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PLANT COMMUNITIES IN DYNAMIC SYSTEMS: HOW DISTURBANCE INFLUENCES COASTAL PLANT COMMUNITY STRUCTURE AND FUNCTION

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PLANT COMMUNITIES IN DYNAMIC SYSTEMS: HOW DISTURBANCE INFLUENCES COASTAL PLANT COMMUNITY STRUCTURE AND FUNCTION

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

by

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Abstract

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By Joseph K. Brown

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Advisor: Julie C. Zinnert, PhD
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Barrier islands are critical landforms that protect mainland coasts from major disturbances. As dynamic systems, barrier islands have ecological mechanisms that aid in sustainable recovery after coastal disturbances. However, as the climate continues to change it is difficult to predict how barrier island function will respond to global change drivers that accompany predicted climate change. Disturbance frequency and nutrient enrichment in coastal regions are drivers of plant community change that are increasing with climate change. Plant communities on barrier islands are not only tightly connected to barrier island function but are also some of the first communities affected by environmental change, making them a critical piece in understanding how current drivers of global change will impact the future of barrier islands. The objective of my dissertation was to observe and manipulate coastal plant communities at local and large-scales to inform community-level species and trait-based alterations caused by differences in response to disturbance and nutrient enrichment. Results presented here indicate that barrier island trait-based communities can vary over local spatial scales depending on overarching topography and historic disturbance response. However, there is scale dependency in relationships between dominant stability domains, barrier island elevation, and dune plant community structure. I show that at large spatial scales, climatic differences among islands contributes more to dune community richness and composition than elevation differences, but at local scales, impacts of elevation, island stability, and local ecological processes on dune plant communities comes into focus. I also show that nutrient enrichment expected to accompany climate change significantly alters both trait-based and species community composition. I show that species composition, trait-based composition, and lifeform abundance all produce conflicting results in response to nutrient additions, but these complexities can be clarified with detailed trait and species analyses when used cooperatively. These results highlight the importance of considering multiple aspects of plant communities in coastal systems if we are to use them to decipher how environmental change will impact large scale ecological processes.

Introduction

Barrier islands have emerged as systems highly vulnerable to disturbances associated with future climate change (Mcfalls et al. 2010, Feagin et al. 2015, Stallins and Corenblit 2018, Zinnert et al. 2019). We are still learning about the many ways disturbances produce feedbacks with barrier island topography, plant community composition, and ecosystem functioning. The dynamic nature of barrier island systems allows for rapid response over short temporal scales depending on plant community composition and function as well as the intensity of press and pulse disturbance events experienced by the system (Stallins 2005, Zinnert et al. 2017). Press disturbances, like nutrient enrichment and sea-level rise, are those that occur over longer time scales and result in gradual change of ecological systems (Bender et al. 1984). Pulse disturbance events, like hurricanes or nor'easters, occur at high intensity and can cause dramatic changes to ecological systems over short time scales (Bender et al. 1984).

Physical processes responsible for shaping barrier islands can influence plant distribution by altering environmental filters and has dominated the literature (Oosting and Billings 1942, Ehrenfeld 1990, Wolner et al. 2013, Durán Vinent and Moore 2014, Fenster et al. 2016, Hsu and Stallins 2020, Stallins et al. 2020). However, recent insights highlight that understanding interactions among plant communities is critical for predicting barrier island response after different disturbance types and can aid in demystifying cross-scale complexities (Young et al. 2011, Brantley et al. 2014, Zinnert et al. 2017, 2019). Further understanding of the interplay between biotic interactions and abiotic conditions is needed to better understand the multiple ways community patterns are affected by environmental factors (Kraft et al. 2015), especially in coastal systems where nature-based solutions are promoted to mitigate climate change.

Considering the important roles barrier islands play in protecting mainland coastal systems from disturbance (Feagin et al. 2015), it is critical that we implement observation and manipulation studies of species and trait-based plant communities to clarify mechanisms of complex biotic/abiotic interactions that may influence barrier island disturbance response. For example, nutrient deposition is an abiotic condition that significantly contributes to biotic interactions as well as community structure and function and is increasing with climate change and anthropogenic influence, especially in coastal systems (Vitousek et al. 1997, Fay et al. 2015, Flores-Moreno et al. 2016, Koerner et al. 2016, Sinha et al. 2017, Firn et al. 2019). Seitzinger et al. (2002) suggest that rates of nutrient inputs are expected to significantly increase in coastal systems by 2050, making it critical to better understand the effects these additions have on plant trait and species community composition and ecosystem functioning on barrier islands.

It is also important that we examine the individualism of barrier island systems and how they form plant communities differently across spatial scales (Stallins 2005, Zinnert et al. 2017, Hsu and Stallins 2020, Stallins et al. 2020). Previous research has highlighted how environmental factors influence species populations in different barrier island habitats (Oosting and Billings 1942, Silander and Antonovics 1982, Carboni et al. 2010, Young et al. 2011, Conti et al. 2017). However, knowledge gaps still remain when considering important community-level plant functional trait patterns that inform mechanisms of habitat maintenance and new community emergence given differences in disturbance responses of coastal systems (De Battisti 2021). Such knowledge gaps are especially obvious across spatial scales, which is a crucial next step in the study of coastal ecology, as we begin to question interactions between barrier island stability and plant community formation in the face of climate change (Zinnert et al. 2017, Hsu and Stallins 2020).

My overall objective was to use observation and manipulation experiments to investigate how species and trait defined plant communities can inform plant community dissimilarity across scales and how disturbances associated with climate change affect these communities. My goals were carried out in four parts: 1) Synthesize large-scale dune plant community composition and structure to identify the influence of barrier island stability across spatial scales, 2) Determine differences in species and trait-based community compositions and ecosystem function existing at local scales among barrier islands with contrasting topography and disturbance responses, 3) Manipulate nutrient deposition to investigate impacts on ecosystem function, community structure, composition, and organization, 4) Quantify nutrient enrichment impacts on trait-based community composition and diversity.

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Chapter 1: Scale dependency of barrier island stability and elevation as drivers of dune plant community composition and structure

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Abstract

Although previous research has identified dune plant communities as important for assessing coastal vulnerability to disturbance, most studies focused on community-level dynamics are often conducted at local-scales. Connections between barrier island stability domains and dune plant community structure are not well-defined at large spatial extents and a knowledge gap remains in identifying the scale dependency of barrier island disturbance response and elevation as drivers of dune plant community difference. Here, we used census and elevation data from five barrier islands along the mid-Atlantic and Gulf coasts (Hog Island, Metompkin Island, South Core, Sapelo Island, and St. George Island) that differ in dominant stability domains to synthesize determinants of plant community dissimilarity among sites. We found that barrier island stability domain classification was not consistently linked to elevation across sites, suggesting that disturbance-resisting and disturbance-reinforcing stability domains can be dominant at high or low elevations. Based on our vegetation analysis we found, at large spatial extents, species richness increased along a decreasing latitudinal gradient, rather than in line with *a priori* stability domains. However, at smaller spatial scales, the influence of dominant stability domains and elevation comes into focus, whereby disturbance-resisting islands are more species rich in the north and have different dune plant community composition in the south compared to disturbance-reinforcing islands. Based on our findings, we conclude that variability of dune plant community structure on barrier islands is dependent on both large-scale climatic patterns that change gradually over a latitudinal gradient and local-scale elevation and ecological processes that influence plant distributions.

Introduction

Coastal ecosystems across the globe are impacted by the changing climate. Increasing rates of sea-level rise with expected increases in frequency and intensity of coastal storms threaten some of the most populated coastlines in the world (Scavia et al. 2002, Mann and Emanuel 2006, Sallenger et al. 2012, Houser 2018). Coastal sand dunes function as a critical geomorphologic formation in coastal systems by dissipating disturbance from wind and waves during high intensity storms (Cowles 1899, Leatherman 1979, Fucella and Dolan 1996, Wolner et al. 2013, Sigren et al. 2014, Feagin et al. 2015, Houser et al. 2015). Dune building dynamics, including initial construction and recovery from disturbance, are often highlighted as relying on feedbacks between physiological/functional-trait responses of a few key species and dominant abiotic factors (i.e., overwash frequency, sediment supply, and aeolian transport) that vary across spatio-temporal scales (Stallins 2003, de Vries et al. 2012, Duran and Moore 2013, Harris et al. 2017, Brown et al. 2018, Hacker et al. 2019, Reijers et al. 2020, Charbonneau et al. 2021). However, dune plant communities as a whole have been noted to function as responsive parts of biogeomophic systems, rather than as collections of a few influential species (Stallins 2003, Stallins and Parker 2003, Acosta et al. 2007, 2009, Gornish and Miller 2010, Miller et al. 2010, Brown and Zinnert 2020).

Plant community composition and diversity of coastal dunes have been identified as critical pieces in assessing coastal dune vulnerability to storm disturbance (García-Mora et al. 2000). Furthermore, previous research has used plant community composition and diversity to disentangle how coastal habitats function as well as how they respond to, and recover from, disturbance events (Acosta et al. 2009, Gornish and Miller 2010, 2013, Young et al. 2011, Brantley et al. 2014, Miller 2015, Brown and Zinnert 2020). Plant community metrics have also been tied to understanding complexities of various biogeomorphic feedbacks in coastal systems that result in differing geographic topography (Stallins 2003, 2006). Such previous work has informed more recent perspectives emphasizing the importance in linking interactions between plant communities and the physical environment to better understand mechanisms driving differences in topographic complexity and stability of coastal systems, specifically barrier islands (Zinnert et al. 2017, Stallins and Corenblit 2018).

Nearly 39% of the global barrier island distribution exists along coastlines in North America (5784 km) (Stutz and Pilkey 2001). Within North America, over 60% of barrier islands are distributed along the Atlantic and Gulf coasts, making them the most heavily barrier island dominated coastlines in the world (Stutz and Pilkey 2001). Due to increased rates of sea-level rise and predicted increase in coastal storms, it is important that we better understand how these vulnerable systems respond to imminent disturbances (Scavia et al. 2002, Schuerch et al. 2018, Nienhuis and Lorenzo-Trueba 2019). Seminal works by Stallins (2005, 2006) aimed to unify ecological and geomorphic patterns to elicit mechanisms of resilience and resistance in barrier island disturbance response. These works applied a refined stability domain framework to concepts originally introduced by Godfrey and Godfrey (1976), linking certain species to specific disturbance response mechanisms (Stallins 2005).

Stability domains on barrier islands are disturbance dependent and have been described as disturbance-reinforcing and disturbance-resisting (Stallins 2005, Zinnert et al. 2017, Stallins and Corenblit 2018). A disturbance-reinforcing stability domain is hypothesized as containing higher abundance of stabilizing species that do not build large dunes, but rather produce dune hummocks and/or stabilize sediment at low elevations that maintain low topography (Stallins 2005, Monge and Stallins 2016, Zinnert et al. 2017). As a result, the probability of overwash events increases and resistance to disturbance decreases (Zinnert et al. 2017). Conversely, a disturbance-resisting stability domain contains higher abundance of species promoting the development of dune-swale complexes, which produces topographic roughness and are less vulnerable to disturbance impacts, but can be more prone to erosional processes (Stallins 2005, Monge and Stallins 2016, Zinnert et al. 2017, 2019, Stallins et al. 2020).

Barrier islands serve as model systems for introducing similar stability-domain hypotheses and as sites for quantifying how differences in elevation and topographic complexity impact island habitats, dune morphology, and disturbance response (Stallins 2003, Young et al. 2011, Vinent and Moore 2015, Goldstein and Moore 2016, Monge and Stallins 2016, Brown and Zinnert 2020). Recently, empirical evidence has suggested that barrier islands populate regions within a multidimensional stability domain space that demarcates similarities in elevation and topographic roughness among different barrier islands at varying scales (Hsu and Stallins 2020, Stallins et al. 2020). For example, at large spatial extents, Virginia barrier islands have been grouped as low-resilience and low-resistance compared to other barrier island systems along the mid- and southern-Atlantic coast (Hsu and Stallins 2020). However, at a more localized scale, the Virginia barrier island system separates into groups of low, flat topography (disturbance-reinforcing) islands and erosion remnant islands, which provides evidence of a disturbance-resisting stability domain (Stallins et al. 2020).

Despite such progress in understanding elevational and topographic determinants of barrier island stability domains, there is a still a considerable knowledge gap regarding connections between dune plant communities and barrier island stability across spatial scales (Zinnert et al. 2017). It is particularly important to investigate stability domains across spatial scales because barrier islands have a propensity to exist in multiple stability domain states depending on localized physical conditions and differential plant community presence (Hayden et al. 1991, 1995, Stallins 2005, Guofan et al. 2006, Young et al. 2007, Zinnert et al. 2016). Stability domains are not instantaneously expressed, but rather propagate and shift to create a more complex mosaic of dynamical states (Van De Leemput et al. 2015). Plant communities are important for understanding local scale stability at the sub-island level. For example, Zinnert et al. (2019) and Woods et al. (2019) show connections between dune elevation and shrub expansion on the Virginia barrier islands, which increased local-scale island stability and response to sea-level rise. These shrub expansion processes can impact stability of entire islands, as well as sub-island sections (Zinnert et al. 2019).

In this study we synthesize elevation and dune vegetation data from five barrier islands along the Atlantic and Gulf coasts to 1) investigate large-scale and local-scale relationships between island elevation and *a priori* classifications of stability domains for each barrier island while highlighting the dune plant communities each island supports, 2) inform our understanding of how large-scale climatic patterns vs. local-scale physical processes impact dune plant communities, and 3) detail scale-dependency when classifying barrier island stability domains, especially when using common topographic and vegetation metrics cooperatively.

Methods

Island/Site Descriptions

Vegetation data from five different islands with low direct anthropogenic disturbance along the Atlantic and Gulf coasts were used. Island stability domain type was designated based on quantitative site characterizations from previous studies as well as elevation ranges (Table 1.1). The islands represent a range from mixed-energy microtidal islands dominated by wave energy to mixed-energy mesotidal islands influenced by tidal processes (Stallins 2003, Miller et al. 2010, Wolner et al. 2013, Brantley et al. 2014). Noted differences in accretion rates and landward migration also existed among islands (Miller et al. 2010, Deaton et al. 2017, Haluska 2017, Zinnert et al. 2019). Furthermore, islands varied in mean annual precipitation, temperature patterns, and rates of relative sea-level rise driven by regional differences in climate and geography (Table 1.2).

The northernmost islands included in this study were Metompkin (Lat. 37.74 N, Lon. 75.56 W) and Hog (Lat. 37.42 N, Lon. 75.686 W) Islands; part of the Virginia Coast Reserve Long-term Ecological Research site. Previous research has shown these islands recover from disturbance differently and exist in different states of topographic complexity (Wolner et al. 2013, Brantley et al. 2014, Stallins et al. 2020). Due to differences in topographic complexity and disturbance response, these islands also have substantial vegetation differences in both dune and swale plant communities (Brantley et al. 2014, Brown and Zinnert 2020).

Metompkin Island has a simple topography with low elevations (Wolner et al. 2013, Brantley et al. 2014, Stallins et al. 2020). Low elevation and modest topographic complexity allow for overwash events to occur on this island, even during low energy storms (Wolner et al. 2013, Brantley et al. 2014). Woody shrub expansion is negligible compared to other VCR barrier islands (Zinnert et al. 2016). Metompkin Island also lacks stability on the island scale and has retreated rapidly (~11 m yr^{-1}) in a counter-clockwise rotation, due to higher migration on the north compared to south end of the island (Wolner et al. 2013, Haluska 2017, Zinnert et al. 2019). The geomorphologic characteristics and processes that dominate on Metompkin represent aspects of low-relief on the northern half and disturbance-reinforcing stability domain on the southern end (Table 1.1) (Wolner et al. 2013, Zinnert et al. 2019, Hsu and Stallins 2020, Stallins et al. 2020). The combination of low, simple topography and rapid island migration results in dune and swale plant communities that are similar in plant functional trait composition with low vegetative productivity (Brown and Zinnert 2020).

Hog Island offers a stark contrast to Metompkin in overall elevation, island retreat patterns, and plant community complexity. While Hog Island has exhibited parallel retreat in the past (Stallins et al. 2020), it has been relatively stable in recent years and has experienced extensive shrub expansion in the last 40 years (Zinnert et al. 2016). Shrub expansion may be a cause of modest shoreline erosion on the northern end of the island (Zinnert et al. 2019), but the overall stability of Hog Island has resulted in few overwash events with a net shoreline accretion rate of ~13 m yr^{-1} (Haluska 2017, Stallins et al. 2020). Extended temporal periods between substantial disturbances allows for development of dune swale complexes consistent with disturbance-resisting stability domains (Table 1.1) (Stallins 2005, Houser et al. 2008, Wolner et al. 2013, Zinnert et al. 2017). The resulting heterogenous landscape promotes development of distinct dune and swale communities that differ in species and functional trait composition with high vegetative productivity (Brown and Zinnert 2020).

The next compartment of barrier islands we investigated include South Core Banks (North Carolina; Lat. 34.41 N, Lon. 76.28 W) and Sapelo Island (Georgia; Lat. 31.23 N, Lon. 81.15 W). Both exist as part of a chain of islands in the Georgia Bight, but represent different tidal regimes (Stallins 2003, Stallins and Parker 2003). The average precipitation on South Core in 2010 was approximately double that of Sapelo Island (Table 1.2). This pattern is influenced by increased exposure to seasonal storms with increased latitude, which also results in differences in shoreline disturbance vulnerability (Davis et al. 1993).

South Core exists on the northern margin of the Georgia Bight and is representative of a barrier island dominated by microtidal processes causing long, linear island morphology (Stallins

2003). Topography has been described as having low, discontinuous dunes (Stallins 2003, Stallins and Parker 2003). Due to overarching topographic patterns and island response to disturbance, this island is described as existing in a disturbance-reinforcing domain state (Table 1.1) (Godfrey and Godfrey 1976, Zinnert et al. 2017, Hsu and Stallins 2020). As a result, it is hypothesized that feedbacks between dune species and dominant abiotic factors reinforce exposure to overwash during recurring storm events (Stallins 2005, Hsu and Stallins 2020). Similar to Metompkin Island, South Core is retreating, however not as fast (~1 m yr^{-1} on average), with North Core Banks retreating faster than South Core Banks (Riggs and Ames 2007).

In contrast to South Core, Sapelo Island is dominated by mesotidal processes resulting in short, wide "drumstick" morphology (Stallins and Parker 2003). Topography on Sapelo has been described as rough and complex, consisting of various dune-swale complexes which decreases the impact of overwash events (Stallins and Parker 2003). This type of topography emerges locally in part due to the influence of burial stimulated species on dunes which aid in dune-building, with woody shrubs stabilizing low swales (Stallins and Parker 2003, Stallins 2005, Miller et al. 2010, Corenblit et al. 2011). Presence of dune-swale complexes and infrequent overwash events, as well as feedbacks facilitating success of burial-stimulated dune-building species, produces topographic roughness characteristic of the disturbance-resisting domain state (Table 1.1)(Zinnert et al. 2017, Hsu and Stallins 2020). While descriptions of topographic complexity and vegetative function on Hog and Sapelo Islands seem similar, Georgia Bight and Virginia island topographies occupy distinct regions of domain state space (Stallins et al. 2020). This indicates the need for a better understanding of both regional and local controls on domain state classification and vegetation communities.

The southernmost barrier island included in our analysis was St. George Island (Florida; Lat. 29.38 N, Lon. 84.54 W). St. George is located on the Gulf Coast and therefore experiences fundamental differences in physical processes that influence barrier island morphology. Longshore drift cells exist along St. George resulting in sediment deposition at the termini of the barrier island (Stone and Stapor 1996). Morphology of St. George is controlled by wave-dominated microtidal processes producing a long-linear barrier island (Miller et al. 2010). From shoreline inward, topography is described as consisting of a single fronting line of dunes, with an overwash controlled interdunal zone, followed by the presence of dune-swale complexes (Miller et al. 2010). The study site was located on the eastern tip of the island which has been forming an active spit platform with profile surveys indicating an accretion rate of ~5.5 m yr $^{-1}$ over the last 30 years (Miller et al. 2010, Foster and Chang 2001). Delineation of the island elevation highlights low relief; however, site descriptions indicate presence of topographic roughness characteristic of a disturbance-resisting regime (Table 1.1). Vegetation on this island has been forecasted to change as storm frequency increases with climate change. For example, Gornish and Miller (2010) predict over 60% of foredune, interdune, and backdune species will decrease as storm frequency increases. Most of the species that are expected to increase in occurrence with storm frequency are grasses (Gornish and Miller 2010).

Plot Establishment

Transect and plot establishment varied among island sites. For fully detailed methods of plot establishment, see Wolner et al. (2013) (Metompkin and Hog Islands), Stallins (2003) (South Core and Sapelo Island), and Miller et al. (2010) (St. George Island).

Briefly, transects on Metompkin and Hog were established in 2010 and consisted of one cross-shore transect and two alongshore transects at six sites along the length of each island, 3 southerly sites and 3 northerly sites. Cross-shore transects varied in length between 50-200+ m, beginning at the foredune toe and continued until the start of a stable interior island habitat was reached. Alongshore transects intersected the cross-shore transect at 5 m and at the measured mid-way point. Alongshore transects extended away from the intersection 50 m in either direction, less if a stable interior habitat was reached. Plots were established every 5 m along each transect using a 0.25 m^2 quadrat.

Transects on South Core and Sapelo Island were established at five sites on each island. On South Core, sites extended along the length of the island, while Sapelo sites were constrained to Nannygoat Beach to reduce the influence of tidal inlets. Each of the five sites consisted of 3 randomly placed transects that extended from the mean high-water mark to the first occurrence of shrub thickets, indicative of a stable interior island habitat. Plots were established at different distances on each island to maintain a comparable sampling effort. A 1 x 2 m quadrat was used to establish a plot every meter at Sapelo sites and every other meter at South Core sites.

Plots on St. George Island were established within nine 60 x 60 m grids. Three grids were established in the foredunes, interdunal flat, and backdunes. Each grid consisted of a 7 x 7 array of 1 m^2 quadrats, each 10 m apart. All three grid replicates in each habitat were established by 2010.

Elevation and Vegetation Surveying

Full method descriptions detailing elevation and vegetation data collection can be found in original studies (Stallins 2003, Miller et al. 2010, Wolner et al. 2013). We briefly summarize these methods below and include citations where methods for elevation and vegetation data collection occurred in studies other than those listed above.

Metompkin and Hog elevation was surveyed in 2010 using a high-resolution GPS at the cm-scale every 5 m along established cross-shore transects. Elevation surveys on cross-shore transects were extended to the water line for improved topographic clarity at each site. Vegetation surveying methods are detailed in Brantley et al. (2014). Surveys were completed by visually estimating percent cover of species falling within each quadrat. Individuals of small species were recorded as 1% cover. All other species cover estimates were quantified to the nearest 5% (Wolner et al. 2010). Plant identification and nomenclature followed Radford et al. (1968). Elevation and vegetation data collected for these sites are publicly available on the VCR LTER Data Catalog (Wolner et al. 2010).

On South Core and Sapelo Island, elevation was surveyed using a total station at 1 m (Sapelo) and 2 m (South Core) intervals along each transect. Vegetation was sampled every 10 cm within each quadrat using a 2 m point-frame sampler. Identification and nomenclature followed Radford et al. (1968) and Duncan and Duncan (1987).

Elevation at the St. George Island site was surveyed in 2011 using a rotating TopCon total station relative to mean sea level (Miller 2015). Vegetation census was collected as percent cover of each species within a 1 m^2 quadrat in late fall of 2011 (Miller 2015). Elevation and vegetation data for the St. George site is also publicly available at https://www.bio.fsu.edu/~miller/StGeorge/. Elevations are all expressed as height above the approximate mean sea level.

Climatic and Sea-level Rise Data

Daily average temperature and precipitation totals for 2010 were accessed from the closest National Oceanic and Atmospheric Association (NOAA) meteorological station to each of the islands. Relative sea-level rise (RSLR) for each island was identified using NOAA sea-level trends. We identified the closest NOAA tide gauge location to each of our sites and reported RSLR for each island (Table 2). Hog and Metompkin climate were estimated using temperature and precipitation data from the Painter, VA meteorological station (NOAA, 2020). Rates of RSLR are based on monthly sea-level data from 1978-2020 and were reported from Wachapreague, VA tidal gauges (NOAA 2020).

South Core Banks climatic patterns was estimate using temperature data from the Cedar Island, North Carolina meteorological station, while average precipitation was estimated using data from the Morehead City, North Carolina meteorological station. Rates of RSLR were reported using tidal gauges in Beaufort, NC and are based on monthly sea-level data from 1953-2020 (NOAA, 2020). Sapelo Island climate was estimated using temperature data collected from the Sapelo Island, Georgia meteorological station and precipitation data from Brunswick McKinnon Airport, Georgia meteorological station. The closest tidal gauge reporting RLSR was located in Savannah, GA. Relative SLR rates were reported in Savannah, GA are based on monthly sea-level data from 1935-2020 (NOAA, 2020).

Climatic patterns for St. George Island were estimated using temperature data accessed from the Apalachicola Airport, Florida meteorological station and precipitation data from the Tallahassee Regional Airport, Florida meteorological station. Rates of RSLR were reported based on monthly sea-level data from the Apalachicola, FL tidal gauges between 1967-2020 (NOAA, 2020). Mean temperature (°C) and mean precipitation (cm) were summarized for 2010 and are presented in Table 2 with RSLR rates (mm yr^{-1}).

Data Analysis

All analyses were conducted using R (R Core Team, 2020). Due to unequal sample size and unequal variances among islands we conducted a non-parametric Kruskal-Wallis test (α =

0.05) to determine how elevation varied within and between islands. A Nemenyi test was used for post-hoc analysis, a chi-square distribution was used to correct p-values when ties were present ($\alpha = 0.05$). These analyses utilized functions in the *car* and *PMCMRplus* packages in R.

Species richness and diversity increase with sampling effort (Williams et al. 2009), making it difficult to compare community diversity of sites with varying sampling efforts. Due to differences in sampling effort at our barrier island sites, we used sample-based rarefaction methodology to construct species accumulation curves (SAC) to evaluate species richness among island dune communities. Sample-based rarefaction produces an SAC of the expected number of species in a reduced collection of n samples drawn randomly from a large pool of empirically observed N samples (Simberloff 1972, Gotelli and Colwell 2001, Colwell et al. 2004). We calculated rarefaction as the mean ± standard deviation of 100 random replicate bootstrapping runs without replacement.

We used principal coordinates analysis (PCoA) to visualize differences in dune plant communities among islands. We conducted our PCoA with the wcmdscale function in the *vegan* R package using 2-dimensions (Oksanen et al. 2019). To reduce computing time and the effect of rare species, we only included species with abundance $\geq 5\%$. In addition to filtering replicates based on abundance, we also standardized species cover data using Hellinger standardization with the decostand function in *vegan* (Oksanen et al. 2019). Hellinger standardization is a recommended technique for reducing the weight of rare species (Legendre and Gallagher 2001). Manhattan distance measure was used to calculate a distance matrix based on standardized species abundances. We selected Manhattan distance to reduce the effects of variable species richness and to reduce the probability of producing an arch effect in our ordination diagram, which complicates interpretation (Podani and Miklós 2002). The resulting ordination diagram identifies dissimilarity of community composition between islands based on distances among plots associated with each island. Points (representing plots on each island) closer to one another are more similar in community composition. We aggregated plot scores for each island group to calculate centroids for each island, which can be interpreted as mean community composition. Species correlations were calculated as Pearson correlation coefficients for each species and used to determine how species abundance influences the spread of points in ordination space.

To test differences in island beta-diversity, we calculated the beta dispersion of points around the calculated centroid (median center of each group). Beta-dispersion tests for significance of homogeneity of group dispersions, which is commonly used as a quantitative metric for beta-diversity (Anderson 2006, Anderson et al. 2006). We used the betadisper function in *vegan* to calculate distances from each point to group centroids (Oksanen et al. 2019). An ANOVA was implemented to test for significant differences in mean beta-dispersion among island plant communities, with Tukey HSD as a pairwise post-hoc test ($\alpha = 0.05$).

Traditionally, ordinations on species compositions are followed-up with a permutational multivariate ANOVA (PERMANOVA) to test for differences in spatial organization of groups in ordination space (Anderson 2017). However, in addition to differences in spatial organization, PERMANOVA analyses are strongly influenced by within-group dispersions when analyzing heavily unbalanced designs (Anderson 2017). We elected not to run PERMANOVA analyses due to large sample size disparities in our dataset and the expectation of differences in beta-dispersion. As an alternative, we calculated distances between centroids for each pairwise combination of island groups using the Manhattan distance matrix. Distances between centroids were calculated in the R package *usedist*, which implements a modified formula first presented by Apostol and Mnatsakanian (2003). This calculation provides a value that can be used to quantitatively describe dissimilarity of island plant community composition, higher values indicate large spatial distances between centroids of plant community groups.

Rank abundance curves (RAC) were used to identify species that are most dominant in island dune communities. RACs were constructed by calculating the average species cover across all plots within an island. To simplify interpretation of our RACs, we highlighted the top 10 species at each location.

We used simple linear regression ($\alpha = 0.05$) with different species abundance aggregations to investigate abundance-elevation relationships using the three most dominant species on each island, according to RACs. Abundance and elevation data were standardized using z-score methodology to aid comparison across islands that significantly differ in elevation. Large-scale abundance-elevation relationships were conducted by aggregating dominant dune species across all barrier islands, while local-scale relationships were conducted using species abundance faceted by island. We used 95% confidence intervals (CI) as a measure of error for resulting linear models. On regression plots, where 95% CI regions do not overlap, species abundance can be seen as significantly different ($\alpha = 0.05$).

Results

Elevation

Mean rank of elevation significantly varied among island dune systems (KW test: $X^2 = 1391.4$, $df = 4$, p-value < 0.05). Post-hoc pairwise comparisons indicate that all islands investigated significantly differed in mean elevation (Fig. 1.1). Sapelo and South Core sites had the highest mean elevations, while Metompkin and St. George sites had the lowest mean elevations (Fig. 1.1). We found that Hog Island had the lowest maximum dune elevation (3.6 m), with the highest dune peak found on South Core (5.9 m) (Table 1.1). The lowest elevation was found on St. George which had plots occurring at sea-level (Table 1.1). Metompkin Island also had plots at low elevations, with a minimum dune elevation of 0.94 m (Table 1.1).

