2023

Dune building dynamics impact cross-island connectivity and barrier island characteristics

Alexander Sabo
Virginia Commonwealth University

Dune building dynamics impact cross-island connectivity and barrier island characteristics

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

By

Alexander Barnes Sabo,

B.S. Environmental Science Washington College

Advisor: Dr. Julie Zinnert, Assistant Professor, Department of Biology

Virginia Commonwealth University

Richmond, VA

April 2023

Acknowledgements

First, I would like to thank my advisor and mentor Dr. Julie Zinnert. When I was looking for graduate opportunities, I had no idea what to expect, and even during the COVID-19 pandemic, Julie created an ideal lab environment for students to grow and develop as scientists. None of this would have been possible without her help and dedication. I would also like to thank my family and my parents for their support throughout this journey. I was not sure what I was getting myself into, and they had even less of an idea. My parents and brothers were always there for, ready to help any way that they could. Thank you to my friend, Aidan, for his continued support, and for his willingness to dog sit almost every time I needed to go to the shore for fieldwork. Finally, I thank my partner, Sarah, for all of her support throughout this process. Life for a medical student is busier than imaginable, but she has always been there for me as we have gone through this journey together.

Thank you to Andrew White, Emily Riffe, Natasha Woods, and Megan Canfield for sharing their unbelievable knowledge of coastal ecology, helping with fieldwork, and providing guidance whenever questions arose. Drew, Emily, and Megan have become great friends of mine during my time with the lab, and I am unsure what a career might look like without them there. Thank you to any other past or present members of the Coastal Plant Ecology lab for helping set the groundwork for studying landscape ecology on the Virginia Barrier Islands. Thank you to Michael Cornish for his help obtaining and processing drone data.

I would also like to acknowledge that this research was performed on the ancestral lands of the Accomac tribe. Colonization by English settlers forcibly removed these peoples from their lands. The opportunities that we have as scientists to study barrier island ecology at the Virginia Coast Reserve exists at the expense of this tribe.

Table of Contents

List of Figures

Abstract

Dune building dynamics impact cross-island connectivity and barrier island characteristics

By Alexander Barnes Sabo, Bachelor of Science

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

Virginia Commonwealth University, 2023

Advisor: Dr. Julie Zinnert, Assistant Professor, Department of Biology

Located at the land-sea interface, barrier islands are important protective features that reduce wave energy and erosion from mainland areas. Further, barrier islands provide habitat for many different organisms and serve as popular areas for recreation and tourism. As sandy landforms, barrier islands are easily disturbed, but often recover after disturbance as a result of island plant communities, specifically dune building grasses. Disturbance on barrier islands is driven by storms, tides, and overwash events. After disturbance has occurred, dune grasses colonize the dunes allowing for dune building and habitat restoration. On the Virginia barrier islands, there are three dominant dune building grasses. These include *Ammophila breviligulata*, *Spartina patens*, and *Panicum amarum*. *Uniola paniculata* is also present in the region, but not in high abundance. Dune building has the potential to impact the entire barrier island ecosystem, and these grasses therefore serve as ecosystem engineers. Protection offered by dune ridges directly impacts the adjacent swale habitat, modifying both biotic and abiotic factors. In order to better understand how dune building impacts the island ecosystem as a whole, we quantified sediment accretion, plant percent cover, stem numbers, and soil characteristics (chlorides, bulk density, %OM, %C, %N). These characteristics were assessed on two islands with varied disturbance intensities. Hog island is infrequently disturbed, and resists change driven by storms and overwash. Metompkin island is frequently disturbed and undergoes high rates of overwash and island migration. In order to quantify these characteristics, 3 cross-shore transects were established on each island in 2020. Additional accretion plots were set on each island during fall 2021. Annual drone flights conducted over the islands provided for additional large-scale data collection and allowed for assessment of dune continuity through least cost paths. After one year, sediment accretion occurred at a higher rate on Hog compared to Metompkin. Dune face plots on Hog accreted sediment while dune face plots on Metompkin underwent high rates of erosion resulting in 9 of 15 plots transitioning from dune to open beach. On Hog, plots established in a newly formed dune hummock accreted sediment at a faster rate than those on the dune face. Species-specific effects were also observed on Hog, with *Panicum* accreting sediment at a significantly lower rate compared to *Ammophila* and *Spartina*. Larger, more continuous dunes on Hog offer enhanced protection for the swale habitat, reducing soil chlorides and increasing annual net primary productivity and soil carbon and nitrogen. As climate change continues to modify ecosystems globally, barrier islands will be at the forefront of increased severe weather and increased sea level. It is therefore crucial that we understand how these ecosystems respond to and recover from disturbance, and the many interconnected variables that exist among barrier island ecosystems. Understanding all aspects of the barrier island system will allow these data to be implemented into models to predict future barrier island scenarios.

Introduction

Barrier islands are critically important landforms that protect 10% of global shorelines and 30% of United States Atlantic and Gulf coasts (Stutz & Pilkey, 2001; 2011). These islands provide a variety of services to both humans and surrounding ecosystems including reduction of wave energy and storm surge, carbon sequestration, serving as habitat for a multitude of organisms, as well as recreation and tourism (Sallenger, 2000; Feagin et al., 2010; Enwright et al., 2021). Due to low topography and composition of unconsolidated substrates, barrier islands are susceptible to disturbance driven by storm and tidal induced overwash (Wolner et al., 2013). Barrier islands exist in a variety of forms and often respond differently to disturbance depending on multiple factors, including plant species composition (Wolner et al., 2013; Zinnert et al., 2017; Zinnert et al., 2019). Increasing rates of sea-level rise impact barrier islands, resulting in losses of islands, island migration, and changes to overall island habitats. This reduces the ecosystem services provided by a barrier island.

Barrier islands are highly dynamic and undergo changes on many different spatiotemporal scales. On the largest of these scales, sediment movement and ocean currents can drive broad change including island migration or rotation (Roman & Nordstrom, 1988; Zinnert et al., 2019; Jay et al., 2022; Robbins et al., 2022). This sediment movement can impact a barrier island system regionally and can be influenced by events many kilometers away (e.g. inlet formation/dredging, groin or jetty construction, beach nourishment, etc.; Armstrong & Lazarus, 2019; Stallins et al., 2020; Robbins et al., 2022). Large-scale change on barrier islands is driven by daily wave action and tides, as well as individual storm events. The daily press of wave action can lead to gradual erosion and landscape change, while the rapid pulse of a storm event can cause rapid shifts in island ecology and geomorphology (Hayden et al., 1991; Oertel & Overman, 2004; Zinnert et al., 2017). Along the US Atlantic coast, these storms come in the form of hurricanes and nor'easters. Storm events drive the movement of sediments, changing island shape and causing overwash and island migration (Leatherman et al., 1977; Hayden et al., 1995; Sallenger, 2000; Houser et al., 2008). As climate change occurs, storms will increase in severity and frequency (IPCC, 2022) resulting in further changes to barrier island systems.

On smaller scales (individual islands and habitats) plant species composition and topography can impact how the island responds to storm and overwash events (Wolner et al., 2013; Zinnert et al., 2017; Zinnert et al., 2019), impacting island resistance and resilience. Here, barrier island resilience is defined as the ability of the island to maintain elevation relative to sea-level rise. This can result in various changes on the island, including island migration (FitzGerald et al., 2018; Zinnert et al., 2019). Barrier island resistance is reflected in an island remaining fixed in place, resisting changes that are driven by sea-level rise and severe weather, but over time may result in higher rates of shoreface erosion and loss of sediment to build up interior or marsh elevation (Zinnert et al., 2019). Barrier island sediment and vegetation dynamics can potentially become modified with the effects of climate change. Climate change impacts barrier island systems through species range shifts due to warming temperatures (Huang et al., 2018; Goldstein et al., 2018) and island erosion/migration due to sea-level rise, thus, it is important to understand the many connected interactions that exist within the landscape.

Dune Building Grasses

Dune grasses modify the physical environment around them by trapping moving sediment. Plant growth and sand accretion result in dune formation, land stabilization, and a reduction of wave energy/erosion (Woodhouse et al., 1977; Stallins, 2005; Zarnetske et al., 2012;

Feagin et al., 2019). In coastal dunes, grasses function as ecosystem engineers, modifying and enhancing the topography of the barrier island landscape (Zarnetske et al., 2012; Zinnert et al., 2017). Recent research has worked to better understand the topographic and vegetation interactions that occur across the barrier island habitats, as well as how sediment fluxes and disturbance vary by habitat (Durán Vinent & Moore, 2015; Stallins & Corenblit, 2018; Zinnert et al., 2019). Dune elevation modifies surrounding island ecosystems, impacting swale habitat succession and state transitions between upland and marsh habitat (Woods et al., 2019; Zinnert et al., 2019).

Dominant dune building grasses along the US mid-Atlantic coast include *Ammophila breviligulata, Spartina patens*, *Panicum amarum*, and *Uniola paniculata* (hereafter referred to by genus). All are common on the Virginia coast; however, native ranges vary. *Ammophila* is a C_3 grass limited to more temperate climates with mortality occurring above 35°C (Seneca & Cooper, 1971). *Ammophila* is an abundant grass on the Virginia coast with its southern range extending to Cape Fear, NC (Hacker et al., 2019), although this may be influenced by plantings (Goldstein et al., 2018). *Spartina, Panicum,* and *Uniola* are C_4 grasses, and *Uniola* is most abundant in North Carolina and points south (Goldstein et al., 2018; Hacker et al., 2019). Both *Panicum* and *Spartina* can be found along the entire US east coast and are abundant on the Virginia coastline (Lonard et al., 2010; Hacker et al., 2019; Brown & Zinnert, 2020). Unlike other dune grass species, *Spartina* can thrive in a variety of habitats across the barrier island system, tolerating conditions on the dune ridge, in the swale, and in the back-barrier marsh (Ehrenfeld, 1990; Lonard et al., 2010).

Each of the dune grass species mentioned exhibit different dune building characteristics. *Ammophila, Panicum*, and *Uniola* are known to be effective dune builders; however, *Ammophila* often creates linear dune ridges using lateral rhizomes, resulting in distinct sand accretion and dune stabilization (Woodhouse et al., 1977; Stallins, 2005; Goldstein et al., 2017). Conversely, *Uniola* and *Panicum* exhibit phalanx growth (i.e. more spaced-out bunches that do not spread in the same lateral manner) due to shorter rhizome length (Woodhouse et al., 1977; Stallins, 2005; Goldstein et al., 2017; Walker & Zinnert, 2022). Unlike the other species, dune building patterns of *Spartina* are less documented; however, it has been shown to build dunes, potentially at a slower rate compared to other grasses (Mullins et al., 2019). Each of these four species also exhibits differing aboveground traits (i.e. height, number of shoots, shoot density, plant density; Hacker et al., 2019; Walker & Zinnert, 2022) which may potentially impact sediment accretion (Charbonneau et al., 2021).

Dune building is often impacted by disturbance in the form of severe weather and overwash events that can result in burial of dune grasses or large-scale erosion (Sallenger, 2000). Plant tolerance of high salinity and burial are necessary for dunes to survive these events (Brown & Zinnert, 2018). Disturbance events can also result in the temporary reset of a dune community. In an island setting where disturbance is more frequent, the dune community may not have sufficient time to recover between events, preventing new dune formation (Miller et al., 2009; Brown & Zinnert, 2020). Although recent studies have documented aspects of grass species effect on sediment dynamics, (e.g. Hacker et al., 2019; Mullins et al., 2019; Charbonneau et al., 2021); studies examining natural dune grass populations and sediment capture over time are lacking. Quantifying interactions between dune building grasses and sediment movement at different locations across the entire barrier island system will enhance predictions of future conditions created by storms and sea-level rise disturbance (Wolner et al., 2013; Zinnert et al., 2017; Zinnert et al., 2019).

Barrier Island Habitats

Barrier islands are separated into distinct habitats including beach, dune, swale, and back-barrier marsh (Figure 1). Variability in dune shape and size created by different dune building grasses have an important impact across the barrier island ecosystem. These differences lead to distinct vegetative zones on barrier islands, primarily consisting of dune and swale communities (Brown & Zinnert, 2020). As new dune formation occurs, embryonic dunes (i.e. hummocks) will coalesce into foredunes, which later form dune ridges and additional swale habitats (Goldstein et al., 2017; Walker & Zinnert, 2022). The formation of these separate habitats results in differing elevations and distance from shoreline, with plant species uniquely adapted to living in specific conditions (Young et al., 2011). These topographic separations affect species colonization which can lead to further habitat modification.

Differences in dominant dune building grass may impact an entire barrier island. For example, islands that are dominated by lower, hummock dunes are often impacted more frequently by disturbance events as the dune ridges do not protect the swale habitat (Stallins, 2005; Houser et al., 2008). This leads to swale habitat that is more similar to the surrounding dune and beach (Zinnert et al., 2017; Brown & Zinnert, 2020). Conversely, islands that are dominated by taller, linear dune ridges are more protected from disturbance events and the swale habitat is less frequently impacted. This leads to a swale habitat that is less similar when compared to the surrounding dune and beach habitats (Brown & Zinnert, 2020).

