






ARTICLE

Coastal and Marine Ecology

Sand supply and dune grass species density affect foredune shape along the US Central Atlantic Coast

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Abstract

Coastal foredunes form via biophysical feedbacks between sand accretion and burial-tolerant vegetation and can protect coastlines from hazards such as extreme storms and sea level rise. Predicting how coastal dunes, and the services they provide, will change in the future requires an understanding of the relative roles of the physical and ecological processes that shape their structure and function. Here we assess the relative roles of sand supply, beach morphology, and vegetation in determining foredune morphology, and its change, along a 300-km stretch of the US Central Atlantic coast. In particular, we used the spatial variability inherent in beaches and dunes of this region to determine the relative importance of shoreline change rate (SCR; a proxy for sand supply to the beach), beach morphology, and grass density of four widespread dune grasses (*Uniola paniculata*, *Ammophila breviligulata*, *Panicum amarum*, and *Spartina patens*) to foredune morphology metrics (height, width, and aspect ratio) along the North Carolina Outer Banks barrier islands. Foredune morphology and change metrics are correlated with three main factors: multidecadal SCR (1997–2016), beach slope, and dune grass density and species identity. Multidecadal SCR and beach width explained the most variation in, and were positively correlated with, foredune height and width, and were negatively correlated with foredune aspect ratio (height divided by width). In addition, grass density and changes in grass density contributed significantly to foredune morphology change. We found a positive relationship between change in *A. breviligulata* density and foredune width, which aligns with previous studies on the US Atlantic and Pacific Northwest coasts. Our results demonstrate the interactive roles of beach sand supply and dune grass functional morphology in dune building processes on highly vulnerable coastlines.

KEYWORDS

Ammophila breviligulata, beach and dune morphology, functional morphology, *Panicum amarum*, sand accretion, shoreline change rate, *Spartina patens*, *Uniola paniculata*

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INTRODUCTION

Coastal dunes serve as the first line of defense against erosion and overtopping by ocean waves (Ruggiero et al., 2001; Sallenger, 2000; Seabloom et al., 2013) and provide other substantial ecosystem services including recreation, wildlife habitat, and carbon sequestration (Barbier et al., 2011; Biel et al., 2017; Drius et al., 2016). This coastal ecosystem is increasingly at risk due to “coastal squeeze,” where landward retreat is prevented by development and engineered shorelines, making dunes more vulnerable to sea level rise and heightened storm intensity (Intergovernmental Panel on Climate Change, 2021) and altering critical ecosystem services (Biel et al., 2017; Gilby et al., 2021; Granek et al., 2010; Halpern et al., 2008; Lawler et al., 2014; Mendoza-González et al., 2012). Predicting how coastal dunes, and the services they provide, will change in the future requires an understanding of the relative roles of the physical and ecological processes that shape their structure and function.

Coastal foredunes, or the most seaward dune ridge parallel to the shoreline, are shaped by the interplay between metocean processes (climate and its effects on wind, waves, and sea level), geological processes (sedimentary that determine shoreline and beach morphology), ecosystem factors (interactions between vegetation, sand, and marine nutrients that determine beach and foredune habitats), and human activity (e.g., Hesp, 1989; Martínez et al., 2004; Pye, 1983; Ruggiero et al., 2018). Metocean and sedimentary processes, in particular, have a large influence on shoreline change rate (SCR), or the rate at which sand is deposited or eroded from the beach (Dingler & Reiss, 2002; Farris & List, 2007; Hanson, 1989). Beach morphology ranges from dissipative (shallow with a wide surf zone) to reflective (steep with a narrower surf zone) not only because of differences in SCR, but also due to beach slope, sediment grain size, and wave conditions (Short & Hesp, 1982; Wright & Short, 1984). Observational and modeling studies suggest that foredune morphology is largely shaped by SCR and beach morphology, and can vary depending on the relative importance of beach and dune sediment budgets (e.g., Biel et al., 2019; Duran & Moore, 2013; Hacker et al., 2012; Hesp, 1989, 2002; Keijsers et al., 2015, 2016; Moore et al., 2016; Zarnetske et al., 2012, 2015). For example, short and narrow foredunes are characteristic of highly eroding, reflective beaches, whereas tall and narrow foredunes can form on neutral or slightly retreating shorelines (Davidson-Arnott et al., 2018; Duran & Moore, 2013; Hesp & Walker, 2013). In contrast, tall, wide foredunes and short, wide foredunes are characteristic of wide and dissipative beaches, where SCRs are high and/or progradational (e.g., Hesp, 1984; Psuty, 1986).