It is critical to also examine density of point elevation measurements within given elevation ranges. St. George and Metompkin both have maximum dune elevations higher than maximum dune elevation on Hog Island. However, both Metompkin and St. George have a much lower density of point measurements above ~2 m (61 plots and 23 plots, respectively), compared to Hog Island (197 plots) (Fig. 1.1). A similar pattern can be seen between South Core and Sapelo Island. South Core has a higher maximum dune elevation, but the density of point measurements above ~4 m is higher on Sapelo (220 plots) than South Core (76 plots) (Fig. 1.1).

Species Richness

There were 94 species identified across all barrier island dune sites (Table S1.1). All five islands reached an asymptotic solution within each sampled area (Fig. 1.2). Resulting rarefaction curves detected varying levels of species richness for each barrier island dune community (Fig. 1.2). Metompkin and Hog Islands (northern most islands) had the lowest expected species richness. Metompkin species accumulation reaches an asymptote at 15 species, while Hog reaches an asymptote at 23 species. Sapelo, South Core, and St. George all exhibit similar species richness (Fig. 1.2). Dune plant community richness on these three islands reach asymptotic saturation and begin to converge between 50-54 species (Fig. 1.2).

Community Composition and Beta-diversity

Pairwise distances among mean community composition of barrier island dune communities (represented by group centroids) showed varying plant community dissimilarities in ordination space (Table 1.3). Dune plant communities were the most similar between Hog and Metompkin Islands (0.51) and were most dissimilar between South Core and Hog (1.66), followed by South Core and Metompkin (1.53) (Table 1.3). Centroid distance between Sapelo and St. George was lower than centroid distance between South Core and Sapelo (Table 1.3), indicating that Sapelo dune communities were more similar to St. George communities than South Core dune communities. This was surprising given the pairwise differences we observed in elevation (Fig. 1.1). Lower elevations on St. George paired with quiescent maritime forcing may result in similar dune-swale vegetation as seen on Sapelo Island which exists at higher elevations and thus is also less disturbed. Below, we detail specific species that drive centroid dissimilarities using species correlations in ordination space.

The first two axes of the PCoA ordination explained 32.8% of the total variation (Axis 1 = 18.6%, Axis 2 = 24.2%). Points along PCoA axis 1 were positively correlated with presence of *Uniola paniculata*, a dominant dune building grass found in dune plant communities in the southern U.S. (Table S1.1). Secondarily, *Heterotheca subaxillaris* also positively correlated with axis 1, thus explaining more of the variation along axis 1, although not to the same extent as *U. paniculata* (Table S1.1). These correlations infer higher abundance of these species in plots on the right side of our PCoA ordination, which is exclusively occupied by dune plots from the three more southerly barrier islands in our study (Fig. 1.3).

Divergence of plots along axis 1 was also driven by negative species correlations (Table S1.1). For example, *Spartina patens*, *Centella asiatica*, and *Ammophila breviligulata* were all negatively correlated with axis 1, further explaining site variation along axis 1 (Table S1.1). Specifically, negative correlations of *S. patens* and *A. breviligulata* explain the spatial location of Hog and Metompkin dune communities in ordination space (Fig. 1.3).

Species correlations associated with PCoA axis 2 primarily explained dissimilarity between South Core dune communities and Sapelo-St. George dune communities (Fig. 1.3). We found that ~12 species were negatively correlated axis 2 with an *r* > 0.20, highlighting a large number of species contributing to community dissimilarity between South Core and Sapelo and St. George Islands (Table S1.1). Of these 12 species, overwash stabilizers including *S. patens* and the bryophyte *Ditrichum pallidum* were most negatively correlated with axis 2 (Table S1.1). Species that were positively correlated with axis 2 with an *r* > 0.20 included swale species; *Phyla nodiflora* and a *Fimbristylis spp.* both of which have higher abundances on Sapelo and St. George and therefore further contribute to the spatial separation between South Core and Sapelo and St. George plant communities.

We found that beta-diversity varied significantly among our barrier island dune communities (ANOVA on beta-dispersion: $F_{4,\,1943} = 27.3$, $p < 0.05$). Site-to-site variation of dune plant communities was significantly higher for the three southern barrier islands compared to barrier islands in the northern compartment (Table 1.3). This indicates that diversity is higher in dune communities of our more southerly barrier islands dune sites which is also supported by results from rarefaction analysis (Fig. 1.2).

Rank abundance curves

Rank abundance curves (RACs) highlight the top 10 species with the highest average relative abundance in each barrier island dune plant community (Fig. 1.4). Many species identified as the top 10 most abundant in each community are the same species that correlate with the directional differences among dune communities in our species ordination space. However, this was not always the case, indicating that the presence of rare species can have an impact on community composition dissimilarity, especially in species rich communities.

In the northern most barrier islands, we found that *A. breviligultata* and *S. patens* both rank in the top 3 species (Fig. 1.4). This provides supporting evidence for the influence these species have on community composition dissimilarities exhibited in our PCoA result (Fig. 1.3). *Panicum amarum* was the top ranked species on Hog and second ranked species on Metompkin (Fig. 1.4), which is surprising given the lack of attention it accrues during investigations of critical dune builders on mid-Atlantic barrier island systems. *Panicum amarum* was the third ranked species on Sapelo but was only found sparsely across South Core and St. George Island, not ranking in the top 10 (Fig. 1.4).

Dune plant communities on our southern barrier island sites were dominated by *U. paniculata* (Fig. 1.4), providing evidence that this is an important species driving community composition differences among northern and southern barrier island dune communities. We also identify *S. patens* as a definitive contributor to community composition dissimilarity of southern barrier islands as it ranks highly on South Core dunes but not as highly Sapelo or St. George dunes (Fig. 1.4). Other species like *P. nodiflora*, *H. subaxillaris*, *D. pallidum* and *C. asiatica* correlated highly with PCoA axis 2 and were ranked highly on some southern barrier island dune but not others (Fig. 1.4). This shows that sharing species in top rank positions will not always result in community similarity. This result emphasizes the importance of species richness and dominance when determining community composition similarities.

Species abundance-elevation relationships

Using the top three species for each island, as identified by RACs, we found six species significantly correlated with standardized elevation at a large-scale (Fig. 1.5). *Uniola paniculata*, *S. maritimum*, *P. nodiflora*, and *H. bonariensis* all positively correlated with standardized elevation, indicating higher abundance at higher elevation sites, after z-score standardization (Fig. 1.5). Conversely, *Paspalum* spp. and *S. patens* were negatively correlated with standardized elevation across all barrier island vegetation, while *A. breviligulata* and *P. amarum* were not correlated with elevation (Fig. 1.5).

When species were separated into islands where each are the most dominant, some species abundance-elevation relationships were not consistent with large-scale analysis. On South Core and Metompkin, *S. patens* relationship with elevation was consistent with large-scale analysis with the highest abundance of *S. patens* occurring at low elevations (Fig. 1.6a and 1.6c). However, on Hog Island, *S. patens* abundance shared similar abundance-elevation relationships as *A. breviligulata* and *P. amarum*, occurring at higher elevations than either South Core or Metompkin (Fig. 1.6b). On Sapelo island, none of the three most dominant species occurred at higher abundance in low elevation areas, indicating that high elevation dune communities occur at a high frequency on Sapelo (Fig. 1.6d). Similar to patterns found on South Core and Metompkin, dominant species on St. George Island consisted of two species with increased abundance at high elevation (*U. paniculata* and *S. maritimum*) and one species with increased abundance at low elevation (*Paspalum sp.*) (Fig. 1.6e).

Discussion

Our data show that barrier islands do not have consistent relationships between elevation and dominant stability domains at large spatial extents, highlighting that disturbance-resisting and disturbance-reinforcing domains can exist at either high or low elevations. Further, large-scale investigation showed that dune plant communities become more species rich along a decreasing latitudinal gradient, rather than in accordance with any predetermined stability state. Increased species richness along a latitudinal gradient has been seen in many other systems and is frequently linked to gradual changes in temperature and/or precipitation patterns over large spatial scales, which we found across these islands (Margules et al. 1987, Austin et al. 1996, Pausas and Austin 2001, Pausas et al. 2003, Currie et al. 2004, Mittelbach et al. 2007). However, literature also highlights the importance of interactions between spatial-scale and environmental heterogeneity as it pertains to species richness (Pausas et al. 2003, Rahbek 2005, Santos et al. 2021), which we found evidence for among our barrier islands. For example, at smaller spatial extents, differences in elevation and/or *a priori* stability domain can correlate with differences in species richness (seen among northern barrier islands) or differences in community composition (seen among southern barrier islands). Based on our findings, variability of dune plant community richness and composition depend on both large-scale climatic patterns as well as local-scale elevation and ecological processes.

We found high community dissimilarity between northern barrier islands and southern barrier islands. This was expected based on previously documented species compositions along mid-Atlantic and Gulf coast dune communities (Stallins 2003, Miller et al. 2010, Young et al. 2011, Goldstein et al. 2017, Hacker et al. 2019). The north-south dissimilarity was primarily driven by dominant dune builders in each region. Dune systems in Virginia and north are dominated by *A. breviligulata*, while dunes south of Virginia are dominated by *U. paniculata* (Brantley et al. 2014, Goldstein et al. 2017, Hacker et al. 2019). However, range expansion of *U. paniculata* over time has been documented in Virginia, possibly due to climatic warming (Goldstein et al. 2017). *Uniola paniculata* (C_4) outperforms *A. breviligulata* (C_3) in the south, likely due to differences in photosynthetic efficiency at increased temperatures (Woodhouse et al. 1968, Harris et al. 2017). Warming annual temperatures and winter minimum temperatures documented in Virginia could alter competitive dominance of species (Goldstein et al. 2017, Huang et al. 2018). Although *U. paniculata* was not specifically identified within our northern compartment of barrier island dunes, we found a dominance shift from *A. breviligulata* on Metompkin Island to *P. amarum* (C_4 plant) on Hog Island, indicating a similar C_4 over C_3

replacement phenomena that has been proposed as *U. paniculata* expands its range northward (Goldstein et al. 2017). To our knowledge, this is the first study to comprehensively show that *P. amarum* is a dominant dune building species in Virginia.

Species richness differences between northern islands could be driven by differences in dominant stability domains, especially considering the high rates on RSLR these islands experience. Our data informs theories proposed by Zinnert et al. (2017), regarding relationships between stability domains and species richness. Based on previous work we would expect disturbance-reinforcing islands to be more species rich than disturbance-resisting islands (Zinnert et al. 2017), however our data supported the opposite relationship. Hog Island (disturbance-resisting) had higher species richness than Metompkin Island (disturbance-reinforcing). Our findings would suggest that in the northern geographic compartment, islands with a propensity to resist disturbances may support more species than islands that respond to disturbance through reinforcement processes.

Our data also shows dune community composition was similar between Sapelo and St. George Islands which were both dissimilar from South Core. This result was unexpected due to the significant elevation differences we found between St. George and Sapelo Islands. However, the latitude of Sapelo and St. George are closer than either island is to South Core, resulting in similar mean annual temperature. Precipitation and patterns of increased temperature could promote species richness on South Core which was comparable to islands at lower latitudes (Zhang et al. 2004). However, increased precipitation is also an indicator of increased storm frequency on South Core compared to Sapelo, due to Sapelo's geographic position in the Georgia Bight (Leatherman 1979, Davis et al. 1993, Stallins and Parker 2003). While increased precipitation from storm frequency may aid in maintaining high species richness of South Core, it could also be a driver of community composition difference between South Core and Sapelo. Similarity of dune communities on islands with extreme elevational contrast (e.g., St. George and Sapelo), which we show here, suggests elevation may not be the most important determinant of community composition differences at scales large enough to be primarily impacted by similarities in climatic patterns. As a result, elevation only becomes a selective force at local scales, where species distributions will shift more with subtle changes in elevation, which drives differences in biotic and abiotic interactions of local plant populations (Doing 1985, Young et al. 2011).

It is critical that connections between elevation gradients and specific species populations contributing to overall community composition be investigated across spatial scales. We show that dominant species identified by RAC analysis have varying relationships with elevation depending on the scale in question. For example, at large spatial extents, *S. patens* is found at lower elevation across all islands, consistent with previous observations (Silander 1979, Silander and Antonovics 1982, Bertness 1991, Hester et al. 1996). At local scales however, it is associated with lower elevations on South Core and Metompkin but also exists at higher elevations on Hog Island, coexisting with dominant dune building species like *A. breviligulata* and *P. amarum*. Such inconsistency of species-elevation relationships could suggest that island specific interactions are contributing to factors that result in altered species roles across islands. This type of phenomena highlights the importance of considering plant functional traits when determining similarities of dune plant communities, which can solve complexities that arise from identical species functioning variably in different locations (Bolnick et al. 2011, Violle et al. 2012, Siefert et al. 2015, Siefert and Ritchie 2016). Functional traits can also aid in grouping distinct species that have similar distribution-elevation relationships across locations which we also found on certain barrier islands (e.g., Weiher et al. 1998). For example, on St. George there were not substantial *S. patens* populations contributing to dune plant communities. However, we found a high-ranking *Paspalum* species that fills a similar low-elevation dominance role. As a C_4 graminoid, this species is similar to *S. patens*, and likely fills a similar niche and may contribute to community dynamics in similar ways. Given these inferred points, we provide the perspective that future research should focus more on plant functional trait composition and diversity of dune plant communities across spatial scales to expand our understanding of how species vs. traits inform plant relationships with elevation at different spatial extents.

Elevation gradients not only impact specific species populations within islands, but also the overall communities developing at different elevations. South Core, Sapelo, and St. George dune communities at lower elevations differ from dune communities at higher elevations. The development of different communities at high and low elevation on islands also contributed to significantly higher beta-diversity on these islands compared to Hog and Metompkin. High beta-diversity can infer the number of unique species communities supported on an island (Whittaker 1960, Koleff et al. 2003, Baselga 2010, Anderson et al. 2011). The propensity of barrier islands to support different plant communities at high and low elevations could be a significant connection between vegetation dynamics and barrier islands stability domains.

Stallins (2005) hypothesized specific dune plant species are connected with island stability domains. Our results could imply that at large spatial extents topographic heterogeneity is more important than elevation with regard to plant community establishment. For example, St. George Island has not been described in terms of stability domains, but site descriptions mirror those of Sapelo and Hog Island, which are described as disturbance-resisting (Miller et al. 2010, Hsu and Stallins 2020, Stallins et al. 2020). However, all three differ in elevation, suggesting that barrier island elevation (high or low) is independent from an island stability domain state (disturbance-resisting or disturbance-reinforcing). This pattern would result in islands existing as high disturbance-resisting and/or low disturbance-resisting, which is supported by geographic analyses of mid-Atlantic barrier islands (Hsu and Stallins 2020). With this knowledge we can continue to probe how different multi-dimensional domain states impact plant communities at different spatial scales.

This study provides evidence supporting the scale dependent context of relationships between dominant stability domains, barrier island elevation, and dune plant community structure. We show that at large spatial scales, macroclimatic differences among islands plays a more important role in dune community richness and composition than elevation differences. However, at more localized scales, the influence elevation, island stability, and local ecological processes have on dune plant communities comes into focus. Information gained from this cross-scale analysis highlights the importance of continuing research that aims to inform interactions between plant communities and barrier island stability. Future work focusing on plant functional trait similarities across spatial scales could provide a clearer picture of how plant communities are connected to dominant stability domains across latitudinal gradients.

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Tables and Figures

Table 1.1 Elevation ranges and *a priori* stability domain states for each island. Dominant stability domain states are based on either topographic analysis or site descriptions from previous studies.

Island	Max Elevation (MASL)	Min Elevation (MASL)	*A priori* Stability Domain
Metompkin	4.76	0.94	Disturbance-reinforcing[a]
Hog	3.67	1.22	Disturbance-resisting[a]
South Core	5.90	1.89	Disturbance-reinforcing[b]
Sapelo	5.76	2.53	Disturbance-resisting[b]
St. George	3.77	0.00	Disturbance-resisting[c]

[a] Based on quantitative topography analysis in Stallins et al. 2020
[b] Based on quantitative topography analysis in Hsu and Stallins 2020
[c] Based on site description in Miller et al. 2010

Table 1.2 Large-scale meteorologic and environmental data for each island.

Island	Mean temperature (°C)	Mean precipitation (cm)	Relative Sea-level rise (mm yr^{-1})
Metompkin	14.9 ± 0.73	64.9 ± 28.4	5.52 ± 0.66
Hog	14.9 ± 0.73	64.9 ± 28.4	5.52 ± 0.66
South Core	17.5 ± 0.66	99.5 ± 29.3	3.29 ± 0.32
Sapelo	19.8 ± 0.59	50.8 ± 11.2	3.39 ± 0.27
St. George	20.2 ± 0.57	123.9 ± 21.7	2.70 ± 0.61

Table 1.3 Island pairwise beta-dispersion difference and pairwise centroid distance. Statistical significance of beta-dispersion is based on results from Tukey HSD, bold indicates significant difference.

Island Comparison	Beta-dispersion difference	Beta-dispersion significance (*p*-value)	Pairwise centroid distance
Sapelo – Metompkin	0.48	< 0.0001	1.37
St. George – Metompkin	0.47	< 0.0001	1.09
South Core - Metompkin	0.43	< 0.0001	1.53
Sapelo – Hog	0.39	< 0.0001	1.41
St. George – Hog	0.37	< 0.0001	1.20
South Core – Hog	0.33	< 0.0001	1.66
Hog – Metompkin	0.09	0.7265	0.51
Sapelo – South Core	0.05	0.5634	1.24
St. George – South Core	0.04	0.8703	1.36
Sapelo – St. George	0.01	0.9956	0.95

Figure Legends

Figure 1.1 Elevation distributions for all five islands. Points represent elevations of specific sites at each island. Distribution lines indicate density of plots within given elevation ranges. Letters represent significant differences based on Nemenyi pairwise comparison (p-value < 0.05).

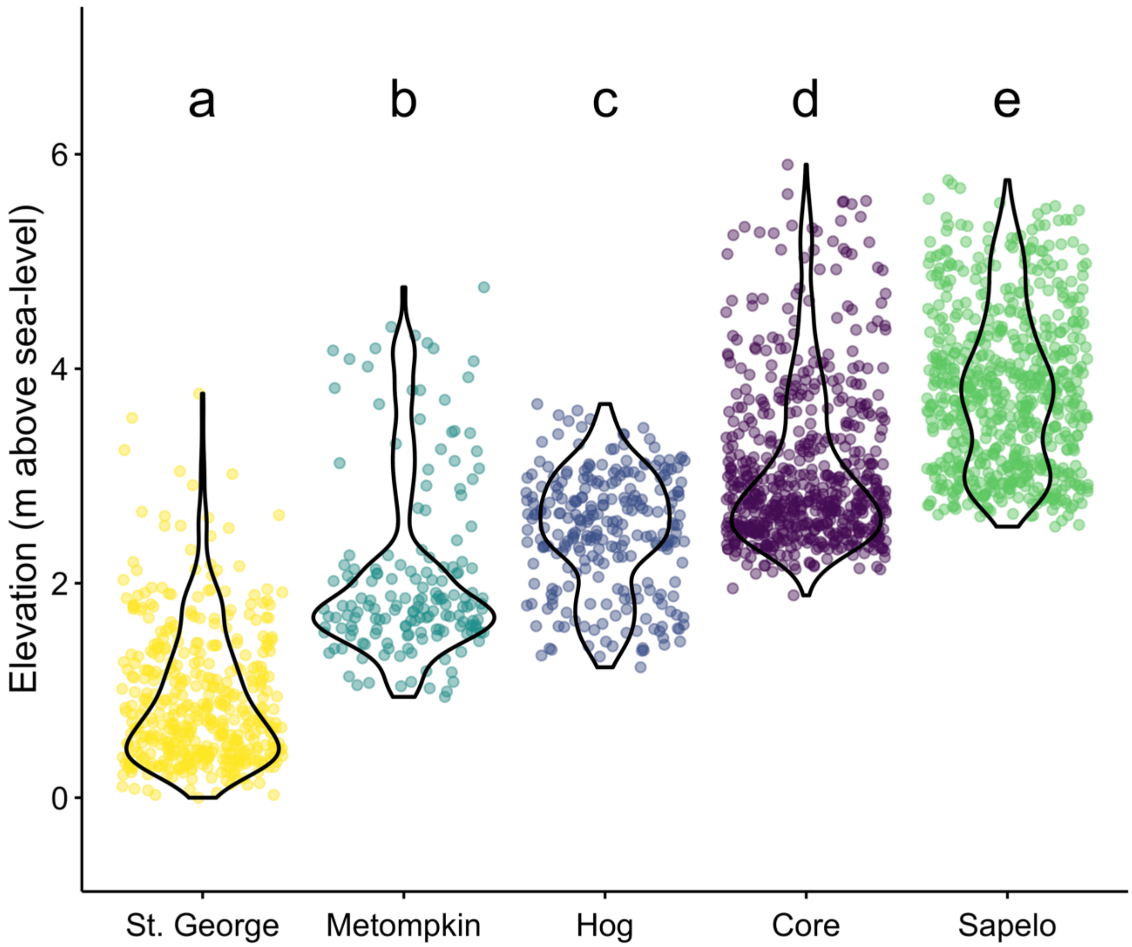
Figure 1.2 Sample-based rarefaction curves based on random subsampling. Lines represent richness trajectories as sites are added. Halos indicate ± standard deviation around mean richness of each mean calculated. Asymptotic saturation represents maximum species richness.

Figure 1.3 Principal coordinate plot representing species community composition for each barrier island. Points represent site replicates which are grouped by convex hulls. Stars represent within island centroids. Centroids can be viewed as a distance-based mean community composition in ordination space.

Figure 1.4 Rank abundance curves highlighting the relative abundance of the top 10 species for each island site, ranked in order from most abundant to least abundant. Panels represent each island (**A** = Metompkin, **B** = Hog, **C** = South Core, **D** = Sapelo, and **E** = St. George).

Figure 1.5 Simple linear regressions of abundance-elevation relationships for the top 3 dune species on each island after z-score standardization. Colors and line types correspond to different species and are coordinated with the reported Pearson correlation coefficients and p-values. Halos around trendlines represent 95% confidence intervals.

Figure 1.6 Simple linear regressions of abundance-elevation relationships for the top 3 dune species on each island after z-score standardization. Panels represent each island (**A** = Metompkin, **B** = Hog, **C** = South Core, **D** = Sapelo, and **E** = St. George). Colors and line types correspond to different species and are coordinated with the reported Pearson correlation coefficients and p-values. Halos around trendlines represent 95% confidence intervals.



a
b
c
d
e
Elevation (m above sea-level)
0
2
4
6
St. George
Metompkin
Hog
Core
Sapelo

Figure 1.1

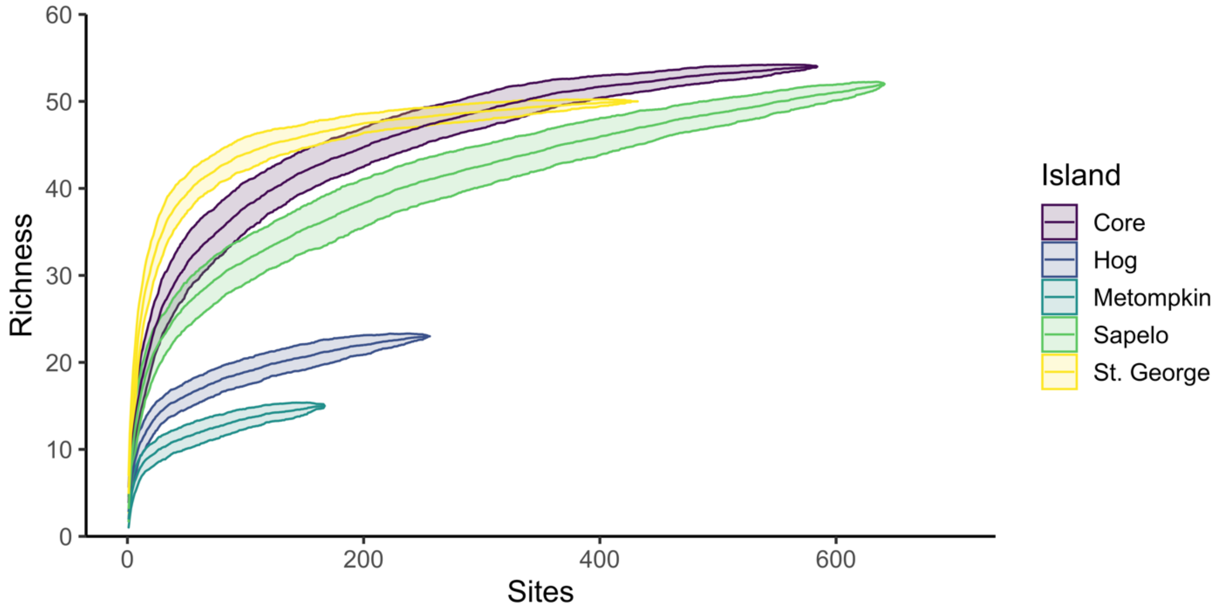
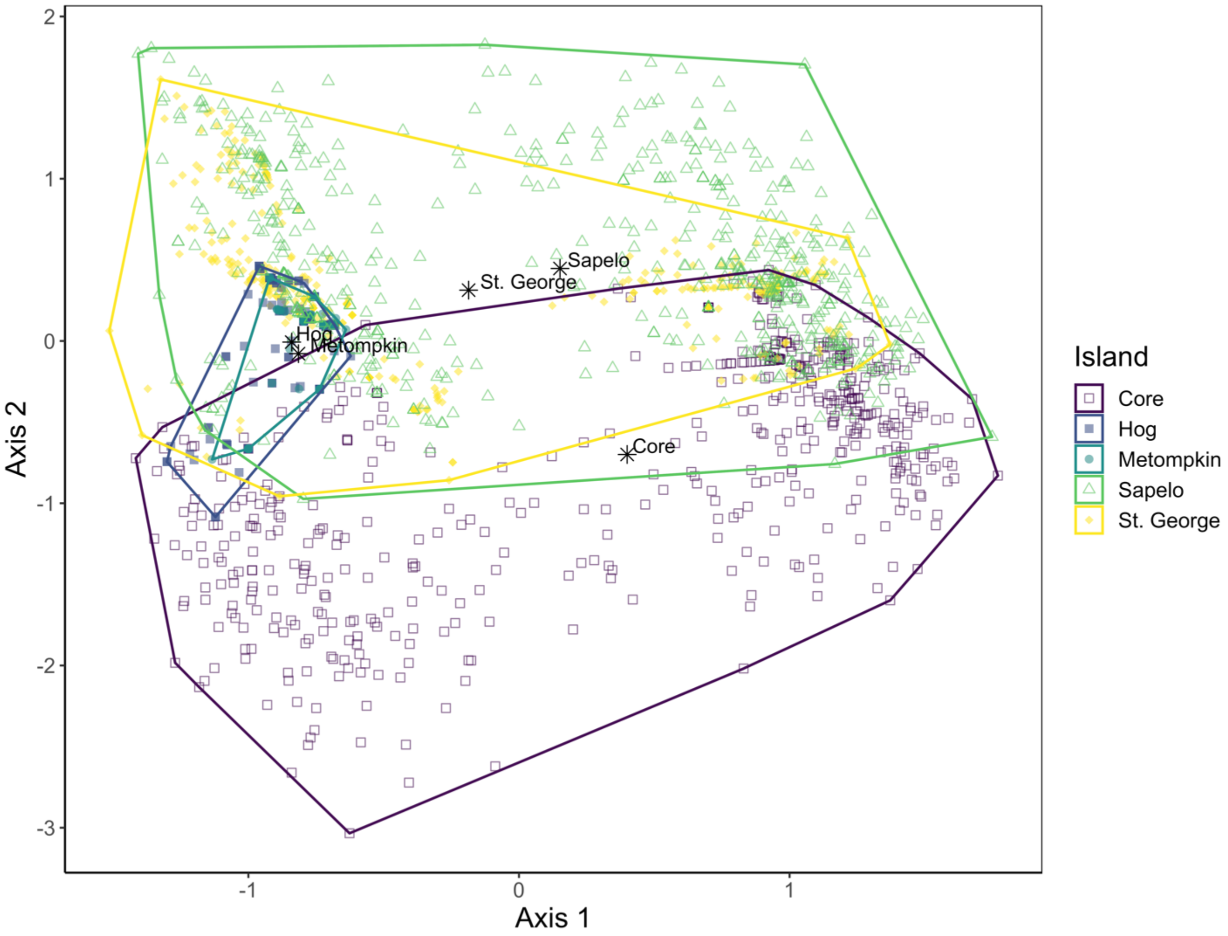

Richness
60
50
40
30
20
10
0
0
200
400
600
Sites
Island
Core
Hog
Metompkin
Sapelo
St. George

Figure 1.2



Axis 2
Axis 1
2
1
0
-1
-2
-3
-1
0
1
Sapelo
St. George
Hog
Metompkin
Core
Island
Core
Hog
Metompkin
Sapelo
St. George

