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CONSEQUENCES OF VINE INFESTATION: LINKING ABIOTIC INFLUENCES AND BIOTIC INTERACTIONS TO SUCCESSIONAL AND STRUCTURAL CHANGES IN COASTAL COMMUNITIES

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CONSEQUENCES OF VINE INFESTATION: LINKING ABIOTIC INFLUENCES AND BIOTIC INTERACTIONS TO SUCCESSIONAL AND STRUCTURAL CHANGES IN COASTAL COMMUNITIES

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Virginia Commonwealth University

by

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Abstract

CONSEQUENCES OF VINE INFESTATION: LINKING ABIOTIC INFLUENCES AND BIOTIC INTERACTIONS TO SUCCESSIONAL AND STRUCTURAL CHANGES IN COASTAL FORESTS

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A Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Virginia Commonwealth University.

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Located at the interfaces of terrestrial and marine environments, coastal habitats are inherently vulnerable to the effects of global change. Barrier island systems in particular serve not only as protective buffers against storm events, but also as sentinel ecosystems for observation of the impacts of sea level rise, and of increasing storm frequency and intensity. In the mid-Atlantic region, shrub thickets of *Morella* species compose the dominant forest community. The often monospecific nature of these plant community assemblages is advantageous to ecological studies and cross-scale applications; the relatively low diversity facilitates transitions between scales. My objective was to investigate the distribution and community roles of lianas in mid-Atlantic barrier island forest communities. I quantified environmental variables at two barrier habitats with differing site management histories and corresponding topography, and found that abiotic factors affected distributions of woody species, which subsequently affected vine species distributions. Some association of prevalent vine species with the common woody plants *Prunus serotina* and *Morella cerifera* was observed, though neither vines nor woody species demonstrated significant species-specific phytosociological associations. Vines demonstrated a long-lasting effect of arresting or delaying succession, and are potentially responsible for the lack of redevelopment of mature maritime forest at these sites. At Hog Island, Virginia, remotely-sensed data were utilized to determine the three-dimensional structural effects of vine infiltration in woody canopies. Vines were found to reduce canopy height and depth, and increase density, short-term diversity, and light-intercepting biomass. Significant vine infiltration can accelerate senescence of shrub thickets, but often results in persistent tangled masses of vegetation which reduce recruitment of later-successional species. These effects may represent long-term, lasting impacts of vine establishment and expansion in these habitats, affecting community succession towards diverse and stable maritime forest, and significantly altering resource dynamics in these sensitive ecosystems.

CHAPTER ONE

ECOLOGICAL CONSEQUENCES OF VINE INFILTRATION AND EXPANSION

Spencer N. Bissett

Introduction

Published works inspiring Charles Darwin's interest in climbing plants in the late 1800s (Darwin, 1865; Isnard and Silk, 2009) speak to the long history of interest in this globally common growth form. Research has been conducted in temperate, montane, island, subtropical, and particularly, tropical systems (Gentry, 1991), but while the physiology of climbers (generically, "vines") has been addressed in studies spanning multiple ecosystems and systematic groups, the particular roles and implications of climbing plant species in coastal environments have received relatively little focus.

Coastal systems impose severe and recurrent stresses on resident species, such as intense sunlight, sea spray, saltwater intrusion, nutrient-poor soils, low freshwater availability, high winds and shifting sand, and storm-related disturbances (Ehrenfeld, 1990; Stalter and Odum, 1993; Hayden et al., 1995; Shao et al., 1996). Because both elevation above sea level and proximity to the shore determine the severity of these and other factors, environmental gradients are linked to position within the landscape and influence plant community composition. Therefore, increasing distance from the ocean is typically reflected by a predictable pattern of successional seral stages (Ehrenfeld, 1990; Levy, 1990; Stalter and Odum, 1993). In the context of barrier islands, the physical pressures associated with most coastal landscapes are compounded by the unique transitional nature of the environment. Drivers such as constantly shifting sand and storm-related overwash, erosion, and accretion contribute to the long-term migration of the islands and further influence the gradients which determine plant community distribution across the landscape, between the beach, island interior, and bay (Stallins and Parker, 2003; Davis and Fitzgerald, 2004). In addition to these processes, both persistent and episodic, global change predictions suggest that sea level will rise in coming decades, to varying degrees of significance depending on the realized scenario (IPCC, 2007). These predictions indicate also that storm event intensity and frequency will increase, particularly with respect to warm-season events (IPCC, 2007; Knutson et al., 2008).

Both climbing plant species and barrier island systems have been the subjects of extensive research, but these areas rarely overlap in the literature. I conducted a multiple-scale investigation of climbing plants in coastal environments, including investigations of environmental drivers of species distributions, biotic interactions with co-occurring woody species, and plant- and community-scale structural effects of vine infiltration in coastal temperate shrub thickets.

Background and Objectives

Previous research has explored the unique set of environmental characters and processes common to coastal systems in general, and to barrier islands in particular (Levy, 1990; Stalter and Odum, 1993; Hayden et al., 1995; Shao et al., 1996). Coastal systems are distinguished from inland environments largely by physical factors, including edaphic characteristics, aerosol (sea spray) chemistry, substrate (sand) movement, and unique climate features such as storm occurrence (Ehrenfeld, 1990; Young et al., 1995). These qualities and events contribute to development of successional vegetation communities with varying distance from the shore. Barrier islands are further distinguished from other coastal systems by their transitional nature. Well-defined plant communities often develop, influenced by elevation and distance from the shore, and these communities may reach a stable state of development in the absence of major disturbances (Hayden et al., 1995). On islands of the Mid-Atlantic region, the dominant community found behind stable and protective sand dunes is composed of dense-canopied thickets of *Morella* shrubs (Young et al., 1995). In many cases, thickets may be considered a climax community because their dense, monospecific nature can prevent the transition to a mature maritime forest. However, as these shrub thickets age and senesce, they are subject to deterioration which is accelerated by storm events, high winds, and winter build-up of ice (Crawford and Young, 1998).

Frequently contributing to the collapse of thickets is the presence of vines in the canopy. Deterioration of thickets provides the existing seed bank, as well as incoming seed rain from avian deposition, with decreased above- and belowground competition and thereby facilitates community succession toward a more ecologically and structurally diverse maritime forest (Ehrenfeld, 1990; Crawford and Young, 1998). Vines often experience greater success than other herbaceous plants in these dense-canopied shrub thickets, as their growth tends to be rapid, owing partly to reduced investment in both support tissues and root biomass (Putz, 1983). Putz (1983) described the highly efficient above- and belowground growth in vines, where architecture is devoted not to supporting the plant itself, but to effective hydraulic transport and competition for nutrients. These qualities allow vines to be among the first successful colonizers of nutrient-rich soils such as that found in the understory of *Morella cerifera* thickets (Putz, 1983; Brantley and Young, 2008). Because these soils are of relatively high quality, and because vines tend to grow rapidly upwards, they often reach the canopy prior to autonomous thicket senescence, and consequently may advance deterioration and succession. And because vines penetrate and permeate the canopy of densely-vegetated communities such as shrub thickets, they physically tie shrubs and trees to one another, adding mass to the canopy (Rowe et al., 2006; Schnitzer and Carson, 2001), and thereby multiplying the damage wrought by wind and winter precipitation, further contributing to gap formation.

The vine growth form also provides a significant advantage in allowing plants to separately locate leaves and roots. Not only is this beneficial in an understory, where vines may germinate in a nutrient-rich but heavily shaded site and grow towards a patch of open canopy, but also on the coast itself, where physiological integration is a similarly effective strategy for some non-climbing species (Klimeš and Klimešová, 1999; Amsberry et al., 2000).

My objective was to investigate the roles of vines in coastal ecosystems across multiple scales. I selected two sites in the mid-Atlantic region, and explored the distribution and effects of vine species at each. Specific goals were carried out in three parts: 1) Vine and woody species distributions were related to environmental variables including topography, abiotic and edaphic characteristics, with regard to differing management histories of two field research sites. 2) Biotic associations of vines with woody structural hosts were investigated. 3) Remotely-sensed data were used to link vine infiltration to structural, long-term, and broad-scale impacts on woody plant canopies.

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CHAPTER TWO

LINKING HABITAT WITH ASSOCIATIONS OF WOODY VEGETATION AND VINES ON TWO MID-ATLANTIC BARRIER ISLANDS

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Abstract

Coastal habitats are inherently vulnerable to global change, as the first areas to be impacted by sea level rise and to experience more frequent and intense storms. Shrubs and vines dominate the climax communities in these environments, and with comparatively long regeneration periods, are highly vulnerable to shifting topography and climate. We investigated abiotic and biotic components of two barrier island landscapes with similar plant communities but different site histories to clarify relationships among physical factors, woody plants, and vines. On Hog Island, VA and at Duck, NC, intra-site comparisons with reference to distance from shoreline and elevation were made to evaluate relationships between woody and vine communities as well as edaphic characteristics. Elevation was significantly related to woody species presence, and vine presence was significantly related to presence of woody structure, indicating an indirect association of the climbing species to elevation. Differing histories of management and development at the two sites have resulted in varying degrees of both topographic complexity and stability. Greater topographic complexity has resulted in similar species richness values for the two sites, despite the considerable difference in total area. Presumably, stabilization and prior management efforts at the Duck site have enabled a community assemblage comparable to that of the much larger Hog Island; however, the Duck site may be more vulnerable because of a decreased potential migrate in response to continued sea level rise and storm impacts.

Introduction

Publications documenting Charles Darwin’s interest in climbing plants in the late 1800s (Darwin, 1865; Isnard and Silk, 2009) speak to the long history of curiosity regarding this globally common growth form. Research on climbing plants (generically, “vines”) has been conducted in temperate, montane, island, subtropical, and tropical systems (Gentry, 1991). While the physiology and phytosociology of vines have been addressed across ecosystems and systematic groups, the particular ecological roles of climbing plants in coastal environments have received little focus. In coastal systems, climbing species may provide a successional link between early colonization by thicketizing woody shrubs, and the later establishment of a mature and diverse maritime forest. A well-developed vine community may therefore be a good indicator of coastal site stability.

Coastal systems impose severe, recurrent, and persistent stresses, including intense sunlight, sea spray, saltwater intrusion, nutrient-poor soils, low freshwater availability, high winds and shifting sand, and storm-related disturbances; all are significant challenges for local flora (Ehrenfeld, 1990; Hayden *et al*., 1995; Miller, Gornish, and Buckley, 2009; Shao, Shugart, and Hayden, 1996; Stalter and Odum, 1993). Elevation above sea level and proximity to shoreline (referenced jointly as "landscape position") determine the severity of these and other environmental gradients, so they may be considered proxies integrating a suite of biotic and abiotic factors that are associated with position within the landscape and affect ecological processes and plant communities (Young *et al*., 2011). Increasing distance from the ocean should, therefore, result in a predictable pattern of community types (Ehrenfeld, 1990; Levy, 1990; Stalter and Odum, 1993). Barrier islands are further distinguished from other coastal systems by their transitional nature, though well-defined and stable plant communities often develop in the absence of major disturbances (Hayden *et al*., 1995; Miller, Gornish, and Buckley, 2009), and this may facilitate vine establishment and proliferation.

Vines are among the first successful colonizers of Mid-Atlantic barrier island soils, following modification by nitrogen-fixing shrubs of the genus *Morella* (Brantley and Young, 2008; Putz, 1983). These shrubs often colonize the area behind stable and protective sand dunes, forming dense-canopied thickets which then expand rapidly (Young, Shao, and Porter, 1995; Young *et al.*, 2007). The monospecific, often impenetrable nature of these thickets may persist for decades, preventing the transition to a mature maritime forest. However, following the onset of senescence, they are subject to deterioration which is accelerated by storm events, high winds, and ice accumulation (Crawford and Young, 1998). Presence of vines in shrub canopies also contributes to the collapse of thickets (Crawford and Young, 1998). Vines often experience greater success than understory species in these dense-canopied shrub thickets, as their growth tends to be rapid, owing partly to reduced investment in both support tissues and root biomass (Putz, 1983). Putz (1983) noted that both above- and belowground growth in vines is highly efficient, with architecture devoted far less to mechanical support than to effective hydraulic transport and competition for nutrients.

Occurrence and expansion of vines in woody canopies influence a multitude of ecological processes. Because vines penetrate and permeate the canopies of densely-vegetated communities such as shrub thickets, they physically tie woody plants to one another, add mass to the canopy (Rowe *et al*., 2006; Schnitzer and Carson, 2001), and may affect carbon balance of these woody-dominated systems. Increased canopy diversity and structural complexity may maintain productivity in aging forests, increasing total carbon uptake (Hardiman *et al*., 2011). Alternately, by accelerating senescence of woody plants on which they structurally depend, vine infiltration may result in eventual carbon release (Durán and Gianoli, 2013). Expansion and encroachment of woody species are now understood to be occurring worldwide and in a variety of ecosystems (Knapp *et al*., 2008), and the concomitant effects of vine expansion have yet to be fully explored.

In the tropics, these trends are already being observed and may even contribute to a positive feedback favoring vine success (Wright *et al*., 2004).

While both climbing plants and barrier island systems have been subjects of previous research, they have not been evaluated in tandem, and the particular roles of vines in coastal habitats are not well understood. To investigate the importance of vines in coastal plant communities, we compared species composition, physical structure, and soil characteristics of two coastal sites, focusing on woody and vine species present. We compared the physical ranges of woody vegetation and vines at each site, and evaluated these sites for dependence of vines on woody cover. We also considered differences in site history, as physical and community stability are strongly affected by human influences.

Methods

Study Sites

Sites were selected during the spring of 2011 and preliminary visits were conducted during summer of that year. Hog Island (Figure 2.1a), a barrier island located within Northampton County, VA and included in the Virginia Coast Reserve (VCR) Long-Term Ecological Research (LTER) site, is the northern of the two sites (37° 27' N, 75° 40' W). The VCR LTER is owned and managed by The Nature Conservancy. Hog Island is ~1200 ha in area, 10 km in length and up to 2.5 km across at its widest point. The Duck Pier Field Research Facility (Duck FRF; Figure 2.1b), the southern site (36° 11’ N, 75° 45’ W), is owned and managed by the United States Army Corps of Engineers (USACE). The site is located on the Outer Banks barrier islands of Dare County, North Carolina. The terrestrial portion of the property is ~80 ha, 1 km in length and ~0.5 km in width.

Site Histories

Both sites represent mixed coastal communities with open sand and beach habitat, regions of grassland composed of dunes and swales, shrub thickets with dense canopies and often low species richness, and occasionally, patches of maritime forest with higher density and species diversity (Harris, Levy, and Perry, 1983; Levy, 1990; Shao, Shugart, and Hayden, 1996). Hog Island is now a relatively pristine coastal system; human occupation ceased in the 1930s when the occupants and structures were moved to the mainland in response to accelerating oceanside erosion and increasing storm impacts (Badger and Kellam, 1989; Fenster and Hayden, 2007; Hayden *et al.*, 1991). Woody species expansion has been documented at Hog Island over the last 30 years along the accreting northeast portion, and also southward down the long axis of the island (Young *et al.*, 2007; Zinnert *et al.*, 2011). The Duck FRF site is located near the midpoint between Cape Henry and Oregon Inlet. It is the narrowest portion of this region (Havholm *et al*., 2004), and is maintained as a 1 km shoreline stretch of naturalized mixed-habitat area. Historically it served as a US Navy bombing range (1941-1965) and was the subject of dune grass plantings and fertilizer enrichment experiments for dune stabilization in spring 1979, 1980, and 1981 (Dolan, 1972; Harris, Levy, and Perry, 1983). No surveys have been conducted since 1997, and no artificial introduction of plants has occurred for more than three decades (Brock *et al*., 2001; Harris, Levy, and Perry, 1983), but much of the Outer Banks, including Duck FRF neighboring areas, is heavily developed and artificially stabilized. This anthropogenic influence still affects the Duck FRF property, primarily by requiring a continuous and stable primary dune to be maintained (Harris, Levy, and Perry, 1983).

Plot Identification

Transects were selected using orthorectified aerial imagery to maximize site coverage while evenly sampling both sites and minimizing bias towards particular areas or communities.

Aerial images used for initial site selection were downloaded using Google Earth version 7.0.2, and coordinates were recorded in degree, minute, second format according to the geographical coordinate system WGS 1984. Four transects were established on Hog island, three were established at Duck FRF. Plots were assigned along transects from west to east in 50 m increments (Table 2.1). Latitude and longitude for each plot were georeferenced for future site visits in summer 2011. Transect plots were identified using a Garmin 60CSx GPS receiver with an accuracy of ± 3 m.

Plant Community and Edaphic Sampling

At each plot, all stems of woody and vine species within a 3 m radius were counted, and canopy coverage was scored on a scale of 0 (no canopy constituent) to 5 (dense coverage over entire plot) for both woody and vine species. Density and complexity of woody and vine canopies in some plots prevented differentiation between species of *Smilax* and *Rubus*; these species are identified to genus. Soil samples were collected in each plot, and 5 m north and south of each plot, for chloride and pH analysis ($n_{Hog} = 116$; $n_{Duck} = 98$).

Soil Chloride and pH Analysis

Soil samples were oven-dried for 72 h at 80 °C and analyzed for pH and chloride content following Wijnholds and Young (2000). For each sample, 50 g of soil was mixed with 200 mL of deionized water. Soil sample pH values were measured with a calibrated pH meter (Hanna Instruments, Woonsocket, RI). Prior to soil chloride analysis, 4 mL of 5 M $NaNO_3$ was added as an ionic equalizer, and chloride content was determined using a chloride electrode (Catalog no. 13-620-526; Accumet, Fisher Scientific, Pittsburgh, PA).