Landscape Characteristics

Coastal dunes are nutrient limited as nutrients rapidly leach into the groundwater from the sandy substrates (Skiba & Wainwright, 1984; Wood, 2021). This creates a soil environment that is limited in available nutrients for plant use (Ehrenfeld, 1990). Even with nutrients leaching from the soil, there are a variety of sources that add and modify the available concentrations including local and oceanic flora and fauna, often through decomposition of debris (Olson, 1958; Skiba & Wainwright, 1984; Ehrenfeld, 1990; Conn & Day, 1996). Other nutrients may enter the dune system from meteorological sources such as rain, snow, or ocean aerosols (Art et al., 1974; Ehrenfeld, 1990). Nitrogen, an important nutrient for plant growth, is often introduced to these systems through nitrogen fixing shrubs or animal waste (Permar & Fisher, 1983; Skiba & Wainwright, 1984). In the mid-Atlantic region, *Morella cerifera* (hereafter referred to by genus) is a common nitrogen fixing shrub with an expanding range in coastal ecosystems due to warming temperatures (Huang et al., 2018). *Morella* grows in the swale habitat behind protective foredunes, modifies the local grassland microclimate, and inputs nitrogen and carbon into the system (Brantley & Young, 2010; Woods et al., 2019; Wood et al. 2020). The relationship between foredune development and *Morella* expansion may alter nutrient availability, further influencing landscape dynamics.

Across the barrier island landscape, soil carbon concentrations vary between the hummock, dune ridge, and swale habitats (Rossi & Rabenhorst, 2019). This is driven by increases in soil age across the landscape, with swale soils being older than dune soils, as well as the spatial transition from herbaceous to woody vegetation (Brantley & Young, 2010; Rossi & Rabenhorst, 2019). Although barrier island carbon processes are not well documented, these soils have the potential to store large amounts of organic carbon (Rossi & Rabenhorst, 2019), depending on overall landscape topography and species composition. Thus, differences in dune topography and the vegetation of adjacent swales have large-scale impacts on all components of the barrier island system (Zinnert et al., 2019; Reeves et al., 2022).

The objective of my research is to understand dune species interactions with sediment dynamics and impacts of dune topography on interior island ecosystem processes (i.e. carbon, productivity, species composition) in islands differing in disturbance histories. Using two barrier islands that differ in disturbance intensity (based on prior landscape change; Zinnert et al., 2019; Brown & Zinnert, 2020), I quantified 1) how sediment availability and disturbance interact with dominant dune grasses to influence rates of sediment accretion and soil characteristics over time and 2) how dune topography-disturbance interactions influence swale vegetation and soil characteristics. Quantifying these factors on islands differing in disturbance intensity provides insight into the roles that dune grasses have on barrier island landscape development and change.

Methods

The study area for this research was two islands on the Virginia Eastern Shore, located within the Virginia Coast Reserve (VCR). The VCR is a collection of islands spanning from Assateague Island in the north to Fisherman Island in the south (Hayden et al., 1991; Figure 2). This reserve was designated by the National Science Foundation (NSF) as a Long-Term Ecological Research (LTER) site and is managed by The Nature Conservancy (Hayden et al., 1991). Since the evacuation of the town of Broadwater from Hog Island in the 1930s, these islands have been primarily uninhabited. This has created a vast barrier island system with limited direct human influence (Hayden et al., 1991). Prior to European settlement, these islands, along with the Virginia Eastern Shore were inhabited by the Accomac tribe, members of the Powhatan Confederacy. Throughout the 17th century, this land was taken from this group by colonizers through force and coercion (Rountree, 1996).

This work was focused on Hog and Metompkin Islands (hereafter referred to as 'Hog' and 'Metompkin'; Figure 2). Both islands are currently undergoing differing responses to disturbance. Hog is infrequently disturbed and undergoes rotational change. This is evidenced by changes in the northern and southern ends of the island gaining and losing sand over time. Recently, sand has been eroding from the north end of the island and depositing on the south end, creating a wide beach allowing for establishment of dune grasses forming new dune hummocks. Hog is characterized by multiple linear dune ridges with swale habitat in between. The island is on average 1.70 m above mean sea-level, with an average thickness below mean sea-level of 4.5 m (Wolner et al., 2013). Island thickness below sea level refers to how much material separates the island surface from the continental shelf (Robbins et al., 2022). Hog has been characterized as rotationally unstable, where sediment shifts between the northern and southern ends of the island, but the center remains relatively consistent (Fenster et al., 2016).

Metompkin is frequently disturbed and experiences extensive overwash, causing the island to retreat landward over time (Wolner et al., 2013; Zinnert et al., 2019). Metompkin has recently had a linear dune ridge; however, overwash fans have broken through this ridge causing it to be discontinuous (Brown & Zinnert, 2020). Unlike Hog, Metompkin is on average 1.64 m above mean sea-level, with an average thickness below mean sea-level of 1.0 m (Wolner et al., 2013), and experiences parallel retreat, moving closer to the mainland over time (Fenster et al., 2016). Further contributing to the disturbance response of Metompkin is downdrift sediment starvation caused by development on islands to the north (Stallins et al., 2020). This interrupts southward longshore sediment movement, preventing Metompkin from accreting new sediment naturally. Additional contributing factors to the differences seen among the two islands are ancient geological features that dictate island placement in relation to the mainland. This comes in the form of underlying topographic highs around Hog that are absent near Metompkin (Robbins et al., 2022).

Ammophila, *Spartina*, and *Panicum* are abundant on the Virginia barrier islands. *Uniola* is not dominant on these islands, and experimental plantings of *Uniola* on Hog have led to localized populations (Mullins et al., 2019).

Study locations and sampling procedure

To quantify herbaceous species abundance and elevation over time, cross-shore transects were established in August 2020 (n =3) on the south end of both islands. Transects were spaced 100 m apart and 0.25m^2 plots were placed every ~5 m from the 2020 high tide line spanning the beach, dune, and into the swale, stopping prior to a shrub thicket when present (n=30). At each plot, location and elevation were recorded with Trimble R10-2 and TSC7 units (Trimble Inc., Westminster, CO). In August 2020, 2021, and 2022, plots were quantified for % cover by species. Seasons end biomass was sampled in a 10 x 100 cm plot adjacent to each composition plot to quantify seasons end biomass (i.e. aboveground annual net primary productivity, ANPP). Due to logistical constraints, biomass was not collected on Hog in August 2022.

In November 2021, additional sampling plots were established on the south ends of both islands, located on the foredune and in the swale. To quantify species interactions with sediment and soil characteristics, 0.25m^2 plots were established based on species presence in naturally occurring monocultures (i.e. *Ammophila, Spartina, Panicum*, n = 5) on the foredune face. On Hog, additional plots were placed in the new dune hummock formation for *Ammophila, Spartina, Panicum* (n = 5). Within the swale, plots were located behind dunes in mixed species grassland (n = 15). Snow poles (123 cm in height and 0.8 cm in diameter) were installed in the center of each plot to monitor sediment accretion. Poles were driven into the ground, leaving ~70 cm above the soil surface. Baseline measurements of exposed pole heights were obtained to indicate starting sand level at each sample location.

Seasonal measurements of sediment accretion, species cover, stem density, and soil characteristics were conducted in 2021 (November) and 2022 (March, August, and November). Species percent cover and stem count were quantified within the 0.25 m^2 plot. Soil cores were obtained directly outside of the 0.25 m^2 plot using a 30 cm metal tube and a mallet. Height of the soil core was measured in the field, and cores were stored in soil collection bags to be transported back to the lab for processing.

Bulk density was quantified to determine soil compaction by measuring the volume of soils in the field, and dry weight of the soil samples after drying at 100°C for 48 hours. Soil organic matter (OM) content was measured using the loss on ignition method by placing 1 g dry soil in a muffle furnace at 550°C for 6 hours (Marchante et al., 2008). Additional samples were sent to the Cornell Isotope Lab for additional analysis of total carbon and nitrogen content. Soil chlorides were quantified to assess salinity content using an Orion Research digital ion analyzer (model: 501, Orion Corporation, Espoo, Finland) to measure the conductivity (mV) of each sample and compare to known saline concentrations.

Drone Imagery

To quantify ease of movement across the landscape, orthomosaic and digital elevation models (DEM) were obtained through the completion of annual drone flights in 2020 and 2022 with the assistance of the Castaroni lab at the University of Virginia and VCR staff. After drone flights, images were analyzed, modified, and corrected by the Castorani lab using Agisoft

Metashape version 1.7 (Agisoft, St. Petersburg, Russia). This created usable raster datafiles (.TIF) that contained imagery and elevation information as a DEM (Figure S1).

To determine topographic factors impacting dune-swale connectivity, DEM imagery analysis was performed using ArcGIS Pro version 2.8.3 (Esri, Redlands, CA). Least cost path analysis was quantified on each island to determine the potential for overwash flow into the swale. Least cost path analysis is a useful tool in determining how water can move across a landscape. This metric (path cost value) is most commonly used when assessing watersheds in mainland areas, however, here we use it as a measure of how continuous dune protection is on the barrier island. The path cost value measures the amount of resistance caused by elevation changes moving from designated start/end points. Least cost path was evaluated starting on the beach (near the high-water mark) to the first swale behind the primary linear dune ridge (n=500, Figure S2).

Statistics

For statistical analysis, dune and swale habitats were considered separately. In order to meet assumptions of normality, percent cover, stem count, OM, and chlorides were log+1 transformed. In the dune habitat, percent cover, stem density, accretion, and soil metrics were analyzed via 3-way ANOVA with habitat locations, species, and season as treatment variables. In the swale habitat, percent cover, ANPP, and soil metrics were analyzed via 2-way ANOVA with island and season as treatment variables. Tukey's Honest Significant Difference tests were performed on significant interactions or main effects of ANOVA tests. Correlations were utilized to determine relationships between sediment accretion and biotic variables mentioned. Path cost values and Trimble elevations were analyzed using a 2-way ANOVA with island and year as treatment variables. Soil carbon and nitrogen percentages were not normally distributed and were analyzed using Wilcoxon Rank Sums tests. Analyses were completed using JMP Pro statistical software version 16.1.0 (SAS, Cary, NC).

Results

Dune Sediment Accretion

Across all dune plots (n=30), sediment accretion rates were significantly higher on Hog (3.4 ± 0.4 cm month^{-1}) compared to Metompkin (-0.2 ± 1.3 cm month^{-1}, F=5.88, p=0.017; Figure 3; Table S1). Because of the wide variation in sediment accretion and erosion on Metompkin, no species effects were seen. Many plots lost elevation on Metompkin, with 5 plots below the high tide line by August 2022 and 4 additional plots lost by November 2022. Additional dune face plots on Metompkin remained above high tide but transitioned to open beach.

Dune and hummock accretion, Hog Island

On Hog, monthly sediment accretion rates in newly formed dune hummocks (n=15) was 35% higher than in plots on the existing dune face (F=12.70, p=0.0007; Table S2). Within these two habitats, dune building grasses accreted sediments at different rates. Sediment accretion rate was highest for *Ammophila* (5.4 ± 0.7 cm month^{-1}) and *Spartina* (5.0 ± 0.5 cm month^{-1}) compared to *Panicum* (2.6 ± 0.5 cm month^{-1}, F=12.09, p<0.0001; Figure 4). Sediment accretion rate was highest in fall (6.8 ± 0.7 cm month^{-1}) compared to winter (3.1 ± 0.3 cm month^{-1}, F=23.44, p<0.0001). No species-specific effects were observed on Metompkin.

Dune plant composition

Along cross-island transects, *Ammophila*, *Spartina*, and *Panicum* were all dominant. Over the three-year sampling period, *Panicum* cover increased, resulting in a decrease in cover for other species (Figure 5).

Dune Plant Characteristics

Plant cover on dunes (n=30) was significantly higher (>40%) on Hog compared to Metompkin (F=43.54, p<0.0001; Figure 6; Table S3). During the sampling period, plant cover was lowest in fall due to plant dormancy (F=9.09, p<0.0001) and significantly lower during fall 2022 on Metompkin coinciding with foredune plots transitioning to open beach (F=11.20, p<0.0001).

Stem numbers in dune plots (n=30) were twice as high on Hog (36 ± 5 stems 0.25 m^{-2}) as compared to Metompkin (14 ± 3 stems 0.25 m^{-2}, F=12.54, p=0.0008; Figure 7; Table S4). Species specific differences were observed in stem number, with *Spartina* having the most stems compared to *Ammophila* and *Panicum* (F=5.94, p=0.0045; Figure 8).

Soil characteristics

Dunes

Soil characteristics varied both spatially and temporally. Within the dune habitat, the lowest OM content occurred in summer 2022 on Hog (0.20 ± 0.05%) and was highest in fall 2021 on Hog (0.34 ± 0.02%, F=4.44, p=0.015; Table S5). All other samples were statistically similar. Soil chlorides were highest on Metompkin in fall 2022 (222,179 ± 96,210 $\mu g\ g^{-1}$) and lowest on Hog in fall 2022 (12,669 ± 11,438 $\mu g\ g^{-1}$, F=8.07, p=0.0007; Table S6). Between islands, chlorides were higher on Metompkin (85,221 ± 32,717 μg g^{-1}) compared to Hog (9,217 ± 5,364 μg g^{-1}, F=61.03, p<0.0001). Seasonally, chlorides were highest in fall 2022 (109,942 ± 48,484 μg g^{-1}) compared to fall 2021 and summer 2022 (F=15.66, p<0.0001). Bulk density differed by island and within season. Bulk density was higher on Metompkin (1.39 ± 0.01 g cm^{-3}) compared to Hog (1.35 ± 0.01 g cm^{-3}, F=19.02, p<0.0001; Table S7) and was highest in summer 2022 (1.45 ± 0.003 g cm^{-3}) and lowest in fall 2021 (1.27 ± 0.008 g cm^{-3}, F=140.37, p<0.0001). Soil carbon and nitrogen were significantly higher in Hog dune soils (0.09 ± 0.04% C, 0.005 ± 0.002% N) than Metompkin dune (0.03 ± 0.005% C, 0.002 ± 0.0001%, N, p<0.0001 for both).