Figure 1.3

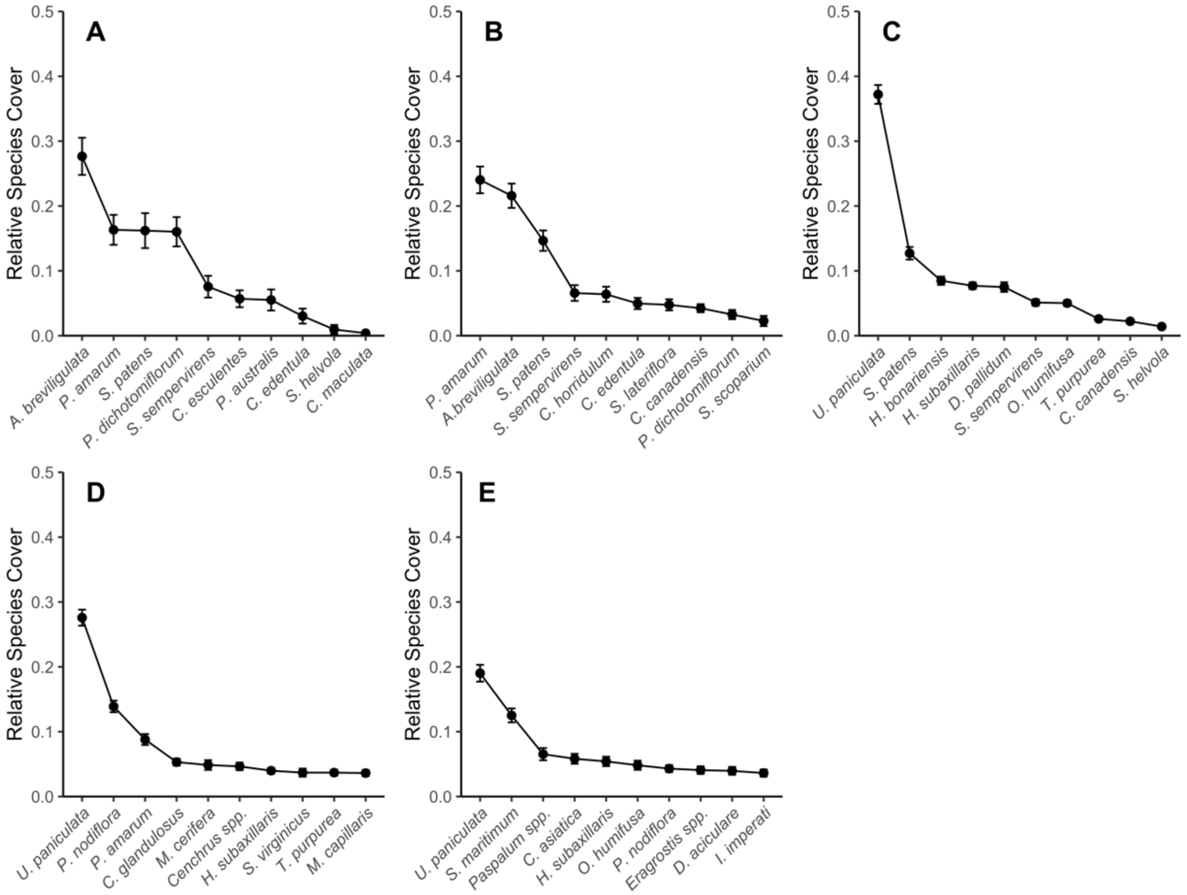
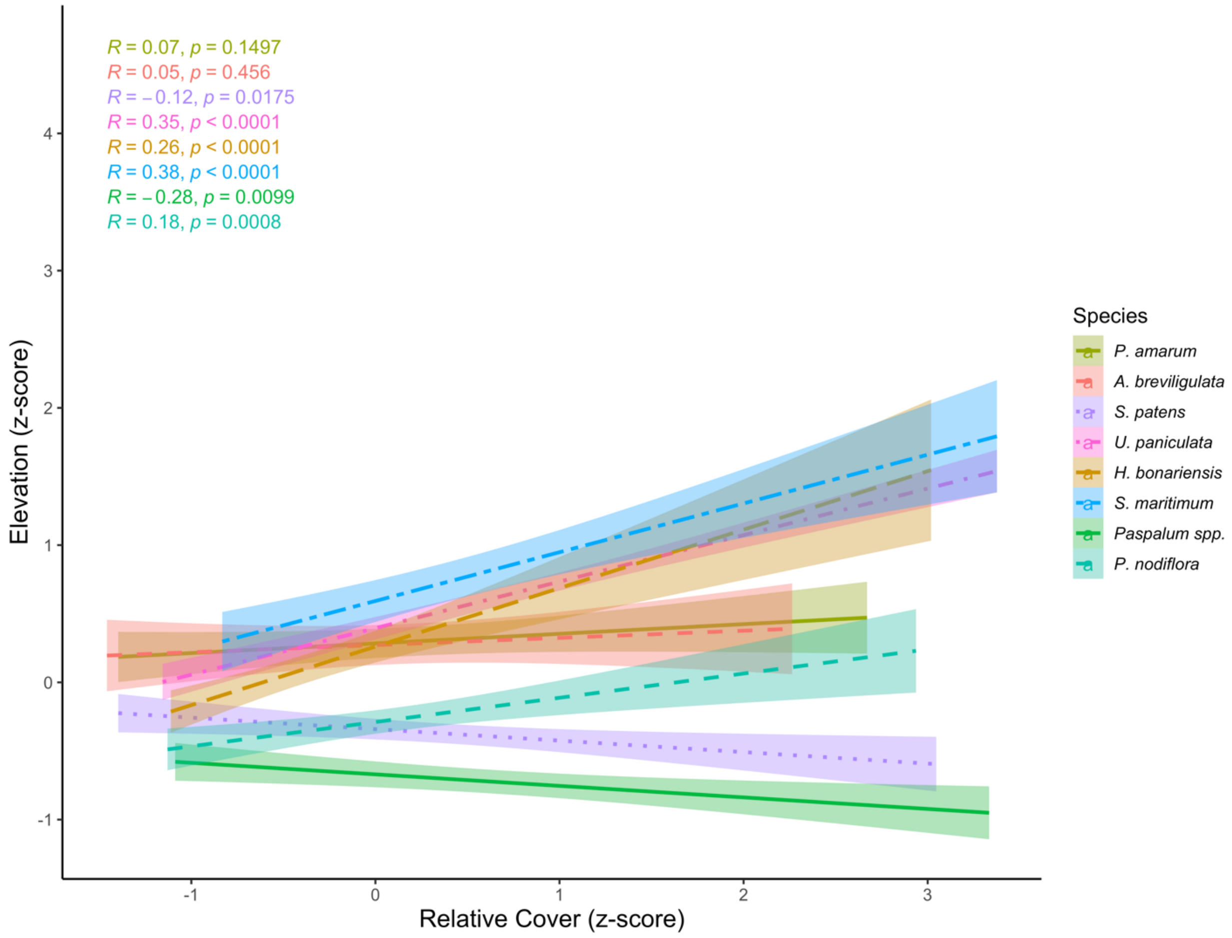

A
B
C
D
E
Relative Species Cover
0.0
0.1
0.2
0.3
0.4
0.5
A. breviligulata
P. amarum
S. patens
P. dichotomiflorum
S. sempervirens
C. esculentes
P. australis
C. edentula
S. helvola
C. maculata
P. amarum
A.breviligulata
S. patens
S. sempervirens
C. horridulum
C. edentula
S. lateriflora
C. canadensis
P. dichotomiflorum
S. scoparium
U. paniculata
S. patens
H. bonariensis
H. subaxillaris
D. pallidum
S. sempervirens
O. humifusa
T. purpurea
C. canadensis
S. helvola
U. paniculata
P. nodiflora
P. amarum
C. glandulosus
M. cerifera
Cenchrus spp.
H. subaxillaris
S. virginicus
T. purpurea
M. capilaris
U. paniculata
S. maritimum
Paspalum spp.
C. asiatica
H. subaxillaris
O. humifusa
P. nodiflora
Eragrostis spp.
D. aciculare
I. imperati

Figure 1.4



$R = 0.07$, $p = 0.1497$
$R = 0.05$, $p = 0.456$
$R = -0.12$, $p = 0.0175$
$R = 0.35$, $p < 0.0001$
$R = 0.26$, $p < 0.0001$
$R = 0.38$, $p < 0.0001$
$R = -0.28$, $p = 0.0099$
$R = 0.18$, $p = 0.0008$
Elevation (z-score)
4
3
2
1
0
-1
-1
0
1
2
3
Relative Cover (z-score)
Species
P. amarum
A. breviligulata
S. patens
U. paniculata
H. bonariensis
S. maritimum
Paspalum spp.
P. nodiflora

Figure 1.5

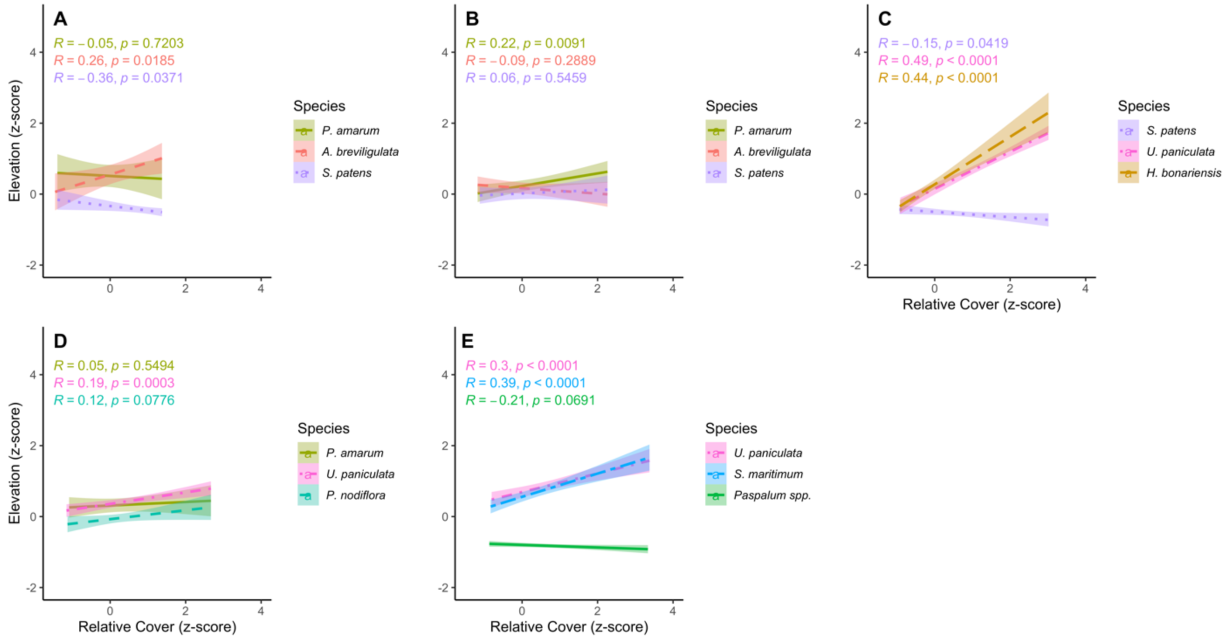

A
R = −0.05, p = 0.7203
R = 0.26, p = 0.0185
R = −0.36, p = 0.0371
Species
P. amarum
A. breviligulata
S. patens
B
R = 0.22, p = 0.0091
R = −0.09, p = 0.2889
R = 0.06, p = 0.5459
Species
P. amarum
A. breviligulata
S. patens
C
R = −0.15, p = 0.0419
R = 0.49, p < 0.0001
R = 0.44, p < 0.0001
Species
S. patens
U. paniculata
H. bonariensis
D
R = 0.05, p = 0.5494
R = 0.19, p = 0.0003
R = 0.12, p = 0.0776
Species
P. amarum
U. paniculata
P. nodiflora
E
R = 0.3, p < 0.0001
R = 0.39, p < 0.0001
R = −0.21, p = 0.0691
Species
U. paniculata
S. maritimum
Paspalum spp.
Elevation (z-score)
Relative Cover (z-score)
4
2
0
-2
0
2
4

Figure 1.6

Appendix

Supplemental Tables

Table S1.1 Binomial species list with Pearson correlation coefficients for PCoA axis 1 and axis 2.

Species	**Axis 1**	**Axis 2**
Ammophila breviligulata	-0.21	0.04
Ampelopsis arborea	-0.05	0.04
Andropogon spp.	-0.03	0.13
Arenaria serpyllifolia	-0.02	-0.24
Aristida purpurascens	-0.03	0.02
Atriplex mucronata	-0.02	-0.01
Baccharis glomeruliflora	-0.03	0.02
Baccharis halimifolia	-0.06	-0.02
Bulbostylis ciliatifolia	-0.11	0.07
Cakile edentula	-0.05	0.03
Centella asiatica	-0.22	0.12
Cenchrus spp.	0.08	0.16
Chamaesyce spp.	0.12	-0.01
Chloris petrea	-0.06	-0.32
Cirsium spp.	-0.10	0.01
Cladonia sp.	0.00	-0.05
Cnidoscolus stimulosus	0.00	0.01
Commelina erecta	0.08	-0.20
Conyza canadensis	0.09	-0.22
Croton glandulosus	0.18	0.10
Cuscuta gronovii	-0.03	-0.04
Cyperus croceus	0.03	0.03
Cyperus esculentes	-0.04	0.01
Cyperus polystachos	-0.04	0.06
Dichanthelium aciculare	-0.16	0.10
Dicanthelium acuminatum	-0.09	-0.17
Diodia teres	0.01	-0.15
Ditrichum pallidum	0.00	-0.49
Eragrostis spp.	-0.20	0.11
Eupatorium spp.	-0.06	0.05
Fimbristylis sp.	-0.17	0.28
Fuirena scirpoidea	-0.13	0.08
Gaillardia pulchella	-0.05	-0.22
Gnaphalium purpureum	0.01	0.04

Heterotheca subaxillaris	0.27	-0.37
Hydrocotyle bonariensis	0.18	-0.32
Hypercium gentianoides	-0.05	0.06
Hypericum hypericoides	-0.04	0.04
Ipomoea imperati	0.08	0.04
Ipomoea sagittata	-0.04	-0.07
Iva frutescens	-0.03	0.01
Iva imbricata	0.00	0.01
Juncus marginatus	-0.12	0.10
Juncus megacephalus	-0.09	0.08
Juncus roemerianus	-0.07	-0.06
Lepidium spp.	0.05	-0.11
Limonium carolinianum	-0.02	0.01
Linum medium	-0.05	-0.04
Ludwigia maritima	-0.03	0.04
Melothria pendula	-0.03	0.01
Morella cerifera	-0.17	0.07
Muhlenbergia capillaris	-0.15	0.19
Muhlenbergia filipes	-0.08	-0.25
Oenothera humifusa	0.14	-0.30
Oldenlandia uniflora	0.00	0.01
Opuntia humifusa	-0.03	0.04
Opuntia pusilla	0.04	0.11
Panicum amarum	-0.15	0.15
Panicum dichotiflorum	-0.12	0.01
Paronychia erecta	-0.02	0.01
Parietaria floridana	-0.05	0.02
Parthenocissus quinquefolia	-0.06	-0.10
Paspalum sp.	-0.17	0.16
Phragmites australis	-0.03	0.01
Physalis angustifolia	0.02	0.02
Phyla nodiflora	-0.14	0.57
Physalis spp.	-0.04	-0.07
Pinus taeda	-0.04	0.04
Plantago virginica	-0.06	-0.18
Polypremum procumbens	0.01	0.05
Polygonum spp.	-0.03	0.02
Quercus geminata	0.04	-0.01
Rhynchospora colorata	-0.08	0.05
Rubus spp.	-0.06	-0.09

Rumex acetosella	-0.03	0.01
Rumex hastatulus	-0.04	0.03
Sabatia stellaris	-0.15	-0.06
Salicornia depressa	-0.02	0.01
Salsola kali	0.00	0.01
Schoenoplectus americanus	-0.06	0.03
Schizachyrium maritimum	0.08	0.08
Schizachyrium scoparium	-0.05	0.01
Scleria spp.	-0.03	-0.01
Scutellaria lateriflora	-0.11	-0.01
Setaria parviflora	-0.05	0.00
Seutera angustifolium	-0.10	-0.18
Sideroxylon tenax	-0.02	0.04
Smilax spp.	-0.01	0.02
Solidago sempervirens	-0.11	-0.33
Spartina patens	-0.33	-0.54
Spermolepsis divaricata	-0.04	-0.13
Sporobolus virginicus	-0.14	0.07
Stenotaphrum secundatum	0.00	0.09
Stipulicida setacea.	-0.02	0.01
Stipulicida setacea.	0.11	-0.05
Toxicoddendron radicans	-0.04	-0.07
Triplasis purpurea	0.20	-0.02
Uniola paniculata	0.91	0.10
Vulpina octoflora	0.03	-0.10

Chapter 2: Topography and disturbance influence trait-based composition and productivity of adjacent habitats in a coastal system

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Abstract

Coastal systems experience frequent disturbance and multiple environmental stressors over short spatial and temporal scales. Investigating functional traits in coastal systems has the potential to inform how variation in disturbance frequency and environmental variables influence differences in trait-based community composition and ecosystem function. Our goals were to (1) quantify trait-based communities on two barrier islands divergent in topography and long-term disturbance response and (2) determine relationships between community trait-based composition and ecosystem productivity. We hypothesized that locations documented with high disturbance would have habitats with similar environmental conditions and trait-based communities, with the opposite relationship in low-disturbance locations. Furthermore, we expected higher productivity and lower site-to-site variation with low disturbance. Functional traits, biomass, and environmental metrics (soil salinity, elevation, and distance to shoreline) were collected and analyzed for two habitat types (dune and swale) on two Virginia barrier islands. Our results show that trait-based community composition differed among habitat types and was related to disturbance. Habitats exhibited more similarity on the high-disturbance island in both trait-based composition and environmental variables. Conversely, the low-disturbance island habitats were more dissimilar. We found the habitat with the lowest disturbance had the highest ecosystem productivity and had trait-based communities indicative of highly competitive environments, while the high-disturbance trait-based communities were influenced by traits that indicate rapid recovery and growth. Site-to-site variation was similar in all dune habitats but differed among inter-island swale habitats that varied in disturbance. These results highlight the importance of incorporating trait-based analyses when approaching questions about community structure and ecosystem productivity in disturbance-mediated habitats, such as coastal systems.

Introduction

Differences in ecosystem functioning (i.e. productivity) often emerge from variations in plant community composition in response to disturbance, demonstrating the importance of quantifying variability in species traits and relationships with ecosystem function resulting from disturbance events (Fukami et al. 2010, Bardgett et al. 2014, Mori et al. 2018). Recently, functional trait-based metrics have been used to understand plant community response to environmental change with potential of disentangling ecosystem response to disturbance (Larsen et al. 2005, Mcfalls et al. 2010, Vellend et al. 2014, Kraft et al. 2015, Fortunel et al. 2016). By providing a mechanistic understanding to community dynamics, trait-based approaches may be more informative in emergence of community patterns than species diversity (Tilman et al. 1997, Lavorel and Garnier 2002, Suding et al. 2008). Here, plant functional traits are defined as plant characteristics that indicate ecological strategies of plant resource uptake/allocation, competitive ability, and spatial distribution relative to environmental conditions (Westoby and Wright 2006). Past research has shown that plant functional traits can be used to inform vegetation zonation of coastal systems in Mediterranean and Gulf coast plant communities (Feagin and Wu 2007, Ciccarelli 2015, Conti et al. 2017). Although driven by disturbance, trait-based community composition has been rarely utilized in Atlantic barrier island systems, with species approaches dominating our understanding of communities and habitats (e.g. Monge and Stallins 2016).

Barrier islands occur on every continent except Antarctica and are present on 30% of US coastlines, with over 2500 km protecting the Atlantic coast (Stutz and Pilkey 2001). Barrier islands are unique systems and are rarely used to study interactions among disturbance, environment, and trait-based community composition, as well as feedbacks with ecosystem function. However, recent research suggests that barrier islands respond individualistically to similar disturbances due to topographic heterogeneity, making them ideal systems for studying disturbance response across multiple scales (Zinnert et al. 2017, 2019). Relationships between plant presence and coastal topography have been documented but these are largely species-based (Stallins 2006, Monge and Stallins 2016, Goldstein et al. 2017, Hacker et al. 2019). A knowledge gap remains as to how differences in topographic heterogeneity influence trait-based community composition and relationships with ecosystem productivity in high disturbance coastal systems.

Large episodic disturbances, such as hurricanes, nor'easters, and other storm events reset coastal plant communities that have been developing since the previous disturbance (Mcfalls et al. 2010, Buma 2015). On barrier islands, it has been theorized that areas of low topographic heterogeneity (i.e. low dunes or dune hummocks) are disturbed more frequently and do not protect areas behind the primary dune (i.e. swales) when disturbances hit. This results in dune and swale habitats similar in how they are influenced by environmental factors like wind, sea-spray, and flooding (Fig.1a Young et al. 2011, Zinnert et al. 2017, 2019, Stallins and Corenblit 2018). If disturbance influences the difference in inter- and intra-island topographic and environmental factors, we would expect to see plant communities differ in overall trait-based community composition and/or site-to-site variability of dune/swale habitat types (Chase 2007).

In this study we address a knowledge gap by investigating how topographic heterogeneity influence environmental factors, and trait-based community composition in terrestrial barrier island systems that differ in long-term disturbance response (Stallins 2006, Zinnert et al. 2019). Where trait-based composition differences exist, we determine how those differences influence ecosystem productivity. 1) We hypothesize that when an island has low topographic heterogeneity (i.e. disturbance is more frequent), environmental conditions between adjacent habitats (i.e. dune and swale) will be homogenous, trait-based community composition will be similar, and ecosystem productivity will be reduced. Conversely, when an island has high topographic heterogeneity (i.e. disturbance is less frequent), there will be more dissimilarity between adjacent dune and swale habitats in environmental conditions and trait-based community composition, with high productivity in the protected inland habitat (swale). 2) Since rapidly resetting plant communities could open niche space for dispersal driven plants that are not necessarily similar in trait-based metrics (Leibold et al. 2004, Leibold and McPeek 2006), we further hypothesize increased site-to-site variation of traits on the island with low topographic heterogeneity (i.e. experiencing more frequent disturbance).

Methods

Site description and plot establishment

This study focuses on two islands, Hog Island and Metompkin Island, within the Virginia Coast Reserve (VCR) Long-Term Ecological Research site that represent different geomorphology classes based on various geographic variables (i.e. shape, size, disturbance regime, and topographic complexity) and long-term response to disturbance (Zinnert et al. 2019).

Metompkin Island (Lat. 37.737 N, Lon. 75.563 W) is a rapidly retreating island, with higher rates of overwash disturbance that has been documented over multiple decades as transition from marsh to upland (Brantley et al. 2014, Fenster et al. 2016, Zinnert et al. 2019). Metompkin Island has lower topographic heterogeneity with swale habitats existing behind low, hummocky dunes that likely do not protect against stressors like sea-spray and overwash (Fig. 2.1a;Shiflett and Young 2010, Brantley et al. 2014). Furthermore, due to the size of the beach on Metompkin Island, plots are much closer to the high tide line than on Hog Island, likely making sea-spray a prominent and consistent stressor (Fig. 2.1a). A continuous, stabilized dune ridge exists ~120 m west of the shoreline, but low topographic relief and lack of dominant woody species makes the island particularly prone to frequent overwash events during even mild storm events (Brantley et al. 2014, Zinnert et al. 2019).

Relative to Metompkin Island, Hog Island (Lat. 37.417 N, Lon. 75.686 W) is characterized as having high topographic heterogeneity with a long continuous foredune ridge that protects swale communities from overwash events caused during disturbance, as well as general sea-spray, sand burial, and other environmental stressors associated with coastal systems (Fig. 2.1b; Woods et al. 2019, Zinnert et al. 2019). This is evidenced by no change in the marsh-upland boundary over the last ~30 years (Zinnert et al. 2019). The low elevation swale habitats exist between primary and stabilized dune systems (Fig. 2.1b). Swale habitats have been characterized by noted increases in plant biomass and plant cover (Fahrig et al. 1993, Miller et al. 2009). Plots (1 m^2, N = 60) were established on both Hog (n = 28) and Metompkin (n = 32) islands along 5 east-west transects spanning dune and swale habitats. Due to differences in island size, Hog Island transects were established every ~200 m with plots 50 m apart, while Metompkin Island transects were established every ~100 m with plots 30 m apart.

Environmental Variables and Species Composition

Young et al. (2011) first presented elevation above sea-level and distance to shoreline as important functional proxies for abiotic factors affecting plant communities including water availability, blowing sand, and sea-spray. These findings were later corroborated by studies conducted on the Mediterranean coast (Bazzichetto et al. 2016). Burdick and Mendelssohn (1987) also used elevation to define dune, swale, and marsh habitats on a Gulf coast barrier island. In accordance with these studies we used elevation above sea-level as a principle component in defining plot affiliation with each habitat type (e.g. dune or swale). Elevation of plots was collected using a LiDar images of study areas (1-3 m spatial accuracy; CoNED

TBDEM, USGS). Distance to shoreline was collected by measuring distance (m) from each plot to high-tide line in ArcMap (ArcGIS, ESRI, Redlands, California, USA). To assess salinity, soil (to 10 cm) was collected at each plot, dried at 105° C for 72 h, and 50 g of dried soil was analyzed for total chlorides with a chloride electrode (model 9617b, Orion, Boston, Massachusetts, USA) with a 1:5 ratio (w/v) of soil distilled with water, using 5 M $NaNO_3$ (2 mL per 100 mL of sample) as an ionic equalizer (Young et al. 1994).

Percent aerial cover was estimated for each plant species separately in each plot in summer of 2017. Species cover was used to calculate the community-weighted mean (CWM) of trait variables for each species in each plot (see below).

Trait Selection and Sampling

Trait metrics selected for this study represent a range of above- and belowground growth strategies, particularly highlighting trade-offs between resource conservatism, rapid growth, and competition. We highlight functional roles for each trait selected for this study (Table 2.1).

Aboveground Traits

Aboveground traits were sampled from a total of 287 individuals across both islands which included a total of 39 different species found across all plots. Maximum plant height (cm) was measured for the tallest individual of each species in each plot. Aboveground samples for one randomly selected individual of each species were harvested and immediately wrapped in moist paper towel, stored in plastic bags, and transferred to a dark refrigerator while processing took place. Specific leaf area (SLA) was measured using computer scanning method. Leaves were removed from stems, laid flat on scanning area and digitized using WinRhizo software (Regent Instruments Inc., Quebec, Canada) to capture projected area. Scanned leaves were dried at 60° C for 72 h, then weighed (g) using a precision scale. Dried leaf samples were ground into a fine powder using a mini Wiley mill and shipped to Cornell University Stable Isotope Laboratory (COIL, Ithaca, New York, USA) for elemental percent (%C and %N) and isotope ($\delta^{13}C$) analysis. Species abundance was used to calculate CWM for each functional trait in each plot:

$$CWM = \sum_{i}^{R} p_i \, t_i$$

Where R is the number of samples, p_i is the relative abundance of species i, and t_i is the mean trait value of species i (Garnier et al. 2004). Using CWM of traits as plot level averages allows for comparisons between habitats while weighting trait values by the most abundant species in each plot.

Belowground Traits

Root samples were collected from a single soil core taken at each plot, cores were bagged and stored in a dark refrigerator while processing took place. Soil cores were washed to separate roots from soil using a series of sieve stacks (3.35 mm, 1.00 mm, and 500 µm). Separation of live and dead roots was based on visual inspection. Cleaned roots were submerged in water and stored in a dark freezer until root morphology measurements were obtained via scanning. Root samples were thawed and suspended with water in a clear acrylic tray and scanned with an Epson Perfection V800 picture scanner (Epson America Inc., Long Beach, California, USA). Digitized root images were processed using WinRhizo to determine root volume and root length. Roots were dried at 60° C for 72 h and weighed (g) using a precision scale to calculate specific root length (SRL) and root tissue density (RTD). Dried root preparation for elemental analysis (%C and %N) and isotope analysis ($\delta^{13}C$) followed the same procedure as aboveground samples. Root trait measures represent CWM as they were obtained through community level soil cores (Birouste et al. 2014).

Biomass Sampling

Annual net primary productivity (ANPP), defined as aboveground biomass at the end of the 2017 growing season, was collected to assess ecosystem function. Standing vegetation was harvested in plots at three selected transects. All vegetation was harvested to ground within a 0.1 x 1 m frame. Samples were dried at 60° C for 72 h and weighed (g). Biomass weights for each plot were extrapolated to estimate productivity (g m^{-2}).

Data Analysis

Environmental variables

Dune and swale habitats were defined based on affiliation to a specific elevation value. We used island median elevation to define habitat types (values over median elevation = dune, values under median elevation = swale). A Kolmogorov-Simonov (KS) test was used to analyze elevation frequency distribution on each island, inferring differences in topographic heterogeneity ($\alpha = 0.05$) between Hog and Metompkin Island.

A principal component analysis (PCA) was used to incorporate multiple environmental variables (i.e., elevation, distance to shoreline, soil salinity) to determine whether habitat types based on elevation differ in multiple environmental variables. Multiple response permutation procedure (MRPP; Euclidean distance) was used to test group differences in multivariate space. A pairwise post-hoc test was run to investigate differences among community types (Bonferroni adjusted $\alpha = 0.008$). Analyses were conducted using PC-ORD (software v. 7.0, MJM Software Design, Gleneden Beach, Oregon, USA).

Trait-based community composition

For trait-based analyses, CWM traits were standardized to have mean zero and unit variance, preventing over influence of traits that are numerically different by orders of magnitude. Investigation of differences in trait-based community composition among island habitats was conducted in three-parts. First, non-metric multidimensional scaling (NMDS) was used to investigate variation of CWM traits among habitat types using Euclidean distance measure. This distance metric was chosen to best represent the data used in the NMDS analysis. The ordination was run (max. iteration of 999) with 3-dimensions to a minimized stress value (stress value < 0.2). NMDS ordination was performed in R (R Core Team, v. 3.5.0, 2018) using the vegan package (Oksanen et al. 2019). For interpretation, a PCA rotation was performed on each NMDS such that the first two axes represent maximum variation of the data. Trait correlations were modeled in multivariate space using the envfit function in the vegan package (Oksanen et al. 2019), this further facilitates interpretation of multivariate patterns. To further aid interpretation of trait-based community composition, we ran a secondary NMDS ordination of species using Bray-Curtis distance measure to a minimized stress value.

Second, centroids for each predefined habitat type were calculated by aggregating site scores in multivariate space, this can be interpreted as an average community composition based on community-weighted traits. Differences in trait-based community composition was then tested using MRPP to determine if trait-based composition significantly differed among habitat types ($\alpha = 0.05$). Pairwise tests were performed to determine which habitat types differed in trait-based composition (PC-ORD; Bonferroni adjusted $\alpha = 0.008$). This analysis was also conducted on species composition to facilitate interpretation of trait-based community differences (Appendix S1).

Third, we used betadisper function (Oksanen et al. 2019) in R to calculate distance values from each plot to respective centroids, an indicator of differences in trait-based community variation among habitat types (Anderson 2006). This method for testing homogeneity of group dispersion is a common quantitative metric for beta-diversity, or site-to-site variation (Anderson et al. 2006). An ANOVA was used to test differences in dispersion among habitat types ($\alpha = 0.05$). Tukey HSD was used as a pairwise post-hoc test. Analysis of variance and post-hoc tests were performed using JMP statistical software (JMP Pro 14, SAS Institute, Cary, North Carolina, USA).

