2020

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

Joseph K. Brown
Virginia Commonwealth University

Julie C. Zinnert
Virginia Commonwealth University, jczinnert@vcu.edu

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

Joseph K. Brown[1,2] and Julie C. Zinnert [1,†]

[1]Department of Biology, Virginia Commonwealth University, 1000 West Cary Street, Richmond, Virginia 23284 USA
[2]Integrative Life Sciences Doctoral Program, Virginia Commonwealth University, 1000 West Cary Street, Richmond, Virginia 23284 USA

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.

Key words: Barrier islands; dune; elevation; functional traits; Hog Island; Metompkin Island; swale; topography; vegetation; Virginia Coast Reserve.

† **E-mail:** jczinnert@vcu.edu

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 Ben 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 (Monge and Stallins 2016).

Barrier islands occur on every continent except Antarctica and are present on 30% of U.S. 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 such as 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 influences 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).

MATERIALS AND 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
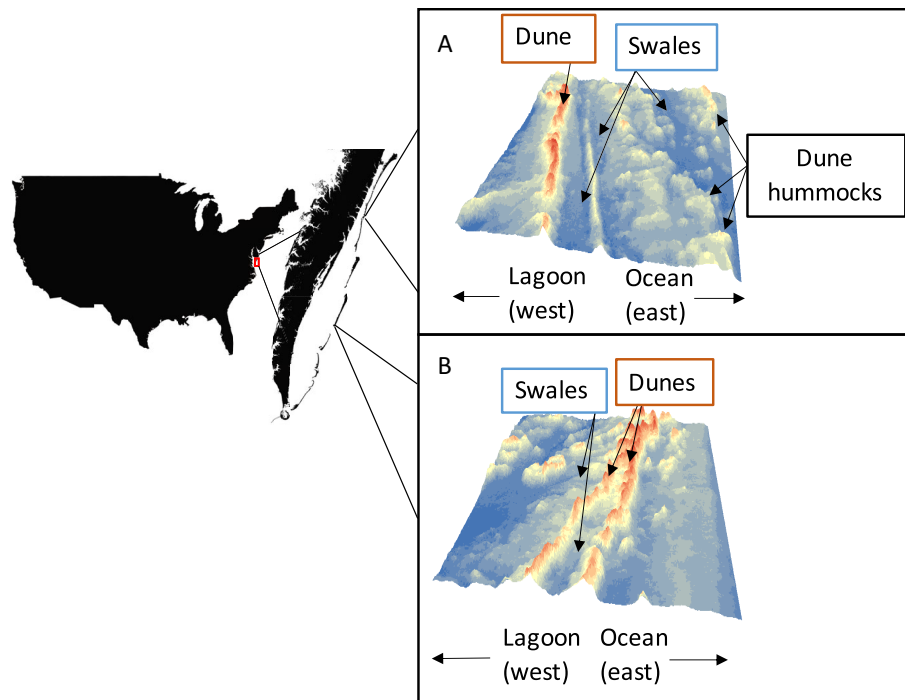
Fig. 1. Map of locations and topographic representation of sites on Metompkin Island (A) and Hog Island (B). The right-side limit of the figures indicates high-tide line on ocean side of each island.

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 such as sea spray and overwash (Fig. 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. 1a). A continuous, stabilized dune ridge exists ~120 m west of the shoreline, but low topographic relief and lack of dominant woody species make 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. 1b; Woods et al. 2019, Zinnert et al. 2019). This is evidenced by no change in the marsh–upland boundary over the last ~30 yr (Zinnert et al. 2019). The low-elevation swale habitats exist between primary and stabilized dune systems (Fig. 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 five 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.

Table 1. Summary of functional roles of traits selected for this study with trait relation to functional role in ecosystems.

Functional role	Traits	References
Aboveground		
Plant growth functions related to photosynthetic rate, relative growth rate, light capture, and leaf life span.	Height; Specific leaf area (SLA); Leaf nitrogen content (leaf %N)	Reich et al. (1998), Cornelissen (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		
Root growth strategies related to trade-offs between proliferation of low-density roots for resource uptake and increased root tissue construction for long root life span 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)

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 principal component in defining plot affiliation with each habitat type (e.g., dune or swale). Elevation of plots was collected using LiDAR images of study areas (1- to 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 and 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 (detailed in Trait selection and sampling).