Cross-island connectivity

Elevation differed between islands, habitats, and over time. There was an island by habitat interactions (F=4.32, p=0.039; Table S8) with Hog dunes exhibiting the highest overall elevation (2.33 ± 0.11 m) followed by Hog swale (1.99 ± 0.09 m). Metompkin dunes (1.75 ± 0.09 m) and swale (1.74 ± 0.05 m) were not statistically different from one another. There was also a significant island by year interaction with Metompkin 2022 exhibiting the lowest overall elevation (1.51 ± 0.10 m), while Hog 2022 had the highest (2.31 ± 0.13 m, F=6.99, p=0.001).

Average path cost (resistance against movement across the landscape) was 7% higher on Hog compared to Metompkin (F=133.05, p<0.0001; Table S9), creating more topographical resistance of seawater and sediment when traveling from the beach to the interior swale.

Swale characteristics

Grassland swale plant cover was highest on Hog (52 ± 5%) compared to Metompkin (13 ± 9%, F=45.21, $p<0.001$; Table S10). Further, cover on both islands was higher in August 2022 (54 ± 9%) compared to November 2021 (32 ± 13%, F=2.95, p=0.04). Swale annual net primary productivity (ANPP) was higher on Hog (299 ± 45 g m^{-2} yr^{-1}) compared to Metompkin (191 ± 23 g m^{-2} yr^{-1}, F=11.21, p=0.001; Figure 10; Table S11).

Soil characteristics differed by island and/or time. A significant island by time interaction was seen in soil chlorides with highest values in summer and fall 2022 on Metompkin (10,800 ± 7,296 µg g^{-1}, 47,782 ± 33,239 µg g^{-1}, F=4.41, p=0.0188; Table S13). Soil chlorides were higher in Metompkin swale (19,785 ± 11,813 µg g^{-1}) compared to Hog swale (539 ± 462 µg g^{-1}, F=9.44, p=0.0039).

Bulk density in the swale habitat varied by island and over time. Bulk density was highest in Metompkin swale (1.37 ± 0.02 g cm^{-3}) compared to Hog swale (1.32 ± 0.02 g cm^{-3}, F=13.38, p=0.0008; Table S14). It was highest in summer 2022 (1.43 ± 0.01 g cm^{-3}), and lowest in fall 2021 (1.21 ± 0.02 g cm^{-3}, F=85.41, $p<0.0001$).

OM content was higher in Hog swale (0.41 ± 0.03%) compared to Metompkin swale (0.26 ± 0.04%, F=4.41, p=0.0429; Table S12). Soil carbon and nitrogen percentages in the swale varied between Hog and Metompkin. Carbon in Hog swale soils (0.07 ± 0.005%) was higher than that in Metompkin swale soils (0.03 ± 0.003%, $p<0.0001$). Similarly, nitrogen in Hog swale soils (0.009 ± 0.0006%) was higher than that in Metompkin swale soils (0.003 ± 0.0002%, $p<0.0001$).

Discussion

Barrier islands are highly dynamic ecosystems and are frequently impacted by disturbance events (i.e. hurricanes, nor'easters). Under future climate scenarios these storms will intensify (IPCC, 2022), resulting in increased impacts to barrier island systems. Barrier islands are at risk of drowning when unable to migrate under increasing rates of sea-level rise (FitzGerald et al., 2018). Although we understand ecological processes that lead to dune formation and succession on barrier islands (Woodhouse et al., 1977; Ehrenfeld, 1990; Day et al., 2001; Miller et al., 2009; Brown & Zinnert, 2020; Charbonneau et al., 2021; Enwright et al., 2021), knowledge gaps remain in our understanding of how adjacent ecosystems on the islands interact and how dune shape and size impacts interior island function. My results show that dominant dune grass species accrete sediment at different rates depending on island and habitat type, with the highest rates of accretion occurring among *Ammophila* and *Spartina* in areas with sufficient sediment supply, such as those found on south Hog. As these dunes develop, increased protection is provided for the adjacent swale habitat, allowing for higher ANPP, soil carbon and nitrogen, and decreased soil salinity. On Metompkin, reduced sediment supply to the island leads to slower dune building and dune erosion, allowing seawater to reach the swale more frequently, leading to lower ANPP, soil carbon and nitrogen, and higher soil chlorides. My work provides additional information for understanding barrier island ecosystems, dune building processes, and how these differences impact surrounding habitats, which can be used in modeling evolution under different climate change scenarios. Continued changes in climate warming, sea-level rise, and sediment dynamics impact species distributions that lead to differences in dune building and overall community composition on the Virginia barrier islands.

Dune grass presence and abundance is important in determining dune formation which alters barrier island landscape characteristics. Over the last several decades, the Virginia climate has warmed, resulting in shifting species distributions (Huang et al., 2018; Goldstein et al., 2018). Climate warming has likely resulted in an increase in the cover and frequency of *Panicum*, a C_4 grass, in the Virginia barrier system. Two decades prior, dunes on Hog Island were dominated by *Ammophila* and *Spartina*, with *Panicum* only comprising ~2% of dune relative cover (Day et al., 2001). By 2022 *Panicum* relative cover increased to >40% on both Hog and Metompkin. While *Ammophila* and *Spartina* are still present on the islands, this shift may have implications for overall dune structure as explained below.

Previous literature suggested the potential expansion of C_4 grasses northward with warming temperatures, but these predictions focused on the expected expansion of *Uniola* (Harris et al., 2017; Goldstein et al., 2018). Contrary to these predictions, our results demonstrate that *Panicum* has expanded on the islands, while *Uniola* has not. Declines in relative cover of *Ammophila* may be due to warming temperatures as the species has high mortality rates at temperatures above 35°C (Seneca & Cooper, 1971). Expansion of *Panicum* rather than *Uniola* is likely a result of *Panicum* having a larger presence and longer history on the islands. *Uniola* was introduced to Hog through experimental plantings in 2014 (Mullins et al., 2019) while *Panicum* has been documented on the Virginia Barrier Islands since the beginnings of dune grass research in the area in 1975 (McCaffrey & Dueser, 1990).

Hog and Metompkin have a history of linear dune ridges that formed as a result of high dominance of *Ammophila* due to long rhizomes and high lateral growth rates (Woodhouse et al., 1977; Wolner et al., 2013; Goldstein et al., 2018; Walker & Zinnert, 2022). Change in species abundance documented on the Virginia barrier islands may result in dunes with characteristics more commonly associated with *Panicum* dune building. Unlike *Ammophila*, *Panicum* exhibits phalanx growth due to shorter rhizomes (Walker & Zinnert, 2022) and traps 50% less sediment than *Ammophila* or *Spartina*, forming smaller, hummocky dunes based on results from this research. Growth traits of *Panicum* will not result in the continuous linear dune ridges associated with *Ammophila* dominated dunes and could have implications for the broader landscape connectivity patterns in the future.

In addition to sediment accretion interactions with grasses (Woodhouse et al., 1977; Stallins, 2005; Zarnetske et al., 2012), dune building is controlled by large scale geophysical factors that influence sediment availability and abundance (Roman & Nordstrom, 1988; Jay et al., 2022; Robbins et al., 2022). Even among islands that are geographically close to one another, the abundance and movement of sediment has an influence on island processes (Armstrong & Lazarus, 2019) and response to disturbance. In the Virginia barrier island system, both Hog and Metompkin are impacted by similar seasonal weather conditions and disturbance events in the form of hurricanes and nor'easters, and even a moderate storm can have long lasting effects on various island habitats (Tuley, 2020). Storm events can lead to varied impacts with storm surge causing erosion in some places and sediment deposition in others (Leatherman et al., 1977; Hayden et al., 1995; Sallenger, 2000; Houser et al., 2008; Tuley, 2020). Although dune building processes on the two islands are impacted by similar environmental factors, sediment accretion was highest on Hog compared to Metompkin, with all plots increasing elevation during the 1-year sampling period. On Metompkin, many plots lost elevation as the habitat transitioned from dune face to open beach (9 plots) and in some cases, plots were submerged at high tide as the shoreline has been moving landward (Zinnert et al., 2019; Mariotti & Hein, 2022).

Larger scale geomorphic processes factor into dune development on these two islands. With an abundance of sediment, the south end of Hog offers increased protection to the established foredune face, allowing dune building to continue even during winter months (although at a lower rate than in new dune hummock formation). Metompkin does not have the same sediment abundance, resulting in island migration and overwash events (Zinnert et al., 2019). Thus, disturbance events prevent year-round sediment accretion, and dunes are washed away as sediment is redistributed. Due to high variation in sediment accretion and erosion on Metompkin, species differences were not observed at the island scale.

Species differences emerge when sediment is abundant, as seen on the south end of Hog. In the new dune hummock formation, accretion occurred at a faster rate (35% higher) than in adjacent foredune plots. Accretion may be initially faster in newly developing dunes, but as sediments continue to accrete and as the dune develops, sediment availability is altered and accretion slows (Davidson-Arnott & Law, 1996; Charbonneau et al., 2021). Regardless of dune location (i.e. foredune or hummock), *Ammophila* and *Spartina* had the highest rates of accretion and were ~50% higher than *Panicum*. Mullins et al. (2019) utilized leaf growth to quantify rates of sediment accretion among transplants of *Ammophila*, *Spartina*, and *Uniola*, suggesting *Ammophila* builds dunes more quickly compared to *Spartina* and *Uniola*. After the 1-year sampling period, my results suggest that natural populations of *Ammophila* and *Spartina* accrete sediment at similar rates in foredunes and newly developing dunes. The significantly lower accretion rate in *Panicum* may be of increased importance due to increased abundance across the Virginia barrier islands and continued climate warming. *Panicum* has the potential to alter dune dynamics and growth from those previously documented in Virginia, creating new climate-vegetation scenarios that current models may not predict.

As a result of differing disturbance regimes and sediment supply, dune plant cover on Hog was >40% higher than on Metompkin, and remained relatively consistent throughout the sampling period, whereas Metompkin dune cover decreased as dunes eroded and transitioned to open beach. Metompkin dunes also had ~50% lower stem numbers on average compared to Hog due to disturbance. These trends in vegetation on Metompkin can be attributed to disturbance events that cause the ecosystem to reset frequently (Ehrenfeld, 1990). Unlike on Hog where succession can continue, plant communities on Metompkin may reset each time a disturbance event occurs, in line with island migration patterns (Day et al., 2001; Brown & Zinnert, 2020).

Among species, *Panicum* had significantly lower stem numbers which may explain lower sediment accumulation. Although not statistically significant, *Spartina* had more stems than *Ammophila*, a trait that has been previously documented in lower latitudes (Hacker et al., 2019). Stem numbers have been suggested to impact on the ability of dune grasses to capture sand, however we found no relationships for any of our species. There are a variety of other mechanisms utilized by dune grasses to increase elevation including rhizomatic growth (Goldstein et al., 2017; Hacker et al., 2019).

Dune soil characteristics followed expected trends between the two islands based on disturbance history. Organic matter content, soil carbon, and soil nitrogen were higher in Hog dunes compared to Metompkin. As Metompkin experiences higher disturbance, accumulated soil carbon may be removed as new sand is deposited or leached out of sandy soils (Rossi & Rabenhorst, 2019). Organic matter also varied by season which may reflect growth and dormancy of above and belowground vegetation, but little is known about the temporal carbon dynamics within dunes alone. Organic matter was lowest during summer months, a time when dune grasses actively increase biomass and lower in fall when plants enter dormancy. Dune soil chlorides also varied spatially and seasonally. They were 89% higher on Metompkin compared to Hog, likely due to increased overwash events as indicated by bulk density. Temporal dynamics of soil chlorides may be due to seasonal weather conditions. Heavy rain events can cause leaching of both chlorides and organic matter from sandy soils, but little is known about the controls on these dynamics. Soil metrics further reinforce our understanding that there are critical differences in the dune ridges and dune development between the two islands. Although Hog and Metompkin are geographically close and experience the same extreme weather events, the dunes, dune development, and dune sediment characteristics are significantly different and lead to impactful changes in the adjacent swale habitat.

Dune building directly impacts the interior island swale habitat by providing protection from disturbance and seawater (Brown & Zinnert, 2020). This connectivity of sediment and seawater (or lack thereof) impacts ecosystem function of the interior island. In order to relate these ground-obtained metrics to a larger scale, least cost path analysis was used to compare the ease of water movement from the shoreline into the island interior. Overall, path cost values were highest on Hog compared to Metompkin, aligning with previous understandings that the dune ridge on Hog is more continuous and robust (Wolner et al., 2013; Brown & Zinnert, 2020). Dune elevation was also higher on Hog (2.33 ± 0.11 m), relative to Metompkin (1.75 ± 0.09 m).

