Plant Community Development in Storm-induced Overwash Fans of the Otis Pike Fire Island High Dune Wilderness Area, New York

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PLANT COMMUNITY DEVELOPMENT IN STORM-INDUCED OVERWASH FANS OF
THE OTIS PIKE FIRE ISLAND HIGH DUNE WILDERNESS AREA, NEW YORK

by

Chellby R. Kilheffer

A dissertation
submitted in partial fulfillment
of the requirements for the
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ABSTRACT


Barrier island systems are driven by disturbance, climate, and geomorphology. Previously, barrier island vegetation communities were primarily described by microclimate variability. The purpose of this dissertation is to better understand effects of white-tailed deer on developing plant communities on barrier islands after a catastrophic disturbance. I used distance-based Moran's eigenvector maps to identify spatial structures in vegetation communities of overwash fans in the third and fourth years after Hurricane Sandy. Spatial structures were present and significant at two or more frequencies in all overwash fans and explained the greatest amount of variation in vegetation community composition. Induced spatial dependence was predominantly controlled by proximity to foredune. I identified five biotic and abiotic influences to community composition in overwash fans and ranked their importance through canonical correspondence analysis. Gradients in productivity and elevation were primarily responsible for community composition and deer effects were not identifiable at the plot level. I identified effects of deer on vegetation cover and richness through a paired exclosure experiment, though only cover effects were statistically significant. Deer effects on cover were starker than those observed on species richness, suggesting assessments of deer effects on depauperate communities should focus on richness and cover. Lastly, I assessed effects of white-tailed deer on the rate of vegetation recovery in overwash fans through imagery classification and assessments of local white-tailed deer density. Though deer affect vegetation cover through trampling, grazing, and browsing in overwash fans, their effects on recovery rates were minimal and not statistically significant. Two overwash fans are expected to recover to pre-Sandy conditions within the decade since a nascent foredune is present and growing. Two overwash fans may never recover due to continued disturbance. The five remaining overwash fans have a slowly-forming nascent foredune, and changes in climate and frequency of storm events make their futures uncertain. Though deer do not pose a threat to the resilience of the barrier island, selective foraging behaviors may change composition and developmental trajectories of recovering vegetation communities over time.

Keywords: barrier island, community development, Fire Island National Seashore, Hurricane Sandy, overwash fan, recovery rate, resilience, white-tailed deer.

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PROLOGUE

Coastal systems, including barrier islands, provide approximately $33 trillion per year through economic services (Martínez et al. 2007), including development and recreation. Recreation activities damage natural coastal systems, particularly dunes, and are increasingly prevalent on coastal areas (Martínez and Psuty 2004). Barrier islands are separated from a mainland by unique coastal ecosystems (Ehrenfeld 1990, Maun 2009), including bays, lagoons, and marshes, each of which is rich in biodiversity and breeding habitat for wildlife (Conover et al. 2005, Hinga 2005). Other coastal ecosystem services include climate regulation, disturbance mitigation, water regulation, soil formation, nutrient cycling, pollination, and biological control (Martínez et al. 2007). Though coastal areas provide important services, they are fraught with dense human development (Ehrenfeld 1990, Kennish 2001) and frequent coastal disturbance (Sallenger 2000, Hapke et al. 2013).

Barrier islands are inherently dynamic due to both natural and anthropogenic processes (Tanski 2007), and they have persisted for thousands of years despite frequent disturbance (Ehrenfeld 1990, Snyder and Boss 2002, Feagin et al. 2010). Barrier islands protect nearby mainlands from tidal erosion (Stone and McBride 1998, Feagin et al. 2010) and storm events (Vinient and Moore 2015). Foredunes along the ocean-coast of barrier islands erode during storm events and serve as natural defenses against disruption of inland ecosystems (Sallenger 2000, Durán and Moore 2013, Hapke et al. 2013). Where erosion rates are high, vegetation communities often remain disturbed and leave the area vulnerable to future storms (Roman and Nordstrom 1988). Natural dune recovery occurs over decadal time scales after such a disturbance (Olson 1958, Wallen 1980, Lichter 1998).
The importance of vegetation in dune formation has always been implicated (Olson 1958), but only recently recognized for controlling aspects of foredune size (Durán and Moore 2013) and vulnerability to future disturbance (Pendleton et al. 2004, Brantley et al. 2014, Vinent and Moore 2015). Plant species tolerant of salt, wind, saline flooding, freshwater and nutrient limitation, and sand burial colonize newly overwashed areas and rebuild a foredune (Stuckey and Gould 2000, Kent et al. 2001, Maun 2009). Together, dune-building plant species and aeolian sand transport determine vegetation recovery time, a key parameter in models of dune formation (Vinent and Moore 2015). Recovery times shorter than the periodicity of high-water events lead to rapid dune growth. Conversely, longer recovery times lead to little or no dune growth because overwashed areas do not recover before the next high-water event (Vinent and Moore 2015). High water events occur over large spatial extents (> 100 km), so adjacent areas typically experience a similar frequency of coastal disturbance. Vegetation recovery time, however, is determined by finer-scale processes, including pre-disturbance vegetation cover conditions and subsequent development rates, and can vary greatly among adjacent disturbed areas (Brantley et al. 2014).

The idea of directional community development has long been debated (Egler 1954, Connell and Slatyer 1977). Theories of dune succession have evolved from strictly temporal sequences (Cowles 1899, Whitford 1901, Lichter 1998) to spatio-temporal sequences (Grime 1977, Tilman 1990, Johnson and Miyanishi 2008) over the last several decades. If spatially-controlled microclimates influence vegetation community development, recovery will differ among adjacent overwash fans based on plant species present and their tolerances of the new environmental conditions (i.e., abiotic factors). Barrier island soils are typically < 200 years old (Ehrenfeld 1990), and they remain young and relatively infertile due to frequent erosion and
overwash events (Ehrenfeld 1990, Titus 1990). Consequently, development of barrier island plant communities is primarily physiographic (Oosting 1954, Martin 1959) and frequent disturbance limits community development in some areas. Microclimates on barrier islands vary based on the presence and size of foredunes, which protect the interior of the island from harsh oceanic conditions (Maun 2009). Without the protection of foredunes, inland ecosystems are subject to salt spray, inundation by seawater, and high winds. Consequently, the growth of foredunes is necessary for the establishment and resilience of characteristic plant communities on barrier islands after a storm event.

Resilience is a system’s ability to adapt to a disturbance or changing environment (Holling 1973). Resilience is scale-dependent and varies with the type and duration of disturbance (Stalling et al. 2015). For example, resilience of a barrier island to low-frequency, high-intensity disturbance (i.e., coastal storms) differs from its resilience to high-frequency, low-intensity disturbance (i.e., human activity, herbivory) as the mechanisms responsible for each differ. Subsequently, resilience of a barrier island after a coastal storm depends on the factors that influence the recovery process, including dune growth, frequency and magnitude of future high water events, and vegetation establishment and growth (Stallins and Parker 2003).

Several geologically recent, unnatural disturbances threaten barrier island resilience. Anthropogenic disturbances, including human development and beach modification (e.g., replenishment, scraping), compromise the resiliency of coastal systems by increasing loss of sand volume on beaches and dunes during tidal cycles and periodic storms (Kratzmann and Hapke 2012). Recreation activities (e.g., walking, camping) compromise barrier island resiliency by breaking stabilizing plant structures (i.e., roots, rhizomes) and impeding the ability of vegetation to trap sand (Hosier and Eaton 1980, Martínez et al. 2006, Santoro et al. 2012).
Recreation activities are particularly harmful if they are frequently conducted on dunes (Gómez-Pina et al. 2002, Lemauviel and Rozé 2003). In addition, a menagerie of native and exotic ungulates have inhabited barrier islands along the Atlantic coast for centuries (Lowney et al. 2005) and chronic herbivory impacts dune vegetation differently according to the dominant herbivore present in the ecosystem (Maun 2009).

Mammalian herbivores are characterized along a spectrum from browsers to grazers based on their digestive systems and subsequent forage preferences (McNaughton et al. 1988). Browsers consume leaves, forbs, woody stems, and other plant material. Browse material tends to contain a heterogeneous assortment of plant materials high in lignin and varied in nutritional quality. In contrast, grazers consume grasses and other monocot vegetation in bulk and nutritional quality is mostly homogeneous (Shipley 1999). While limited grazing and browsing can induce greater growth rates in defoliation-tolerant vegetation (Frank et al. 1998) and aid in dispersal of seeds (Maun 2009), selective browsing can change understory composition in forests (Eschtruth and Battles 2008, Eschtruth and Battles 2009, Goetsch et al. 2011), alter nutrient cycles (Augustine et al. 2003), reduce community biodiversity (Bakker et al. 2006), alter species competition (Augustine and McNaughton 1998), and reduce ecosystem productivity (Bråthen et al. 2007) over time.

Horses, classified as grazers, reduce cover and diversity of herbaceous maritime vegetation (Seliskar 2003, Porter et al. 2014). Deer, however, are classified as browsers, though they also consume grass regularly (Bryant et al. 1981, Hobbs et al. 1983). On barrier islands where both horses and deer are present, herbivore effects on dune vegetation have been attributed predominantly to horses (Keiper 1990). Browsers and grazers occasionally exhibit dietary overlap, but documented cases are uncommon (Hansen and Reid 1975, Hobbs et al.
1983). Little is known about effects of deer on dune vegetation in the absence of horses (Carruthers et al. 2013). Hooved animals are also known to crush vegetation and reduce cover through trampling (McNaughton et al. 1988, de Mazancourt et al. 1998). Trampling in dune systems has significant negative impacts to vegetation cover (Hylgaard and Liddle 1981, Bowles and Maun 1982, Andersen 1995, Santoro et al. 2012, Carruthers et al. 2013) and composition (Šilc et al. 2017). Compared to other ecosystems, dune vegetation communities are especially vulnerable to trampling (Andersen 1995, Santoro et al. 2012) since intact root and rhizome systems are easily crushed or broken and sandy soils are compacted, hindering establishment of nearby plants (Maun 2009).

Previously, barrier island plant communities were primarily characterized by abiotic factors (i.e., erosion, sand burial, salt spray, and freshwater limitation) and microclimate variability (Art 1976, Ehrenfeld 1990, Maun 2009). The goal of my research is to postulate the effects of biotic influences on barrier island resilience through impacts to post-disturbance vegetation recovery (Figure 1). Ecosystem drivers, natural or anthropogenic factors that induce ecosystem change (Nelson et al. 2006), of barrier islands include disturbance, climate, and geomorphology (Brantley et al. 2014). Stressors acting upon the vegetation communities in overwash fans include changes in climate, visitor use, non-native plant species, erosion, sand burial, salt spray, freshwater limitation, and herbivory (Art 1976, Ehrenfeld 1990, Maun 2009, Brantley et al. 2014). Several environmental conditions exhibit gradients on barrier islands, with greater concentrations nearer to the ocean (i.e., visitor use, sand burial, salt spray, and freshwater limitation). Other environmental conditions affect bay and ocean coasts, including climate change and erosion.
The purpose of this dissertation is to better understand how deer affect developing plant communities on barrier islands after a catastrophic disturbance. In the first chapter, I describe spatial structures in vegetation community composition in areas disturbed by a storm event. I intend to submit Chapter One with several co-authors for peer-reviewed publication by July 2018. The anticipated audience for Chapter One includes spatial or coastal ecologists. In the second chapter, I identify and rank the relative influences of biotic and abiotic factors on community composition in overwash fans. I intend to submit Chapter Two with several co-authors for peer-reviewed publication by October 2018, and the anticipated audience includes coastal botanists and managers. In the third chapter, I explore effects of white-tailed deer exclusion on vegetation cover and richness through a conventional experiment. I intend to submit Chapter Three with several co-authors for peer-reviewed publication by July 2018. The anticipated audience for Chapter Three includes coastal managers and disturbance ecologists. In the fourth chapter, I calculate the recovery rates of vegetation in overwash fans and assess the importance of pre-storm vegetation cover and local deer density. I intend to submit Chapter Four with several co-authors for peer-reviewed publication by October 2018, and the anticipated audience includes coastal managers and climate change specialists.
STUDY AREA

The focal study area is on Fire Island, New York, USA (40.703586 N, 72.952014 W). Fire Island is a barrier island located approximately 6 km from the south shore of Long Island (Figure 2). Fire Island National Seashore is unique within the National Park Service network because its boundaries include 17 private residential communities, a county park, two towns, three villages, a globally rare maritime forest community, and the Otis Pike Fire Island High Dune Wilderness Area (OPWA), the only federally designated wilderness area in the state of New York. Eastern shorelines of Fire Island are highly erosive, while shorelines of many western areas are accretive (Allen et al. 2002, Psuty et al. 2018). Prevailing winds are strongest in the spring and summer months from the south and west. Highest wind speeds occur in winter months and originate from the north (Art 1976). Mean annual temperature is 10.7 °C and mean annual precipitation is 117 cm (Art 1976, Forrester 2004). Sands on Fire Island are composed of quartz (98%), tourmaline, magnetite, and garnet (Art et al. 1974), and nutrient leach rates are high (Art 1976). Major storms typically occur in autumn and winter (Art 1976) approximately once every 8 years (USACE 1960).

On October 29, 2012, a catastrophic combination of weather events caused devastation to the coastal northeastern United States. Hurricane Sandy, a post-tropical cyclone with a massive wind radius (>185 km), caused prodigious storm surge and inundation of coastal New York, especially barrier islands like Fire Island (Blake et al. 2013). Across Fire Island, 200 homes were destroyed, many protective sand dunes were overwashed, and two breaches were formed when abnormally high tides and wave heights of up to 10 m caused extensive erosion (Blake et al. 2013, Hapke et al. 2013). Subsequent to landfall of Hurricane Sandy, several nor’easter storms,
which typically have larger wave heights than hurricanes (Dolan and Davis 1992), caused additional and significant erosion across Fire Island (Hapke et al. 2013).

White-tailed deer (*Odocoileus virginianus borealis*) inhabited Fire Island long before the National Seashore was established (O’Connell and Sayre 1989). The deer population appears to separate into sub-populations, one of which shares the OPWA and adjacent National Park Service housing development (unpublished data). The deer populations on western Fire Island (excluding the OPWA population) have access to supplemental food sources through garbage and frequent hand-feeding (O’Connell and Sayre 1988, Underwood 2005). The western deer populations exhibit high densities (average: 51 deer km$^{-2}$) and are documented to negatively impact understory composition, and potentially tree canopy recruitment, of the globally rare maritime forest community (Art 1987, Forrester et al. 2006, Forrester et al. 2007, Raphael 2014).

Fire Island National Seashore natural resource managers recognize the strong cultural and natural resources present on the island and aim to enhance both through their management actions. Fire Island staff intends to develop a management plan for post-storm recovery and coastal land use in conjunction with nearby agencies and communities, and enhance their public outreach and education programs. Communities on Fire Island are responsible for mitigating concerns regarding visitor use due to the National Park Service’s limited authority on private land (FIIS 2016a). Fire Island staff will initiate a deer management plan within the next few years, the goal of which is to enhance public outreach and education in the western communities regarding high deer densities, reduce deer densities on federal tracts of land throughout Fire Island, and, subsequently, protect cultural and natural resources that are negatively affected by high deer densities (FIIS 2016b).
My research focuses on the OPWA (Figure 2), which was designated a federal wilderness area in 1980 (Klopfer et al. 2002). The OPWA is managed in accordance with philosophy espoused in the Wilderness Act of 1964 (Underwood et al. 1998, FIIS 2016c) and efforts are taken to minimize human disturbance. Overnight camping is limited to behind dunes to avoid danger of beach vehicles and public vehicle use is prohibited on OPWA beaches. Mechanical management is also strictly limited in the OPWA and human recreation is monitored through camping and hunting permits issued by Fire Island National Seashore.

As with most Atlantic barrier islands, plant communities in the OPWA exhibit zonation parallel to the shoreline (Ehrenfeld 1990). Community zones begin with the ocean-side beach (Figure 3), where annual plants survive with high amounts of salt and sunlight, consistent sand burial, occasional tidal overwash, and low freshwater availability. The foredunes on Fire Island are dominated by American beachgrass, *Ammophila breviligulata*, a perennial grass with a strongly positive growth response to sand burial (Maun 2009). The back-side of the foredune transitions to swale, where protection from wind, salt spray, and sand abrasion provides a very different growing environment for plants. Many small pitch pine (*Pinus rigida*) groves exist in areas of swale where soils are acidic (Stuckey and Gould 2000). The OPWA does not have an established secondary dune or holly maritime forest (Klopfer et al. 2002), but occasional remnant patches of American holly (*Ilex opaca*) and *P. rigida* exist between shrub and marsh communities. Grassland plant species richness is low (S=1), but it increases farther inland (Ehrenfeld et al. 1989).

Before Hurricane Sandy, foredunes in the OPWA were 4-15 m high (Hapke et al. 2010). Many stretches of foredune in Fire Island’s OPWA were flattened and overwashed by Hurricane Sandy’s high storm surge, depositing large volumes of sand inland and leaving overwash fans
(Figure 3) ranging in size from 0.60 ha to 3.24 ha. A breach occurred at Old Inlet (Figure 4), a previous inlet that remained a low-lying area of the OPWA for nearly 200 years (Psuty et al. 2005). The Old Inlet breach remains open and connects the Atlantic Ocean to Great South Bay. After only one growing season, *A. breviligulata* established on the beach and in overwash fans. Characteristic of dune vegetation (Maun 2009), a positive feedback between beach grass growth and sand entrapment is evident in some areas since Hurricane Sandy.

Deer in the OPWA have consistently exhibited densities of approximately $25 \pm 8$ deer km$^{-2}$ since the mid-1980s based on aerial and ground surveys (O’Connell and Sayre 1989, Underwood 2005). Trampling by deer results in structural damage to above-ground and below-ground vegetation, leaving a legacy network of trails lacking vegetation throughout the OPWA (NYSC 2010, NOAA 2012). Deer apparently graze *A. breviligulata* and other plants in overwash fans of the OPWA (unpublished data; Figure 5). However, the degree to which deer exert an impact to the composition and structure of recovering vegetation in overwash fans after storms like Hurricane Sandy is speculative.
Figure 1. Conceptual model showing ecosystem drivers, environmental stressors acting upon vegetation communities in overwash fans (OW), and useful measures of OW characteristics (i.e., function and composition). Stressors highlighted in green are well-documented in literature and are addressed in some capacity in this dissertation, though my primary focus is on the role of deer as a stressor to developing vegetation communities in overwash fans. Erosion and climate change effects occur on both coasts, though other stressors exhibit gradients in concentration from ocean (i.e., high) to bay (i.e., low).
Figure 2. Fire Island National Seashore is located off the southern coast of Long Island, New York, USA and contains the Otis Pike Fire Island High Dune Wilderness Area.
Figure 3. Cross-section of a barrier island with vegetation communities documented in the Otis Pike High Dune Wilderness Area showing (a) typical vegetation community zonation, (b) after an overwash event, and (c) as the foredune begins to rebuild over time. Details regarding species commonly present in vegetation zones are present in the text.
Figure 4. Nine locations where foredunes were overwashed by Hurricane Sandy in 2012 in the OPWA, Fire Island, NY.
Figure 5. Trail camera photograph taken on January 11, 2015 in an overwash fan of the OPWA, Fire Island, NY showing a group of white-tailed deer grazing senescent *Ammophila breviligulata*. 
CHAPTER ONE: Patterns of vegetation cover and species composition in overwash fans on Fire Island recovering from Hurricane Sandy

**Introduction**

Barrier islands are linear landforms where several environmental factors (i.e., abiotic) exhibit gradients perpendicular to the shoreline (Ehrenfeld 1990, Maun 2009). The presence of a foredune prevents most salt, sand, and wind from impacting vegetation on the leeward side of the dune. Consequently, salt spray, wind velocity, soil acidity, and sand deposition are highest on the ocean coast and decrease farther inland (Lichter 1998, Kim and Yu 2009, Maun 2009). Soil moisture and nutrient contents (i.e., nitrogen and phosphorus) increase farther inland, where a soil horizon forms (Art 1976, Lichter 1998, Maun 2009, Fenu et al. 2013). Depth to the freshwater table also decreases farther inland (Schubert 2009). Soil characteristics vary with relative humidity, temperature, light, sediment grain size, pH, and conductivity (Maun 2009).

Plant communities on barrier islands often contain subsets of the species present on the adjacent mainland (Ehrenfeld 1990), and they exhibit roughly parallel bands of composition and density as a result of abiotic gradients. Abiotic conditions often mediate plant survival and reproduction (Houle 1996, Maun 2009), and several gradients, including salt spray (Oosting and Billings 1942), sand burial (Oosting and Billings 1942, Hewett 1970, van der Valk 1974, Moreno-Casasola 1986), freshwater limitation (Schubert 2009), and nutrient limitation (Gilbert et al. 2008, Maun 2009, Fenu et al. 2013, Jass 2015), can be assumed based on location alone (Maun 2009, Young et al. 2011, Jass 2015). Differences in abiotic conditions can induce multi-scale spatial patterns of vegetation establishment and growth (Watt 1947, Dale and Fortin 2014, Zinnert et al. 2016), and location as a proxy for abiotic stress is worthy of investigation at different spatial and temporal scales (Stallins and Parker 2003).
Knowledge of spatial scales present in ecological data is necessary to identify processes structuring communities (Borcard et al. 2004, Chase 2014), and many spatial patterns present in species communities result from both niche and neutral processes (Chen 2014). Niche theories suggest that environmental conditions are responsible for species presence and community structure (Chen 2014). Conversely, neutral theories state that speciation, dispersal, and ecological drift dominate over niche-based processes in structuring communities due to differences in temporal and spatial scale (Mikkelson 2005: from Hubbell 2001). Chase (2014) posited that neutral processes occur over small spatial extents within which environmental conditions are relatively constant, and niche processes occur over broad spatial extents. Differentiation of niche and neutral processes responsible for these patterns is possible after accounting for spatial scale in analysis (Gilbert and Bennett 2010, Chase 2014).

Scale sensitivity influences the kinds of statistical analyses of ecological data used (Legendre and Fortin 1989, Legendre 1993). Borcard and Legendre (2002) introduced distance-based Moran’s eigenvector maps (dbMEM) as a tool for extracting and testing the significance of spatial variation in georeferenced data. The dbMEMs represent a spectral (i.e., “eigen-“) decomposition of the spatial relationships within the sampling frame (Legendre et al. 2009). Eigenfunctions describe the spatial scales that can be accommodated in the sampling design, and are obtained by a principal coordinate analysis of a truncated Euclidean distance matrix among the sampling sites.

