morella* seeds were captured during the winter of 2012-13 (Table 2). The greatest proportions of seeds were captured at sites at 0 and 50 m from the thicket edge, 0.403 and 0.406, respectively. At distances 100 m and greater, proportions of seeds captured were less than or equal to 0.010 with the exception of the 200 m distance traps, where 0.098 of seeds were captured (Table 2).

The distribution of seeds dispersed throughout the encroachment zone declined from 0 to 150 m and peaked at 200 m (Figure 3). Among the non-linear regressions of the dispersal throughout the encroachment zone (Table 3), the Exponential model was the best fit kernel (AIC = 88.29), followed by the Gaussian (Δ AIC = 4.76) and the Power model (Δ AIC = 5.89) (Figure 4). The exponential model fit is indicative of a leptokurtic dispersal distribution (Turchin 1998).

Seed shadow group

Approximately half (0.503) of all seeds were captured within 0 – 0.46 m of fruiting *Morella*. Distances under fruiting *Morella* shrubs: 0.46 – 0.91 m, 0.91 – 1.37 m, and 1.37 – 1.83 m yielded proportions of: 0.176, 0.140, and 0.072, respectively. A histogram of the proportional distribution of the seed shadow group with the range of each distance

class specified for ease of visualization as the traps of this group were arranged such that sampling was continuous from 0 to 1.83 m from cover by fruiting *Morella* (Figure 5). Seed dispersal drops off rapidly between the first and second distance classes and may appear to extend further than the total range sampled (0 – 1.83 m) (Figure 5).

Among the results of the regression analyses of the seed shadow group, the kernel best fit was the Power formula (AIC = 50.74) (Table 4). This was followed by the Exponential (Δ AIC = 2.43) and both were better than the Gaussian model (Δ AIC = 9.06) (Figure 6). The best fit by the Power model indicates that seed dispersal in the immediate vicinity of fruiting *Morella* is strongly leptokurtic (Turchin 1998).

Dispersal among cover types

The proportion of seeds captured under non-fruiting *Morella* was 0.064. Seeds captured under co-occurring shrub species *B. halimifolia* and *I. frutescens* contributed proportions of 0.024 and 0.015 respectively, and traps placed under no-shrub-cover captured 0.006 of all seeds collected (Table 2).

A box plot of seeds captured among cover types revealed that mean and range of dispersal under fruiting *Morella* was much greater than all other cover types with little overlap between the range of dispersal under fruiting *Morella* and the other cover types (Figure 7). The ANOVA that included both the closest (frt.morella.1) and farthest (frt.morella.4) traps of the seed shadow group found significant differences ($F = 10.31$, $p < 0.001$) in seeds captured among cover types (Table 5). The corresponding Tukey test (Table 6) found that significant differences in dispersal occurred between the traps closest to fruiting *Morella* (frt.morella.1) and every other group (all $p < 0.001$), but no

differences were found between the other groups included in this test. Dispersal under fruiting *Morella* cover was much greater than under other cover types; however, it was of interest to determine whether there were differences in dispersal among the other cover types because dispersal among other cover types may influence dispersal patterns throughout the landscape.

The second ANOVA and Tukey tests that included the farthest traps of the seed shadow group (frt.morella.4) revealed differences with and among the other cover types (Table 7 and Table 8). A box-plot of these groups revealed that dispersal varied among these groups with the highest mean and range in the non-fruiting *Morella* group (non.frt.morella) and lowest mean in the no-cover group (no.cover) (Figure 8). The ANOVA conducted on these groups, summarized in Table 7, found significant differences among the groups (F: 5.605, $p = 0.00108$). The corresponding Tukey test is summarized in Table 8. Significant differences were found between the farthest traps of the seed shadow group (frt.morella.4) and: *B. halimifolia* (bac: $p = 0.035$), *I. frutescens* (iva: $p = 0.0030$), and no shrub cover (no.cover: $p = 0.002$), but no significant difference from the non-fruiting *Morella* group (non.frt.morella: $p = 0.312$). Dispersal under non-fruiting *Morella* was not different from dispersal at the farthest traps of the seed shadow group (frt.morella.4: $p = 0.313$) nor from dispersal under either of the co-occurring species sampled, *B. halimifolia* ($p = 0.678$) nor *I. frutescens* ($p = 0.1.89$). Dispersal under *B. halimifolia* and *I. frutescens* was not different ($p = 0.950$) from each other, nor was either group different from dispersal where there was no shrub cover ($p = 0.856$ and 0.997). Dispersal was lowest where there was no cover and was only significantly

different from farthest traps of the seed shadow group (frt.morella.4: $p = 0.002$), but not any other cover type.

Established *Morella* and Soil Conditions

From 0 to 150 m of the thicket edge, average *Morella* cover decreased, from 23.3% (SE \pm 17.11) down to < 1% (SE \pm 1.3) (Figure 9). However, at 200 m average cover of *Morella* was slightly higher (6.8%, SE \pm 10.82), but remained very low (< 1%) at greater distances (250 and 300 m) from the thicket edge. Grass cover was about 50 % (+/- 5%) for 0 – 150 m from the thicket edge, highest at 200m (79.5%, SE \pm 14.41) and lowest at 250 and 300 m away (38.9%, SE \pm 17.98 and 38.1% SE \pm 14.61, respectively) (Figure 9).

Most quadrats with *Morella* cover had soil chlorides below 500 $\mu\text{g/g}$ dry soil (Figure 10). However, a few quadrats near the thicket edge had chloride contents greater than expected in both months, March and April (Figure 10), suggesting that the spatial/ temporal variation in soil salinity may affect *Morella* shrubs differently throughout the life cycle. There was no direct relationship between soil salinity and established *Morella* in March ($r^2 = 0.004$, $p = 0.92$) and a weak, but significant relationship between soil salinity and established *Morella* in April ($r^2 = 0.69$, $p << 0.001$) (Figure 10). Neither was a direct relationship found between percent cover of grasses and soil salinity in March ($r^2 = 0.05$, $p = 0.23$), nor in April ($r^2 = 0.06$, $p = 0.20$) (Figure 10).