Once sediment reaches the back beach via aeolian and wave-driven sediment transport (Cohn et al., 2019), vegetation can play a key role in shaping foredunes. Burial-tolerant vegetation, such as dune grasses and forbs, slows sand-laden wind and leads to deposition, which stimulates plant growth and, in turn, leads to further sand deposition (Biel et al., 2019; Brown & Zinnert, 2018; Charbonneau et al., 2021; Charbonneau & Casper, 2018; Duran & Moore, 2013; Hacker et al., 2012; Harris et al., 2017; Hesp, 1989, 2002; Keijsers et al., 2015; Maun, 1998; Maun & Lapierre, 1984; Mullins et al., 2019; Woodhouse, 1978; Zarnetske et al., 2012, 2015). Early studies noted relationships between grass species and dune shape (e.g., Godfrey, 1977; Godfrey & Godfrey, 1973; Van der Valk, 1975; Woodhouse et al., 1977), and more recent empirical and modeling studies suggest that plant density, plant morphology, and differences in lateral versus vertical belowground growth patterns can contribute to the development of a wide range of foredune shapes from short and wide to tall and narrow and from discontinuous (hummocky or nebkha dunes) to continuous (linear foredunes) (Biel et al., 2019; Goldstein et al., 2017; Hacker et al., 2012; Hesp, 2002; Hesp et al., 2021; Zarnetske et al., 2012). Previous research has shown that in addition to sand supply to the beach, dune grass density and growth form are significant moderating factors to dune morphology (Arens, 1996; Biel et al., 2019; Esler, 1970; Hacker et al., 2012; Hesp et al., 2019; Olson, 1958; Zarnetske et al., 2012, 2015). In one study on the US Pacific Northwest coast, Zarnetske et al. (2015) found that timescale determined the relative importance of geomorphic and ecological factors; at an annual scale, sand supply to the beach explained a greater proportion of the variation in foredune morphology, but at a decadal scale, beach grass density was more important. In another study, over a greater spatial extent, Biel et al. (2019) found that ~50% of the variability in foredune height was attributed to measures of sand supply to the beach, while invasive *Ammophila* beach grass density comprised another 10% of the variability. Interestingly, as a result of its thinner and denser shoots, the presence of *Ammophila arenaria* (European beachgrass) led to more vertical sand deposition and taller, steeper foredunes (Hilton, 2006) compared with *Ammophila breviligulata* (American beachgrass) dominated dunes, which tended to be shorter and wider.

Here, we build on these previous studies by assessing the relative roles of beach sand supply, beach morphology, and vegetation in determining foredune morphology, and its change, along a 300-km stretch of the US Central Atlantic coast. These dunes are highly vulnerable to sea level rise, coastal erosion, and extreme storms because of the juxtaposition of dunes and human activity (Hovenga et al., 2021). Despite their vulnerability,

we know surprisingly little about the processes determining dune morphology, which plays a key role in wave attenuation and flooding risk on barrier islands (Sallenger, 2000), particularly at regional spatial scales. The most widespread species of dune grass in this region is *Uniola paniculata* L. (sea oats), a drought-tolerant C₄ grass that extends from Virginia (VA) to Florida (Goldstein et al., 2018; Seneca, 1969). Secondary in abundance is *A. breviligulata* Fernald (American beachgrass), a mid-Atlantic C₃ grass that extends from North Carolina (NC) to Canada and is thought to be heat-intolerant (Goldstein et al., 2018). A transition zone between these species occurs in the NC Outer Banks, where *U. paniculata* dominates dunes in the southern Outer Banks and *A. breviligulata* dominates farther north (Goldstein et al., 2018; Hacker et al., 2019). Two other dune grass species that are prevalent in the Outer Banks and have similar distributions to *U. paniculata* are *Spartina patens* (Aiton) Muhlenberg (saltmeadow cordgrass) and *Panicum amarum* Elliott (bitter panicgrass).