Ecosystem productivity

ANOVA was used to determine if ecosystem productivity was different among habitat types ($\alpha = 0.05$). Tukey HSD was performed to test for pairwise differences in habitat biomass production. All analyses on biomass were completed using in R.

Results

Environmental variables of habitat types

Frequency distributions of elevation among plots on Hog and Metompkin were significantly different ($P < 0.05$), suggesting topography is more homogenous on Metompkin Island (high disturbance) compared to Hog Island (low disturbance; Fig. 2.2). Environmental parameters explained 82.2% of total variation among habitat types (PC 1 = 60.7%, PC 2 = 21.5%), with PC 1 as the primary driver of variation. Site separation along PC 1 was correlated with elevation ($r^2 = 0.79$), soil salinity ($r^2 = -0.80$) and distance to shoreline ($r^2 = -0.74$, Appendix S1: Fig. S2.1). Soil chloride values on Metompkin dune and swale had a lower range (7.2 – 88.2 and 8.2 – 118.1 $\mu g\ g^{-1}$, respectively) than soil chlorides on Hog dune and swale habitats (10.1 – 575.9 and 88.2 – 7968.2 $\mu g\ g^{-1}$, respectively). We found separation of habitat types in environmental multivariate space based on MRPP ($t = -15.07$, $P < 0.0001$). Pairwise post-hoc testing revealed significant differences between all habitat types except Metompkin dune and Metompkin swale (Table 2.2). These results indicate that while Metompkin dune and Metompkin swale are distinct habitats based on elevation (and are classified this way in many studies, e.g. Brantley et al. 2014), multiple environmental variables reflect little difference in abiotic factors of the two areas.

Trait-based community composition

Trait-based composition resulted in a three-dimensional solution (final stress = 0.118, Fig. 2.3a). We found differences in mean trait-based community composition between habitats as well as differences of site-to-site variation within habitat types (Fig. 2.3a). Hog swale was positively correlated with above- and belowground traits of dominant competitors (e.g. height, and SRL; Fig 3b). Interestingly, we also found that multiple habitat types were positively correlated with leaf C:N (Fig. 2.3b), suggesting higher amounts of structural carbon in leaves. Hog dune, Metompkin dune, and Metompkin swale all showed positive correlations with resource conservation traits as well as traits that can be utilized by rapid growth/disturbance response (e.g. RTD, leaf $\delta^{13}C$, SLA, root C:N and leaf %N; Fig. 2.3b). A full list of trait correlation coefficients and goodness of fit results can be viewed in the supplementary appendix (Appendix S1: Table S2.1).

Community level functional trait composition differed significantly among habitats (MRPP, $T = -11.70$, $P < 0.0001$). Pairwise comparisons indicated high dissimilarity of trait-based community composition among Hog Island dune and swale habitats, while Metompkin dune and swale habitats had similar trait-based community compositions (Table 2.3; Fig. 2.3a). The trait-based communities associated with the Hog dune habitat did not significantly differ from trait-based communities of Metompkin swale habitats but were different from Metompkin dune habitat (Table 2.3). Similar results were found when analyzing communities based on species dissimilarities (Appendix S1: Table S2.2, Fig. S2.2). A full list of species and NMDS axes correlations are provided in supplementary appendix (Appendix S1: Table S2.3). Site-to-site variation of trait-based communities within habitat type differed significantly between Hog swale and Metompkin swale habitats (Table 2.4), indicating higher site dispersion based on traits in Metompkin swale habitats (Fig. 2.3a).

Ecosystem productivity

Ecosystem productivity varied significantly among habitats ($F = 5.81$, $P < 0.05$; Fig. 2.4) and was highest in Hog swale habitat (870.1 ± 135.02 g m^{-2}) compared to all other habitat types (Fig. 2.4). Hog dune habitats had an average productivity of 364.5 ± 198.14 g m^{-2}, while Metompkin dune and swale had mean biomass of 419.44 ± 84.61 g m^{-2} and 204.1 ± 57.30 g m^{-2}, respectively.

Discussion

Barrier island systems, and coastal systems in general, are dominated by the effects of disturbance (Mcfalls et al. 2010, Ciccarelli 2015). We demonstrate that islands differing in disturbance (Zinnert et al. 2019), also vary in topographic heterogeneity and environmental metrics. We find that inter- and intra-island habitats differ in trait-based community and ecosystem productivity. This research contributes to literature linking indirect drivers like disturbance to altered trait-based community composition and ecosystem productivity (Haddad et al. 2008, Pakeman et al. 2011).

In support of our primary hypothesis, intra-island habitats with lower topographic heterogeneity (i.e. Metompkin dune and Metompkin swale) were more similar in both environmental variables and trait-based community composition, while habitats with higher topographic heterogeneity (i.e. Hog dune and Hog swale) were more dissimilar. As predicted, Hog swale had the highest amount of productivity, likely due to increased protection by a large linear dune ridge from ocean water flooding during storm disturbance (Oster and Moore 2009).

Our data also partially support our secondary hypothesis that site-to-site variation of trait-based communities would be higher in habitats on the island with lower topographic heterogeneity (i.e. higher disturbance). Through inter-island analysis we found that while not all high disturbance habitats had significantly higher dispersion, Metompkin swales had more site-to-site variation of trait-based communities compared to low disturbance Hog swales.

Topography and environmental variables

Metompkin dune and swale habitats, which differed based on elevation, were similar when considering multiple environmental variables. As suggested by Shiflett and Young (2010) and Brantley et al. (2014), the low and hummocky nature of dunes on Metompkin does not protect plant communities of inner swale habitats, as there is no physical barrier from disturbance events. Therefore, frequent interruption (i.e. storm disturbance) of ecosystem processes, that normally lead to construction of primary dune ridges, result in environments more similar across a geographic area that would otherwise be characterized as distinct habitats (Stallins and Corenblit 2018). Habitats experiencing disturbance more frequently correlated with lower soil salinity. Although seemingly counter intuitive, this is evidenced by the negative correlation with soil salinity of Metompkin swale habitats as well as dune habitats on both islands along PCA 1. It is possible that correlations are caused by frequent sandy-soil overwash during storms. Salt leaches more readily through large pores of sandy sediment (Liu et al. 2011). Therefore, newly deposited sand with little to no organic matter may leach salts faster than older sandy-soils with organic matter build-up, as seen in the Hog swale habitat. Increased salinity in soils have been proposed to provide important nutrient inputs for coastal systems (Art et al. 1974).

The difference in topographic heterogeneity we show here likely leads to variability in inter-island disturbance frequency, which has been recently demonstrated from remote imaging (Zinnert et al. 2019). Higher rates of disturbance likely reset plant communities rapidly in dune and swale habitats on Metompkin Island (Mcfalls et al. 2010, Buma 2015). Pronounced disturbance and low environmental variation likely serve as primary drivers influencing the intra-island similarity of trait-based communities on Metompkin Island. Conversely, the lack of disturbance mediation and increased variation in environmental stress between habitats on Hog Island may be the primary drivers of intra-island dissimilarity of trait-based community development when disturbance is low.

Trait-based community composition and productivity

Similar to other systems, when barrier islands exist in a state of prolonged recovery from disturbance (e.g. Hog swale), plant functional traits become a primary force in community development as abiotic factors influence species interactions (Díaz et al. 1998, Feagin and Wu 2007, Cornwell and Ackerly 2009, Fang et al. 2018). Interactions between species and environments shape communities as plants with suitable trait values dominate and ultimately develop feedbacks with ecosystem function (Tilman 1994, Kunstler et al. 2015). In this study, dissimilarity between trait-based communities of Hog swale compared to all other habitats is likely due to feedbacks that develop between low disturbance, increased ecosystem productivity, and functional trait profiles indicative of survival in productive habitats.

Ecosystem productivity was found to be highest in Hog swale habitat, suggesting that lower disturbance is related to increased biomass production in dune-swale systems. Relationships between increased productivity and trait-based composition of plant communities indicate competitive interactions in Hog swales. For example, higher max height and SRL in

Hog swale habitats may result from competitive communities developing in high production environments (Feagin and Wu 2007, Mommer et al. 2011, Laliberté et al. 2012a). High leaf C:N was positively correlated with Hog swale habitats along NMDS 1 suggesting increased structural carbon in leaves, a pattern also seen in competitively dominant species of other highly productive habitats (Poorter and De Jong 1999). Elevated levels of structural carbon per unit nitrogen in competitive habitats helps provide support for plants to compete for light and would explain low SLA values seen in Hog swales, as presence of structural carbons typically has negative trade-off effects on SLA (Poorter and De Jong 1999). In contrast, the positive correlation of dune habitats with SLA values can be attributed to a higher abundance of annual strand species in mobile dune zones (e.g. *Cakile edentula* and *Conyza canadensis*; Ciccarelli 2015). In these dune habitats, the positive correlation with leaf C:N along NMDS 1 can also be explained by increased structural carbon. However, rather than contributing to competitive outcomes (like we propose for Hog swale), the structural carbon benefits dune grasses (e.g. *Spartina patens* and *Ammophila breviligulata*) that stand prostrate and contribute to dune building processes.

Increased root %N was also highly correlated with Hog swale trait-based communities and is often related to development of more nutritious soils over prolonged recovery time, with newly created N being rapidly taken up by plants (Du et al. 2007, Laliberté et al. 2012b). Thus, existing on a topographically heterogeneous island experiencing the effects of disturbance less frequently may influence community structure in productive habitats by selecting for competitive traits that promote growth and structure (Leibold et al. 2004). These findings are generally supported by Grime's (1974) description of competitive species. Traits that are shaping these competitive communities are most influenced by those responsible for capture of light, water, nutrients, and space which may be causing the trait-based dissimilarity between Hog swale habitats and all other habitats investigated in this study.

Similarities between inter- and intra-island trait-based community compositions (e.g. Hog dune – Metompkin swale and Metompkin dune – Metompkin swale comparisons) may also be driven by the frequency at which each habitat experiences disturbance. Aboveground traits that influenced communities of highly disturbed habitats include those that promote survival in well drained sandy soils of recently overwashed areas (e.g. $\delta^{13}C$) as well as belowground traits that maintain species persistence during disturbance (e.g. RTD; Roumet et al. 2006). Trait-based communities in habitats experiencing increased disturbance also had traits associated with rapid growth (e.g. high %N and SLA). We suggest that %N and SLA are elevated in high disturbance habitats because they are important for growth of annuals and young perennials that quickly colonize newly disturbed resource space (e.g. *Eragrostis spectabilis*, *Gnaphalium purpureum,* and *Dysphania ambrosioides*), a phenomena that has been traditionally described as ruderal strategy (Grime 1974, Ciccarelli 2015). We show here that rapid growth traits do not necessarily correlate with high productivity communities. For example, disturbance as an indirect driver of trait-based community composition could decrease productivity, limiting biotic competitive interactions, elucidating why competitive traits like height, C:N, and SRL lack influence in our high disturbance habitats. Thus, lower productivity may not only be a response of trait-based communities of these habitats but may act as a driver of mean trait-based community composition differences between Hog dune, Metompkin dune, and Metompkin swale habitats compared to Hog swale.

Trait-based community site-to-site dispersion

Trait-based dispersion is often positively correlated with biomass; however this is not true for all systems (Cadotte 2017). Our inter-island comparison of swale habitats found that highly productive Hog swale habitat had significantly lower dispersion than low productivity Metompkin swale habitat. Trait-based dispersion may not reflect increases in productivity when traits influencing species coexistence do not also specifically affect productivity function (Cadotte 2017), a mechanism that may explain patterns in our coastal system. More specifically, traits that promote coexistence of species in competitive Hog swale plant communities may also be responsible for increased productivity, while traits that promote coexistence in highly disturbed Metompkin swale plant communities do not affect productivity.

However, research has also suggested that differences in community dispersion could be a result of divergent assembly processes. It has been suggested that severe levels of disturbance allows stochastic assembly to predominate community development and structure, resulting in high site-to-site variation (Lepori and Malmqvist 2009). Conversely, reduced variability among sites, as seen in Hog swale trait-based communities, might be explained by lower disturbance and high similarity of trait values because communities would be driven by dominant species that share similar traits and persist as species compete for resource space (Li and Shipley 2018). While we did not specifically test for difference in community assembly rules (deterministic vs. stochastic) in this study, the differences in site-to-site variation of the trait-based communities in Hog and Metompkin swale habitats show potential for future studies using barrier islands as models to further understand how disturbance and topographic heterogeneity mediate trait-based community structure and assembly.

Conclusion

Our study shows the importance of incorporating trait-based analyses when approaching questions about community structure of barrier island habitats differing in disturbance regimes. Our results suggest that inter-island differences in topography influences environmental variability of adjacent dune-swale habitats. Moreover, inter- and intra-island differences in trait-based community composition and dispersion are likely linked to topographic heterogeneity, disturbance frequency, and ecosystem productivity. Low disturbance swale habitats were influenced by traits that promote success in highly competitive environments and feedback with increased productivity. High disturbance trait-based communities of dune and swale habitats were primarily characterized by rapid growth traits that promote quick response to disturbance events. Questions regarding relationships between trait-based dispersion and productivity remain, but this analysis provides insights of how barrier islands may serve as good systems to study assembly processes and linkages with productivity.

DATA AVAILABILITY

Functional trait, species, and biomass productivity data from this project is available on the Virginia Coast Reserve data portal: Brown, J. and J. Zinnert. 2017. Species composition and plant functional traits on Hog and Metompkin Islands, VA 2016-2017. Virginia Coast Reserve Long-Term Ecological Research Project Data Publication knb-lter-vcr.296.2

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Tables and Figures

Table 2.1 Summary of functional roles of traits selected for this study with trait relation to functional role in ecosystems.

Aboveground		
Functional Role	Traits	References
Plant growth functions related to photosynthetic rate, relative growth rate, light capture, and leaf lifespan.	Height Specific leaf area (SLA) Leaf nitrogen content (leaf %N)	Reich et al. 1998, Cornelissen et al. 2003, Wright et al. 2004
Resource conservation strategies related to functional stress tolerance, nutrient use efficiency, gas exchange, and water use efficiency.	Leaf carbon content Leaf ^{13}C:^{12}C (δ^{13}C) Leaf carbon:nitrogen (leaf C:N)	Díaz et al. 2004, Pérez-Harguindeguy et al. 2013, Liu et al. 2017
Belowground		
Functional Role	Traits	References
Root growth strategies related to tradeoffs between proliferation of low density roots for resource uptake and increased root tissue construction for long root lifespan and drought resistance.	Specific root length (SRL) Root tissue density (RTD)	Eissenstat 1991, Craine et al. 2001, Craine and Lee 2003, Birouste et al. 2014
Root chemical traits as indicators of root nutrient and water use patterns, root growth rate, and root construction	Root carbon content (leaf %C) Root nitrogen content (root %N) Root ^{13}C:^{12}C (δ^{13}C)	Reich et al. 1998b, Tjoelker et al. 2005, Roumet et al. 2006

Table 2.2 Pairwise comparison of MRPP results on environmental factors between habitat types on Hog and Metompkin Island. Bold indicates significance with a corrected α = 0.008.

Habitat type comparison	T	*P*
Hog dune – Hog swale	-8.82	**<0.0001**
Hog dune – Metompkin dune	-10.29	**<0.0001**
Hog dune – Metompkin swale	-9.38	**<0.0001**
Hog swale – Metompkin dune	-10.65	**<0.0001**
Hog swale – Metompkin swale	-10.48	**<0.0001**
Metompkin dune – Metompkin swale	-0.28	0.2698

Table 2.3 Pairwise comparison of MRPP results on trait-based community composition differences between habitat types on Hog and Metompkin Island. Bold indicates significance with a corrected α = 0.008.

Habitat comparison	T	*P*
Hog dune – Hog swale	-6.10	**0.0002**
Hog dune – Metompkin dune	-5.13	**0.0012**
Hog dune – Metompkin swale	-3.29	0.0107
Hog swale – Metompkin dune	-13.27	**<0.0001**
Hog swale – Metompkin swale	-12.07	**<0.0001**
Metompkin dune – Metompkin swale	0.03	0.4092

Table 2.4 Beta-dispersion Tukey HSD comparison of trait-based community dispersion differences among habitat types on Hog and Metompkin Island, with differences of mean distance to centroid indicated as absolute values. Bold indicates *P* < 0.05.

Habitat type comparison	Difference	SE Difference	*P*
Hog dune – Hog swale	0.59	0.406	0.4725
Hog dune – Metompkin dune	0.30	0.393	0.8754
Hog dune – Metompkin swale	0.50	0.393	0.5834
Hog swale – Metompkin dune	0.29	0.393	0.8770
Hog swale – Metompkin swale	1.09	0.393	**0.0367**
Metompkin dune – Metompkin swale	0.78	0.380	0.1668

Figures Legends

Figure 2.1 Map of locations and topographic representation of sites on Metompkin Island (A) and Hog Island (B). The right-side limit of the figures indicates high-tide line on ocean side of each island.

Figure 2.2 Frequency distribution of plot elevations on Metompkin Island (A) and Hog Island (B). Histogram bars are overlaid by Kernel density curve to represent non-parametric probability distribution.

Figure 2.3 A) Non-metric multidimensional scaling of community level trait-based composition grouped by habitat type by convex hulls. Points represent plots in trait space with plus symbols (+) representing centroids for each habitat type. Colors are matched to island and habitat association. Centroids indicate mean trait-based composition. B) Vector plot of functional trait correlations modeled using envfit. Vectors are labeled with the functional trait they represent, and lengths indicate goodness of fit. Full correlation coefficient (r^2) values and significance of trait fits are reported in supplementary data (Appendix S1: Table 2.1).

Figure 2.4 Primary productivity (mean ± SE) as measured by end of season biomass for each island and community type. Letters indicate significant differences based on Tukey HSD pairwise comparisons, such that bars that do not share the same letter are significantly different ($P < 0.05$).

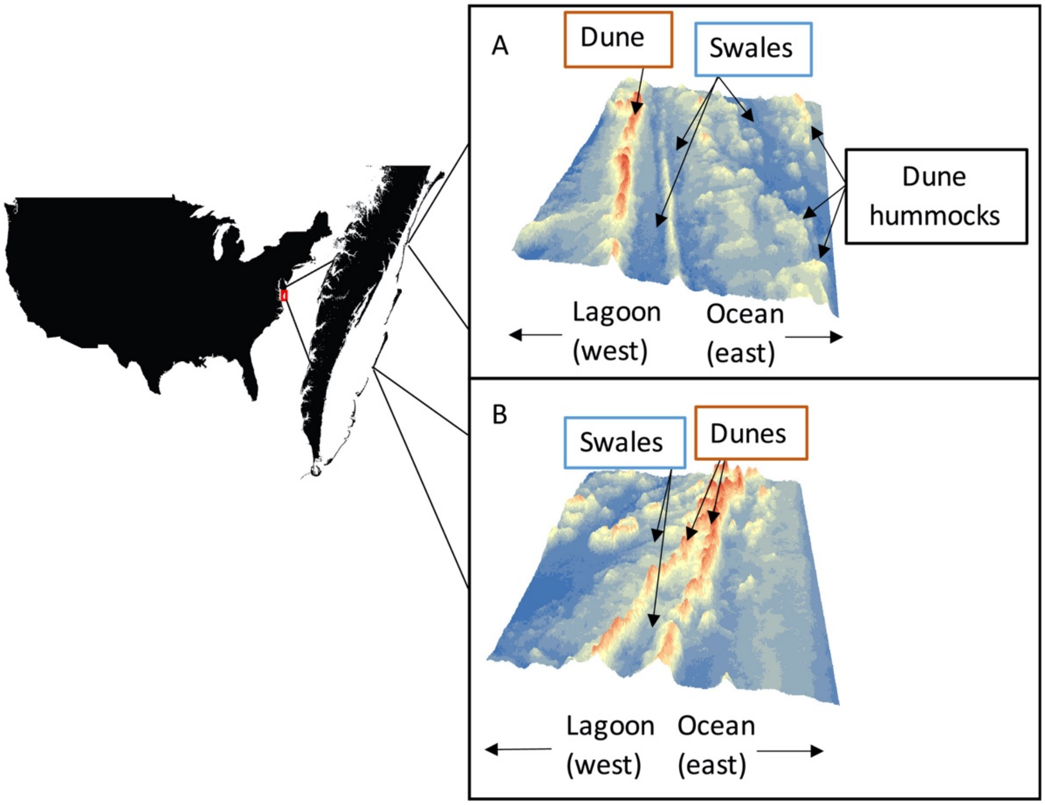
A
Dune
Swales
Dune hummocks
Lagoon (west)
Ocean (east)
B
Swales
Dunes
Lagoon (west)
Ocean (east)

Figure 2.1

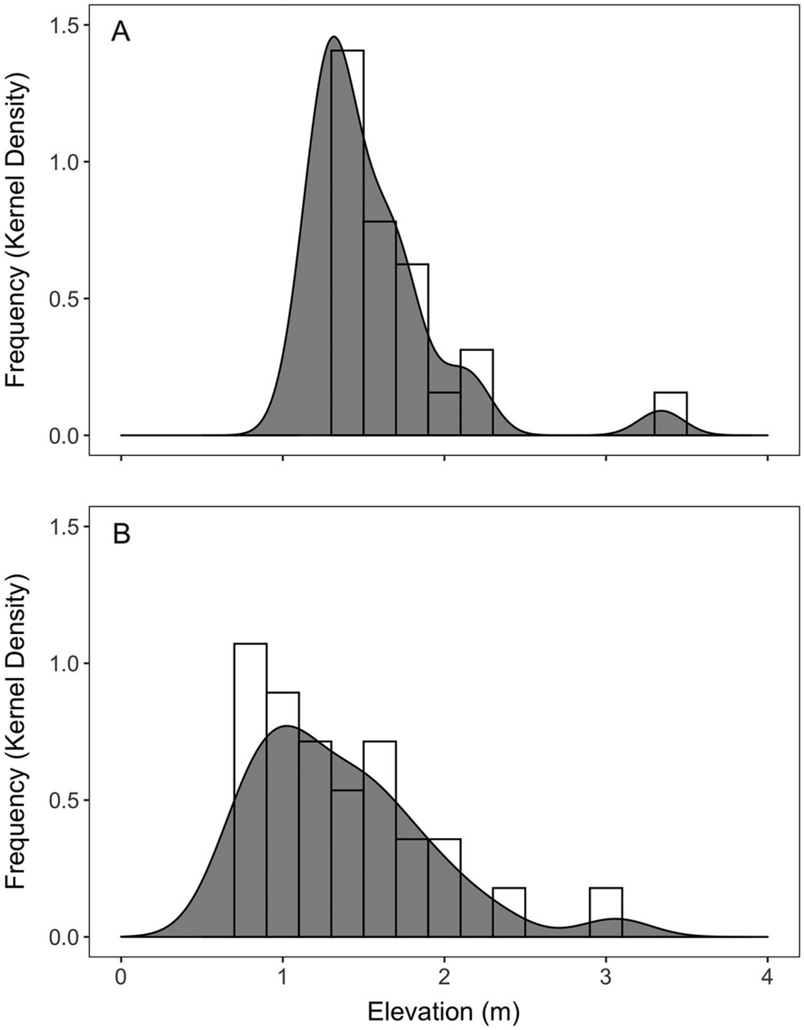
A
B
1.5
1.0
0.5
0.0
1.5
1.0
0.5
0.0
Frequency (Kernel Density)
Frequency (Kernel Density)
0
1
2
3
4
Elevation (m)

Figure 2.2

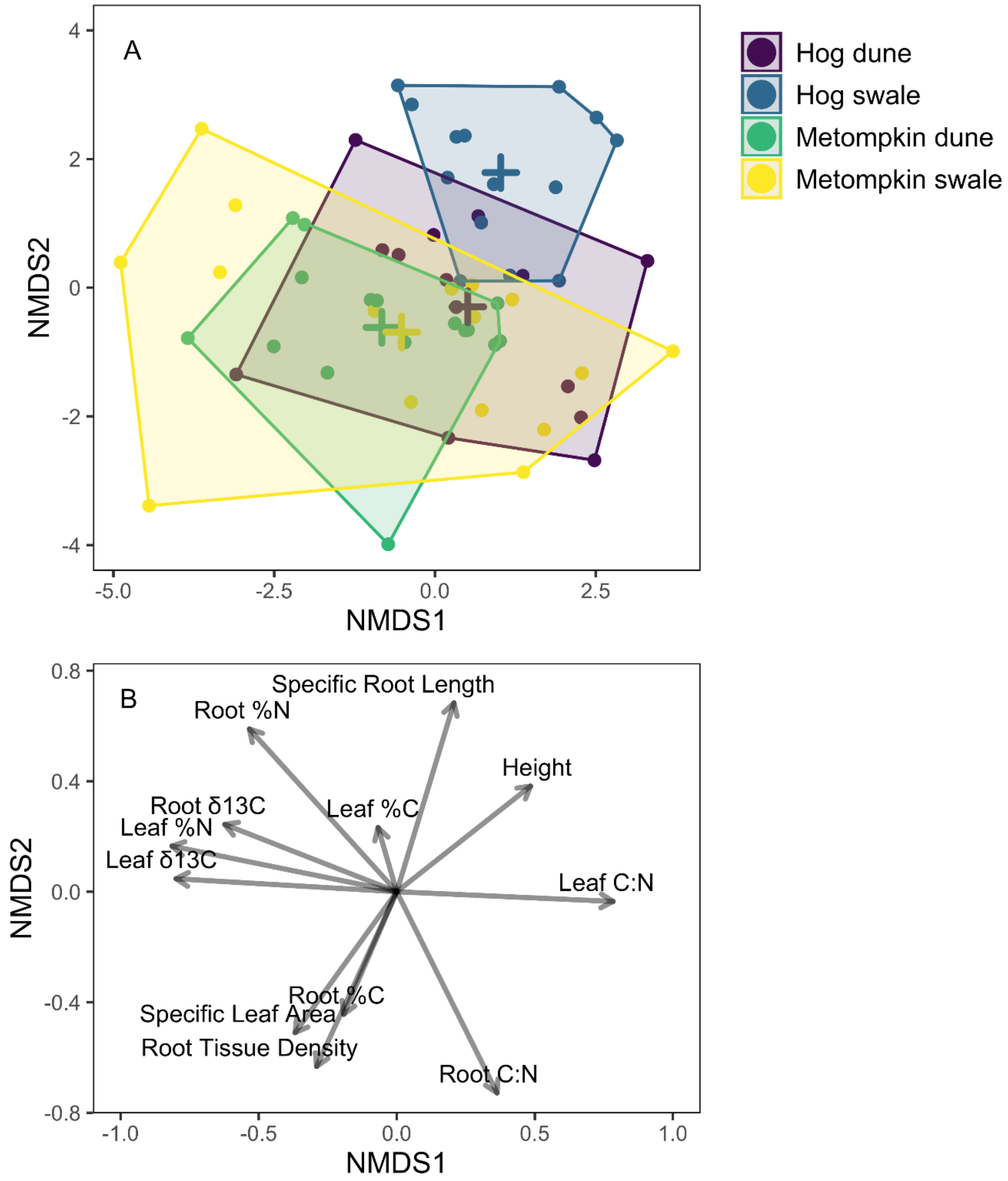
A
NMDS2
4
2
0
-2
-4
NMDS1
-5.0
-2.5
0.0
2.5
Hog dune
Hog swale
Metompkin dune
Metompkin swale
B
NMDS2
0.8
0.4
0.0
-0.4
-0.8
NMDS1
-1.0
-0.5
0.0
0.5
1.0
Specific Root Length
Root %N
Height
Root δ13C
Leaf %C
Leaf %N
Leaf δ13C
Leaf C:N
Root %C
Specific Leaf Area
Root Tissue Density
Root C:N

Figure 2.3

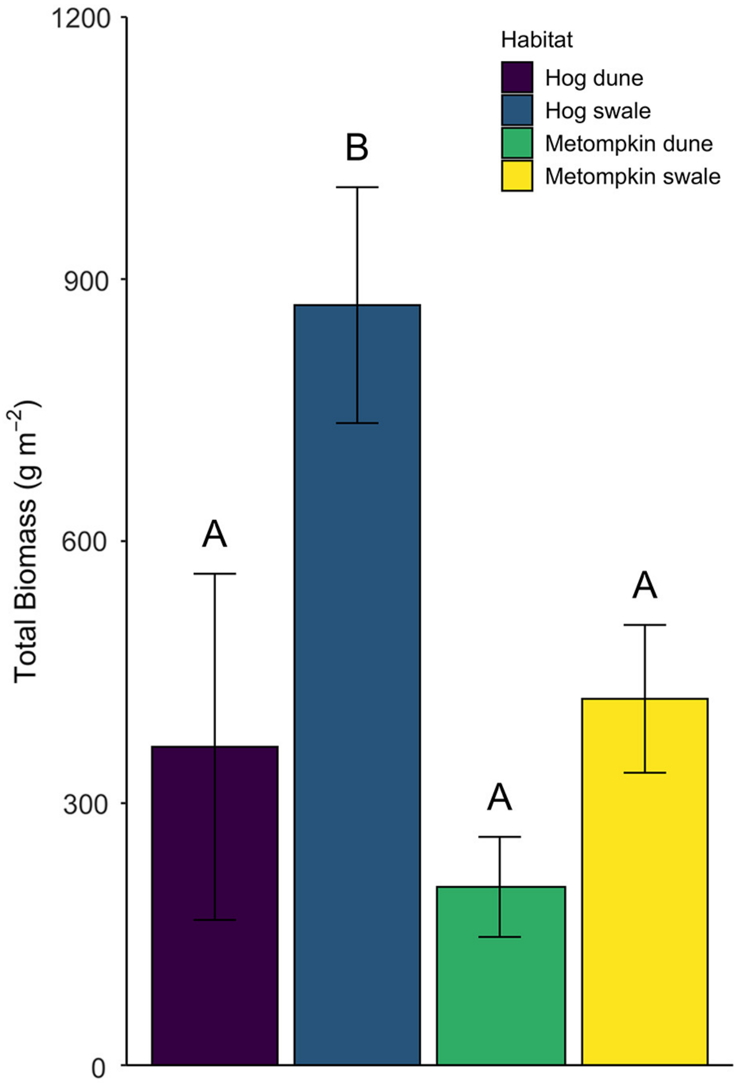
1200
900
600
300
0
Total Biomass (g m^{-2})
Habitat
Hog dune
Hog swale
Metompkin dune
Metompkin swale
A
B
A
A

Figure 2.4

Appendix

Methods for species composition analysis

Non-metric multidimensional scaling (NMDS) was used to investigate variation of species cover among community types. Bray-Curtis distance measure was used to calculate a distance matrix for species-based analysis. Ordinations were run (max. iteration of 999) with 3-dimensions to a minimized stress value (stress value < 0.2). Ordinations were performed in R (R Core Team, v. 3.5.0, 2018) using the vegan package. For interpretation, a PCA rotation was performed on each NMDS (first two axes represent maximum variation). Pearson correlation coefficients were calculated to facilitate interpretation of multivariate patterns (Appendix S1. Table 3).