Tall, continuous dunes provide increased protection for interior island habitats where successional processes can dominate. The disturbance-moderating effects of these continuous dune ridges also influence interior soil characteristics (Stallins, 2001; Zinnert et al., 2017; Woods et al., 2019; Brown & Zinnert, 2020). Community composition and soil characteristics are highly dependent on ocean water or salt spray extending past the primary beach to the dune ridges and further into the swale. Increased salinity serves as a stressor for plant species, including those with elevated salt tolerance (Oosting & Billings, 1942). Plants in the swale habitat are more heavily burdened by this salinity, reducing ANPP and soil carbon inputs. In swale grassland, ANPP, organic matter content, soil nitrogen, and soil carbon were higher on Hog than Metompkin. Dune protection also allows for increased plant biodiversity where a wide variety of plant species thrive (Brown & Zinnert, 2020). Eventually, grasslands transition to *Morella* shrubs, and as swale protection continues, *Morella* seedlings begin to grow in new swales closer to the ocean, a direct result of the increased protection provided by the new dune formation (Woods et al., 2019; Wood, 2021).

Although *Morella* and other woody vegetation are present on Metompkin (Zinnert et al., 2019), expansion of woody plants is limited due to the enhanced seawater movement into the interior portions of the island. Soil chlorides were >36 times higher in Metompkin swales than those on Hog, limiting the growth of *Morella* (Tolliver et al., 1997). As a result of reduced vegetative cover and ANPP, soil organic matter content, soil carbon, and soil nitrogen were also very low in Metompkin swale habitat.

Bulk density in the swale followed the trend seen in dune habitat (i.e. higher in Metompkin swale compared to Hog swale). This may further indicate soil movement and compaction on Metompkin past the dune due to overwash events. Previous work suggests that barrier island soil surface bulk density decreases moving inland (Tackett & Craft, 2010). Metompkin swale bulk density values were higher than those observed on Hog dunes, aligning with the theory that disturbance is driving high bulk density values on Metompkin. With repeated overwash events, sediments on Metompkin can become more compacted in wide overwash fans. Conversely, Hog dunes and swales are not exposed to the same level of disturbance, and do not experience compaction events frequently. Further differences in sediments on the two islands such as grain size may contribute to these differences in sand availability and movement (Fenster et al., 2016).

Conclusion

Barrier islands consist of distinct adjacent habitats that are frequently impacted by disturbance. This disturbance is an important driver of long-term change, and island systems exist with it. Of the species that inhabit barrier islands, dune building grasses have a critical role in landscape modification. These species, *Ammophila breviligulata*, *Spartina patens*, and *Panicum amarum* grow in the beach habitat, gradually transforming the landscape into a protective dune ridge when sediment is abundant. Dunes built by these grasses allow for the ecological community in the swale to thrive as it is protected from the effects of the ocean. With a changing climate, nearly all aspects of the barrier island ecosystem will be impacted, and it is important to understand and predict these changes on multiple levels. Warming temperatures and increased abundance of *Panicum* on the Virginia barrier islands will drastically modify dune development, driving changes across the island landscape. As *Panicum* accumulates less sediment than *Ammophila* and *Spartina*, increased abundance may result in lowered dune protection and reduced productivity in the grassland swale, impacting ecosystem carbon and nitrogen cycling. *Panicum* dominance on an island that is already undergoing rapid change (Metompkin) could further enhance the erosive properties of the island and prevent the system from adapting to rising sea-levels. This will also have implications for more stable islands (Hog) as a landscape dominated by multiple linear dune ridges transitions to more hummocks. As scientists work to better understand barrier island systems, it is ever more important that biological feedbacks from island ecosystems are incorporated into future scenario modeling and predictions.

Figures

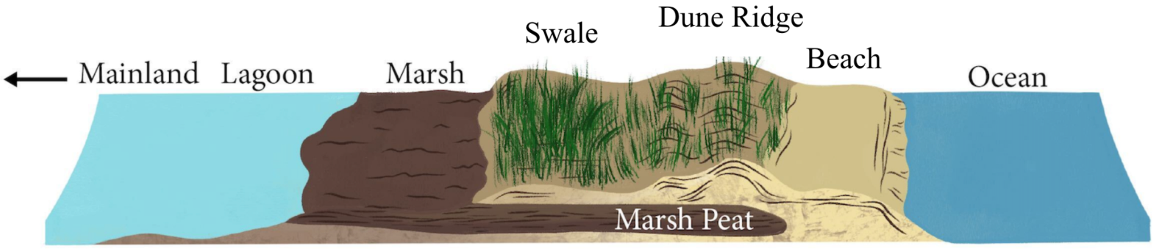

Figure 1. Cross-section of a typical barrier island. Image created by Julia Yee.

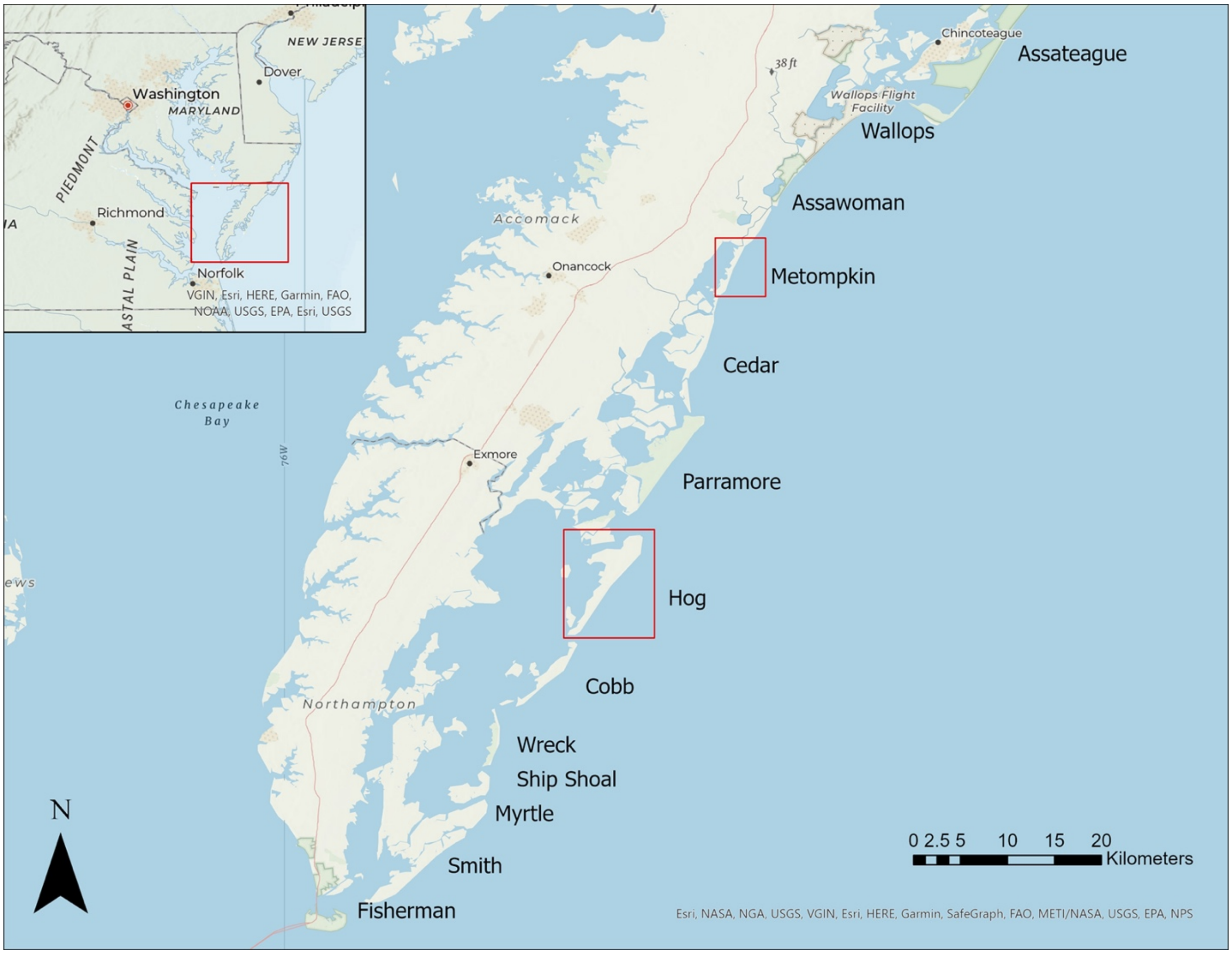

Figure 2. The barrier islands of the Virginia Coast Reserve. Islands studied marked in red. Study areas are located on the southern ends of both Hog and Metompkin Islands.

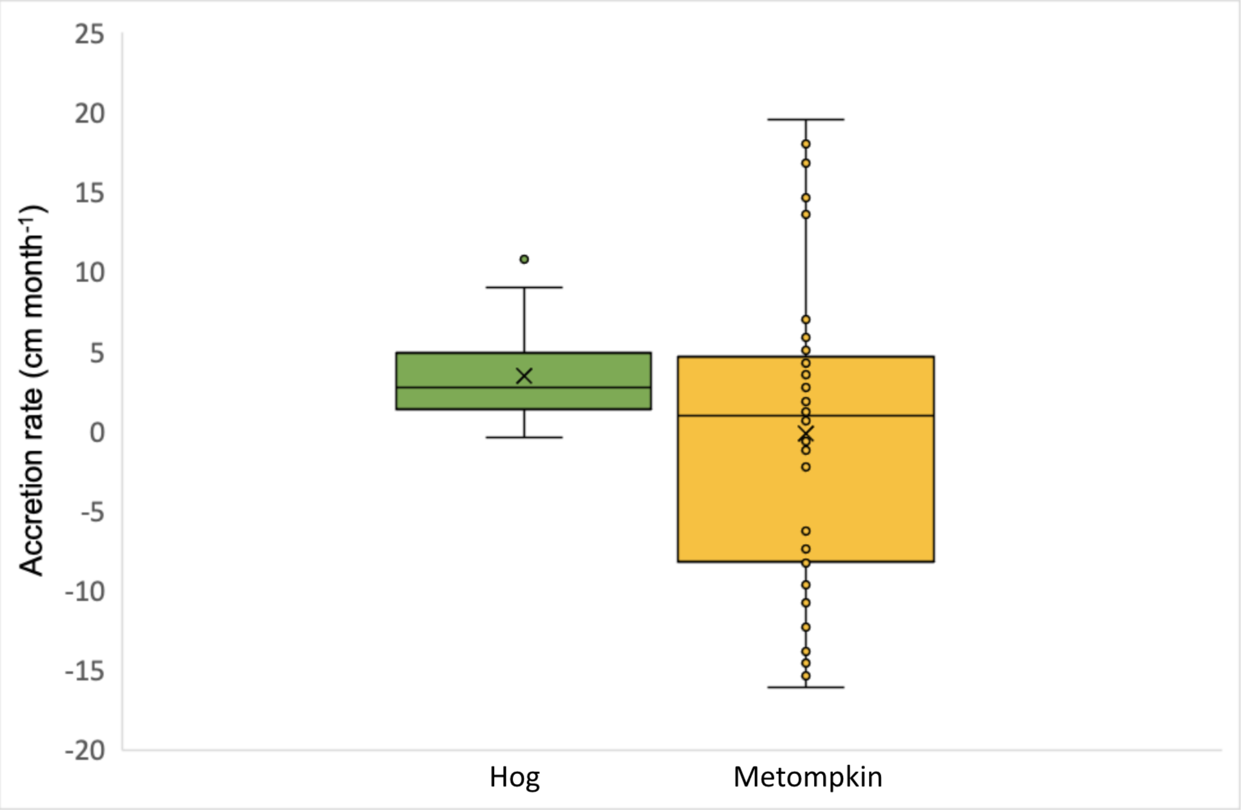

Figure 3. Average sediment accretion rate (cm month^{-1}) for Hog and Metompkin.