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 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 the 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 (δ^{13}C) analyses. 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, and 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, 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 (δ^{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 × 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 (α = 0.05) between Hog Island 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 α = 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 overinfluence 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 three 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 were then tested using MRPP to determine whether trait-based composition significantly differed among habitat types (α = 0.05). Pairwise tests were performed to determine which habitat types differed in trait-based composition (PC-ORD; Bonferroni-adjusted α = 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 (α = 0.05). The 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 whether ecosystem productivity was different among habitat types (α = 0.05). The Tukey HSD was performed to test for pairwise differences in habitat biomass production. All analyses on biomass were completed using 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). 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. S1). Soil chloride values on Metompkin dune and swale had a lower range (7.2–88.2 and 8.2–118.1 µg/g, respectively) than soil chlorides on Hog dune and swale habitats (10.1–575.9 and 88.2–7968.2 µg/g, 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). 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. 3a). We found differences in mean trait-based community composition between habitats and differences in site-to-site variation within habitat types (Fig. 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. 3b), suggesting higher amounts of structural carbon in leaves. Hog dune, Metompkin dune, and Metompkin swale all showed positive correlations with resource conservation traits and traits that can be utilized by rapid growth/disturbance response (e.g., RTD, leaf δ¹³C, SLA, root C:N, and leaf %N; Fig. 3b). A full list of trait correlation coefficients and goodness-of-fit results can be viewed in the supplementary appendix (Appendix S1: Table S1).

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
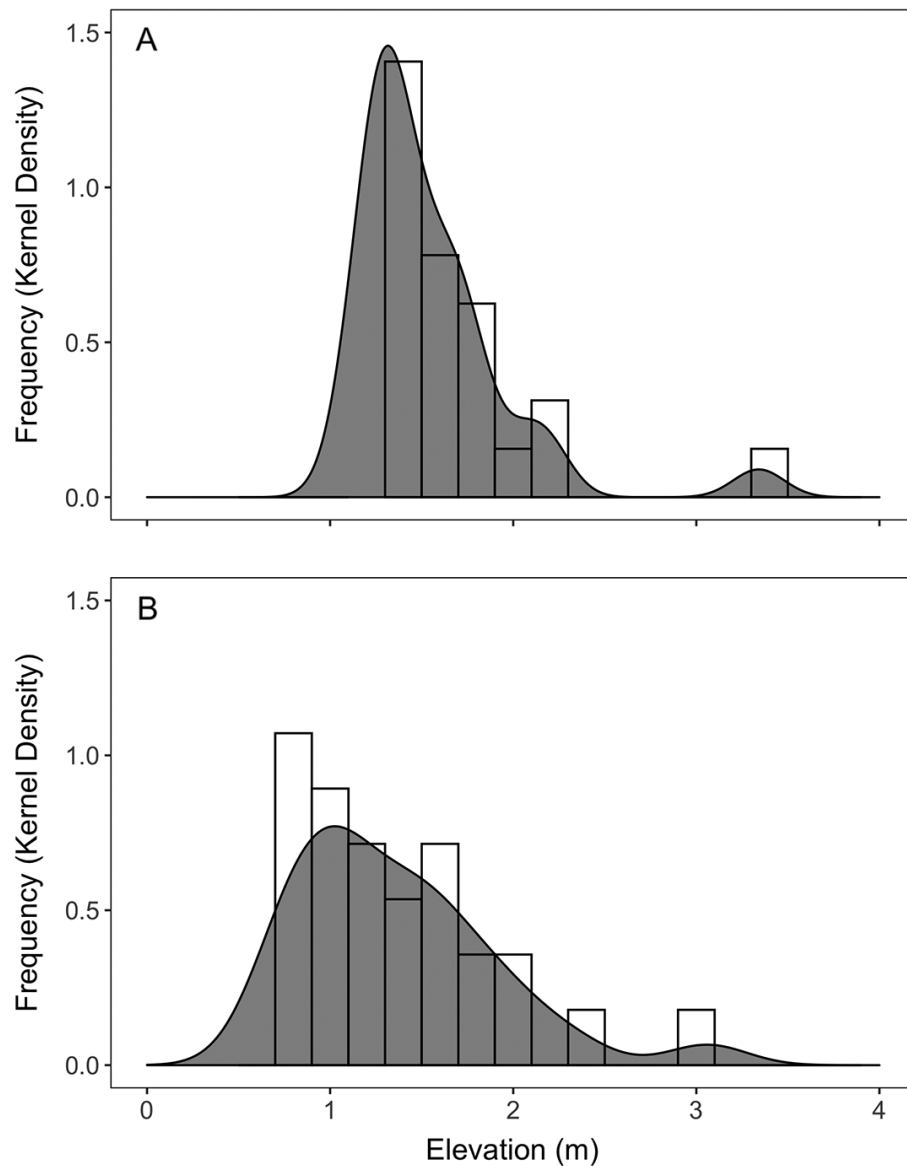
Fig. 2. Frequency distribution of plot elevations on Metompkin Island (A) and Hog Island (B). Histogram bars are overlaid by Kernel density curve to represent nonparametric probability distribution.