Landscape position determination

Remotely-sensed data were used to physically characterize and compare plot elevation and distance to shoreline (landscape position) at each study site. Hog Island LiDAR data were collected in July 2011 (Tuck Mapping Solutions, Inc.). Data were collected with a Riegl LMS-Q680i system, with full waveform capability operating at 400 kHz pulse repetition frequency (PRF), mounted on a Bell 407VFR helicopter. Accuracy of this system is ± 20 mm, and precision is ± 20 mm. Duck FRF LiDAR data were retrieved from the National Oceanic and Atmospheric Administration's (NOAA) Digital Coast program online database. Horizontal accuracy for NOAA LiDAR data is at least ± 2.0 m, and vertical accuracy is ± 15 cm root-mean-square-error (RMSE) in open areas. Following collection, data were processed using previously-surveyed geo-referenced ground points and known-elevation reference points including USGS survey monuments. Elevations used for analyses were averaged from all LiDAR returns within a 5 m radius of each transect sample point.

Statistical Analyses

Mann-Whitney U-tests ($\alpha = 0.05$) were used to test for differences between mean elevation, mean soil Cl, and mean soil pH at Hog Island and Duck FRF. The non-parametric test was chosen because these data were not normally distributed, as determined by Kolmogorov-Smirnoff tests. For statistical analyses, woody species and vine species were each pooled for consideration as two functional groups. Logistic regression analysis (Keating and Cherry, 2004) was used to evaluate woody and vine species presence / absence for relationship to soil edaphic characteristics (soil Cl, soil pH) and site physical characteristics (elevation, distance to shoreline). Additionally, vine presence / absence was tested for relationship with woody cover score (0-5). Relationships with a *p*-value of 0.05 or less were considered significant.

Results

Topography

Topography differed significantly between Hog Island and Duck FRF sites (Figures 2.2 and 2.3). Mean elevation above sea level of sample plots on Hog Island was 1.19 m ± 0.05 m while the Duck FRF site mean was significantly greater ($z = -7.51$; $p < 0.001$) at 5.01 m ± 0.34 m (Table 2.1). Duck FRF elevation ranges were also greater (Table 2.1), reflecting the much wider variation across transects for these plots. It is noteworthy that even the maximum Hog Island plot elevation (2.20 m) is lower than the minimum Duck FRF plot elevation (2.36 m).

Edaphic characteristics

Soil chloride and pH values were greater and more widely varied on Hog Island than at Duck FRF (Figures 2.4 and 2.5). Mean soil chloride value for Hog Island was significantly greater ($z = 5.91$; $p < 0.001$) than Duck FRF, and varied widely between 101 and 125172 ppm with a mean of 12196 ± 4312 ppm (Figure 2.4; Table 2.2). Duck FRF soil Cl values ranged from 135 to 1152 ppm with a mean value of 333 ± 36 ppm (Figure 2.5; Table 2.2). At Duck FRF, all transect mean soil Cl values were lower than those measured for Hog Island; the lowest Hog Island transect mean value (1829 ± 781 ppm) was higher even than the maximum Duck FRF transect mean value (235 ± 24 ppm). Mean soil pH at Hog Island was 5.9 ± 0.1, while Duck soils were slightly but significantly ($z = 8.32$; $p < 0.001$) more acidic; mean soil pH for all Duck plots was 5.0 ± 0.1 (Table 2.2).

Plant Community Distributions

Species Richness and Cover— Woody and vine communities were similar at Hog Island and Duck FRF, with both sites dominated by *Morella* species. At Hog Island, *M. cerifera* thickets occupied much of the upland portion of the island across all transects, while stands of the congener *M. pensylvanica* occurred across all transects at Duck FRF. Woody species richness values at Hog Island and Duck FRF were 6 and 8, respectively (Table 2.3). Vine species richness values at Hog Island and Duck FRF were 8 and 7, respectively, and vine communities also were similar between the two sites. Presence of *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans, Vitis aestivalis* and *V. rotundifolia*, and similar *Rubus* and *Smilax* species was recorded at both (Table 2.3). Cover scores assigned for plots at each site showed a notable disparity between woody and vine cover for Hog Island, but similar values for Duck FRF (Figure 2.6). Of particular interest was the heavy woody cover and sparse vine cover observed on Hog Island transect 3, and the complete absence of vine species at Hog transect 4, a sample area representing the southern edge of woody expansion. Compared to the closely-matched cover scores for vines and woody plants at Duck FRF, this was suggestive of a relationship between woody species pre-existence and vine establishment.

Landscape Position— Across each transect, presence of woody and vine species were compared to physical characteristics of each plot. Elevation range of woody plant inhabited plots was greater at Duck FRF than at Hog Island; woody species presence ranged 0.76 - 1.73 m on Hog Island, and 2.63 – 7.24 m at Duck FRF (Figures 2.2 and 2.3). Vine species presence ranged 0.76 – 1.73 m on Hog Island and 2.36 – 8.14 m at Duck FRF; slightly higher at Duck due to the presence of *Smilax bona-nox* on dune ridges (Figures 2.2 and 2.3). With respect to distance to ocean shoreline, woody habitat range was 137 – 1278 m and 44 – 546 m for Hog Island and Duck FRF, respectively (Figures 2.2 and 2.3). Vine habitat range was 175 – 1175 m and 44 – 546 m for Hog Island and Duck FRF, respectively (Figures 2.2 and 2.3). No woody or vine species were present within 100 m of the shoreline on Hog Island transects, but logistic regression analysis did not indicate a significant effect of distance to shore on the presence of these species (Table 2.4). Logistic regression analyses did show significant relationships between elevation and woody species presence at Hog Island (β = -4.45; p = 0.007), and at Duck FRF (β = -0.70; p = 0.016) (Table 2.4). Further, vine species presence was significantly related to woody plant cover score at Hog Island (β = 0.47; p = 0.023), though the relationship was not significant at Duck (Table 2.4).

Edaphic Characteristics

No relationship was found between edaphic characteristics (soil Cl or pH) and presence of either woody species or vines, despite the significant difference in soil chloride levels between the two sites (Table 2.4).

Discussion

We compared physical characteristics and plant community composition of two differing coastal barrier habitats to investigate how the distribution of vine species in coastal regions may be differentially dependent on abiotic site physical characteristics and on plant community biotic interactions. Edaphic characteristics and presence / absence of woody and vine species relative to landscape position (Young *et al*., 2011) were compared to evaluate habitat ranges for representatives of each growth form and to determine relationships between site characteristics and plant community composition.

Site History

Comparison of physical characteristics between the two sites revealed significant differences between topographies, which relate to site histories and affect habitability by woody plant communities, and by extension, vine species presence. Hog Island and the Virginia barrier system in general are situated on an extremely active and dynamic coastline, and are experiencing greater erosion rates than other Mid-Atlantic barrier systems (Dolan, Hayden, and Lins, 1980); they are consequently lower in elevation and shorter lengthwise than other Mid-

Atlantic islands. These features are well-preserved and without the influence of recent human intervention; thus the VCR islands are subjected to the influence of storm events and sea level rise, including overwash and roll-over (Dolan, Godfrey, and Odum, 1973).

By comparison, Duck, NC and the Outer Banks in general have a long history of human influences including dune construction and stabilization, beach nourishment, and plantings and fertilization (Dolan, Godfrey, and Odum, 1973; Harris, Levy, and Perry, 1983; Magliocca, McNamara, and Murray, 2011). These efforts indirectly stabilize Duck FRF, though the site itself has not been the subject of stabilization projects or plantings since 1981 (Harris, Levy, and Perry, 1983). The artificially created and maintained dunes are higher and steeper than natural dunes, so storm-induced overwash and sea spray effects are greatly reduced (Havholm *et al.*, 2004), as seen in our soil chloride results. This protection from the influence of storms and past use of the FRF as a bombing range has contributed to a complex topography behind foredunes; however, the FRF may still be considered unstable over the long term (Dolan, Godfrey, and Odum, 1973; Magliocca, McNamara, and Murray, 2011). Elsewhere on the Outer Banks, well-developed maritime forests have persisted nearer the baysides of wider islands, but Duck may not be expected to continue development into self-stabilizing maritime forest (similar to Nags Head or Kitty Hawk Woods), given sufficient time (Havholm *et al.*, 2004). Duck FRF is a particularly narrow segment of land which has been largely cut off from natural sand addition (overwash) by artificial dune stabilization, so migration of dunes and large-scale, long-term site stability that would facilitate maritime forest development are unlikely. These differences in location, geomorphic processes, and human influence presumably contribute to observed differences in woody communities and associated vines.

Landscape Position

Duck FRF has more varied topography and greater elevations than Hog Island due largely to artificial maintenance and stabilization of neighboring dunes, but Hog Island encompasses a far greater range of distances from shoreline due to its natural state. Logistic regression analysis indicated that, for both sites, woody plant distribution patterns are significantly related to elevation, but not to distance to shoreline. While previous research has shown that woody plant distribution across barrier island habitats may be determined by edaphic characteristics, especially total soil chloride concentration (Wijnholds and Young, 2000; Young, Erickson, and Semones, 1994) and pH (Houle, 2008), such patterns were not observed in our study. Elevation above sea level and distance to shoreline are considered to be integrative predictors of woody plant distributions in these systems (Ehrenfeld, 1990; Young *et al*., 2011), and our analyses reinforced the relationship of woody species with elevation, though not with distance to shore. However, the absence of both woody and vine species on Hog Island transects less than 100 m from the ocean demonstrates that distance to shoreline is important within a short range of the ocean front. Low elevation exaggerates many coastal stressors within close proximity to the shoreline (Ehrenfeld, 1990). By comparison, at Duck FRF, woody and vine presence within 100 m of the ocean front at all transects may be facilitated by the greater primary dune elevation and associated protection from high winds, sea spray, and overwash events. This tradeoff between spatial and topographical range is reflected by species richness values, which at Hog Island and Duck FRF were very similar at 13 and 14, respectively, despite the far larger area (~1200 ha) sampled on Hog Island. The high level of topographic variation due to land management history and the resulting habitat heterogeneity may provide for this relatively high species richness in a smaller area (~80 ha) at Duck FRF (Crawford, Marcucci, and Bennett, 2013; Stallins and Parker, 2003).

Edaphic Characteristics

Soil chlorides were universally greater on Hog Island, due partly to the inclusion of bayside salt marsh plots inhabited by the shrub, *Iva frutescens* (Young, Erickson, and Semones, 1994), and partly to the low topographic character of Hog Island, enabling greater overwash and reach of sea spray (Stallins and Parker, 2003). Soils at Hog Island were less acidic compared to Duck FRF. Neither soil Cl concentration nor soil pH was significantly related to woody or vine presence at either site. In addition, neither soil Cl nor soil pH was related to elevation above sea level at either site. Differences between site soil chloride values warrant further investigation, as there was no significant effect of soil chloride on shrub or vine presence / absence, despite the wide range of soil chloride found at Hog Island. However, intensive sampling including a wider temporal range incorporating pre- and post-storm measurement would be necessary to properly evaluate the importance of soil Cl in plant distributions at these sites.

Plant Community Patterns

While vine presence / absence was not directly related to the physical environment, the significant relationship between vine presence and woody cover score highlights the indirect effect of physical characteristics on vine presence. With the exceptions of *Smilax bona-nox* at Duck FRF and *Mikania scandens* at Hog Island, no vines occurred independently of woody vegetation. This relationship can be attributed to the similar physical limits of both woody species and vines; these plants largely share the same habitat requirements, including edaphic characteristics, protection from ocean and storm impacts, and access to freshwater (Young *et al*., 2011). Further, in both habitats, the primary woody colonizer is a nitrogen-fixing shrub of the genus *Morella*, and both *Morella* species form dense monospecific thickets following colonization (Harris, Levy, and Perry, 1983; Young, Erickson, and Semones, 1994). These actinorhizal shrub species facilitate colonization of other species by increasing soil nitrogen and organic matter content (Brantley and Young, 2010).

Following these soil modifications, vines have an advantage due to their rapid growth, comparatively low investment in support tissues, and exploitation of existing vegetation structure (Putz, 1983). As "structural parasites," vines are therefore most successful in areas where woody plants are well established, and may be expected to become more prevalent as well, following the well-documented expansion of woody species in a wide range of habitats (Knapp *et al.*, 2008; Zinnert *et al.*, 2011). Hog Island transect 4, which has no vine cover, represents a front of expansion for *Morella cerifera*, and as these now-healthy thickets further age and begin to experience decline, vine species may be expected to colonize following the pattern observed in older thickets (e.g. transects 1 and 2) on Hog Island. This pattern was not observed at Duck FRF, and this may be attributed to the differences in landscape management between the two sites.

Conclusion

When considered as a single functional group, woody plant distribution was significantly related to elevation above sea level, but not to distance from shoreline, soil chloride, or soil pH, perhaps due to the narrow range of tolerances exhibited among the species considered (Young *et al.*, 2011). These findings seem in partial contrast to past studies in this area, which have indicated that both elevation and distance to shoreline impact coastal plant community distributions (Ehrenfeld, 1990; Young *et al.*, 2011). However, this comparison between community drivers at an essentially natural site and a managed one suggests that in a compressed landscape, greater topographic variation can act as a substitute for greater distance to shoreline by providing similar protection against shoreline-related stressors. Woody plants often occurred independently, but when considered as a single functional group, vine distribution was significantly related to woody plant cover, but not to other environmental characteristics. At the naturally-developing landscape of Hog Island, this relationship and the progression of succession is apparent as younger shrub canopies (i.e. southern and eastern fronts of woody expansion) exhibit less or no vine colonization compared to older, more advanced sites. While the stable, formerly-managed nature of the Duck FRF has enabled a community assemblage comparable to that of the much larger Hog Island, Duck will be more vulnerable in the near future, due to its species and associated communities' decreased ability to shift with imminent environmental presses. Future studies should address the distributions of individual species at these sites, and investigate the question of species-specific preferences by vines for woody substrate plants, which have yet to be thoroughly quantified.

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Table 2.1: Elevation (m) by site and transect for Hog Island, VA and Duck FRF, NC. All plot elevations were greater at Duck FRF than at Hog Island, as were means and ranges by both site and transect. Site mean elevations were significantly ($p \leq 0.05$) different.

	Plots	**Mean ± SE**	**Max.**	**Min.**	**Range**
Hog Island T1	n = 22	1.17 ± 0.06	1.98	0.82	1.16
T2	n = 9	1.20 ± 0.12	1.73	0.76	0.98
T3	n = 6	1.30 ± 0.12	1.79	0.87	0.91
T4	n = 7	1.16 ± 0.21	2.20	0.76	1.44
Total	n = 44	1.19 ± 0.05	2.20	0.76	1.45
Duck FRF T1	n = 11	5.88 ± 0.50	8.14	2.65	5.49
T2	n = 10	5.27 ± 0.80	10.16	2.64	7.52
T3	n = 12	3.99 ± 0.37	6.36	2.36	4.00
Total	n = 33	5.01 ± 0.34	10.16	2.36	7.80

Table 2.2: Summary of edaphic characteristics for Hog Island, VA and Duck FRF, NC. Values are mean ± SE. Maximum, minimum, and range are included for soil Cl to illustrate variability between both transects and sites. Site mean soil pH values and mean soil Cl values were significantly ($p \leq 0.05$) different.

	Soil pH	**Soil Cl**	**Cl Max.**	**Cl Min.**	**Cl Range**
Hog Island T1	5.3 ± 0.2	18434 ± 8592	125173	157	125016
T2	6.4 ± 0.1	14804 ± 8658	79850	104	79746
T3	6.1 ± 0.1	1829 ± 781	5279	101	5178
T4	6.5 ± 0.1	2580 ± 1004	6557	420	6137
Total	5.9 ± 0.1	12196 ± 4312	125173	101	125072
Duck FRF T1	4.9 ± 0.1	461 ± 91	1152	208	944
T2	5.1 ± 0.2	310 ± 34	525	189	336
T3	5.1 ± 0.2	235 ± 24	410	135	275
Total	5.0 ± 0.1	333 ± 36	1152	135	1017

Table 2.3: Listing of woody and vine species and species richness for Hog Island, VA and Duck FRF, NC study transects.

Trees / Shrubs	**Hog Island**	**Duck FRF**
Aralia spinosa (Araliaceae)	-	+
Baccharis hamilifolia (Asteraceae)	+	+
Diospyros virginiana (Ebenaceae)	-	+
Iva frutescens (Asteraceae)	+	-
Juniperus virginiana (Cupressaceae)	+	-
Morella cerifera (Myricaceae)	+	-
Morella pensylvanica (Myricaceae)	-	+
Persea borbonia (Lauraceae)	+	+
Prunus serotina (Rosaceae)	+	+
Quercus virginiana (Fagaceae)	-	+
Zanthoxylum clava-herculis (Rutaceae)	-	+
Woody Species Richness	**6**	**8**
Vines		
Lonicera japonica (Caprifoliaceae)	+	+
Mikania scandens (Asteraceae)	+	-
Parthenocissus quinquefolia (Vitaceae)	+	+
Rubus spp. (Rosaceae)	+	+
Smilax spp. (Smilacaceae)	+	+
Toxicodendron radicans (Anacardiaceae)	+	+

Vitis aestivalis (Vitaceae)	+	+
Vitis rotundifolia. (Vitaceae)	+	+
Vine Species Richness	**8**	**7**
Total Richness	**14**	**15**

Table 2.4: Logistic regression analysis summary with *p*-values for each analysis shown and significant values ($p \leq 0.05$) indicated with *. Woody species presence was significantly related to elevation at both sites. Vine presence was significantly related to woody cover score at Hog Island, but not to other environmental variables.