Past research in this system shows evidence that dune grasses may be important in determining foredune morphology. Previous studies in NC starting in the 1960s used experimental plantings to compare the dune building properties of *U. paniculata*, *A. breviligulata*, and *P. amarum* (Seneca et al., 1976; Woodhouse, 1978; Woodhouse et al., 1977). Results showed that foredunes with monocultures of each species achieved similar crest elevations after 8 years, but foredunes with *A. breviligulata* monocultures were wider and larger in volume compared with the steeper, narrower dunes created by the other two species (Woodhouse et al., 1977). A recent study by Hacker et al. (2019) described the functional morphology and sand accretion properties of four dune building grass species (the three mentioned above and *S. patens*), providing mechanisms for the observed differences in dune building capabilities of these plants, as previously observed by Esler (1970). They found that *U. paniculata* had fewer, taller shoots compared with *A. breviligulata*, which had dense, clumped shoots and was correlated with the highest rate of sand accretion (Appendix S1: Figure S1a,c,e). In addition, their findings suggested that shoot density and growth form were stronger factors in determining sand accretion than shoot morphology per se.

In this study, our goal was to consider the relative role of geological and ecological factors in explaining the variability in foredune morphology across the Outer Banks of NC, one of the most vulnerable shorelines to erosion and inundation in North America (Thieler, 2000). We asked the following questions:

1. What is the relative contribution of beach sand supply (hereafter shortened to sand supply), beach morphology,

and dune grass density and species in shaping foredune morphology over space and time?

2. Do the dune grass species *A. breviligulata* and *U. paniculata* affect foredune morphology in species-specific ways, and if so, how?

Based on the results of previous studies (e.g., Biel et al., 2019; Davidson-Arnott et al., 2018; Hesp, 1989; Zarnetske et al., 2015), we hypothesized that multidecadal SCR (used here as a proxy for sand supply to the beach) and beach slope would be some of the most important factors shaping dune morphology in our study region. Further, we also expected a positive relationship between dune grass density and foredune morphology, with increases in foredune height associated with the more vertical growth of *U. paniculata* and increases in foredune width associated with the more horizontal growth of *A. breviligulata*.

To explore these questions and hypotheses, we collected two years of vegetation and beach and dune morphometric data at 90 cross-shore transects spread over a 300-km stretch of the Outer Banks coastline. We used the spatial variability in the dataset to conduct multivariate regression analyses, model selection (Akaike information criterion [AIC]), and hierarchical partitioning to first explore the possible correlations between foredune morphology metrics (i.e., height, width, toe elevation, and aspect ratio) and the explanatory variables of dune grass density (including *U. paniculata*, *A. breviligulata*, and both combined), beach morphometrics (i.e., width, backshore slope, and foreshore slope), and sand supply metrics (i.e., annual and multidecadal SCR) at a regional scale. In this analysis, we harnessed the large variability in explanatory metrics across space to explore whether differences in vegetation density and species identity, as well as measures of sand supply across space, are related to foredune morphology. The second analysis that we conducted considered whether a change in foredune morphology over a year-long period was related to the same explanatory variables across the coast and thus included a change in foredune morphology over time component.

MATERIALS AND METHODS

Study region

The study region encompasses foredunes along the NC coastline from Shackleford Banks, NC, to False Cape, VA (Figure 1; Appendix S1: Table S1), a 300-km stretch of sandy barrier islands exhibiting spatial variability in beach geomorphology (Hovenga et al., 2021), vegetation