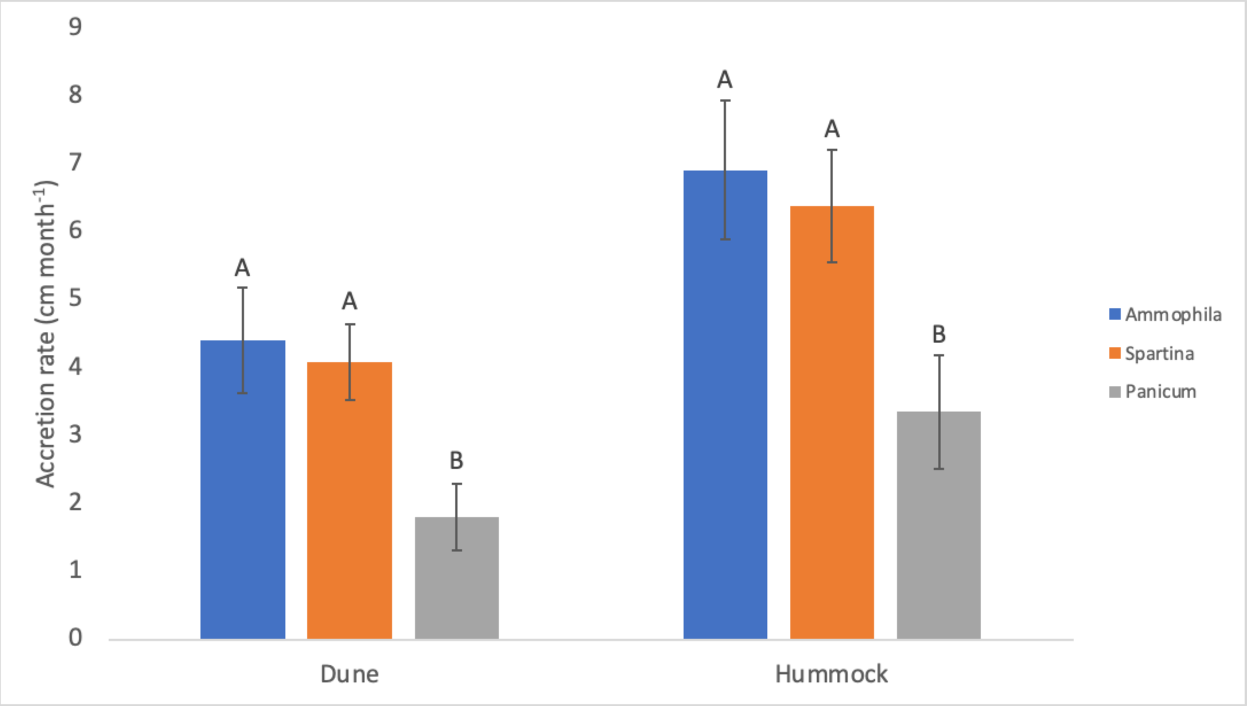

Figure 4. Average sediment accretion rate (cm month^{-1}) by habitat and dominant species on Hog. Letters indicate statistical difference, error bars show standard error.

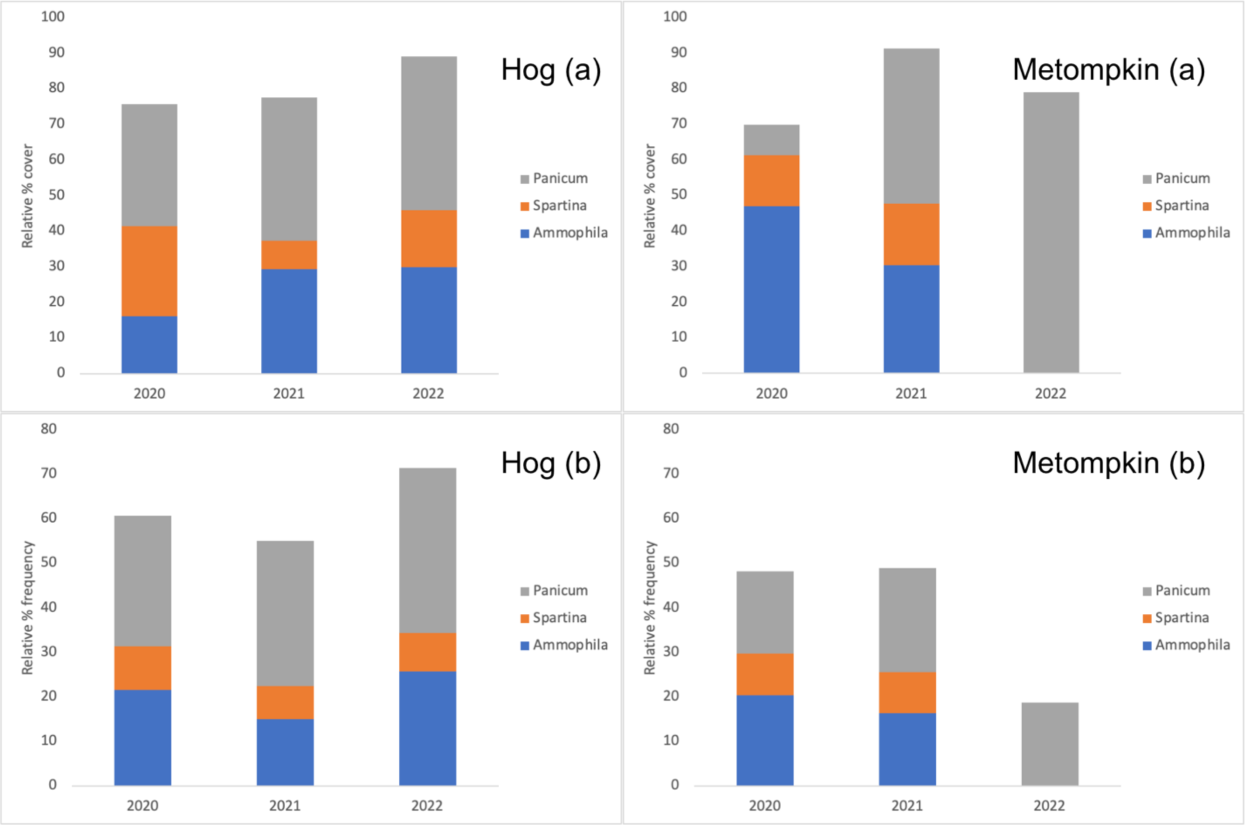

Figure 5. Relative % cover (a) and relative % frequency (b) for dune grass species along cross-island transects on Hog and Metompkin.

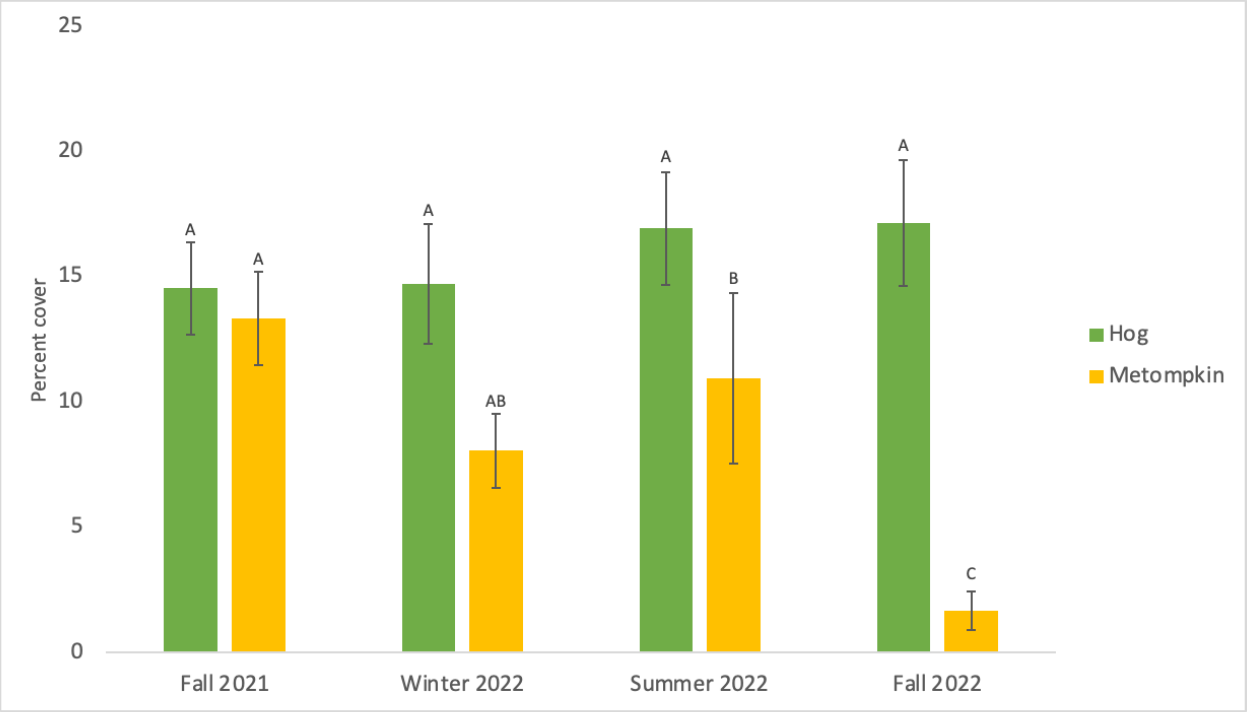

Figure 6. Average percent cover of dominant dune grasses by season on Hog and Metompkin.

Letters indicate statistical difference, error bars show standard error.

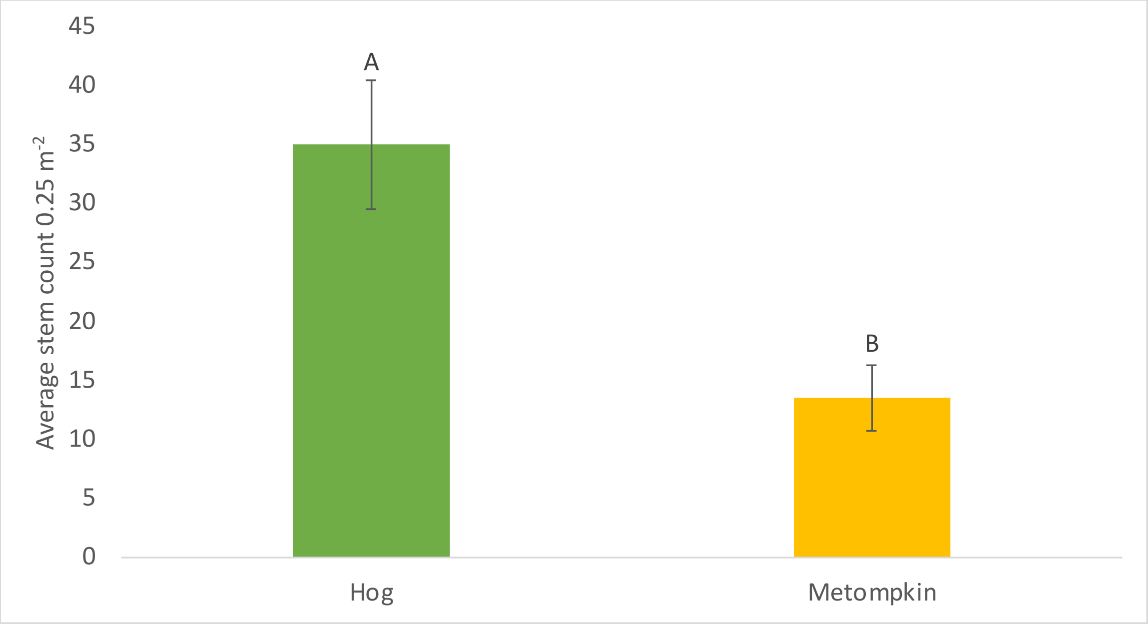

Figure 7. Mean stem count for all species by island. Letters indicate statistical difference, error bars show standard error.

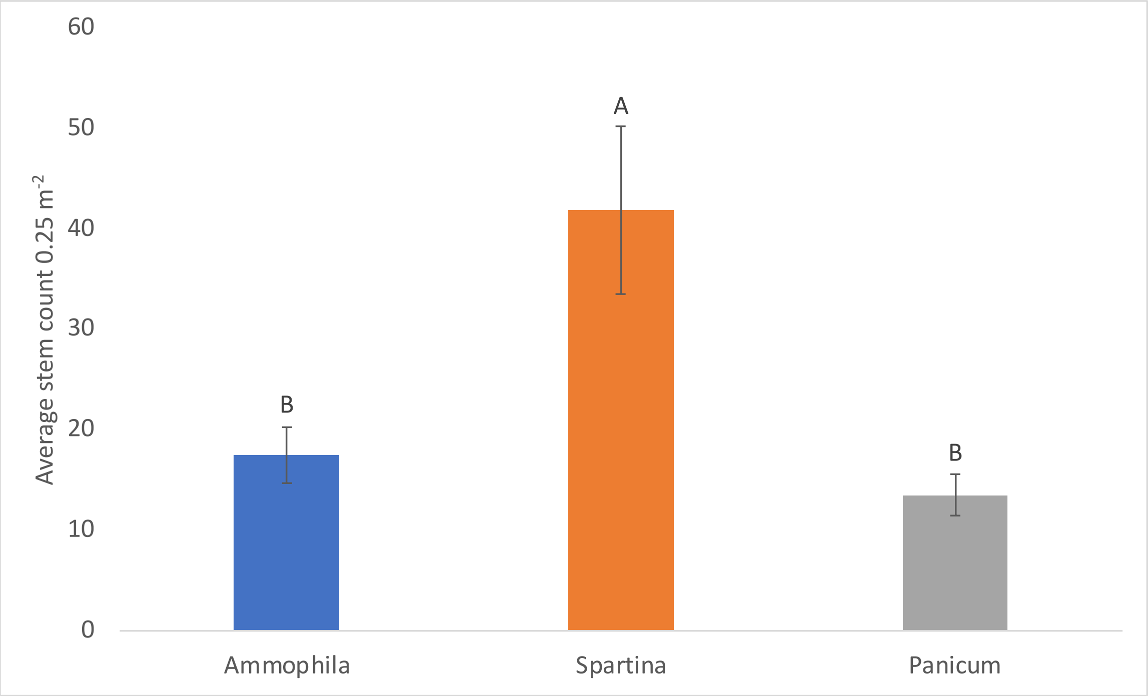

Figure 8. Mean stem count for both islands by dune grass species. Letters indicate statistical difference, error bars show standard error.