swale habitats had similar trait-based community compositions (Table 3, Fig. 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 3). Similar results were found when analyzing communities based on species dissimilarities (Appendix S1: Table S2,

Fig. S2). A full list of species and NMDS axes correlations are provided in supplementary appendix (Appendix S1: Table S3). Site-to-site variation of trait-based communities within habitat type differed significantly between Hog swale and Metompkin swale habitats (Table 4), indicating higher site dispersion based on traits in Metompkin swale habitats (Fig. 3a).

Table 2. Pairwise comparison of MRPP results on environmental factors between habitat types on Hog and Metompkin Island.

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

Note: Bold indicates significance with a corrected $\alpha = 0.008$.

Ecosystem productivity

Ecosystem productivity varied significantly among habitats ($F = 5.81$, $P < 0.05$; Fig. 4) and was highest in Hog swale habitat (870.1 ± 135.02 g/m^2) compared to all other habitat types (Fig. 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 found that inter- and intra-island habitats differ in trait-based community and ecosystem productivity. This research contributes to literature linking indirect drivers such as 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, which normally lead to construction of primary dune ridges, results 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 counterintuitive, this is evidenced by the negative correlation with soil salinity of Metompkin swale habitats and 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 buildup, as seen in the Hog swale habitat. Increased salinity in soils has 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
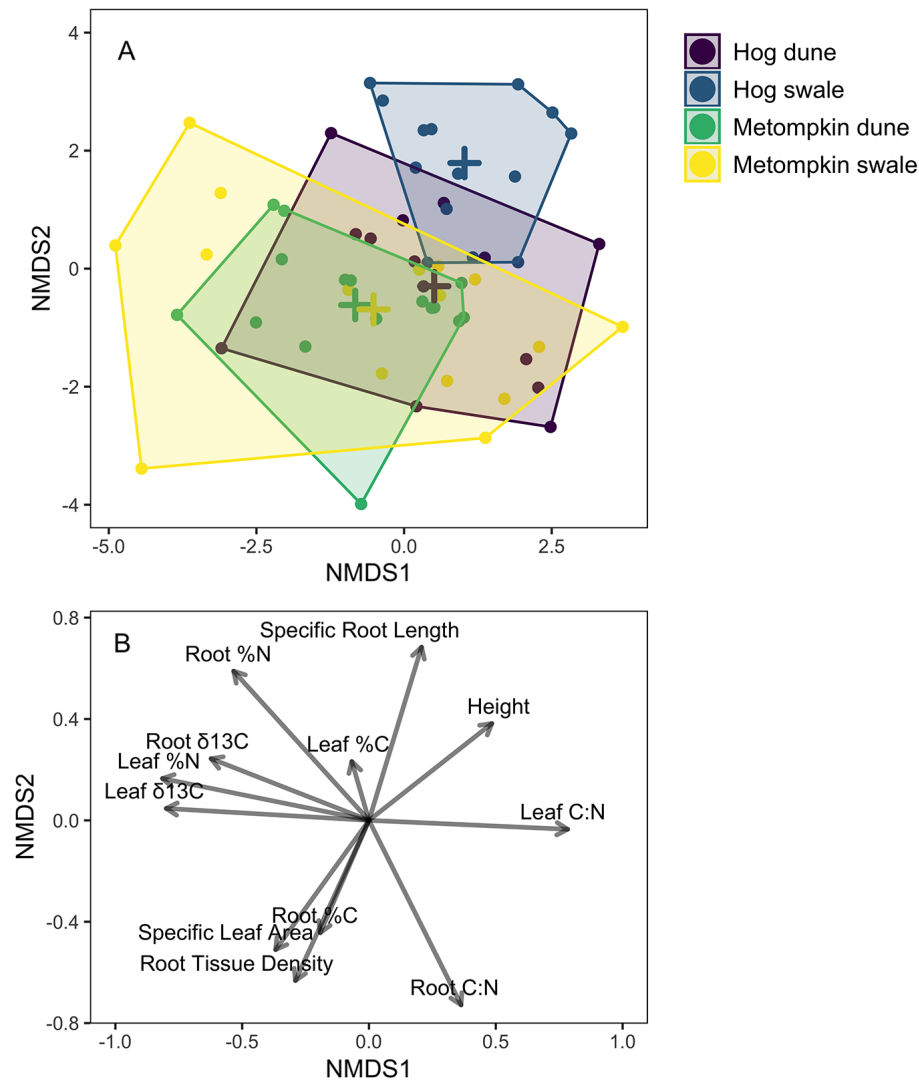
Fig. 3. (A) Non-metric multidimensional scaling of community-level trait-based composition grouped by habitat type by convex hulls. Points represent plots in trait space with plus symbols (+) representing centroids for each habitat type. Colors are matched to island and habitat association. Centroids 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 S1).