Discussion and Conclusions

Study objectives were to investigate the roles of *Morella* seed dispersal and environmental filters that influence establishment patterns as barrier island grasslands are converted to shrub thickets. A multi-step process of dispersal and environmental filtering determines expansion patterns of shrubs and the extent of thicket distribution. As I hypothesized, the spatial distribution of *Morella* propagules dispersed into a landscape under encroachment pressure had leptokurtic qualities. *Morella* seed dispersal throughout the encroachment zone was best fit to the exponential dispersal kernel. An exponential rate of decrease in density of propagules dispersed across a landscape is characteristic of a 'fat tailed' dispersal distribution and that of a spreading population (Turchin 1998, Kot et al. 1996). The leptokurtic distribution suggests that *Morella* cover will continue to expand on Hog Island provided the availability of suitable habitat. However, as the dispersal was a better fit to the Gaussian than the Power model, the distribution may not be strongly leptokurtic or the rate of spread may be slowing down. This may be due to a variety of factors, such as availability of suitable habitat on Hog Island. Zinnert et al. (2011) noted that only 46% of available habitat to *Morella* was occupied as of 2010. Granted, this estimate characterized suitable habitat available to *Morella* on Hog Island by using only the conditions of elevation and distance to shoreline. It does not take into account biotic or abiotic interactions that may influence *Morella* establishment patterns.

Leptokurtic distributions have a higher concentration either at the tails or about the mean (corresponding to the thicket edge in this case) than mesokurtic (synonymous with normal or Gaussian) distributions (Zar 2010). While an exponential model indicated a leptokurtic dispersal distribution, a model using a power formula would indicate

dispersal with stronger leptokurtic quality than an exponential whereas, a Gaussian model would indicate more mesokurtic distribution (Turchin 1998). By this reasoning, one might expect a rapidly expanding population with a variety of dispersal agents, as in the present case, to be fit more closely by the power model. However, the Gaussian model was the second best fit kernel which suggests the dispersal distribution of *Morella* propagules may not be strongly leptokurtic at the landscape scale and the expansion rate may be slowing.

In the area from 0 to 150 m from the thicket edge, the density of seeds dispersed declined; this may be considered the population front, the direct interface between shrub thicket and grassland. At 200 m from the thicket edge, there was a peak in seed dispersal. At 200 m, nearly 10 % of all seeds collected coincided with a peak in *Morella* cover (6.8%, SE \pm 10.82). Thus, established fruiting shrubs contribute to seeds dispersed in this part of the encroachment zone. The peak of dispersed seeds far ahead of the population front contributed to the leptokurtic quality of the dispersal kernel. Turchin (1998) describes common characteristics of expanding populations as the establishment of individuals far ahead of the population front and becoming sources of propagules, thus leading to “great leaps forward” as the population expands; a pattern which seems apparent on Hog Island as evidenced by the peaks of *Morella* cover and propagules dispersed far ahead of the population front. The peaks of established *Morella* and seed dispersal at a long distance occurred at two points along the transect that was 200 m from the thicket edge. In an environment with a more homogenous distribution of suitable habitat, distant establishment may have been more common throughout the encroachment zone. Heterogeneous landscapes typically have irregular

dispersal kernels (Levey et al. 2008). However, barrier islands are heterogeneous landscapes which results in patchy distributions of plants (Hayden et al. 1991)

In the immediate vicinity of fruiting *Morella* (i.e. shadow group traps) seed dispersal was best represented by a power formula: $y = a * (x + 1)^b$, and may extend farther than the range sampled (0 – 1.83 m). This strongly leptokurtic dispersal may be attributable to the variety of avian dispersers known to consume *Morella* fruit (Nathan and Muller-Landau 2000, Borgmann et al. 2004). This pattern of local dispersal influenced by behavior of foraging birds (Levey et al. 2008), or possibly wind blown seeds or fruit as they are small and light and winds can be strong on the coast. However, neither bird foraging behavior on the Virginia Barrier Island nor effects of wind on *Morella* dispersal have been studied. To better understand the mechanisms that influence dispersal patterns and their respective importance, will require monitoring the behavior of frugivorous, overwintering birds of the Virginia Barrier Islands, especially the Yellow rumped Myrtle Warbler (*Dendroica coronata coronata*) and possibly the effects of wind on fruit dispersal.

Seed predation was evident, but not directly quantified or observed, only as broken seed coats found in the seed traps and in what appeared to be rodent scat. Only three rodents have been documented on Hog Island: house mouse (*Mus musculus*), Marsh Rice Rat (*Oryzomys palustris*) and Norway Rat (*Rattus norvegicus*). Dietary habits are not presently documented (Ray Deuser, personal communication). If granivory of *Morella* propagules is occurring on Hog Island, it may happen disproportionately more where seeds are in greater supply (within and near *Morella* thickets and fruiting adults), then seeds dispersed farther from the thicket may have

greater chances of survival as the Janzen and Connell hypothesis would predict (Janzen 1970, Connell 1971, Dennis et al. 2007). If such processes apply to the present system then seed dispersal near the thicket edge or near fruiting *Morella* may have been underestimated.

In order for *Morella* propagules to be dispersed away from a fruiting parent, they are mostly if not entirely dependent on birds to forage the fruit and defecate seeds elsewhere. Joy and Young (2002) demonstrated the significance of *Juniperus virginiana* as perches and modifiers of microenvironmental conditions in barrier island grasslands and thereby functioning as facilitators of dispersal and seedling survival of bird dispersed plants. They also found that of the woody, bird dispersed plant species present in soil seed banks under *J. virginiana*, *Morella* were the most abundant and *B. halimifolia*, which is wind dispersed, was the only other woody species found with higher abundance (Joy and Young 2002). In the present study, the sample portion of *Morella* seeds dispersed under *B. halimifolia* cover was 0.024. The Tukey tests found this portion to be significantly different from that directly under fruiting *Morella*, but not significantly different from any other cover type sampled, including non-fruiting *Morella*. However, dispersal of *Morella* seeds under co-occurring shrubs such as *B. halimifolia* may be of similar ecological significance to *J. virginiana* by serving as perches for birds dispersing seeds. Shiflett and Young (2008) also demonstrated the importance of perch structures to avian seed dispersal on the Virginia barrier islands. They installed fecal collection traps in both grassland and woody sites to investigate dispersal throughout the Virginia barrier islands. Further investigation into whether *B. halimifolia* and other co-occurring shrubs alter microenvironmental conditions enough to significantly affect

Morella seed germination may provide further insight into biotic interactions that influence patterns of woody expansion into coastal grasslands.

Density of grass cover has been previously found to influence *Morella* seedling survival (Tolliver 1997). The spatial association of grass cover with established *Morella* cover suggests that biotic interactions determine germination and seedling success and thus *Morella* establishment. Within the first 100 m of the encroachment zone, percent cover of both *Morella* and grass decreased; it appears that *Morella* is replacing grasses. Other parts of the encroachment zone where both *Morella* and grass cover are low suggest that some minimum of grass cover may be necessary for *Morella* seed germination. However, this heterogeneity of vegetative cover may be simply reflect the heterogeneity of favorable environmental conditions available to either grasses or *Morella*. The coincidence of high grass (79.5 %) and *Morella* (6.8 %) cover at 200 m from the thicket edge suggests positive influences of grass cover on *Morella* establishment. Further investigation of microenvironmental conditions associated with grass cover is necessary to determine the significance of these potential relationships.