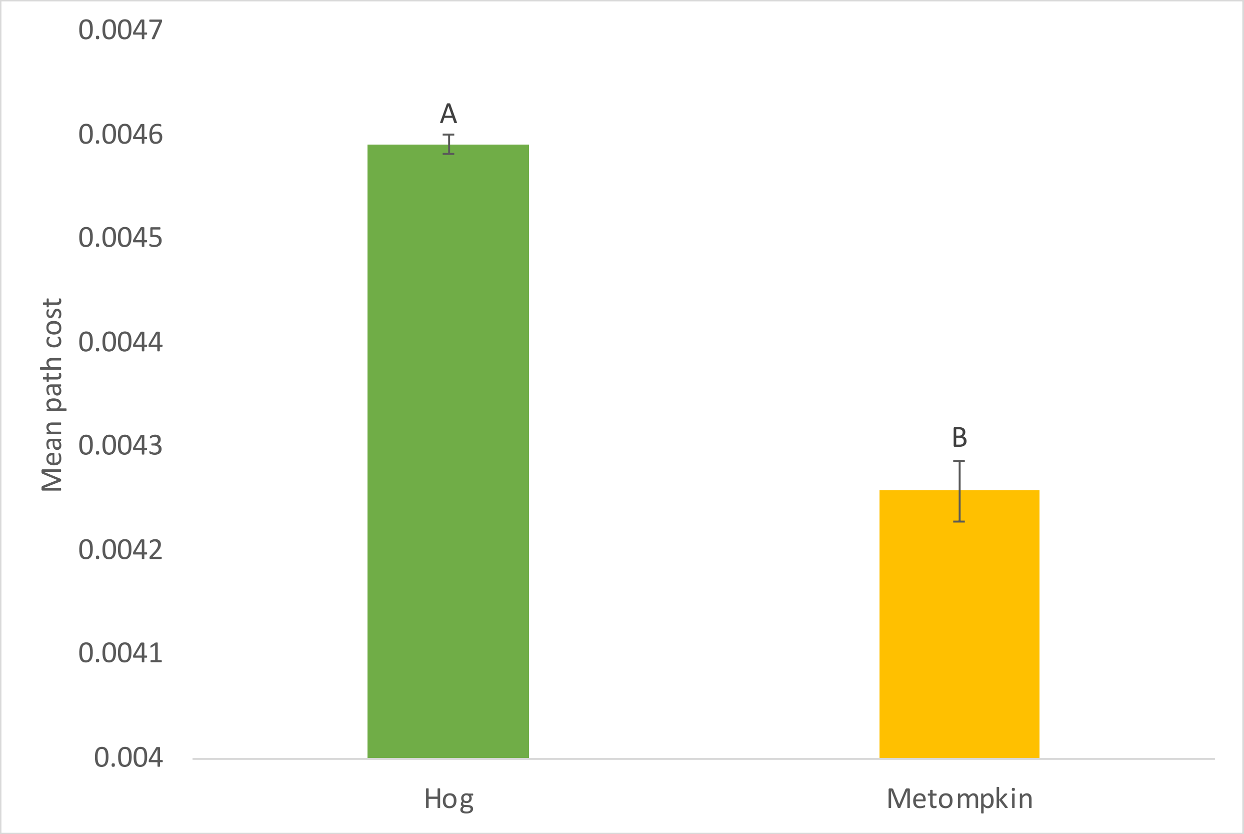

Figure 9. Mean path cost values for Hog and Metompkin. Letters indicate statistical difference, error bars show standard error.

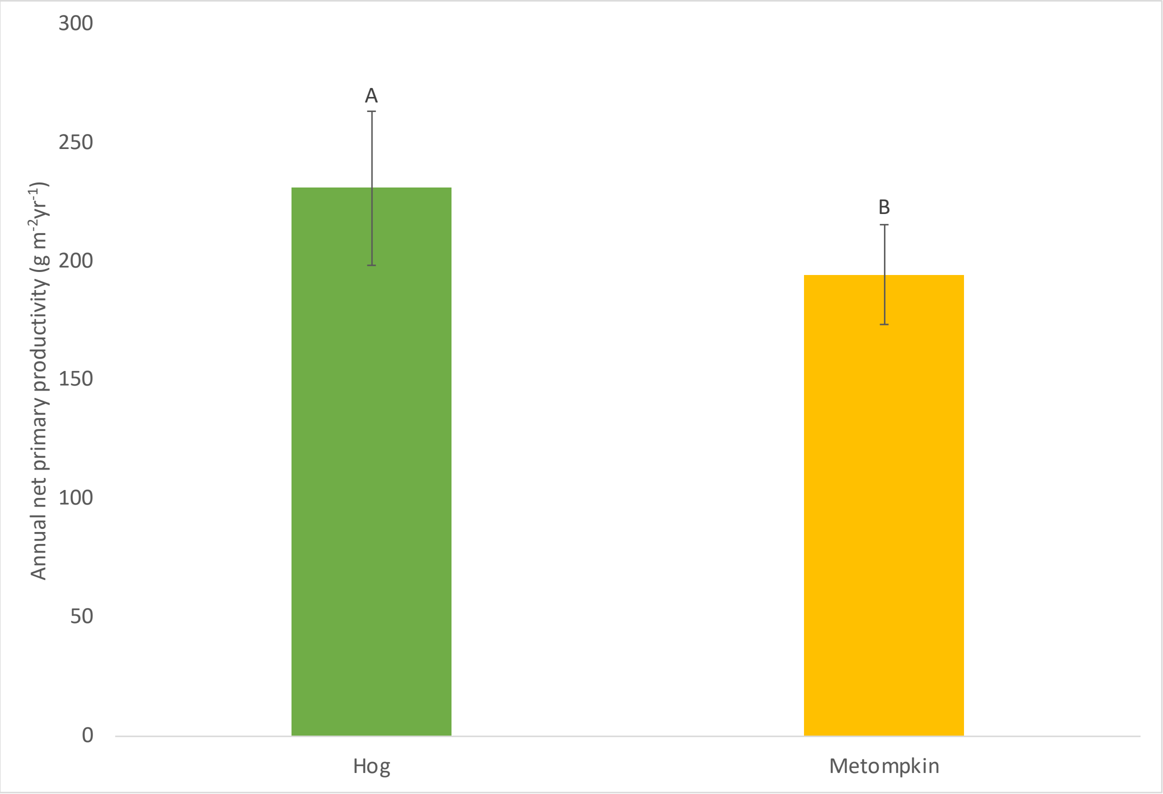

Figure 10. Annual net primary productivity in grassland swale on Hog and Metompkin. Letters indicate statistical difference, error bars show standard error.

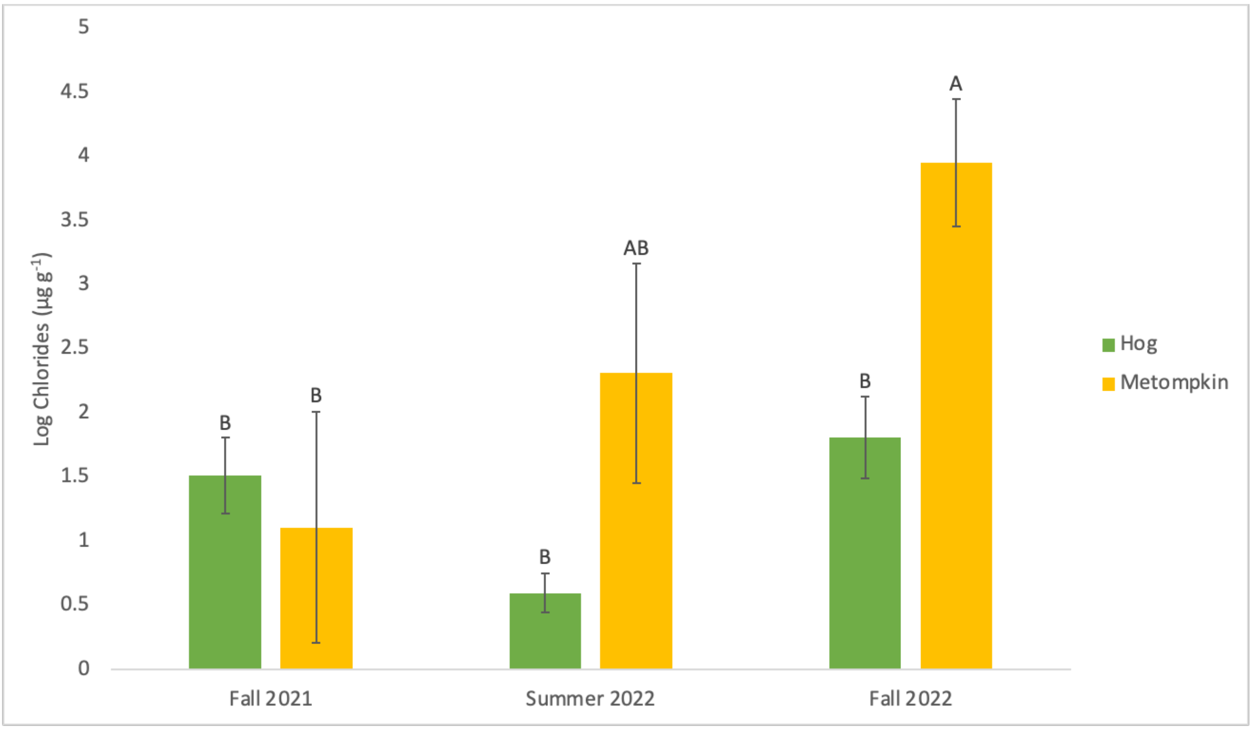

Figure 11. Average log transformed seasonal chlorides for both habitats on Hog and Metompkin. Letters indicate statistical difference, error bars show standard error.

References

Armstrong, S. B., & Lazarus, E. D. (2019). Masked Shoreline Erosion at Large Spatial Scales as a Collective Effect of Beach Nourishment. *Earth's Future*, *7*(2), 74-84. https://doi.org/10.1029/2018EF001070

Arp, W. J., Drake, B. G., Pockman, W. T., Curtis, P. S., & Whigham, D. F. (1993). Interactions between C_3 and C_4 Salt Marsh Plant Species during Four Years of Exposure to Elevated Atmospheric CO2. *Vegetatio*, *104/105*, 133-143.

Art, H. W., Bormann, F. H., Voigt, G. K., & Woodwell, G. M. (1974). Barrier Island Forest Ecosystem: Role of Meteorologic Nutrient Inputs. *Science*, *184*(4132), 60-62. https://doi.org/10.1126/science.184.4132.60

Barbier, E. B., Hacker, S. D., Kennedy, C., Koch, E. W., Stier, A. C., & Silliman, B. R. (2011). The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169-193. https://doi.org/10.1890/10-1510.1

Beaumont, N. J., Jones, L., Garbutt, A., Hansom, J. D., & Toberman, M. (2014). The value of carbon sequestration and storage in coastal habitats. *Estuarine, Coastal and Shelf Science*, *137*, 32-40. https://doi.org/10.1016/j.ecss.2013.11.022

Brantley, S. T., & Young, D. R. (2010). Shrub expansion stimulates soil C and N storage along a coastal soil chronosequence. *Global Change Biology*, *16*(7), 2052-2061. https://doi.org/10.1111/j.1365-2486.2009.02129.x

Brown, J. K., & Zinnert, J. C. (2018). Mechanisms of surviving burial: Dune grass interspecific differences drive resource allocation after sand deposition. *Ecosphere*, *9*(3). https://doi.org/10.1002/ecs2.2162

Brown, J. K., & Zinnert, J. C. (2020). Topography and disturbance influence trait-based composition and productivity of adjacent habitats in a coastal system. *Ecosphere, 11*(5). https://doi.org/10.1002/ecs2.3139

Charbonneau, B. R., Dohner, S. M., Wnek, J. P., Barber, D., Zarnetske, P., & Casper, B. B. (2021). Vegetation effects on coastal foredune initiation: Wind tunnel experiments and field validation for three dune-building plants. *Geomorphology*, *378*. https://doi.org/10.1016/j.geomorph.2021.107594

Conn, C. E., & Day, F. P. (1996). Response of root and cotton strip decay to nitrogen amendment along a barrier island dune chronosequence. *Canadian Journal of Botany, 74*(2), 276-284. https://doi.org/10.1139/b96-033

Davidson-Arnott, R. G. D., & Law, M. N. (1996) Measurement and Prediction of Long-Term Sediment Supply to Coastal Foredunes. *Journal of Coastal Research*, *12*(3), 654-663.

Day, F. P., Crawford, E. R., & Dilustro, J. J. (2001). Aboveground Plant Biomass Change along a Coastal Barrier Island Dune Chronosequence over a Six-Year Period. *Journal of the Torrey Botanical Society*, *128*(3), 197-207. https://doi.org/10.2307/3088711

Drius, M., Carranza, M. L., Stanisci, A., & Jones, L. (2016). The role of Italian coastal dunes as carbon sinks and diversity sources. A multi-service perspective. *Applied Geography*, *75*, 127-136. https://doi.org/10.1016/j.apgeog.2016.08.007

Durán Vinent, O., & Moore, L. J. (2015). Barrier island bistability induced by biophysical interactions. *Nature Climate Change*, *5*(2), 158-162. https://doi.org/10.1038/nclimate2474

Ehrenfeld, J. G. (1990). Dynamics and Processes of Barrier Island Vegetation. *Aquatic Sciences, 2*(3,4), 437-480.