		Elevation (m)	**Distance to shoreline (m)**	**Soil Cl**	**Soil pH**	**Woody cover score**
Hog Island	**Woody**	*0.007	0.108	0.551	0.075	--
	Vine	0.642	0.131	0.097	0.959	*0.023
Duck FRF	**Woody**	*0.016	0.130	0.171	0.384	--
	Vine	0.884	0.515	0.488	0.711	0.177

Figure Legends

Figure 2.1: Site locations along Mid-Atlantic U.S. coastline. (a) Four transects were established across Hog Island, VA. (b) Three transects were established across the Duck FRF site in NC.

Figure 2.2: Transect elevation profiles for Hog Island, Virginia, showing woody species presence at majority of plots and almost no independent vine presence. Closed circles denote presence of woody vegetation, open squares denote vines. Higher elevation and lack of both woody and vine species presence on dune ridges is apparent $\leq$ 100 m from shoreline.

Figure 2.3: Transect elevation profiles for Duck FRF, North Carolina. Closed circles denote presence of woody vegetation, open squares denote vines. A greater elevation range compared with Hog Island is apparent. Woody species are present in nearly all plots, and independent vine presence is rare. Note presence of both growth forms within 100 m of shoreline at all transects.

Figure 2.4: Soil Cl (mean ± SE) for each plot along Hog Island transects. There is wide variability of soil Cl and very high salinity in northern bayside marshy areas. No significant ($p \leq 0.05$) relationship was detected between soil Cl and woody / vine species presence at either site.

Figure 2.5: Soil Cl (mean ± SE) for each plot along Duck FRF transects. Duck FRF exhibited smaller range and lower values of soil Cl.

Figure 2.6: Cover scores (0-5; mean ± SE) by transect for Hog Island and Duck FRF. Hog Island Transects 3 and 4 had little or no vine presence, as these woody communities are younger,

still expanding, and not yet subject to extensive deterioration, though T3 may be expected to resemble T2 in the near future. Duck FRF transects are more similar to each other, partly as a result of greater stability.

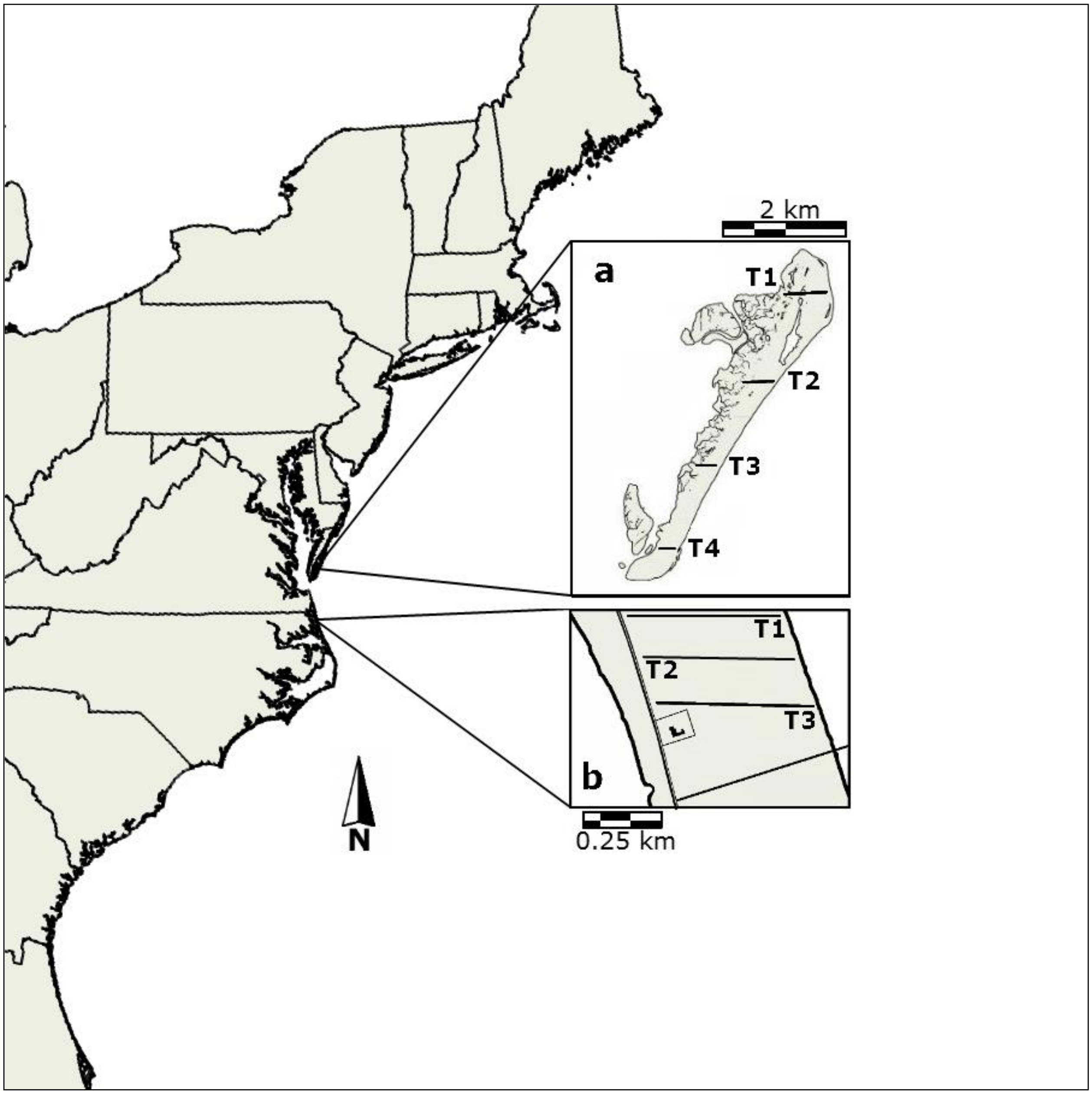


Figure 2.1

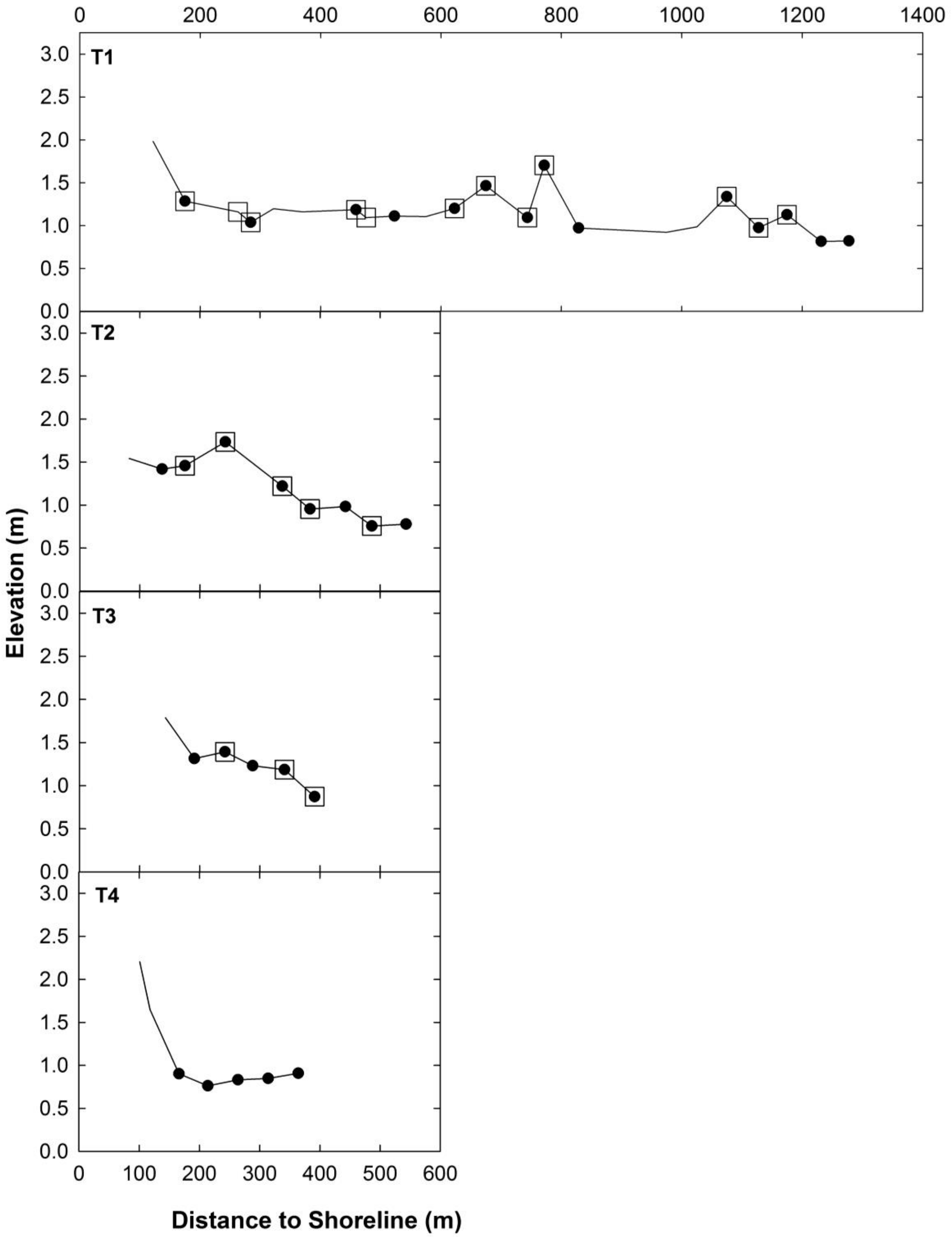
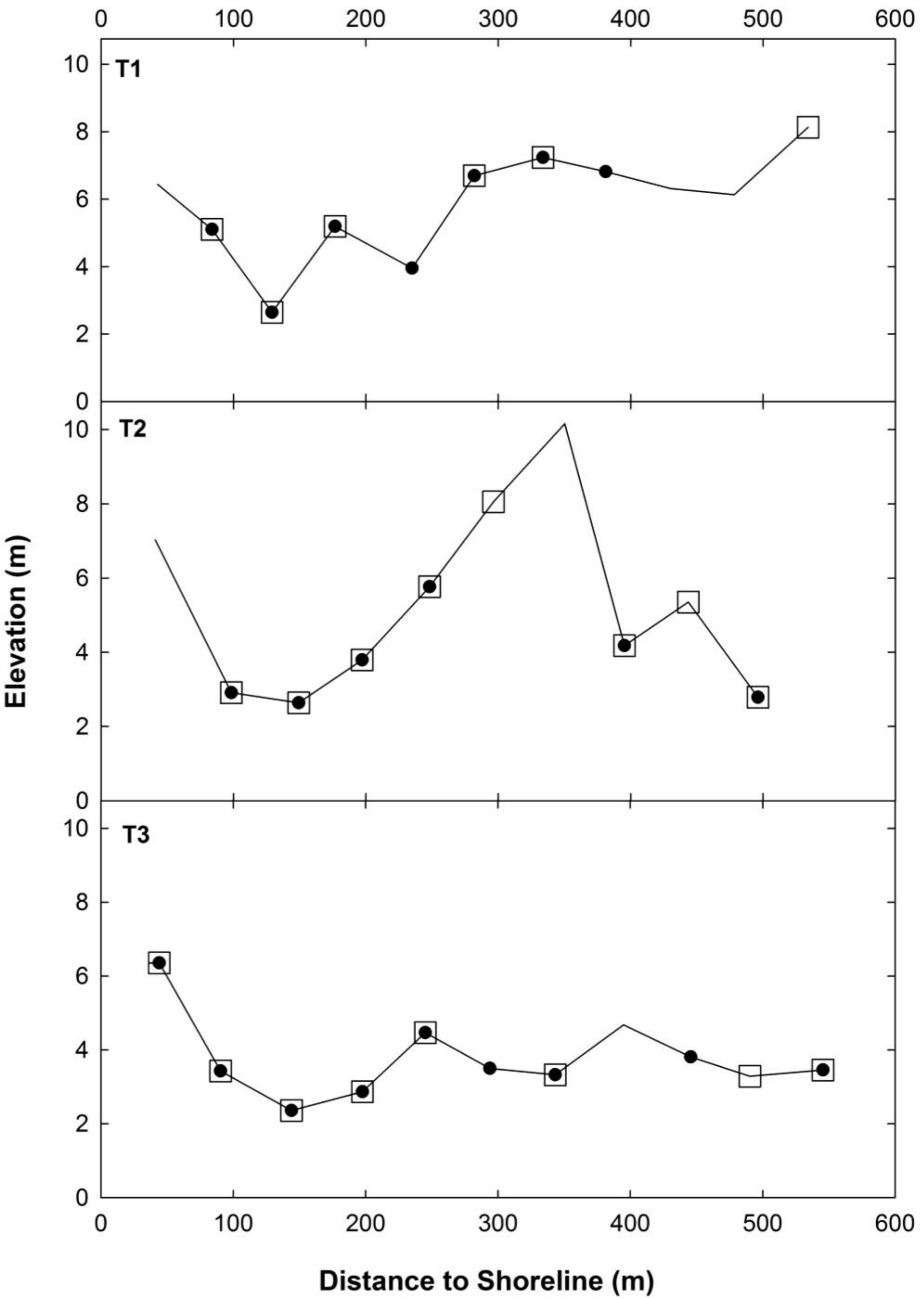
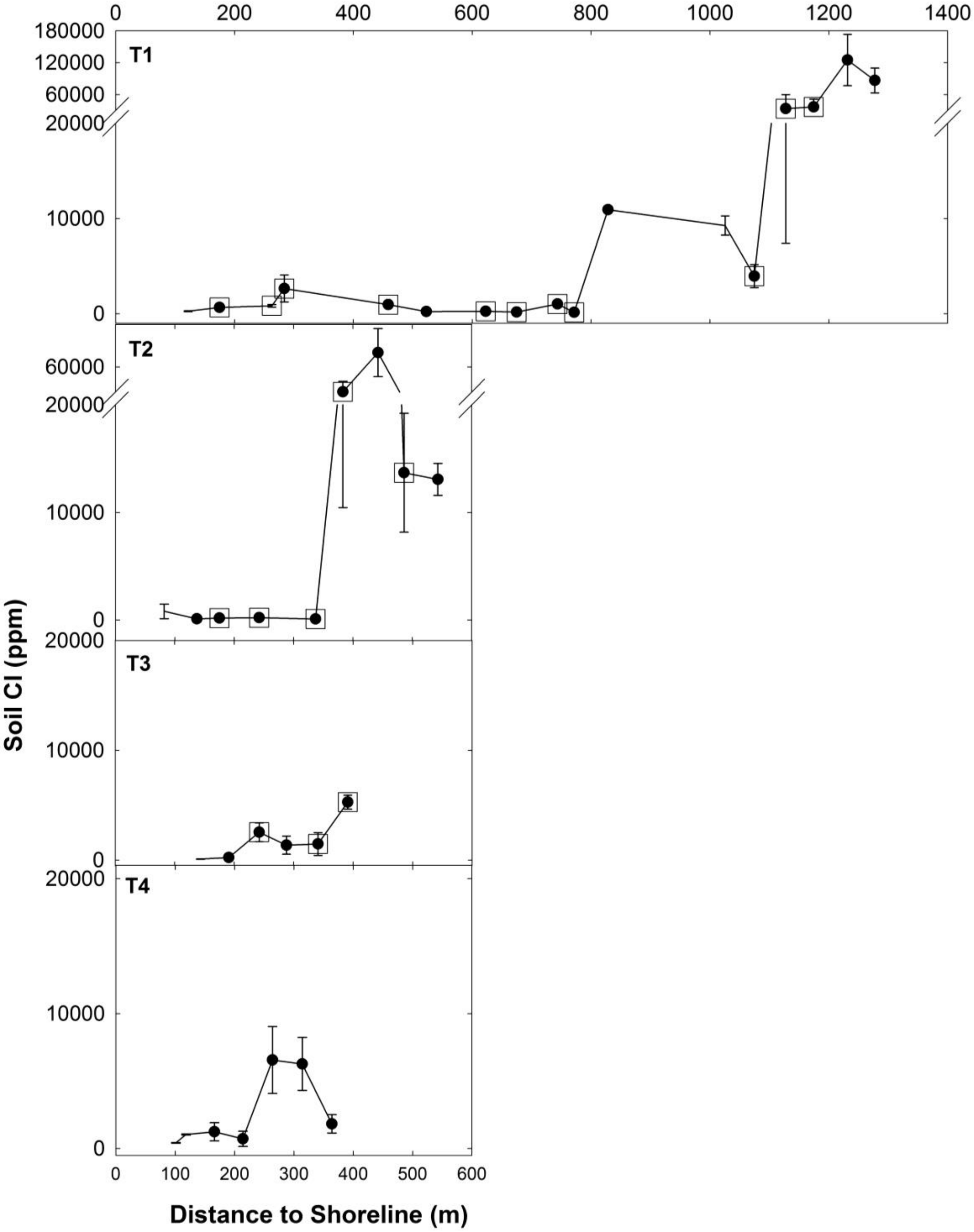

0
200
400
600
800
1000
1200
1400
T1
T2
T3
T4
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Elevation (m)
0
100
200
300
400
500
600
Distance to Shoreline (m)

Figure 2.2



T1
T2
T3
Elevation (m)
Distance to Shoreline (m)
0
100
200
300
400
500
600
0
2
4
6
8
10

Figure 2.3


T1
T2
T3
T4
0
200
400
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800
1000
1200
1400
180000
120000
60000
20000
10000
0
60000
20000
10000
0
20000
10000
0
20000
10000
0
Soil Cl (ppm)
0
100
200
300
400
500
600
Distance to Shoreline (m)