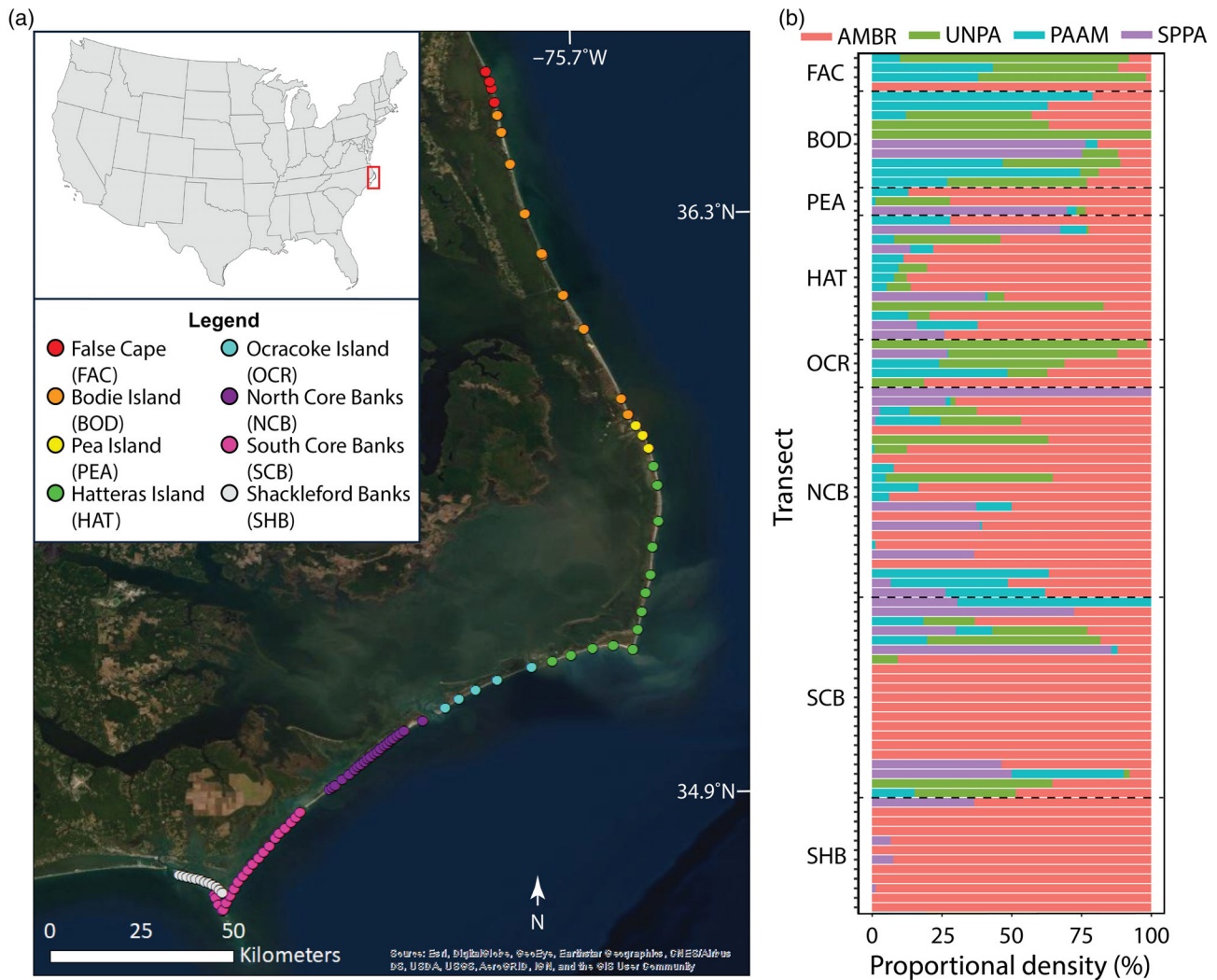


FIGURE 1 Transect locations and dune grass abundance within the study area from north to south. (a) Map of study sites and transect locations along the 300-km stretch of the Atlantic coast from Shackleford Banks, NC to False Cape, VA, USA. (b) Proportional density (tillers/0.25 m²) of four dominant NC dune grasses (*Uniola paniculata* [UNPA], *Ammophila breviligulata* [AMBR], *Panicum amarum* [PAAM], and *Spartina patens* [SPPA]). Island abbreviations are given in the legend and dashed lines represent borders between islands.

species and density (Hacker et al., 2019), wave energy, shoreline orientation, and underlying stratigraphy (Lazarus & Murray, 2011). The region is characterized by varying levels of development and management, ranging from relatively undeveloped and unmanaged protected national seashores (e.g., Cape Lookout National Seashore [CALO] and Cape Hatteras National Seashore) to developed, populated areas with management practices including beach nourishment, sand fencing, and grass planting (Itzkin et al., 2021). Most of our sites fell within the protected national seashores, but Hatteras Island and Bodie Island had several sites within developed areas that were included in this study, so as to maintain spatial coverage along the coastline.

The Outer Banks coastline is highly dynamic, which has resulted in a large range in beach and dune

morphology over the 300-km distance (Appendix S1: Figure S1). For example, foredune height and beach width range from 1.5–5.5 m and ~30–55 m, respectively, within CALO (Hovenga et al., 2021), while dunes along Cape Hatteras and northward are typically between 3 and 11 m tall (Woolard & Colby, 2002). Some sites have taller, steeper dunes paired with narrower, steeper beaches (e.g., Shackleford Banks dunes), while other areas within the region have lower, more gently sloping dunes, associated with wider beaches (e.g., parts of North Core Banks). Dunes tend to be shorter and more eroded near inlets, while the central regions of the islands tend to alternate between periods of erosion and accretion (Hovenga et al., 2021). On average, dune crest heights accreted by 0.01–0.02 m/year from 1997 to 2016, while dune toe locations typically retreated at the decadal scale

(rates varied widely), resulting in steeper foredune faces over time (see Hovenga et al., 2021 for additional details).