Enwright, N. M., Wang, L., Dalyander, P. S., Wang, H., Osland, M. J., Mickey, R. C., Jenkins, R. L., & Godsey, E. S. (2021). Assessing Habitat Change and Migration of Barrier Islands. *Estuaries and Coasts*, *44*, 2073-2086. https://doi.org/10.1007/s12237-021-00971-w

Feagin, R. A., Furman, M., Salgado, K., Martinez, M. L., Innocenti, R. A., Eubanks, K., Figlus, J., Huff, T. P., Sigren, J., & Silva, R. (2019). The role of beach and sand dune vegetation in mediating wave run up erosion. *Estuarine, Coastal and Shelf Science*, *219*, 97-106. https://doi.org/10.1016/j.ecss.2019.01.018

Feagin, R. A., Smith, W. K., Psuty, N. P., Young, D. R., Martínez, M. L., Carter, G. A., Lucas, K. L., Gibeaut, J. C., Gemma, J. N., & Koske, R. E. (2010). Barrier Islands: Coupling Anthropogenic Stability with Ecological Sustainability. *Journal of Coastal Research*, *26(6)*, 987-992. https://doi.org/10.2112/09-1185.1

Fenster, M. S., Dolan, R., & Smith, J. J. (2016). Grain-size distributions and coastal morphodynamics along the southern Maryland and Virginia barrier islands. *Sedimentology*, *63*(4), 809-823. https://doi.org/10.1111/sed.12239

FitzGerald, D. M., Hein, C. J., Hughes, Z., Kulp, M., Georgiou, I., Miner, M. (2018). Runaway Barrier Island Transgression Concept: Global Case Studies. In: Moore, L., Murray, A. (eds) Barrier Dynamics and Response to Changing Climate. Springer, Cham. 3-56. https://doi.org/10.1007/978-3-319-68086-6_1

Goldstein, E. B., Moore, L. J., & Durán Vinent, O. (2017). Lateral vegetation growth rates exert control on coastal foredune “hummockiness” and coalescing time. *Earth Surface Dynamics*, *5*(3), 417-427. https://doi.org/10.5194/esurf-5-417-2017

Goldstein, E. B., Mullins, E. V., Moore, L. J., Biel, R. G., Brown, J. K., Hacker, S. D., Jay, K. R., Mostow, R. S., Ruggiero, P., & Zinnert, J. C. (2018). Literature-based latitudinal distribution and possible range shifts of two US east coast dune grass species (*Uniola* *paniculata* and *Ammophila breviligulata*). *PeerJ*, *6*, e4932. https://doi.org/10.7717/peerj.4932

Hacker, S. D., Jay, K. R., Cohn, N., Goldstein, E. B., Hovenga, P. A., Itzkin, M., Moore, L. J., Mostow, R. S., Mullins, E. V., & Ruggiero, P. (2019). Species-Specific Functional Morphology of Four US Atlantic Coast Dune Grasses: Biogeographic Implications for Dune Shape and Coastal Protection. *Diversity*, *11*(5), 82. https://doi.org/10.3390/d11050082

Harris, A. L., Zinnert, J. C., & Young, D. R. (2017). Differential response of barrier island dune grasses to species interactions and burial. *Plant Ecology*, *218*(5), 609-619. https://doi.org/10.1007/s11258-017-0715-0

Hayden, B. P., Dueser, R. D., Callahan, J. T., & Shugart, H. H. (1991). Long-Term Research at the Virginia Coast Reserve. *BioScience*, *41*(5), 310-318.

Hayden, B.P., Santos, M. C. F. V., Shao, G., & Kochel, R. C. (1995). Geomorphological controls on coastal vegetation at the Virginia Coast Reserve. *Geomorphology*, 13, 283-300.

Houser, C., Hapke, C., & Hamilton, S. (2008). Controls on coastal dune morphology, shoreline erosion and barrier island response to extreme storms. *Geomorphology*, *100*(3-4), 223–240. https://doi.org/10.1016/j.geomorph.2007.12.007

Huang, H., Zinnert, J. C., Wood, L. K., Young, D. R., & D'Odorico, P. (2018). Non-linear shift from grassland to shrubland in temperate barrier islands. *Ecology*, *99*(7), 1671-1681. https://doi.org/10.1002/ecy.2383

IPCC, 2022: *Climate Change 2022: Impacts, Adaptation, and Vulnerability.* Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [H.-O. Pörtner, D.C. Roberts, M. Tignor, E.S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.)]. Cambridge University Press. Cambridge University Press, Cambridge, UK and New York, NY, USA, 3056 pp., doi:10.1017/9781009325844.

Jay, K. R., Hacker, S. D., Hovenga, P. A., Moore, L. J., & Ruggiero, P. (2022). Sand supply and dune grass species density affect foredune shape along the US Central Atlantic Coast. *Ecosphere*, *13*(10). https://doi.org/10.1002/ecs2.4256

Leatherman, S. P., Williams, A. T., & Fisher, J. S. (1977). Overwash sedimentation associated with a large-scale northeaster. *Marine Geology*, *24*(2), 109-121. https://doi.org/10.1016/0025-3227(77)90004-4

Lonard, R. I., Judd, F. W., & Stalter, R. (2010). The Biological Flora of Coastal Dunes and Wetlands: *Spartina patens* (W. Aiton) G.H. Muhlenberg. *Journal of Coastal Research*, *265*, 935-946. https://doi.org/10.2112/JCOASTRES-D-09-00154.1

Marchante, E., Kjøller, A., Struwe, S., & Freitas, H. (2008). Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Applied Soil Ecology*, *40*(2), 210-217. https://doi.org/10.1016/j.apsoil.2008.04.004

Mariotti, G., & Hein, C. J. (2022). Lag in response of coastal barrier-island retreat to sea-level rise. *Nature Geoscience*, *15*(8), 633-638. https://doi.org/10.1038/s41561-022-00980-9

McCaffrey, C. A., & Dueser, R. D. (1990). Plant associations on the Virginia Barrier Islands. *Virginia Journal of Science*, 41(4A), 282-299.

Miller, T. E., Gornish, E. S., & Buckley, H. L. (2009). Climate and coastal dune vegetation: disturbance, recovery, and succession. *Plant Ecology*, 206, 97-104. https://doi.org/10.1007/s11258-009-9626-z

Mullins, E., Moore, L. J., Goldstein, E. B., Jass, T., Bruno, J., & Durán Vinent, O. (2019). Investigating dune building feedback at the plant level: Insights from a multispecies field experiment. *Earth Surface Processes and Landforms*, *44*(9), 1734-1747. https://doi.org/10.1002/esp.4607

Oertel, G. F., & Overman, K. (2004). Sequence morphodynamics at an emergent barrier island, middle Atlantic coast of North America. *Geomorphology*, *58*(1-4), 67-83. https://doi.org/10.1016/S0169-555X(03)00187-9

Olson, J. S. (1958). Rates of Succession and Soil Changes on Southern Lake Michigan Sand Dunes. *Botanical Gazette*, *119*(3), 125-170. https://doi.org/10.1086/335973

Oosting, H. J., & Billings, W. D. (1942). Factors Effecting Vegetational Zonation on Coastal Dunes. *Ecology*, *23*(2), 131-142. https://doi.org/10.2307/1931081

Permar, T. A., & Fisher, R. F. (1983). Nitrogen fixation and accretion by wax myrtle (*Myrica cerifera*) in slash pine (*Pinus elliottii*) plantations. *Forest Ecology and Management*, *5*(1), 39-46. https://doi.org/10.1016/0378-1127(83)90067-1

Reeves, I. R., Goldstein, E. B., Moore, L. J., & Zinnert, J. C. (2022). Exploring the impacts of shrub-overwash feedbacks in coastal barrier systems with an ecological-morphological model. *Journal of Geophysical Research: Earth Surface*, *127*(3). https://doi.org/10.1029/2021jf006397

Robbins, M. G., Shawler, J. L., & Hein, C. J. (2022). Contribution of longshore sand exchanges to mesoscale barrier-island behavior: Insights from the Virginia Barrier Islands, U.S. East Coast. *Geomorphology*, *403*, 108163. https://doi.org/10.1016/j.geomorph.2022.108163

Roman, C. T., & Nordstrom, K. F. (1988). The effect of erosion rate on vegetation patterns of an east coast barrier island. *Estuarine, Coastal and Shelf Science*, *26*(3), 233-242. https://doi.org/10.1016/0272-7714(88)90062-5

Rossi, A. M., & Rabenhorst, M. C. (2019). Organic carbon dynamics in soils of Mid-Atlantic barrier island landscapes. *Geoderma*, *337*, 1278-1290. https://doi.org/10.1016/j.geoderma.2018.10.028

Rountree, H. C. (1996). *Pocahontas's people the Powhatan Indians of Virginia through four centuries*. University of Oklahoma Press.

Sallenger, A. H. (2000). Storm Impact Scale for Barrier Islands. *Journal of Coastal Research*, *16*(3), 890-895.

Seneca, E. D., & Cooper, A. W. (1971). Germination and seedling response to temperature, daylength, and salinity by *Ammophila breviligulata* from Michigan and North Carolina. *Botanical Gazette*, *132*(3), 203-215. https://doi.org/10.1086/336580

Skiba, U., & Wainwright, M. (1984). Urea hydrolysis and transformations in coastal dune sands and soil. *Plant and Soil*, *82*(1), 117-123. https://doi.org/10.1007/BF02220775

Stallins, J. A. (2001). Soil and vegetation patterns in barrier-island dune environments.*Physical Geography*, *22*(1), 79-98. https://doi.org/10.1080/02723646.2001.10642731

Stallins, J. A. (2005). Stability domains in barrier island dune systems. *Ecological Complexity*, *2*(4), 410-430. https://doi.org/10.1016/j.ecocom.2005.04.011

Stallins, J. A., & Corenblit, D. (2018). Interdependence of geomorphic and ecologic resilience properties in a geographic context. *Geomorphology*, *305*, 76-93. https://doi.org/10.1016/j.geomorph.2017.09.012

Stallins, J. A., Hsu, L.-C., Zinnert, J. C., & Brown, J. K. (2020). How bottom-up and top-down controls shape dune topographic variability along the U.S. Virginia barrier island coast and the inference of dune dynamical properties. *Journal of Coastal Conservation*, *24*(3), 30. https://doi.org/10.1007/s11852-020-00747-7

Stutz, M. L., & Pilkey, O. H. (2001). A Review of Global Barrier Island Distribution. *Journal of Coastal Research*, Special Issue 34. International Coastal Symposium, 15-22.

Stutz, M. L., & Pilkey, O. H. (2011). Open-Ocean Barrier Islands: Global Influence of Climatic, Oceanographic, and Depositional Settings. *Journal of Coastal Research*, *27*(2), 207-222. https://doi.org/10.2112/09-1190.1

Tackett, N. W., & Craft, C. B. (2010). Ecosystem Development on a Coastal Barrier Island Dune Chronosequence. *Journal of Coastal Research*, *264*, 736-742. https://doi.org/10.2112/08-1167.1

Tolliver, K. S., Martin, D. W., & Young, D. R. (1997). Freshwater and saltwater flooding response for woody species common to barrier island swales. *Wetlands*, *17*(1), 10-18. https://doi.org/10.1007/BF03160714

Tuley, P. A. (2020). Comparing coastal storm impact to decadal changes in barrier island ecosystems. Thesis dissertation.

Walker, S. L., & Zinnert, J. (2022). Whole plant traits of coastal dune vegetation and implications for interactions with dune dynamics. *Ecosphere*, *13*(5), e4065. https://doi.org/10.1002/ecs2.4065

Wolner, C. W., Moore, L. J., Young, D. R., Brantley, S. T., Bissett, S. N., & McBride, R. A. (2013). Ecomorphodynamic feedbacks and barrier island response to disturbance: Insights from the Virginia Barrier Islands, Mid-Atlantic Bight, USA. *Geomorphology, 199*, 115-128. https://doi.org/10.1016/j.geomorph.2013.03.035

Wood, L.K. (2021). The Mechanisms and Consequences of Shrub Encroachment on the Virginia Barrier Islands. Thesis dissertation.