Figure 2.4

Figure 2.4

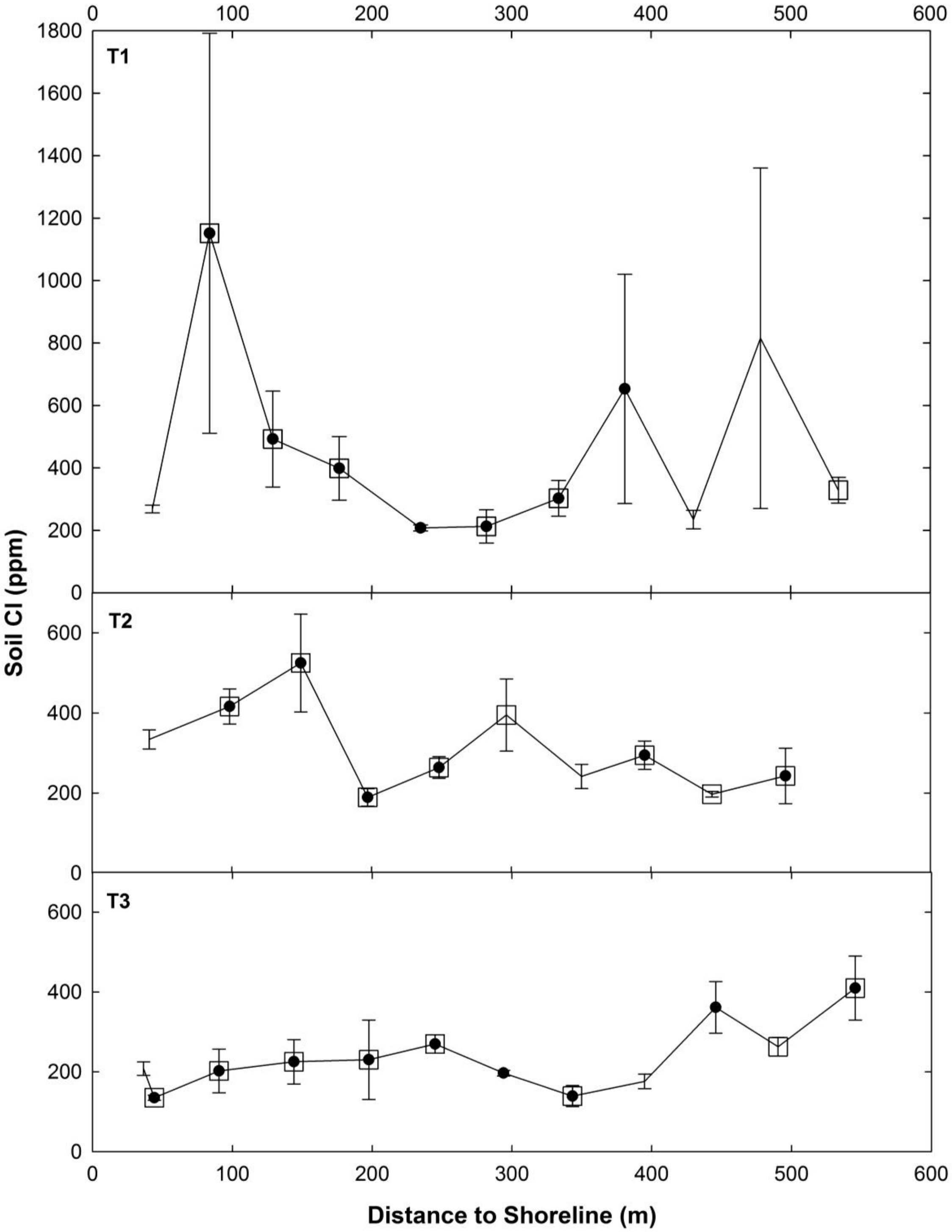

Figure 2.5

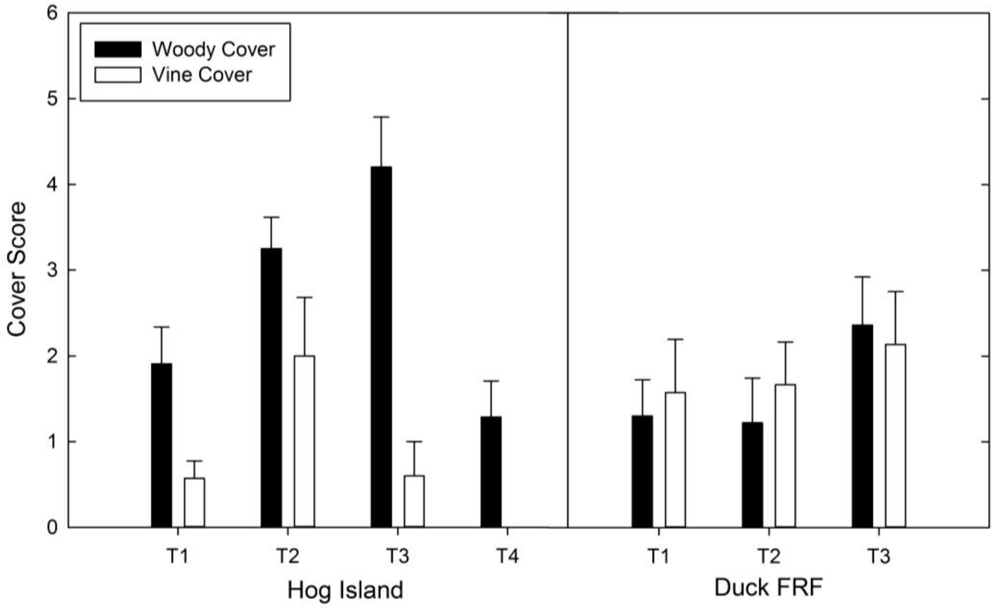
Woody Cover
Vine Cover
Cover Score
0
1
2
3
4
5
6
T1
T2
T3
T4
Hog Island
T1
T2
T3
Duck FRF

Figure 2.6

CHAPTER THREE

SHRUB ENCROACHMENT FACILITATES LIANA EXPANSION AND AFFECTS PHYSICAL STRUCTURE IN TEMPERATE COASTAL COMMUNITIES

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Abstract

Successional theory historically has predicted linear progression through a series of environment-modifying communities, resulting in a highly stable climax community. A recent surge of interest in the concept of alternate stable states focuses on non-linear progression. Both frameworks have been successfully applied to coastal ecosystems, where biotic facilitation and competition occur amidst strong abiotic drivers. The concept of arrested succession or recalcitrant states also suggests that alternate stability may be only temporary within the process of succession. We evaluated shrub / tree and liana communities at barrier island sites in Virginia and North Carolina to determine the extent to which environmental variables affect plant distributions, whether species-specific phytosociological associations existed, and what changes in community structure result from liana infiltration of woody canopies. These two mid-Atlantic barrier island sites share similar plant communities but differ in geomorphology and management history. Dominant species were *Morella* shrubs, with high frequencies of the lianas *Parthenocissus quinquefolia, Smilax* spp., and *Rubus* spp. We identified woody and liana species, counted individuals, and assigned cover scores. Soil chloride and pH were measured across each site, and we evaluated woody and liana species distributions with respect to environmental variables. We tested for associations between lianas and woody species using correlative and multivariate analyses. Species-specific associations were not observed, but woody plant distributions were significantly correlated with environmental variables at the Virginia site. Liana distribution was correlated with woody species presence and diversity, and at the northern site, there was a relationship between prevalent liana species and presence of *Morella cerifera* and *Prunus serotina*. We observed a lack of maritime forest development at

both sites, and suggest that the expansion of both liana and shrub species may have a synergistic effect in preventing or delaying maritime forest re-establishment.

Introduction

Coastal ecosystems are subjected to numerous unique stressors by virtue of their generally low relief, close proximity to salt water, and vulnerability to storm events (Ehrenfeld 1990, Stalter and Odum 1993, Young et al., 2011). In addition, abiotic stressors such as nutrient and freshwater limitations, windblown sand, temperature and light extremes, and storm events severely limit plant establishment and success in these habitats, and anticipated effects of global change may be anticipated to intensify these challenges (Ehrenfeld 1990, Naumann et al. 2009). Frequent large-scale disturbances may set back community development to earlier successional stages or re-direct succession in an altered trajectory (Hayden et al. 1991, Hayden et al. 1995). Many of these abiotic factors can be coarsely integrated by the concept of landscape position (Young et al. 2011). In the barrier island context, landscape position defines plant species distributions by distance to shoreline and elevation, two variables that integrate multiple abiotic factors (Ehrenfeld 1990, Young et al. 2011). These complex factors not only interact to limit the development of long-term stable plant communities, but also result in multiple successional stages across a chronosequence (Ehrenfeld 1990, Day et al. 2001, Miller et al. 2010). Secondary succession is readily observed at the patch and landscape scales (Crawford and Young 1998*b*, Miller 2015), while primary succession is observable at smaller spatial and temporal scales due to the frequency and severity of disturbances, particularly in the highly dynamic mid-Atlantic region of North America (Dolan et al. 1980, Hayden et al. 1995, Miller et al. 2010).

Classical ecological theory suggests that in many habitats, a linear progression through early, mid, and late-successional communities proceeds to a point at which a slow-growing and highly interconnected climax community results (Clements 1936, Odum 1969, Pickett et al. 1987, Levy 1990, Pickett and Cadenasso 2005). Recent renewed interest in alternate stable state theory places a greater emphasis on the concept that some systems also exhibit non-linear changes from one stable equilibrium state to another (Beisner et al. 2003, D'Odorico et al. 2012, Bowman et al. 2015). Both frameworks have been applied to coastal systems in general, and to barrier islands in particular (Odum 1969, Ehrenfeld 1990, Hayden et al. 1995, Crawford and Young 1998*a*, Jiang et al. 2013). Frequent disturbance and successional processes are readily observed, but a true climax community may never be reached (Levy 1990, Hayden et al. 1991).

Both herbaceous lianas and woody lianas (hereafter jointly referred to as lianas) play important ecological roles in forests and other plant communities, particularly with regard to succession. Lianas depend on and compete with existing tree and shrub species (hereafter, woody plants) (Whigham 1984, Dillenburg et al. 1993, Hegarty 1991, Young et al. 1995, Schnitzer and Bongers 2002, Londré and Schnitzer 2006). Lianas have long garnered interest for their structure-parasitizing growth strategies, and this growth form is advantageous in colonization of new habitat. In the mid-Atlantic region, most liana species are also bird-dispersed (Ehrenfeld 1990, Levy 1990, Shiflett et al. 2013), facilitating colonization to and across the landscape. Canopy gaps in woody communities caused by storm events and onset of shrub senescence provide establishment sites for lianas where abundant soil resources and protection from abiotic stresses are available, and seed rain is high (Ehrenfeld 1990, Crawford and Young 1998*a, b*, Mabey et al. 1998, DeWalt et al. 2000, Brantley and Young 2008).

Canopy gaps occur extensively in the shrub thickets of mid-Atlantic barrier islands, which encourage bird-dispersed seed deposition, provide shelter for seedling establishment, and ameliorate low-nutrient soil conditions via symbiotic nitrogen fixation and organic matter deposition (Wijnholds and Young 2000, Brantley and Young 2008). Initial exclusion of other plant species by dense shrub canopies gives way to facilitation as senescence and external physical stressors create gaps in monospecific thickets (Crawford and Young 1998*b*, Shiflett and Young 2010). As lianas establish and expand to permeate the canopies of woody vegetation, the resulting community increases in species diversity and typically progresses through a coastal sere towards maritime forest (Stalter and Odum 1993), provided that the physical environment remains sufficiently stable. As communities develop, liana establishment both accelerates the decline of the woody community and encourages seed rain which will develop the post-shrub forest (Young et al. 1995, Ladwig and Meiners 2009).

We studied species-specific establishment and association patterns of lianas and woody plants at two barrier island sites, to focus our inquiry on the interactions within a relatively simple plant community assemblage in a highly dynamic physical environment with understood abiotic patterns (Oosting and Billings 1942, Ehrenfeld 1990, Hayden et al. 1991, Stalter and Odum 1993). At these sites, successional processes are limited spatially and temporally, and this facilitates a more focused appraisal of between-species interactions (Walker and Wardle 2014). We investigated individual liana species preferences for environmental microhabitat characteristics, as well as phytosociological relationships to the woody support species and possible influences on successional transitions between coastal plant communities. Our sites, selected off the coasts of Virginia and North Carolina, were distant enough from one another to represent entirely unconnected systems but sufficiently similar in climate and species composition to allow comparison. Differences between site topographies affect environmental variables and community distributions, and differences in management history and strategy affect storm response and influence on plants and geomorphology.

Methods

Study sites

Field research was conducted on Hog Island, in Northampton County, VA (37° 27' N, 75° 40' W) and at the Duck Field Research Facility (FRF) in Dare County, NC (36° 11’ N, 75° 45’ W), ~137 km south (Fig. 3.1). Hog Island is part of the National Science Foundation-funded Virginia Coast Reserve Long-Term Ecological Research (VCR LTER) site, and is owned and managed by The Nature Conservancy. The island is ~12 km in length, and ~2 km across at its widest point. It has been unoccupied since the mid-1930s and persists as a natural barrier island of low elevation (mean elevation approximately 6 m) with oceanfront strand and grassland habitat, grass- and forb-colonized dune / swale complexes, expanding shrub thickets, isolated patches of maritime forest, inland freshwater ponds and marshes, and bayside salt marshes (Badger and Kellam 1989, Levy 1990, Hayden et al. 1991, Shao et al. 1996, Young et al. 2007).

The Duck FRF is a former (1941-1965) US Navy bombing range that is currently maintained as a ~1 km stretch of naturalized shoreline and island habitat, up to 0.70 km wide (Harris et al. 1983). The FRF and surrounding areas underwent significant artificial stabilization efforts beginning in the 1930s, and while these activities at the FRF itself were discontinued in 1981, stabilization via dredged sand addition continues for the beach, for the primary dune and for adjacent inhabited areas north and south (Dolan 1972, Harris et al. 1983). Mean elevation of the Duck FRF site is approximately 5 m greater than that of Hog Island. Vegetation is patchy, consisting of discontinuous shrub thickets and tree islands with large areas of bare sand in between. General site environmental characteristics have been previously described by Bissett et al. (2014), and showed the Duck FRF site to be more complex topographically, narrower from ocean to lagoon, more acidic, and lower in total soil chloride content as compared to Hog Island. Higher elevations at Duck FRF may confer similar protection from shoreline stressors as has been noted at Hog Island, where distance from the shoreline ameliorates exposure (Naumann et al. 2009, Young et al. 2011).

Plot selection and sampling

To avoid biases toward specific plots or communities, transects and plots were selected using orthorectified aerial imagery, and initially visited in June and July of 2011. Aerial imagery was acquired using Google Earth (version 7.0.2) and coordinates were recorded in degree-minute-second format according to the 1984 World Geodetic System format. We established seven east-west cross-island transects with plots spaced 50 m equidistant; four on Hog Island and three at Duck FRF (Fig. 3.1). Per plot, woody and liana species were identified using floristic manuals (Radford et al. 1968, Duncan and Duncan 1987, Weakley et al. 2012), and stems were counted within a 3 m radius of plot central point. Canopy coverage by lianas and by woody species was scored on a scale of 0 (no coverage) to 5 (coverage $\geq$ 90%). Basal area was not measured, as it is unrelated to liana effects on woody vegetation in temperate habitats (Ladwig and Meiners 2009) and presented a considerable logistical challenge in shrub thickets and tree islands.

For soil total chloride and pH analysis, samples ($n_{Hog} = 116$; $n_{Duck} = 98$) were collected at the center, 5 m north, and 5 m south of each plot. Samples were oven-dried for 72 h at 80 °C. Soil pH and total chloride content analysis by water extraction followed Wijnholds and Young (2000). 50 g from each soil sample was mixed with 200 mL of deionized water. pH was measured with a calibrated pH electrode (Hanna Instruments, Woonsocket, Rhode Island, USA). For soil chloride analysis, 4 mL of 5 M $NaNO_3$ was added as an ionic equalizer, and chloride content was determined with a chloride electrode (Accumet, Fisher Scientific, Pittsburgh, Pennsylvania, USA).

Elevation and distance to shoreline for each plot were determined with remotely-sensed data. Plot distances perpendicular from shoreline were derived from geo-rectified aerial imagery, and Lidar data were used for elevation measurements. Plot elevations for analyses were averaged from all Lidar last (ground) returns within a 5 m radius of each central point. Hog Island Lidar data were collected in July 2011 (Tuck Mapping Solutions, Inc., Big Stone Gap, Virginia, USA), using a Riegl LMS-Q680i system (Riegl Laser Measurement Systems GmbH, Horn, Austria), with full waveform capability operating at 400 kHz pulse repetition frequency, mounted on a Bell 407VFR helicopter. System accuracy was ± 20 mm; precision was ± 20 mm. Duck FRF Lidar data were retrieved from the National Oceanic and Atmospheric Administration’s (NOAA) Digital Coast program online database. Horizontal accuracy for NOAA Lidar data is at least ± 2.0 m, and vertical accuracy is ± 0.15 m root-mean-square-error in open areas. Data were post-processed using geo-referenced ground points and known-elevation reference points including USGS survey monuments. Lidar data were analyzed using Quick Terrain Modeler software version 8.0.3.4 (Applied Imagery, Chevy Chase, Maryland, USA).

Analyses

Species importance values were determined using a relative abundance calculation (Derksen et al. 1993) to incorporate relative density and relative frequency of each species at each site and within the two functional groups: woody and liana. For each functional group and for each site, summary values for environmental variables were calculated (Table 3.1). We performed Sorensen-distance Mantel analyses to test for environmental controls of plant community composition at plots (PC-ORD 5.33 for Windows, MjM software, Gleneden Beach, Oregon, USA). Sorensen-distance Bray-Curtis ordinations with variance-regression endpoint selection were used to evaluate plot differences based on species composition at each plot, and to identify the strength of environmental variables (distance from shoreline, elevation above sea level, soil pH, total soil Cl) as community drivers (PC-ORD 5.33). Pearson correlation analyses of liana abundance, liana cover score, and liana species richness versus woody species richness and cover score for each site were conducted (JMP Pro 11.0.0, SAS Institute, Inc., Cary, North Carolina, USA). Pearson correlations of environmental variables were also evaluated (JMP Pro 11.0.0).