Difference in species composition among habitat types were tested using multiple response permutation procedure (MRPP; $\alpha = 0.05$). Pairwise tests were performed to determine which habitat types differed in species composition (PC-ORD; Bonferroni adjusted $\alpha = 0.008$).

Table S2.1 Coordinates of traits in multivariate space (NMDS 1 and NMDS 2) and correlation coefficients (r^2) values from envfit model (Fig.3). Asterisks on r^2 values represent significance ($P < 0.05$).

Trait	**NMDS 1**	**NMDS 2**	r^2
Height (cm)	0.785	0.619	0.38*
Specific leaf area (g cm^{-2})	-0.585	-0.811	0.40*
Leaf nitrogen content (% N)	-0.980	0.199	0.69*
Leaf carbon content (% C)	-0.280	0.960	0.06
Leaf δ^{13}C	-0.999	0.059	0.64*
Leaf C:N	0.999	-0.045	0.62*
Root tissue density (g cm^{-3})	-0.417	-0.909	0.48*
Specific root length (g m^{-2})	0.290	0.957	0.51*
Root nitrogen content (% N)	-0.672	0.741	0.63*
Root carbon content (% C)	-0.398	-0.918	0.23*
Root δ^{13}C	-0.931	0.364	0.45*
Root C:N	0.446	-0.895	0.66*

Table S2.2 Pairwise comparison of MRPP results on species- and trait-based community composition differences between community types on Hog and Metompkin Island. Bold indicates significance with Bonferroni corrected α = 0.008.

Community type comparison	T	*P*
Hog dune – Hog swale	-6.10	**<0.0001**
Hog dune – Metompkin dune	-6.07	**<0.0001**
Hog dune – Metompkin swale	-3.06	0.0115
Hog swale – Metompkin dune	-10.20	**<0.0001**
Hog swale – Metompkin swale	-6.07	**<0.0001**
Metompkin dune – Metompkin swale	-2.54	0.0218

Table S2.3 Species Pearson correlation coefficients for 3-dimensional NMDS solution (Fig. 3).

Species	NMDS 1	NMDS 2	NMDS 3
Achillea millefolium	-0.000	-0.005	0.104
Ammophila breviligulata	0.149	-0.279	-0.454
Andropogon virginicus	0.073	0.213	0.489
Baccharis halimifolia	0.019	-0.172	0.334
Borrichia frutescens	-0.434	-0.029	0.049
Cakile edentula	0.095	-0.141	-0.319
Carex lurida	0.079	0.017	0.152
Cenchrus tribuloides	0.031	0.109	-0.093
Chenopodium ambrosioides	0.097	-0.116	-0.219
Cirsium horridulum	0.003	0.078	-0.143
Conyza canadensis	0.243	0.258	-0.032
Cyperus esculentes	0.255	0.555	-0.000
Distichlis spicata	-0.544	0.069	0.044
Eragrostis spectabilis	0.125	-0.582	-0.061
Fimbristylis castanea	-0.283	-0.028	-0.126
Gnaphalium purpureum	0.112	-0.346	-0.016
Hypericum gentianoides	-0.040	0.097	-0.011
Iva frutescens	-0.209	-0.061	-0.017
Juncus gerardi	-0.055	-0.04	0.358
Krigia virginica	0.125	-0.029	-0.201
Lepidium virginicum	0.020	0.014	-0.093
Limonium carolinianum	-0.479	0.075	-0.029
Linum virginianum	-0.002	-0.088	0.235
Morella cerifera	-0.059	-0.163	0.459
Monarda punctata	-0.009	0.075	-0.162
Oenothera humifusa	0.170	-0.078	0.129
Panicum amarum	0.249	0.194	-0.228
Panicum dichotomiflorum	0.210	-0.034	0.129
Phragmites australis	0.135	-0.160	0.353
Pseudognaphalium obtusifolium	0.025	-0.144	-0.036
Rumex acetosella	0.122	0.219	-0.078
Salicornia depressa	-0.479	0.002	-0.161
Schoenoplectus americanus	-0.056	0.121	-0.023
Setaria parviflora	-0.047	0.033	0.097
Solidago sempervirens	0.328	-0.033	0.097
Spartina alterniflora	-0.528	0.127	-0.014
Spartina patens	-0.278	0.272	-0.064
Strophostyles helvola	-0.034	0.021	-0.107

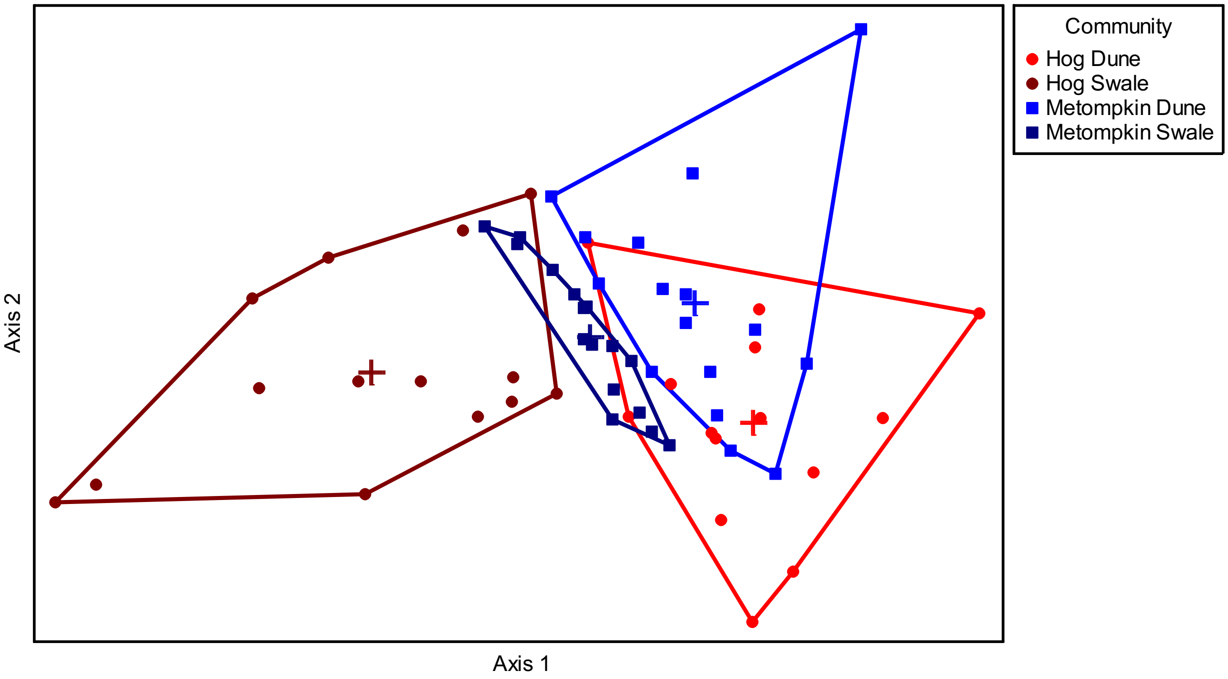

Figure S2.1 Principal Components Analysis (PCA) of environmental variables (elevation, distance to shoreline, and soil salinity). Axes 1 and 2 explained 82.2% of the total variation (PC1 = 60.7%, PC2 = 21.5%). Colors and convex hulls highlight groups based on habitat type.

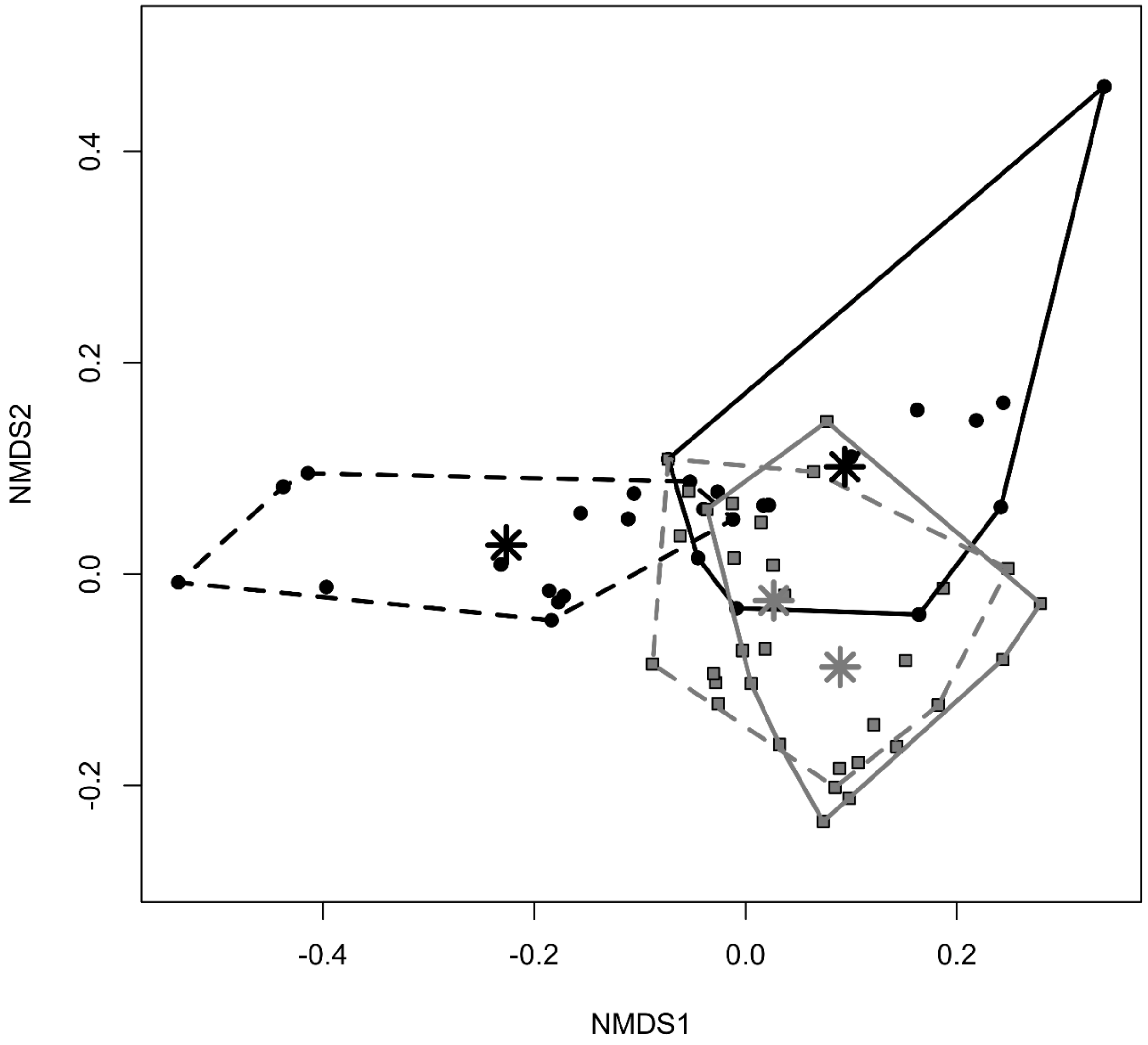

Figure S2.2 Non-metric multidimensional scaling of species-based community composition grouped by habitat type. Black circles represent plots located on Hog Island and gray squares represent plots on Metompkin Island. Solid lines group plots on each island defined as dune habitats, while dotted lines group plots on each island defined as swale habitats. Asterisks represent centroids for each habitat with colors matched to island association. Convex hulls cluster habitat types for each island, with centroids for each habitat type providing a measure of “mean” species composition for each community.

Chapter 3: Plant community re-organization and increased productivity caused by multi-year nutrient enrichment of a coastal grassland

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Abstract

Nutrient enrichment alters plant community structure and function at a global scale. Coastal plant systems are expected to experience increased rates of nitrogen and phosphorus deposition by 2100, caused mostly by anthropogenic activity. Despite high density of studies investigating connections between plant community structure and ecosystem function in response to nutrient addition, inconsistencies in system response based on the ecosystem in question calls for more detailed analyses of nutrient impacts on community organization and resulting productivity response. Here, we focus on nutrient addition impacts on community structure and organization as well as productivity of different lifeforms in a coastal grassland. We established long-term nutrient enrichment plots in 2015 consisting of control (C), nitrogen (N), phosphorus (P), and nitrogen + phosphorus (NP) treatments. In 2017 we collected graminoid and fob productivity, root productivity, and community composition for each plot. We found that N and NP enrichment significantly increased productivity, while P did not, highlighting N limitation in coastal systems. Importantly, nutrient enrichment treatments did not alter root productivity. However, all treatments caused significant differences in community composition. Using rank abundance curves, we determined that community composition differences were driven by increased dominance of nitrophilous graminoids, re-organization of subordinate species, and species absences in N and NP plots. Results of this study highlight how coastal grassland communities are impacted by nutrient enrichment. We show that community re-organization is an important consideration that helps disentangle community-level impacts of nutrient enrichment that include increased dominance and absence of critical species.

Introduction

As global N and P enrichment becomes more common, researchers are investigating the effects nutrient enrichment has on plant communities around the world (Fay et al. 2015, Harpole et al. 2016, Firn et al. 2019). Increased nutrient enrichment can alter multiple aspects of plant community composition, plant functional trait expressions, and ecosystem functionality (Avolio et al. 2014, Borer et al. 2014, Fay et al. 2015, La Pierre and Smith 2015, Koerner et al. 2016, Firn et al. 2019, Brown and Zinnert 2021). Nutrient enrichment influences species composition as well as other components of community structure and organization (i.e., species diversity, richness, evenness, and dominance), often times at large scales (Carson and Barrett 1988, Clark and Tilman 2008, Hautier et al. 2009, Bobbink et al. 2010, Avolio et al. 2014, Koerner et al. 2016, Harpole et al. 2017, Soons et al. 2017, Zhang et al. 2019). However, scientific literature reflects a lack of consistency regarding community response to nutrient enrichment and fewer studies include coastal grasslands. For example, many studies have found increased N and P result in decreased species diversity, evenness, and richness, with species disappearance identified as a common occurrence (Wilson and Tilman 1991, Clark et al. 2007, Hautier et al. 2009, De Schrijver et al. 2011, Ceulemans et al. 2013, Flores-Moreno et al. 2016, Demalach and Kadmon 2017). Others found no difference in community structure after nutrient treatments (Sundqvist et al. 2014, Read et al. 2018, Yang et al. 2018). Likewise, there are also studies that demonstrate how nutrient enrichment can influence some facets of community composition and structure but not others (Avolio et al. 2014). Similar inconsistencies occur with productivity response to nutrient enrichment. Most studies find nutrient additions significantly impact primary productivity level (e.g., Borer et al. 2014, Fay et al. 2015, Harpole et al. 2016, Zhao et al. 2019), while others found no impact on productivity, specifically within different lifeforms (Li et al.

2018). However, Li et al. (2018) attribute this finding to low levels of N added in their experiment. These variabilities highlight the importance of identifying how nitrogen impacts different lifeforms in different ecosystems (Tang et al. 2017).

Increased productivity can promote mechanisms responsible for altering community composition and structure by decreasing space and increasing composition for light (Hautier et al. 2009, 2014, Ceulemans et al. 2013, Borer et al. 2014, Demalach and Kadmon 2017, DeMalach et al. 2017, Harpole et al. 2017). The unpredictability of system response to nutrient enrichment highlights how ecosystem differences in regional species pools as well as pre-existing environmental conditions may influence the final result of community and ecosystem shifts in response to various nutrient enrichment treatments. Thus, it is critical that we investigate how N and P (both individually and synergistically) influence plant community dynamics in coastal ecosystems that differ in abiotic stressors from other grasslands. For example, barrier island grasslands are uniquely impacted by environmental factors that could influence how plant communities respond to nutrient enrichment (Young et al. 2011). Furthermore, barrier islands are present globally in the same areas that are expected to increase in nutrient deposition (Sinha et al. 2017).

In this study we focus on a mid-Atlantic coastal grassland. The mid-Atlantic region may experience dramatic increases in nutrient loading in the next 80-100 years (Sinha et al. 2017). Projections show that in the continental U.S., the Atlantic coast is expected to see the largest regional increase in N enrichment by 2100 (Sinha et al. 2017). Previous nutrient enrichment models suggest coastal areas in the northern hemisphere have also been dramatically impacted by N deposition in the last 30 years, with recent work highlighting the role reduced N deposition has on global N flux (Seitzinger et al. 2002, Li et al. 2016, Ackerman et al. 2019). Increases in P enrichment through run-off and deposition has accrued less focus but research has found that coastal waters are some of the most at-risk ecosystems for P enrichment (Peñuelas et al. 2013). For example, a model from Mahowald et al. (2008) suggests a net gain in atmospheric total P by oceans, while most other terrestrial systems show a net loss of total P.

Barrier islands occur along 30% of U.S. coastlines with more than half existing on the Atlantic coast where nutrient enrichment is expected to spike (Stutz and Pilkey 2001, Sinha et al. 2017). Barrier island dynamics including disturbance response and resilience are tightly coupled with plant communities and how they feedback with physical processes (Ehrenfeld 1990, Young et al. 2011, Zinnert et al. 2019, Brown and Zinnert 2020). High nutrient enrichment via run-off and deposition onto barrier islands can play a substantial role in driving plant community differences in species and functional trait compositions given N-limitations of sandy soils constituting these islands (Art et al. 1974, Ehrenfeld 1990, Day et al. 2004, Brantley et al. 2014, Brown and Zinnert 2021). As a result, hypotheses have been established that attempt to explain how altered plant communities in response to nutrient enrichment lead to subsequent changes in barrier island dynamics, specifically disturbance response and successional processes in dune slacks (Bobbink et al., 2010; Zinnert, Stallins, Brantley, & Young, 2017).

Past nutrient enrichment studies in coastal systems have shown that N enrichment can cause long-term plant community change on sand dunes (Day et al. 2004, Heyel and Day 2006, Aggenbach et al. 2017). Day et al. (2004) found that after N enrichment on a dune system, species re-ordering ensues with longstanding shifts in species dominance and species disappearance. Both aboveground biomass and belowground biomass were higher just one year after N fertilization treatment with effects lasting nearly 10 years (Heyel and Day 2006). Similar conclusions have been made in European dune systems where elevated nutrient deposition increases productivity and alters plant community structure, specifically reducing species richness (Soons et al. 2017). Previous research in calcareous European sand dunes also shows that decalcified, acidic sand dunes are more sensitive to N-deposition due to the increased availability of P, making both N and P important components if we are to understand plant community response to expected nutrient enrichment (Kooijman et al. 2017).

Phosphorus enrichment in coastal systems has gathered less focus, especially in coastal grasslands. It has been proposed that P is not a limiting nutrient in terrestrial coastal systems (Kachi and Hirose 1983, Osgood and Zieman 1993, Kooijman et al. 1998). However, Kooijman et al. (2017) showed sensitivity of dune vegetation to N-deposition when P is abundantly available in the soil, justifying the investigation of N, P, and NP treatments in coastal systems. Furthermore, N and P can influence plant communities synergistically, such that productivity is higher in NP treatments than either N or P treatments individually (Elser et al. 2007, Fay et al. 2015). Despite work on coastal sand dunes, knowledge gaps remain in non-dune coastal grassland systems regarding research investigating feedbacks between nutrient enrichment, increased productivity, plant community response, and systematic plant community reorganization.

We address these knowledge gaps by conducting a 3-year nutrient enrichment study to understand prolonged N, P, and NP treatments affect coastal grassland communities. Specifically, we aim to understand how nutrient enrichment alters lifeform productivity and plant community composition after 3 years of nutrient treatments. For this study we focus on how plant community structure (evenness, richness, and diversity) and reorganization explain altered community composition. We used visualization of rank abundance curves (RACs) to explore whether systematic plant community re-organization contribute to community differences

(Avolio et al. 2019). We hypothesize that 1) both aboveground and belowground graminoid and forb productivity will increase with N and NP treatments, 2) that N and NP additions will causes differences in common community structure metrics (species diversity, richness, and evenness), and 3) compared to control plots (serving as a reference of a natural community), N and NP, enrichment will cause differences in community composition.

Methods

Study site, plot establishment, and nutrient application

Hog Island (37.417 N, 75.686 W) is a barrier island part of the Virginia Coast Reserve (VCR) Long-term Ecological Research along the U.S. Atlantic coast. Nutrient fertilization plots were established on the southern end of the island in a dune slack environment composed of perennial graminoid and annual/biennial forb species. The site consists of sandy, well-drained soils and has been described as stable due to presence of a linear dune ridge which provides protection from coastal disturbances (Brown and Zinnert 2020).

Plots were established on the Hog Island grassland in 2015 following a modified Nutrient Network approach (Moulton 2017). Experimental set-up followed a randomized block design with four treatments (N = nitrogen, P = phosphorus, NP = nitrogen + phosphorus, and C = control) with each treatment replicated five times (n = 5). Treatment units within each block were 3 m^2 with 1 m walkways, which were not recognized as usable plot space. Units were subdivided into four 1 m^2 subplots to allow for separate spaces for productivity and species composition data collection. Phosphorus was applied as triple super phosphate, while N was applied as ammonium nitrate in particulate solid form. Fertilization application occurred twice per growing season (May and June) from 2015-2017, each nutrient treatment was administrated at 5 g m^{-2} yr^{-1}, totaling 10 g m^{-2} yr^{-1} by the end of each season.

Lifeform productivity sampling

Productivity was defined as all aboveground vegetation biomass at the end of the growing season (September 2017). Productivity was sampled from one subplot within a haphazardly placed 0.1 x 1 m frame and extrapolated to represent plot level productivity (g m^{-2}). Samples were sorted by lifeform (graminoid or forb), oven dried separately for 72 h at 60^{o} C, and weighed (g). Belowground productivity was also collected in 2017. We used a single root core taken in a haphazardly selected spot in the same subplot where aboveground biomass was collected. For each root core, large roots were identified visually and collected from each soil core before the remainder of the cores were washed in a series of sieve stacks to collect smaller roots. All roots were rinsed with water before samples were oven dried for 72 h at 60^{o} C and weighed (g).

Species composition and community structure

In July of 2017 we recorded aerial species cover to the nearest 1% using an undisturbed subplot designated for species composition data collection. We calculated species evenness, richness, and diversity using the *codyn* package in R (Hallett et al. 2016). Species richness was computed as the number of different species in each replicate while species evenness was calculated as *Evar* for each replicate, this evenness index is recommended for general use compared to a number of other evenness indices (Smith and Wilson 1996). *Evar* produces an index between 0-1, where 0 represents minimum evenness within a replicate and 1 represents maximum evenness within a replicate (Smith and Wilson 1996). Species diversity was calculated as Shannon's diversity index for each replicate (H').

Abundance differences were calculated for each species using control plots as a reference treatment and pooled all replicates to create a single species pool (Hallett et al. 2016). This calculation allowed us to investigate how abundance species present in the species pool differed between control plots and each treatment group. For example, a positive value indicated that a species had higher abundance in the treatment community than control community, while negative values indicated that a species had lower abundance in the treatment community than in the control community. Averaged species abundances were ranked in order of most abundant to least abundant to visualize the RACs for each treatment. RACs have been utilized in previous studies to inform differences in species compositions among treatment groups (Koerner et al. 2016, Avolio et al. 2019).

Statistical analysis

All analyses were conducted using R statistical program (R Core Team 2019). We conducted a one-way analysis of variance (ANOVA) to determine whether mean (± SE) graminoid and forb productivity significantly varied among nutrient treatments groups ($\alpha = 0.05$). We performed ANOVAs on log transformed productivity data to meet assumptions of normality and homogeneity of variance. Tukey HSD was used as a post-hoc test to determine significant pairwise differences among specific nutrient treatments ($\alpha = 0.05$).

Significant differences in community structure metrics (species diversity, richness, and evenness) among nutrient enrichment treatment groups was tested using a one-way ANOVA ($\alpha = 0.05$), after confirming assumptions of normality (checked visually using QQ-plots) and homogeneity of variance (assessed using Levene's test). Tukey HSD was used as a pairwise post-hoc test for each community structure metric ($\alpha = 0.05$).

Non-metric multidimensional scaling (NMDS) ordination was used to visualize community composition of nutrient enrichment treatments. Resulting NMDS visualization identifies replicate similarity based on distance in ordination space. Points (represent experimental replicates) closer together are more similar in community composition than points that are further apart. Prior to conducting the NMDS, species abundances were standardized to represent a relative abundance for each replicate. We conducted the NMDS in the *vegan* R package using Bray-Curtis distance measure to calculate a distance matrix of relative species abundances for each treatment replicate (Oksanen et al. 2019). The NMDS was performed using 3-dimensions to a minimized stress value (maximum iteration = 999). We used Monte Carlo randomization test to determine whether the final NMDS solution had a lower stress than would be expected by chance ($\alpha = 0.05$). A principal component analysis (PCA) rotation was applied to the finalized NMDS to aid interpretation. This technique rotates the finalized plot such that NMDS axis 1 and 2 represent maximum variation of the data.

We used the envfit function in *vegan* to calculate species correlations in ordination space (Oksanen et al. 2019). Significance of fitted species correlations was assessed within the envfit function using permutation test (permutation = 999). Species that produced significant *p*-values are more correlated in ordination space than would be expected by chance and thus explain a large proportion of variation in the data. These species were highlighted in RACs to examine the impact of rank order shuffling on community composition dissimilarity.

Centroids for each treatment group were calculated by aggregating site scores. Centroids can be interpreted as mean community composition for each treatment group. We used a permutational multivariate-ANOVA (PERMANOVA) to determine significant differences among community composition of nutrient enrichment treatments (permutation = 999, $\alpha = 0.05$) (Anderson 2017). A pairwise post-hoc test was conducted to determine which pairwise treatment groups had different community compositions (FDR adjusted $\alpha = 0.05$). We calculated multivariate homogeneity of group dispersion using the betadisper function in *vegan* to determine within-group replicate variation (Anderson 2006, Oksanen et al. 2019). Testing homogeneity of multivariate group dispersion has been identified as a distance-based method of identifying differences in beta-diversity among groups (Anderson et al. 2006). We used an ANOVA on mean distance between each point and their respective median centroid to determine significant differences of beta-dispersion among treatment groups ($\alpha = 0.05$). A Tukey HSD test was used as a post-hoc test for pairwise differences in mean beta-dispersion ($\alpha = 0.05$).

Results

Lifeform and belowground productivity

Graminoid productivity was significantly different among our nutrient enrichment treatments (ANOVA: $F_{3,16} = 13.57$, *p*-value = 0.0001). Graminoid productivity was significantly higher in N (744 ± 102 g m^{-2}) and NP (1187 ± 262 g m^{-2}) plots compared to C (186 ± 46 g m^{-2}) and P (271 ± 71 g m^{-2}) plots (Fig. 3.1a). While graminoid productivity in N and NP treatments were not significantly different from one another, it is important to highlight NP treated plots were more than 1.5 and 4.3 times more productive than N and P treated plots, respectively. We did not find significant differences in forb productivity among nutrient treatments (ANOVA: $F_{3,}$

$_{16} = 2.98$, p-value = 0.0625), but did find NP plots were ~32 times more productive than C plots, ~9 times more productive than P plots, and ~2 times more productive than to N plots (Fig 3.1b).

Despite clear differences in graminoid productivity across nutrient enrichment treatments, we found no difference in belowground productivity among nutrient enrichment treatments (ANOVA: $F_{3, 16} = 0.15$, p-value > 0.05) (Fig. S3.1).

Community structure, composition, and organization

There were 22 different plant species identified across all plots consisting of 10 graminoid species and 12 forb species (Table 3.1). Neither species diversity (ANOVA: $F_{3, 16} = 1.71$, p-value > 0.05) nor species richness (ANOVA: $F_{3, 16} = 1.37$, p-value > 0.05) were significantly affected by nutrient treatment (Table 3.2). However, species evenness was significantly different among treatment groups (ANOVA: $F_{3, 16} = 4.73$ and p-value = 0.0150). Based on pairwise test results, we found mean species evenness of NP treated communities was significantly lower than P treated communities (Table 3.2).

Our NMDS on treatment community composition reached a final 3-dimensional solution with a minimized stress = 0.08 (Fig. 3.2). Nutrient enrichment treatments caused all treatments to differ in mean community composition (PERMANOVA: $F_{3, 16} = 4.52$, p-value = 0.001). Community composition of all treatment groups clearly varied along NMDS1 (Fig. 3.2). Within-group dispersion did not vary, suggesting similar beta-diversity among nutrient treated communities ($F_{3, 16} = 2.05$, p-value > 0.05).

Species correlated with NMDS1 and/or NMDS2 were used to disentangle species specific contributions to the dissimilarity of communities (Table 3.1). Nutrient treated communities (N, P, and NP) correlated with perennial graminoid species (*Ammophila* *breviligulata, Spartina patens, Cyperus esculentes, Panicum amarum,* and *Setaria parviflora*), suggesting higher abundance of these species in treated communities compared to control communities (Table 3.1). Alternatively, control communities were correlated with forb species, including *Conyza canadensis*, *Gnaphalium purpurea*, and *Linum virginianum* as well as a perennial graminoid, *Andropogon virginicus* (Table 3.1).

RACs and Abundance Differences

Differences in species rank order, as well as species absences, existed between treatment and control communities (Fig. 3.3). This is especially true for species that non-randomly correlated with NMDS axes. Differences in species rank order were directly informed by abundance differences between treatment and control communities. Similar species (e.g., *S. patens*, *A. breviligulata*, *S. parviflora*, and *C. esculentes*) had higher abundance across treatment communities compared to control communities (Fig. 3.4). For some species (i.e., *S. patens* and *A. breviligulata*) this resulted in increased dominance, as these species did not differ in rank position across treatments (Fig. 3.3). For example, in P treated communities, *S. patens* abundance was, on average, ~6% higher while *A. breviligulata* was 2% higher than in control communities (Fig 3.4a). In N treated communities we found that *A. breviligulata* had abundance >10% higher compared to control communities, while *S. patens* was still ~6% higher (Fig. 3.4b). In NP treated communities, we again found both *A. beviligulata* and *S. patens* had a higher abundance compared to control communities, but by larger percentages (11% and 8%, respectively) (Fig. 3.4c). In other cases, abundance differences were coupled with re-ordering of species ranks. For example, *S. parviflora* abundance was between 7-11% higher and ranked higher in all treatment communities compared to controls (Fig. 3.3, Fig. 3.4). In NP treated communities, a similar pattern was exhibited for *C. esculentes*, with abundance 11% higher in

NP communities compared to controls, which coupled with an increased species rank order (Fig. 3.3a and 3.3d, Fig. 3.4a and 3.4c).