Like other eigenanalyses, dbMEM results in new variables (i.e., eigenvectors) that are orthogonal and proportional to Moran’s I, a commonly computed statistic characterizing spatial autocorrelation (Mitchell 2005). Significant dbMEM eigenvectors are chosen using standard statistical methods and are representative of variation at a particular spatial scale (Borcard and
Legendre 2002, Dray et al. 2006). Variation partitioning can then be used to measure the amounts of variation explained by multiple factors (Peres-Neto and Legendre 2010, Oksanen et al. 2008), including spatial eigenvectors and environmental proxy variables.

Understanding how plant communities recover after a major disturbance has been a priority in ecology for decades (Grime 1974, Chaneton and Facelli 1991, Grace 1991, Dornelas 2010). The role of environmental variability is a key concern in understanding how communities are organized (Wiens 1977), but environmental conditions often exhibit spatial patterns (Legendre 1993, Cottenie 2005, Gao et al. 2014). Spatial autocorrelation, structure in community data resulting from spatial gradients, often contributes significantly to community structuring (Borcard et al. 2011, Bannar-Martin 2014), but it is usually considered a nuisance. However, spatial autocorrelation can improve interpretation of processes from spatial patterns (Dormann et al. 2007), including scales at which they act (Borcard et al. 2004). Spatial patterns of barrier island vegetation communities are obvious (Art 1976, Ehrenfeld 1990, Maun 2009), but factors controlling recovering community composition and cover are not well-understood. The purpose of this chapter is to characterize vegetation community development in overwash fans of the OPWA by partitioning the variation among environmental, spatial, and shared components.

In this chapter, I use dbMEM analysis to identify spatial structures in vegetation communities of overwash fans, and test spatial eigenvectors in a canonical analysis with several environmental proxies. My main objectives are to (1) describe spatial patterns in vegetation composition and cover, (2) identify scales at which the plant community is structured, and (3) explore the relationship between community spatial structure and environmental proxies in nine areas overwashed by Hurricane Sandy in the OPWA.
Methods

In preparation for vegetation surveys, I delineated boundaries of nine large-extent storm-induced overwash fans from aerial imagery (NOAA 2012) in ArcGIS. I used the Create Fishnet tool in ArcGIS (version 10.2, ESRI, Redlands, CA) to overlay a 10x10-m lattice within each overwash boundary. I determined optimal grid size from preliminary sampling of inter-patch distances (Legendre and Legendre 2012, page 787) measured from aerial imagery and field sampling of emerging plant density and cover conducted in 2014. I retained at least 60 plots in each overwash (range: 61 - 99) at grid intersections to ensure vegetation cover estimates were within defined precision targets.

Digital point intercept vegetation surveys (see Appendix J) were conducted three times per year in 2015 and 2016 to capture the entire growing season (i.e., July, September, October). I used a Canon T3i digital single-lens reflex camera (DSLR) with 18-55 mm zoom lens mounted approximately 2-m above the ground on an adjustable, aluminum frame (Booth et al. 2004) with a 1-m$^2$ base. The camera was placed in the nadir position to record vegetation cover contained with the boundary of the frame base. I wrote survey date, plot location and number on a small dry-erase board, which was placed within the camera field of view for plot identification. I set the camera shutter speed to 1/2000th of a second to minimize blurring of photographs from windblown vegetation, and I released the shutter remotely using a Bluetooth connection to the camera. Photographs of each plot were stored in native and compressed formats for later processing (Johnson et al. 2009). The sampling protocol was executed with two people.

I downloaded plot locations into a handheld Trimble GeoXT 2008 Series GPS unit with TerraSync™ and sub-meter horizontal accuracy. I navigated to plot locations using the real-time, satellite-based augmentation system available through the TerraSync application. Navigation was
suspended at horizontal accuracies >60 cm. I inserted a pin flag into the ground at the plot location, and with the aid of a mounted compass, I oriented the camera frame due north with the pin flag in the southeast corner (Figure 6). A bed sheet attached to two 122-cm wooden dowels was used to shade the plot from direct sunlight, which aided in image processing by reducing glare and shadows (Cox and Booth 2008).

Post-processing of photographs required three main steps: (1) label each image with survey date and plot number, (2) crop the image to within the quadrat boundary, and (3) analyze the image for species frequency. A grid of 100 points was created using the Generate Regular Points in Polygons tool from Geospatial Modelling Environment (version 0.7.3.0, Spatial Ecology LLC, Queensland, Australia). The grid was placed with a 5-cm buffer around the inside boundary of each plot image to minimize edge effects. The 100-grid-point file was used as input to PointSampler in ArcGIS (Gobbett and Zerger 2014), which sequentially prompted the user to identify any species present at each point location using user-defined categories, which I used as species labels. PointSampler created a tabulated file containing the plant species identified at each point, which I used to calculate species frequencies. I used species frequency as a proxy for cover (Elzinga et al. 1998) and applied Inverse-Distance Weighting in ArcGIS to visualize vegetation coverage in overwash fans. Plants were identified using several resources (Gleason and Cronquist 1991, Silberhorn 1982, Stuckey and Gould 2000) and were verified (Jordan Raphael and Eric Lamont, pers. comm.). I used nomenclature published by the United States Department of Agriculture Natural Resources Conservation Service Plants Database (USDA 2018).

Distance-based Moran’s eigenvector methods consist of three main steps: (1) distance-based eigenvector decomposition of response (i.e., community) data, (2) division of significant
latent variables (i.e., dbMEMs) into sub-models representing fine (10-20 m), broad (~100 m), or other metric of spatial patterns, and (3) interpretation of sub-models using explanatory variables. An optional fourth step is to partition the variance with respect to explanatory variables and several sub-models of dbMEMs (i.e., fine- and broad-scale patterns). I use all four steps to assess spatial patterns in community data in recovering overwash fans. Before attempting to pool data from two years, I tested the effects of month and year on community composition using multivariate analysis of variance (i.e., MANOVA) in R (version 3.2.0). The matrices of plant species frequency values (i.e., cover) were transformed using the Hellinger equation (“Model 1”) prior to analyses. Hellinger transformations are used to reduce the effect of large values and many zeroes in response data (Borcard et al. 2011, Legendre and Legendre 2012).

To identify spatial scales at which vegetation cover varied, I first calculated a Euclidean distance matrix of UTMX and UTMY coordinates for survey locations, which was truncated according to Borcard and Legendre (2002). I then computed distance-based Moran’s eigenvector maps (i.e., Principal Coordinates of Neighbor Matrices) on Hellinger-transformed response matrices for each overwash fan in each year (n=18) with the PCNM (Legendre et al. 2010) function in R. Eigenvectors (i.e., dbMEMs) of the neighborhood matrix represent patterns of vegetation structure at increasing spatial frequencies. Eigenvectors with Moran’s I > 0 indicate positive autocorrelation and those with Moran’s I < 0 indicate negative autocorrelation. I used forward selection to identify significant eigenvectors and created sub-models corresponding to broad and fine spatial structures (Borcard and Legendre 2002).

I evaluated the importance of environmental proxies in the structuring of Hellinger-transformed community response matrices through redundancy analysis (RDA). Environmental proxies included plot elevation (AG 2015, AG 2016), proximity (m) of the plot location to the
foredune (i.e., “dune”), and proximity (m) of the plot location to the bay-side salt marsh (i.e., “marsh”). Proximity to the dune was used to represent gradients in salt spray and sand burial. Proximity to the marsh was used to represent freshwater availability, and elevation was used to represent access to freshwater (i.e., points at higher elevations are farther from the water table), exposure to wind abrasion, and concentration of salt spray. I used forward selection to test significance of environmental proxies in the RDA on (1) the community response matrix, (2) broad-scale, and (3) fine-scale spatial sub-models. I also calculated average change in dune height between 2015 and 2016 to assist the interpretation of the roles of environmental proxies in structuring recovery of plant communities in overwash fans.

I tested the response matrix of each overwash fan for the presence of a bi-linear trend with location (i.e., UTMX, UTMY) using a redundancy analysis and MANOVA with 1,000 permutations. Significant linear trends reveal changes in the community response at potentially broader scales than the sampling extent (Borcard et al. 2004). Where linear trends were significant, response matrices were regressed against UTM coordinates, and the residuals were used as response variables in a “detrended” set of analyses (“Model 2”). For Model 2 analyses, positive spatial dbMEMs were not separated into broad and fine spatial sub-models. I computed dbMEMs for detrended response matrices to capture significant spatial structures present in the nine overwash fans that are unrelated to geographic location (Borcard et al. 2004) and identified environmental proxies important to detrended vegetation community composition through RDA and forward selection.

Finally, I used the varpart function in the vegan R package (version 2.4-1; Oksanen et al. 2008) to identify variation in community data that was attributable to environmental proxies, spatial sub-models, and induced spatial dependence. Induced spatial dependence is explained by
environmental and spatial variables, but contributions of each individual variable are indistinguishable. I used adjusted R² value as an indicator of the amount of variation explained by each explanatory matrix (Borcard et al. 2004, Peres-Neto et al. 2006, Bannar-Martin 2014). All R code used in this chapter is available in Appendix A.

**Results**

I photographed an average of 661 plots (range: 581 - 683) during each of six survey periods (Table 1). Overwash 1 was inaccessible during October 2016. Vegetation cover was dominated by *A. breviligulata*. Interpolated vegetation cover maps revealed patchy cover in overwash fans, with greater numbers of species observed (Appendix B) and percent cover of *A. breviligulata* (Appendix C) in bayside areas of all overwash fans (Figure 7).

MANOVA results indicated a significant effect of year but not month (year*month interaction: F=1.003, df=5, 3423, p=0.392; year: F=1.089, df=1, 3422, p=0.001; month: F=1.401, df=2, 3423, p=0.199) on plant community composition, so subsequent analyses were conducted for individual overwash fans for the month of September in each year (2 years, 9 overwash fans: n=18). I chose to model September surveys for two reasons: (1) overwash 1 was not surveyed in October 2016 and (2) species diversity and vegetation cover were greater in September than in July (unpublished data). A bi-linear trend in the community response matrices was detected in every overwash fan (p=0.001).

Moran’s eigenvector maps of community data revealed an average of 6.1 positive dbMEMs (range: 3 - 11) and 24 negative dbMEMs (range: 5 - 44) per overwash. Individual negative dbMEMs did not significantly improve the fit of models (α=0.10), and thus were not further investigated. Significance of broad- and fine-scale positive dbMEMs were indicated for
every overwash fan, and an average of 3 (range: 2 - 5) dbMEMs was significant (Figure 8). Variability captured by dbMEMs was visually represented by one-dimensional sine waves for interpretability, though dbMEMs vary across space and therefore describe two spatial dimensions. Broad positive dbMEMs described spatial processes occurring at ~100 m (Appendix D). Fine positive dbMEMs represented spatial patterns occurring at ~10-20 m. Broad-scale spatial structures explained more variation in the community than fine-scale spatial structures in 2015 (average: 13.4% vs. 9.4%) and 2016 (average: 16.1% vs. 11.5%; Figure 9). A comparatively large percentage of variance (range: 4.0% - 40.3%) was shared among environmental proxies and positive dbMEMs.

Though proportions of variation explained by environmental proxies were low, they significantly contributed to vegetation community composition in all overwashes (Table 2). Many environmental proxies also contributed to the spatial structures identified by the dbMEMs. Relationships between environmental proxies and sub-models remained consistent between years for most overwash fans. Broad-scale spatial structures were explained primarily by proximity to dune. Fine-scale spatial structures were rarely explained by environmental proxies. In the overwash fan with the greatest decline in dune height, none of the environmental proxies explained spatial structures identified using dbMEM.

Moran’s eigenvector maps of detrended community data revealed an average of 5 positive dbMEMs (range: 1 - 11) and 26 negative dbMEMs (range: 11 - 48) per overwash fan. None of the negative dbMEMs was significant. Environmental proxies contributed more significantly to vegetation community composition in four overwash fans in 2015 (average: 28.7%) than in 2016 (average: 23.5%; Figure 10). Positive spatial processes explained more community variance in 2015 than in 2016. Little variation was explained by the environmental
proxies or induced spatial dependence after removing the bi-linear trends in community composition. Greater proportions of variation in the detrended response matrices were unexplained (i.e., residual) than in the response matrices containing the bi-linear spatial trends.

**Discussion**

Spatial structuring of the plant communities was apparent in every recovering overwash I sampled. On average, over one-half (i.e., 54%) of the variation in plant community composition was explained by the selected dbMEM eigenfunctions. Interestingly, non-spatial environmental forcing (i.e., sand burial, salt spray, limited fresh water) explained less than 1% of the variation in community composition on average, yet was important in 3 overwash fans. One instance was in overwash 1 during 2015, the largest overwash fan, where all the environmental proxies were correlated with community composition. That pattern was not observed in 2016 due to an intervening inundation of the overwash fan caused by the remnants of Hurricane Joaquin (Berg 2016). The other two overwash fans (i.e., 3 and 8), with clear environmentally-controlled responses in the vegetation community, exhibited the largest increases in dune formation between years. The persistence of a nascent foredune dictated the degree to which environmental proxies influenced plant community composition in recovering overwash fans; in overwash fans where a budding foredune was removed between surveys, environmental control was less important than where a budding foredune persisted.

Fine-scale positive autocorrelation (10-20 m) describes neutral processes, including dispersal of species besides *A. breviligulata*. Broad-scale positive autocorrelation (~300 m) describes niche processes acting upon the community, including gradients in harsh beach conditions, productivity from bayside marshes (Art 1976, Maun 2009), and radial growth of *A. breviligulata* rhizomes and subsequent shoots (Ehrenfeld 1990). While fine scale spatial
structuring was demonstrated in all overwash fans, it was not consistently correlated with the environmental proxies I modeled with a single exception. I observed significant induced spatial dependence between all environmental proxies and fine-scale spatial structure in overwash 9, where *A. breviligulata* cover was nearly one-half (i.e., 0.54x) of all other overwash fans. Because fine-scale spatial structures are typically associated with “neutral” processes (Legendre et al. 2009), plant species other than *A. breviligulata* are more likely to be dispersal-limited (i.e., *Chamaesyce polygonifolia*) and reflected in the sub-models in these overwash fans.

Use of proxies to assess abiotic factors in overwash fans is supported in the analysis of barrier island plant communities (Ehrenfeld 1990, Maun 2009). Positive spatial autocorrelation in all overwash fans showed strong environmental forcing, and the proportion of variance in community composition that was shared between spatial structures and environmental proxies (i.e., induced spatial dependence) was approximately 24% and consistent between years. That proximity to the dune induced significant spatial dependence is not surprising due to its overwhelming influence on plant communities (Ehrenfeld 1990, Maun 2009). The correlation between spatial structures and proximity to the dune was most evident at broad spatial scales. I attribute this phenomenon to variation in *A. breviligulata* cover across each overwash fan. Elevation and proximity to the marsh also induced spatial dependence, especially in overwash fans where the dune was severely eroded (e.g., overwash fan 2 in 2015 and 2016) or non-existent (e.g., overwash fan 1 in 2016).

Plants in overwash fans must tolerate sand burial and freshwater limitation, two factors determined largely by elevation and proximity to the dune (Ehrenfeld 1990, Maun 2009). Acosta et al. (2007) found that alteration of dune morphology highly influenced changes in coastal vegetation zonation and the disappearance of some vulnerable plant communities. Proximity to
the dune significantly contributed to spatial patterns observed in seven of nine overwash fans in 2015, but was only significant in five overwash fans in 2016. Kim and Yu (2009) found that distance to coastline was a significant indicator of exchangeable cations (Ca$^{2+}$, Mg$^{2+}$, K$^+$), with greater concentrations of salt spray nearer to the coastline. The switch in significance of proximity to dune in this study describes reductions in salt spray as a result of emerging foredunes in 2016.

Nitrogen availability may become more important to vegetation community composition as a foredune blocks salt spray and communities diversify (Maun 2009). *A. breviligulata* interacts with *Morella pensylvanica* (Shumway 2000) and *Lathyrus japonicus* (Stuckey and Gould 2000), two plants associated with nitrogen-fixing bacteria in root nodules, to secure nutrients. *M. pensylvanica* and *L. japonicus* are primarily found on the leeward-side of foredunes and swale (Ehrenfeld 1990). Both species were observed more frequently in 2016 than 2015 in the OPWA, suggesting the growth of foredunes enhanced spread of *M. pensylvanica* and *L. japonicus* between years.

Negative autocorrelation explained large amounts of variation in community composition in developing overwash fans. Negative autocorrelation often manifests in regular sampling schemes (Dray et al. 2012) and describes the high likelihood that adjacent plots exhibit extreme differences in vegetation composition and cover. In the process of choosing between an appropriate plot spacing and time available to sample, my sampling scheme probably induced some negative autocorrelation. However, negative autocorrelation explained smaller proportions of variation in community composition in 2016 than 2015 and plant cover increased substantially between years. Expression of negative autocorrelation in plant communities of overwash fans
will continue to decrease as patches of vegetation coalesce, as was documented for sand dunes in Ontario, Canada (Morrison and Yarranton 1974).

On average, 25% of the variation in the community data was unexplained (Legendre et al. 2009). Stochasticity in community data can be explained by environmental variability (Tilman 1990), demographic variability (Hubbell 2005), or more likely a combination of both (Adler et al. 2007). Statistical methods do not allow for differentiation of potentially explainable and real stochasticity present in the community data. It is often infeasible to measure all environmental gradients acting within a study system, particularly interactions among environmental variables, but many of these structures are captured in the spatial components defined by the dbMEM analysis (Borcard et al. 1992). Brantley et al. (2014) used constrained ordination and several environmental conditions to describe overwash fan plant communities, but their results only explained approximately 20% of the variation present. I explained a greater amount of variation in overwash fan plant communities by including effects of spatial structures not attributable to a particular environmental condition.

The use of variation partitioning in ecology has drawn recent criticism (Gilbert and Bennett 2010, Smith and Lundholm 2010) for two reasons. First, variation partitioning is scale-sensitive (Angeler et al. 2013). Second, the covariance between environmental variables and spatial structures confounds a clear interpretation of niche and dispersal limitation (Gilbert and Bennett 2010). In studies that seek to understand factors controlling beta diversity over large spatial extents, these are serious shortcomings. In my study, however, the spatial extent of inference is short (<300 m) and clearly demarcated, the number of plant species is low (~30), and putative, underlying environmental gradients are well-defined. Finally, because I divided
dbMEMs structures into spatial sub-models, the ability to distinguish between neutral (i.e., fine-scale) and niche (i.e., broad-scale) processes was facilitated.

I sought to understand spatial structuring in recovering plant communities after a major storm event. I anticipated strong environmental forcing and important spatial structuring as the communities developed. High proportions (~70%) of variation in plant community composition and cover were explained by spatial structuring. Environmental forcing contributed little to community variability except in one instance, but induced spatial dependence was important in all overwash fans. Proximity to foredune was the principle influence on community and spatial structures. Some overwash fans may not recover from Hurricane Sandy due to ongoing inundation during high water events, but those with persistent foredunes will continue to develop in the absence of subsequent overwash.
Table 1. Six total vegetation surveys were conducted in overwash fans in the OPWA, Fire Island, New York throughout the growing seasons in 2015 and 2016.

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<td>61</td>
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<td>Survey Date</td>
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<td>9/9</td>
<td>9/9</td>
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<td>9/10</td>
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<td></td>
</tr>
<tr>
<td>Num. Plots</td>
<td>97</td>
<td>90</td>
<td>77</td>
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<tr>
<td>Num. Plots</td>
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<td>77</td>
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<td>69</td>
<td>77</td>
<td>65</td>
<td>80</td>
<td>58</td>
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</table>
Table 2. Environmental proxies for sub-models ("SM") ordered by change in dune height: (1) community composition ("Comm."), (2) broad-scale, and (3) fine-scale spatial structures in overwash fans ("OW") in the OPWA, Fire Island, New York for 2015 and 2016. Variables include elevation, proximity to foredune ("Dune"), and proximity to marsh ("Marsh"). Significance values (i.e., p-values) are reported; “-” denotes a statistically insignificant relationship.

<table>
<thead>
<tr>
<th>OW</th>
<th>SM</th>
<th>2015</th>
<th>2016</th>
<th>Change in Dune Height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Elevation</td>
<td>Dune</td>
<td>Marsh</td>
</tr>
<tr>
<td>2</td>
<td>Comm.</td>
<td>0.010</td>
<td>0.009</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Comm.</td>
<td>0.009</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Comm.</td>
<td>&lt; 0.001</td>
<td>0.011</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>5</td>
<td>Comm.</td>
<td>0.011</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
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<td>Broad</td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>6</td>
<td>Comm.</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
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</tr>
<tr>
<td>9</td>
<td>Comm.</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
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<td></td>
<td>Fine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Comm.</td>
<td>0.009</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>8</td>
<td>Comm.</td>
<td>0.002</td>
<td>0.001</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td></td>
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<td></td>
<td>Fine</td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>0.003</td>
<td>&lt; 0.001</td>
<td>0.012</td>
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</tbody>
</table>
Figure 7. Percent *A. breviligulata* cover and number of plant species observed during September 2015 in three overwash fans of the OPWA, Fire Island, New York.

Interpolation was performed using inverse-distance weighting.
Figure 8. A trend surface analysis showing dbMEM values for positive axes of Hellinger-transformed community composition (Model 1) in two post-Hurricane Sandy (i.e., 2015) overwash fans in the OPWA, Fire Island, New York.

The size of the circles correspond to dbMEM values (dark circles > 0, white circles < 0), and bands of like symbols describe spatial patterns captured by the significant axes from broad (left-most) to fine (right-most) scale. Relationships shown are more useful to interpret than the dbMEM values themselves.
Figure 9. Percentage of variation explained by environmental proxies, spatial autocorrelation, and residual variation for Hellinger-transformed community composition in post-Hurricane Sandy (i.e., 2015 and 2016) overwash fans in the OPWA, Fire Island, New York. Important environmental variables included elevation, proximity to foredune, and proximity to marsh, and Hellinger-transformation was used to reduce the effect of large species frequency values in the community composition matrix.
Figure 10. Percentage of variation explained by environmental proxies, spatial autocorrelation, and residual variation for detrended (i.e., UTMX, UTMY) community composition data in post-Hurricane Sandy (i.e., 2015 and 2016) overwash fans in the OPWA, Fire Island, New York. Important environmental variables included elevation, proximity to foredune, and proximity to marsh, and Hellinger-transformation was used to reduce the effect of large species frequency values in the community composition matrix.
CHAPTER TWO: Abiotic and biotic constraints to barrier island plant community recovery after Hurricane Sandy.