In previous works, biotic interactions among co-occurring plants was found to influence both dispersal and seedling survival (Tolliver 1997, Joy and Young 2002) and the current work raises the question of the influence of *B. halimifolia* on dispersal patterns. The ecological significance of *B. halimifolia* on dispersal and seedling survival on invasion patterns of *Morella* into coastal grasslands may be of interest to future researchers.

While there are important biotic interactions in coastal ecosystems that influence patterns of plant distribution, abiotic factors are also extremely influential (Art et al.

1974, Young et al. 2011). Soil salinity, in particular, is known to be a strong determinant of plant distributions in coastal environments (Ehrenfeld 1990, Young et al. 1994). My second hypothesis that establishment patterns of *Morella* will be a subset of areas where dispersal occurs and suitable soil conditions are common was only partially supported. *Morella* is limited to soils with chloride content below $500 \mu\text{g} \cdot \text{g}^{-1}$ dry soil however, some of the soil samples from plots with established *Morella* were higher in chloride content than expected. Young et al. (1994) sampled soils during the growing season, from June to October, whereas samples taken for the current study were from March and April. In both March and April soils from plots along the thicket edge and near the middle of the island had chloride content $> 500 \mu\text{g} \cdot \text{g}^{-1}$. The spatiotemporal variability of soil salinity on barrier islands may explain the unexpectedly high chloride content at these locations (Young et al. 1994), or suggest that the effects of soil salinity on *Morella* survival varies throughout the shrub life cycle. The interaction of this important abiotic factor with the process of *Morella* establishment may be more complex in scope than the current study, thus requiring further investigation of salinity effects throughout the life cycle of *Morella* and demonstrating a need for a better understanding of the spatiotemporal dynamics of soil salinity on barrier islands.

The establishment process of *Morella* encroachment into grasslands may be mediated by the interaction of many biotic and abiotic factors. Seed dispersal patterns throughout a landscape under encroachment pressure are leptokurtic and are influenced by the distribution of co-occurring plants that function as perches for frugivorous birds. By acting as perches, co-occurring shrubs facilitate the spread of bird dispersed plants such as *Morella*. The suitability of an environment to which seeds are

dispersed seems to depend on a combination of interactions between biotic and abiotic factors: predation by granivores, plant – plant resource competition, water availability and soil salinity. The indication that these factors all interact as filters, with varying degrees, on *Morella* establishment suggests the process from seed dispersal to thickening in coastal environments is multi-stepped and complex. Understanding importance of each of these relationships to plant community shifts will enable more informed predictions of ecosystems responses to global change.

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Appendix

Table 1 Model formulas fit to the *Morella* dispersal kernel of landscape scale dispersal data (dispersal throughout encroachment zone) and to dispersal in immediate vicinity of fruiting *Morella* (seed shadow group)

| Formula type | Equation |
|---------------------|------------------------|
| Exponential | $y = a * e^{(-x * b)}$ |
| Power | $y = a * (x + 1)^b$ |
| Gaussian | $y = (b * x^2) - a$ |

Table 2 *Morella* seed count with relative proportions by distance from thicket edge and by cover type on Hog Island, VA.

| Distance from thicket edge (m) | Distance from fruiting | | | | | | | | No shrub cover | Perches | | | Total | Relative Proportion |
|-----------------------------------|---------------------------|------------------------------|------------------------------|------------------------------|--------------------------------|----------------------|-----------------------|------------|----------------|-------------------|--|--|-------|------------------------|
| | <i>Morella</i> (m) | | | | | | | | | Co-occurring spp. | | | | |
| | 0 – 0.46 frt.morella.1 | 0.46 – 0.91 frt.morella.2 | 0.91 – 1.37 frt.morella.3 | 1.37 – 1.83 frt.morella.4 | non-fruiting <i>Morella</i> | <i>I. frutescens</i> | <i>B. halimifolia</i> | | | | | | | |
| 0 | 932 | 332 | 276 | 141 | 0 | 111 | 13 | 76 | 1881 | 0.403 | | | | |
| 50 | 1104 | 397 | 275 | 119 | - | - | 0 | - | 1895 | 0.406 | | | | |
| 100 | 63 | 52 | 66 | 16 | 1 | 116 | 2 | 26 | 342 | 0.073 | | | | |
| 150 | - | - | - | - | 20 | 20 | 0 | 9 | 49 | 0.010 | | | | |
| 200 | 248 | 39 | 36 | 58 | 2 | 53 | 21 | - | 457 | 0.098 | | | | |
| 250 | - | - | - | - | 0 | - | 35 | - | 35 | 0.007 | | | | |
| 300 | - | - | - | - | 7 | - | 1 | - | 8 | 0.002 | | | | |
| Total | 2347 | 820 | 653 | 334 | 30 | 300 | 72 | 111 | 4667 | | | | | |
| Relative Proportion | 0.503 | 0.176 | 0.140 | 0.072 | 0.006 | 0.064 | 0.015 | 0.024 | | 1 | | | | |

Table 3 Dispersal kernel: Comparison of non-linear regressions of *Morella* seed dispersal density throughout the *Morella* encroachment zone on Hog Island, VA.

| Model Formula type | a | b | RSS | AIC | Δ AIC |
|---------------------------|-----------|------------|------------|------------|--------------|
| Exponential | 484.8 | 0.0088 | 52243 | 88.29 | 0 |
| Gaussian | - 0.00318 | - 0.000419 | 103175 | 93.05 | 4.76 |
| Power | 456.94 | -0.235 | 121153 | 94.18 | 5.89 |

Table 4 Seed shadow group distribution: non-linear regressions of density of *Morella* seeds dispersed within the immediate vicinity of fruiting *Morella* cover on Hog Island, VA.

| Model formula type | a | b | RSS | AIC | Δ AIC |
|---------------------------|----------|----------|------------|------------|--------------|
| Power | 1510.21 | - 2.46 | 16858 | 50.74 | 0 |
| Exponential | 1267.46 | 1.52 | 30970 | 53.17 | 2.43 |
| Gaussian | - 671.5 | - 215.2 | 162608 | 59.80 | 9.06 |

Table 5 ANOVA of *Morella* seeds captured among cover types, including the closest, (frt.morella.1) and farthest (frt.morella.4) traps of the seed shadow group.