A variety of oceanographic, geologic, and aeolian processes shape sand supply to these beaches and influence the alongshore variability in beach and dune morphometrics, including relative sea level (RSL), shoreline orientation, wind and wave conditions, and sediment grain size distributions. For example, over the past 2000 years, RSL has risen at an average rate of 1.11 ± 0.03 mm/year along the northern NC coastline (Kopp et al., 2015). However, recent RSL change rates have accelerated over the past century, with areas north of Cape Hatteras experiencing greater acceleration; for example, rates averaged 3.3 ± 0.9 and 2.3 ± 0.7 mm/year in Duck and Wilmington, NC, respectively (Hay et al., 2015). Moreover, the NC coastline as a whole, including the study region, is eroding by ~ 0.7 m/year on average, but there is significant spatial variability in shoreline erosion and accretion (Hovenga et al., 2021; Miller et al., 2005).

The shoreline orientation of the beaches and dunes also varies along the NC coastline (Figure 1), meaning that dunes are not always oriented toward the dominant wind direction. Differences in shoreline orientation can influence dune morphology along the coastline. For example, Hovenga et al. (2021) found that east/west oriented shorelines within CALO, which are exposed to the dominant cross-shore wind direction, tended to have larger foredunes. The region is characterized by a moderately energetic seasonal wind and wave climate, including average wind speeds of ~ 6.8 m/s and average annual significant wave heights of ~ 1.2 m (Bryant et al., 2016). Wind and wave direction can vary alongshore, with the region primarily experiencing waves from the east in the fall and winter and from the south during the spring and summer (U.S. Army Corps of Engineers, 1997; Park & Wells, 2005). Tropical hurricanes frequently occur in the summer and fall (along with the heaviest precipitation) and nor'easters occur in the winter and spring, enhancing wave energy and storm surges associated with beach and foredune erosion (Boyles & Raman, 2003; Dolan & Lins, 1985).

Finally, sand grain size can be important to beach and dune morphology (Short & Hesp, 1982). The mean surface grain size is that of medium sand—approximately 0.3 mm within CALO and 0.4 mm in the northern Outer Banks—although grain size distributions and shell content can vary greatly across the region and depending on the timing of storm events (Hovenga et al., 2019, 2021; Inman & Dolan, 1989; Shideler, 1973). Increased shell content on the beach can decrease aeolian sediment transport to the dune, while finer sands are transported more easily and often lead to increased aeolian sediment flux to the dunes compared with coarser sands (Hovenga et al., 2019).

Vegetation and topography field surveys

To characterize a suite of ecological and geomorphic variables, we conducted plant community surveys and collected beach and foredune topography at 90 transects in October 2016 (CALO transects) and June 2017 (northern Outer Banks transects) (Jay et al., 2022) following the methods of Hacker et al. (2012) (Figure 1; Appendix S1: Table S1). Most of the transects were placed 2–5 km apart but the distance ranged from 0.4 to 20.4 km depending on island size and beach access, with greater distances between transects occurring particularly in developed areas where beaches were not accessible by vehicle. Transects were placed perpendicular to the shoreline at each site, starting at approximately mean lower low water and extending through the dune toe (the seaward-most dune extent, marked by the topographic inflection point between the backshore and the foredune, and often denoted by the vegetation line), the dune crest (the highest point of foredune elevation), and the dune heel (the lowest point on the landward side of the foredune; Figure 2). Quadrats (0.25 m^2) were established every 5 m along the transect within which we counted the tiller density of each grass species. We used a Network Real Time Kinematic Differential Global Positioning System (R7 unit, Trimble, Sunnyvale, CA, USA), which typically has a total vertical uncertainty of less than 8 cm (Ruggiero et al., 2005), to measure the elevation along the beach and dune profile and at each quadrat along the foredune. We resampled all 90 cross-shore transects one year after they were originally surveyed (October 2017 for CALO transects and June 2018 for northern Outer Banks transects).