Results

Community Structure

Species diversity of shrubs, trees, and lianas was low at both sites. Shannon-Wiener diversity index values were 0.82 for Hog Island, and 0.43 at Duck FRF. Liana species compositions were similar between study sites, with few exceptions. The native species, *Parthenocissus quinquefolia* L. Planchon (Vitaceae) (PAQU) and *Toxicodendron radicans* L. (Anacardiaceae) (TORA), and invasive *Lonicera japonica* Thunb. (Caprifoliaceae) (LOJA), were common to both sites (Fig. 3.2a). Natives *Smilax bona-nox* L.*, S. glauca* Walter, and *S. rotundifolia* L. (Smilacaceae) were also identified, and were pooled as *Smilax* spp. (SMSP), due to difficulty in distinguishing *Smilax* species at ground level, often within dense shrub understory where simultaneous access to both leaves and stems for verification was impossible. Intra-specific variation in morphology further complicates definitive identification (Steyermark 1963), but the growth strategy and community role of these lianas were deemed similar enough to permit combination (Duncan and Duncan 1987). *Mikania scandens* L. (Asteraceae) (MISC), *Rubus argutus* Link (Rosaceae) (RUAR), and *Vitis labrusca* L. (Vitaceae) (VILA), were documented only on Hog Island, and *Rubus trivialis* Michaux (Rosaceae) (RUTR) and *Vitis aestivalis* Michaux (Vitaceae) (VIAE) were limited to Duck FRF. The congeners, *S. rotundifolia, S. bona-nox,* and *S. glauca,* were pooled as *Smilax* spp., due to difficulty in distinguishingMost frequently occurring liana species were *P. quinquefolia* and *R. argutus* at Hog Island and *Smilax* spp. and *R. trivialis* at Duck FRF (Fig. 3.2a). Liana species richness at Hog Island and at Duck FRF were seven and six, respectively, and liana species diversity values (Shannon H') were 0.58 and 0.32, respectively.

Liana species compositions were more similar between sites than were shrub / tree species compositions. Woody species richness values were six and eight at Hog Island and Duck FRF, respectively (Fig. 3.2b). The sites shared three species and had no documented woody exotics. Species with highest importance values at both sites were *Morella* shrubs: evergreen *M. cerifera* L. Small (Myricaceae) (MOCE) at Hog Island and deciduous *M. pensylvanica* Mirbel Kartesz (Myricaceae) (MOPE) at Duck FRF. *Baccharis halimifolia* L. (Asteraceae) (BAHA), *Persea borbonia* L. Sprengel (Lauraceae) (PEBO), and *Prunus serotina* Ehrhart (Rosaceae) (PRSE) were found at both sites. *Iva frutescens* L. (Asteraceae) (IVFR) and *Juniperus virginiana* L. (Cupressaceae) (JUVI) were found only at Hog Island. *Aralia spinosa* L. (Araliaceae) (ARSP), *Diospyros virginiana* L. (Ebenaceae) (DIVI), *Quercus virginiana* Miller (Fagaceae) (QUVI), and *Zanthoxylum clava-herculis* L. (Rutaceae) (ZACL) were found only at Duck FRF. Woody relative density and relative frequency were positively correlated for both sites, but more strongly at Duck FRF (r = 0.85) than at Hog Island (r = 0.30), due to extremely high densities of *M. pensylvanica* stems in near-shore plots. Shrub / tree species diversity values were 0.45 and 0.20 at Hog Island and Duck FRF, respectively.

Relationships to environmental variables

Results of multivariate analyses differed conspicuously between sites. At Hog Island, a Mantel test of all plots considering all species in both functional groups indicated a strong and significant ($p < 0.01$; r = 0.37) relationship with environmental variables. When separated by functional group, a significant correlation remained for woody species ($p < 0.01$; r = 0.46), but was absent for lianas ($p < 0.40$; r = 0.07). Bray-Curtis ordination showed strong clustering of liana species around dominant woody species at Hog Island, especially *M. cerifera* and *P. serotina*, with the strongest drivers being elevation ($r_{\text{axis 1}} = 0.68$; $r_{\text{axis 2}} = -0.22$) and total soil chlorides ($r_{\text{axis 1}} = -0.48$; $r_{\text{axis 2}} = 0.66$; Fig. 3.3). Soil pH ($r_{\text{axis 1}} = -0.40$; $r_{\text{axis 2}} = -0.16$) and distance from shoreline ($r_{\text{axis 1}} = -0.22$; $r_{\text{axis 2}} =0.48$) were weaker drivers, but were related to one another (Table 3.2), and are also thought to co-vary across the significant physical gradients of this barrier island landscape (Dilustro and Day 1997, Young et al. 2011). While liana species composition at Hog Island plots was not related to abiotic environmental gradients, significant correlations of liana cover score with woody cover score, and of liana species richness with both woody cover score and woody species richness were found (Table 3.3).

At Duck FRF, environmental variables showed no relationship to plant community compositions. Mantel test results showed no significant correlations between species composition and environmental variables ($p > 0.08$; r < 0.171). Bray-Curtis ordination results also showed no clustering of species, and no evidence of abiotic environmental drivers on distributions of plots with regard to species composition (Fig. 3.4). Despite lack of strong significant species relationships, correlations existed at the functional group level, between liana cover score and woody richness and cover score, and between liana species richness and woody richness and cover score (Table 3.3).

Discussion

Interacting and possibly synergistic effects of woody plant expansion, shrub thicket re-establishment, and liana proliferation may alter successional processes in coastal environments. Our study suggests that woody communities on stable, unmanaged mid-Atlantic barrier islands are demonstrating arrested succession, rather than progressing towards maritime forest which occupied the sites prior to disturbance. As shrub thickets senesce and decline, gaps foster increasing establishment of tree species and development of maritime forest, provided that the physical environment remains sufficiently stable (Levy 1983, Levy 1990, Ehrenfeld 1990, Crawford and Young 1998*b*). However, maritime forest was not identified at either site, and isolated tree islands, self-reinforcing shrub thicket and liana tangle gaps are the most stable woody communities (Harris et al. 1983, Crawford and Young 1998*a*). Liana expansion through canopies can accelerate canopy collapse and contribute to gap formation, depending on forest age and storm events (Putz 1984, Garrido-Pérez 2008). Success of lianas has been linked to existing woody communities in terms of both competition and facilitation, particularly with regard to liana climbing strategy and woody species and community characteristics (Dillenburg et al. 1993, Carter and Teramura 1988, Nabe-Nielsen 2001, Campanello et al. 2007, Nesheim and Økland 2007, Leicht-Young et al. 2010, Pasquini et al. 2015). In the mid-Atlantic coastal region, lianas establish early in the lifespan of woody communities, both accelerating woody species decline and encouraging seed rain (Young et al. 1995, Ladwig and Meiners 2009). Because differences between structural host species and community composition can affect type and rate of liana colonization and expansion (Carter and Teramura 1988, Campanello et al. 2007, Leicht-Young et al. 2010), colonizing species assemblage and successional processes may be affected (Schnitzer and Bongers 2002, Ladwig and Meiners 2009, Schnitzer and Bongers 2011).

Strong correlations existed between liana frequency and woody vegetation, especially in the unmitigated environment of Hog Island, where stronger correlations also existed between woody plant distributions and environmental factors. Multivariate analysis demonstrated a significant correlation of environmental factors with woody species distribution at Hog Island, but not at Duck FRF. Geomorphological differences between the two sites likely account for this disparity, as the greater potential distance from shoreline at Hog Island introduces a wider range of soil salinities, soil ages and development stages, and protection from shoreline-related abiotic stressors (Ehrenfeld 1990, Levy 1990, Young et al. 2011). At the Duck FRF site, a high primary dune is maintained by dredged sand addition and beach nourishment, and reduces abiotic stressors associated with the oceanfront (Dolan 1972, Young et al. 2011). This artificial stabilization and habitat management limits the potential ranges of the abiotic variables measured here, but reduces these stressors within a smaller distance from the shore.

Prevalent lianas and lianas present at the two sites were generalist species (Carter and Teramura 1988) and thus did not demonstrate a clear relationship with the environment at either site. At Hog Island, ordination analysis indicated an association of lianas with *Morella cerifera* and *Prunus serotina,* though it is likely that this is indirectly due to environmental variables (soil saturation, saltwater intrusion) preventing association with *Iva frutescens*, and to the overwhelming prevalence of *M. cerifera* across Hog Island (Levy 1990, Young et al. 1995, Duncan and Duncan 1987). We found no species-specific associations at Duck FRF, likely due to abiotic homogeneity and patchiness of the landscape. Environmental variables did not affect woody or liana species distributions at the FRF, and significant filtering is unlikely as the range of soil salinities was far less than for Hog Island. We did not measure soil moisture, but the higher mean elevation of the FRF would also reduce cross-site availability to freshwater, and the narrower land area would not support an equivalent freshwater lens (Hayden et al. 1995, Young et al. 2007, Masterson et al. 2014). Further, the prevalence of tree islands as opposed to continuous shrub thicket increases edge effects at the FRF, (Turner 1990, Schnitzer et al. 2000).

We documented very low diversity in woody and climbing species for both sites, with partial species overlap. On Hog Island, species distribution of both functional groups was influenced by abiotic factors, but when separated into woody and liana groups, only woody species distributions were significantly related to environmental variables. At Duck FRF, there was no significant relationship of measured abiotic factors to species distributions. While edaphic factors affect liana success in other systems (Dillenburg et al. 1993, DeWalt et al. 2006, Álvarez-Cansino et al. 2015), here the effect is overwhelmed by the impact of woody plant presence or absence. Woody species facilitate liana establishment and growth in multiple ways including microclimate moderation, soil development, seed rain enhancement, and physical support (Ehrenfeld 1990, Levy 1990, Crawford and Young 1998*a*, *b*, Bissett et al. 2014).

Due to the overall low species diversity at both of these sites as well as to the overwhelming dominance of *M. cerifera* and *M. pensylvanica* at the two sites, strong species-specific relationships do not emerge, largely because *Morella* shrubs provide an extremely accommodating structure for all climbing types of lianas (Carter and Teramura 1988). Abundance of small branches to act as trellises, and connectivity within patches facilitates liana ascension and infiltration throughout the canopy (Balfour and Bond 1993, Schnitzer et al. 2000, Leicht-Young et al. 2010). Leicht-Young et al. (2010) found that tree diameter, tree bark type, and size, number, and placement of branches all can affect colonization and ascension by lianas.

Both *Morella* species possess great numbers of low and small branches and form dense groupings which allow lianas to expand easily after reaching the canopy (Brantley and Young, 2010, Shiflett et al. 2014). Therefore these shrubs are accommodating to ascension by twining, tendril-climbing, and root-climbing lianas (Carter and Teramura 1988).

Woody species diversity, community stability, and soil age all increase with distance from shoreline (Ehrenfeld 1990, Levy 1990, McCaffrey and Dueser 1990). Community age increases (Ehrenfeld 1990, Day et al. 2001), and later successional stages occur and persist in the island interior. On mid-Atlantic barrier islands, the dominant woody species are *Morella* shrubs, which grow densely together, producing monospecific thickets that can persist for decades (Harris et al. 1983, Levy 1990, Young et al. 2007). Recent research on the Virginia barrier islands suggests that the shrub thicket is a self-reinforcing stable state that expands even as island area decreases (Young et al. 2007, Zinnert et al. *unpublished manuscript*). It has been documented that *M. cerifera* effectively recolonizes after thicket decline (Levy 1990), and limits establishment of other species within thickets (Tolliver et al. 1995, Crawford and Young 1998*b*). Despite this, significant areas of mature maritime forest historically existed on Hog Island (Badger and Kellam 1989), but our results show that maritime forest is not establishing. Today, dense *M. cerifera* thicket, isolated tree islands, and patches of liana-dominated canopy are the most developed plant communities (Young et al. 2007, Bissett et al. 2014).

Our finding of a functional relationship between lianas and woody vegetation is significant in coastal communities and may play a role in arresting of succession prior to maritime forest development. Lianas compete for resources with supporting vegetation, and also add significant mass to the canopy, advancing community change by hastening the collapse of tree canopies. This additional mass can significantly alter the three-dimensional structure of the shrub thickets, having lasting effects on the community. Physical structure of the canopy directly affects the absorption of incoming radiation and the percentage of light reaching the ground below (Bonan 1993, Runyon et al. 1994, Brantley and Young 2010). Long-term implications of this trend in reduced structure and diversity may include changes in carbon balance and vertebrate habitat, as well as changes in the physical stability of the barrier island landscape. Additionally, as global change has been linked to both shrub expansion (Archer et al. 1995, Knapp et al. 2008, Zinnert et al. 2011) and liana proliferation (Schnitzer 2005, Schnitzer and Bongers 2011, Pasquini et al. 2015), we may expect to see a more extensive decline of maritime forests as shrub- and liana-dominated communities expand.

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Table 3.1: Summary values (mean ± SD) for environmental variables at Hog Island and Duck FRF. Sample size in parentheses. Values are shown for sites in full, for liana species and woody species considered together regardless of site, and individual species at each site.

	Distance (m)	Elevation (m)	Soil pH	Soil Cl
Site				
Hog Island	530.02 ± 342.48 (104)	1.17 ± 0.27 (104)	5.8 ± 0.8 (103)	10845 ± 19734 (103)
Duck FRF	228.95 ± 134.34 (86)	4.05 ± 1.59 (86)	5.0 ± 0.5 (86)	346 ± 215 (86)
Functional Group				
Vine	369.96 ± 292.96 (89)	2.75 ± 1.84 (89)	5.3 ± 0.7 (88)	4018 ± 9525 (88)
Woody	414.71 ± 319.91 (101)	2.23 ± 1.74 (101)	5.5 ± 0.8 (101)	7854 ± 19055 (101)

Table 3.2: Pearson's correlation coefficients between environmental variables.

	Elevation	Soil pH	Total soil Cl
Distance	$p = 0.34$; r = 0.17	$p < 0.01$; r = 0.47	$p < 0.01$; r = 0.61
Elevation		$p < 0.01$; r = 0.52	$p = 0.02$; r = 0.40
Soil pH			$p = 0.69$; r = 0.07

Table 3.3: Pearson's correlation coefficients (*r*) for Hog Island and Duck FRF liana community values versus woody richness (Shannon H') and cover score (0-5). *$p \leq 0.05$, **$p \leq 0.01$.

Hog Island	Woody sp. richness	Woody cover score
Total liana abundance	0.18	0.06
Liana cover score	0.25	0.36*
Liana species richness	0.56**	0.42**
Duck FRF		
Total liana abundance	0.18	0.56**
Liana cover score	0.55**	0.70**
Liana species richness	0.60**	0.70**

Figure Legends

Figure 3.1: Hog Island (H) and Duck FRF (D) site locations. Sites shown at right with study transects identified. Duck Transect 3 (D-T3) shown at bottom to illustrate transect layout and notation of plots D-T3-P01 through D-T3-P11. Number of plots per transect varied with island width from 22 (H-T1) to 6 (H-T3).

Figure 3.2:

Relative frequencies of liana (A) and woody (B) species at Hog Island and Duck FRF. Lianas: *Lonicera japonica* (LOJA), *Mikania scandens* (MISC), *Parthenocissus quinquefolia* (PAQU), *Rubus argutus* (RUAR), *Rubus trivialis* (RUTR), *Smilax* spp. (SMSP), *Toxicodendron radicans* (TORA), *Vitis aestivalis* (VIAE), *Vitis labrusca* (VILA). Woody species: *Aralia spinosa* (ARSP), *Baccharis halimifolia* (BAHA), *Diospyros virginiana* (DIVI), *Iva frutescens* (IVFR), *Juniperus virginiana* (JUVI), *Morella cerifera* (MOCE), *Morella pensylvanica* (MOPE), *Persea borbonia* (PEBO), *Prunus serotina* (PRSE), .*Quercus virginiana* (QUVI), *Zanthoxylum clava-herculis* (ZACL).