| | df | MS | SS | F | p |
|-----------|-----------|-----------|-----------|----------|----------|
| Cover | 5 | 61875 | 309374 | 10.31 | < 0.001* |
| Residuals | 52 | 6001 | 312056 | | |

Table 6 Tukey test (with closest and farthest traps of the shadow group) of *Morella* seed dispersal. Groups are designated as: frt.morella.1 = closest of ‘shadow group’, frt.morella.4 = farthest of ‘shadow group’, non.frt.morella = non-fruiting *Morella*, bac = *B. halimifolia*, iva = *I. frutescens* and no.cover = no shrub cover.

| Comparison | Difference | p |
|----------------------------------|------------|----------|
| frt.morella.1 – bac | 181.7 | < 0.001* |
| frt.morella.1 – iva | 189.0 | < 0.001* |
| frt.morella.1 – no.cover | 192.3 | < 0.001* |
| frt.morella.1 – non .frt.morella | 168.3 | < 0.001* |
| frt.morella.1 – frt.morella.4 | 147.9 | < 0.001* |
| frt.morella.4 – bac | 33.8 | 0.96 |
| frt.morella.4 – iva | 41.2 | 0.88 |
| frt.morella.4 – no.cover | 44.4 | 0.86 |
| frt.morella.4 – non.frt.morella | 20.4 | 0.99 |
| non.frt.morella – bac | 13.4 | 0.99 |
| bac – iva | 7.3 | 0.99 |
| bac – no.cover | 10.5 | 0.99 |
| iva – no.cover | 3.2 | 0.99 |
| non.frt.morella – iva | 20.7 | 0.99 |
| non.frt.morella – no.cover | 23.9 | 0.98 |

Table 7 ANOVA of *Morella* seeds captured among vegetation cover types on Hog Island, VA, including only the farthest traps of the seed shadow group (frt.morella.4).

| | df | MS | SS | F | p |
|-----------|-----------|-----------|-----------|----------|-----------|
| Cover | 4 | 2658.5 | 10634 | 5.605 | 0.00108 * |
| Residuals | 41 | 474.5 | 19445 | | |

Table 8 Tukey test including only the farthest traps of the seed shadow group (frt.morella.4) of *Morella* dispersal. Group designations are the same as Table 6.

| Comparison | Difference | p |
|---------------------------------|-------------------|----------|
| frt.morella.4 – no.cover | 44.4 | 0.002* |
| frt.morella.4 – iva | 41.2 | 0.003* |
| frt.morella.4 – bac | 33.8 | 0.035* |
| frt.morella.4 – non.frt.morella | 20.4 | 0.313 |
| non.frt.morella – no.cover | 23.9 | 0.124 |
| non.frt.morella – iva | 20.7 | 0.189 |
| non.frt.morella – bac | 13.4 | 0.678 |
| bac – iva | 7.3 | 0.950 |
| bac - no.cover | 10.5 | 0.856 |
| iva - no.cover | 3.2 | 0.997 |

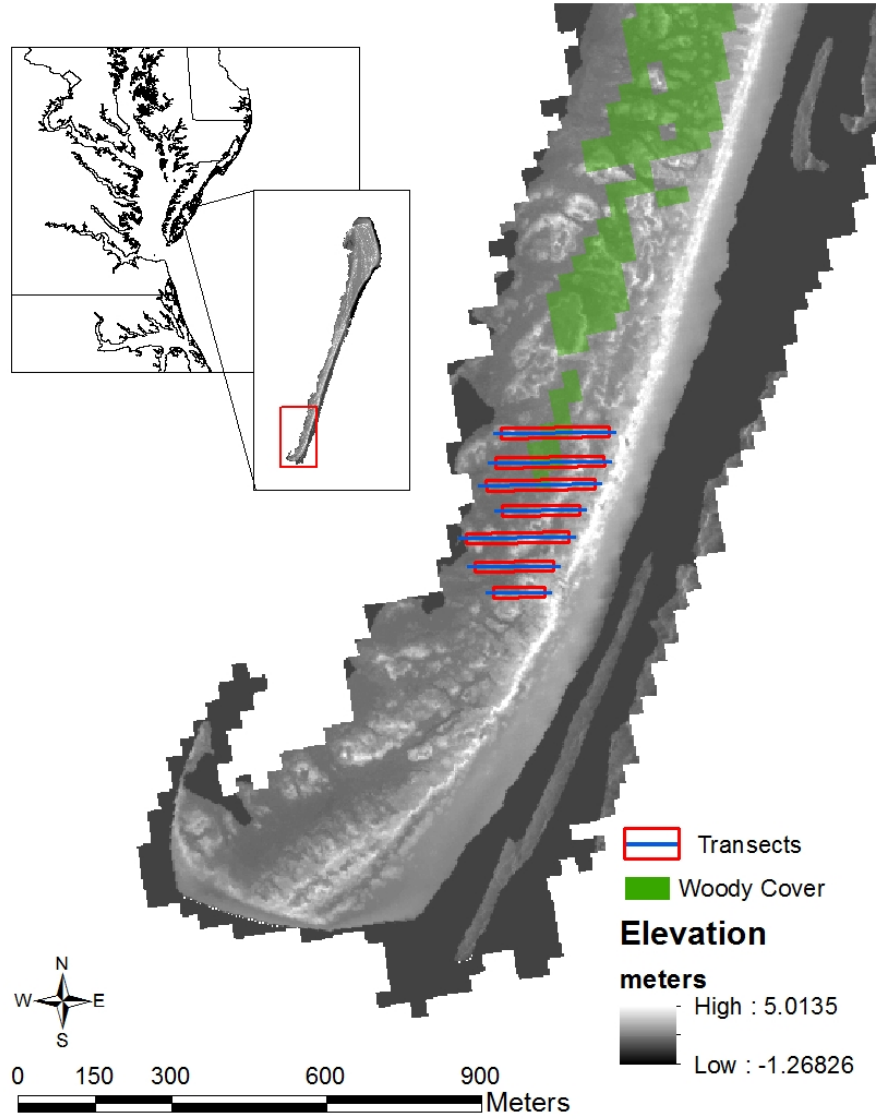


Figure 1 Study site – Hog Island, Eastern Shore, VA



Figure 2 Seed traps deployed near fruiting *Morella*; those pictured were of the ‘seed shadow’ group.