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

Table 3. Pairwise comparison of MRPP results on trait-based community composition differences between habitat types on Hog Island and Metompkin Island.

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

Note: Bold indicates significance with a corrected $\alpha = 0.008$.

Table 4. Beta-dispersion Tukey HSD comparison of trait-based community dispersion differences among habitat types on Hog Island and Metompkin Island, with differences in mean distance to centroid indicated as absolute values.

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

Note: Bold indicates $P < 0.05$.

Fig. 4. Primary productivity (mean ± standard error) as measured by end-of-season biomass for each island and community type. Letters indicate significant differences based on the Tukey HSD pairwise comparisons, such that bars that do not share the same letter are significantly different ($P < 0.05$).

become a primary force in community development as abiotic factors influence species interactions (Díaz et al. 1998, Feagin and Ben 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
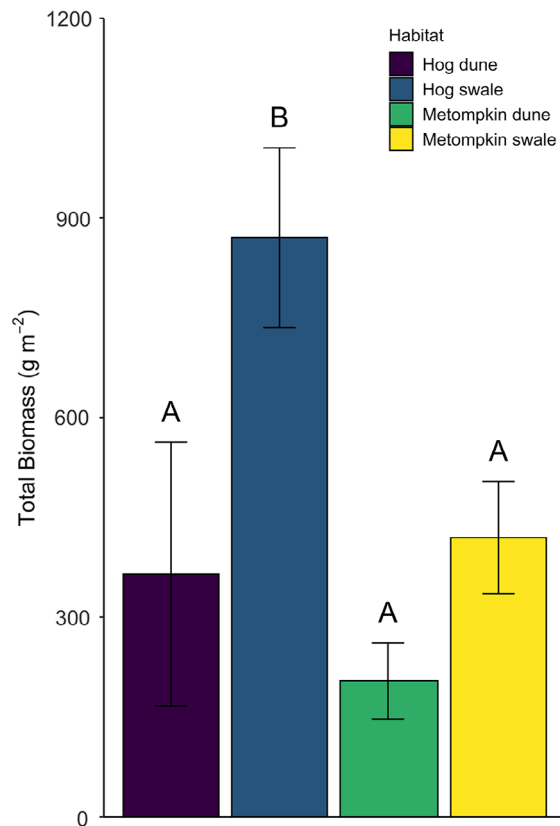
disturbance is related to increased biomass production in dune–swale systems. Relationships between increased productivity and trait-based composition of plant communities indicate competitive interactions in Hog swales. For example, higher max height and SRL in Hog swale habitats may result from competitive communities developing in high-production environments (Feagin and Ben 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 help provide support for plants to compete for light and would explain low SLA values seen in Hog swales, as the 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. 2012*b*). 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., δ^{13}C) and 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 such as 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 allow 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 influence 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 into how barrier islands may serve as good systems to study assembly processes and linkages with productivity.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

None declared.