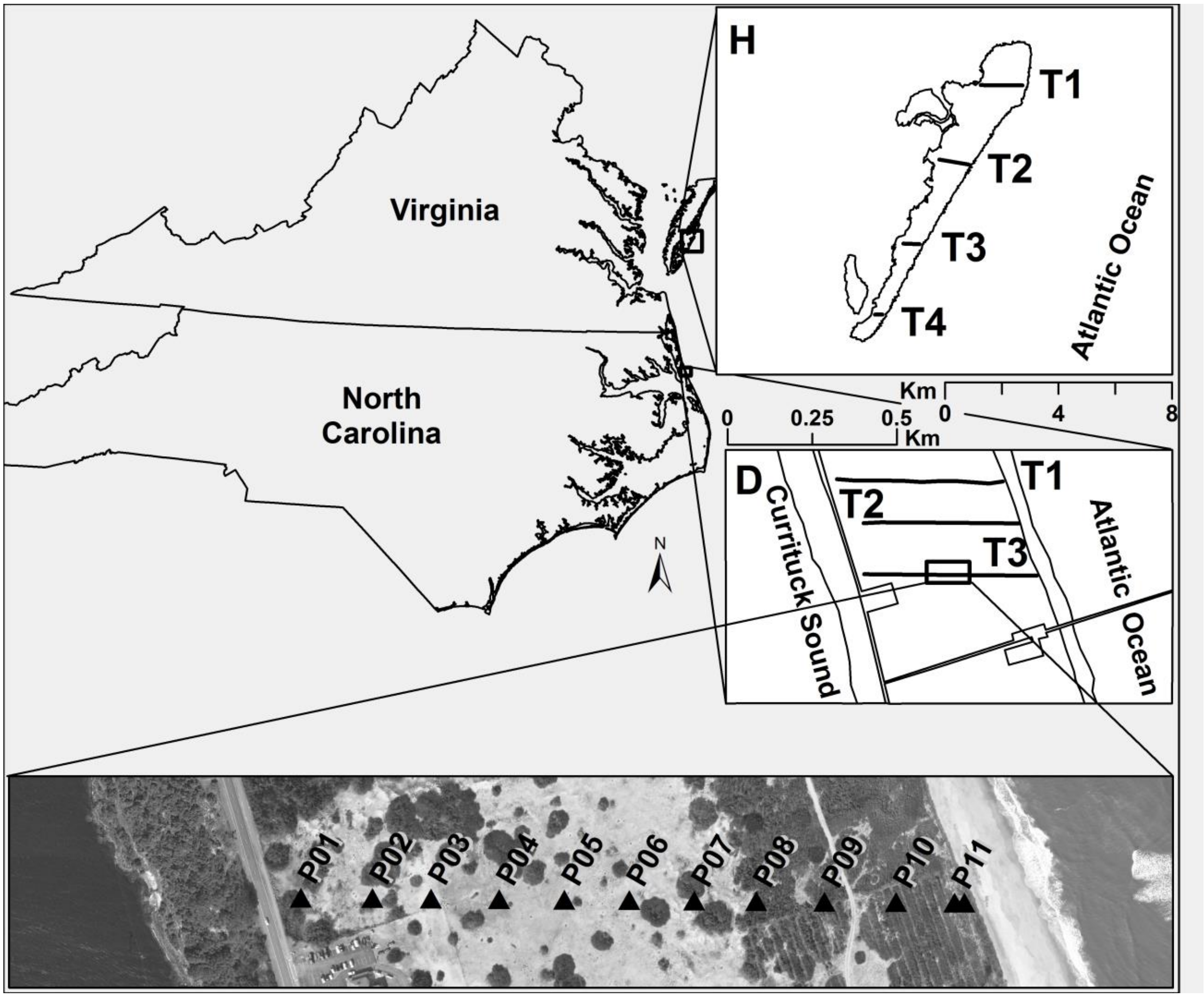
Figure 3.3:

Bray-Curtis ordination results for Hog Island. Triangles indicate plots, X's indicate species, and lines from center represent environmental variables. Liana species are shown in blue, woody species are shown in red. Length of line indicates strength of environmental driver. Lianas: *Lonicera japonica* (LOJA), *Mikania scandens* (MISC), *Parthenocissus quinquefolia* (PAQU), *Rubus argutus* (RUAR), *Rubus trivialis* (RUTR), *Smilax* spp. (SMSP), *Toxicodendron radicans* (TORA), *Vitis aestivalis* (VIAE), *Vitis labrusca* (VILA). Woody species: *Aralia spinosa*

(ARSP), *Baccharis halimifolia* (BAHA), *Diospyros virginiana* (DIVI), *Iva frutescens* (IVFR), *Juniperus virginiana* (JUVI), *Morella cerifera* (MOCE), *Morella pensylvanica* (MOPE), *Persea borbonia* (PEBO), *Prunus serotina* (PRSE), .*Quercus virginiana* (QUVI), *Zanthoxylum clava-herculis* (ZACL).

Figure 3.4:

Bray-Curtis ordination results for Duck FRF. Triangles indicate plots, X's indicate species, and lines from center represent environmental variables. Liana species are shown in blue, woody species are shown in red. Lianas: *Lonicera japonica* (LOJA), *Mikania scandens* (MISC), *Parthenocissus quinquefolia* (PAQU), *Rubus argutus* (RUAR), *Rubus trivialis* (RUTR), *Smilax* spp. (SMSP), *Toxicodendron radicans* (TORA), *Vitis aestivalis* (VIAE), *Vitis labrusca* (VILA). Woody species: *Aralia spinosa* (ARSP), *Baccharis halimifolia* (BAHA), *Diospyros virginiana* (DIVI), *Iva frutescens* (IVFR), *Juniperus virginiana* (JUVI), *Morella cerifera* (MOCE), *Morella pensylvanica* (MOPE), *Persea borbonia* (PEBO), *Prunus serotina* (PRSE), .*Quercus virginiana* (QUVI), *Zanthoxylum clava-herculis* (ZACL).



Virginia
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H
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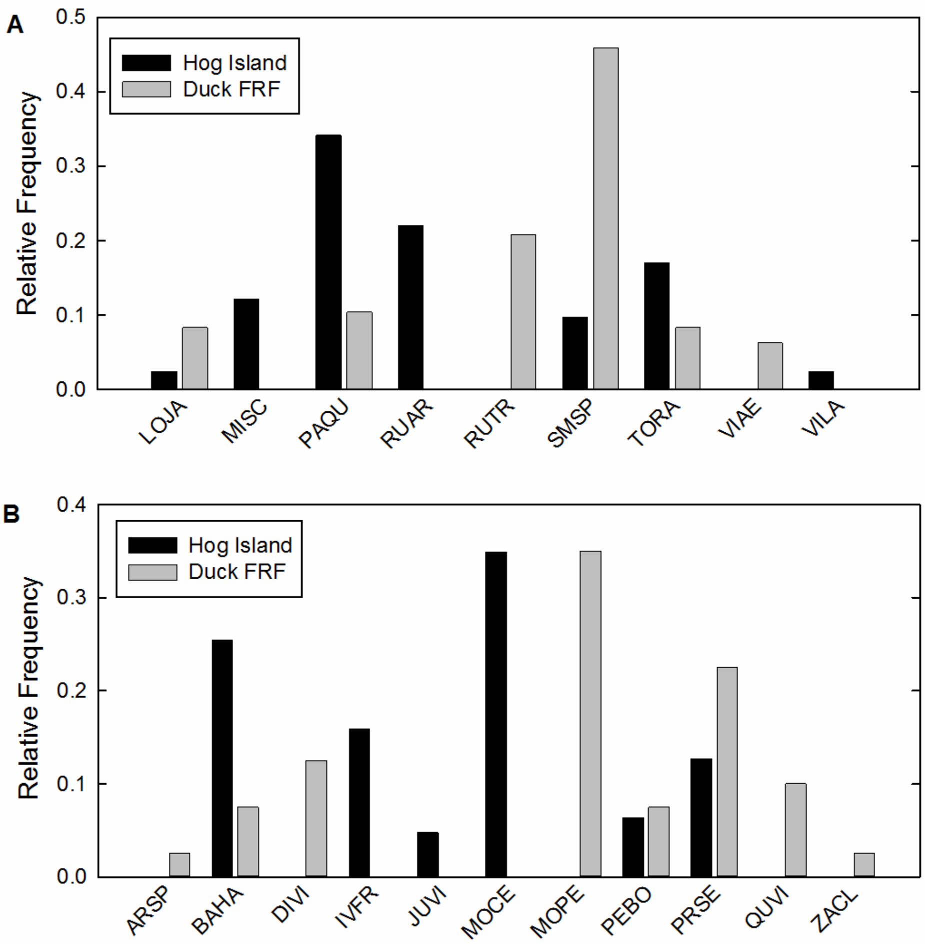
Figure 3.1


A
Relative Frequency
0.0
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Hog Island
Duck FRF
LOJA
MISC
PAQU
RUAR
RUTR
SMSP
TORA
VIAE
VILA
B
Relative Frequency
0.0
0.1
0.2
0.3
0.4
Hog Island
Duck FRF
ARSP
BAHA
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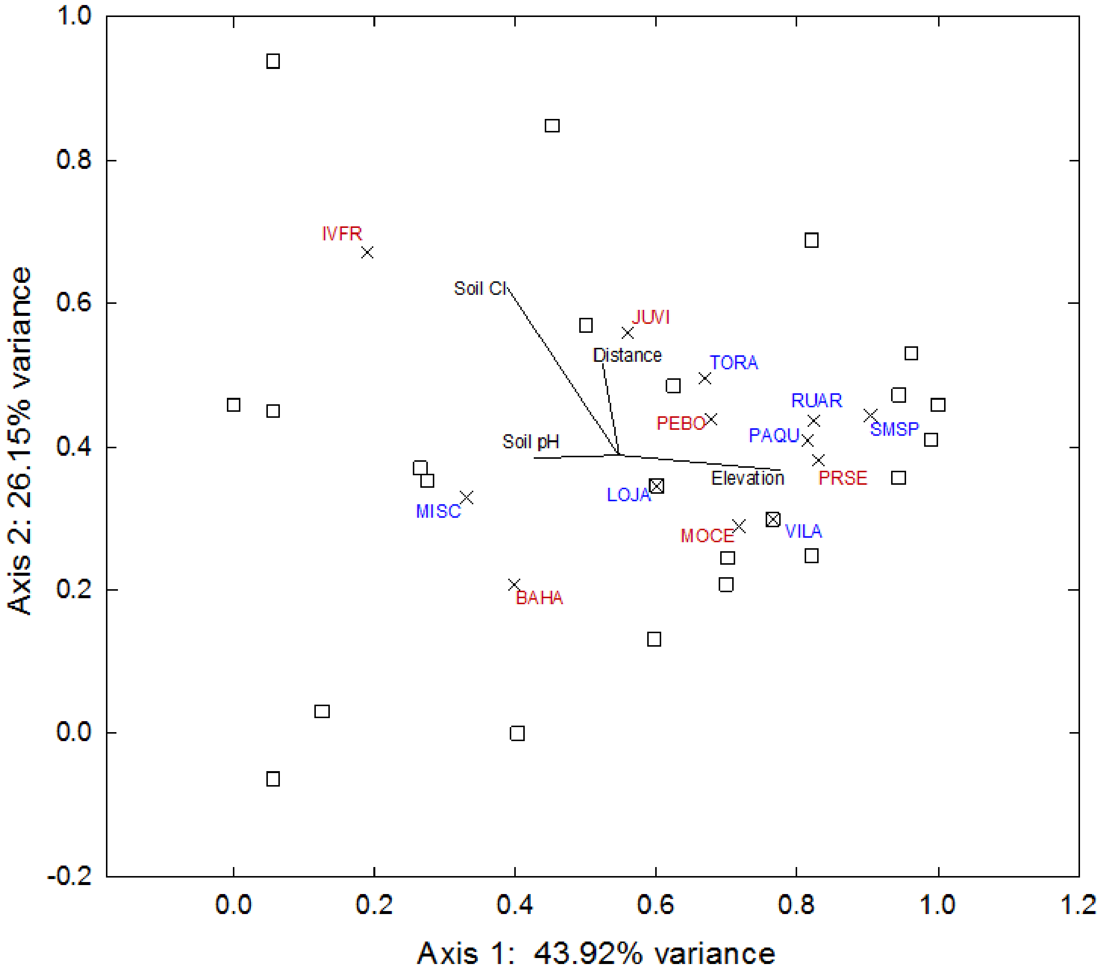
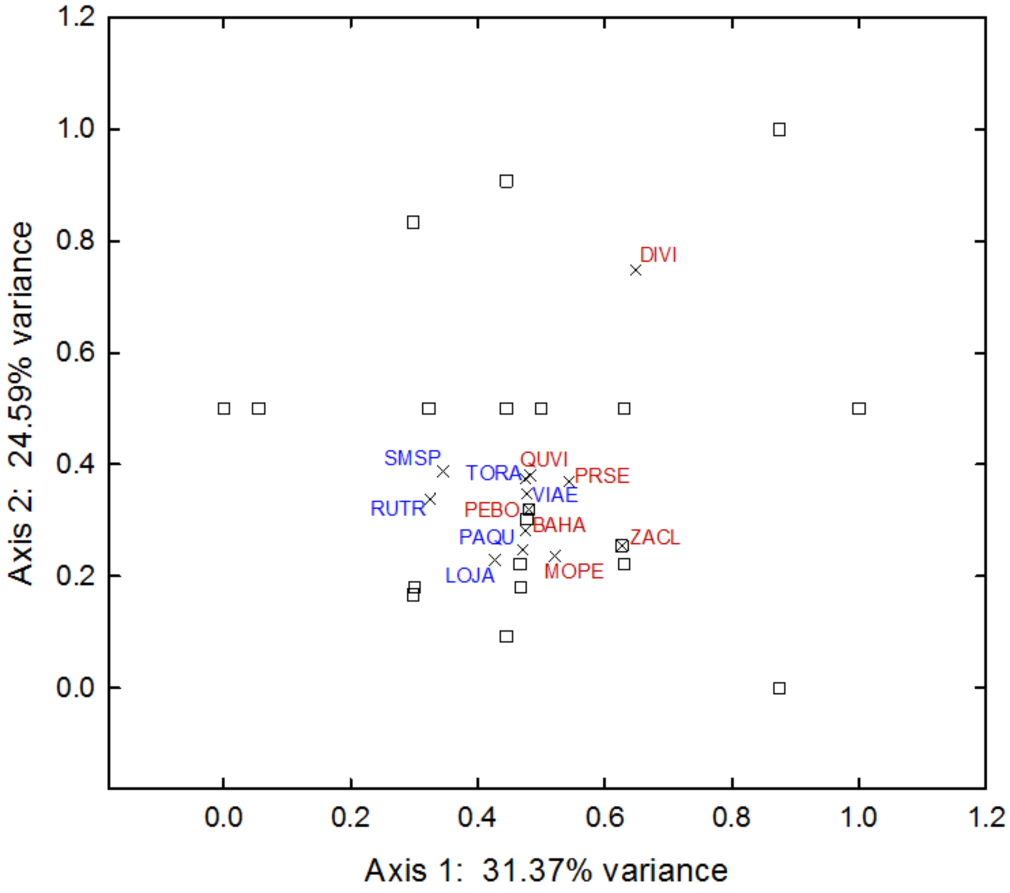
IVFR
JUVI
MOCE
MOPE
PEBO
PRSE
QUVI
ZACL

Figure 3.2



Axis 2: 26.15% variance
Axis 1: 43.92% variance
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
IVFR
Soil Cl
JUVI
Distance
TORA
RUAR
SMSP
PEBO
PAQU
Soil pH
Elevation
PRSE
LOJA
MISC
VILA
MOCE
BAHA

Figure 3.3


1.2
1.0
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Axis 2: 24.59% variance
0.0
0.2
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0.6
0.8
1.0
1.2
Axis 1: 31.37% variance
DIVI
SMSP
TORA
QUVI
PRSE
VIAE
RUTR
PEBO
BAHA
PAQU
ZACL
LOJA
MOPE

Figure 3.4

CHAPTER FOUR

REMOTE DETECTION OF THREE-DIMENSIONAL CHANGE IN SHRUB THICKET CANOPY FOLLOWING INFILTRATION AND EXPANSION BY COMPETITIVE VINES

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Abstract

Located at interfaces between terrestrial and marine ecosystems, coastal regions are uniquely sensitive to the predicted effects of global climate change. Barrier islands in particular will be the first habitats affected by sea level rise and by increasing storm frequency and intensity. As both size and geological stability of these islands change, consequences for mainland coastlines may be severe. Large-scale and long-term study and monitoring of these habitats and ecosystems are therefore important for our prediction and understanding of future changes, and remotely-sensed data provides useful methods for such research. As remote sensing methods and platforms have advanced, interest in and ecological applications of these techniques have grown commensurately. Particularly, the combination of spectral and structural information derived from air- and space-borne sensors permits scaling from the leaf, plant, and community level to the ecosystem, landscape, and regional levels. We analyzed both structural (Lidar) and spectral (hyperspectral imagery) data collected from a mid-Atlantic barrier island. To better understand successional processes and changes in this system, we specifically evaluated community-level effects of vine / liana expansion into the dominant woody community. Areas of greatest geomorphic and ecological stability at this site are occupied by established and expanding *Morella cerifera* shrub thickets. Well-developed maritime forest is not found on the island, despite both historical presence and extant occurrence elsewhere at coastal sites of similar stability. We compared three-dimensional structural effects of vine infiltration, using a forest characterization scheme with Lidar data which permitted comparisons between plot types of canopy density and canopy openness at multiple aboveground heights. Hyperspectral imagery also was tested for utility in detecting vine species presence across the landscape, but limitations in resolution prevented identification of multiple-species vine

occurrence atop and within canopies, due to overwhelming prevalence of *M. cerifera* foliage. Our results indicate that heavy incidence of vines significantly changes three-dimensional structure of shrub canopy. Vine-colonized canopy is lower, denser, and reduced in depth. Light-intercepting biomass is increased, reducing light penetration to the understory. Increased light attenuation combined with greater biomass weighing on low vegetation reduces recruitment of shrubs and other woody species, and delays or prevents progress through historically evident successional pathways towards a maritime forest. Persistent liana tangles and self-reinforcing *M. cerifera* thicket continue to dominate the stable regions of the island. These community types are less structurally and ecologically diverse than maritime forest, but because of their considerable physical and ecological stability, we anticipate lasting effects on community development and response of this and similar islands.

Introduction

Three-dimensional architecture and physical structure of plant canopies have important implications for community successional processes and ecosystem structure and function [Ellison et al., 2005]. Plant community canopy structure and constituent species are major determinants of carbon dynamics, seed rain and seedling recruitment, and light absorption and interception [Ellison et al., 2005; Brantley et al., 2010]. These factors are also important in understanding ecosystem function as well as position in the context of succession. Additionally, canopy structure and composition are well-suited for study using remotely-sensed datasets, which are of great utility in transitions between leaf- and plant-scale measurements to community-, ecosystem-, and landscape-scale applications.