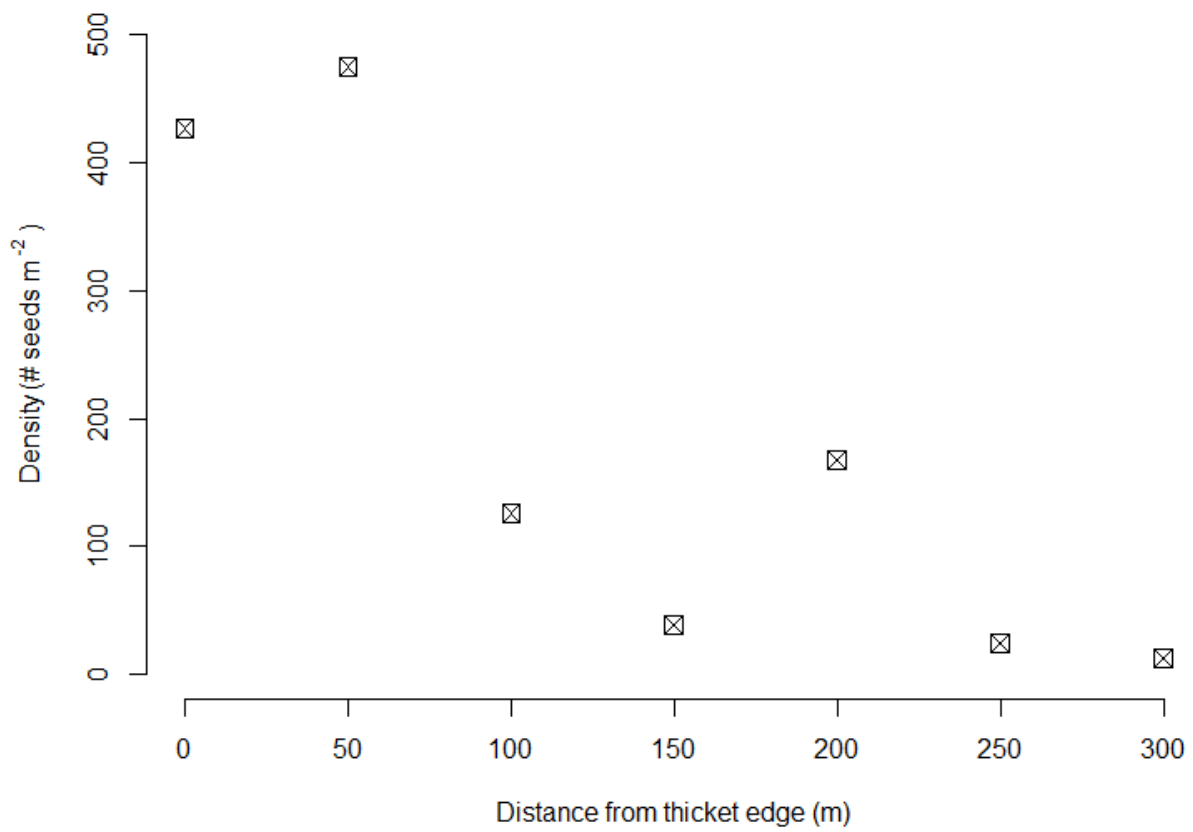


Figure 3 Density of seeds dispersed throughout encroachment zone of *Morella* into grassland on Hog Island, VA.

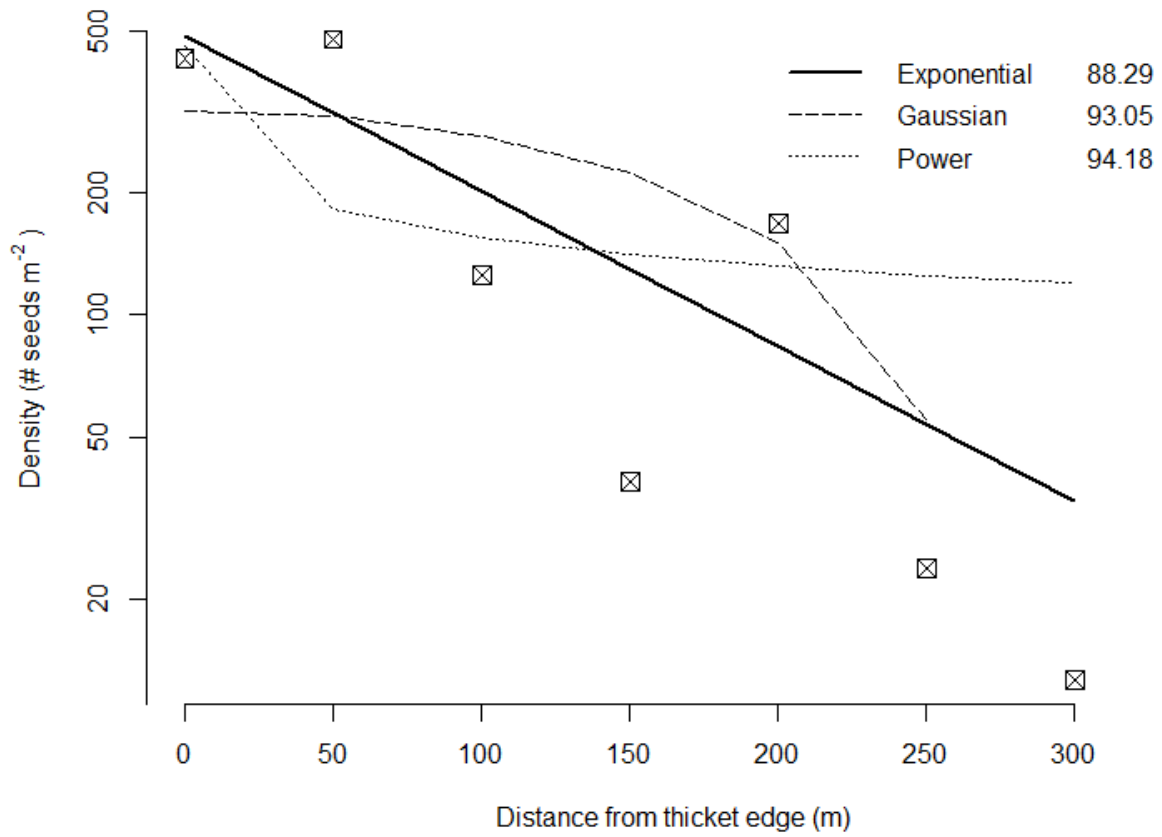


Figure 4 Dispersal kernel: density of *Morella* seeds dispersed (log scale) vs. distance from thicket edge on Hog Island, VA. Lines are of non-linear regressions of Exponential, Power and Gaussian models, with corresponding AIC values.