Introduction

Foredunes serve as a barrier against coastal storms and wave run-up (Sallenger 2000, Houser et al. 2008). All coastal plants must be stress-tolerators (Grime 1977) to establish and persist, and have evolved different life history strategies to exploit disturbed areas (Maun 2009). Species tolerances to environmental conditions (i.e., sand burial, wind, direct sunlight, salt spray, soil characteristics; Ehrenfeld 1990, Maun 2009) determine where they grow along gradients. Some annual herbs are tolerant of high winds, direct sunlight, sand burial, and moderately saline conditions, and are thus present on high beaches and dune areas flattened by storms. Many plants common on beaches and other areas frequently disturbed are annuals that exhibit thick cuticles, prostrate growth forms, high water use efficiency, and high phenotypic plasticity. Dispersal is predominantly by wind and wave action (Maun 2009). These species are common on middle beaches, but not so on high beaches where perennial grasses establish (Cowles 1899).

The presence of a budding foredune drastically changes environmental conditions farther inland, allowing less tolerant plant species to establish, and facilitates the zonal characteristics of barrier islands (Ehrenfeld 1990). Many authors attribute barrier island plant community zonation primarily to plant tolerance to sand burial (Martínez and Psuty 2004, Maun 2009). Perennial dune grasses cannot tolerate the periodic wave action on lower beaches, but they thrive on high beaches and foredunes where sand accretion occurs. Dune grasses typically grow rapidly and clonally (Maun 2009). After a storm event, dune grasses grow in high density in overwash fans until a nascent foredune forms. Salt-intolerant plants establish on the leeward side of foredunes, increasing dune stability. On leeward slopes, wind speed is greatly diminished and many biennial
herbs grow interspersed among grasses and shrubs. Some additional shrub species grow farther inland of the dune, predominantly in swale, and eventually out-compete grasses (Ehrenfeld 1990, Maun 2009).

Abiotic forcing on barrier island vegetation development is well-documented (Ehrenfeld 1990, Maun 2009), but effects of biotic factors are less understood. The purpose of this chapter is to explore relationships among abiotic and biotic (i.e., net primary productivity, white-tailed deer) factors that influence vegetation community development in overwash fans while controlling for spatial autocorrelation. Spatial variables in this chapter describe patterns in overwash fan plant communities that are not necessarily abiotic or biotic, and likely describe combinations of both factors. In this chapter, I test multiple characteristics of overwash fans that may influence vegetation community development after Hurricane Sandy, including important spatial structures (see Chapter One), white-tailed deer presence, elevation, and vegetation productivity. My main objectives are to (1) explore relationships between community vegetation characteristics and biotic and abiotic factors, and (2) rank biotic and abiotic factors in terms of their significance to vegetation community structure in recovering overwash fans.

**Methods**

I used the Normalized Difference Vegetation Index (NDVI) as a proxy for vegetation productivity in overwash fans. I obtained Landsat 7 ETM+ Surface Reflectance imagery for the OPWA for 24 June 2015 and 26 June 2016 (courtesy of United States Geological Survey). Landsat 7 sensors were replete with gaps in data after a Scan Line Corrector failed in 2003 (Andrefouet et al. 2003). To accommodate these gaps in imagery data, I used imagery from 12 July 2016 where necessary. I scaled the red, green, blue and near-infrared (NIR) bands to
between 1-255 using the scaling parameter provided in the Landsat 7 metadata. I used the Image Analysis toolbar in ArcGIS to create a composite of the red (band 3), green (band 2), blue (band 1), and near-infrared (band 4) bands. I calculated NDVI using the following equation:

\[
NDVI = \frac{\text{NIR}-\text{RED}}{\text{NIR}+\text{RED}}
\]

NDVI values range from -1 to +1, where negative values typically correspond to pixels with no green vegetation present and positive values correspond to pixels with highly productive green vegetation present (Pettorelli et al. 2005).

I surveyed vegetation communities in nine areas overwashed by Hurricane Sandy in the OPWA in 2015 and 2016 (see Chapter One). I transformed frequency values using the Hellinger equation for each species present in vegetation plots to reduce the influences of zeroes and large values (Borcard et al. 2011, Legendre and Legendre 2012). It is difficult to identify signs of browsing and grazing on herbaceous vegetation using commonly-used indices (Blossey et al. 2017, Nuzzo et al. 2017), so I recorded deer pellet groups in nadir photographs as an indicator of deer use at the plot scale. I averaged the number of deer pellet groups over all surveys within a year to account for minor variations in plot location among surveys.

Ordination can be used to interpret relationships among species or explanatory variables and to rank the relative importance of environmental gradients as they relate to structure of the community (ter Braak and Verdonschot 1995, Legendre and Legendre 2012). Canonical correspondence analysis (CCA) is a type of constrained ordination that uses regression methods and allows for statistical hypothesis testing. CCA assumes unimodal explanatory variables and can be used to model linear relationships if the response data contains species composition information (ter Braak 1986). I used the *cca* function in the R package vegan (version 2.4-1; Oksanen et al. 2008) to conduct a Canonical Correspondence Analysis (CCA) between...
community composition data (i.e., Y) and scaled versions of explanatory variables as constraints, including deer presence (i.e., presence of deer pellet groups; “Deer”), productivity (“NDVI”), elevation (“DEM”), broad-scale spatial structures (“Broad”), and fine-scale spatial structures (“Fine”). Spatial sub-models were identified as the most significant axis describing either broad- or fine-scale structures in the community (see Chapter One). I conducted CCA separately for each year, but pooled plots across all overwash fans to assess overall patterns in the vegetation community in overwash fans. I used variable selection, ordistep function in vegan package in R, to select significant variables based on the F-statistic of the model after a variable was added to the null model. Akaike’s Information Criterion was used to determine variable importance if two models shared an F-statistic (Oksanen et al. 2008). The F-statistic was also used to calculate the p-value, the probability that the null statistical hypothesis is true.

I created biplots of species and explanatory variable scores from each CCA using scaling 2 to assess species responses to environmental gradients in explanatory variables (Palmer 1993, Borcard et al. 2011). Rare species (i.e., observed in <5 plots) were included in the CCA using community composition data, though I did not infer environmental relationships from the biplots to avoid misinterpretation (ter Braak and Verdonschot 1995). I used envfit to fit significant environmental variables on an ordination plot and ordihull to draw convex hulls around plots in each overwash fan. All R code used in this chapter is available in Appendix E.

Results

I identified 29 plant species among all surveys and overwash fans (Table 3). Vegetation cover was dominated by A. breviligulata, which was observed in 72.8% of plots in 2015 and 75.8% of plots in 2016. Other common species included: Toxicodendron radicans, Chamaesyce
polygonifolia, Prunus maritima, Lathyrus japonicus, and Smilax glauca. Productivity differed among years and overwash fans (Appendix F). Deer sign was observed in only 1% of plots surveyed. In both years, A. breviligulata (AMBR) was positively correlated with NDVI (Figure 11). In 2015, T. radicans (TORA), S. glauca (SMGL), Morella pensylvanica (MOPE), L. japonicus (LAJA), Parthenocissus quinquefolia (PAQU), C. polygonifolia (CHPO), and Rosa multiflora (ROMU) were found in plots associated with high NDVI and Fine-scale spatial structures. Hudsonia tomentosa (HUTO) was observed in plots with strong Broad-scale spatial structure. Variables significant (α=0.10) to the CCA were NDVI, DEM, and Fine (Table 4), and plots exhibited gradients in Fine and NDVI (Figure 12) for many overwash fans. In 2016, LAJA, Juncus species, POAR, CHPO, Pseudognaphalium obtusifolium (PSOB), and PAQU were found in areas of relatively high elevation (Figure 11). SYPI, PRMA, TORA, SMGL, AMBR, and Triplasis purpurea (TRPU) were associated with Fine-scale spatial structures. MOPE was found in areas with strong Broad-scale structuring (Figure 12). Significant (α=0.10) contributions to the CCA were from NDVI, DEM, and Fine (Table 4). Deer did not significantly contribute to the CCA in either year studied.

In 2015 and 2016, NDVI exerted the strongest influences on overall community composition (Figure 12). In 2015, vegetation communities in overwash fans 2 and 5 were expressed across all significant variables. Vegetation communities in overwash fans 1, 3, 6, and 7 were expressed mostly along a gradient in NDVI. Vegetation communities in overwash fans 4, 8, and 9 were expressed in Fine-scale spatial gradients. In 2016, vegetation communities in overwash fans 1, 2, 4, 5, 8 and 9 exhibited hulls across all significant variables. Vegetation communities in overwash fans 3, 6, and 7 contained predominantly Fine-scale spatial patterns.
The CCA results for each overwash fan revealed low constrained variation (Table 5). Variables in overwash fans 8 and 9 consistently explained more variance (16-25%) than in other overwash fans (5-12%). The variables studied did not explain the vegetation communities in overwash fan 3. NDVI and DEM significantly contributed to the ecological gradients captured in community composition for nearly all overwash fans. Broad-scale processes were only significant for the largest site, overwash fan 1 (area: 3.24 ha).

Discussion

Community composition in many overwash fans was strongly associated with gradients in net primary productivity, fine-scale spatial structures, and elevation. Broad-scale spatial structures were statistically insignificant in the CCA due to their high correlation with NDVI among overwash fans. In essence, broad-scale spatial structures are induced by the spread of *A. breviligulata*, whose greenness signature is reflected in the NDVI (Pettorelli et al. 2005). Deer sign was only observed in ~1% of vegetation plots, so its statistical insignificance in the canonical correspondence analysis was not surprising.

The greatest increases in *A. breviligulata* result from moderate levels of sand burial (Ehrenfeld 1990, Maun 2009), which occur in coastal areas lacking a foredune (i.e., overwash fans), and not necessarily from increases in nutrient availability. *A. breviligulata* grows radially and clonally, so increases in cover of this species occur rapidly and in close proximity (Ehrenfeld 1990). NDVI increased toward marshes in all overwash fans (Appendix F) where species richness and cover of species other than *A. breviligulata* were greatest (Appendix C), suggesting NDVI also captured changes in species richness. Productivity decreased along the old primary dune line, where erosion and inundation still periodically occur.
Plant species relationships with productivity remained consistent between years. Niches identified in CCA plots for two common species (i.e., *L. japonicus*, *C. polygonifolia*) were defined by fine-scale spatial structures in 2015 and shifted to follow the elevation gradient in 2016. Both of these species are typically found on the leeward sides of budding foredunes (Stuckey and Gould 2000) and both were more frequently observed in 2016 than in 2015. In 2015, community structure in eight overwash fans exhibited important gradients in either productivity or fine-scale spatial structures, as evidenced by thin hulls along an environmental vector in the CCA. In 2016, three overwash fan communities showed gradients in productivity, but all others showed variation in both productivity and fine-scale spatial gradients.

Though physiological factors are important determinants of coastal vegetation communities, island geomorphology, particularly elevation, is also important. Brantley et al. (2014) found that island geomorphology affected both elevation and community structure in overwash fans off the Virginia coast. Dune-building plant species must tolerate sand burial, the primary limiting factor for seedling establishment and growth (Maun 1994, Maun 2009) for most coastal plants. Leatherman (1977) posited that sand movement between the beach and overwash fans on barrier islands is primarily influenced by wind direction. On Fire Island, winds predominate from the ocean during the growing season (Art 1976), increasing sand accretion farther inland and eliciting a positive growth response in *A. breviligulata* in overwash fans (Ehrenfeld 1990, Maun 2009). During the stage of post-Hurricane Sandy recovery discussed in this chapter, the dominance of beach grass and annual increases in elevation are expected (Stallins and Parker 2003, Stallins 2005, Maun 2009). Hayden et al. (1995) attributed changes in elevation to variability in depth to water table and subsequent vegetation patterning on frequently-disturbed barrier islands. Several dune-stabilizing shrubs and herbs found in the
OPWA also respond positively to mild sand burial, including *M. pensylvanica*, *P. maritima*, and *L. japonicus* (Ehrenfeld 1990). Only *L. japonicus* was confined to primary dune areas and showed a positive relationship with elevation in this study. *P. maritima* and *M. pensylvanica* were observed in many areas of overwash fans, and were not confined to dune areas.

Of the plant species observed in overwash fans, nearly half were found in greater proportions of plots in 2016 than 2015. *C. polygonifolia* is a prostrate annual commonly found on dunes and beaches (Cowles 1899, Silberhorn 1982), and nearly doubled in frequency in 2016. This species was recorded near the dune, but was overwhelmingly present in and influences the significance of fine-scale spatial structures in overwash 9. The three herbaceous Asteraceae species observed (i.e., *S. pilosum*, *E. caroliniana*, and *P. obtusifolium*) increased at least three-fold in the second survey in overwash fans with significant influences of elevation (i.e., overwash fans 7 and 8). These species prefer disturbed habitat (Dowhan and Rozsa 1989) and disperse effectively through wind, suggesting their presence may be reliant upon the presence of a nascent foredune and subsequent changes in wind in disturbed coastal areas. Dune-stabilizing shrubs (i.e., *L. japonicus*, *P. maritima*, and *M. pensylvanica*) increased in frequency in most overwash fans where dunes increased in height between years (i.e., overwash fans 9, 8, 7, 5), supporting the suggested importance of these species in building a persistent foredune after establishment of *A. breviligulata* (Ehrenfeld 1990).

CCAs of individual overwash fans revealed stronger effects of elevation and a greater proportion of variation was explained by constraining variables in western overwash fans. Fire Island is oriented east-northeast, and the east end of the OPWA is narrower and closer to sea level than the western portion, increasing the risk of inundation and overwash events farther east (Sallenger 2000). Barrier islands are known to migrate landward through wave action and sand
movement (Ehrenfeld 1990), and eastern areas of Fire Island migrate northwest faster than western areas due to lesser off-shore sediment supplies (Schwab et al. 2000), further exaggerating differences in elevation between eastern and western overwash fans.

Barrier islands are generally considered poor deer habitat due to relatively infertile soils (Ray et al. 2001), including low nutrients and freshwater availability, and prevalence of unpalatable species (Stuckey and Gould 2000). When compared to abiotic factors, plot-level effects of deer on vegetation community structure were inconclusive. The index of deer activity that I used was very sparse as pellet groups were only present in 1% of vegetation plots, so plot-level assessments of deer effects are not robust. Because I sampled from a lattice of points covering most of the overwash fan, adding more plots to increase the probability of encountering more fecal pellets was not possible. Previous studies exploring effects of deer on coastal vegetation were either inconclusive (Art 1987) or found no effects of deer in dune areas (Keiper 1990, Porter et al. 2014). Deer usually exhibit more browsing than grazing foraging behavior, so the proportion of grass in their diets is typically low (Hobbs et al. 1983, Beier 1987, Weckerly and Nelson 1990, Johnson et al. 1995). However, deer may compensate for limited forage availability in the OPWA by increasing grazing of beachgrass. To accurately assess effects of an herbivore to species cover and richness in post-Hurricane Sandy overwash fans, experimental methods may be necessary.

The use of canonical correspondence analysis in ecology is not without controversy (Borcard et al. 2011). Canonical correspondence analysis was designed to elucidate gradients in environmental conditions from ecological community data (ter Braak and Verdonschot 1995). Results of the constrained ordination are visualized in a diagram (i.e., bi- or triplot) to differentiate habitat associations of the species in the community data along environmental
gradients. Species are ordered along canonical axes according to their environmental similarities, so biplots can be used to interpret among-species relationships and environmental tolerances (Borcard et al. 2011). CCA uses a chi-square metric calculated from species composition data, which reduces effects of common species and inflates effects of rare species (Legendre and Gallagher 2001, Dray et al. 2012). The chi-square metric is not universally accepted by ecologists, and Borcard et al. (2011) suggest chi-square should only be used when rare species are seen as potential indicators of ecosystem gradients. CCA also relaxes linearity assumptions, increasing its applicability to community data that occurs over large environmental gradients (Legendre and Legendre 2012). Appropriate use of CCA requires cautious interpretation of large environmental gradients and species responses (Borcard et al. 2011, Legendre and Legendre 2012). In post-Hurricane Sandy overwash fans in the OPWA, environmental gradients are strong and I expected rarer species to indicate the presence of microclimates along these gradients.

I aimed to understand relationships among abiotic, spatial, and biotic controls to vegetation communities in recovering overwash fans. Like Brantley et al. (2014), overwash fans in the OPWA were dominated by *A. breviligulata* cover. Community structure exhibited strong gradients in NDVI, fine-scale spatial structures, and elevation, but effects of deer were indiscernible at the plot-level. The importance of fine-scale spatial structures in western overwash fans suggests that the neutral patterns of species present besides *A. breviligulata* in the communities were identifiable in these overwash fans. Fire Island is wider and higher in elevation farther west, suggesting that impacts of Hurricane Sandy were less severe in these areas and they may better absorb storm energy and reduce local effects of disturbance.
Table 3. List of plant species observed during surveys of overwash fans in the OPWA, Fire Island, New York in 2015 and 2016. *Juncus* were identified to the Genus taxonomic level.

<table>
<thead>
<tr>
<th>No.</th>
<th>Scientific Name</th>
<th>Common name</th>
<th>Life Hist.*</th>
<th>Growth Form*</th>
<th>% Plots Present (2015)</th>
<th>% Plots Present (2016)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Ammophila breviligulata</em></td>
<td>American beachgrass</td>
<td>P</td>
<td>Gram.</td>
<td>72.83</td>
<td>75.79</td>
</tr>
<tr>
<td>2</td>
<td><em>Toxicodendron radicans</em></td>
<td>poison ivy</td>
<td>P</td>
<td>Herb.</td>
<td>7.42</td>
<td>7.45</td>
</tr>
<tr>
<td>3</td>
<td><em>Chamaesyce polygonifolia</em></td>
<td>sandmat</td>
<td>A</td>
<td>Herb.</td>
<td>4.86</td>
<td>7.19</td>
</tr>
<tr>
<td>4</td>
<td><em>Prunus maritima</em></td>
<td>beach plum</td>
<td>P</td>
<td>Shrub</td>
<td>4.03</td>
<td>3.52</td>
</tr>
<tr>
<td>5</td>
<td><em>Lathyrus japonicus</em></td>
<td>beach pea</td>
<td>P</td>
<td>Herb.</td>
<td>3.93</td>
<td>4.71</td>
</tr>
<tr>
<td>6</td>
<td><em>Smilax glauca</em></td>
<td>cat greenbrier</td>
<td>P</td>
<td>Shrub</td>
<td>3.49</td>
<td>3.41</td>
</tr>
<tr>
<td>7</td>
<td><em>Juncus</em></td>
<td>rush</td>
<td>P</td>
<td>Gram.</td>
<td>1.67</td>
<td>1.09</td>
</tr>
<tr>
<td>8</td>
<td><em>Hudsonia tomentosa</em></td>
<td>beach heather</td>
<td>P</td>
<td>Shrub</td>
<td>1.57</td>
<td>1.97</td>
</tr>
<tr>
<td>9</td>
<td><em>Morella pensylvanica</em></td>
<td>northern bayberry</td>
<td>P</td>
<td>Shrub</td>
<td>1.38</td>
<td>1.71</td>
</tr>
<tr>
<td>10</td>
<td><em>Rosa multiflora</em></td>
<td>multiflora rose</td>
<td>P</td>
<td>Shrub</td>
<td>1.03</td>
<td>0.83</td>
</tr>
<tr>
<td>11</td>
<td><em>Parthenocissus quinquefolia</em></td>
<td>Virginia creeper</td>
<td>P</td>
<td>Herb.</td>
<td>0.88</td>
<td>0.93</td>
</tr>
<tr>
<td>12</td>
<td><em>Phragmites australis</em></td>
<td>common reed</td>
<td>P</td>
<td>Gram.</td>
<td>0.79</td>
<td>1.03</td>
</tr>
<tr>
<td>13</td>
<td><em>Triplasis purpurea</em></td>
<td>purple sandgrass</td>
<td>A</td>
<td>Gram.</td>
<td>0.74</td>
<td>1.40</td>
</tr>
<tr>
<td>14</td>
<td><em>Symphyotrichum pilosum</em></td>
<td>hairy white aster</td>
<td>P</td>
<td>Herb.</td>
<td>0.59</td>
<td>1.91</td>
</tr>
<tr>
<td>15</td>
<td><em>Prunus serotina</em></td>
<td>black cherry</td>
<td>P</td>
<td>Shrub</td>
<td>0.49</td>
<td>0.26</td>
</tr>
<tr>
<td>16</td>
<td><em>Vaccinium corymbosum</em></td>
<td>Highbush blueberry</td>
<td>P</td>
<td>Shrub</td>
<td>0.49</td>
<td>0.52</td>
</tr>
<tr>
<td>17</td>
<td><em>Polygonella articulata</em></td>
<td>sand jointweed</td>
<td>A</td>
<td>Herb.</td>
<td>0.39</td>
<td>2.28</td>
</tr>
<tr>
<td>18</td>
<td><em>Smilax rotundifolia</em></td>
<td>roundleaf greenbrier</td>
<td>P</td>
<td>Shrub</td>
<td>0.25</td>
<td>0.21</td>
</tr>
<tr>
<td>19</td>
<td><em>Euthamia caroliniana</em></td>
<td>slender goldenrod</td>
<td>P</td>
<td>Herb.</td>
<td>0.20</td>
<td>0.62</td>
</tr>
<tr>
<td>20</td>
<td><em>Panicum amarum</em></td>
<td>bitter panicgrass</td>
<td>P</td>
<td>Gram.</td>
<td>0.20</td>
<td>0.10</td>
</tr>
<tr>
<td>21</td>
<td><em>Salsola kali</em></td>
<td>Russian thistle</td>
<td>A</td>
<td>Herb.</td>
<td>0.20</td>
<td>0.10</td>
</tr>
<tr>
<td>22</td>
<td><em>Lechea maritima</em></td>
<td>beach pinweed</td>
<td>P</td>
<td>Herb.</td>
<td>0.15</td>
<td>0.67</td>
</tr>
<tr>
<td>23</td>
<td><em>Pseudognaphalium obtusifolium</em></td>
<td>sweet everlasting</td>
<td>B</td>
<td>Herb.</td>
<td>0.10</td>
<td>0.36</td>
</tr>
<tr>
<td>24</td>
<td><em>Artemisia stelleriana</em></td>
<td>dusty miller</td>
<td>P</td>
<td>Herb.</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>25</td>
<td><em>Cakile edentula</em></td>
<td>searocket</td>
<td>A</td>
<td>Herb.</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>26</td>
<td><em>Solidago sempervirens</em></td>
<td>seaside goldenrod</td>
<td>P</td>
<td>Herb.</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>27</td>
<td><em>Verbascum thapsus</em></td>
<td>common mullein</td>
<td>B</td>
<td>Herb.</td>
<td>0.05</td>
<td>0</td>
</tr>
<tr>
<td>28</td>
<td><em>Ilex opaca</em></td>
<td>American holly</td>
<td>P</td>
<td>Shrub</td>
<td>0</td>
<td>0.16</td>
</tr>
<tr>
<td>29</td>
<td><em>Rosa rugosa</em></td>
<td>beach rose</td>
<td>P</td>
<td>Shrub</td>
<td>0</td>
<td>0.05</td>
</tr>
</tbody>
</table>

* Life History: P = perennial, A = annual, B = biennial
* Growth Form: Gram. = Graminoid, Herb. = Herbaceous
Table 4. Canonical Correspondence Analysis and variable selection of plot-scale environmental variables (i.e., elevation [DEM], productivity [NDVI], deer sign [Deer], and spatial processes [Fine, Broad]) on species composition in overwash fans of the OPWA, Fire Island, New York in 2015 and 2016.