Conversely, similar species existed at lower abundance across all treatment communities compared to control communities. For example, *C. canadensis* and *G. purpurea* (annual forbs) had lower abundance in treatment communities compared to control communities (Fig. 3.4). *Gnaphalium purpurea* abundance was consistently ~1% lower in nutrient treated communities compared to control communities. For *G. purpurea* this small negative difference in abundance was substantial as it caused *G. purpurea* to decrease between 3-5 rank positions across treatment communities compared to controls (Fig. 3.3). *Conyza canadensis* abundance was only 1% lower in P treated communities compared to controls and resulted in a similar rank in both communities (Fig. 3.3a-b, Fig. 3.4a). However, in N and NP treated communities, *C. canadensis* abundance was between 2-5% lower compared to controls which decreased the species by 4-5 rank positions (Fig. 3.3, Fig. 3.4).

Certain abundance differences, and associated species rank order, were treatment dependent. Phosphorus and NP treated communities had depressed abundance of *A. virginicus* compared to control communities (-4% and -7%, respectively), causing the species to decrease in rank (Fig. 3.3, Fig. 3.4). *Andropogon virginicus* existed at the same rank in control and N treated communities, and actually increased in abundance by ~3% in N plots (Fig. 3.3 and 3.4).

Many species fluctuated in presence/absence among communities, most of which could be caused by plot spatial differences and thus were not significantly correlated with community composition dissimilarity (Fig. 3.3, Table 3.1). However, some notable species were systematically absent in N and NP treated communities. We found *L. virginianum* (a low-ranking species that contributes to community dissimilarity) was absent in both N and NP treated communities (Fig. 3.3c-d, Table 3.1). In NP communities, *F. castanea* (which also significantly contributed to community divergence) was absent (Fig. 3.3d). *Fimbristylis castanea* also significantly contributed to community divergence in ordination space (Table 3.1).

Discussion

Our study shows N and NP enrichments increase graminoid productivity 4-6 times that of controls in our coastal grassland system but did not significantly increase forb productivity. This finding was expected given the level of N-limitation in coastal grassland soils (Art et al. 1974, Ehrenfeld 1990, Young et al. 2011). Our results complement studies in coastal dune systems that found increased aboveground productivity following N fertilization (Day et al. 2004, Heyel and Day 2006). Phosphorus enrichment did not have a significant impact on graminoid productivity. These findings support those identifying N as a more limiting nutrient than P in coastal systems (Kachi and Hirose 1983, Osgood and Zieman 1993, Kooijman et al. 1998, 2017). Our data show that NP enrichment caused the largest graminoid productivity increase of any nutrient enrichment treatment, which is consistent with European coastal system response to nutrients (Kooijman et al. 2017). Although we did not find a significant impact of nutrient enrichment on forb productivity, we identified trends of increased forb biomass in N and NP plots. Similar lifeform dependencies have been found in other studies (Li et al. 2018).

Unexpectedly, we did not find difference among treatments in root productivity. We expected root productivity to increase in response to nutrient enrichment based on previous research indicating that N can have long-lasting effects on belowground biomass in coastal dune systems (Heyel and Day 2006). However, given that our study was conducted in a coastal grassland swale, interactions that influence plant success differ from those dominating in dune plant communities, like increased competitive interactions and more frequent access to freshwater (Young et al. 2011, Brown and Zinnert 2020). Similar to our findings, global scale research shows that aboveground and belowground productivity does not always correlate in the presence of nutrient enrichment (Cleland et al. 2019).

Cleland et al. (2019) suggest belowground biomass increases with nutrient enrichment (N addition), but only when coupled with high light. However, as light competition increases at the soil surface, N additions decreased belowground biomass (Cleland et al. 2019). We suggest a similar response in our grassland system. Nutrient additions into sandy, nutrient poor soils likely increase aboveground productivity enough to effectively decrease light at the soil surface, causing decreased belowground production. Increased aboveground biomass also results in competition for light and space which has been shown to impact multiple aspects of community structure, composition, and organization which we also found in our study.

Multiple aspects of plant community structure can be altered as competition for light and space increases (e.g., Clark and Tilman 2008, Harpole et al. 2016, 2017, Koerner et al. 2016, Demalach and Kadmon 2017). Our results show that in a coastal grassland system, nutrient enrichment did not have impacts on species diversity or species richness. However, we did find that species evenness differed between specific nutrient enrichment treatments (NP and P). Plots fertilized with NP had significantly lower species evenness compare to P enriched plots. This pattern is likely driven by increased dominance of the top ranked species in the community (*A. breviligulata* and *S. patens*), a well-documented response to N additions in coastal dunes (Day et al. 2004, 2018).

Nutrient enrichments do not always influence traditional community structure metrics but can still impact community composition and organization (Avolio et al. 2014). Our data show this to be the case in our study system. Nutrient enrichment treatments drive significant differences in community composition, causing distinct communities associated with each treatment. Interestingly, we found that N and NP enrichment increase productivity and community composition compared to controls, while P enrichment only influence community composition, which is not common in other systems. Nutrient impacts on community composition, but not productivity highlights benefits of understanding both species and functional trait response to nutrient enrichment, as both can inform different community-ecosystem function relationships (Brown and Zinnert 2021). For studies focusing on species response, like we do here, investigating abundance differences and rank order reshuffling in each community, provide an outlet for detailing how increased dominance, species re-ordering, and even absences of specific species ignite community differences among nutrient treatment groups.

Our data shows that N, P, and NP enrichment all result in species re-ordering of a few key species and increased dominance of top-ranking species. These findings expand on previous dune research showing N fertilization increases the dominance of certain species over time (Day et al. 2004, 2018). *Ammophila breviligulata* and *S. patens* systematically increased abundance across treatment groups but did not contribute to species re-organization, as they remained the top ranked species across treatment groups. These findings are similar to those found in dune systems (Day et al. 2004). Additionally, other graminoid species displayed systematic increase in our grassland system across nutrient enrichment plots. For example, *S. parviflora* increased abundance across all treatment groups, which caused significant re-organization of species ranks within nutrient treated communities. *Setaria parviflora* became one of the top ranked species in each nutrient enrichment treatment, shifting from 9th ranked species in C plots to 3rd-4th ranked species in nutrient enrichment plots. *Cyperus esculentes* also increased abundance across all nutrient enrichment treatments, with a major increase in NP plots, where it became the 3rd most dominant species. The increase in abundance and rank order of graminoid species compared to other lifeforms has been found in many systems, as graminoids (especially those that are nitrophilous) tend to infiltrate N fertilized plots rapidly (Bobbink et al. 2010). As a result, literature describes nitrophilous graminoids as "winners" in nutrient driven competitive scenarios (Bobbink et al., 2010).

We also found certain species systematically decrease or become entirely absent in response to nutrient enrichment, contributing to community re-organization and community composition differences. *Andropogon virginicus* decreased abundance in P and NP plots, impacting its within-community rank position, driving differences in community composition. Species presence/absence differences exist among treatments, however only *F. castanea* and *L. virginianum* were significantly correlated with community divergence and also absent in N and NP plots. Nutrient enrichment (N, P, or NP) can cause differences among communities driven by dominant species re-ordering, while N and NP also can cause absence of key species in coastal grasslands. We posit that mechanisms leading to these responses are caused by interactions between increased productivity and traits of successful vs. unsuccessful species.

Previous research suggests long-standing community change on barrier island dunes by altered N flux is primarily driven by competitive exclusion (Day et al. 2004, 2018). We expand upon these findings by showing similar patterns in coastal grasslands and propose that certain characteristics of successful species promote increased abundance in nutrient enrichment plots, thus altering community organization and composition. Gross and Mittelbach (2017) show tall clonal species have substantial impacts on community structure in fertilized grasslands. Clonal species were found to increase in abundance after fertilization and correlated with decreased species richness, driven by the ability to spread vegetatively as decreased light limited seedling recruitment (Gross and Mittelbach 2017). In our study, species that increased dominance and rank order in fertilized plots (i.e., *S. patens*, *A. breviligulata*, *S. parviflora*, and *C. esculentes*) are clonal and do not rely on seedling recruitment in competitive environments. Furthermore, lower abundance and/or rank order of *G. purpurea* (annual forb) and *C. canadensis* (annual forb) across all treatments compared to controls. As annual forbs, abundance of these species can be limited by competitive exclusion, primarily through decreased dispersal ability and seedling recruitment in densely vegetated areas.

Competitive exclusion mechanisms can also explain lower abundance and rank order of *A. virginicus* (short-lived, ruderal, non-rhizomatous graminoid) in NP treated communities. We suggest increased productivity in NP treated plots influences *A. virginicus* recruitment. Previous studies have identified decreased *A. virginicus* abundance as competition increases (Bazzaz 1968, 1990). Peters and Lowance (1974) found *A. virginicus* abundance decreased in N fertilized plots, eventually leading to species replacement by other dominant graminoids. Interestingly, we found *A. virginicus* conserved its rank order in N treated communities, compared to controls, suggesting that abundance may not be consistently impacted across treatments. Alternatively, *A. virginicus* abundance may be impacted by other biotic/abiotic interactions in our system that were not measured in the current study.

Species absence was a significant factor influencing community composition differences and was most common in N and NP treated communities. While previously mentioned sub-optimal recruitment conditions can explain the absence of *L. virginianum* in N and NP plots, it does not explain the absence of *F. castanea* in NP plots. The *Fimbristylis* genera are often clonal and grow in dense caespitose tufts, which are traits that would indicate success in highly competitive environments. However, *F. castanea* has also been found to be an early successional species that pioneers newly developed swales and is eventually replaced by other mid- to late-successional species after 4-7 years (Johnson 1997). Nutrient enrichment has been shown to increase successional rate in a number of terrestrial systems around the world including coastal dune and grassland systems (Bobbink et al. 2010). Here, NP enrichment may alter rates of succession by the third year of enrichment.

Conclusions and implications for barrier island systems

Nutrient enrichment impacts on a barrier island grassland systems has not accrued much focus despite previous work indicating community composition and productivity changes in coastal dune systems (Day et al. 2004, 2018, Heyel and Day 2006). We show that some patterns are conserved across dune and grassland habitats. For example, we found nutrient enrichment increases aboveground graminoid biomass. However, belowground productivity has also been shown to increase in response to nutrient enrichment on barrier island dune systems (Heyel and Day 2006), which we did not find in our coastal grassland site. This suggests that adjacent habitats may be influenced by nutrients in different ways. Increased aboveground growth response could decrease light levels in at the soil surface in grasslands, which has been shown to stagnate N-driven belowground productivity at a global scale (Cleland et al. 2019).

Similar to dune studies, we also found nutrients impact community composition and organization by increasing dominance of *S. patens* and *A. breviligulata*, enhancing our understanding their role in grassland competitive interactions and influence over species evenness. Community composition differences without major changes in common community structure metrics (i.e., species diversity and richness) is evidence large impacts on community composition can occur from community re-organization of species ranks rather than changes in basic community structure metrics (Avolio et al. 2014, 2019).

By investigating abundance and RAC differences in nutrient enrichment plots compared to control plots, we found increased abundance and rank order of specific species inform how nutrient enrichment alters coastal grassland community organization. Species exhibiting clonal growth strategy may be better competitors as nutrient additions increase productivity and decrease light availability, a mechanism found in other grassland systems (Gross and Mittelbach 2017).

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Tables and Figures

Table 3.1 Species information with NMDS correlations along axis 1 and 2 and results from envfit randomization test. Bold represents significance (*p*-value < 0.05).

Species	**Lifeform**	**NMDS1**	**NMDS2**	***p*-value (envfit)**
Ammophila breviligulata	Graminoid	-0.65	0.23	**0.004***
Andropogon virginicus	Graminoid	0.44	0.81	**0.001***
Chamaesyce maculate	Forb	0.05	0.17	0.768
Conyza canadensis	Forb	0.32	-0.76	**0.002***
Cyperus esculentes	Graminoid	-0.75	-0.18	**0.001***
Dicanthelium longiligulatum	Graminoid	0.58	0.01	0.060
Dysphania ambrosioides	Forb	-0.07	-0.13	0.817
Festuca rubra	Graminoid	0.18	-0.15	0.622
Fimbristylis castanea	Graminoid	0.47	0.48	**0.016***
Gnaphalium purpurea	Forb	0.34	-0.61	**0.010***
Krigia caespitosa	Forb	-0.04	0.14	0.843
Lepidium virginicum	Forb	-0.26	-0.05	0.568
Linum virginianum	Forb	0.50	0.47	**0.022***
Monarda punctata	Forb	-0.34	-0.06	0.315
Oenthera humifusa	Forb	0.20	-0.41	0.165
Panicum amarum	Graminoid	-0.42	-0.52	**0.007***
Panicum dichotomiflorum	Graminoid	-0.17	0.09	0.720
Physalis walteri	Forb	-0.35	0.05	0.305
Sabatia stellaris	Forb	0.51	0.46	0.066
Setaria parviflora	Graminoid	-0.56	0.49	**0.001***
Solidago sempervirens	Forb	-0.51	0.00	0.083
Spartina patens	Graminoid	-0.57	0.40	**0.010***

Table 3.2 Effects of nutrient additions on plant community metrics (richness, evenness, and Shannon's diversity index [H']). Significant differences ($p < 0.05$) are indicated by shared letter codes based on post-hoc pairwise comparison results. Values that do not share the same letter are significantly different.

Treatment	**Richness**	**Evenness**	**H'**
Control	9.8 ± 0.6	0.42 ± 0.02^{ab}	1.74 ± 0.06
Phosphorus	10.4 ± 0.7	0.48 ± 0.01^{b}	1.89 ± 0.07
Nitrogen	10.2 ± 0.4	0.40 ± 0.10^{ab}	1.83 ± 0.06
Nitrogen + Phosphorus	9.0 ± 0.3	0.35 ± 0.01^{a}	1.73 ± 0.05

Table 3.3 Pairwise comparisons of plant community composition between nutrient treatments based on PERMANOVA post-hoc test. Bolded values indicate significant differences (*p*-value < 0.05).

Pairwise comparison	**F-statistic**	***p*-value (FDR adjusted)**
Control vs Phosphorus	3.14	**0.0240**
Control vs Nitrogen	4.32	**0.0120**
Control vs Nitrogen + Phosphorus	8.89	**0.0120**
Phosphorus vs Nitrogen	2.52	**0.0348**
Phosphorus vs Nitrogen + Phosphorus	4.35	**0.0140**
Nitrogen vs Nitrogen + Phosphorus	2.77	**0.0380**

Figure Legends

Figure 3.1 Productivity of graminoid (A) and forb (B) lifeforms among nutrient treatments in coastal mesic grassland. Productivity axes are adjusted to best represent data within lifeform groups. Treatments include C (control), P (phosphorus), N (nitrogen), and NP (Nitrogen + Phosphorus). Treatments that do not share letters are significantly different ($p < 0.05$) based on Nemenyi post-hoc pairwise comparison test.

Figure 3.2 Non-metric multidimensional scaling (NMDS) ordination of species composition grouped into convex hulls by nutrient treatment. Points represent within treatment replicates with stars indicating centroids of each treatment group. Centroids can be viewed as a representation of mean community composition. Colors and symbols are matched to nutrient treatment (C = control, P = phosphorus, N = nitrogen, NP = nitrogen + phosphorus).

Figure 3.3 Rank abundance curves for all species in each treatment group. Species that were found to significantly correlate with the spread on plots in our NMDS (Fig. 2) are highlighted with a colored halo.

Figure 3.4 Abundance difference of each species present in a: control and phosphorus (P) plots, b: control and nitrogen (N) plots, and c: control and nitrogen + phosphorus (NP) plots. Control plots are used as a reference to the natural coastal grassland community. Black bars indicate species that are more abundant in nutrient treated plots compared to control plots, while white bars indicate species that are less abundant in control plots compared to treated plots.

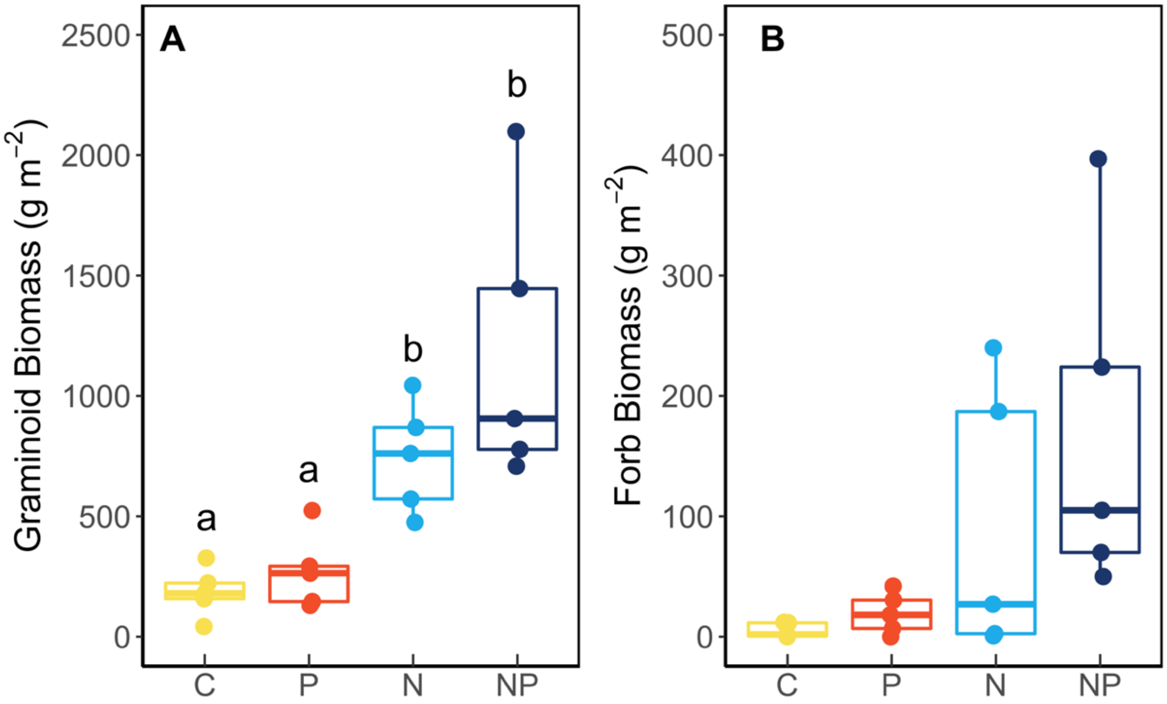
A
Graminoid Biomass (g m^{-2})
2500
2000
1500
1000
500
0
a
a
b
b
C
P
N
NP
B
Forb Biomass (g m^{-2})
500
400
300
200
100
0
C
P
N
NP

Figure 3.1

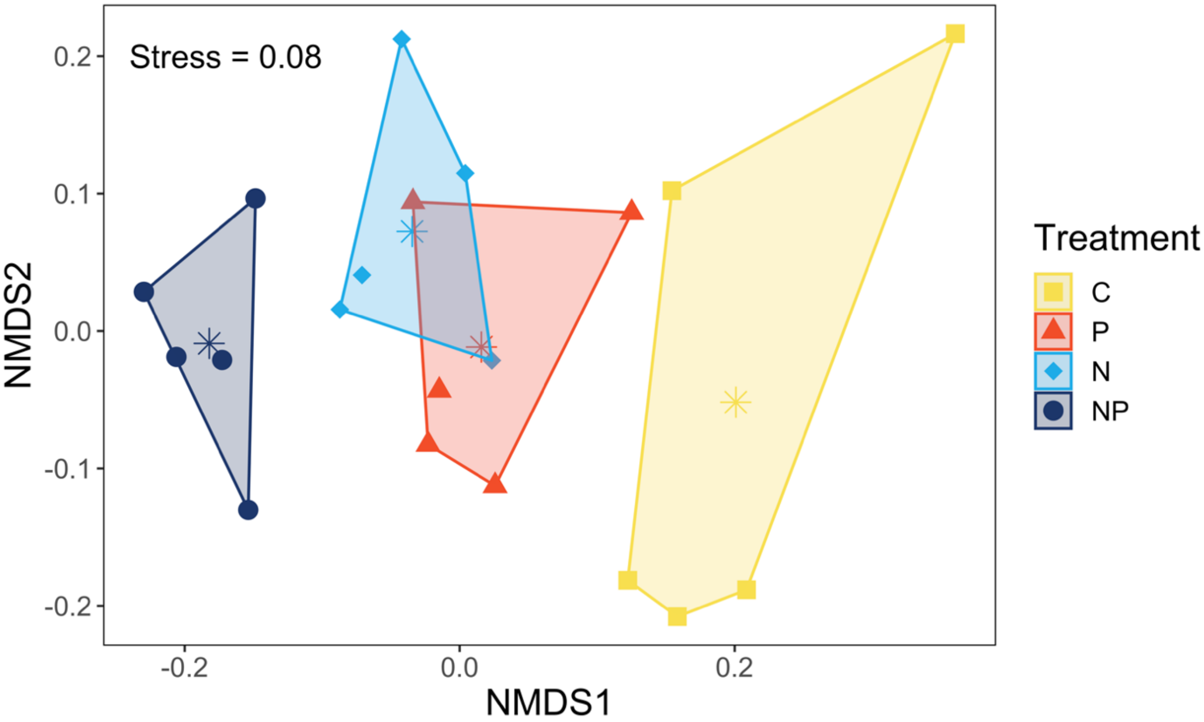

Figure 3.2

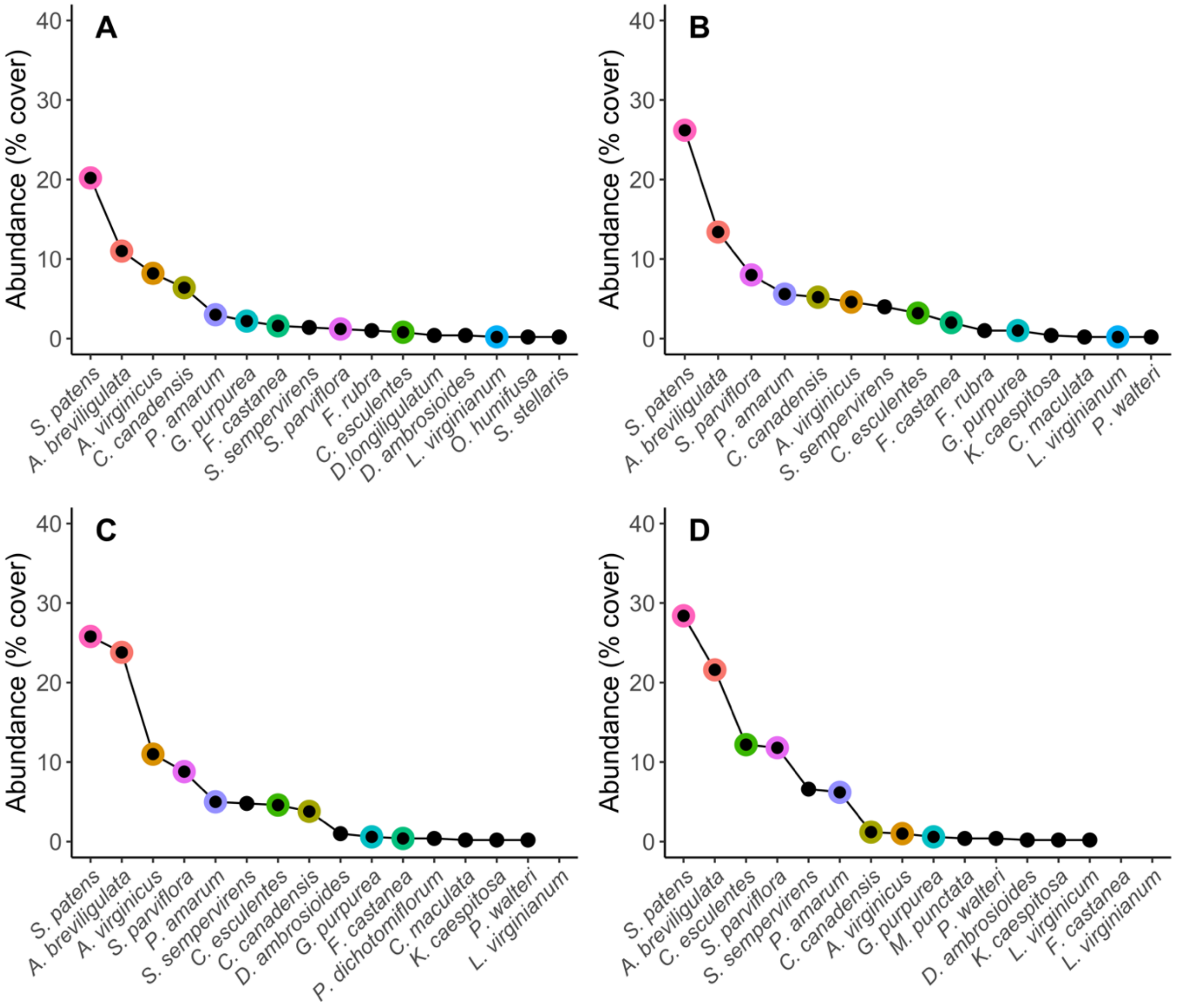
A
B
C
D
Abundance (% cover)
0
10
20
30
40
S. patens
A. breviligulata
A. virginicus
C. canadensis
P. amarum
G. purpurea
F. castanea
S. sempervirens
S. parviflora
F. rubra
C. esculentes
D.longiligulatum
D. ambrosioides
L. virginianum
O. humifusa
S. stellaris
S. patens
A. breviligulata
S. parviflora
P. amarum
C. canadensis
A. virginicus
S. sempervirens
C. esculentes
F. castanea
F. rubra
G. purpurea
K. caespitosa
C. maculata
L. virginianum
P. walteri
S. patens
A. breviligulata
A. virginicus
S. parviflora
P. amarum
S. sempervirens
C. esculentes
C. canadensis
D. ambrosioides
G. purpurea
F. castanea
P. dichotomiflorum
C. maculata
K. caespitosa
P. walteri
L. virginianum
S. patens
A. breviligulata
C. esculentes
S. parviflora
S. sempervirens
P. amarum
C. canadensis
A. virginicus
G. purpurea
M. punctata
P. walteri
D. ambrosioides
K. caespitosa
L. virginicum
F. castanea
L. virginianum

Figure 3.3

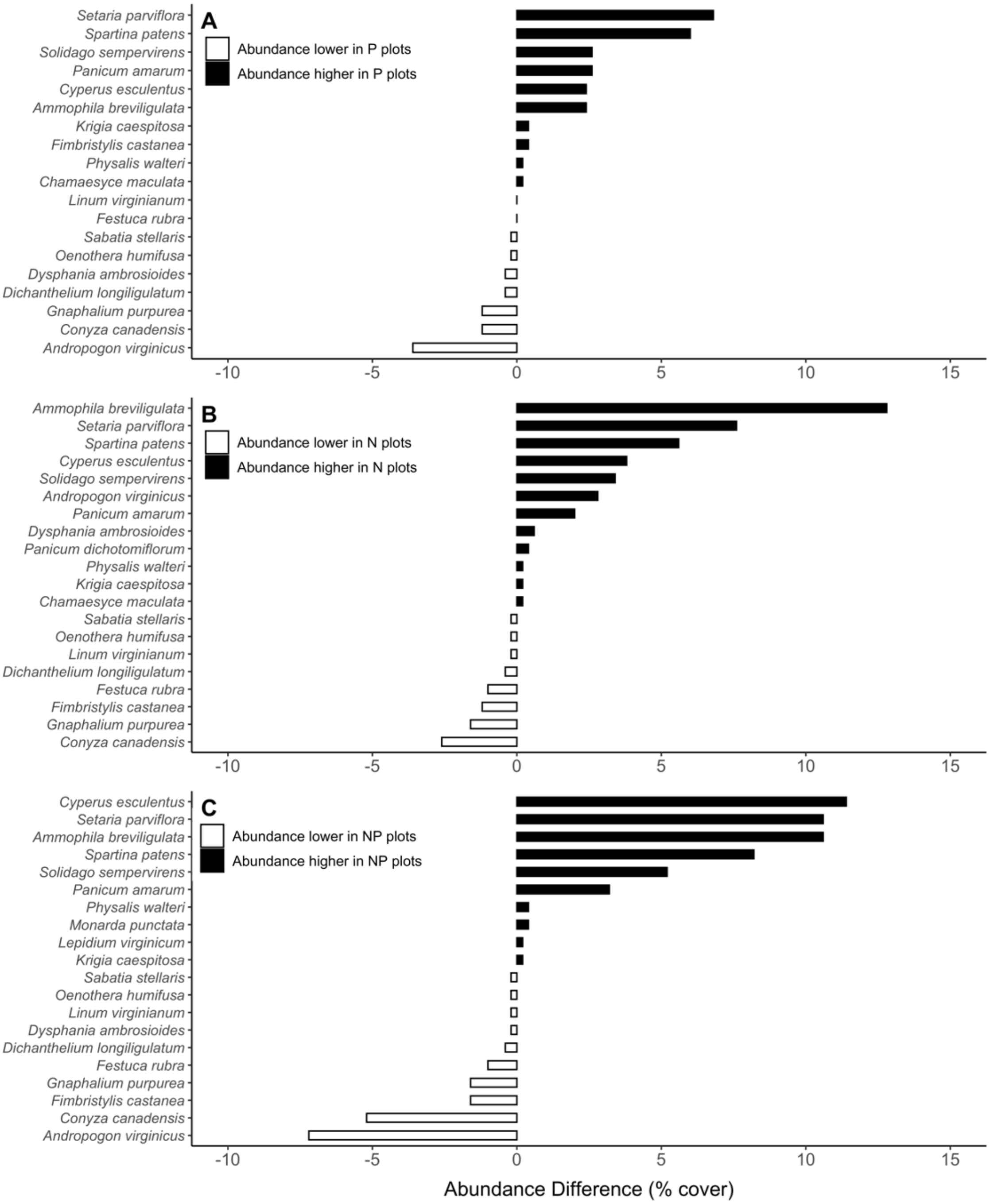
A
Abundance lower in P plots
Abundance higher in P plots
Setaria parviflora
Spartina patens
Solidago sempervirens
Panicum amarum
Cyperus esculentus
Ammophila breviligulata
Krigia caespitosa
Fimbristylis castanea
Physalis walteri
Chamaesyce maculata
Linum virginianum
Festuca rubra
Sabatia stellaris
Oenothera humifusa
Dysphania ambrosioides
Dichanthelium longiligulatum
Gnaphalium purpurea
Conyza canadensis
Andropogon virginicus
-10
-5
0
5
10
15
B
Abundance lower in N plots
Abundance higher in N plots
Ammophila breviligulata
Setaria parviflora
Spartina patens
Cyperus esculentus
Solidago sempervirens
Andropogon virginicus
Panicum amarum
Dysphania ambrosioides
Panicum dichotomiflorum
Physalis walteri
Krigia caespitosa
Chamaesyce maculata
Sabatia stellaris
Oenothera humifusa
Linum virginianum
Dichanthelium longiligulatum
Festuca rubra
Fimbristylis castanea
Gnaphalium purpurea
Conyza canadensis
-10
-5
0
5
10
15
C
Abundance lower in NP plots
Abundance higher in NP plots
Cyperus esculentus
Setaria parviflora
Ammophila breviligulata
Spartina patens
Solidago sempervirens
Panicum amarum
Physalis walteri
Monarda punctata
Lepidium virginicum
Krigia caespitosa
Sabatia stellaris
Oenothera humifusa
Linum virginianum
Dysphania ambrosioides
Dichanthelium longiligulatum
Festuca rubra
Gnaphalium purpurea
Fimbristylis castanea
Conyza canadensis
Andropogon virginicus
-10
-5
0
5
10
15
Abundance Difference (% cover)

Figure 3.4

Chapter 4: Trait-based investigation reveals patterns of community response to nutrient enrichment in coastal mesic grassland

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Abstract

Despite recent advances, we still do not understand how chronic nutrient enrichment impacts coastal plant community structure and function. We aimed to clarify such impacts by testing for differences in ecosystem productivity and multiple community metrics in response to fertilization. We established plots in 2015 consisting of control (C), nitrogen (N), phosphorus (P), and nitrogen + phosphorus (NP) treatments in a mid-Atlantic coastal grassland. In 2017 we collected aboveground biomass, functional traits, and species abundance for each plot. Our findings indicate a synergistic co-limitation, such that NP plots were more productive than all other treatments. A combination of traits responsible for competition and nutrient uptake (i.e., height and $\delta^{15}N$) caused trait-based divergence of N and NP plots from C and P plots. Functional trait-based composition patterns differed from species composition and lifeform abundance patterns, highlighting complexities of community response to nutrient enrichment. While trait-based functional alpha-diversity did not differ among nutrient treatments, it was positively correlated with biomass production, suggesting nutrients may impact functional alpha-diversity indirectly through increased productivity. Increased functional alpha-diversity could be a mechanism of co-existence emerging as productivity increases. These results have important implications for understanding how plant communities in low-productivity coastal systems are altered by fertilization.