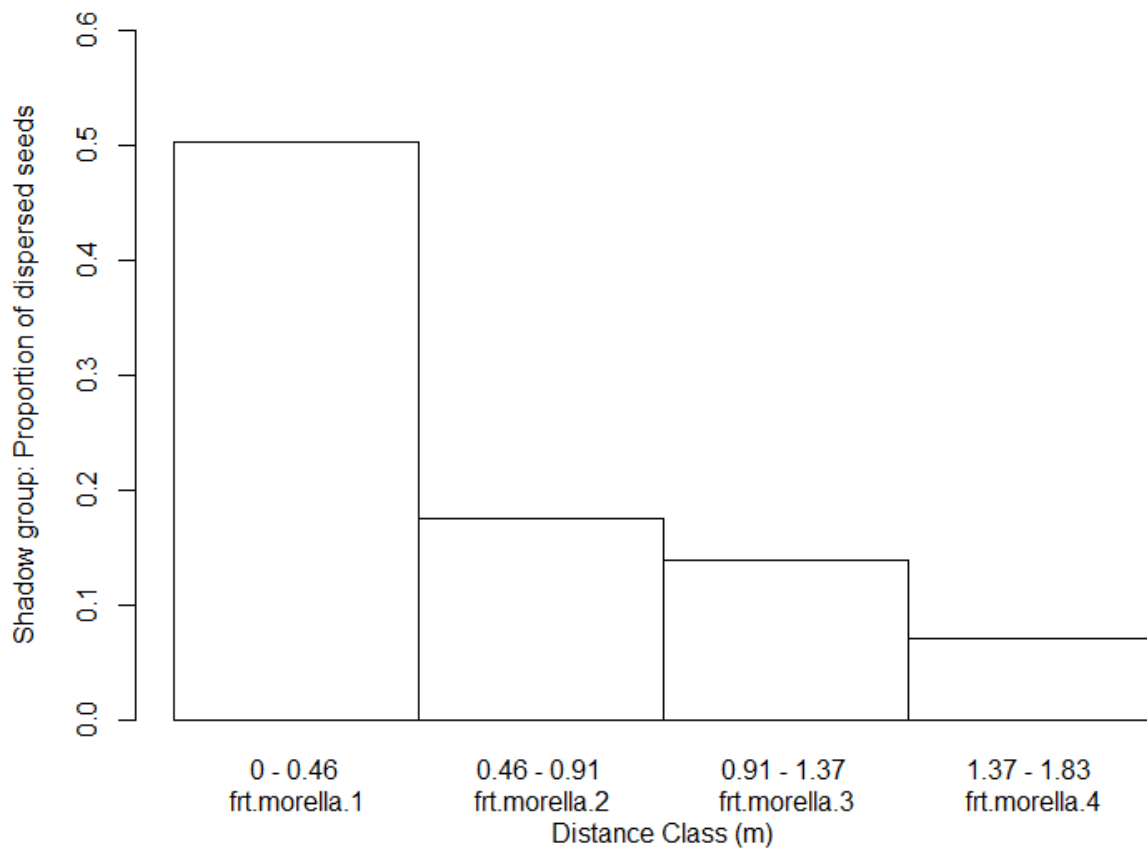


Figure 5 Histogram proportions of the seed shadow of fructing *Morella* on Hog Island, VA.

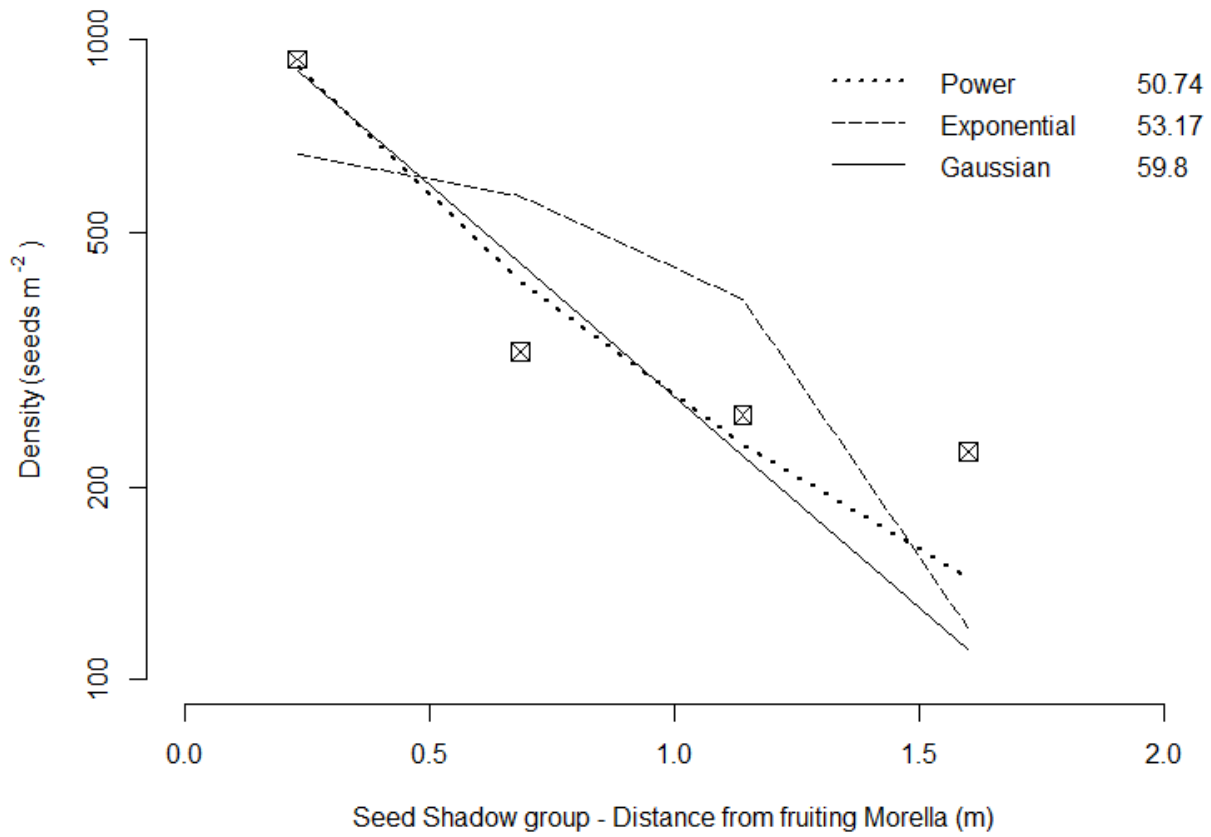


Figure 6 Non-linear regressions of seed dispersal (log scale density) in the immediate vicinity of fruiting *Morella* on Hog Island, VA with model types and AIC values. X-values are the distance to the middle of seed traps from fruiting *Morella* cover.