<table>
<thead>
<tr>
<th>Year</th>
<th>Global Model</th>
<th>df</th>
<th>Chi²</th>
<th>F</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>DEM+Broad+Fine+NDVI+Deer</td>
<td>5</td>
<td>0.057</td>
<td>2.47</td>
<td>0.022 *</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>662</td>
<td>3.071</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2016</td>
<td>DEM+Broad+Fine+NDVI+Deer</td>
<td>5</td>
<td>0.075</td>
<td>2.31</td>
<td>0.021 *</td>
</tr>
<tr>
<td></td>
<td>Residual</td>
<td>662</td>
<td>4.273</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Variable Selection</th>
<th>df</th>
<th>AIC</th>
<th>F</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td>NDVI</td>
<td>1</td>
<td>3749.9</td>
<td>4.782</td>
<td>0.005 **</td>
</tr>
<tr>
<td></td>
<td>DEM</td>
<td>1</td>
<td>3747.6</td>
<td>4.290</td>
<td>0.030 *</td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td>1</td>
<td>3747.9</td>
<td>1.625</td>
<td>0.070</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td>1</td>
<td>3748.1</td>
<td>1.478</td>
<td>0.130</td>
</tr>
<tr>
<td></td>
<td>Deer</td>
<td>1</td>
<td>3749.4</td>
<td>0.189</td>
<td>0.505</td>
</tr>
<tr>
<td>2016</td>
<td>NDVI</td>
<td>1</td>
<td>3917.1</td>
<td>3.982</td>
<td>0.005 **</td>
</tr>
<tr>
<td></td>
<td>Fine</td>
<td>1</td>
<td>3915.8</td>
<td>3.232</td>
<td>0.005 **</td>
</tr>
<tr>
<td></td>
<td>DEM</td>
<td>1</td>
<td>3914.7</td>
<td>3.117</td>
<td>0.025 *</td>
</tr>
<tr>
<td></td>
<td>Broad</td>
<td>1</td>
<td>3915.6</td>
<td>1.142</td>
<td>0.365</td>
</tr>
<tr>
<td></td>
<td>Deer</td>
<td>1</td>
<td>3916.7</td>
<td>0.033</td>
<td>0.980</td>
</tr>
</tbody>
</table>

Significance codes: < 0.001 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1
Table 5. Canonical Correspondence Analysis of vegetation communities in overwash fans in the OPWA, Fire Island, New York in 2015 and 2016 revealed increases in effects of environmental control on species composition from eastern (OW 1) to western (OW 9) overwash fans.

<table>
<thead>
<tr>
<th>OW</th>
<th>Year</th>
<th>Variables</th>
<th>Sign.</th>
<th>% Const.</th>
<th>% Unconst.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2015</td>
<td>Broad, NDVI</td>
<td>**</td>
<td>9.16</td>
<td>90.84</td>
</tr>
<tr>
<td>1</td>
<td>2016</td>
<td>Broad</td>
<td>*</td>
<td>5.71</td>
<td>94.29</td>
</tr>
<tr>
<td>2</td>
<td>2015</td>
<td>NDVI</td>
<td>*</td>
<td>6.46</td>
<td>93.54</td>
</tr>
<tr>
<td>2</td>
<td>2016</td>
<td>NDVI</td>
<td>.</td>
<td>8.13</td>
<td>91.87</td>
</tr>
<tr>
<td>3</td>
<td>2015</td>
<td>--</td>
<td></td>
<td>5.06</td>
<td>94.94</td>
</tr>
<tr>
<td>3</td>
<td>2016</td>
<td>--</td>
<td></td>
<td>4.83</td>
<td>95.17</td>
</tr>
<tr>
<td>4</td>
<td>2015</td>
<td>NDVI</td>
<td>*</td>
<td>6.62</td>
<td>93.38</td>
</tr>
<tr>
<td>4</td>
<td>2016</td>
<td>--</td>
<td></td>
<td>5.23</td>
<td>94.77</td>
</tr>
<tr>
<td>5</td>
<td>2015</td>
<td>NDVI</td>
<td>**</td>
<td>9.19</td>
<td>90.81</td>
</tr>
<tr>
<td>5</td>
<td>2016</td>
<td>NDVI</td>
<td>**</td>
<td>10.32</td>
<td>89.68</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>DEM</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>2015</td>
<td>NDVI</td>
<td>*</td>
<td>7.68</td>
<td>92.32</td>
</tr>
<tr>
<td>6</td>
<td>2016</td>
<td>Fine</td>
<td>.</td>
<td>8.01</td>
<td>91.99</td>
</tr>
<tr>
<td>7</td>
<td>2015</td>
<td>DEM</td>
<td>*</td>
<td>7.05</td>
<td>92.95</td>
</tr>
<tr>
<td>7</td>
<td>2016</td>
<td>DEM</td>
<td>**</td>
<td>11.61</td>
<td>88.39</td>
</tr>
<tr>
<td>8</td>
<td>2015</td>
<td>NDVI</td>
<td>*</td>
<td>16.69</td>
<td>83.31</td>
</tr>
<tr>
<td>8</td>
<td>2016</td>
<td>NDVI</td>
<td>**</td>
<td>19.98</td>
<td>80.02</td>
</tr>
<tr>
<td>9</td>
<td>2015</td>
<td>NDVI</td>
<td>*</td>
<td>16.66</td>
<td>83.34</td>
</tr>
<tr>
<td>9</td>
<td>2016</td>
<td>NDVI</td>
<td>***</td>
<td>25.13</td>
<td>74.87</td>
</tr>
</tbody>
</table>

Significance ("Sign.") codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’
"Const." describes constrained variance explained, while "Unconst." describes unexplained variance.
Figure 11. Canonical Correspondence Analysis (CCA) biplots (scaling=2) for vegetation communities in overwash fans in the OPWA, Fire Island, New York in 2015 and 2016. The CCA was constrained by elevation [DEM], productivity [NDVI], and spatial structures [Fine, Broad]). The five most frequently observed species are enlarged for emphasis: *Ammophila breviligulata* (AMBR), *Toxicodendron radicans* (TORA), *Chamaesyce polygonifolia* (CHPO), *Prunus maritima* (PRMA), *Lathyrus japonicus* (LAJA).
Figure 12. Canonical Correspondence Analysis biplots (scaling=2) for vegetation communities in overwash fans in the OPWA, Fire Island, New York constrained by elevation (DEM), productivity (NDVI), and spatial processes (Fine, Broad) in 2015 and 2016. Vectors of significant variables are shown.
CHAPTER THREE: Putative effects of white-tailed deer (*Odocoileus virginianus borealis*) exclusion on vegetation recovery in overwash fans created by Hurricane Sandy

**Introduction**

Browsing and grazing by large herbivores can decrease survival and reproduction of plants (Waller and Alverson 1997, Ruhren and Handel 2000, Rooney and Waller 2003), decrease plant diversity (Urbanek et al. 2012, Pendergast et al. 2015), and change community composition (Tilghman 1988, Kittredge and Ashton 1995, Long 1999, Blumenthal and Augustine 2009, Raphael 2014). On Assateague Island, grazing by feral horses changed dune vegetation structure (Seliskar 2003). In areas where horses and white-tailed deer were present, deer minimally browsed dune vegetation (Keiper 1990, Porter et al. 2014) and used dunes less frequently than available (Sherrill et al. 2010). It is unknown, however, if deer impact dune vegetation when other large herbivores are not present. Unlike populations on Assateague Island, deer on Fire Island are not hunted and densities vary greatly (Underwood 2005). The National Park Service has resisted managing deer in the OPWA due to its Wilderness designation. However, the park's enabling legislation permits public hunting and managers are currently considering regulated deer harvest in support of natural resource objectives in the OPWA.

Many studies have demonstrated that deer density is positively correlated with the level of impact the population exerts on a vegetation community (Anderson 1994, Augustine et al. 1998, Augustine and Freligh 1998). After a major disturbance, selective browsing by deer, even at low density (Holmes and Webster 2011), can change the trajectory of plant communities as they regenerate (Rooney 2009, Raphael 2014). Human trampling is well-documented and can have lasting effects on vegetation in areas with sandy soils (Hylgaard and Liddle 1981, Bowles and Maun 1982, Andersen 1995, Santoro et al. 2012, Šilc et al. 2017), though little is known
about trampling effects of herbivores on barrier islands (Carruthers et al. 2013). Deer are the largest and most impactful herbivore inhabiting Fire Island (O’Connell and Sayre 1989, Forrester et al. 2006). Art (1987) assessed changes in vegetation composition using exclosures in the OPWA after Hurricane Gloria in 1985, but was unable to discern a significant effect of deer on swale vegetation. Fire Island’s white-tailed deer population has increased dramatically (Underwood 2005) since the 1980s, exposing plant communities to a novel biotic stressor with which to contend.

An opportunity to better understand the potential effects of white-tailed deer on recovering vegetation in overwash fans arose after the storm surge from Hurricane Sandy overwashed many areas of the OPWA (Hapke et al. 2013), depositing large volumes of sand where herbs, grasses, and shrubs once dominated. The purpose of this chapter is to elucidate the nature of white-tailed deer impacts to vegetation recovering from catastrophic disturbance. My primary objective is to assess impacts of a locally-abundant deer population to plant community richness and cover among overwash fans. Secondarily, I will explore factors that impinge on the determination of a biologically meaningful deer effect, including aspects of experimental design and plant responses to sand burial.

Methods

Sixty-one 1-m² paired permanent plots were deployed randomly in post-Hurricane Sandy overwash fans during spring 2013 (Figure 13) and marked with Carsonite™ posts in the southeast corner. The number of plots placed in each overwash fan (range: 4 - 10) was roughly proportional to the size of the overwash fan. Each overwash fan received at least two pairs of permanent plots (i.e., 4 plots: 2 fences, 2 controls), but more control plots were placed due to
logistical constraints of transporting fencing materials and people to remote locations. Fences were constructed from 1.5-m high woven wire fence with 5 cm x 10 cm openings. Each fence was buried approximately 30 cm into the sand to prevent deer access from beneath. I assessed vegetation cover in all permanent plots in September 2015 and 2016 using methods outlined in Chapter One.

Two concerns need to be addressed to properly interpret an effect of deer exclusion in the paired permanent plot experiment. First, when the fences were erected, overwash fans were nearly denuded of vegetation (NOAA 2012). Consequently, some permanent plot locations may not represent conditions throughout the rest of the overwash fan, which I refer to as initial location bias. Second, many colonizing plant species in overwash fans exhibit increased rates of spread when partially buried by sand, particularly A. breviligulata (Maun 2009). The potential for increased sand burial caused by the interception of windblown sand by the woven wire around treatment plots caused me to explore plot elevation changes between 2015 and 2016 and subsequent changes in vegetation cover.

To address initial location bias, I compared total cover in open plots located throughout each overwash fan on a lattice (hereafter, “lattice” plots; see Chapter One) with control plots. Large observed differences in cover between control and lattice plots suggest location bias that could lead to misinterpretation of an effect of excluding deer. While treatment plots were generally located in close proximity to control plots, random chance acting on a small sample size could result in absolute differences in cover and species richness unrelated to the presence of deer. I used a split-plot analysis, sp.plot function in the agricolae R package (version 1.2-8), to assess differences in vegetation cover between control and lattice plots. Split-plot designs are often employed when one factor is more readily applied to large experimental units (i.e.,
overwash fan) and another factor can be applied to smaller units (i.e., treatment vs. control; Littell et al. 2002). I considered the overwash fan as the “whole plot” factor, the paired plots as the “treatment” factor, and year as the split-plot factor. The sp.plot function ensures that the proper error mean squares was applied to test for a “treatment”, or effect of deer exclusion, three years after Hurricane Sandy. I performed a similar analysis to assess differences in vegetation cover and species richness between treatment and control plots. I imposed a decision-limit on the whole-plot by treatment interaction to determine which overwash fans might be contributing to statistically significant responses (Nelson et al. 2005). Because the hypothesis was treatment > control for all response comparisons, use of a decision-limit essentially results in a paired-test and increased statistical power. All R code used in this chapter is available in Appendix G.

To explore the changes in vegetation cover that may be attributed to partial or complete sand burial, I used quantile regression of the change in live, green vegetation cover observed in the lattice plots on their location (i.e., UTM coordinates) and the change in elevation as derived from high-resolution LiDAR data (i.e., DEM) between 2015 and 2016. I performed quantile regression using the qr function in the R package quantreg (version 5.33). Quantile regression is a type of robust regression that models the effects of covariates on the conditional quantiles of a response variable without assuming normality in response data (SAS 2017). Quantile regression is particularly useful when the rate of change in the conditional quantile, expressed by the regression coefficients, depends on the quantile itself (Cade and Noon 2003). Increases in vegetation cover due to increases in plot elevation might indicate a sand burial effect, independent of the presence of deer.
Results

Initial Location Bias

I surveyed at least two control, two treatment, and 57 lattice plots in each overwash fan in 2015 and 2016 (Table 6) and recorded total vegetation cover and species richness. The split-plot analysis of variance comparing vegetation cover between lattice and control plots was significant (F=7.3, df=19, 35, p<0.0001), but highly variable (CV=96.1%) and poor-fitting (R²=0.10). While mean vegetation cover in lattice plots (31.2%) was lower than in control plots (39.6%), the effect was statistically insignificant (p=0.18). However, there was a significant effect of year in the analysis (F=10.5, df=1, 16, p=0.0012). There was more cover in all plots measured in 2016 (41.2%) than in 2015 (29.6%; Figure 14).

Sand Burial Effects

The quantile regression of the change in total live vegetation cover among lattice plots between 2015 and 2016 indicated important contributions of all covariates, but at different quantiles of response (Figure 15a). In plots exhibiting changes in vegetation cover below the median, the effect of sand accretion was equivocal and variable (Figure 15b). In plots exhibiting changes in vegetation cover above the median, however, the effect of sand accretion was positive and significant (Table 7) to at least the 75th quantile. In plots with the greatest vegetation cover increases (>75th quantile), the effect of sand accretion was large and positive, but with substantially greater variation. The effect of west to east variation in plot location (i.e., UTM east-west) exerted a significantly negative effect on the change in plot cover (Figure 15c), while the opposite effect was true for north-south variation (i.e., UTM north-south) in plot location (Figure 15d). In lattice plots at the 75th quantile, where vegetation cover changes were
significantly related to sand burial, vegetation cover increased between 2% and 10%. Nine permanent plots, one treatment and eight controls, exhibited vegetation cover changes in that range (Figure 16).

Effects of Deer Exclusion

The split-plot analysis of variance for species richness was significant (F=2.31, df=19, 98, p=0.004), somewhat predictive (R²=0.31), and moderately variable (CV=51.6%). Average species richness across all overwash fans was 18.2% higher in treatment plots than in control plots (Figure 17), but the effect was statistically insignificant (p=0.27). The analysis revealed a significant effect of overwash (F=2.9, df=8, 35, p=0.008).

The split-plot analysis of variance for total vegetation cover between control and treatment plots was significant (F=3.19, df=19, 98, p<0.0001). The model explained 38% of the variation in total vegetation cover between years with moderate variability (CV = 53.5%). The Type III hypothesis test for an effect of deer exclusion was also significant (F=7.23, df=1, 8, p=0.03). There was significantly more vegetation cover in treatment (61.6%) versus control plots (39.6%). In addition, year (F=6.93, df=1, 16, p=0.013) and overwash (F=2.55, df=8, 35, p=0.014) were important sources of variation in the model (Figure 18).

Discussion

Despite a liberal decision-limit, (i.e., α = 0.20) only 4 of 9 overwash fans exhibited a demonstrable effect of deer exclusion. In addition, three (i.e., 3, 4, and 8) of the remaining 5 overwash fans exhibited initial location bias because means for the lattice plots were larger than means for the control plots. The primary effect of deer exclusion that I observed was a reduction
in total plant cover outside of fenced plots. Impacts to species richness, while compelling, were highly variable and statistically insignificant. Only a subset of the species present on the nearby mainland is able to withstand environmental conditions on barrier islands (Ehrenfeld 1990), so species richness is inherently low (≤ 4 species per survey plot). Coastal microclimates are also highly variable (Maun 2009), so I cannot fully rule out the possibility that some of the observed differences in species richness among overwash fans results from natural variability.

When the vegetation community is depauperate, vegetation cover may provide a better indication of herbivore effects than species richness, which is consistent with a recent meta-analysis of community-level impacts of white-tailed deer (Habeck and Schultz 2015). While deer impacts to herbaceous plants have been documented in other natural areas of Fire Island (Art 1976, Forrester et al. 2006, Raphael 2014), this is the first attempt to describe them in a relatively tree-less barrier island wilderness beach.

However, interpretation of the effects of deer exclusion on recovering plant communities in overwash fans requires some qualification. I expected vegetation cover to be lower in lattice plots than control plots due to the increased sampling fraction and higher probability of including bare sand. Greater average cover in lattice plots than control plots would lead to a finding of a deer exclusion effect when none was warranted, which I refer to as initial location bias. Disregarding the possibility of initial location bias increases the Type I error rate when lattice plot means are larger than control means, or rejecting a true null hypothesis of no mean difference between treatment (i.e., deer exclusion) and control.

Although I did not detect fence-induced stimulation of plant cover, it is possible that this effect occurred shortly after deployment (i.e., 2013-2014). The dominant vegetation species detected in overwash fans, *A. breviligulata*, responds to sand burial by increasing growth of both
shoots and roots (Ehrenfeld 1990, Maun 2009) and decreases in growth as sand burial diminishes (Disraeli 1984). The effects of deer exclusion I documented are compounded since the study initiation, while the effect of time in the split-plot analysis is instantaneous (i.e., 2015-2016). Though the contemporary evidence suggests that sand burial bias occurs in both control and treatment plots, hysteresis associated with fence-induced stimulation of vegetation cover vis-à-vis sand burial cannot be objectively evaluated.

Effects of deer exclusion on vegetation cover in overwash fans indicate both grazing and trampling components. Grazing was documented in survey plots and year-round in camera images (unpublished data) in overwash fans. Because I was unable to differentiate effects of grazing from trampling in this study, the effects of deer exclusion captures both forms of impact. Some plant species are more resistant to trampling than others (Dale and Weaver 1974, Davidson and Fox 1974, Pellerin et al. 2006), but sandy soils exacerbate effects of trampling on barrier islands (Andersen 1995, Santoro et al. 2012). *A. breviligulata* is vulnerable to trampling when underground rhizomes are compromised (Maun 2009), but may only be deleteriously affected under severe trampling conditions (McDonnell 1981).

Differences in vegetation cover I observed in control and treatment plots include both deer and human influences in overwash fans. Local deer densities were high in overwash fans, but humans were also frequently recorded by trail cameras in overwash fans. While human activity was greatest in overwash fans 1, 6, and 9, deer activity was at least twice as high based on photo documentation (unpublished data). However, Weaver and Dale (1978) found that trampling by hooved animals (i.e., horses) was more damaging to sand dunes than human foot traffic. Human use was predominantly on beaches and flat areas of overwash fans, while deer were observed climbing dunes frequently (unpublished data). My findings implicate effects of
deer trampling on vegetation, but a close examination of human recreation impacts in overwash fans is warranted.

Sample size of permanent plots in this study was small, with four to ten 1-m$^2$ permanent plots per overwash fan. For example, the interpretation of an effect of deer exclusion for overwash fan 1 is particularly suspect since only one treatment plot was available for analysis after two treatment plots were inundated by Hurricane Joaquin’s high storm surge (Berg 2016). The remaining treatment plot is adjacent to the salt marsh and well-protected from beach conditions. Human visitors tampered with plot markers in overwash fan 1 in 2015, though vegetation cover appeared to be undisturbed. The reduction in sample size resulted in it failing to exceed the control-limit imposed by the statistical analysis, so was not included among those overwash fans exhibiting demonstrable effects of deer exclusion.

In this study, I attempted to document the biotic impacts of an abundant deer herd to dune vegetation recovering from catastrophic storm surge. Due to the unique nature of the barrier island beach, I attempted to control for important intervening factors related to experimental design, the nature of plant responses to sand burial and small sample sizes. Three years after landfall of Hurricane Sandy, I documented a compelling but statistically insignificant difference in plant species richness between treatment and control plots among overwash fans, but substantial and variable reductions in total plant cover. I attribute this variation to differences in local deer density, geomorphology, and human activity among overwash fans. While deer graze and browse vegetation in overwash fans, deer and humans trample vegetation in some overwash fans and separating effects of each is not possible from exclusion studies alone.
Table 6. Number of plots surveyed in each overwash fan in the OPWA, Fire Island, New York in 2015 and 2016, including permanent control and treatments plots used to assess deer effects.

<table>
<thead>
<tr>
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<th>Treatment</th>
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<tr>
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</tbody>
</table>
Table 7. Results of quantile regression of change in elevation (“delta_dem”) and UTM coordinates on change in total vegetation cover between 2015 and 2016 in lattice plots located throughout overwash fans in the OPWA, Fire Island, New York.