Beach and dune morphometrics

We extracted beach and foredune morphometrics at each transect from field topography data following the methods of Mull and Ruggiero (2014) (see Figure 2 for details of the morphometric measures). Shoreline position, defined as the approximate location of mean high water (MHW), was extracted using the 0.4-m contour referenced to the North American Vertical Datum 1988 (NAVD88) (Hovenga et al., 2021). Foredune morphometric (response) variables included foredune toe and foredune crest elevation (in meters; relative to MHW, as defined above), foredune width (in meters; defined as one half foredune width, or the horizontal distance between the foredune toe and crest), and foredune aspect ratio (foredune height divided by width). Beach morphometric parameters included beach width (distance between MHW and foredune toe), backshore beach slope (slope between MHW and foredune toe), and foreshore

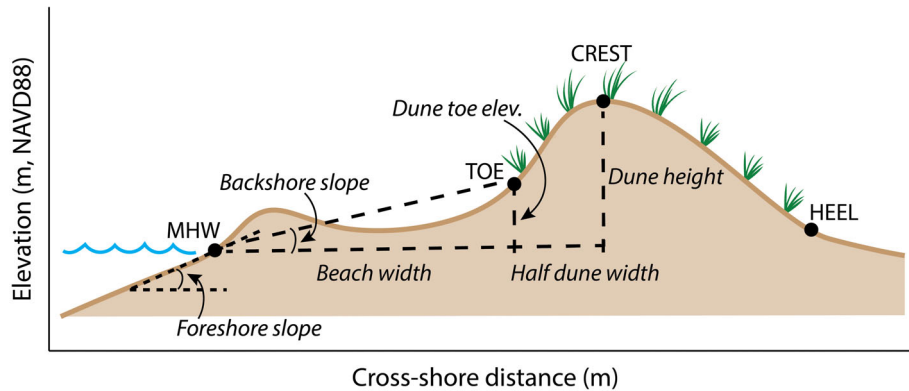


FIGURE 2 Diagram of beach and dune morphometric parameters measured and calculated using data from real-time kinematic GPS surveys following the methods of Mull and Ruggiero (2014). MHW refers to mean high water, extracted using the 0.3-m MHW contour (NAVD88). Foredune morphometrics measured included the position and elevation of the foredune toe (the seaward extent of the foredune, marked by the topographic inflection point between the backshore and the foredune), the foredune crest (the highest point of the foredune), and the foredune heel (the landward extent of the foredune ridge, determined by an elevation minimum). Foredune height and toe elevation were calculated as the difference between MHW and foredune crest and foredune toe elevations, respectively. Foredune width was calculated as one-half dune width, or the horizontal distance between the foredune toe and crest, in order to capture changes in the width of the foredune face. Beach width was calculated as the horizontal distance between MHW and the foredune toe. Changes in morphology metrics were calculated as the difference between these parameters from 2016 to 2017. We determined backshore slope as the slope between MHW and the dune toe, and foreshore slope was calculated as the slope in the vicinity of MHW.

beach slope (slope in the vicinity of the shoreline position). Change in foredune and beach morphometrics was calculated as the annual difference between these values.

Shoreline change rate data

We used SCR (i.e., the rate at which the shoreline position at a given location moves seaward or landward) as a proxy for sand supply to the beach. This metric has been shown to be a reliable measure of the volume of sand gained or lost from the beach over time, particularly at decadal or longer timescales (Dingler & Reiss, 2002; Farris & List, 2007; Hanson, 1989). However, we recognize that shoreline positions can shift for a variety of reasons including RSL changes and seasonal and multiyear variation in metocean conditions, and it is therefore important to account for potential biases in the calculation of SCR (e.g., by using a datum-based shoreline; Moore et al., 2006; Ruggiero et al., 2003).

We calculated two SCR metrics: annual and multidecadal. Both SCR metrics were annual measures (meters of change per year). Annual SCR was calculated for each survey transect using the topographic data to measure the change in shoreline position (and beach width) from one year to the next. Multidecadal SCR was calculated in two ways due to the varying availability of airborne lidar data for different locations within the study region. For the CALO transects, multidecadal SCR was calculated as the average annual change in shoreline

position from 1997 to 2016 using airborne lidar data from NOAA's Digital Coast website as described in Hovenga et al. (2021). For the northern Outer Banks from Ocracoke Island to False Cape, VA, multidecadal SCR was calculated as the average annual change in shoreline position from 1997 to 2010 using USGS data from Kratzmann et al. (2017). For both multidecadal SCR calculations, cross-shore profiles were extracted at survey transect locations and shoreline positions were defined with a spatially varying MHW contour ranging from 0.33 to 0.46 m (referenced to NAVD88).