Wood, L. K., Hays, S., & Zinnert, J. C. (2020). Decreased temperature variance associated with biotic composition enhances coastal shrub encroachment. *Scientific Reports*, *10*(1), 8210. https://doi.org/10.1038/s41598-020-65161-3

Woods, N. N., Dows, B. L., Goldstein, E. B., Moore, L. J., Young, D. R., & Zinnert, J. C. (2019). Interaction of seed dispersal and environmental filtering affects woody encroachment patterns in coastal grassland. *Ecosphere*, *10*(7), e02818. https://doi.org/10.1002/ecs2.2818

Woodhouse, W. W., Seneca, E. D., & Broome, S. W. (1977). Effect of species on dune grass growth. *International Journal of Biometeorology, 21*(3), 256-266. https://doi.org/10.1007/BF01552879

Young, D. R., Brantley, S. T., Zinnert, J. C., & Vick, J. K. (2011). Landscape position and habitat polygons in a dynamic coastal environment. *Ecosphere*, *2*(6), 1-15. https://doi.org/10.1890/ES10-00186.1

Zarnetske, P. L., Hacker, S. D., Seabloom, E. W., Ruggiero, P., Killian, J. R., Maddux, T. B., & Cox, D. (2012). Biophysical feedback mediates effects of invasive grasses on coastal dune shape. *Ecology*, *93*(6), 1439-1450. https://doi-org.proxy.library.vcu.edu/10.1890/11-1112.1

Zinnert, J. C., Stallins, J. A., Brantley, S. T., & Young, D. R. (2017). Crossing Scales: The Complexity of Barrier-Island Processes for Predicting Future Change. *BioScience*, *67*(1), 39-52. https://doi.org/10.1093/biosci/biw154

Zinnert, J. C., Via, S. M., Nettleton, B. P., Tuley, P. A., Moore, L. J., & Stallins, J. A. (2019). Connectivity in coastal systems: Barrier island vegetation influences upland migration in a changing climate. *Global Change Biology*, *25*(7), 2419-2430. https://doi.org/10.1111/gcb.14635

Vita

Alexander Barnes Sabo was born in Baltimore, Maryland to Michael and Michelle Sabo in 1997. His family lived in Westminster, Maryland, and this is where he resided throughout his childhood. In 2016, he graduated from Westminster High School and later attended Washington College in Chestertown, Maryland. At Washington College, he pursued the degree of Bachelor of Science in Environmental Science with minors in Hispanic Studies and Public Health, graduating in May 2020. In June 2020, Alex and his partner, Sarah, moved to Richmond and he began working as an aquatics coordinator for the YMCA of Greater Richmond. While aquatics has always been a passion of his, this was not a long-term career path, and Alex applied for a laboratory technician position in the Coastal Plant Ecology lab at VCU with the hope of eventually entering the lab as a graduate student. In Fall 2021, Alex enrolled as a Masters Student in Dr. Julie Zinnert's lab and began working toward his degree. Alex will complete this degree in May of 2023 and pursue a future career path in environmental science.

Supplementary Tables and Figures

Table S1. Three-way ANOVA results for sediment accretion rate (cm month^{-1}) by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	*p*
Season	0.0367	0.9639
Dominant Species	0.8391	0.4363
Island	**5.8823**	**0.0178**
Season*Dominant Species	0.0761	0.9893
Season*Island	1.3445	0.2671
Dominant Species*Island	0.3261	0.7228
Season*Dominant Species*Island	0.0692	0.9911

Table S2. Three-way ANOVA results for sediment accretion rate (cm month^{-1}) on Hog by season, habitat, and island. Significant factors are shown in bold.

Source	F	*p*
Season	**23.4416**	**<0.0001**
Habitat	**12.6978**	**0.0007**
Dominant Species	**12.0853**	**<0.0001**
Season*Habitat	2.7746	0.0691
Season*Dominant Species	1.862	0.1664
Habitat*Dominant Species	0.0077	0.9924
Season*Habitat*Dominant Species	0.2422	0.7859

Table S3. Three-way ANOVA results for percent cover by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	*p*
Season	**9.0867**	**<0.0001**
Dominant Species	0.3416	0.7115
Island	**43.5384**	**<0.0001**
Season*Dominant Species	0.3726	0.8948
Season*Island	**11.1973**	**<0.0001**
Dominant Species*Island	1.2564	0.2893
Season*Dominant Species*Island	0.1493	0.9888

Table S4. Three-way ANOVA results for stem count by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	*p*
Season	1.8481	0.1667
Dominant Species	**5.9413**	**0.0045**
Island	**12.5352**	**0.0008**
Season*Dominant Species	1.6662	0.1702
Season*Island	2.2204	0.1177
Dominant Species*Island	2.0149	0.1426
Season*Dominant Species*Island	0.1869	0.9443

Table S5. Three-way ANOVA results for OM in the dune habitat by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	p
Season	1.5936	0.2105
Dominant Species	0.8905	0.4151
Island	0.0025	0.9603
Season*Dominant Species	1.4530	0.2258
Season*Island	**4.4362**	**0.0153**
Dominant Species*Island	3.2269	0.0457
Season*Dominant Species*Island	0.8785	0.4813

Table S6. Three-way ANOVA results for soil chlorides (μg g^{-1}) in the dune habitat by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	*p*
Season	**15.6630**	**<0.0001**
Dominant Species	0.5018	0.6076
Island	**61.0270**	**<0.0001**
Season*Dominant Species	**3.1593**	**0.0191**
Season*Island	**8.0657**	**0.0007**
Dominant Species*Island	0.4347	0.6492
Season*Dominant Species*Island	1.1075	0.3600

Table S7. Three-way ANOVA results for bulk density (g cm^{-3}) in the dune habitat by season, dominant dune grass species, and island. Significant factors are shown in bold.

Source	F	p
Season	**140.3707**	**<0.0001**
Dominant Species	0.0691	0.9333
Island	**19.0211**	**<0.0001**
Season*Dominant Species	1.4527	0.2259
Season*Island	1.0055	0.3711
Dominant Species*Island	0.8120	0.4481
Season*Dominant Species*Island	1.9579	0.1105

Table S8. Three-way ANOVA results for elevation (m) by habitat, island, and year. Significant factors are shown in bold.

Source	F	*p*
Habitat	**4.6658**	**0.0316**
Island	**25.9781**	**<0.0001**
Year	0.9156	0.4015
Habitat*Island	**4.3234**	**0.0385**
Habitat*Year	2.2420	0.1081
Island*Year	**6.9928**	**0.0011**
Habitat*Island*Year	1.5599	0.212

Table S9. Two-way ANOVA results for path cost value by island and year. Significant factors are shown in bold.

Source	F	*p*
Island	**133.0454**	**<0.0001**
Year	**159.7671**	**<0.0001**
Month*Island	**113.2582**	**<0.0001**

Table S10. Two-way ANOVA results for plant cover in the swale habitat by season and island. Significant factors are shown in bold.

Source	F	*p*
Season	**2.9458**	**0.0413**
Island	**45.2111**	**<0.0001**
Season*Island	0.1122	0.9526

Table S11. Two-way ANOVA results for ANPP (gm^{-2} yr^{-1}) in the swale habitat by year and island. Significant factors are shown in bold.

Source	F	*p*
Year	0.0319	0.8585
Island	**11.2087**	**0.0010**
Year*Island	0.9894	0.3215

Table S12. Two-way ANOVA results for OM in the swale habitat by season and island. Significant factors are shown in bold.

Source	F	*p*
Season	0.3606	0.6998
Island	**4.4058**	**0.0429**
Season*Island	1.6593	0.2045

Table S13. Two-way ANOVA results for chlorides ($\mu g\ g^{-1}$) in the swale habitat by season and island. Significant factors are shown in bold.

Source	F	*p*
Season	**7.1718**	**0.0022**
Island	**9.4438**	**0.0039**
Season*Island	**4.4085**	**0.0188**

Table S14. Two-way ANOVA results for bulk density (g cm^{-3}) in the swale habitat by season and island. Significant factors are shown in bold.

Source	F	*p*
Season	**85.4091**	**<0.0001**
Island	**13.3786**	**0.0008**
Season*Island	2.6898	0.0805

Correlations

Table S15. Correlations of sediment accretion with % cover, previous cover, stem count, and previous stem count.

March 2022		Correlation
Hog Dune	Cover (%)	-0.3421
	Lag cover (%)	0.3348
	Stem count	0.2081
Hog Hummock	Cover (%)	0.3714
	Lag cover (%)	**0.5427**
	Stem count	0.3952
Metompkin Dune	Cover (%)	-0.0015
	Lag cover (%)	0.4712
	Stem count	0.0409
August 2022		
Hog Dune	Cover (%)	-0.3516
	Lag cover (%)	0.2750
	Stem count	-0.0704
	Lag stem count	0.4251
Hog Hummock	Cover (%)	-0.2902
	Lag cover (%)	0.2588
	Stem count	0.2865
	Lag stem count	0.3354
Metompkin Dune	**Cover (%)**	**0.7852**
	Lag cover (%)	0.3738
	Stem count	**0.7031**
	Lag stem count	0.2594
November 2022		
Hog Dune	Cover (%)	-0.0139
	Lag cover (%)	-0.3663
	Stem count	-0.0101
	Lag stem count	-0.0580
Hog Hummock	Cover (%)	-0.3755
	Lag cover (%)	-0.3336

	Stem count	0.2162
	Lag stem count	0.2058
Metompkin Dune	**Cover (%)**	**0.8142**
	Lag cover (%)	0.2513
	Stem count	**0.7900**
	Lag stem count	0.1695

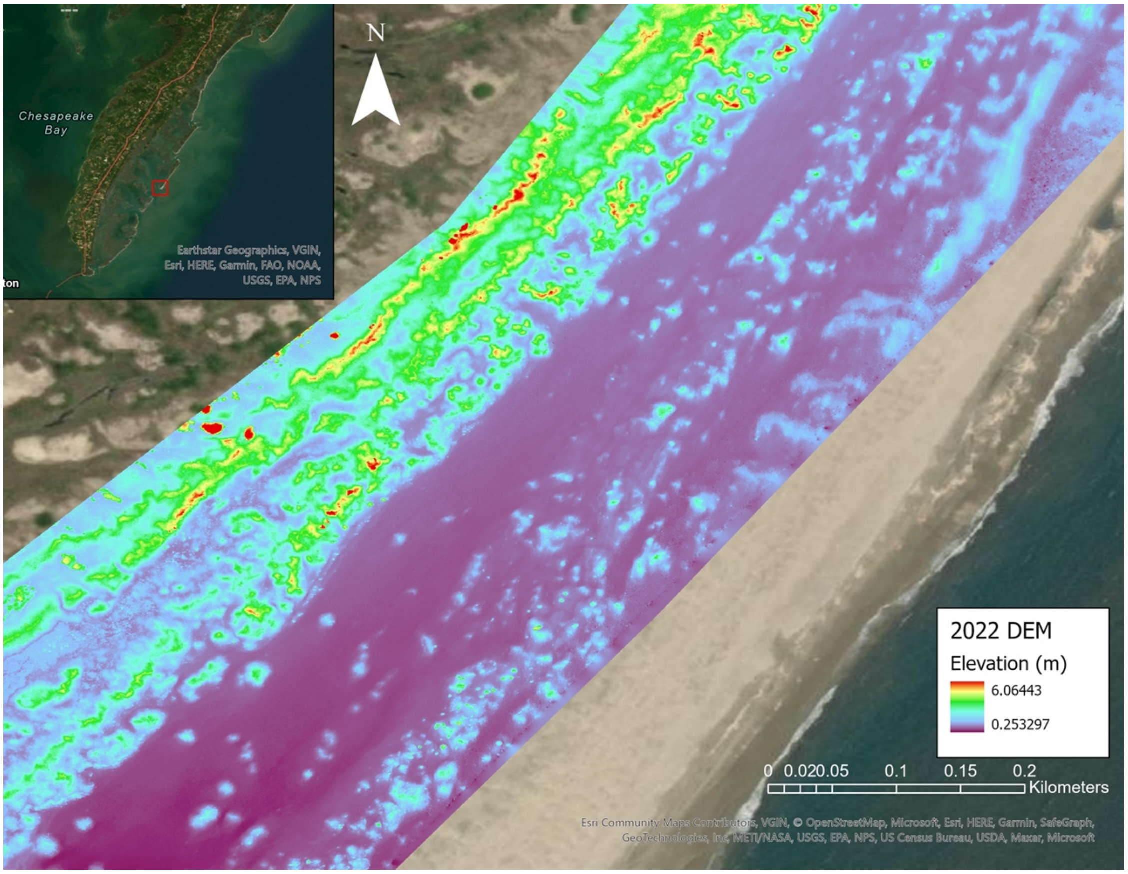

Figure S1. Digital elevation model overlayed on Hog Island.

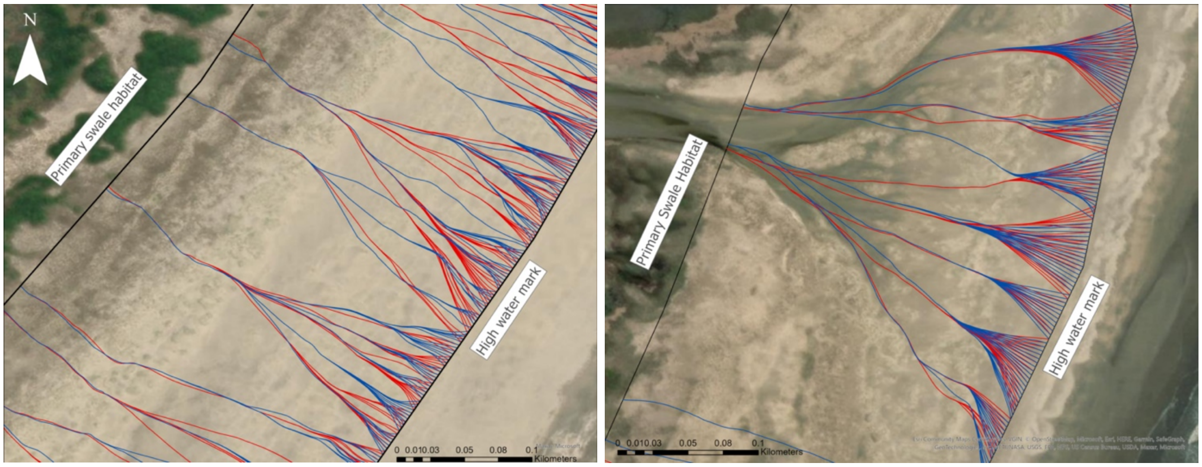

Figure S2. Visual representation of least-cost paths across Hog (left) and Metompkin (right) Islands. 2020 paths are shown in red, 2022 paths shown in blue.