Quantile Level: 0.1
Predicted Mean Value: -12.71

| Parameter | df | Estimate | SE | 90% Confidence Limits | t-value | Pr > |t| |
|-----------|----|----------|----|------------------------|---------|------|---|
| Intercept | 1  | -12.737  | 1.349 | -14.959 | -10.515 | -9.44 | < 0.0001* |
| delta_dem | 1  | 0.009    | 0.020 | -0.025    | 0.043 | 0.44 | 0.6629 | |
| utmx      | 1  | 0.000    | 0.011 | -0.019    | 0.019 | -0.02 | 0.9813 | |
| utmy      | 1  | -0.005   | 0.023 | -0.043    | 0.033 | -0.23 | 0.8177 | |

Quantile Level: 0.5
Predicted Mean Value: 1.73

| Parameter | df | Estimate | SE | 90% Confidence Limits | t-value | Pr > |t| |
|-----------|----|----------|----|------------------------|---------|------|---|
| Intercept | 1  | 1.703    | 0.245 | 1.299 | 2.107 | 6.94 | < 0.0001* |
| delta_dem | 1  | 0.008    | 0.002 | 0.05 | 0.012 | 3.76 | 0.0002 * |
| utmx      | 1  | -0.008   | 0.002 | -0.01 | -0.005 | -5.13 | < 0.0001* |
| utmy      | 1  | 0.016    | 0.003 | 0.011 | 0.021 | 5.03 | < 0.0001* |

Quantile Level: 0.75
Predicted Mean Value: 9.65

| Parameter | df | Estimate | SE | 90% Confidence Limits | t-value | Pr > |t| |
|-----------|----|----------|----|------------------------|---------|------|---|
| Intercept | 1  | 9.497    | 0.740 | 8.278 | 10.716 | 12.84 | < 0.0001* |
| delta_dem | 1  | 0.048    | 0.014 | 0.025 | 0.071 | 3.37 | 0.0008 * |
| utmx      | 1  | -0.024   | 0.004 | -0.03 | -0.018 | -6.23 | < 0.0001* |
| utmy      | 1  | 0.050    | 0.008 | 0.036 | 0.063 | 6.12 | < 0.0001* |

Quantile Level: 0.95
Predicted Mean Value: 28.01

| Parameter | df | Estimate | SE | 90% Confidence Limits | t-value | Pr > |t| |
|-----------|----|----------|----|------------------------|---------|------|---|
| Intercept | 1  | 27.682   | 1.696 | 24.888 | 30.476 | 16.32 | < 0.0001* |
| delta_dem | 1  | 0.105    | 0.070 | -0.010 | 0.220 | 1.50 | 0.1331 | |
| utmx      | 1  | -0.039   | 0.015 | -0.063 | -0.015 | -2.70 | 0.0071 * |
| utmy      | 1  | 0.079    | 0.031 | 0.029 | 0.130 | 2.60 | 0.0095 * |

(*) denotes significant parameters as determined by the p-value.
Figure 13. Maps of permanent plot locations in each overwash fan in the OPWA, Fire Island, New York, including an insert photo showing permanent plots in overwash 9.
Figure 14. Average vegetation cover (i.e., between 2015 and 2016) and standard errors measured in lattice and control plots in overwash fans in the OPWA, Fire Island, New York.
Figure 15. Change in total vegetation cover (i.e., delta_total_cover) between 2015 and 2016 as a function of changes in (b) elevation (i.e., delta_DEM) and (c, d) UTM coordinates as calculated through quantile regression for post-Hurricane Sandy overwash fans in the OPWA, Fire Island, New York.
Figure 16. Vegetation cover change between 2015 and 2016 in the 75\textsuperscript{th} quantile of lattice plots ranged from 2 - 10\% in overwash fans in the OPWA, Fire Island, New York.
Figure 17. Plant species richness and standard error measured in control and treatments plots, averaged between 2015 and 2016, in overwash fans in the OPWA, Fire Island, New York.
Figure 18. Vegetation cover and standard error measured in control and treatments plots, averaged between 2015 and 2016, in overwash fans in the OPWA, Fire Island, New York.
CHAPTER FOUR: Vegetation recovery in overwash fans of the Otis Pike Fire Island High Dune Wilderness Area after Hurricane Sandy

Introduction

Few plant species can tolerate the harsh conditions on coastal beaches (Maun 2009). *Ammophila breviligulata* is tolerant of salt spray and its long, slender leaves allow it to blow freely in high winds without excessive damage. Sand deposition hinders growth of most coastal plants, but several species, including *A. breviligulata*, respond positively to sand burial and are largely responsible for dune growth. When foredunes are overwashed in the northeastern United States, *A. breviligulata* establishes (Stuckey and Gould 2000) as vegetative fragments wash up during tidal wave action and underground rhizomes of inland plants spread (Maun 1985). As dunes form, salt and sand deposition decrease farther inland and several species of shrubs establish on the leeward side of the dune, further increasing its strength and sand entrapment capabilities (Ehrenfeld 1990).

Growth rates of *A. breviligulata* remain positive on the dune, but decrease inland as sand burial diminishes and other species less tolerant of beach conditions expand. Expansion rates of *A. breviligulata* are often quite high in areas with consistent sand deposition (Olson 1958, Kent et al. 2001, Maun 2009), though they vary geographically (Maun 2009). Consequently, annual mapping of the expansion of *A. breviligulata* and other plants after a disturbance can increase our understanding of the factors that impinge on the recovery process, and aid in developing potential mitigation strategies. Mapping plant cover can be done through satellite imagery and digital image classification methods (Kerr and Ostrovsky 2003).

The use of image classification to assess temporal vegetation change is not new (Tucker et al. 1985, Mas 1999, Hassan and Southworth 2018). The random forest image classification
method (RF) is widely considered the most-accurate machine-learning technique available (Cutler et al. 2007, Xie et al. 2008). RF uses multiple classification trees in a regression framework to classify land cover from spectral, geographic, or other user-defined raster layers. Similar to maximum likelihood classification methods, the user trains samples from imagery (Lillesand et al. 2014). Instead of strictly using spectral information to identify land cover, classification trees use linear combinations of input layers and decision trees to partition the image into regions that are increasingly homogeneous. Because RF methods use a subset of training data to classify land cover, use of an independent dataset for accuracy assessment is unnecessary (Breiman 2001).

Rates of vegetation recovery directly influence the resilience of barrier island systems after a major storm event like Hurricane Sandy (Durán and Moore 2013, Vinent and Moore 2015). Thus, factors that impinge on vegetation recovery rates have the potential to also affect resilience to future disturbance events (Houser et al. 2015, Vinent and Moore 2015). For example, expansion of A. breviligulata through time and space, in addition to facilitating the formation of dunes, promotes rapid increases in net primary productivity in recovering overwash fans, which in turn modifies microhabitats conducive to the establishment of other plant species (Wallen 1980, Ehrenfeld 1990). Fifty years ago, this simple feedback mechanism alone would have led to rapid vegetation recovery and enhanced island resiliency.

Since then, populations of feral, native and exotic large herbivores have irrupted to numbers that pose serious challenges to the management of other significant natural resources of barrier islands (Art 1987, Wood et al. 1987, Cromwell 1999, Seliskar 2003, Forrester et al. 2006, Sherrill et al. 2010, Carruthers et al. 2013, Porter et al. 2014). Hyper-abundant populations of large herbivores on barrier islands may reduce resiliency by impeding rates of vegetation
recovery through the combined effects of browsing, grazing and trampling. It has long been established that ungulates seek out highly productive patches of forage (Ritchie et al. 1998, Bråthen et al. 2007), especially in nitrogen-limited habitats. Alteration in the distribution of herbivores in response to variation in net primary productivity could exert disproportional effects on recovering vegetation and compromise resilience.

The purpose of this chapter is to better understand the effects of locally abundant white-tailed deer populations on vegetation recovery rates, and therefore island resiliency, in areas of the OPWA overwashed by Hurricane Sandy. My main objectives are to (1) classify high-resolution digital orthoimagery into relevant land cover categories, (2) estimate vegetation recovery rates for nine overwash fans, (3) explore the effects of local deer density and pre-storm vegetation cover on observed rates of vegetation, and (4) document the relationship between net primary productivity and local deer density among overwash fans.

Methods

Vegetation Cover Assessment

I obtained digital orthoimagery tiles for the OPWA before Hurricane Sandy (NYSC 2010), in the aftermath of Hurricane Sandy (NOAA 2012), in the third growing season post-Hurricane Sandy (AG 2015) and in the fourth growing season post-Hurricane Sandy (NYSC 2016). The imagery resolutions were 0.15 meters for 2010 and 2016, 0.35 meters for 2012, and 1 meter for 2015. I mosaicked tiles for each year using the Mosaic to New Raster tool in ArcGIS (version 10.5, ESRI, Redlands, CA) into a continuous image.

I used a RF image classification method to characterize vegetation cover in and around nine overwash fans in the OPWA. I created training samples using the ArcGIS Image
Classification tools. I identified samples over the entire mosaicked image for each year to account for differences in atmospheric correction and spectral signature, and aggregated samples into nine land cover categories: water, waves (i.e., white), wet sand, dry quartz sand, magnetite and garnet sand, marsh grass, beach grass, shrubs, and trees. I used the Train Random Trees classifier in ArcGIS to define classification trees using three combinations of spectral bands and elevation for each year: (1) only red, green, and blue spectral bands, (2) red, green, blue, and near-infrared spectral bands, and (3) red, green, blue, and near-infrared spectral bands and the digital elevation model. I used the Boundary Clean function in ArcGIS to smooth boundaries between classes of land cover. I further aggregated land cover into water, sand, marsh grass, beach grass, shrubs, and trees.

Many classification accuracy assessment methods are available, but there is strong debate over which methods are most appropriate (Xie et al. 2008). I chose to use the ArcGIS accuracy assessment tools to calculate confusion matrices of user’s and producer’s accuracies proportionally for each class (n=500 points) in each year and a kappa statistic (Van Deusen 1996, Stehman and Czaplewski 1998) since the resolution of the imagery used was very high. User’s accuracy measures the probability that a randomly selected point classified in a category actually depicts that category in truth. Producer’s accuracy measures error of omission by comparing the number of points classified in a category to the number of points actually within that category in the image (Congalton 2005). Kappa statistics between 0.61-0.80 indicate substantial agreement between the classified image and true land cover, and >0.81 are believed to be nearly perfect (Landis and Koch 1977).

Finally, I compared total classified vegetation cover with that estimated from a lattice of 1-m² plots extending the length and width of each overwash fan (see Chapter One). I regressed
average vegetation cover in each overwash fan on classified total cover, pooled over both years of sampling (i.e., 2015-2016). I tested the statistical hypothesis of a slope not significantly different from unity and intercept not significantly different from zero.

Local Deer Density in Overwash Fans

I used Reconyx brand Hyperfire Covert-IR HC600 cameras to monitor deer use of overwash fans in the OPWA. I programmed trail cameras to take photographs every hour from 0400 to 1000 and 1700 to 2300 each day, and to take three photographs at one-second intervals when motion was detected, including at night using an infra-red sensor. I positioned trail cameras in the bayside portion of each overwash fan near a deer trail crossing, away from the beach to avoid abrasion by wind-blown sand and salt spray. Cameras were pointed in a direction to avoid glaring sun contact and angled downward approximately 12 degrees. Cameras were secured in metal enclosures and attached to 10x10-cm, pressure-treated posts buried in the sand so the camera position was approximately 1.2-m above ground level. One camera was placed in each overwash fan, and they were monitored at approximately biweekly intervals from August to November in 2015 and 2016.

I downloaded trail camera photographs from memory cards, renamed them using Renamer (http://smallcats.org/CTA-executables.html, Accessed 04 October 2014), and manually organized photographs by overwash fan and species captured. I separated photographs containing deer into folders of group size for each independent observation (i.e., 15-minute interval). To analyze photographs, I used the program DataAnalyze (Sanderson and Harris 2013), which calculated total effort per camera, species activity patterns, and density uncorrected for imperfect detection.
In a companion study, a sample of female deer was captured and marked individually with radio-collars (unpublished data). I identified all marked female deer and as many antlered males as possible from trail camera images. I created encounter histories for every identifiable individual in each overwash fan from 1 August to 24 November of each year and calculated an estimate of local abundance (Jacobson et al. 1997). I used the “species abundance by location by year by month” from DataAnalyze as the total number of deer observations. Lastly, I divided total number of deer by area of the overwash fan to calculate a local deer density in each overwash fan. Because no identifiable deer were recorded in overwash fans 1 and 2 during 2015, I imputed values for these two overwash fans by regressing local abundance on the total number of deer observed in camera images.

I treated local deer densities as representing the average number of resident animals using each overwash fan during the growing season and not as global population estimates. I used analysis of covariance to assess the relationship between local deer density and average NDVI for each overwash fan in 2015 and 2016. Finally, I used multiple linear regression to assess effects of local deer density (average of 2015 and 2016) and pre-Sandy (i.e., 2010) vegetation cover on the estimated rates of vegetation recovery for each overwash fan. All R code used in this chapter is available in Appendix H.

Vegetation Recovery Rates

I reclassified each image into a binary raster of vegetation cover (grass, shrubs, trees = 1, sand, water = 0). I then used Zonal Statistics in ArcGIS with overwash fan boundaries as zones to calculate the sum of pixels of vegetation cover. I divided the sum of vegetation pixels by the total number of pixels processed to obtain a percent vegetation cover estimate. I ln-transformed
average percent cover values for each year and overwash fan and used ordinary linear regression to estimate the exponential recovery rate (i.e., exp(slope)).

I used the Normalized Difference Vegetation Index (NDVI) as a proxy for vegetation productivity in overwash fans (see Chapter Two). I obtained Landsat 7 ETM+ Surface Reflectance imagery for the OPWA for the following dates: 15 June 2012, 04 July 2013, 21 June 2014, 24 June 2015, 26 June 2016, and 29 June 2017 (courtesy of United States Geological Survey). I used Zonal Statistics in ArcGIS (version 10.2) to calculate average NDVI within each overwash fan.

**Results**

*Vegetation Cover Assessment*

The best-fit classification used red, green, blue and near-infrared spectral bands. Classifications using only red, green, and blue spectral bands fit the data well, but several land cover classes were difficult to distinguish (i.e., beach grass and marsh grass, shrubs and trees). Classifications using red, green, blue, and near-infrared bands and the digital elevation model misclassified many low elevation sandy areas as water. Overall accuracy calculated for each year was between 81% and 98%, indicating strong agreement between the classification and visible land cover (Table 8). In 2010, vegetation cover in areas that were overwashed by Hurricane Sandy varied between 23.6 % and 72.0 % (Table 9), and contained mostly shrubs with small patches of *A. breviligulata* (Figure 19, Appendix I). The regression of average vegetation cover derived from plot sampling on classified cover was significant (F = 32.7; df = 1, 16; p < 0.0001), predictive (R² = 0.67) and relatively precise (CV = 19.1%). The regression slope was not
different from unity ($\beta_1 = 0.97; \text{SE} = 0.17$) but the intercept was significantly different from zero ($\beta_0 = 16.8\%; \text{SE} = 3.3\%; \text{Figure 20}$).

**Local Deer Density in Overwash Fans**

I identified three female and 22 male deer from trail camera photographs taken in 2015, but I was unable to identify individual deer photographed in overwash fans 1 and 2. I calculated between 10 and 39 total deer in overwash fans (Table 10) using equations from Jacobson et al. (1997). I identified three adult females and 31 adult males from trail camera photographs taken in 2016, and calculated between 5 and 63 total deer in overwash fans.

**Vegetation Recovery Rates**

Vegetation cover decreased by 96-99% after Hurricane Sandy and only small patches of shrubs remained intact. By the third growing season post-Hurricane Sandy (i.e., 2015), all overwash fans had established vegetation communities dominated by *A. breviligulata* with small patches of shrubs. Vegetation cover continued to increase in 2016 in all overwash fans. Two overwash fans (i.e., 1 and 2) experienced significant inundation and coastal erosion between 2015 and 2016.

Exponential rates of vegetation recovery ranged from 1.5% to 2.2% yr$^{-1}$ (Figure 21, Table 11). Average pre-Sandy vegetation cover positively influenced vegetation recovery rates from 2012 to 2016 (Figure 22). Averaged across both years, local deer density ranged from 4 to 78 individuals ha$^{-1}$. Multiple linear regression of vegetation recovery rates on pre-Sandy vegetation cover and local deer density was significant ($F = 6.5; \text{df} = 2, 6; p = 0.032$). Sixty-eight percent of the variation in vegetation recovery rates of overwash fans was explained by the model. Standardized regression coefficients revealed a positive and significant effect of pre-Sandy
vegetation cover ($\beta = 0.18; t = 3.2; p = 0.019$), and a negative but statistically insignificant effect of local deer density ($\beta = -0.08; t = -1.5; p = 0.192$) on vegetation recovery rates (Figure 23).

Net primary productivity differed among years and overwash fans (Appendix F). Two overwash fans (i.e., 3 and 8) did not have Landsat imagery available on any dates between 01 June and 30 August 2017, so NDVI was calculated from 2012-2016 only. For all nine overwash fans, average NDVI decreased between 2012 and 2013, increased from 2013 to 2015, and decreased from 2015 to 2016 (Table 12). The maximum and range of NDVI values were greater in 2015 than 2016. Local deer density increased with average NDVI in overwash fans ($F=5.651$, $df=1, 15$, $p=0.031$) and the relationship was the same between years.

Discussion

I did not find an effect of local density of white-tailed deer on the rates of vegetation recovery in storm-induced overwash fans of the OPWA. Instead, pre-storm vegetation cover was a better predictor of vegetation recovery rates. While the estimated coefficient associated with local deer density was negative, the effect was neither statistically significant nor compelling and amounted to about four percentage points of total cover over a 10-year period. The combination of its low palatability and rhizomatous growth habit, the spread of $A. \text{breviligulata}$ is not deleteriously affected by grazing and trampling of deer in overwash fans. While I did occasionally record grazing on green and growing shoots, by far, $A. \text{breviligulata}$ was consumed by deer during the non-growing season when fodder of any kind is not readily available, and my trail camera images bear that out. Similar observations have been made for other grazing species (Gadgil 2002).

Although use of aerial or satellite imagery in vegetation assessment is increasingly popular in ecology (Symeonakis et al. 2017, Melville et al. 2018), it has limitations. The RF
classifier performed adequately in capturing changes in important land cover in and around overwash fans of the OPWA. Despite using relatively high resolution satellite imagery, however, plot data recorded on average 16.8% more vegetation cover than classifications. Patchy vegetation, like that I encountered in overwash fans, can easily be misclassified using digital imagery if cover in 1-m\(^2\) plots is highly variable. Imagery used for this study was collected before the beginning of the growing season (i.e., April) and ground methods were conducted during the growing season (i.e., September), so differences in total vegetation cover estimated through each method was unsurprising. Bias in estimated recovery rates was not evident since the regression slope between total cover measured using ground methods and image classification was not different from unity. Since Hurricane Sandy, the rate of vegetation recovery in overwash fans has increased at an average exponential rate of 1.8% per year and cover is dominated by *A. breviligulata*. At current rates, vegetation coverage will return to pre-Sandy conditions within the decade for most overwash fans. However, transition from grasses to shrubs and small trees will take much longer and depends on how quickly a protective dune forms.

However, *A. breviligulata* is very sensitive to the effects of trampling (USDA 2018). Deer trails are clearly evident in pre-Sandy classified land cover images (Figure 19, Appendix I). Vegetation, including *A. breviligulata*, is eliminated over time as a consequence of repeated trampling. Pellerin et al. (2006) found that deer trampling decreased ground vegetation cover, increased coverage of bare peat, and subsequently prevented future establishment of plants in peat lands. Similar legacy effects persist in the OPWA from the Burma Road, a vestige of anticipated development of the island that prompted the creation of the National Seashore and the OPWA (USNPS 2016). Local densities I computed in overwash fans were unprecedented; in
fact, one might argue that the effect of deer in the initial recovery of vegetation is primarily trampling that leads to an overall reduction in *A. breviligulata* cover, but does not affect its rate of spread.

While vegetation cover was greater in 2016 than 2015, the productivity index decreased for all overwash fans between 2015 and 2016. A drought spanning most of the northeastern United States in 2016 (data courtesy of NOAA: https://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers/) is the likely cause of plant stress, earlier senescence (unpublished data) of *A. breviligulata*, and reduced productivity in all overwash fans despite increases in vegetation cover. In spite of the local drought, local deer density exhibited a positive, linear relationship with productivity in overwash fans in both years. Herbivore migration is related to timing and amount of rain in the Serengeti (Sinclair and Norton-Griffiths 1979, Holdo et al. 2009), Yellowstone National Park (Sawyer and Kauffman 2011), and steppes of Mongolia (Leimgruber et al. 2001), similarly to what I found in the OPWA.

Due to the short window of my analysis of vegetation recovery, I can only speculate on the future development of the vegetation community in overwash fans. Should the overwash fan develop a budding foredune, the site should eventually transition to a shrub-dominated swale (Ehrenfeld 1990, Tilman 1990). Shrub encroachment in overwash fans has been attributed to the absence of subsequent storm events (Schroder et al. 1979), which would allow dunes time to develop. Shrubs are more likely to encroach in areas with denser grass cover where soil nutrients are present (Young et al. 1995). In a coastal system in Florida, time needed for shrub encroachment into *A. breviligulata*-dominated overwash fans ranged from 19 to 52 years (Johnson 1997). Because overwash fans 1 and 2 remain highly vulnerable to continued inundation, they may never fully recover from the impact of Hurricane Sandy.

UA = User’s Accuracy. PA = Producer’s Accuracy. Bolded values = overall accuracy.

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<td>20.1</td>
<td>27.7</td>
<td>37.2</td>
<td>11.3</td>
</tr>
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</table>
Table 10. Individual deer observed in trail cameras in overwash fans (OW) in the OPWA, Fire Island, New York in 2015 and 2016, including results of local deer density calculations. Many deer were observed in multiple overwash fans, so values in this table are not population estimates.

<table>
<thead>
<tr>
<th>OW</th>
<th># Unique Deer</th>
<th># Unique Obs.</th>
<th>Pop. Factor</th>
<th># Total Deer Obs.</th>
<th># Deer Using OW</th>
<th>OW Area (ha)</th>
<th>Dens. Deer Use (deer ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2015</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>32</td>
<td>19*</td>
<td>3.2</td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>13</td>
<td>10*</td>
<td>2.6</td>
<td>4</td>
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<td>3</td>
<td>5</td>
<td>24</td>
<td>0.21</td>
<td>58</td>
<td>12</td>
<td>0.7</td>
<td>18</td>
</tr>
<tr>
<td>4</td>
<td>3</td>
<td>3</td>
<td>1.00</td>
<td>34</td>
<td>34</td>
<td>1.1</td>
<td>32</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>23</td>
<td>0.26</td>
<td>71</td>
<td>19</td>
<td>1.4</td>
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<td>6</td>
<td>8</td>
<td>18</td>
<td>0.44</td>
<td>66</td>
<td>29</td>
<td>0.7</td>
<td>44</td>
</tr>
<tr>
<td>7</td>
<td>11</td>
<td>93</td>
<td>0.12</td>
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<td>31</td>
<td>0.6</td>
<td>52</td>
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<tr>
<td>8</td>
<td>10</td>
<td>18</td>
<td>0.56</td>
<td>70</td>
<td>39</td>
<td>1.4</td>
<td>28</td>
</tr>
<tr>
<td>9</td>
<td>9</td>
<td>44</td>
<td>0.20</td>
<td>105</td>
<td>21</td>
<td>0.8</td>
<td>27</td>
</tr>
<tr>
<td>2016</td>
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<td></td>
<td></td>
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<td></td>
</tr>
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<td>2</td>
<td>4</td>
<td>0.50</td>
<td>10</td>
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<td>3.2</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
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<td>2.6</td>
<td>9</td>
</tr>
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<td>3</td>
<td>8</td>
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<td>0.53</td>
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<td>0.7</td>
<td>38</td>
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<tr>
<td>4</td>
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<td>5</td>
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<td>14</td>
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<td>5</td>
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<td>21</td>
<td>0.43</td>
<td>63</td>
<td>27</td>
<td>1.4</td>
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<td>6</td>
<td>11</td>
<td>23</td>
<td>0.48</td>
<td>68</td>
<td>33</td>
<td>0.7</td>
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<td>7</td>
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<td>74</td>
<td>0.24</td>
<td>259</td>
<td>63</td>
<td>0.6</td>
<td>104</td>
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<tr>
<td>8</td>
<td>3</td>
<td>4</td>
<td>0.75</td>
<td>15</td>
<td>11</td>
<td>1.4</td>
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</tr>
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<td>9</td>
<td>10</td>
<td>38</td>
<td>0.26</td>
<td>54</td>
<td>14</td>
<td>0.8</td>
<td>18</td>
</tr>
</tbody>
</table>

* Values imputed from a regression of deer using the overwash fan on total deer observed in camera images during 2016.
Table 11. Rates of change in percentage of total vegetation cover among years since Hurricane Sandy (i.e., 2012, 2015, and 2016) and overwash fans in the OPWA, Fire Island, New York.