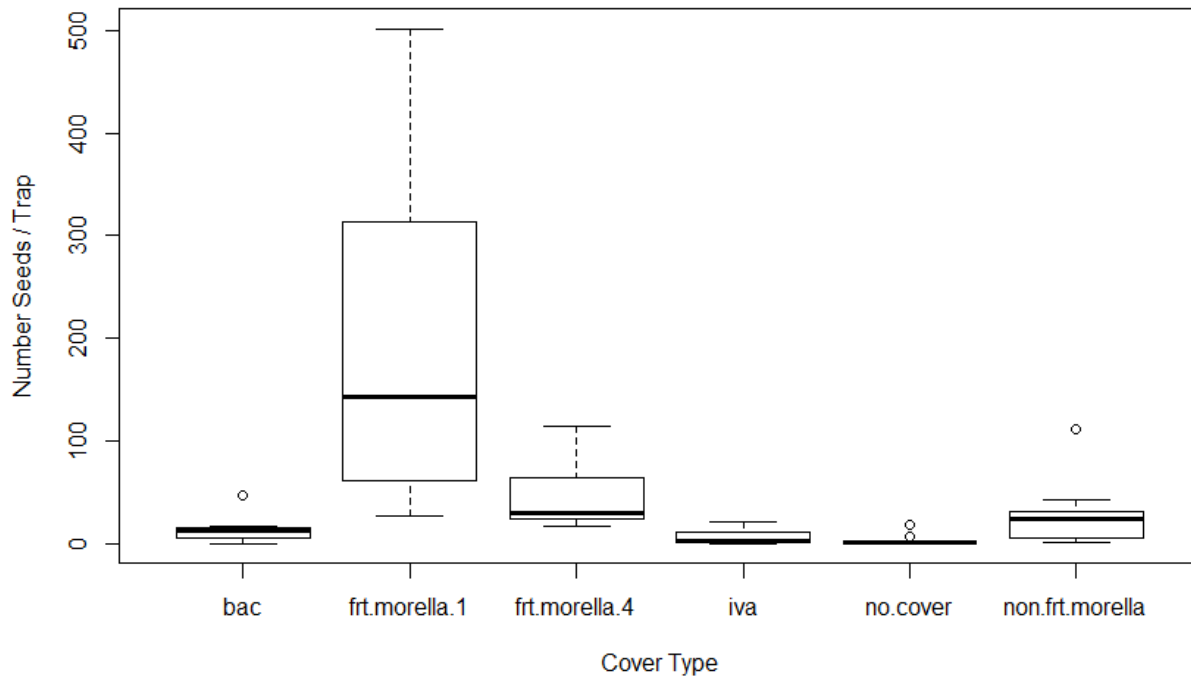


Figure 7 Mean, Standard Deviation and Range of *Morella* seeds dispersed under cover types on Hog Island, VA. Groups are designated as: frt.morella.1 = closest traps of the ‘shadow group’, frt.morella.4 = most distant traps of the ‘shadow group’, non.frt.morella = traps under non-fruiting *Morella*, bac = traps under *B. halimifolia*, iva = traps under *I. frutescens* and no.cover = traps placed where there was no shrub cover.

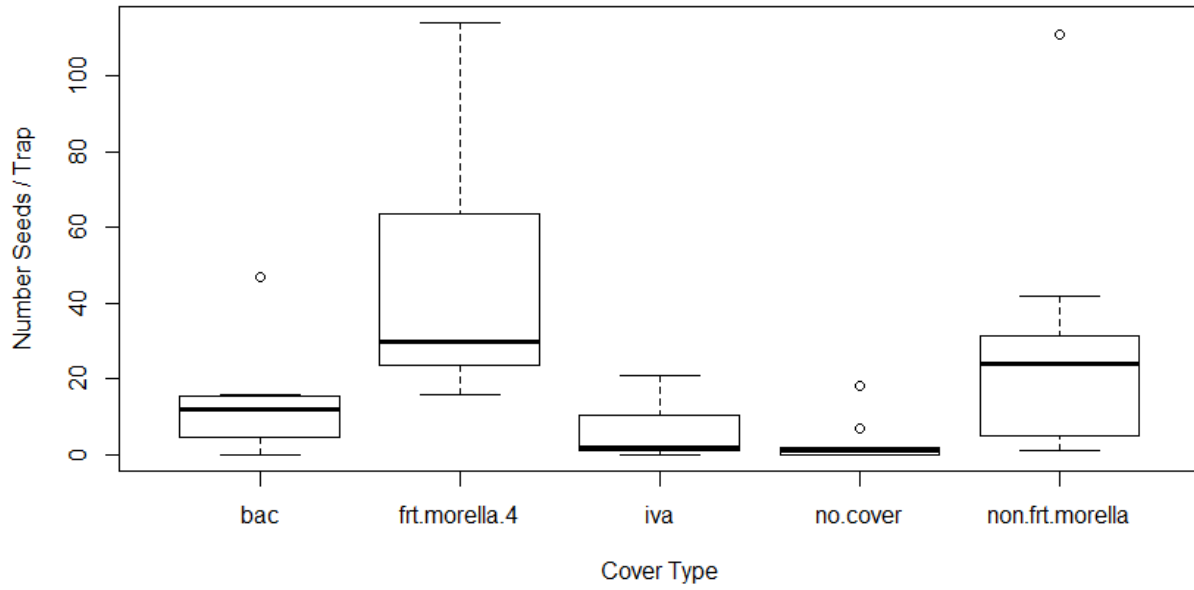


Figure 8 *Morella* seeds captured under cover types on Hog Island, VA. Groups are designated same as in Figure 7 (above).