REFERENCES

Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62:245–253.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693.

Art, H. W., F. H. Bormann, G. K. Voigt, and G. M. Woodwell. 1974. Barrier island forest ecosystem: role of meteorologic nutrient inputs. Science 184:60–62.

Bardgett, R. D., L. Mommer, and F. T. De Vries. 2014. Going underground: root traits as drivers of ecosystem processes. Trends in Ecology and Evolution 29:692–699.

Bazzichetto, M., M. Malavasi, A. T. R. Acosta, and M. L. Carranza. 2016. How does dune morphology shape coastal EC habitats occurrence? A remote sensing approach using airborne LiDAR on the Mediterranean coast. Ecological Indicators 71:618–626.

Birouste, M., E. Zamora-Ledezma, C. Bossard, I. M. Pérez-Ramos, and C. Roumet. 2014. Measurement of fine root tissue density: A comparison of three methods reveals the potential of root dry matter content. Plant and Soil 374:299–313.

Brantley, S. T., S. N. Bissett, D. R. Young, C. W. V. Wolner, and L. J. Moore. 2014. Barrier island morphology and sediment characteristics affect the recovery of dune building grasses following storm-induced overwash. PLOS ONE 9:e104747.

Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6:1–15.

Burdick, D. M., and I. A. Mendelssohn. 1987. Waterlogging responses in dune, swale and marsh populations of Spartina patens under field conditions. Oecologia 74:321–329.

Cadotte, M. W. 2017. Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters 20:989–996.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the

National Academy of Sciences USA 104:17430–17434.

Ciccarelli, D. 2015. Mediterranean coastal dune vegetation: Are disturbance and stress the key selective forces that drive the psammophilous succession? Estuarine, Coastal and Shelf Science 165:247–253.

Conti, L., F. de Bello, J. Lepš, A. T. R. Acosta, and M. Carboni. 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. Journal of Vegetation Science 28:762–773.

Cornelissen, J. H. C., et al. 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Craine, A. J. M., J. Froehle, D. G. Tilman, D. A. Wedin, and F. S. Chapin. 2001. The relationships among root and leaf traits of 76 grassland species and relative abundance along fertility and disturbance gradients. Oikos 93:274–285.

Craine, J. M., and W. G. Lee. 2003. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. Oecologia 134:471–478.

Díaz, A. S., et al. 2004. The plant traits that drive ecosystems : evidence from three continents. Journal of Vegetation Science 15:295–304.

Díaz, S., M. Cabido, and F. Casanoves. 1998. Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122.

Du, F., H. B. Shao, L. Shan, Z. S. Liang, and M. A. Shao. 2007. Secondary succession and its effects on soil moisture and nutrition in abandoned old-fields of hilly region of Loess Plateau, China. Colloids and Surfaces B: Biointerfaces 58:278–285.

Eissenstat, D. 1991. On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytologist 118:63–68.

Fahrig, L., B. Hayden, and R. Dolan. 1993. Distribution of barrier island plants in relation to overwash disturbance: a test of life history theory. Journal of Coastal Research 9:403–412.

Fang, S., M. W. Cadotte, Z. Yuan, F. Lin, J. Ye, Z. Hao, and X. Wang. 2018. Intraspecific trait variation improves the detection of deterministic community assembly processes in early successional forests, but not in late successional forests. Journal of Plant Ecology 12:593–602.

Feagin, R. A., and X. Ben Wu. 2007. The spatial patterns of functional groups and successional direction in a coastal dune community. Rangeland Ecology and Management 60:417–425.

Fenster, M. S., R. Dolan, and J. J. Smith. 2016. Grain-size distributions and coastal morphodynamics along the southern Maryland and Virginia barrier islands. Sedimentology 63:809–823.