<table>
<thead>
<tr>
<th></th>
<th>OW 1</th>
<th>OW 2</th>
<th>OW 3</th>
<th>OW 4</th>
<th>OW 5</th>
<th>OW 6</th>
<th>OW 7</th>
<th>OW 8</th>
<th>OW 9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slope</td>
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<td>1.9</td>
<td>2.0</td>
<td>1.6</td>
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<td>1.8</td>
<td>1.7</td>
<td>2.2</td>
<td>1.5</td>
</tr>
<tr>
<td>Intercept</td>
<td>1.8</td>
<td>1.0</td>
<td>1.4</td>
<td>1.9</td>
<td>1.3</td>
<td>1.8</td>
<td>4.1</td>
<td>1.9</td>
<td>2.2</td>
</tr>
</tbody>
</table>

* Year in which total vegetation cover is predicted to return to pre-storm condition
Table 12. Average Normalized Difference Vegetation Index (NDVI) for each overwash fan from 2012 to 2017 in the OPWA, Fire Island, New York. Values in parentheses indicate standard deviations.

<table>
<thead>
<tr>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.70 (0.11)</td>
<td>0.36 (0.08)</td>
<td>0.44 (0.16)</td>
<td>0.48 (0.16)</td>
<td>0.44 (0.13)</td>
<td>0.24 (0.04)</td>
</tr>
<tr>
<td>2</td>
<td>0.57 (0.10)</td>
<td>0.33 (0.08)</td>
<td>0.39 (0.09)</td>
<td>0.43 (0.10)</td>
<td>0.40 (0.09)</td>
<td>0.41 (0.11)</td>
</tr>
<tr>
<td>3</td>
<td>0.62 (0.09)</td>
<td>0.45 (0.10)</td>
<td>0.53 (0.10)</td>
<td>0.54 (0.11)</td>
<td>0.53 (0.08)</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
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<td>0.40 (0.08)</td>
<td>0.44 (0.08)</td>
<td>0.46 (0.08)</td>
<td>0.40 (0.06)</td>
<td>0.45 (0.07)</td>
</tr>
<tr>
<td>5</td>
<td>0.57 (0.15)</td>
<td>0.43 (0.13)</td>
<td>0.49 (0.15)</td>
<td>0.51 (0.17)</td>
<td>0.43 (0.11)</td>
<td>0.51 (0.14)</td>
</tr>
<tr>
<td>6</td>
<td>0.53 (0.09)</td>
<td>0.50 (0.08)</td>
<td>0.50 (0.06)</td>
<td>0.52 (0.09)</td>
<td>0.45 (0.07)</td>
<td>0.52 (0.09)</td>
</tr>
<tr>
<td>7</td>
<td>0.59 (0.06)</td>
<td>0.55 (0.06)</td>
<td>0.56 (0.07)</td>
<td>0.60 (0.07)</td>
<td>0.48 (0.05)</td>
<td>0.55 (0.07)</td>
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<tr>
<td>8</td>
<td>0.60 (0.10)</td>
<td>0.43 (0.11)</td>
<td>0.49 (0.01)</td>
<td>0.53 (0.11)</td>
<td>0.51 (0.10)</td>
<td>-</td>
</tr>
<tr>
<td>9</td>
<td>0.54 (0.18)</td>
<td>0.52 (0.14)</td>
<td>0.54 (0.15)</td>
<td>0.55 (0.16)</td>
<td>0.45 (0.11)</td>
<td>0.27 (0.05)</td>
</tr>
</tbody>
</table>

* Overwash fan 7 used 07/01/2012 imagery. Overwash fans 3 and 8 used 07/12/2016 imagery.
Figure 19. Image classifications for post-Hurricane Sandy Overwash 1 in the OPWA, Fire Island, New York show changes in vegetation cover from grass and shrubs in 2010, to bare sand as a result of Hurricane Sandy, to expanding grass cover in 2015 and 2016. Classifications of all other overwash fans are shown in Appendix I. In all overwash fans, the presence of deer trails is evident in 2010.
Figure 20. Average percent cover calculated from imagery classification versus average percent cover measured in 1-m$^2$ plot surveys in nine overwash fans in the OPWA, Fire Island, New York between 2015 and 2016.
Figure 21. Regressions of log-transformed percent vegetation cover from classified imagery as a function of Year (i.e., 2012, 2015, 2016) in post-Hurricane Sandy overwash fans in the OPWA, Fire Island, New York.
Figure 22. Linear regressions suggest a positive effect of pre-Sandy (i.e., 2010) vegetation cover on rate of post-Hurricane Sandy vegetation change (i.e., 2012 to 2016) in overwash fans (“OW”) in the OPWA, Fire Island, New York. Points are labeled with overwash fan number as defined in Figure 4 and 95% confidence intervals are shown.
Figure 23. Multiple linear regressions of the effects of average local deer density (i.e., 2015, 2016) and pre-Sandy cover (i.e., 2010) on exponential rates of vegetation recovery in overwash fans in the OPWA, Fire Island, New York. Contours represent predicted exponential rates of vegetation cover.
Figure 24. Local deer densities were greater in more productive overwash fans in 2015 and 2016 in the OPWA, Fire Island, New York. Points are labeled with overwash fan number as defined in Figure 4 and 95% confidence intervals are shown.
EPILOGUE

The goal of this research was to investigate the effects of abiotic and biotic factors on barrier island resilience through impacts to post-disturbance vegetation recovery. The presence of a foredune is the primary force controlling plant community development in overwash fans in the Otis Pike Fire Island High Dune Wilderness Area after Hurricane Sandy. Effects of deer were consistent between years, highly variable among overwash fans, but minor when compared to abiotic forcing captured in spatial structures. Deer affected species richness and cover of vegetation communities, but local densities of deer did not negatively affect the rate of vegetation recovery in overwash fans.

Fine-scale and broad-scale spatial structures are important to the development of plant communities in overwash fans. Like other studies (Legendre et al. 2009, Smith and Lundholm 2010), only broad-scale structures were related to environmental conditions. Fine-scale spatial structures represent neutral processes, including dispersal and ecological drift (Adler et al. 2007, Dray et al. 2012). Broad-scale spatial structures, which represent niche properties (Smith and Lundholm 2010, Dray et al. 2012), did not significantly contribute to the niche partitioning in plant communities. Productivity was the primary contributor to niche partitioning in overwash fans plant communities, and it was strongly positively correlated with broad-scale spatial structures. Successional stage may influence the roles of niche and neutral processes in communities (Gravel et al. 2006, Chu et al. 2007), suggesting that the relationships I uncovered in overwash fans may shift as plant communities continue to mature.

Two overwash fans are not expected to recover in the near future due to continued overwash and erosion events. Two additional overwash fans have developed nascent foredunes, which is reflected in plant community composition and cover. The futures of the five remaining
overwash fans remain uncertain, as dune growth is positive but comparatively slow. When a foredune is present and plant communities diversify from graminoids to shrubs and herbs, the biotic effects of deer browsing, grazing and trampling may become more important to species composition and community structure.

Because deer preferentially forage easily digestible species and new growth of many other species (Halls 1984), I chose to study the nature of their effects, and then to ascertain which are actually meaningful to plant community recovery in overwash fans. For example, differences in species richness that I documented between treatment and control plots, while not statistically significant, could compound over time as species richness increases with community development. This is a common observation from long-term deer exclusion studies — it often takes a long time for effects to evince (Kain et al. 2011, Pendergast et al. 2015). Deer are attracted to high productivity sites and their effects manifest from unprecedented local densities. However, at the present time, white-tailed deer do not appear to threaten the resilience of Fire Island’s wilderness as most overwash fans continue to rapidly recover from Hurricane Sandy.

High local deer densities may contribute to the productivity in some overwash fans through dung and urine soiling that provides temporary, local nutrients to plants (Petrusewicz and Grodzinski 1975), especially in nutrient-poor sites (Ritchie et al. 1998). Although leach rates in sandy soils are very high, dense vegetation roots and thin soil horizons found in inland areas mitigate rapid losses (Maun 2009), which could explain the denser and lusher vegetation found nearer to the marsh in all overwash fans. Because deer use the adjacent marsh (unpublished data), which is highly productive, they transport nutrients into the swale and recovering overwash fans through daily and seasonal foraging movements. Further research on the
biogeochemical cycling of nutrients and cross-habitat transport will be required to fully understand the role of deer in shaping recovering plant communities.

A strong driver of barrier island systems is climate (Figure 1), which has changed over global and local extents since the last storm event that caused extensive overwash on Fire Island (i.e., Hurricane of 1938). Of the many consequences of a changing climate, coastal areas are most heavily impacted by sea level rise and changes in coastal storm frequency and intensity (NAST 2001). Sea level rise increases erosion (Kratzmann and Hapke 2012), frequency of wash-over events and breaching, and frequency and magnitude of oceanic inundation (Sallenger 2000, Masterson et al. 2014). Though sea level rise occurs evenly along barrier islands, vulnerability to storm damage, including surge, varies with geomorphology (i.e., elevation). The northeastern United States, including New York, are a sea level hotspot (Sallenger et al. 2012) and Psuty et al. (2005) suggested that the rate of sea level rise for Fire Island has been increasing. As sea levels rise, storm surges will reach areas farther inland and greater in height than storm surges from decades ago (Psuty et al 2005). Frequent high water events may hinder vegetation recovery between storms (Vincent and Moore 2015) and further increase erosion (Houser and Hamilton 2009), limiting the island’s natural defense. Sea level rise reduces the distance separating the freshwater lens from underlying brackish groundwater, causing saltwater intrusion into the freshwater lens and cascading effects on vegetation communities (Masterson et al. 2014).

The ability of coastal ecosystems to adapt to changes in ecosystem drivers, like climate change, is compromised by other stressors acting upon the system. Mitigation of extant stressors, like effects of white-tailed deer herbivory, can aid in the recovery of coastal systems after a coastal disturbance (Scavia et al. 2002). On Fire Island, two types of resilience were addressed in this dissertation: (1) resilience to impacts from Hurricane Sandy, a high-intensity, low-
frequency disturbance, and (2) resilience to deer herbivory, a low-intensity, high-frequency disturbance. The results of my study suggest that Hurricane Sandy exceeded storm resilience for two overwash fans where I documented continued coastal disturbance. Hurricane Sandy did not exceed storm resilience for the two overwash fans with rapidly recovering foredunes. The storm resilience of the five remaining overwash fans may be compromised if a future storm impacts Fire Island before the foredunes are able to provide adequate protection. Though deer do not currently impact resilience of the OPWA, deer will impact the transition of plant communities as more palatable, shrubby plant species encroach into overwash fans. Effects of deer foraging in mature plant communities could impact the resilience of overwash fans over a temporal scale greater than the results of this dissertation. Human activities, particularly recreation, may also affect vegetation recovery in overwash fans in the OPWA, but was not assessed in this study. Future monitoring and research is necessary to assess impacts of deer and human activity as overwash fans continue to recover from Hurricane Sandy.
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VegMeasure 2: a software package that facilitates measurement of foliar cover, litter and 
bare ground on rangelands. Department of Rangeland Resources, Oregon State 
University, Corvallis, OR, USA.
a depauperate forest dominated by an understory tree: results from a 60-year-old deer 
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APPENDICES

Appendix A. R code for Chapter One analysis, including MANOVA, PCA, RDA, and dbMEM using vegetation community composition in overwash fans (i.e., Y) and environmental proxies (i.e., X).

# Load the required packages
library(ade4)   #version: 1.7-6
library(vegan) #version: 2.4-3
library(AEM)   #version: 0.6
library(adespatial) #version: 0.0-8
library(spdep) #version: 0.6-6
library(packfor) #version: 0.0-8

setwd("...")

# Load source files for additional functions
source("PCNM.R")
source("pcoa.all.R")
source("R_functions_for_Practicals.txt")

# percent cover of all vegetation species detected in OW plots
flora.all <- read.csv("flora_999.csv", header=TRUE, row.names=1)
flora <- flora.all[,4:29]

# schedule of sampling events
sampling <- read.csv("sampling_999.csv", header=TRUE, row.names=1)

# all variables used in analysis
all.vars <- read.csv("dbMEM_vars_999.csv", header=TRUE, row.names=1)

Year <- "2015"  #change for each run
OW <- "1"

#### MANOVA among OWs 2-9, all surveys ####
curr.siteS <- c(2,3,4,5,6,7,8,9)
sampling.manova <- sampling[,sampling$OW %in% curr.siteS,]
rn.man1 <- rownames(sampling.manova)
flora.manova <- flora[rn.man1,]
# Create a factor for YEAR by transforming vector
sampling.manova1$YEAR
year.fac <- as.factor(sampling.manova1$Surv_Yr)

# Create a factor for SEASON
season.fac <- sampling.manova1$Surv_Mo
table(season.fac, year.fac)

# Create Helmert contrasts for factors and interaction
year.season.helm <- model.matrix(~ season.fac * year.fac,
contrasts=list(season.fac="contr.helmert", year.fac="contr.helmert"))

# Helmert contrast variables should all sum to 0
apply(year.season.helm[, 2:ncol(year.season.helm)], 2, sum)

# Cross products of Helmert contrasts should equal 0
res <- t(year.season.helm[, -1]) %*% year.season.helm[, -1]
# Check that non-diagonal terms of matrix "res" are 0.
head(res)

# Transform data
flora.hel.manova1 <- decostand(flora.manova1, method="hellinger")

# Hellinger distance matrix from transformed data
flora.hel.manova1.D1 <- dist(flora.hel.manova1)

# Cross season & year factors to create groups
year.season.fac <- as.factor(paste(year.fac, season.fac, sep="."))

# Test homogeneity of the multivar within-group covariance matrices
flora.hel.manova1.MHV <- betadisper(flora.hel.manova1.D1,
year.season.fac)

# MANOVA:
season.year.rda1 <- rda(flora.hel.manova1, year.season.helm[, 2:4],
year.season.helm[, 5:6])
anova(season.year.rda1, step=1000, perm.max=1000, model="direct")
RsquareAdj(season.year.rda1)

# Can factor Season explain significant portion of dispersion?
season.rda1 <- rda(flora.hel.manova1, year.season.helm[, 2:3],
year.season.helm[, 5:6])
anova(season.rda1, step=1000, perm.max=1000, strata=year.fac,
model="direct")
RsquareAdj(season.rda1) # Measure of effect size

# Can factor Year explain significant portion of dispersion?
year.rda1 <- rda(flora.hel.manova1, year.season.helm[, 4],
year.season.helm[, c(5:6)])
anova(year.rda1, step=1000, perm.max=1000, strata=season.fac,
model="direct")
RsquareAdj(year.rda1) # Measure of effect size

##### PCA of X variables #####
vars <- all.vars[,5:11]
head(vars)
#PCA of env data, including standardization of vars (scale=TRUE)
vars.pca <- rda(vars, scale=TRUE)
vars.pca
vars.pca.sum <- summary(vars.pca) #default scaling 2
names(vars.pca.sum)
plot(vars.pca)

#### RDA, Y ~ X ####
flora.hel <- decostand(flora, method="hellinger")
flora.rda <- rda(flora.hel ~ ., location)
anova(flora.rda, step=10000, perm.max=10000)
R2adj <- RsquareAdj(flora.rda)$adj.r.squared
flora.rda.sum <- summary(flora.rda)
flora2.sc <- scores(flora.rda, choices=1:2, display="sp")
windows(title="RDA scaling 2 + lc")
plot(flora.rda, display=c("sp", "lc", "cn"),
     main="Triplot RDA flora.hel ~ location - scaling 2 - lc scores")
arrows(0, 0, flora2.sc[,1], flora2.sc[,2], length=0, lty=1, col="red")

# Global test of RDA result
anova.cca(flora.rda, step=10000)
# Test of significance by axis
anova(flora.rda, by="axis", step=1000)
# Variance inflation factors (VIF)
vif.cca(flora.rda)

# Forward selection
step.forward <- ordistep(rda(flora.hel ~ 1, data=location),
                    scope=formula(flora.rda),
                    direction="forward", pstep=1000)
flora.rda.pars <- rda(flora.hel~UTMX + UTMY + DEM, data=location)
anova(flora.rda.pars, step=1000)
anova(flora.rda.pars, step=1000, by="axis")
vif.cca(flora.rda.pars)
RsquareAdj(rda(flora.hel ~ UTMX+UTMY+DEM,
         data=location))$adj.r.squared

#### dbMEM ####
# Isolate Flora and UTM for September surveys
utm_Sep <- all.vars[all.vars$Surv_Mo=="September",]
flora_Sep <- flora.all[flora.all$Surv_Mo=="September",]
# Hellinger transformation of all response data
flora.hel <- decostand(flora_Sep, method="hellinger")
# Is there a linear spatial trend in the full response matrix?
flora.trend <- rda(flora.hel, utm_Sep)
anova(flora.trend, step=10000, perm.max=10000)
RsquareAdj(flora.trend)
utm_Sep <- utm_Sep[utm_Sep$Surv_Yr==Year,]
utm_Sep <- utm_Sep[utm_Sep$OW == OW,]
utm_Sep <- utm_Sep[,7:8]

# Isolate flora data for individual overwash fan and year
# Code was iterated for each overwash and year combination (n=18).
flora_Sep <- flora_Sep[flora_Sep$Surv_Yr==Year,]
flora_Sep <- flora_Sep[flora_Sep$OW == OW,]
flora_Sep <- flora_Sep[,4:29]

# Hellinger transformation
flora.hel <- decostand(flora_Sep, method="hellinger")
# Is there a linear spatial trend in the response data?
flora.trend <- rda(flora.hel, utm_Sep)
anova(flora.trend, step=10000, perm.max=10000)
RsquareAdj(flora.trend)
# Remove linear trend
flora.detrend <- resid(lm(as.matrix(flora.hel)~., data=utm_Sep))

# Calculate distance matrix
distmat <- dist(utm_Sep[,1], utm_Sep[,2], diag=TRUE, upper=TRUE,
                method="euclidean")
spatial.mem <- PCNM(distmat, dBMEM=TRUE, moran=TRUE, all=TRUE)
summary(spatial.mem)
# Which dBMEM model positive temporal correlation?
spatial.mem$Moran_I

#RDA of fauna by dBMEM eigenvectors modeling positive spatial corr.
spatial.mem.pos <-
    as.data.frame(spatial.mem$vectors[,spatial.mem$Moran_I$Positive])
flora.mem.pos <- rda(flora.hel ~ ., spatial.mem.pos)
anova(flora.mem.pos, step=10000, perm.max=10000)
RsquareAdj(flora.mem.pos)
anova(flora.mem.pos, by="axis")

spatial.mem.neg <-
    as.data.frame(spatial.mem$vectors[,!spatial.mem$Moran_I$Positive])
flora.mem.neg <- rda(flora.hel ~ ., spatial.mem.neg)
anova(flora.mem.neg, step=10000, perm.max=10000)
RsquareAdj(flora.mem.neg)
anova(flora.mem.neg, by="axis")

plot(utm_Sep[,1], scores(flora.mem.neg, display="lc",
            choice=1), type="b", pch=19, main =
paste("RDA Axis 1 Negative Spatial Correlation Model"), xlab="X Coordinate", ylab="RDA axis")
plot(utm_Sep[,2], scores(flora.mem.neg, display="lc",
            choice=1), type="b", pch=19, main =
paste("RDA Axis 1 Negative Spatial Correlation Model"), xlab="Y Coordinate", ylab="RDA axis")
plot(utm_Sep[,1], scores(flora.mem.neg, display="lc",
            choice=2), type="b", pch=19, main =
paste("RDA Axis 2 Negative Spatial Correlation Model"), xlab="X Coordinate", ylab="RDA axis")

plot(utm_Sep[,1], scores(flora.mem.neg, display="lc",
            choice=2), type="b", pch=19, main =
paste("RDA Axis 2 Negative Spatial Correlation Model"), xlab="X Coordinate", ylab="RDA axis")
plot(utm_Sep[,2], scores(flora.mem.neg, display="lc", choice=2), type="b", pch=19, main = paste("RDA Axis 2 Negative Spatial Correlation Model"), xlab="Y Coordinate", ylab="RDA axis")
plot(utm_Sep[,1], scores(flora.mem.pos, display="lc", choice=1), type="b", pch=19, main = paste("RDA Axis 1 Positive Spatial Correlation Model"), xlab="X Coordinate", ylab="RDA axis")
plot(utm_Sep [,2], scores(flora.mem.pos, display="lc", choice=1), type="b", pch=19, main = paste("RDA Axis 1 Positive Spatial Correlation Model"), xlab="Y Coordinate", ylab="RDA axis")

sel.mem <- forward.sel(flora.hel, spatial.mem$vectors, nperm=9999, alpha=0.1)
mem.select <- sort(sel.mem$order[sel.mem$pval<=0.1])
select <- which(spatial.mem$Moran_I$Positive == TRUE)
# Number of PCNM with I > E(I)
len <- length(select)
num.pos <- which(mem.select <= len)
max <- max(num.pos)
mem.select.pos <- mem.select[1:max]
n <- length(mem.select.pos)
n. <- n/2
mem.select.pos.b <- head(mem.select.pos, n=n.)
mem.select.pos.f <- tail(mem.select.pos, n=n.) #check for duplicates
end <- length(mem.select)
mem.select.neg <- mem.select[(max+1):end]
len.n <- length(mem.select)

#### Fine and Broad Scale ####
vars_Sep <- all.vars[all.vars$Surv_Mo=="September",]
vars_Sep <- vars_Sep[vars_Sep$Surv_Yr==Year,]
vars_Sep <- vars_Sep[vars_Sep$OW ==OW,]
vars_Sep <- vars_Sep[,c(9:11)]

# Check each significant dbMEM for normality using Shapiro
shapiro.test(resid(lm(spatial.mem.pos[,1] ~ ., data=vars_Sep)))
sel.mem1.env <- lm(spatial.mem.pos[,1] ~ ., data=vars_Sep)
summary(sel.mem1.env)