Introduction

Global scale research has revealed effects of nutrient additions on productivity, species diversity/composition, and functional trait expressions of plant communities (Borer et al. 2014, Fay et al. 2015, La Pierre and Smith 2015, Harpole et al. 2016). It is recognized that anthropogenic activity alters global nutrient availability and deposition, most notably nitrogen (N) and phosphorus (P) (Vitousek et al. 1997, Mahowald et al. 2008). Anthropogenic sources now surpass any natural process contributing to nutrient deposition (Galloway et al. 2003, Rockström et al. 2009, Fay et al. 2015). Rapidly increasing rates of N and P addition through anthropogenic sources result in the emergence of questions regarding the effects nutrients, both individually and synergistically, have on the plant community and ecosystem dynamics.

Elser et al. (2007) and Fay et al. (2015) detail synergistic effects of N and P, demonstrating that in terrestrial ecosystems, simultaneous addition of N and P (NP) causes a larger response than either nutrient does individually. Studies have shown increased deposition affects more than just productivity. For example, increases in vegetative biomass after three years of nutrient addition cause subsequent decreases in sub-canopy light availability (Borer et al. 2014, Harpole et al. 2017), often resulting in plant species loss (Wilson and Tilman 1991, Clark et al. 2007, Hautier et al. 2009, Demalach and Kadmon 2017). Studies investigating plant community response to nutrient additions indicate that nutrient enrichment can change community spatial and temporal variability, as well as alter succession patterns and community structure (Carson and Barrett 1988, Clark and Tilman 2008, Koerner et al. 2016). La Pierre and Smith (2015) found that species experiencing chronic fertilization express differences in functional traits compared to species in ambient conditions. These previous works highlight the importance of investigating plant traits to understand mechanisms altering community structure in response to chronic nutrient enrichment (Suding et al. 2005, Tatarko and Knops 2018, Firn et al. 2019). Although the aforementioned research has laid the foundation regarding potential effects of nutrient enrichment on global change, gaps remain. For example, a number of studies have investigated trait-based community patterns in response to nutrient enrichment (Ceulemans et al. 2011, Zhang et al. 2019), but uncertainties still remain regarding effects of nutrient enrichment on functional trait-based diversity (i.e., diversity of traits).

Limitations using species diversity to express plant diversity have increased interest in quantifying functional trait-based diversity (functional diversity) to answer questions regarding plant community organization, species interactions, and response to disturbances (Kraft et al. 2008, Hu et al. 2014). Functional diversity has become an important metric for understanding how species, as dynamic parts of a community, change organismal traits through interactions with the environment, which can impact ecosystem functioning (Calow 1987, Laureto et al. 2015). Functional diversity metrics are indicators of community structural response to environmental perturbations (Mouillot 2007) and can be measured across multiple scales (Carmona et al. 2016). Both functional alpha- and beta-diversity are computed using quantitative functional trait data collected on members of the plant community. Here we define functional beta-diversity as the site-to-site variation among functional trait defined communities, while functional alpha-diversity is defined as functional trait diversity at the local-scale (i.e., within a plot). These diversity metrics, along with analysis of specific differences in functional trait expression, can help decipher mechanisms of altered trait-based community structure in response to nutrient enrichment and increased productivity. Current research focusing on functional diversity does not identify unified patterns of plant communities in response to nutrient enrichment, suggesting that responses may be dependent on combinations of nutrient treatments and regional or local pressures (Mason et al. 2012, Helsen et al. 2014, Niu et al. 2014).

Most prominent nutrient enrichment studies have been conducted in agroecosystems or prairie grasslands with different soil profiles than coastal grasslands. Coastal grassland soils are characterized by their highly leached sandy composition resulting in low nutrient content and low water holding capacity (Ehrenfeld 1990). Increased N deposition is expected to occur in coastal ecosystems (Seitzinger et al. 2002, Aggenbach et al. 2017), and previous work has highlighted the need to understand how nutrients influence coastal plant communities (Day et al. 2004, Pakeman et al. 2016). Focusing on the coastal system response to nutrient accumulation will identify mechanisms altering coastal plant community function, leading to improved predictions of community trajectory and future functional change (Pakeman et al. 2016, Aggenbach et al. 2017). This is especially true for barrier island systems, where plant communities are tied closely to disturbance response (Zinnert et al. 2017).

Barrier islands are coastal systems occurring along 15% of coastlines globally with most occurring in the northern hemisphere (Stutz and Pilkey 2001). Geographic areas where barrier islands are common coincide with areas expected to experience increased synthetic fertilizer use (Seitzinger et al. 2002, Sinha et al. 2017). By 2100, N enrichment in the continental U.S. is expected to increase by 19%, with the Atlantic coast experiencing the largest regional increase (Sinha et al. 2017). High nutrient enrichment from run-off and atmospheric deposition is a major influence on barrier island plant communities given the prominence of sandy-soil compositions and high N limitation (Ehrenfeld 1990, Day et al. 2004). Nutrient enrichment studies on coastal dune systems show that N addition causes long-term plant community change (Day et al. 2004), yet P has not been identified as a limiting nutrient in terrestrial coastal systems (Osgood and

Zieman 1993, Smith et al. 1999). Patterns revealing NP synergistic co-limitation at global scales necessitates investigation of both nutrients in coastal systems (Elser et al. 2007, Fay et al. 2015). We build upon previous research by investigating effects of nutrient enrichment on trait-based communities of a mid-Atlantic coastal mesic grassland.

Our goal was twofold. First, we tested how chronic (3 year) nutrient addition affects trait-based community structure and function. Specifically, we tested whether N, P, and NP enrichment increases community-level biomass and/or modifies specific functional trait expressions. We hypothesize that, due to N limitation in coastal systems, biomass will show notable increase under N and NP treatments, with NP prompting a co-limitation effect such that biomass produced after NP fertilization will be significantly higher than biomass produced by N or P alone. Furthermore, we predict that functional traits promoting resource acquisition (e.g., height, specific leaf area, and leaf N traits) will be expressed in N and NP treatments, due to increased competition for light in nutrient-rich environments. Second, we investigated community-level functional trait change using trait-based community composition and trait diversity (functional alpha- and beta-diversity). We hypothesize that N and NP treatments will alter trait-based community composition and that such changes will be accompanied by increased functional alpha- and beta-diversity. Furthermore, we expect that functional alpha- and beta-diversity will have a significant relationship with biomass productivity. Identifying how nutrients impact productivity, specific functional trait expressions, and trait-based community composition and diversity may improve predictions of trait-based vegetation change in sand-based coastal grasslands as global change drivers like nutrient enrichment persist.

Methods

Study Site

Hog Island (37.417 N, 75.686 W) is one of 13 barrier islands in the Virginia Coast Reserve (VCR) Long-Term Ecological Research site along the US Atlantic coast. The VCR is experiencing shrub encroachment by *Morella cerifera* on a landscape scale (Zinnert et al. 2016). *M. cerifera* is a N-fixing shrub that dominates later successional swales and may be facilitated by the presence of a grass canopy (Young et al. 2011, Sinclair et al. 2020). Due to extensive shrub cover on the northern end of Hog Island, plots were established on the southern end in a recently developed swale (i.e., dune slack) composed of perennial grass and annual/biennial forb species. Dominant graminoids at our grassland site included *Spartina patens*, *Setaria parvifolia*, *Andropogon virginicus*, and *Ammophila breviligulata,* which is a common dune grass in this region but also occurs frequently in swales (Young et al. 2011). Other graminoid species like *Fimbrystylis castanea* and *Cyperus esculentes* were less abundant but were also found at the site. Forb species were generally less dominant but included *Solidago sempervirens* and *Conyza canadensis*. Soils at our nutrient enrichment plots are sandy and well-drained, and relatively young due to high overwash occurrence in the early 2000s. Untreated areas indicate that %N in the soils ranged from 0.02–0.03%, while P ranged from 6–10 ppm.

Plot Establishment and Nutrient Application

Nutrient enrichment plots were installed on Hog Island in 2015 (Moulton 2017). Plots followed a randomized design modified from the Nutrient Network (https://nutnet.org/) to include three treatments (N = nitrogen, P = phosphorus, NP = nitrogen + phosphorus, and C = Control), replicated five times per treatment (N = 20 total experimental units, n = 5 per treatment). Each unit was 3 m^2 with 1 m walkways, which were not recognized as usable plot space. Units were subdivided into four 1 m^2 subplots. Nutrient applications were completed twice per growing season (May and June) from 2015-2017. Annual N and P application totaled

10 g m^{-2} yr^{-1}, while NP plots totaled 20 g m^{-2} yr^{-1} (10 g m^{-2} of N and 10 g m^{-2} of P). Phosphorus was applied as triple super phosphate, while N was applied as ammonium nitrate in particulate solid form.

Biomass and Species Composition Sampling

Biomass was defined as all aboveground vegetation at the end of the 2017 growing season (September 2017) and was collected to assess ecosystem productivity. Aboveground vegetation was harvested from one subplot to ground level within a haphazardly placed 0.1 × 1 m frame and extrapolated to represent plot level productivity (g m^{-2}). Samples were oven-dried for 72 h at 60 °C and weighed (g). Species composition was sampled using areal cover estimation (%) of each species, bare ground, and dead plant material, such that total cover of each plot summed to 100%. In July of 2017, species cover was assessed in a subplot that had not previously been used for destructive sampling. For logistical purposes, the five most abundant species in each plot were used for trait sampling. The top five species accounted for ~75% of the relative vegetation cover in all plots. *Spartina patens* and *A. breviligulata* were consistently the most dominant species in each plot. The annual forb *C. canadensis* had top five abundance in C and N plots but not in P or NP plots. This was the only difference in lifeform of the top five species as all other species were graminoids.

Functional Trait Selection and Sampling

Functional traits were selected to best understand the mechanisms of plant response to ecological dynamics including environmental and biotic interactions. Aboveground traits we selected highlight some trade-offs between rapid growth and resource conservatism. Investigating plant traits that exist on a resource use spectrum aids in understanding mechanisms of survival for plants in areas of different limiting factors (Funk et al. 2016). Maximum height was selected as a competitive trait, as it likely indicates plant response to low light from shading during increased biomass productivity (Laliberté et al. 2013). Height covaries with other plant growth traits including photosynthetic rate, relative growth rate, and leaf lifespan (Wright et al. 2004). Leaf traits including specific leaf area (SLA) leaf nitrogen content (%N), and leaf carbon content (%C) indicate trade-offs between rapid growth and resource conservation in highly productive and resource-limited communities (Poorter and De Jong 1999, Díaz et al. 2004). Last, ^{15}N:^{14}N (δ^{15}N) was selected to investigate mechanisms of nutrient uptake or fixation through symbiotic relationships (Hobbie and Högberg 2012, Kleinebecker et al. 2014, Liu et al. 2017).

Maximum height was measured in cm before harvesting by extending the longest leaf of the three tallest individuals for each species. Aboveground samples were harvested for one randomly selected individual for each of the top five species in each plot. Samples were immediately wrapped in the moist paper towel, stored in a plastic bag, and were stored in a dark refrigerator while processing took place. One leaf from each plant was re-hydrated and used to measure SLA using a computer scanning method to digitize leaf samples and capture projected leaf area (cm^2). Leaf samples were then oven-dried at 60^{o} C for 72 h and weighed (g). Dried leaf samples were ground into powder with a Wiley Mini-Mill and shipped to the Cornell Isotope Laboratory (COIL, Ithaca, New York, USA) for carbon and nitrogen elemental analysis (%C and %N) and isotope analysis (δ^{15}N). All samples for aforementioned foliar traits were collected in the summer of 2017. Species abundance was used to calculate community-weighted means (CWMs) for each functional trait:

$$\mathrm{CWM} = \sum_{\mathrm{i}}^{\mathrm{R}} p_{\mathrm{i}}\, \mathrm{t_i}$$

where R is the number of samples, p_i is the relative abundance of species i, and t_i is the mean trait value of species i (Garnier et al. 2004).

Statistical Analysis

All analyses conducted as part of this study were performed using R (R Core Team, v. 3.5.0, 2018). To determine the effect of nutrient enrichment on plot scale productivity, we performed a one-way ANOVA on mean biomass production in 2017 ($\alpha = 0.05$). Tukey HSD was performed to test for pairwise differences among treatments. Similarly, after confirming assumptions of normality and equal variance, we used ANOVAs to determine whether any CWM functional traits differed among treatment groups ($\alpha = 0.05$). When significant differences existed between groups, Tukey HSD was used as a post-hoc test to determine which treatments differed significantly.

Principal components analysis (PCA) ordination was used to visualize how nutrient enrichment affected community-level variation in CWM functional trait profiles (solution checked using scree plot). CWM traits were standardized to a mean of zero and unit variance to ensure no single trait would over-influence plot relationships in the trait space. We used the envfit function in vegan to create a vector overlay of CWM trait values indicating how specific traits are influencing plot position in trait space (Oksanen et al. 2019). Centroids were calculated for each of the convex hulled treatment groups.

Species community composition was visualized using non-metric multidimensional scaling (NMDS) ordination. We utilized Bray–Curtis distance measure to calculate a distance matrix of relative species abundance for each treatment replicate. The NMDS was run to a minimized stress value (stress < 0.2) using 3 dimensions (maximum iteration = 999). We performed the ordination in the vegan R package (Oksanen et al. 2019). For purposes of interpretation, a PCA rotation was applied to the finalized NMDS, such that NMDS axis 1 and 2 represent maximum variation of the data.

For both trait and species composition analysis, treatment groups were tested using a permutational MANOVA (PERMANOVA) to determine if nutrient enrichment significantly changed CWM trait and/or species composition (Anderson 2017) (max iteration = 999; α = 0.05). PERMANOVA makes no assumptions about the distribution of response variables or dissimilarities and is robust to assess heterogeneity of variances when used on balanced designs (Anderson 2017). Post-hoc pairwise testing was conducted to determine which treatments significantly differed in CWM trait composition (α = 0.05, FDR adjustment).

To satisfy assumptions of normality and variance we log transformed our cover data prior to performing a two-way ANOVA on % cover of graminoid and forb lifeforms among nutrient treatments (α = 0.05) to determine whether lifeform abundance differed among communities receiving different nutrient treatments. We found no significant lifeform x treatment interaction, and thus proceeded to testing for significant differences of main effects. Tukey HSD was used as a post-hoc test when appropriate (α = 0.05).

Functional alpha-diversity was calculated as Rao's quadratic entropy (FD_Q). We selected FD_Q because it handles multiple trait variables and aims to estimate species dispersion in multidimensional trait space at the plot level, weighting solutions by relative abundance (Botta-Dukát 2005, Laliberte and Legendre 2010). Functional alpha-diversity indices were calculated using the FD package (Laliberté et al. 2015). Functional beta-diversity was calculated using betadisper in the R vegan package which calculates beta dispersion, or the distance of each plot to the mean center of each treatment group (Oksanen et al. 2019). Beta dispersion tests for homogeneity of group dispersion and is a common quantitative metric of beta-diversity

(Anderson 2006, Anderson et al. 2006). We used ANOVA (with Tukey HSD post-hoc) and simple linear regression analysis ($\alpha = 0.05$) to determine the impact of nutrients on functional diversity and the relationship between functional diversity and biomass, respectively.

Results

Biomass Response to Nutrients

Biomass production significantly differed among nutrient treatments (Fig. 4.1; $F_{3, 16} = 18.5$, $p < 0.0001$). Of all the nutrient treatment groups, NP had the highest biomass production with the lowest biomass production occurring in C and P plots (Fig. 4.1). NP plots were significantly more productive than both P and N plots (Fig. 4.1), suggesting a nutrient synergistic co-limitation. Although N plots produced lower biomass than NP plots, we found that mean biomass was still significantly higher than P and C plots, with mean productivity approximately three to four times higher (Fig. 4.1).

Community-Level Trait Response

Individual Trait Differences Among Treatments

Community-weighted functional traits varied across nutrient treatments. Community-weighted height was significantly different among nutrient treatments ($F_{3, 16} = 72.2$, $p < 0.0001$), with N and NP plots having the tallest communities on average (Fig. 4.2a). We found that N and NP fertilization increased community-weighted plant height between 34–55% compared to P and C plots. There was no significant treatment effect on SLA (Fig. 4.2b). Although aboveground tissue in NP plots was enriched in ^{15}N isotope, the difference was not significant compared to C and P plots (Fig. 4.2c). Aboveground tissues in N plots had enriched ^{15}N isotope levels compared to C and P plots, shifting $\delta^{15}N$ from below 0 to above 3 ppt (Fig. 4.2c). Values of foliar %C showed a small but significant increase in N plots compared to C plots (+4.6%, Fig. 4.2d). Leaf %N did not differ among treatments (Fig. 4.2e).

Trait, Species, and Lifeform Composition

A total of 68.9% of the variation in our data was explained by the functional trait metrics used in the PCA (PC1 = 40.9%, PC2 = 28.0%). We found that nutrient treatments resulted in significantly different trait-based community composition (Fig. 4.3, PERMANOVA: $F_{3, 16} = 4.65$, $p < 0.001$). Trait-based communities of N and NP plots occupied significantly different functional trait space compared to C and P plots, primarily diverging along PC1 (Fig. 4.3, Table 4.1). All traits were significantly correlated with PC1 and/or PC2 and can be used to indicate how nutrients drive trait-based community position in trait space (Table S4.1). For example, height, $\delta^{15}N$, and %C, were strongly correlated with PC1, indicating plots treated with N/NP are separate from C/P-treated plots because N- and NP-treated communities are taller and have higher levels of foliar $\delta^{15}N$ and %C (Table S4.1, Fig. 4.3). Our multivariate analysis shows more clearly how traits like foliar $\delta^{15}N$ and %C impact the dissimilarity of N/NP communities and C/P communities compared to investigations of these traits using univariate analysis alone. Likewise, SLA had a strong positive correlation with PC2, while %N and %C had negative correlations with PC2, influencing separation of N and NP plots in trait space (Table S4.1, Fig. 4.3), a pattern that is not as clear after investigating univariate trait response of SLA, %N, and %C.

Differences in species composition were also found among treatments (Fig. S4.1, PERMANOVA: $F_{3, 16} = 4.52$, $p < 0.001$). Species composition was significantly different among all treatments, despite the similarities we find in functional composition of N/NP and C/P communities (Table S4.2). We also found that, across all treatments, mean graminoid cover was significantly higher than mean forb cover (Fig. S4.2, ANOVA: $F_{3, 16} = 77.65$, $p < 0.0001$).

However, abundance of lifeforms did not differ among communities experiencing different nutrient enrichment treatments (Fig. S4.2; ANOVA: $F_{1, 16} = 0.53$, $p > 0.05$). For example, graminoid abundance did not differ among treatment groups. These results indicate that trait, species, and lifeform composition provide different perspectives regarding community-level response to nutrient addition in a coastal mesic grassland.

Trait-based Alpha and Beta Diversity

Neither functional alpha- nor beta-diversity of trait-based communities were significantly different based on nutrient treatment (Fig. 4.4a,b; ANOVA: $F_{3, 16} = 1.42$, $p = 0.2746$ and $F_{3, 16} = 1.91$, $p = 0.1693$, respectively). However, there was a significant positive correlation between aboveground biomass and functional alpha-diversity (Fig. 4.4c), while the relationship between functional beta-diversity and biomass was weak and non-significant (Fig. 4.4d). This pattern indicates that functional alpha-diversity is not so much influenced by nutrient treatment as it is linked to biomass production in each plot, which is significantly higher in N and NP plots (Fig. 4.4c).

Discussion

We show the influence of chronic (3 year) nutrient enrichment on community-level biomass, specific functional trait expressions, and trait-based community composition and diversity in a coastal grassland. It is clear that N enrichment had significant impacts on community biomass production. NP exhibited a synergistic co-limitation effect on biomass production such that NP treatments produced higher biomass than either N or P treatments individually. These findings are consistent with previous studies showing synergistic nutrient effects in other terrestrial systems (Elser et al. 2007, Fay et al. 2015). However, it is interesting that P alone had no effect on productivity because it has been shown to increase productivity in other grassland systems (Fay et al. 2015). This is particularly surprising at our grassland site because, according to our NMDS results, P alters community species composition, even without evidence of causing differences in productivity or functional trait-based composition. We found that biomass production in N and NP plots are on average four and seven times higher than C plots, respectively. This follows global scale trends which indicate that N and NP deposition increases biomass production by, on average, 18% and 40% compared to C plots, respectively (Fay et al. 2015). Considering the extent of coastal grassland distribution worldwide, our findings emphasize the importance of including more coastal grasslands when investigating response to nutrient enrichment at the global scale.

Our investigation of specific functional traits shows that some functional trait expressions associated with competition and altered nutrient acquisition (i.e., height and $\delta^{15}N$) were significantly higher in N and NP plots, similar to other nutrient enrichment studies (Siefert and Ritchie 2016, Tatarko and Knops 2018). Differences in plant height are likely driven by increased competition for light, as N and NP increase aboveground biomass production (Siefert and Ritchie 2016, Tatarko and Knops 2018). It is important to note that increased height can also be a result of higher N acquisition, allowing for species to grow more prolifically than if they were in an N-limited environment. We found that other traits remained unchanged among nutrient enrichment treatments (i.e., %N and SLA), indicating that certain traits are conserved in coastal systems regardless of nutrient additions. These trait responses stray from what global patterns have shown, such as those found by Firn et al. (2019), which identify leaf N content as an important indicator of nutrient inputs. As leaf N was not affected by fertilization, investigating root traits in future studies may inform aboveground responses. Previous research highlights that increased N acquisition by roots may affect other functional traits, like $\delta^{15}N$, which correlates with leaf N content (Hobbie et al. 2000).

Foliar $\delta^{15}N$ is traditionally used as the primary metric for whole plant $\delta^{15}N$ and varies as a result of multiple environmental changes including N deposition (Craine et al. 2015). Increased availability and uptake of N can result in $\delta^{15}N$ enrichment in plant tissues (Jung et al. 1997, Michelsen et al. 1998, Hobbie et al. 2000), most typically through mechanisms of decreasing plant dependence on fungal and microbial associates to capture and fix N (Högberg et al. 2011, Hobbie and Högberg 2012). In our study, we found that CWM $\delta^{15}N$ values in C plots was ~0 ppt, which could suggest plants in untreated communities rely on N_2 fixation through symbiotic rhizosphere relationships, a mechanism found in the dominant coastal shrub *M. cerifera* (Bond 1967, Robinson 2001). Symbiotic relationships are an important N acquisition strategy in N-limited coastal systems (Young et al. 1992) and may be disrupted by N additions. While we did not specifically test for changes in microbial communities associated with plant root systems, increased $\delta^{15}N$ enrichment has been linked to plant dissociation from N-fixing bacteria, mycorrhizal fungi, or both when N becomes more readily available during fertilization (Johnson et al. 2003, Craine et al. 2009, Grman and Robinson 2013). Previous research has also shown that soil microbial communities can be directly affected by nutrient inputs (Zhang et al. 2008, Chen et al. 2018). If microbial community changes occur in a way that effectively decreases microbial support to plants, functional trait differences could emerge as plants compensate for the loss of microbial relationships. Further studies are necessary to understand how nutrient enrichment impacts microbial communities and their plant associations in coastal soils.

Surprisingly, we found that different patterns emerged depending on whether we analyzed trait-based composition, species composition, or lifeform abundance. As hypothesized, trait-based community analysis provided evidence that N and NP treatments filter trait combinations that favor survival when biomass is high (i.e., in biotically competitive scenarios). Directional divergence of communities experiencing different nutrient enrichment treatments (in multivariate trait space) indicates the importance of incorporating multiple aboveground trait combinations when investigating drivers of trait-based community composition. In contrast with these trait-based patterns, we uncovered distinct differences in species composition among our nutrient treatments, such that all communities were significantly different from one another, while abundance of different lifeforms in each treatment community exhibit yet another pattern, in which all treatments were similar in relative forb and graminoid cover. Contrasting patterns between trait, species, and lifeform response presents an important complexity that has lacked focus in nutrient enrichment studies. It is critical to determine how each type of community investigation technique contributes to our understanding of plant community response to nutrient enrichment. While we did not specifically test why these community-level analyses differ in their response to nutrient enrichment, we recognize that contrasting patterns among trait, species, and lifeform analyses could be relevant to questions that are currently being pursued in other investigations of plant community response to nutrient enrichment. For this reason, we highlight two possible explanations for such community responses below and encourage future work emphasizing these points.

First, these patterns could indicate that nutrient enrichment influences functional traits, species composition, and lifeform abundance independently. For example, it is possible that functional trait responses would not match species composition changes if nutrient treatments were not causing complete species turnover. Global change drivers like nutrient enrichment can influence species composition in a plethora of ways including species rank and evenness changes

(Avolio et al. 2019). If differences in species composition among nutrient treatments are caused by reordering of subordinate species or increased dominance of the most abundant species, we may not see differences reflected in community level functional traits because the dominant species still contribute most to the community functional trait expression.

Second, to fully understand how nutrient additions impact plant communities, it is of interest to determine whether altered functional trait expressions lead to changes in species composition, or vice versa. In our coastal grassland system, it is possible that functional traits, species composition, and lifeform abundance may change sequentially. Such a phenomenon could exist because nutrient additions play a critical role in increasing biomass production which consequentially changes plant competitive interactions through modified functional traits of community members. This mechanism leads to competitive exclusion of certain species under a new highly productive community, resulting in altered species composition. However, the inverse relationship could also be true. Nutrients could reorganize species abundances by opening a niche space for species that would otherwise be unable to germinate and colonize a given resources space, resulting in new plant species contributing to community-level functional trait compositions. Given these complexities, we encourage the use of other community-level functional trait metrics to disentangle changes in functional trait compositions, like functional alpha- and beta-diversity which we tested at our coastal grassland site.

We did not find that functional alpha-diversity varied significantly among nutrient treatments. However, we did find a significant positive correlation signifying that functional alpha-diversity is coupled with increased biomass production which is caused by N and NP enrichment. The coupled response of biomass and functional alpha-diversity response is likely a critical piece in identifying mechanisms of local-scale co-existence. In this case, when biomass is high, competitive interactions result in dissimilar trait values for co-occurring species at the alpha-level (Swenson et al. 2012). However, it is surprising that the pattern of increased alpha-diversity was only seen in relation to biomass and not among different nutrient enrichment treatments. This pattern may indicate an indirect influence of nutrient enrichment on functional diversity at the alpha-level. For example, nutrient enrichment may have an influence on specific functional trait responses, but the diversity of traits at the plot level are more influenced by biomass productivity. This information supports that functional diversity at the alpha-level can help determine how modified functional trait expressions influence species compositions as varying nutrient treatments increase biomass production. Similar findings have been found in other grassland communities (Laliberté et al. 2013).