In coastal ecosystems, both woody lianas and herbaceous climbers (hereafter collectively labeled as *vines*) play an important role in community succession [Crawford and Young, 1998a, b; Bissett et al., *in revision*]. The dominant woody species of the mid-Atlantic coast is the actinorhizal shrub *Morella cerifera*, an evergreen shrub which forms dense, often monospecific thickets ~5-7 m in height. They can persist for decades and are expanding markedly [Young et al., 1995; Young et al., 2007]. Gaps in these thickets result from shrub senescence and from collapse due to external factors including storm events, high winds, and ice accumulation [Ehrenfeld, 1990; Young et al., 1995]. Introduction of vines into shrub canopies adds mass, ties shrubs together, and multiplies damage inflicted by these external drivers [Crawford and Young, 1998b]. We have previously investigated vine-shrub interactions in this habitat [Bissett et al., 2014; Bissett et al., *in revision*] and have shown a significant association between vines and woody plants. Coupled with the observation that vine occurrence is increasing in tropical forests, this association with the expanding woody community suggests that the vine component of coastal communities will increase [Schnitzer and Bongers, 2011; van der Heijden et al., 2015].

Remote detection and analysis of plant communities, species, habitats, and environments have become widely-used and invaluable methods for investigation and prediction of habitat range and extent [Guisan and Thuiller, 2005]. These data and their derivatives allow extrapolation across spatial and temporal scales. For example, Guisan and Thuiller [2005] described species distribution models (SDMs) for the quantification of species' environmental niches by relating field observations to known predictive environmental variables. Similarly, Young et al. [2011] described distribution of several coastal plant species in terms of habitat polygons and integrated a variety of environmental variables into a two-dimensional model for each species. Schnitzer and Bongers [2011] suggested initiating a long-term, large-scale liana abundance monitoring project, and as use of remotely-sensed data continues to increase, a pre-existing dataset will enable comparisons across temporal as well as spatial extents.

Recent advances in remote sensing of vegetation have increased the potential for utilizing vegetative features beyond traditional cover metrics [Miura and Jones, 2010; Ussyshkin and Theriault, 2011]. The capability of active infrared laser scanning (Lidar) systems to acquire direct, three-dimensional measurements of canopy with very high density point clouds allows for improved retrieval of vegetation structural information. Lidar systems have improved both in spatial resolution and spectral capability; full-waveform Lidar systems can deliver detailed and accurate profiles of vertical structure of plant canopies and provide information using reflected spectra from the laser pulses [Lefsky et al., 2002; Hakala et al., 2012]. Traditional systems have demonstrated the ability of Lidar data-based predictions of aspects of forest structure (biomass, density, canopy height, etc.) [Lefsky et al., 2002; Hyde et al. 2005, Omasa et al. 2007, Asner et al. 2008, Estornell et al. 2011]. Although analysis of understory vegetation cover with airborne Lidar has received more attention in recent years, it is still considered an understudied area [Miura and Jones, 2010; Wing et al., 2012].

The spatial and spectral resolution of hyperspectral imagery allows for extraction of plant features such as pigment content, biochemical characteristics, and structural qualities [Adam et al., 2010; Alonzo et al., 2014]. Application of the Normalized Difference Vegetation Index (NDVI) over the last two decades has enabled quantification and mapping of photosynthetic vegetation with the goal of estimating above-ground net primary productivity (ANPP) and other landscape-level fluxes [Asner et al., 2000; Naumann et al., 2009; Brantley et al., 2011]. Leaf Area Index (LAI) also has been related to hyperspectral indices including NDVI, variations of MCARI (Modified Chlorophyll Absorption Ratio Index), and red-edge indices [Zarco-Tejada et al., 2002; Zhang et al., 2008; Brantley et al., 2011]. These approaches provide means of detecting both structural and spectral changes in plant communities. Infiltration of vines in plant canopies affects these signatures by altering physical structure and by adding biomass and species richness [Foody et al., 2003; Chambers et al., 2007; Sanchez-Ázofeifa et al., 2009].

To better understand physical changes resulting from vine infiltration of woody plant canopies, we used field measurements and remotely-sensed data to investigate three-dimensional structural changes to barrier island shrub thickets experiencing significant vine proliferation. Specifically, we evaluated whether vine infiltration adds or replaces structure, mass, and density in the canopies of these woody communities using remote sensing methods, and validated our findings with ground-based measurements in the field. We hypothesized that both vegetation reflectance and three-dimensional structure would differ due to differences in species composition, stress effects of vine competition, and differences in LAI.

Methods

Field site, selection, and measurements

Plots located on Hog Island (37° 27’ N, 75° 40’ W) in Northampton County, Virginia were visited in June, 2015. Hog Island is within the Virginia barrier chain and is included in the Virginia Coast Reserve (VCR) Long-Term Ecological Research (LTER) site, owned and overseen by The Nature Conservancy (TNC). Island length is approximately 12 km, and width at the widest point is approximately 2.4 km, including the stabilizing bayside marsh area (Figure 4.1). Though the island was colonized, it has been unoccupied since the 1930s and is regarded as a pristine system [Hayden et al., 1991]. We established field plots (3 m diameter; n = 22) across the age range of *Morella cerifera* shrub thickets on Hog Island, to explore differences in physical structure between stands with and without heavy vine coverage. In the field, we scored plot coverage for woody plants and vine species on a scale from zero (no presence) to five (total or near-total coverage). Canopy height and depth were measured at the center of every plot with a stadia rod. We identified all woody and vine species and counted woody stems in each plot. Leaf area index (LAI) was recorded using a LAI-2000 plant canopy analyzer (LI-COR Biosciences, Inc., Lincoln, NE). Mean cover scores, shrub density, and LAI were compared between plot types using Student's t-tests.

Remotely-sensed data acquisition

Lidar and hyperspectral imagery were collected concurrently on June 4, 2013 on Hog Island by the Joint Airborne Lidar Bathymetry Technical Center of Expertise (JALBTCX). These data were field-validated and post-processed prior to delivery to VCR LTER personnel. Lidar data were collected using the Coastal Zone Mapping and Imaging Lidar (CZMIL) system using a green laser (532nm) for simultaneous topographic / bathymetric survey. Vertical accuracy is better than ± 0.20 m, horizontal accuracy is better than ± 0.75 m. In addition to point clouds, bare-earth digital elevation models (DEMs) were derived from topographic Lidar data and used to extract mean ground elevation in each plot for calculation of canopy height and depth figures.

Hyperspectral imagery covering 375 to 1050 nm were collected under near cloud-free conditions at 1700 m (above ground level) providing a data set representing 1-4 $m^2 \cdot pixel^{-1}$ on the ground and a final spectral cube 96 bands deep (6 nm bandwidth) using an Itres Compact Airborne Spectrographic Imager (CASI)-1500. Data were field-validated using an ASD FieldSpec HandHeld 2 spectroradiometer (Analytical Spectral Devices, Inc., Boulder, CO) Data were radiometrically corrected by converting raw digital numbers to sensor radiance values with a calibration technique in Itres' Radcorr software program [Macon, 2009; Wozencraft et al., 2007]. Imagery was geopositioned using position and orientation data collected during the flight and orthorectified. The at-sensor radiance images were normalized to reflectance by utilizing the downwelling solar irradiance model from the Simple Model of the Atmospheric Radiative Transfer of Sunshine (SMARTS). Geocorrected reflectance images were mosaicked using a process for the overlap region that selects the brighter pixel on land or the water pixel with a higher land-water-index [Kim et al., 2010].

Lidar Analysis

Miura and Jones [2010] developed a forest characterization scheme (FCS) to stratify a Lidar dataset into vertical layers and to subsequently analyze Lidar return type. Return type may be: 1- singular, as a bare-earth reflection; 2- first-of-many, as an initial top-of-canopy return; 3- intermediate, as an above-ground mid-canopy return; or 4- last-of-many, as a return from the ground below a tree or shrub canopy. This innovative assessment of Lidar data allows for fuller estimation of forest structure at various vertical layers. Herbaceous vegetation, shrubs, and understory trees may be differentiated from one another, and distribution of biomass from ground to canopy ceiling may also be evaluated. Using a FCS modified from that described by Miura and Jones [2010], data from each flight line were extracted from each return type (1 – 4) and subset into 4 vertical layers based on ground measurements of the canopy: ground (0 – 0.2 m from ground); low vegetation (0.2 – 1 m from the ground); medium vegetation (1 – 3 m from the ground); and high vegetation (> 3 m), using Quick Terrain modeler 7.1.5 (Applied Imagery, Silver Spring, MD) (Figure 4.2). Height ranges were determined based on long-term field observations including multiple year shrub productivity analyses [Brantley and Young, 2008; Young, *unpublished data*]. From these classifications, and using equations adapted from Miura and Jones [2010], canopy characterizations were calculated. These equations deliver values for open canopy above bare ground, (O_G), open canopy above low vegetation (O_L), low vegetation (V_L), open canopy above medium vegetation (O_M) and medium vegetation (V_M), high vegetation

(V_H) and vertically-dense high canopy (D_H), and canopy cover (CC). Variances were unequal for canopy structure metrics except V_L, and so we conducted pairwise comparisons for all metrics using independent-sample Mann-Whitney U-tests.

Hyperspectral Analysis

Hyperspectral reflectance data were extracted and analyzed in ENVI version 5.1 (Excelis Visual Information Solutions, Inc., Boulder, CO). Plot spatial extents were imported as shapefiles, and spectra were extracted for the 9 m^2 area encompassing each plot completely, following findings by Brantley et al. [2011] that aggregated pixel spectra are more effective indicators of LAI. Due to the patchiness of vegetation in this environment, however, we also extracted spectra for the 1 m^2 pixel covering the central point in each plot for comparison. Reflectance spectra for monospecific shrub canopies were compared to spectra for vine-infested canopies at each wavelength using Student's t-tests. We compared derivative spectra and multiple hyperspectral indices to test for remotely-detectable stress effects of vines on shrubs, and other indicators of community differences following infestation by vines. Many of these indices are related to differences in the red-edge region, which are usually associated with stress detection but may also be affected by differences in LAI, as increases in leaf area also increase the scattering of light associated with leaf mesophyll cells. Red-edge reflectance (R) and first-derivative (D) indices were D_{730}/D_{706}, R_{740}/R_{850}, R_{761}/R_{757}, D_{705}/D_{722}, D_{715}/D_{705}, D_{max}/D_{720}, and the chlorophyll index (CI) [Zarco-Tejada et al., 2002, 2009; Gitelson et al., 2005; Campbell et al., 2007; Zhang et al., 2008]. We also evaluated the normalized difference vegetation index (NDVI), a standard red reflectance region index used to quantify and map photosynthetic vegetation [Asner et al., 2000]. Hyperspectral indices were tested for correlations with LAI (IBM SPSS Statistics 22, International Business Machines, Inc.).

Results

Field Measurements

Hog Island plots with heavy vine coverage had significantly different three-dimensional structure compared to plots with near-complete coverage by *Morella cerifera* (Table 4.1). Stem density of woody plants did not differ significantly between *M. cerifera* thicket canopies and those of vine-heavy plots ($p = 0.41$). However, LAI was 16.35 % higher ($p = 0.02$) in vine-infiltrated canopies than in *M. cerifera* canopies (Table 4.1), demonstrating that vines contribute a significant amount of light-intercepting mass. As well as showing an increase in biomass, vine-infiltrated canopies were significantly lower in height than were shrub canopies ($p < 0.01$). Vine-heavy canopies were also less vertically deep than shrub canopies ($p < 0.01$) (Table 4.1).

Forest canopy characterization

Significant differences between shrub- and vine-covered plots existed across most forest canopy structure metrics (Figure 4.3). Only aboveground canopy opening (O_G) and canopy cover (CC) did not significantly differ between plot types. Greatest differences existed in the middle and high canopies of plots. Amount of medium-height vegetation (V_M; 1 - 3 m height) was much greater for vine-infested plots (0.39 ± 0.06) than for shrub-dominated plots (0.15 ± 0.02; $p < 0.01$). Opening above medium vegetation (O_M) was also greater for vine-infested plots (0.34 ± 0.06) than for plots dominated by *M. cerifera* (0.06 ± 0.01; $p < 0.01$). High vegetation (V_H) was greater in shrub plots (0.67 ± 0.03) than in vine plots (0.34 ± 0.07; $p < 0.01$). Despite the similarity in shrub density, the greater incidence of high vegetation in shrub plots is evident, as is the more even through-canopy distribution of biomass in vine plots (Figure 4.4).

Hyperspectral analysis

We used eight hyperspectral indices to test for detectable differences between spectra of shrub and vine canopies. Neither 1 m^2 (Table 4.2) nor 9 m^2 (Table 4.3) area analyses revealed detectable differences between shrub and vine canopies. Hyperspectral indices were correlated with LAI for plots lacking vine infiltration (Table 4.4). Five indices (NDVI, CI, R_{740} / R_{850}, D_{705} / D_{722}, and D_{730} / D_{706}) showed significant predictive relationships with LAI at the 9 m^2 pixel scale. One index, D_{max}/D_{720}, was significantly predictive at the 1 m^2 scale (Table 4.4). No significant correlations existed between hyperspectral indices and LAI for vine-dominated plots.

Discussion

We combined field and remotely-sensed measurements to assess differences in canopy structure resulting from vine expansion through shrub canopy thickets on a Virginia barrier island. *Morella cerifera* shrub thickets are the dominant community type on this and other islands in the mid-Atlantic region and are expanding independently of island area change [Young et al., 2007; Zinnert et al., *in review*]. The physical structure of these shrubs is particularly accommodating to colonization by climbing plants and upon reaching the canopy, vines and lianas proliferate and add mass while negatively affecting the inferior vegetation through competition for both light and soil resources [Dillenburg et al., 1993; Crawford and Young, 1998b; Schnitzer et al., 2005]. Our results show significant changes in the three-dimensional structure of shrub thicket canopies. LAI, canopy height, canopy depth, and canopy density were significantly affected, despite the lack of change in woody stem density.

Changes in canopy structure directly affect many community processes, particularly with regard to light interception. Leaf shape, size, arrangement, and orientation affect absorption of incoming radiation and the percentage of light reaching understory vegetation and ground level [Bonan, 1993; Runyon, 1994; Ellison et al., 2005; Brantley and Young 2007; Brantley and

Young, 2010]. Both woody lianas and herbaceous climbing plants play important roles in natural successional processes, where the vine component of an advanced forest can comprise nearly half of the stem density and as much as a quarter of the species diversity [Schnitzer and Bongers, 2011], and competition within the canopy can be significant, as vines have very high foliage-to-stem ratios [Putz, 1984]. Their advantageous morphology is permitted by a structure-parasitizing growth habit, highly-efficient transport tissues, and consequent low investment in support tissues, all of which permit rapid vertical growth [Putz, 1983; Schnitzer and Bongers, 2011].

In our study, vine infiltration affected the distribution of canopy biomass, by reducing height and depth and by increasing LAI. As vines compete with supporting vegetation for above- and belowground resources, they add significant mass to the canopy and can advance community change by accelerating the collapse of the woody constituent, particularly in coastal areas which are subject to frequent and intense storms events. As a result, both canopy height and canopy depth decrease, and this increases the effective density of the canopy with regard to ground level vegetation, further reducing recruitment from the seed bank [Schnitzer and Bongers, 2011]. These resultant tangled patches of vines self-reinforce, and are indicative of the increase in vines which has also been documented in tropical forests [Schnitzer, 2005; van der Heijden et al., 2015]. In areas lacking substantial vine presence, shrub senescence may still result in autonomous gap formation, but this will typically give rise to a more complex forest with greater species richness and longer-lived woody species [Badger and Kellam, 1989; Crawford and Young, 1998b; Ellison et al., 2005].

As determined by the canopy structure analysis [Miura and Jones, 2010], there was a decrease in high canopy vegetation (V_H) with heavy vine infiltration. This was unexpected, as vine proliferation adds biomass to the highest layers of the canopy. However, the similarity in canopy cover (CC) and increases in low vegetation (V_L), medium vegetation (V_M), and LAI suggest that vine infiltration primarily results in thicket teardown, and often persistent vine tangles. Schnitzer et al. [2000] investigated persistent liana tangles in tropical forests, and attributed their success in gaps to four primary features, which are common to the vine species found at Hog Island [Crawford and Young, 1998b; Bissett et al., *in review*]. Vines survive in gaps following treefalls, are abundant in forests prior to gap appearance, can recruit successfully from seed rain and the existing seed bank, and also re-sprout profusely from fallen stems [Schnitzer et al., 2000]. Yavitt et al. [1995] noted rapid and heavy liana colonization of gaps, and Whitmore [1989] also pointed out that succession can be arrested in liana-colonized gaps. Many studies of liana-driven changes in canopy dynamics have been conducted in tropical systems; ours is one of the first studies to document such effects of vines on three-dimensional canopy structure in a temperate ecosystem using ground and remotely-sensed datasets.

Hyperspectral imagery has been recently used in detection of vines in tropical environments, based on differences in leaf functional traits and pigment composition [Sánchez-Azofeifa et al., 2009; Asner et al., 2012; Ball et al., 2015]. In this study, hyperspectral signatures and derived indices did not provide a reliable discrimination method for vine-colonized canopy, despite significant physical differences of the plot types and significant variation in species diversity. Cross-seasonal studies may enable greater success as vine species are deciduous and *M. cerifera* is evergreen. We were able to detect correlations with multiple hyperspectral indices and LAI of shrub canopy lacking vine infiltration, similar to results of Brantley et al. [2011]. This relationship was not observed with respect to vine-infiltrated plots, despite the significant increase in LAI. This may have been due to increased shadowing as a result of three-dimensional changes (i.e. increased structural heterogeneity) as observed from Lidar data, or to saturation of the reflectance signal due to the high LAI [Asner et al., 2000; Middleton et al., 2009].