# broad submodel on comm
mem.sel.pos.b <- as.data.frame(spatial.mem$vectors[,mem.select.pos.b])
flora.mem.sel.pos.b <- rda(flora.hel ~ ., mem.sel.pos.b)
anova(flora.mem.sel.pos.b, step=10000, perm.max=10000)
RsquareAdj(flora.mem.sel.pos.b)

# fine submodel on comm
mem.sel.pos.f <- as.data.frame(spatial.mem$vectors[,mem.select.pos.f])
flora.mem.sel.pos.f <- rda(flora.hel ~ ., mem.sel.pos.f)
anova(flora.mem.sel.pos.f, step=10000, perm.max=10000)
RsquareAdj(flora.mem.sel.pos.f)
# env on community
flora.env <- rda(flora.hel ~ ., vars_Sep)
anova(flora.env, step=10000, perm.max=10000)
RsquareAdj(flora.env)

# env on broad submodel
sel.mem.b.env <- rda(mem.sel.pos.b~., vars_Sep)
anova(sel.mem.b.env, step=10000, perm.max=10000)
RsquareAdj(sel.mem.b.env)

# env on fine submodel
sel.mem.f.env <- rda(mem.sel.pos.f~., vars_Sep)
anova(sel.mem.f.env, step=10000, perm.max=10000)
RsquareAdj(sel.mem.f.env)

# for sel, env on comm
res.sel1 <- forward.sel(flora.hel, vars_Sep, nperm=9999, alpha=0.05)

# for sel, env on fine
res.sel2 <- forward.sel(mem.sel.pos.f, vars_Sep, nperm=9999, alpha=0.05)

# for sel, env on broad
res.sel3 <- forward.sel(mem.sel.pos.b, vars_Sep, nperm=9999, alpha=0.05)

### Variation Partitioning ###
head(vars_Sep)
vars <- c(1,2,3) # Varies for each OW and year (res.sel1)

res.part <- varpart(flora.hel, vars_Sep[,vars],
                     spatial.mem$vectors[,mem.select.pos.b],
                     spatial.mem$vectors[,mem.select.pos.f],
                     spatial.mem$vectors[,mem.select.neg])

res.part
plot(res.part, digits=3)

mod1 <- rda(flora.hel, vars_Sep[,vars],
            spatial.mem$vectors[,mem.select])
anova(mod1, step=1000, perm.max=10000)
RsquareAdj(mod1) # Contribution of X1 (vars)

mod2 <- rda(flora.hel, spatial.mem$vectors[,mem.select.pos.b],
            cbind(vars_Sep[,vars],
                  spatial.mem$vectors [,mem.select.neg],
                  spatial.mem$vectors [,mem.select.pos.f]))
anova(mod2, step=1000, perm.max=10000)
RsquareAdj(mod2) # Contribution of X2 (broad positive dbMEM)

mod3 <- rda(flora.hel, spatial.mem$vectors[,mem.select.pos.f],
            cbind(vars_Sep[,vars],
                  spatial.mem$vectors [,mem.select.neg],
                  spatial.mem$vectors[,mem.select.pos.b]))
anova(mod3, step=1000, perm.max=10000)
RsquareAdj(mod3) # Contribution of X3 (fine positive dbMEM)
mod4 <- rda(flora.hel, spatial.mem$vectors[,mem.select.neg],
            cbind(vars_Sep[,vars],
                  spatial.mem$vectors[,mem.select.pos.b],
                  spatial.mem$vectors [,mem.select.pos.f]))
anova(mod4, step=1000, perm.max=1000)
RsquareAdj(mod4) # Contribution of X4 (negative dbMEM)

### Stacked Bar Graph ###

Model_10 <- read.csv("Model_10_perc.csv") #non-detrended
head(Model_10)
colnames(Model_10) <- c("X","Year","Env. Vars.", "Shared Spatial & Env.", "Spatial: Broad", "Spatial: Fine", "Spatial: Negative", "Residuals")

melted <- melt(Model_10, id.vars=c("X","Year"))
melted$cat <- ''
melted[melted$X == 'OW 1',]$cat <- "OW 1"
melted[melted$X == 'OW 2',]$cat <- "OW 2"
melted[melted$X == 'OW 3',]$cat <- "OW 3"
melted[melted$X == 'OW 4',]$cat <- "OW 4"
melted[melted$X == 'OW 5',]$cat <- "OW 5"
melted[melted$X == 'OW 6',]$cat <- "OW 6"
melted[melted$X == 'OW 7',]$cat <- "OW 7"
melted[melted$X == 'OW 8',]$cat <- "OW 8"
melted[melted$X == 'OW 9',]$cat <- "OW 9"
melted <- within(melted, Year[Year == '2015']< '15')
melted <- within(melted, Year[Year == '2016']< '16')

windowsFonts(Times=windowsFont("Times New Roman"))
ggplot(melted, aes(x = Year, y = value, fill = factor(variable, levels=c("Env. Vars.", "Shared Spatial & Env.", "Spatial: Broad", "Spatial: Fine", "Spatial: Negative", "Residuals")))) + geom_bar(stat = 'identity', position = 'stack') + facet_grid(~ X) + labs(title="Community Composition Data with Trend", x="Year (20XX)", y="Percentage of Variation", fill="Source") + scale_fill_grey(start = 0.8, end = 0.2, na.value = "red") + theme(panel.background=element_rect("white"),
            panel.grid.major=element_line("white"),
            panel.grid.minor=element_line("white"),
            axis.text.x=element_text(color="black",size=10,margin=margin(-15,0,0,0)),
            axis.text.y=element_text(color="black",size=10),
            axis.title.x=element_text(color="black",size=15),
            axis.title.y=element_text(color="black",size=15),
            axis.ticks.x=element_blank(),
            plot.title=element_text(hjust=0.5),
            text=element_text(family="Times"))

######################################################################## END #################################################################
Appendix B. Percent *A. breviligulata* cover observed during September 2015 and September 2016 in nine post-Hurricane Sandy overwash fans in the OPWA, Fire Island, New York. Interpolation was performed through inverse-distance weighting.
Appendix C. Total number of plant species observed during September 2015 and September 2016 for nine post-Hurricane Sandy overwash fans in the OPWA, Fire Island, New York. Interpolation was performed through inverse-distance weighting.
Appendix D. A trend surface analysis showing dbMEM values for significant positive axes of Hellinger-transformed community composition in post-Hurricane Sandy (i.e., 2015, 2016) overwash fans in the OPWA, Fire Island, New York.

The size of the circles correspond to dbMEM values (dark circles > 0, white circles < 0), and bands of like symbols describe spatial patterns captured by the significant axes from broad (left-most) to fine (right-most) scale. Relationships shown are more useful to interpret than the dbMEM values themselves.
Overwash 2, 2015, plot spacing: 20-m

Overwash 2, 2016, plot spacing: 20-m
Overwash 3, 2015, plot spacing: 10-m

Overwash 3, 2016, plot spacing: 10-m

Broad ——— Fine
Overwash 4, 2015, plot spacing: 10-m

Overwash 4, 2016, plot spacing: 10-m

Broad  ➔  Fine
Overwash 6, 2015, plot spacing: 10-m

Overwash 6, 2016, plot spacing: 10-m

Broad → Fine
Overwash 8, 2015, plot spacing: 10-m

Overwash 8, 2016, plot spacing: 10-m

Broad → Fine
Overwash 9, 2015, plot spacing: 10-m

Overwash 9, 2016, plot spacing: 10-m

Broad  →  Fine
Appendix E. R code for Chapter Two analyses, including Canonical Correspondence Analysis of vegetation community composition in overwash fans (i.e., Y) and environmental factors (i.e., X).

```r
# clear console memory
rm(list = ls())

# load packages
library(ade4) # version: 1.7-6
library(vegan) # version: 2.4-3

# set working directory
setwd("...

# percent cover of all vegetation species detected in OW plots
Vars <- read.csv("vars_999_dens.csv", header=TRUE, row.names=1)
Flora15 <- read.csv("flora_2015.csv", header=TRUE, row.names=1)
Flora16 <- read.csv("flora_2016.csv", header=TRUE, row.names=1)
row.names(Flora15) <- Flora15$Id
row.names(Flora16) <- Flora16$Id

# vegetation data
veg15 <- Flora15[,5:22]
veg16 <- Flora16[,c(5:20,22:27)]

# environmental data
Vars_QDMA <- Vars[,c(1:3,5,10:14,16:22,25:32)]

# brave new world data
Vars_QDMA15a <- Vars_QDMA[Vars_QDMA$Surv_Yr=="2015",]
row.names(Vars_QDMA15a) <- Vars_QDMA15a$Id
Vars_QDMA15 <- Vars_QDMA15a[,c(5,10:13,15)]
Vars_QDMA15o <- Vars_QDMA15[,c(2,5,10:13,15)]
Vars_QDMA16a <- Vars_QDMA[Vars_QDMA$Surv_Yr=="2016",]
row.names(Vars_QDMA16a) <- Vars_QDMA16a$Id
Vars_QDMA16 <- Vars_QDMA16a[,c(5,10:13,15)]
Vars_QDMA16o <- Vars_QDMA16a[,c(2,5,10:13,15)]

colnames(Vars_QDMA15) <- c("DEM","Broad","Fine","NDVI","Deer")
colnames(Vars_QDMA16) <- c("DEM","Broad","Fine","NDVI","Deer")
colnames(Vars_QDMA15o) <- c("OW","DEM","Broad","Fine","NDVI","Deer")
colnames(Vars_QDMA16o) <- c("OW","DEM","Broad","Fine","NDVI","Deer")

# CCA

# vegetation CCA
veg.cca <- cca(veg15~DEM+Broad+Fine+NDVI+Deer, Vars_QDMA15, scale=TRUE)
plot(veg.cca, display=c("sp","cn","wa"))
anova(veg.cca)
```
veg.cca2 <- cca(veg16~DEM+Broad+Fine+NDVI+Deer, Vars_QDMA16, scale=TRUE)
plot(veg.cca2, display=c("sp","cn","wa"),
anova(veg.cca2)

veg.cca.ow2 <- cca(veg15~NDVI+DEM+Deer +Fine+Broad+Condition(OW), Vars_QDMA15o, scale=TRUE)
veg.cca.ow4 <- cca(veg16~NDVI+DEM+Deer+Fine+Broad+Condition(OW), Vars_QDMA16o, scale=TRUE)

selection <- ordistep(cca(veg15~1, Vars_QDMA15),
    scope=formula(veg.cca), direction="forward", pstep=1000)
selection$anova

selection2 <- ordistep(cca(veg16~1, Vars_QDMA16),
    scope=formula(veg.cca2), direction="forward", pstep=1000)
selection2$anova

ef.ow.cca <- envfit(veg.cca.ow2, Vars_QDMA15o, permutations=999)
plot(veg.cca.ow2, display="sites", type="p")
with(Vars_QDMA15o, ordihull(veg.cca.ow2, OW,
    col=c("deeppink","brown","coral","darkgoldenrod",
         "lightgoldenrod3","chartreuse4","green","blue","darkorchid"),
    lty=1, lwd=1.5))
legend("topleft", lty=1, lwd=1.5,
    c("OW1","OW2","OW3","OW4","OW5","OW6","OW7","OW8","OW9"),
    col=c("deeppink","brown","coral","darkgoldenrod","lightgoldenrod3",
         "chartreuse4","green","blue","darkorchid"))
ef.ow.cca2 <- envfit(veg.cca.ow4, Vars_QDMA16o, permutations=999)
plot(veg.cca.ow4, display="sites", type="p")
with(Vars_QDMA16o, ordihull(veg.cca.ow4, OW,
    col=c("deeppink","brown","coral","darkgoldenrod",
         "lightgoldenrod3","chartreuse4","green","blue","darkorchid"),
    lty=1, lwd=1.5))
legend("topleft", lty=1, lwd=1.5,
    c("OW1","OW2","OW3","OW4","OW5","OW6","OW7","OW8","OW9"),
    col=c("deeppink","brown","coral","darkgoldenrod","lightgoldenrod3",
         "chartreuse4","green","blue","darkorchid"))

plot(veg.cca.ow2, display="sites")
plot(ef.ow.cca, p.max=0.1)
plot(veg.cca.ow4, display="sites")
plot(ef.ow.cca2, p.max=0.1)

######################################################################## END ###################################################################
Appendix F. Normalized Difference Vegetation Index calculated for each overwash fan from 2012 (before Hurricane Sandy) to 2017 using Landsat 7 ETM+ Surface Reflectance imagery showed general increases in post-disturbance productivity as vegetation recovers.
OPWA Overwash 7: NDVI

<table>
<thead>
<tr>
<th>Date</th>
<th>NDVI</th>
<th>±</th>
<th>Date</th>
<th>NDVI</th>
<th>±</th>
</tr>
</thead>
<tbody>
<tr>
<td>07/01/2012</td>
<td>0.594</td>
<td>± 0.055</td>
<td>07/04/2013</td>
<td>0.549</td>
<td>± 0.063</td>
</tr>
<tr>
<td>06/21/2014</td>
<td>0.560</td>
<td>± 0.075</td>
<td>06/24/2015</td>
<td>0.604</td>
<td>± 0.066</td>
</tr>
<tr>
<td>06/26/2016</td>
<td>0.484</td>
<td>± 0.048</td>
<td>06/29/2017</td>
<td>0.551</td>
<td>± 0.070</td>
</tr>
</tbody>
</table>

Legend
- OW Boundary NDVI
- High: 1
- Low: -1

Imagery: Landsat 7 (courtesy of USGS)

OPWA Overwash 8: NDVI

<table>
<thead>
<tr>
<th>Date</th>
<th>NDVI</th>
<th>±</th>
<th>Date</th>
<th>NDVI</th>
<th>±</th>
<th>Date</th>
<th>NDVI</th>
<th>±</th>
</tr>
</thead>
<tbody>
<tr>
<td>06/15/2012</td>
<td>0.595</td>
<td>± 0.100</td>
<td>07/04/2013</td>
<td>0.425</td>
<td>± 0.105</td>
<td>06/21/2014</td>
<td>0.493</td>
<td>± 0.111</td>
</tr>
<tr>
<td>06/24/2015</td>
<td>0.525</td>
<td>± 0.106</td>
<td>07/12/2016</td>
<td>0.512</td>
<td>± 0.101</td>
<td>06/29/2017</td>
<td>NDVI: N/A</td>
<td></td>
</tr>
</tbody>
</table>

Legend
- OW Boundary NDVI
- High: 1
- Low: -1

Imagery: Landsat 7 (courtesy of USGS)
Appendix G. R code for Chapter Three analyses, including split-plot analyses and quantile regression of permanent plot data.

```r
rm(list = ls())  # clear console memory

# Load the required packages
install.packages("quantreg")
library("quantreg")
install.packages("agricolae")
library("agricolae")

setwd("...")

### Split-Plot Analyses ###
sp.veg <- read.csv("SplittoR.csv")
head(sp.veg)

sp.veg <- within(sp.veg, OW.F <- factor(OW))
sp.veg <- within(sp.veg, G.F <- factor(Group))
sp.veg <- within(sp.veg, Yr.F <- factor(Year))

sp.veg.ac <- sp.veg[sp.veg$Group!="Treatment",]
str(sp.veg.ac)
sp.veg.ct <- sp.veg[sp.veg$Group!="Lattice",]
str(sp.veg.ct)

gp <- aov(TotalVeg ~ OW.F+G.F+OW.F*G.F+Yr.F+G.F*Yr.F, data = sp.veg)
summary(gp)

ac <- aov(TotalVeg ~ OW.F+G.F+OW.F*G.F+Yr.F+G.F*Yr.F,
          data = sp.veg.ac)
summary(ac)

c <- aov(TotalVeg ~ OW.F+G.F+OW.F*G.F+Yr.F+G.F*Yr.F,
          data = sp.veg.ct)
summary(c)

sp <- sp.plot(sp.veg$Yr.F, sp.veg$OW, sp.veg$G.F, sp.veg$TotalVeg)
sp.ac <- sp.plot(sp.veg.ac$Yr.F, sp.veg.ac$OW, sp.veg.ac$G.F,
                 sp.veg.ac$TotalVeg)
sp.ct <- sp.plot(sp.veg.ct$Yr.F, sp.veg.ct$OW, sp.veg.ct$G.F,
                 sp.veg.ct$TotalVeg)
```

#### Quantile Regression ####

QR <- read.csv("QuanReg_standard.csv", header=TRUE)
head(QR)
#QR$dlta_dem <- QR$dlta_dem*100 #convert delta dem to (cm) instead of (m)
model1 <- rq(dlta_tc~utmX+utmY+dlta_dem, tau=c(0.1, 0.5, 0.75, 0.95), data=QR)
names(model1)
model1$fitted.values
windows()
plot(summary(model1))

#### Slope check: Treatment Vs Control ####

Deltas <- read.csv("slopecheck_treat_control.csv", header=TRUE)
head(Deltas)

lm <- lm(Delta_tc_perc~Delta_DEM_cm, data=Deltas)
summary(lm)
anova(lm)

windows()
plot(Deltas$Delta_DEM_cm, Deltas$Delta_tc_perc, xlab="Delta DEM (cm)",
ylab="Delta Vegetation Total Cover (%)", pch=16, cex=1,
col="blue", ylim=c(0,12))
abline(v=0, lty=3, lwd=1, col="gray")
abline(lm, lty=1, lwd=2, col="black")
points(8.4, 5, cex=1,pch=16,col="red")
legend("topright", cex=1, pch=16, col=c("blue","red"), c("Control", "Treatment"))
text(locator(1), "Delta_VTC = 1.8878 + 0.5791(Delta_DEM), R2 = 0.6428")
Appendix H. R code for Chapter Four analyses, including linear models testing relationships between productivity (NDVI) and vegetation cover, vegetation cover and rate of recovery, and deer density and rate of recovery.

```r
### C. Kilheffer - Dissertation Chapter 4
### March 13, 2018
### R Version 3.2
# Install.packages("visreg") # version 2.5-0
Library("visreg")
rm(list = ls()) # clear console memory

#### NDVI_Cov ####
NDVI_Cov <- read.csv("NDVI_Cov.csv", header=TRUE)
Year <- as.factor(NDVI_Cov$Year)
Cov <- NDVI_Cov$VegCov
NDVI <- NDVI_Cov$NDVI

lm <- lm(Cov~Year+NDVI+Year*NDVI)
summary(lm)
anova(lm)

x2015 <- NDVI_Cov[NDVI_Cov$Year=="2015",]
lm2 <- lm(x2015$VegCov~x2015$NDVI)
summary(lm2)
anova(lm2)

x2016 <- NDVI_Cov[NDVI_Cov$Year=="2016",]
lm3 <- lm(x2016$VegCov~x2016$NDVI)
summary(lm3)
anova(lm3)

windows()
plot(NDVI_Cov$NDVI, NDVI_Cov$VegCov, xlab="NDVI", ylab="Total Vegetation Cover (%)", pch=16, cex=1, col="blue", ylim=c(0,40))
abline(lm2, lty=1, lwd=2, col="blue")
abline(lm3, lty=1, lwd=2, col="red")
points(x2016$NDVI, x2016$VegCov, cex=1, pch=16, col="red")
legend("topright", cex=1, pch=16, col=c("blue","red"), c("2015", "2016"))
text(NDVI_Cov$NDVI, NDVI_Cov$VegCov, NDVI_Cov$OW, cex=0.6, pos=4, col="black")
```
### 2010 Cover and Slope ###
Cov10_Slope <- read.csv("Cov10_Slope.csv", header=TRUE)
lm4 <- lm(Slope~Pre_Cov, data=Cov10_Slope)
summary(lm4)
anova(lm4)

windows()
visreg(lm4, xlab="Pre-Sandy (2010) Vegetation Cover (%)",
ylab="Rate of Vegetation Change (%/yr)",
ylim=c(1,2.5), line.par=c(col="black"))
points(Cov10_Slope$Pre_Cov, Cov10_Slope$Slope, cex=1,pch=16,
col="blue")
legend("topleft", lty=c(NA,1), lwd=c(NA,5),cex=1, pch=c(16,NA),
col=c("blue","grey80"), c("OW","95% CI"))
text(Cov10_Slope$Pre_Cov, Cov10_Slope$Slope, Cov10_Slope$OW, cex=0.6,
pos=4, col="black")
text(locator(1), "Change_Veg = 0.012(Pre_Sandy_Cov) + 1.134, R2 = 0.5082")

### Regressions by OW: Year vs Cover ###
Cov_Yr <- read.csv("Cov_Yr.csv", header=TRUE)
head(Cov_Yr)
lm_o1 <- lm(Cov_Yr$X1~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o1)
anova(lm_o1)
lm_o2 <- lm(Cov_Yr$X2~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o2)
anova(lm_o2)
lm_o3 <- lm(Cov_Yr$X3~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o3)
anova(lm_o3)
lm_o4 <- lm(Cov_Yr$X4~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o4)
anova(lm_o4)
lm_o5 <- lm(Cov_Yr$X5~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o5)
anova(lm_o5)
lm_o6 <- lm(Cov_Yr$X6~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o6)
anova(lm_o6)
lm_o7 <- lm(Cov_Yr$X7~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o7)
anova(lm_o7)
lm_o8 <- lm(Cov_Yr$X8~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o8)
anova(lm_o8)
lm_o9 <- lm(Cov_Yr$X9~Cov_Yr$Year, data=Cov_Yr)
summary(lm_o9)
anova(lm_o9)
Plot Deer vs NDVI

```r
windows()
Deer_NDVI <- read.csv("Deer_NDVI_forR.csv", header=TRUE)
# Deer Density is deer/ha
head(Deer_NDVI)
Year <- as.factor(Deer_NDVI$Year)
DeerDens <- Deer_NDVI$DeerDens
NDVI <- Deer_NDVI$NDVI

lm <- lm(DeerDens~Year+NDVI+Year*NDVI)
summary(lm)
anova(lm)

lm2 <- lm(DeerDens~NDVI)
summary(lm2)
anova(lm2)

x2016 <- Deer_NDVI[Deer_NDVI$Year=="2016",]

windows()
visreg(lm2, ylim=c(0,120), xlab="NDVI", ylab="Density of Deer Use (deer ha\-1)", line.par=c(col="black"))
points(NDVI, DeerDens, cex=1,pch=16,col="blue")
points(x2016$NDVI, x2016$DeerDens, cex=1,pch=16,col="red")
legend("topleft",lty=c(NA,NA,1),lwd=c(NA,NA,5),cex=1,pch=c(16,16,NA),
  col=c("blue","red","grey80"), c("2015", "2016","95% CI"))
text(locator(1), "Dens_Deer = 152.3(NDVI) - 51.8, R2 = 0.225")
```
text(Deer_NDVI_2$NDVI, Deer_NDVI_2$DeerDens, Deer_NDVI_2$OW, cex=0.6, pos=4, col="black")

#### Deer Rec Rates ####
TC_initC <- read.csv("rates.csv", header=TRUE)
# seq = year (0, 3, 4), tcov = ln(%cov), initc = ln(%cov year -2)
head(TC_initC)

glm <- glm(tcov ~ initc+as.factor(ow)+seq+as.factor(ow)*seq, data=TC_initC)
summary(glm)
anova(glm)

Rates <- read.csv("rates2.csv", header=TRUE)
# roc = rate of change (slope), expsl = exponentiated slope,
# avgd = average dens of deer use (2015+2016)/2,
# sodu = sum of deer use (2015+2016), initc = ln(%cov year -2)
head(Rates)

glm2 <- glm(roc ~ avdg+exp(initc), data=Rates)
summary(glm2)
anova(glm2)

#### Classification vs Plot Total Cover ####
Class_Plot <- read.csv("Class_Plot.csv", header=TRUE)

lm.cp <- lm(Plot~Class, data=Class_Plot)
summary(lm.cp)
anova(lm.cp)

x2016 <- Class_Plot[Class_Plot$Year=="2016",]

windows()
plot(Class_Plot$Class, Class_Plot$Plot, xlab="Avg Cover from Classification",
  ylab="Avg Cover from IDW (Plot)", pch=16, cex=1, col="blue",
  ylim=c(0,60), xlim=c(0,60))
abline(lm.cp, lty=1, lwd=2, col="black")
points(x2016$Class, x2016$Plot, cex=1,pch=16,col="red")
legend("topright", cex=1, pch=16, col=c("blue","red"), c("2015", "2016"))
text(locator(1), "Dens_Deer = 146.14(NDVI) - 44.25, R2 = 0.1032")
text(Deer_NDVI$NDVI, Deer_NDVI$DeerDens, Deer_NDVI$OW, cex=0.6, pos=4, col="black")

######################################################################## END ########################################################################
Appendix I. Image classifications show changes in vegetation cover from grass and shrubs in 2010 to grass in 2016 as overwash fans recover from Hurricane Sandy.