Conclusions and Implications for Coastal Systems

Combined deposition of N and P effectively releases plant communities from an environmental filter (i.e., an abiotic factor influencing species success/establishment) and drives feedbacks between altered plant functional trait expressions and community productivity. As biomass increased with nutrient enrichment, we found functional alpha-diversity also increased. The positive relationship between functional alpha-diversity and aboveground biomass may be evidence of a species co-occurrence mechanism stemming from limiting functional trait similarity among species (Laliberté et al. 2013). Limiting similarity of functional traits between co-occurring species in relatively high productivity environments is a common mechanism promoting species co-existence (Schwilk and Ackerly 2005). The increase in functional diversity at the local scale in our system can contribute to our understanding of processes governing community assembly (i.e., competition vs. environmental filtering), which has not been comprehensively investigated through manipulation experiments in high-disturbance, low-productivity coastal systems. Functional alpha-diversity can also specify how environmental perturbations relevant to coastal systems (i.e., nutrient enrichment) influence community structure and ecosystem functions like productivity and resilience (Schwilk and Ackerly 2005, Mouillot 2007).

It is important to recognize that while certain individual functional trait responses may be more unified in response to nutrient enrichment at global scales, others are likely driven by overarching environmental variability specific to certain ecosystem types. For example, we find certain traits (e.g., plant height) follow patterns uncovered in many other systems (Li et al. 2015, DeMalach et al. 2017, Nogueira et al. 2018), but traits like leaf N content, SLA, and others, do not follow patterns seen in other systems or at global scales (La Pierre and Smith 2015, Tatarko and Knops 2018, Firn et al. 2019). Recognition of site-specific influences on functional trait expressions emphasizes the importance of continued nutrient enrichment studies across multiple spatial scales.

Understanding mechanisms of trait-based community change by investigating diversity metrics and specific functional trait expressions sheds light on how low-productivity coastal systems are affected by recurring nutrient enrichment. Such mechanisms feedback to vegetative biomass, leading to increased productivity in N and NP plots that are four to six times higher than C plots. Understanding mechanisms of change and subsequent effects of nutrient enrichment is especially important in these low-production coastal systems, as models project increased nutrient loading by 2100 which will increase overall productivity and ultimately increase coastal resistance at large scales (Storm and Süss 2008, Sinha et al. 2017). We acknowledge barrier islands are unique systems and respond individualistically to long- and short-term environmental forcings across varying spatial scales (Zinnert et al. 2017). However, coastal systems are increasingly vulnerable to climate-associated disturbance, making it critical to understand plant community change in response to nutrient enrichment. To test our results in other regions, we encourage the establishment of more nutrient manipulation studies in low-nutrient coastal grasslands around the globe, especially those located in other barrier island systems. A higher focus on these areas will lead to better predictions of vegetation change as nutrient enrichment continues.

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Tables and Figures

Table 4.1 Pairwise comparisons via PERMANOVA results for trait-based communities between nutrient enrichment treatments on a coastal grassland. Bold indicated $p < 0.05$, using FDR correction.

Comparison	**F-value**	***p*-value**
C vs. P	0.9	0.5260
C vs. N	6.8	**0.0135**
C vs. NP	5.2	**0.0135**
P vs. N	7.4	**0.0135**
P vs. NP	5.4	**0.0135**
N vs. NP	4.4	0.1236

Figure Legends

Figure 4.1 Total biomass (mean ± SE) for each nutrient treatment (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus) on a barrier island grassland community. Letters indicate significant differences based on Tukey HSD pairwise comparison results. Bars with different letters are significantly different ($p < 0.05$).

Figure 4.2 Mean ± SE of community-weighted height (a), specific leaf area (b), leaf nitrogen isotope ratio (c), leaf carbon content (d), and leaf nitrogen content (e) for each nutrient treatment (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus) on a barrier island grassland community. Connecting letters indicate significant differences based on Tukey HSD pairwise comparison results. Bars that do not share the same letter are significantly different ($p < 0.05$).

Figure 4.3 Principal components analysis (PCA) of trait-based community composition grouped in convex hulls by nutrient treatment type on a barrier island grassland community. Points represent individual experimental plots in functional trait space with asterisks indicating centroids for each group. Colors and symbols are matched to nutrient treatment (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus). Centroids can be viewed as mean trait-based community composition. Vectors indicate functional trait correlations with each axis. Vectors are labeled with the functional trait they represent, and lengths indicate goodness of fit (Table S1).

Figure 4.4 Mean (± SE) of functional alpha (FD_Q) (a) and beta-diversity (beta-dispersion) (b) for each nutrient treatment (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus). Relationship between total aboveground biomass and functional alpha-diversity

(c) and functional beta-diversity (d). Regression coefficients and *p*-value are reported at the top of each panel.

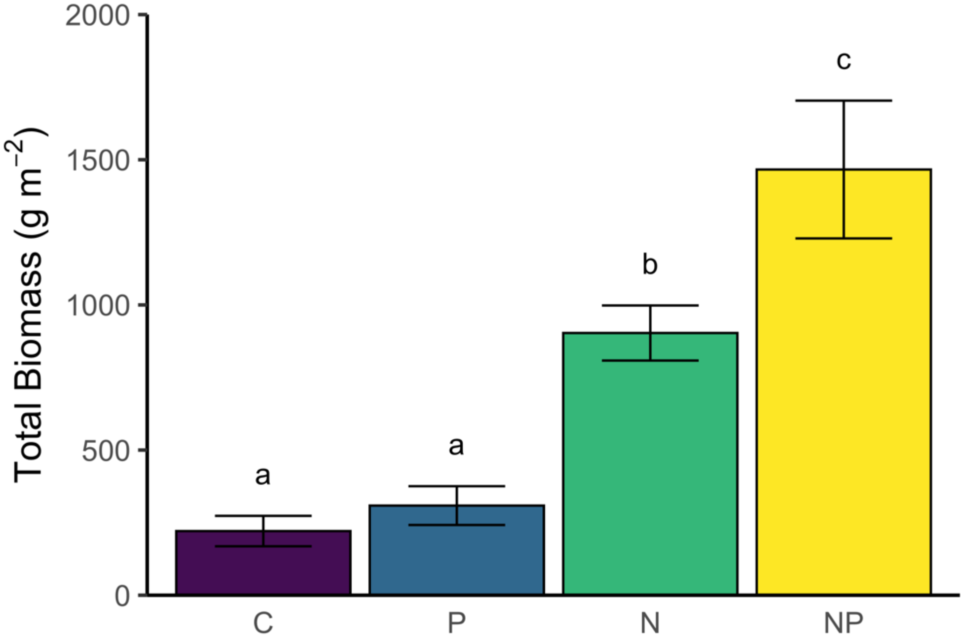

Figure 4.1

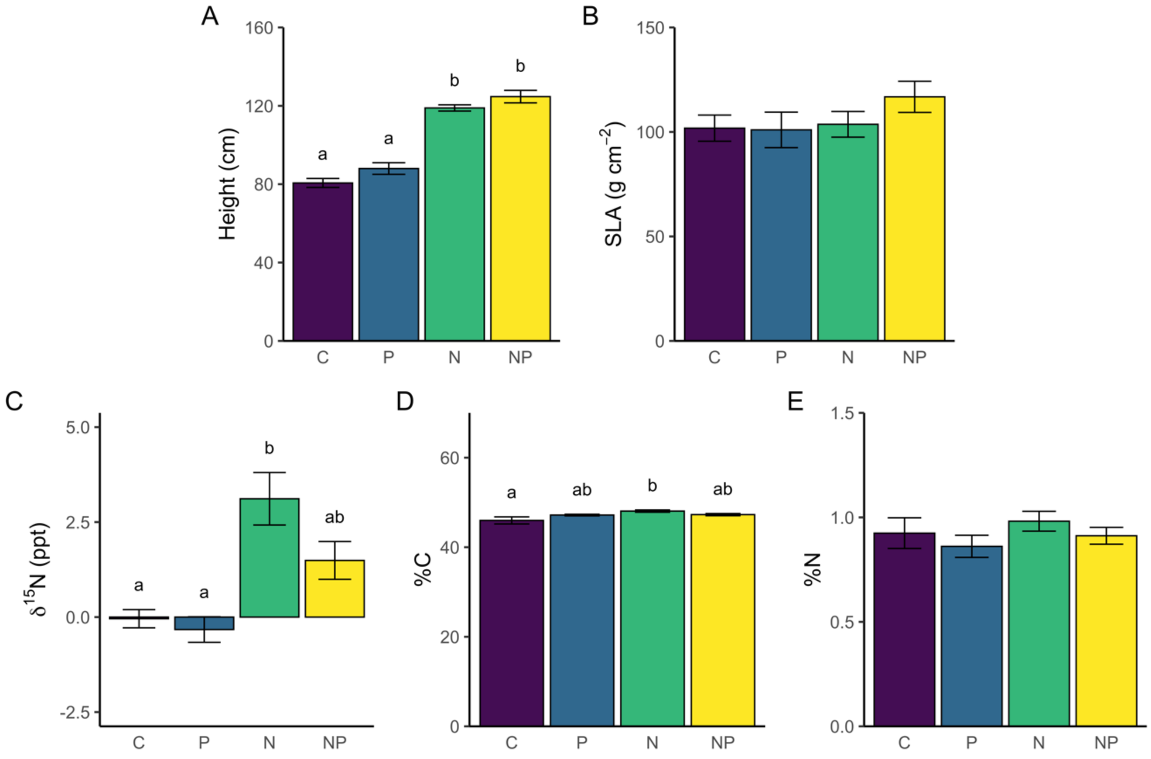
A
Height (cm)
160
120
80
40
0
a
a
b
b
C
P
N
NP
B
SLA (g cm^{-2})
150
100
50
0
C
P
N
NP
C
δ^{15}N (ppt)
5.0
2.5
0.0
-2.5
a
a
b
ab
C
P
N
NP
D
%C
60
40
20
0
a
ab
b
ab
C
P
N
NP
E
%N
1.5
1.0
0.5
0.0
C
P
N
NP

Figure 4.2

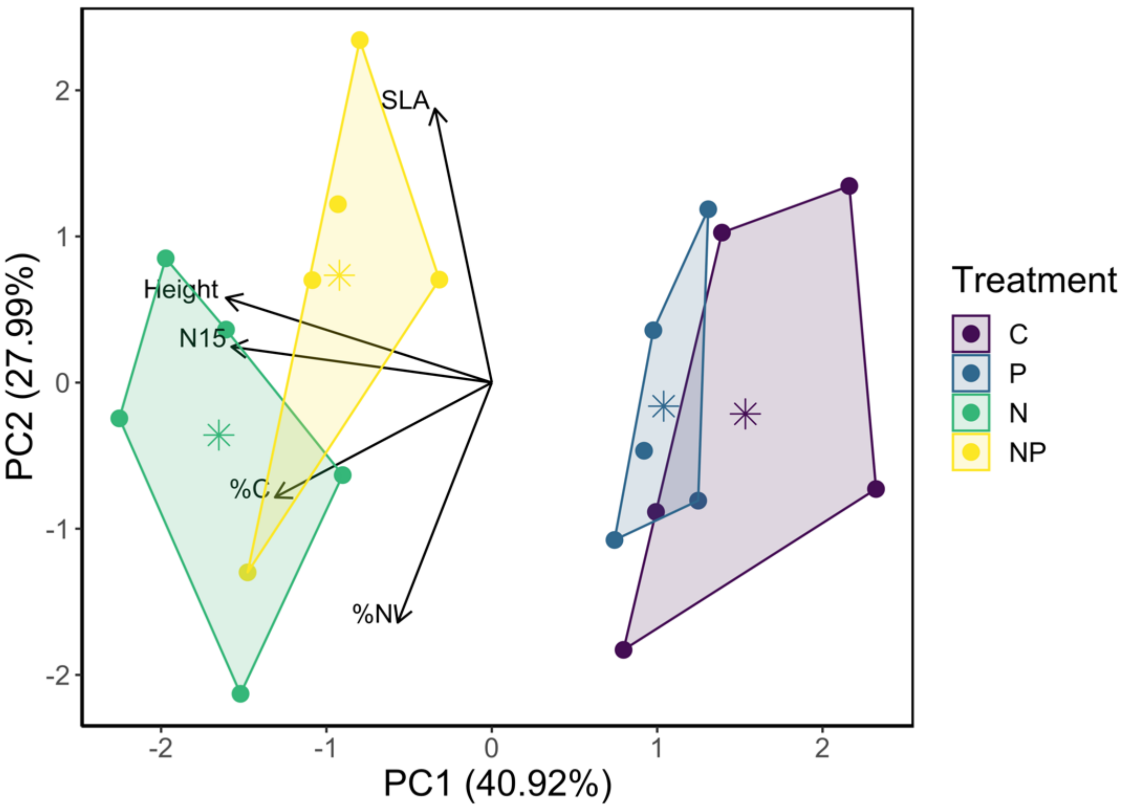
SLA
Height
N15
%C
%N
PC2 (27.99%)
PC1 (40.92%)
2
1
0
-1
-2
-2
-1
0
1
2
Treatment
C
P
N
NP

Figure 4.3

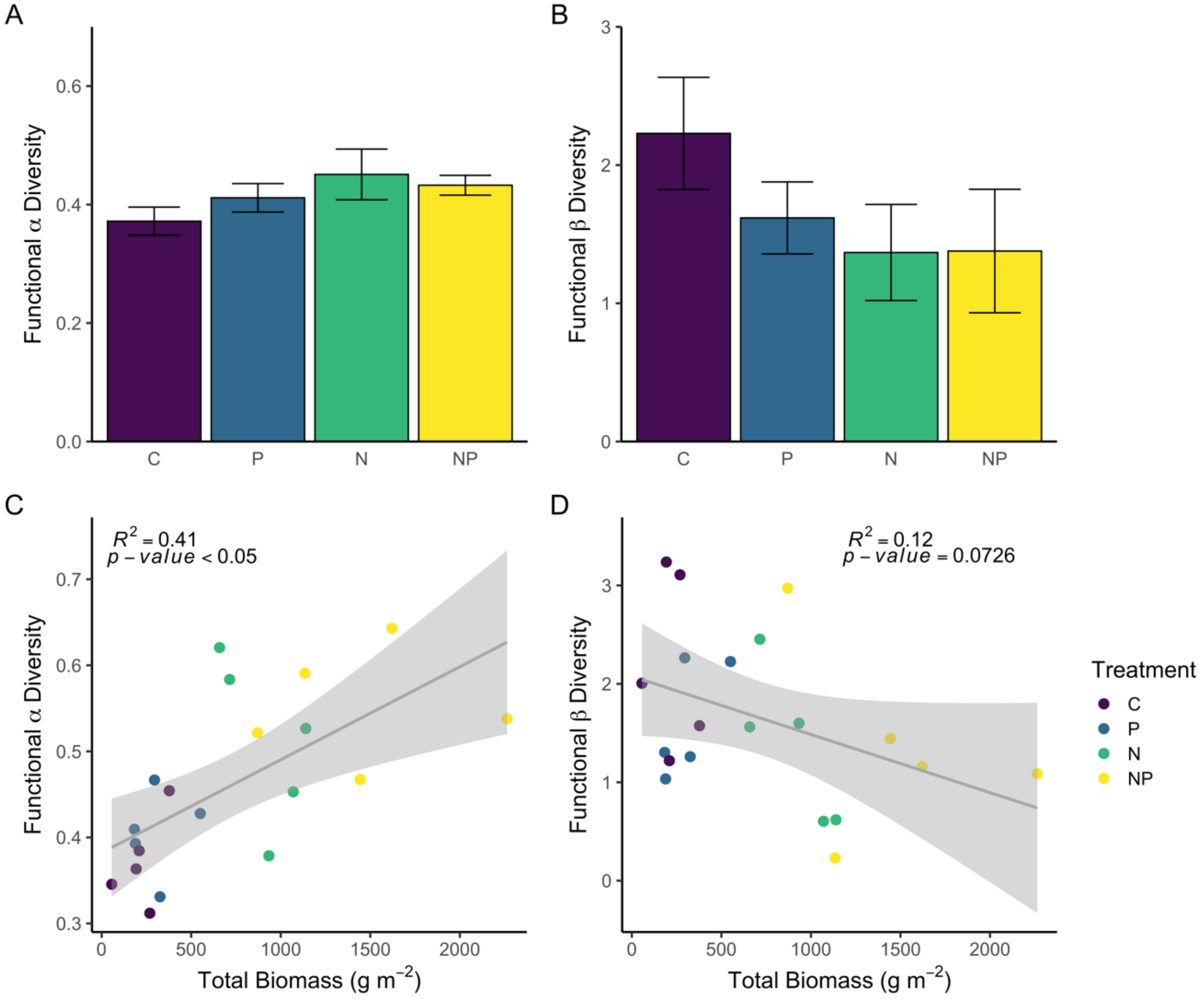
A
B
C
D
Functional α Diversity
Functional β Diversity
C
P
N
NP
$R^2 = 0.41$
$p - value < 0.05$
$R^2 = 0.12$
$p - value = 0.0726$
Total Biomass (g m^{-2})
Treatment
C
P
N
NP

Figure 4.4

Appendix

Supplemental Tables and Figures

Table S4.1 Directional correlations of each functional trait along PC1 and PC2 (Figure 3). Goodness-of-fit is represented as r^2 and correlates with vector lengths in Figure 2. Bold indicates $p < 0.05$. Traits include height, specific leaf area (SLA), leaf carbon content (%C), leaf nitrogen content (%N), and leaf nitrogen isotope ratio ($\delta^{15}N$).

Trait	PC 1	PC 2	r^2	*p* – value
Height	-0.94	0.34	0.80	**0.001**
Specific leaf area (SLA)	-0.18	0.98	0.71	**0.001**
Leaf N content (%N)	-0.33	-0.94	0.61	**0.001**
Leaf C content (%C)	-0.86	-0.51	0.71	**0.001**
Leaf ^{15}N	-0.99	0.15	0.61	**0.001**

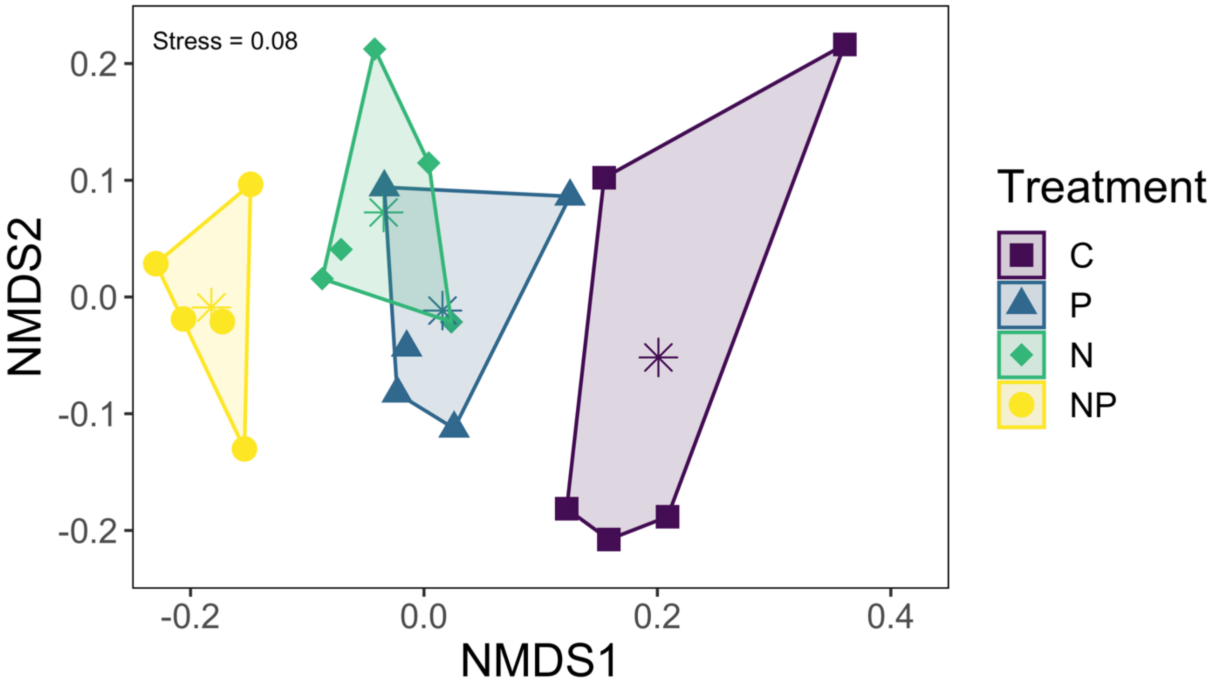

Figure S4.1 Non-metric multidimensional scaling (NMDS) of species composition grouped in convex hulls by nutrient treatment type on a barrier island grassland community. Points represent individual experimental plots in species space with stars indicating calculated centroids for each group. Colors and symbols are matched to nutrient treatment (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus). Centroids can be viewed as mean community compositions.

Table S4.2 Pairwise comparisons via perMANOVA results for species composition between nutrient enrichment treatments in coastal grassland. Bold indicates $p < 0.05$, using FDR correction.

Comparison	**F – value**	***p* – value**
C vs P	3.14	**0.033**
C vs N	4.32	**0.021**
C vs. NP	8.89	**0.026**
P vs N	2.52	**0.033**
P vs NP	4.35	**0.021**
N vs NP	2.77	**0.033**

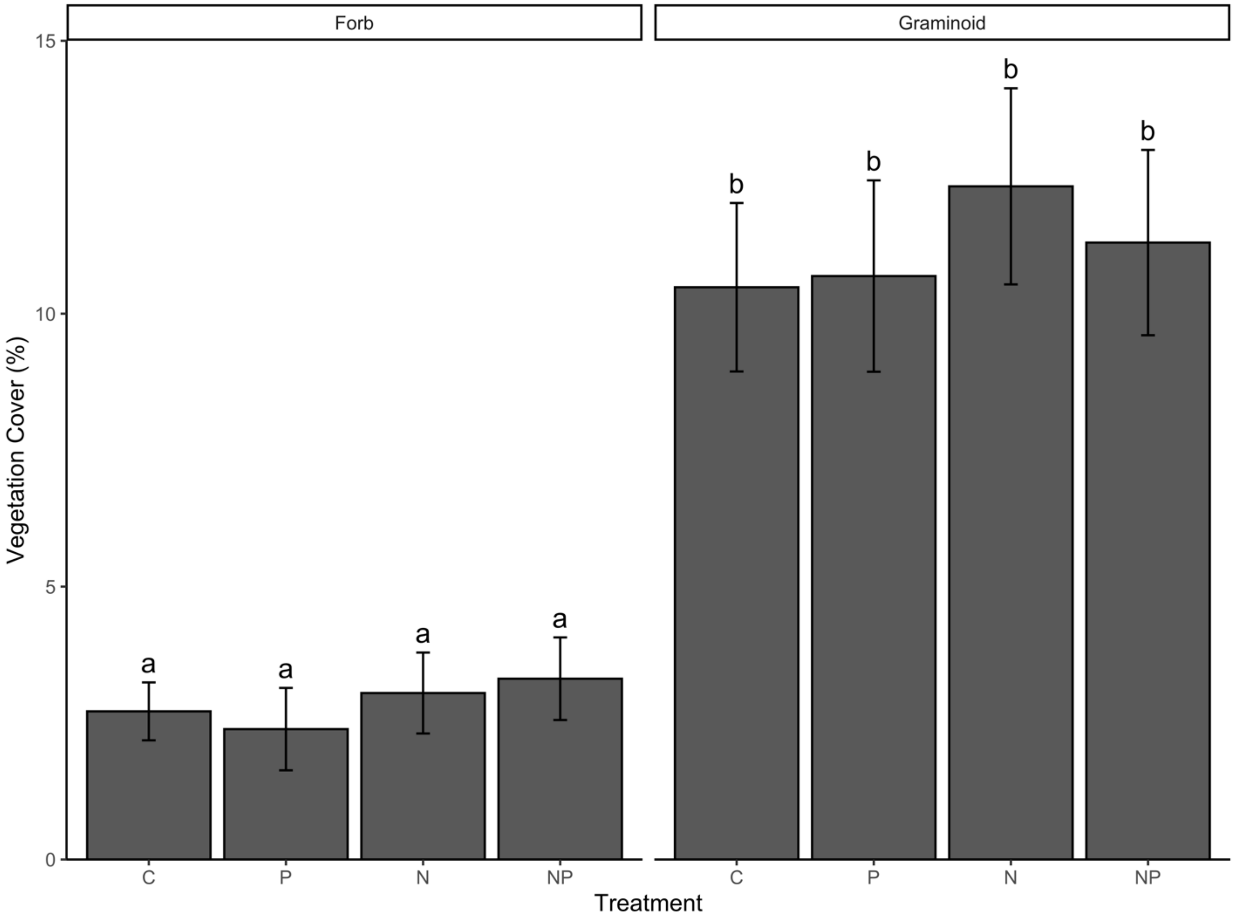

Figure S4.2 Mean percent cover ± SE of forb and graminoid lifeforms in each nutrient treatment group on a barrier island grassland community. Bars are grouped by lifeform type as well as nutrient treatment level (C = control, P = phosphorus, N = nitrogen, and NP = nitrogen + phosphorus). Letter codes represent significant differences, such that bars with different letter codes are significantly different (Tukey HSD, $p < 0.05$).

Conclusions and Significance

Barrier islands are dynamic coastal systems with the ability to actively respond to disturbances that are expected to increase and cause global change. These can exist as press and pulse events which impact ecological systems in different ways (Bender et al. 1984). Disturbance response of barrier island systems can vary depending on the type of disturbance event and pre-exiting feedbacks between island morphology and established plant communities (Godfrey and Godfrey 1976, Stallins 2005, Zinnert et al. 2017). Stability domains (i.e., disturbance resisting vs. disturbance-reinforcing) are mechanisms by which barrier islands respond to pulse storm events that vary across spatial scales, thus impacting environmental filters that act as partial determinants of plant community composition and structure (Stallins and Parker 2003, Stallins 2005, Kraft et al. 2015, Zinnert et al. 2017). Similarly, nutrient enrichment, acting as a press disturbance, effectively alters nutrient limitation in coastal environments (Minchinton and Bertness 2003, Heyel and Day 2006). Resulting plant communities can ultimately influence feedbacks with ecosystem productivity and disturbance response.

This research uses species and trait-based investigation to determine plant community response as different climate change disturbances influence barrier island function. Plant functional traits played a critical role in understanding differences in plant community structure as disturbance response was observed and as novel abiotic factors were introduced (Kraft et al. 2015). By providing a mechanistic understanding to ecosystem function, trait-based approaches in cooperation with species-defined analyses are beneficial for investigating emergence of novel community patterns (Tilman et al. 1997, Lavorel and Garnier 2002, Suding et al. 2008, De Battisti 2021). For example, species-defined and trait-based investigation revealed scale dependency of elevation and dominant barrier island stability domains on plant community structure and function (Chapter 1 and Chapter 2). Vegetation at large spatial scales was impacted more by gradual changes in climatic variables and relative sea-level rise along a latitudinal gradient, rather than in line with *a priori* stability domain characterization (Chapter 1). The effect elevation and dominant stability domain differences have on plant community structure and resulting ecosystem function (i.e., productivity and habitat formation) only comes into focus at smaller spatial extents, which are relevant for coastal management. Within islands that differ in topography and disturbance response (i.e., Hog and Metompkin Islands), local-scale habitat development at disturbance-resisting sites translates to dune-swale habitats that are distinct in trait-based community composition, with swales producing higher productivity levels (Chapter 2). Conversely, at the disturbance-reinforcing site, distinct dune-swale habitats are not developed, and ecosystem productivity is comparatively reduced (Chapter 2). This research highlights how plant community structure and the ways in which plant communities impact ecosystem function are linked to different ecological processes depending on the spatial scale in question.

Species and trait-based community investigations can also be used to better understand how coastal systems will respond to global change drivers that are expected to couple with climate change, like nutrient enrichment. Nitrogen (N) and phosphorus (P) additions have significant impacts on ecosystem productivity and plant composition structure at global scales (Fay et al. 2015, Hautier et al. 2015, Komatsu et al. 2019). Altering aspects of coastal grassland communities can subsequently influence the stability of barrier islands and thus the vulnerability to erosive physical processes (Zinnert et al. 2017, 2019). Nutrient manipulation in this study uncovered the impacts enrichment has on vegetative productivity, species-defined community structure, and trait-based community composition (Chapter 3 and Chapter 4). A synergistic nutrient co-limitation from NP enrichment increased productivity more than N or P did individually (Chapter 4). Complexities at the community-level were highlighted as species-defined community composition differences caused by nutrient enrichment were not replicated in a trait-based investigation, indicating that species and traits can respond independently to nutrient additions (Chapter 3 and Chapter 4). Community difference based on species-defined investigation was driven by in increased dominance of graminoid perennial species with re-organization and, in certain cases, loss of key subordinate species (Chapter 3). Trait-based investigation found that increased productivity in N and NP treated communities likely drove the dominance completive functional traits (Chapter 4). These responses to nutrient enrichment can limit the success of annual forb species by limiting resources required for seedling establishment and success. Plant community reorganization and altered functional trait expressions also explain increased functional alpha-diversity as plants with limiting trait similarities can aid co-existence of species in highly productive plant communities (Laliberté and Legendre 2010, Chapter 4).

Implications of the research presented here can be applied to many other systems experiencing novel change. Understanding connections between topographic patterns and plant community metrics across spatial scales will contribute to disentangling how barrier island plant communities respond to global change drivers while concurrently affecting barrier island spatial heterogeneity. Cooperative research practices using both plant trait-based and species-defined community ecology can benefit investigations of complex questions that involve multiple scales and co-occurring phenomena, helping to inform how plant community structuring processes and future plant community trajectories are influenced by relationships between changing abiotic conditions and biotic interactions.

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Vita

Joseph Karl Brown was born to Stephen and Lisa Brown on November 4, 1990, in Alexandria, VA. He grew up in Fredericksburg, VA and graduated from Massaponax High School, Fredericksburg, VA in 2009. He received his Bachelor of Science in Biology from Virginia Commonwealth University, Richmond, VA in 2013. He went on to teach remedial algebra at Post Oak Middle School in Spotsylvania County, VA, while also coaching the boy's track team. In 2014 he started as a graduate student in the Coastal Plant Ecology Lab and received his Master of Science in Biology from Virginia Commonwealth University in 2016. He subsequently enrolled in the Integrative Life Sciences program at VCU where he continued research on coastal plant ecology. In 2018 he was the lead organizer for an Organized Oral Session at the annual Ecological Society of America (ESA) national conference that synthesized coastal research across the U.S. While enrolled in his PhD program he mentored 3 undergraduate researchers and served as the Student Liaison Coordinator for the ESA Student Section, Student Liaison for the ESA Southeast Chapter, and President of the Society for Ecological Restoration at VCU.