Fortunel, C., R. Valencia, S. J. Wright, N. C. Garwood, and N. J. B. Kraft. 2016. Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. Ecology Letters 19:1062–1070.

Fukami, T., I. A. Dickie, J. P. Wilkie, B. C. Paulus, D. Park, A. Roberts, P. K. Buchanan, and R. B. Allen. 2010. Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters 13:675–684.

Garnier, E., J. Cortez, G. Billès, M. L. Navas, C. Roumet, M. Debussche, G. Laurent, A. Blanchard, D. Aubry, A. Bellmann, C. Neill, and J. P. Toussaint. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85:2630–2637.

Goldstein, E. B., L. J. Moore, and O. D. Vinent. 2017. Lateral vegetation growth rates exert control on coastal foredune "hummockiness" and coalescing time. Earth Surface Dynamics 5:417–427.

Grime, J. P. 1974. Vegetation classification by reference to strategies. Nature 250:26–31.

Hacker, S. D., K. R. Jay, N. Cohn, E. B. Goldstein, P. A. Hovenga, M. Itzkin, L. J. Moore, R. S. Mostow, E. V. Mullins, and P. Ruggiero. 2019. Species-specific functional morphology of four US Atlantic coast dune grasses: biogeographic implications for dune shape and coastal protection. Diversity 11:82.

Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters 11:348–356.

Kraft, N. J. B., P. B. Adler, O. Godoy, E. C. James, S. Fuller, and J. M. Levine. 2015. Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29:592–599.

Kunstler, G., et al. 2015. Plant functional traits have globally consistent effects on competition. Nature 529:204–207.

Laliberté, E., B. Shipley, D. A. Norton, and D. Scott. 2012a. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? Journal of Ecology 100:662–677.

Laliberté, E., B. L. Turner, T. Costes, S. J. Pearse, K. H. Wyrwoll, G. Zemunik, and H. Lambers. 2012b. Experimental assessment of nutrient limitation along a 2-million-year dune chronosequence in the south-western Australia biodiversity hotspot. Journal of Ecology 100:631–642.

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538–547.

Lavorel, S., and E. Garnier. 2002. composition in community changes Predicting from plant traits: functioning ecosystem the Holy Grail revisiting. Functional Ecology 16:545–556.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A., and M. A. McPeek. 2006. Coexistence of the Niche and neutral perspectives in community ecology. Ecology 87:1399–1410.

Lepori, F., and B. Malmqvist. 2009. Deterministic control on community assembly peaks at intermediate levels of disturbance. Oikos 118:471–479.

Li, Y., and B. Shipley. 2018. Community divergence and convergence along experimental gradients of stress and disturbance. Ecology 99:775–781.

Liu, W., H. Xu, X. Yang, and X. Shi. 2011. Extraction of molybdenum from low-grade Ni-Mo ore in sodium hypochlorite solution under mechanical activation. Minerals Engineering 24:1580–1585.

Liu, X., G. Xu, Y. Wu, L. Ma, J. Gao, Y. Zhang, and P. Liu. 2017. Leaf characters of *Ulmus elongata* in fragmented habitats: implications for conservation. Acta Ecologica Sinica 37:346–353.

Mcfalls, T. B., P. A. Keddy, D. Campbell, and G. Shaffer. 2010. Hurricanes, floods, levees, and nutria: vegetation responses to interacting disturbance and fertility regimes with implications for coastal wetland restoration. Journal of Coastal Research 26:901–911.

Miller, T. E., E. S. Gornish, and H. L. Buckley. 2009. Climate and coastal dune vegetation: disturbance, recovery, and succession. Plant Ecology 206:97–104.

Mommer, L., E. J. W. Visser, J. van Ruijven, H. de Caluwe, R. Pierik, and H. de Kroon. 2011. Contrasting root behaviour in two grass species: a test of functionality in dynamic heterogeneous conditions. Plant and Soil 344:347–360.

Monge, J. A., and J. A. Stallins. 2016. Properties of dune topographic state space for six barrier islands of the U.S. southeastern Atlantic coast. Physical Geography 37:452–475.

Mori, A. S., F. Isbell, and R. Seidl. 2018. b-Diversity, community assembly, and ecosystem functioning. Trends in Ecology & Evolution 33:549–564.