**Overwash fan #2**

**Overwash fan #3**

Author Contributions
CRK helped design the study, aided in development of the digital methodology, collected the digital point sampling data, collected some of the traditional point sampling data, analyzed the data for the manuscript and wrote most of the manuscript. JR helped design the study, developed the traditional point sampling methods, collected the traditional point sampling data, and provided feedback to the analyses and final manuscript. LR helped design the study and provided feedback for the analyses and final manuscript. HBU helped design the study, aided in development of the digital methodology, collected the digital point sampling data, aided in analysis, and wrote parts of the manuscript.

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Keywords
Coastal vegetation; digital image analysis; digital point sampling; disturbance; species frequency; rapid ecological assessment; vegetation survey

Introduction
After a broad-scale disturbance like fire, drought or hurricane, post-disturbance ecosystem assessments are essential to quantify impacts and resilience (Sayre et al. 1999). Assessment usually dictates implementation of treatments and allocation of resources, which each aim to increase recovery potential (Miller et al. 2015). Rapid assessment methods are often used to complement or extend long-term studies (Medeiros and Torezn 2012) or to refine landscape-scale assessments from aerial imagery, and they frequently provide reliable information about the status of the disturbed area while requiring a small investment in time and money (Fennessy et al. 2004). Rapid assessment methods are meant to be easy to use, reproducible, and should reduce the cost and time spent assessing resource status (Medeiros and Torezn 2012). Here, we focus on the application and validation of a rapid ecological assessment on coastal vegetation recovery after storm surge inundation.

Many vegetation assessment methods measure species frequency as an alternative to percent cover since it is faster, easier, and induces less individual bias (Elzinga et al. 1998). We used species frequency as a proxy for cover and compared results obtained using two field methods: traditional point intercept and digital point intercept. Traditional point intercept (TPI) methods for assessing species frequency typically use a quadrat containing equally-spaced point
locations. At point locations, vegetation presence is assessed visually. TPI is easy to implement and requires little training, but species frequency may be overestimated under windy sampling conditions. Movement of vegetation within the quadrat can make the natural orientation of the vegetation difficult to estimate. This is referred to as wind bias throughout this paper (Cagney et al. 2011). In coastal environments, wind bias may be considerable owing to the nearly constant presence of onshore and offshore breezes. Digital point intercept (DPI) methods use a mounted camera to take nadir photographs of vegetation plots, which are analyzed using image software (Booth et al. 2005). DPI is less susceptible to wind bias due to camera shutter control (Booth et al. 2006), and allows for species frequency quantification using GIS-based tools (Gobbett and Zerger 2014).

Long-term, plot-based studies often require permanent plot markers, which pose several problems for our study. Marking systematic vegetation plots using a 100-m, reel tape measure is difficult in windy, coastal environments and accuracy is compromised under most field conditions. Permanence of plot markers is generally difficult to maintain in coastal systems due to constant sand movement and disturbance by visitors. In addition, protected natural areas often restrict the use of obtrusive permanent markers (Landres et al. 2008). We combined DPI with sub-meter Differential Global Position System (DGPS) navigation to eliminate the need for permanent plot markers and to facilitate rapid movement between plot locations. Because plot locations are georeferenced, both temporal and spatial analyses of vegetation recovery are possible (Legendre and Legendre 1998).

The purpose of this study was to adapt an existing method for rapidly assessing rangeland vegetation to recovering coastal vegetation in a vulnerable landscape, while minimizing the research footprint on the ecosystem and maximizing time spent in the field collecting data. Our objectives were to (1) compare vegetation species frequency estimates using traditional and digital point intercept methods to support the comparable use of the rapid assessment method, and (2) test sub-meter DGPS navigation as an alternative to conventional plot layout procedures to reduce ecosystem impacts and field time.

Study Area
Fire Island is a barrier island located off the south shore of Long Island, New York, USA, (40.6476° N, 73.1459° W; Figure 1). Fire Island National Seashore consists of a mosaic of natural areas, managed by the US National Park Service, and 17 private residential communities. Within the National Seashore exists a rare Ilex opaca maritime forest and the only federally-designated wilderness area in New York State, the Otis Pike Fire Island High Dune Wilderness (OPWA). Fire Island National Seashore manages the OPWA according to the policies implemented by the federal Wilderness Act of 1964, which aims to reduce human disturbance.

Figure 1. Fire Island National Seashore is located off the southern coast of Long Island, New York, USA. Otis Pike Fire Island High Dune Wilderness Area is located within Fire Island National Seashore.
(i.e., vehicle transportation, field equipment, vegetation trampling, etc.).

Barrier island physiognomy is characterized by strong ocean to bay stratification of vegetation (Ehrenfeld 1990), grading from the presence of a primary dune on the oceanside beach to a flat saltmarsh along the bayside. The beach is highly vulnerable to inundation from coastal storm surge and sea-level rise (Pendleton et al. 2004). Before Superstorm Sandy made landfall in October 2012, the primary dune system in the OPWA was 4-15 m high and relatively intact (Hapke et al. 2010). Superstorm Sandy produced an unprecedented storm surge that obliterated sections of the primary dune at >10 locations and created two breaches of the island (Blake et al. 2013, Hapke et al. 2013). Sand was carried inland by the storm surge, which buried large areas of existing vegetation (Hapke et al. 2013). Plant species such as American beachgrass (Ammophila breviligulata) and beach pea (Lathyrus japonicus) initiate primary succession in these overwashes (Ehrenfeld 1990, Maun 2009).

Methods

Using ArcGIS, we delineated boundaries of eight overwashes from aerial imagery. Posts were randomly placed within each overwash to mark permanent vegetation plots. Fifty-two permanent plots were surveyed between 22-24 Sep 2015 using TPI and between 11-14 Sep 2015 using DPI. We established additional unmarked plots in a grid (i.e., array) in each overwash to (1) increase sample size, (2) estimate time needed to navigate to plots using a handheld GPS, and (3) avoid placing additional permanent markers in the overwashes. We used ArcGIS (version 10.2, ESRI, Redlands, CA) to overlay a 10x10-m grid within each overwash boundary. Optimal grid size was determined from preliminary sampling of inter-patch distances measured from aerial imagery and field sampling of emerging plant density and cover (Legendre and Legendre 1998, page 709). The 527 array plots were surveyed using only DPI from 11-14 Sep 2015. During surveys, navigation was suspended at horizontal accuracies >60 cm. Logistics of the two methods were compared using measured field sampling and data processing times.

Traditional Point Intercept

All permanent plots were surveyed using TPI (n=52). A 1-m² quadrat was oriented along the cardinal directions with the plot post in the southeast corner. The quadrat contained 50 unevenly-spaced points with an approximately 11-cm north-south interval and 25-cm east-west interval (Figure 2). At each point, a pin flag was lowered vertically to the ground and species presence was recorded if vegetation contacted the pin. The

Figure 2. Overwash vegetation plot #861 was photographed on 27 Jul 2015. The pin flag located in the top-left (southeast) corner was located using sub-meter navigation and the frame was oriented north using a mounted compass.
sampling protocol was executed successfully with two people: a vegetation identifier and a recorder. Species presence was later entered into a digital database, verified, and used to estimate percent species frequency for each plot. Percent species frequency was calculated by dividing the total number of contacts of each species by the total number of points and multiplying by 100. Field time included locating permanent plot markers, properly aligning the quadrat, removing vegetation from beneath the quadrat frame, collecting species contacts, and securing all fenced plots before departure. Processing time included transferring species contacts from data sheets to a digital database and verifying each entry.

Digital Point Intercept
All permanent plots (n=52) and additional array plots (n=527) were surveyed using DPI. A digital camera was mounted 2-m above the ground on an adjustable aluminum frame (Booth et al. 2004) with a 1-m² base. Survey date, plot location and number were written on a small dry-erase board that was placed within the photo boundary (Figure 2). A pin flag was inserted into the ground at the plot location and, with the aid of a mounted compass, the camera frame was oriented due north with the pin flag in the southeast corner. A twin-sized bed sheet attached to two 122-cm wooden dowels was used to shade the plot from direct sunlight, which aided in image processing by reducing glare and shadows (Cox and Booth 2008). Camera shutter speed was set to 1/2000th of a second to minimize blurring of photographs from windblown vegetation, and the shutter was released remotely using a Bluetooth connection to the camera. The sampling protocol was executed successfully with two people: a navigator and a camera frame carrier. Post-processing plot data required three main steps: (1) label each image with survey date and plot number, (2) crop the image to within the quadrat boundary, and (3) analyze the image for species frequencies. A 10-cm grid of 100 points was created using the Generate Regular Points in Polygons tool from Geospatial Modelling Environment (version 0.7.3.0, Spatial Ecology LLC, Queensland, Australia). Since plots were small (1 m²), we placed the grid of points with a 5-cm buffer inside the quadrat (Figure 2) to minimize edge effects (Elzinga et al. 1998). The 100-grid-point file was used as input to PointSampler in ArcGIS, which sequentially prompted the user to identify presence at each point location using user-defined categories (i.e., grass, sand, etc.). PointSampler created a tabulated file containing the identified presence category for each point, which was used in percent species frequency estimation as above. Field time for DPI included navigating to all overwash plots (n=579), properly aligning the quadrat, removing vegetation from beneath the quadrat frame, and taking a photograph. Processing time included renaming all photographs, clipping images to within the quadrat boundary, defining species contacts using PointSampler, and extracting the resultant table to a digital database for analysis.

Results
In permanent plots, we identified 11 vegetation species among overwashes. In array plots, we identified an additional 7 species present. Many species were present in multiple overwashes, but several were only observed in unmarked array plots (Table 1).

A.breviligulata was recorded in 50 permanent plots using TPI and 48 permanent plots using DPI. Two species were recorded in five plots (Toxicodendron radicans, Lathyrus japonicus), two were recorded in two plots (Prunus maritima, Smilax spp.), and three were recorded in only one plot (Morella pensylvanica, Rosa multiflora, Vaccinium corymbosum, Hudsonia tomentosa). Due to their small sample sizes, and minimal within-plot coverage, all species besides A. breviligulata were removed from further analyses.
Table 1. Vegetation surveys were conducted in overwashes in the Otis Pike Fire Island High Dune Wilderness Area. Perm. Plots are permanent plots (n=52). Array Plots are those with no plot marker (n=527).

We required 14 field hours to survey 52 permanent plots in eight overwashes using TPI (Table 2). Processing of TPI field data required six hours. TPI required 39.2 person-minutes per plot. We required 16 field hours to survey 579 plots in eight overwashes (i.e., 52 permanent plots, 527 array plots) using DPI. Processing of DPI photos required 12.5 hours. DPI required 4.6 (SE: 0.10) person-minutes per plot.

<table>
<thead>
<tr>
<th>Method</th>
<th># Plots</th>
<th>Total Time (min)</th>
<th>Time Per Plot (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Field</td>
<td>Processing</td>
</tr>
<tr>
<td>TPI</td>
<td>52</td>
<td>1,680&lt;sup&gt;a&lt;/sup&gt;</td>
<td>360&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>DPI</td>
<td>579</td>
<td>1,920&lt;sup&gt;c&lt;/sup&gt;</td>
<td>750&lt;sup&gt;d&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> 14 hr * 60 min/hr * 2 persons = 1,680 person-minutes
<sup>b</sup> 6 hr * 60 min/hr * 1 person = 360 person-minutes
<sup>c</sup> 16 hr * 60 min/hr * 2 persons = 1,920 person-minutes
<sup>d</sup> 12.5 hr * 60 min/hr * 1 person = 750 person-minutes

Table 2. Time allocation needed to complete surveys using traditional point intercept (TPI) and digital point intercept (DPI) vegetation assessment methods. TPI required significantly more time per plot (39.2 minutes) than DPI (4.6 minutes), severely limiting sample size with time available for field work.
TPI methods resulted in higher percent species frequency estimations of beach grass in permanent plots at nearly all values of cover compared to DPI methods (Figure 3). The non-linear least-squares curve shows a peak of 91.4%, which indicates an asymptote. The alpha value, -0.010, determines the stretch or compression of the logistic regression and was calculated after minimizing the sum of squared deviations of the residuals. The DPI value, or the curve inflection point, was 16.73.

Figure 3. Regression of A. breviligulata (AMBR) frequency estimated from traditional point intercept methods on frequency estimated from digital point intercept methods. The grey line indicates a 1:1 relationship. A non-linear least-squares curve-fit is shown (Zar 2010).

Discussion
We documented an order of magnitude difference in time required to collect and process vegetation species frequency between DPI and TPI. Consequently, we were able to incorporate substantially more spatial replicates and achieve greater study area coverage using DPI. Like Booth et al. (2005) and Cagney et al. (2011), we also found image analysis requires significantly less processing time than traditional field methods. We attribute some of the recorded discrepancy between frequency measured using TPI and DPI to windblown vegetation and the difficulty of accurately counting vegetation contacts using TPI methods. For example, at ≥40% DPI coverage, TPI estimates approached 90%. Wind bias was ameliorated in DPI estimates due to the use of camera shutter priority in the field, making DPI particularly effective in inherently windy coastal environments (Booth et al. 2004).

DPI methods are accurate for single-layer vegetation as some plants near the ground are obscured from view in the nadir image. DPI can be reliably implemented in locations with one layer of vegetation cover (Booth et al. 2005, Cagney et al. 2011). The vegetation assessed in this study was predominantly present in one layer due to prostrate growth forms of many coastal plants (Stuckey and Gould 2000) and the sparsely populated nature of recovering overwashes. In a few instances, particularly along the edges of overwashed areas, grasses, forbs and shrubs
overlapped in some plots, creating multi-layered vegetation. In these cases, any obscured vegetation was identified in the field and recorded as present in the plot.

Distinct advantages to using DPI methods include increased sample size due to less time invested per plot, and the ability to reanalyze original plot images from digital archives (Chen et al. 2010). Vegetation plot photos can be used for vegetation cover assessment by using image classification or other processing methods. VegMeasure classified images into user-defined vegetation cover classes (Johnson et al. 2009), but is no longer available for use (D. E. Johnson, pers. comm.). We chose PointSampler because it allows for many (<26) user-identified vegetation cover categories and user-identified sample points. PointSampler is an ArcGIS add-in compatible with multiple versions of ArcMap, and has detailed instructions for its use (Gobbett and Zerger 2014). Methods of ground layer assessment using aerial imagery are progressing, but spatial resolution is often too coarse to identify vegetation community composition and individual species on a <100-m spatial scale (Xie et al. 2008). Other tools exist to assess canopy cover using photos taken by a smart phone (Tichy 2016), but few are available to assess ground layer vegetation.

TP-I methods are useful for temporal analyses of relative vegetation cover and estimates may be easily corrected for wind bias by using an equation derived from another method, such as DPI (Figure 3). DPI methods require less post-processing for accuracy, save time in the field, allow for larger sample sizes, reduce wind bias, minimize edge effects, and allow for future and comparative analyses of archived plot images. DPI methods are ideal when a threshold of vegetation cover dictates management action, especially when limited time is available for assessment. We recommend the use of DPI methods when the research question (1) involves assessment of ground vegetation in mostly a single layer, (2) requires vegetation cover estimates and not necessarily species dominance, and/or (3) allows for sub-meter accuracy in plot navigation. DPI use may be limited in areas with dense understory due to the size of the camera mount, but it is easily dismantled for transportation purposes. Sub-meter navigation was sufficient in this study, but finer-scale research questions may require permanent plot markers. Use of a high-resolution digital camera combined with sub-meter DGPS navigation saves substantial time committed to data collection and analysis, and reduces the research footprint in protected natural areas. An extension of DPI using unmanned aerial vehicles for locations with accessibility concerns is ripe for investigation.

References


Johnson, M.D., Clark, P., Louhaichi, M., Worz, A., Ndzieze, S.K., & Johnson, D.E. 2009. VegMeasure 2: a software package that facilitates measurement of foliar cover, litter and bare ground on rangelands. Department of Rangeland Resources, Oregon State University, Corvallis, OR, USA.


VITA

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Education
Doctor of Philosophy in Fish & Wildlife Biology & Management  GPA: 4.0/4.0
SUNY ESF, May 2014 – May 2018
Master of Science in Conservation Biology  GPA: 4.0/4.0
SUNY ESF, August 2012 – May 2014
Title: Effects of landscape composition and structure on abundance and distribution of urban white-tailed deer
Bachelor of Science in General Biology, Minor in Business  GPA: 3.8/4.0
The Pennsylvania State University, Berks Campus, August 2008 – May 2012

Work Experience
Post-Doctoral Associate – SUNY ESF and NYS Parks, Recreation & Historic Preservation
April 2018 – Present: supervised field technician, data management, meta-analysis
Lead Graduate Ambassador – SUNY ESF Office of Instruction and Graduate Studies
August 2017 – May 2018: managed student databases, facilitated graduate campus tours
Directorate Fellow – United States Fish & Wildlife Service, New York Field Office
May – August 2017: completed impact analysis for species of special concern
Invited Ecologist – Hudson Bay Project @ Wapusk National Park, Manitoba, Canada
July 2017: consulted for research biologists in survey methods and impact analysis
Mid-Atlantic Coastal Storms Graduate Research Fellow – Virginia Sea Grant & NOAA
July 2016 – July 2017: conducted field research, created outreach activities and products
Research Assistant – SUNY Research Foundation & Fire Island National Seashore
July 2014 – July 2016: designed field research, wrote research proposals, trained interns
Teaching Assistant – SUNY ESF Department of Environmental & Forest Biology
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Intern – Ned Smith Center for Nature and Art, Pine Grove, PA
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Berks International Conservation Intern – Penn State Berks, Presqu’ile Provincial Park (Ontario)
August 2010 – July 2011: captured and banded shorebirds, recorded chick feedings

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Field Volunteer and Undergraduate Mentor – Penn State Berks  06/2013 – Present
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Scholarly Communications Librarian Search Committee – SUNY ESF  09/2017 – 12/2017
Instructor, Coastal & Barrier Island Ecology Seminar – SUNY ESF  01/2017 – 05/2017
Vice President for Research Search Committee – SUNY ESF  05/2016 – 12/2016
Field Volunteer – Fire Island National Seashore  05/2014 – 05/2016
Undergraduate Mentor – SUNY ESF  09/2013 – 05/2014
Resident Assistant – Penn State Berks  08/2011 – 05/2012
Blue & White Society Executive Member – Penn State Berks  01/2009 – 05/2012
Lion Ambassador (Campus Leader) – Penn State Berks  06/2009 – 05/2012
Campus Activities Board Executive Member – Penn State Berks  05/2010 – 05/2012
Orientation Leader Team Captain – Penn State Berks  04/2009 – 08/2011
**Interpersonal, Written, & Oral Communication**

**Academic Audiences**
- **Peer-Reviewed Publications:**
  - 4 Journal Articles *in preparation*
  - 2 Journal Articles *in review*
  - 1 Conference Proceedings
  - 1 Book Chapter
- **Campus Presentations:**
  - 2 Inter-departmental Research Reviews
- **Research Posters:**
  - 1 Institutional, 3 Conference
- **Oral Conference Presentations:**
  - 5 International, 3 Regional, 1 Local
- **Guest Lectures:**
  - 5 Undergraduate Lectures

**Agency Partners**
- **Natural Resource Reports:**
  - 5 *in preparation*
- **Resource Briefs:**
  - 2 completed, 1 *in preparation*
- **Oral Presentations:**
  - 1 National Committee Presentation

**Public Outreach**
- **Materials Created:**
  - 1 Interpretive Program
  - 1 Plant Identification Guide
- **Presentations:**
  - 1 TED-style talk

**Public & Political Meetings**
- **Presentations:**
  - 2 Syracuse-Onondaga County Deer Task Force
  - 1 Tomorrow’s Neighborhoods Today (Region 5)

**Honors & Awards**

**Community Service Awards**
- *Penn State Walker Award:* awarded for integrity and services to the College 04/2012
- *Campus Life Award:* awarded by Penn State Berks Staff for services to students 04/2010

**Society Membership**
- New York Academy of Sciences 2015 – Present
- Phi Kappa Phi Honor Society 2012–2014

**Competitive Research & Travel Awards**
- SUNY ESF Alumni Association Grant 11/2017
- Virginia Sea Grant Mid-Atlantic Coastal Storms Graduate Research Fellowship 07/2016
- American Wildlife Conservation Foundation Research Grant 03/2015

**Additional Skills**

**Field**
- Vegetation Sampling: quadrat, transect, ocular estimation, digital point intercept, species ID
- Animal Monitoring: GPS/VHF radio-collar triangulation, trail cameras (inc. antler ID), spatial capture-recapture, distance sampling, passerine and meso-mammal ID
- Animal Handling: mist net, Clover trap, trapping, banding, radio-collaring
- Other: situational awareness, use of 4WD vehicles, behavior surveys

**Technical**
- Programming: R (vegan, Unmarked, R2WinBUGS), C++, Python, SAS
- Spatial Analysis: ArcGIS, FragSTATS, image classification, metadata compilation