Our results show that advanced vine growth significantly affects canopy structure, with lasting community implications, specifically with regard to succession, but also potentially affecting long-term carbon storage and cycling [Hardiman et al., 2011]. These physical changes were observed vertically throughout the stand, and documented both remotely and at ground level via field measurements. We demonstrated that vines significantly change the three-dimensional structure of coastal shrub thicket canopies in temperate ecosystems. These physical changes are important to our understanding of community dynamics, and may prove useful in detecting and analyzing effects of understory species, including invasive plants, which similarly alter the 3-dimensional structure of forests [Asner et al., 2008]. Like vines, understory species will pose challenges in reliable identification beneath woody overstory vegetation. Development and modification of these methods to enhance both detection and prediction of the occurrence of less-dominant members of plant communities may become a valuable means for monitoring and predicting the directions of plant community dynamics, particularly with regard to community-level shifts in response to global change.

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Table 4.1: Field measurements (mean ± SE) for shrub- and lianadominated plots on Hog Island.

		Cover Score				
	LAI ± SE*	Woody*	Vine*	Canopy Height*	Canopy Depth*	Woody stems / m^2
Shrub	4.71 ± 0.21	5 ± 0	0.18 ± 0.12	6.10 ± 0.24	4.39 ± 0.35	0.91 ± 0.26
Vine	5.48 ± 0.23	3.45 ± 1.13	4.36 ± 0.15	3.23 ± 0.38	1.99 ± 0.28	0.62 ± 0.21
p- value	0.02	< 0.01	< 0.01	< 0.01	< 0.01	0.38

Table 4.2: Comparison of center pixel (1 m^2) hyperspectral indices for monospecific *Morella cerifera* and vine-dominated plots on Hog Island.

	Mean ± SE		
Index	Shrub	Vine	*p*- value
NDVI	0.88 ± 0.01	0.86 ± 0.01	0.47
CI	0.53 ± 0.02	0.51 ± 0.02	0.49
R_{740} / R_{850}	0.74 ± 0.01	0.74 ± 0.01	0.57
R_{761} / R_{757}	0.78 ± 0.04	0.82 ± 0.05	0.54
D_{705} / D_{722}	0.94 ± 0.04	0.91 ± 0.05	0.66
D_{730} / D_{706}	0.81 ± 0.04	0.82 ± 0.05	0.87
D_{715} / D_{705}	1.23 ± 0.42	1.24 ± 0.05	0.95
D_{max} / D_{720}	1.02 ± 0.13	1.04 ± 0.02	0.45

Table 4.3: Comparison of 9 m^2 aggregate pixels (3 x 3 pixels) hyperspectral indices for monospecific *Morella cerifera* and vine-dominated plots on Hog Island.

	Mean ± SE		
Index	Shrub	Vine	*p*- value
NDVI	0.87 ± 0.01	0.86 ± 0.02	0.44
CI	0.53 ± 0.01	0.51 ± 0.02	0.53
R_{740} / R_{850}	0.73 ± 0.00	0.75 ± 0.01	0.03
R_{761} / R_{757}	0.76 ± 0.02	0.78 ± 0.03	0.64
D_{705} / D_{722}	0.91 ± 0.03	0.88 ± 0.02	0.56
D_{730} / D_{706}	0.80 ± 0.03	0.85 ± 0.03	0.22
D_{715} / D_{705}	1.30 ± 0.03	1.29 ± 0.03	0.69
D_{max} / D_{720}	1.00 ± 0.00	1.00 ± 0.00	0.33

Table 4.4: Correlation analysis of hyperspectral indices and LAI for monospecific *Morella cerifera* and vine-dominated plots. Results are shown for center pixel (1 m^2) and aggregate pixel (9 m^2) analyses.

	Shrub thicket		Vine-dominated	
Index	1 m^2	9 m^2	1 m^2	9 m^2
NDVI	$r = 0.40; p= 0.21$	$r = 0.65; p= 0.03$ *	$r = -0.29; p= 0.39$	$r = -0.35; p= 0.30$
CI	$r = 0.49; p= 0.13$	$r = 0.65; p= 0.03$ *	$r = -0.39; p= 0.23$	$r = -0.38; p= 0.25$
R_{740} / R_{850}	$r = -0.48; p= 0.13$	$r = -0.69; p= 0.02$ *	$r = 0.16; p= 0.64$	$r = 0.14; p= 0.67$
R_{761} / R_{757}	$r = -0.60; p= 0.05$	$r = -0.58; p= 0.06$	$r = 0.51; p= 0.11$	$r = 0.43; p= 0.19$
D_{705} / D_{722}	$r = -0.13; p= 0.70$	$r = -0.73; p= 0.01$ *	$r = 0.05; p= 0.89$	$r = 0.25; p= 0.46$
D_{730} / D_{706}	$r = 0.48; p= 0.13$	$r = 0.71; p= 0.01$ *	$r = -0.34; p= 0.31$	$r = -0.26; p= 0.43$
D_{715} / D_{705}	$r = 0.14; p= 0.68$	$r = 0.45; p= 0.17$	$r = -0.14; p= 0.68$	$r = -0.15; p= 0.66$
D_{max} / D_{720}	$r = -0.71; p= 0.01$ *	$r = 0.00; p= 1.00$	$r = 0.25; p= 0.45$	$r = 0.32; p= 0.34$

Figure Legends

Figure 4.1: Site locations on Hog Island, Virginia (A). Plots were located on or near previously-established transects [Bissett et al., 2014] across the north end (B) and mid-island region of Hog Island (C).

Figure 4.2: Representative Lidar-derived cross-section of Hog Island shrub thicket. Plots show Lidar pulse returns 1 (top) through 4 (bottom). Dashed lines differentiate FCS canopy depth regions: Ground (0 – 0.2 m); Low Vegetation (0.2 - 1 m); Medium Vegetation (1 – 3 m); and High Vegetation (> 3 m).

Figure 4.3: Summary of canopy structure metric comparisons for plot types of *Morella cerifera* monospecific thicket (black bars) and shrub thicket with heavy vine canopy constituent (grey bars). *, **, *** denote significant differences at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively.

Figure 4.4: Mean number of Lidar pulse returns relative to height above ground (m) for *Morella cerifera* monospecific shrub thicket (left), and vine-dominated canopy (right).

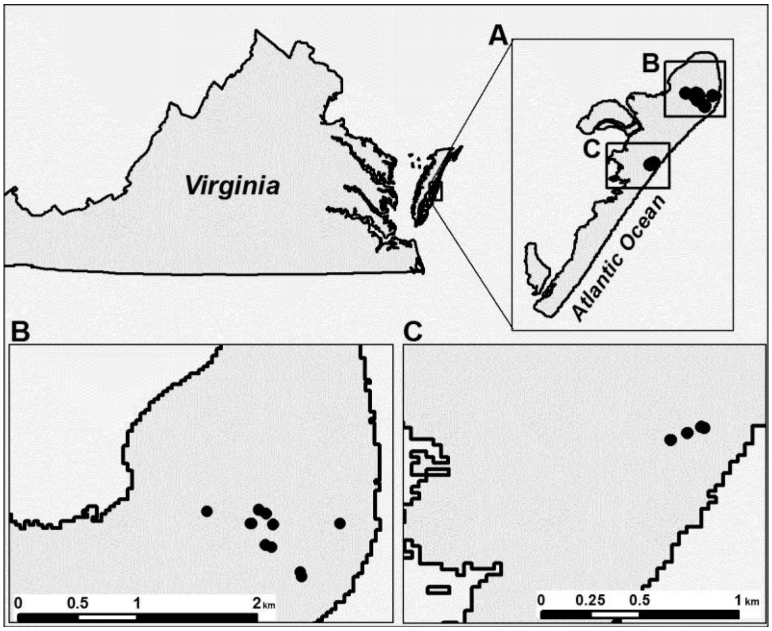

Figure 4.1

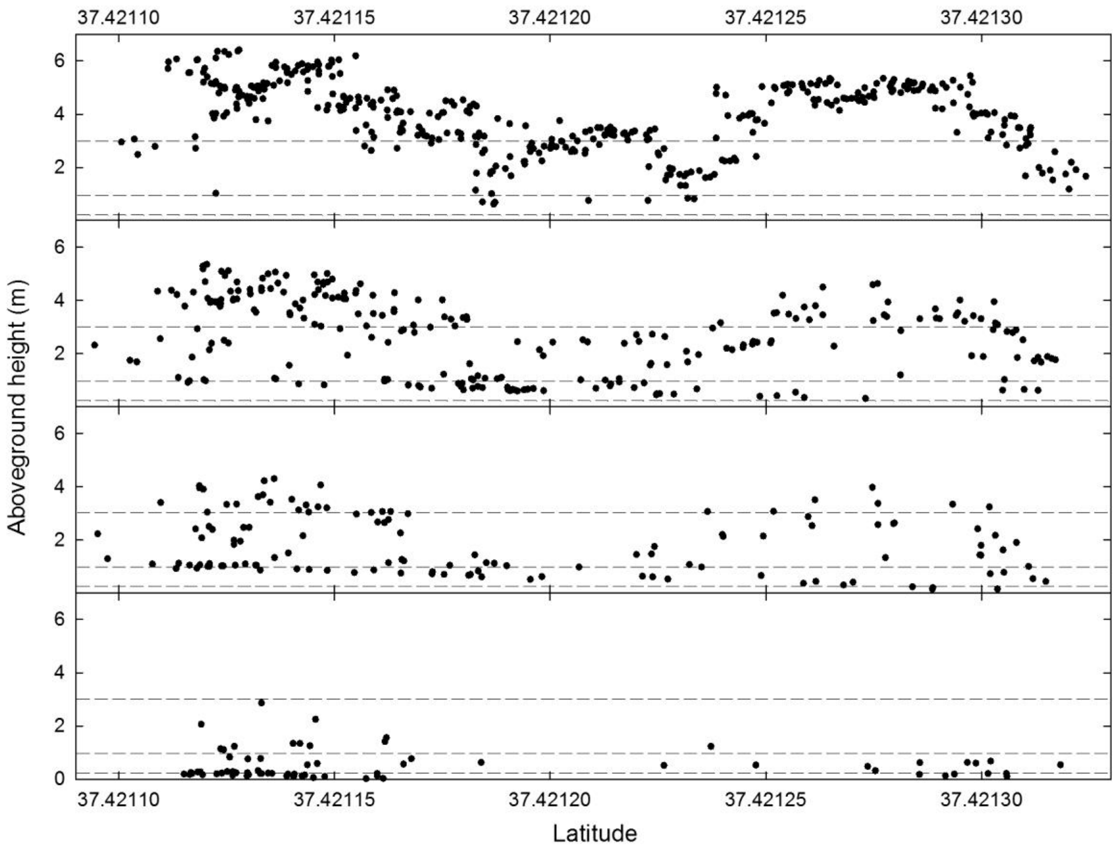
37.42110
37.42115
37.42120
37.42125
37.42130
6
4
2
0
Aboveground height (m)
Latitude

Figure 4.2

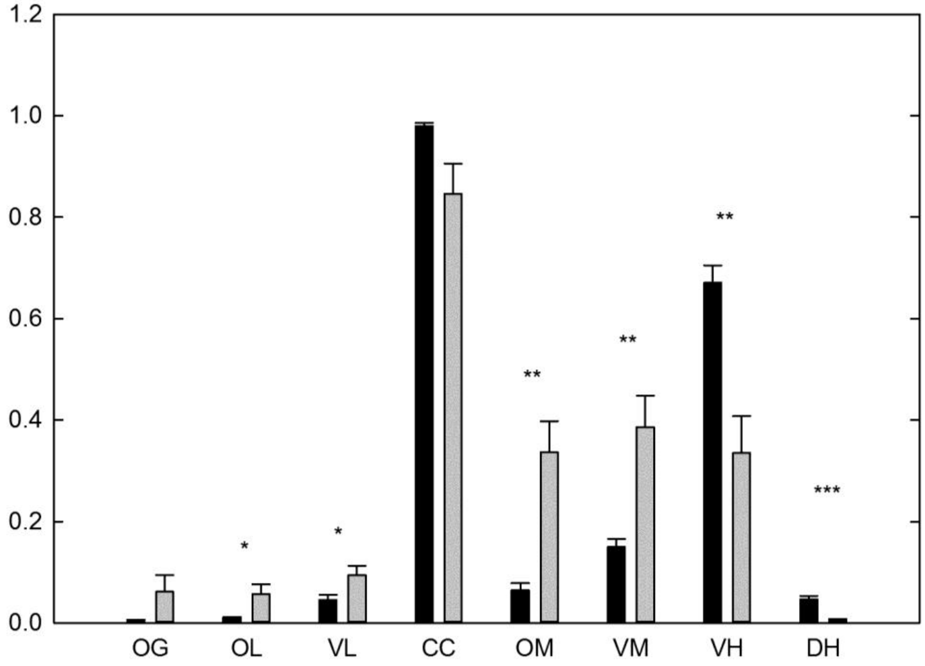

Figure 4.3

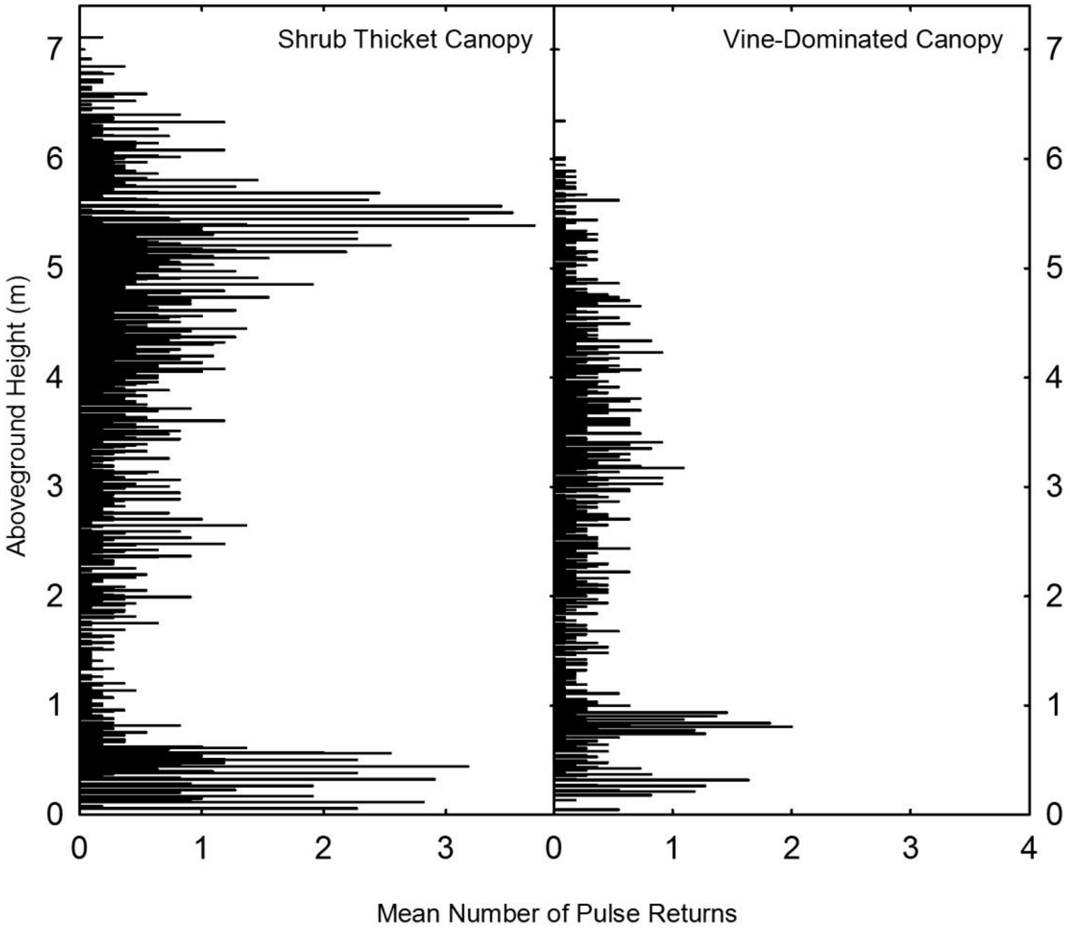
Shrub Thicket Canopy
Vine-Dominated Canopy
Aboveground Height (m)
0
1
2
3
4
5
6
7
0
1
2
3
0
1
2
3
4
Mean Number of Pulse Returns

Figure 4.4

VITA

Spencer Nathaniel Bissett was born on October 26, 1981, in Rockbridge County, Virginia, where his childhood was spent climbing trees, staining his knees green, and pursuing arthropods. A lifelong interest in plants and the outdoors led to a horticulture course during his middle school years, and later to the Virginia Field Biology Governor's School. Spencer graduated with honors from Rockbridge County High School and attended Wake Forest University, where he majored in Biology. Upper-level electives were ecologically-focused, and Dr. Smith's plant ecophysiology course gave a name to the lifelong interest in How Plants Work. Spencer gained experience in field research while working as a Smith Lab technician and research assistant both before and following his graduation in 2004, and after a summer (2006) internship studying pollinator ecology at Archbold Biological Station, he entered Virginia Commonwealth University to pursue graduate study with Dr. Don Young. M.S. research on avian dispersal of a nitrogen-fixing bacterial endosymbiont was concluded in 2008, and Spencer then entered the Integrative Life Sciences Ph.D. program at VCU. After seven years, (nearly) eight publications, numerous lab and field teaching experiences, and innumerable wide-ranging field and lab experiences with fellow students and researchers, Spencer emerges as Dr. Bissett. His immediate plans include teaching undergraduate biology courses at VCU, developing a physiological ecology course focused on invasive species, expanding research performed for his dissertation for further publication, and pursuing the "Bissett and Bissett, 2011" paper with Thad that we've been talking about for so damn long.