Oksanen, J., et al. 2019. vegan: community ecology package. R package version 2.5-4. http://CRAN.R-project.org/package=vegan

Oster, D., and L. Moore. 2009. Beach Morphology of the Virginia Barrier Islands 1998, 2005 and 2009. Environmental Data Initiative. https://doi.org/10.6073/pasta/95bf349362e134e6730b9568f1946b1d

Pakeman, R. J., J. J. Lennon, and R. W. Brooker. 2011. Trait assembly in plant assemblages and its modulation by productivity and disturbance. Oecologia 167:209–218.

Pérez-Harguindeguy, N., et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany 61:167–234.

Poorter, H., and R. De Jong. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. New Phytologist 143:163–176.

Reich, P. B., M. B. Walters, D. S. Ellsworth, J. M. Vose, J. C. Volin, C. Gresham, and W. D. Bowman. 1998*a*. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life span: a test across biomes and functional groups. Oecologia 114:471–482.

Reich, P. B., M. B. Walters, M. G. Tjoelker, D. Vanderklein, and C. Buschena. 1998*b*. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Functional Ecology 12:395–405.

Roumet, C., C. Urcelay, and S. Díaz. 2006. Suites of root traits in species growing differ between annual and perennial. New Phytologist 170:357–367.

Shiflett, S. A., and D. R. Young. 2010. Avian seed dispersal on Virginia Barrier Islands: potential influence on vegetation community structure and patch dynamics. American Midland Naturalist 164:91–106.

Stallins, J. A. 2006. Geomorphology and ecology: unifying themes for complex systems in biogeomorphology. Geomorphology 77:207–216.

Stallins, J. A., and D. Corenblit. 2018. Geomorphology Interdependence of geomorphic and ecologic resilience properties in a geographic context. Geomorphology 305:76–93.

Stutz, M. L., and O. H. Pilkey. 2001. A review of Global Barrier Island distribution. Journal of Coastal Research:15–22.

Suding, K. N., S. Lavorel, F. S. Chapin, J. H. C. Cornelissen, S. Díaz, E. Garnier, D. Goldberg, D. U. Hooper, S. T. Jackson, and M. L. Navas. 2008. Scaling environmental change through the

community-level: a trait-based response-and-effect framework for plants. Global Change Biology 14:1125–1140.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tilman, D., J. Knopps, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302.

Tjoelker, M. G., J. M. Craine, D. Wedin, P. B. Reich, and D. Tilman. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. New Phytologist 167:493–508.

Vellend, M., et al. 2014. Assessing the relative importance of neutral stochasticity in ecological communities. Oikos 123:1420–1430.

Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. Trends in Ecology and Evolution 21:261–268.

Woods, N. N., B. L. Dows, E. B. Goldstein, L. J. Moore, D. R. Young, and J. C. Zinnert. 2019. Interaction of seed dispersal and environmental filtering affects woody encroachment patterns in coastal Grassland. Ecosphere 10, e02818.

Wright, I. J., et al. 2004. The worldwide leaf economics spectrum. Nature 428:821–827.

Young, D. R., S. T. Brantley, J. C. Zinnert, and J. K. Vick. 2011. Landscape position and habitat polygons in a dynamic coastal environment. Ecosphere 2:1–15.

Young, D. R., D. L. Erickson, and S. W. Semones. 1994. Salinity and the small-scale distribution of three barrier island shrubs. Canadian Journal of Botany 72:1365–1372.

Zinnert, J. C., J. A. Stallins, S. T. Brantley, and D. R. Young. 2017. Crossing scales: the complexity of barrier-island processes for predicting future change. BioScience 67:39–52.

Zinnert, J. C., S. M. Via, B. P. Nettleton, P. A. Tuley, L. J. Moore, and J. A. Stallins. 2019. Connectivity in coastal systems: Barrier island vegetation influences upland migration in a changing climate. Global Change Biology 25:2419–2430.

Data Availability Statement

Functional trait, species, and biomass productivity data from this project are 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; and Virginia Coast Reserve Long-Term Ecological Research Project Data Publication knb-lter-vcr.296.2

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3139/full