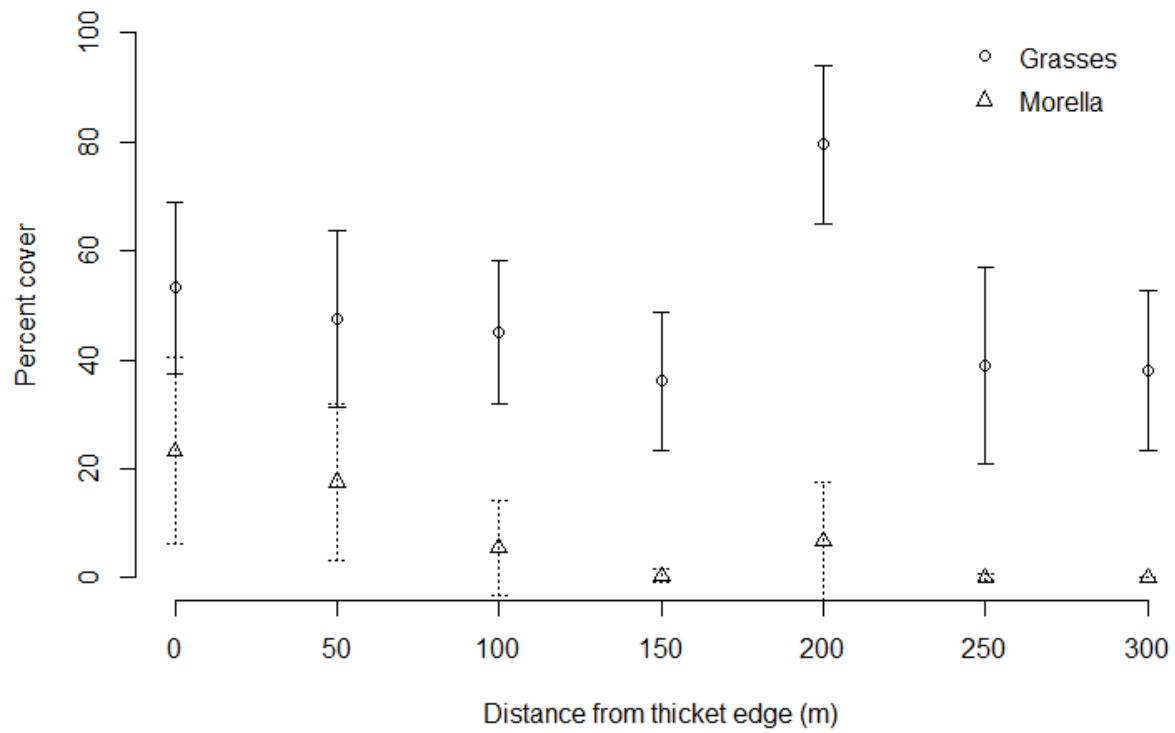


Figure 9 Percent cover of *Morella* and grasses throughout encroachment zone on Hog Island, VA (mean \pm SE).

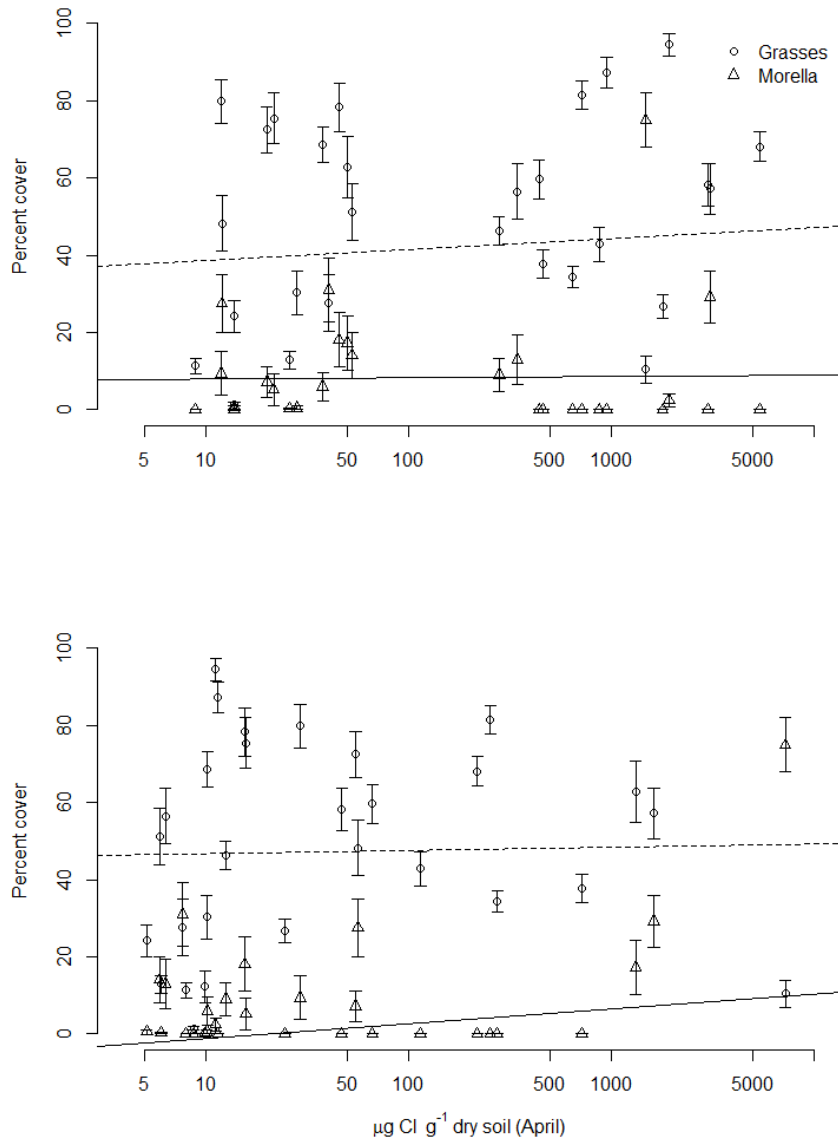


Figure 10 Least squares linear regressions of Soil chlorides and *Morella* (solid lines, March $r^2 = 0.004$, April $r^2 = 0.69$) and grass (dashed lines, March $r^2 = 0.06$, April $r^2 = 0.04$) cover. Points are mean percent cover \pm SE.

Vita

Benjamin Lawrence Dows was born on September 30, 1982 in Richmond, Virginia and graduated from James River High School in 2000. During that interval, he was a member of the Boy Scouts of America, Troop 859, which instilled in him a love of the outdoors and a curiosity that later drew him to pursue studies in the ecological sciences. Benjamin has also been a student of the Ving Tsun (Wing Chun) system of Chinese martial arts since 2003, an endeavor that has been invaluable to him. He earned his Bachelor of Science in Biology from Virginia Commonwealth University in 2008. More recently he has engaged in the more tranquil and increasingly popular hobby of home brewing beer. After some deliberation, he elected to return to VCU with hopes of finding a more intellectually stimulating career. His immediate academic pursuits have lead him to expand on the current work while continuing his doctoral studies at VCU under the advisement of Dr. Young; continuing in the footsteps of three of his predecessors of the Coastal Plant Ecology Lab (CPEL) to obtain what he has coined the, "Young Lab Hat-Trick". Ultimately and more generally his research interests, while constantly evolving, are to model patterns and processes of invasion and range expansion at landscape and regional scales.