Statistical analyses

We used R v.3.6.1 (R Development Core Team, 2019) for all statistical analyses. Additive and multiplicative linear regression models (glm in R) were used to explore correlations between individual foredune morphology variables and multiple explanatory variables. Our first set of analyses used foredune morphology metrics as response variables, while our second set of analyses used the change in the foredune morphology metrics over one year as response variables. We used AIC (multiple top models were considered within 4 Δ AIC; Burnham et al., 2002) to select the top models that best describe the relationships. AIC uses an estimator to predict model error and thus the relative quality of different models for a given set of data. We then used hierarchical partitioning analyses (hier.part in R) with R^2 as the

goodness-of-fit metric to quantify the proportion of variance explained by each explanatory variable. Before models were run, Shapiro–Wilk tests and residual and normal quantile plots were used to assess whether variables conformed to the assumptions of linear regression, and transformations were used if necessary. Two-sided one sample *t* tests were used to quantify whether changes in beach and foredune morphology and vegetation density metrics (the change from one year to the next) differed from the null value of zero (i.e., no change).

For the models, the response variables included foredune morphology metrics (height, width, toe elevation, and aspect ratio for the first analysis, and the annual change in these parameters for the second analysis) and the explanatory variables included beach sand supply (annual and multidecadal SCR), beach morphology (beach width, annual change in beach width, backshore slope, and foreshore slope), and dune grass density. Dune grass density in the quadrats (per 0.25 m²) was averaged within transects and included mean combined tiller density of the four dominant grass species, mean *A. breviligulata* tiller density, mean *U. paniculata* tiller density, mean combined tiller density of *A. breviligulata* and *U. paniculata*, annual change in *A. breviligulata* tiller density, and annual change in *U. paniculata* tiller density. Fifteen transects adjacent to inlets and capes (Figure 3a,b; Appendix S1: Table S1) with high erosional or progradational multidecadal SCRs were excluded, resulting in 75 transects used in the statistical analyses.

RESULTS

Temporal and spatial patterns in beach and foredune morphology and vegetation

Sand supply and beach morphology metrics varied greatly throughout the study region (Figure 3). Of the 75 transects used in our analyses, we found that annual SCR values were more extreme (range: −31.8 to 32.4 m/year, mean ± SE: 2.9 ± 1.5 m/year) than multidecadal values (−3.8 m to 4.2 m/year, −0.5 ± 0.2 m/year) and there was no clear pattern with latitude (Figure 3a,b). By contrast, multidecadal SCRs (measured as the average annual change in shoreline position) show that, over a time period of roughly two decades, beaches in CALO have been primarily eroding (89% have negative values), while many of the beaches from Ocracoke Island northward have been accreting (59% have positive values) (Figure 3b). Beach width ranged from 4.4 to 99.6 m (mean ± SE: 38.0 ± 2.2 m), with generally wider beaches in the north (Figure 3c). Overall, beach width declined on average by −0.7 ± 1.3 m over the year, but this decrease was not statistically significant (*p* = 0.619; Figure 3d). Moreover,

multidecadal SCR and beach width were positively correlated, with wider beaches associated with positive and higher multidecadal SCR values. Backshore and foreshore slopes averaged 0.05 ± 0.003 and 0.08 ± 0.004, respectively, with typically more steeply sloped beaches in the north compared with CALO in the south (Figure 3f).

Foredune morphology also varied greatly across the study region, with some metrics displaying latitudinal trends. In particular, foredune height (5.3 ± 0.2 m), width (42.4 ± 3.5 m), and toe elevation (2.1 ± 0.01 m) increased northward (Figure 4a–c), while foredune aspect ratio showed no latitudinal trend (Figure 4d). Changes in foredune morphology also occurred at the annual timescale, with an average increase in crest elevation of 0.11 ± 0.03 m (Figure 4e; *t* = 3.165, *df* = 71, *p* = 0.002) and an average increase in toe elevation of 0.15 ± 0.06 m (Figure 4g; *t* = 2.317, *df* = 71, *p* = 0.023). Foredune aspect ratio did not change at the annual timescale (Figure 4h; *p* = 0.914).

Our results also show differences in dune grass species tiller density across the study region and over the year. *Uniola paniculata* was the most abundant, *A. breviligulata* and *P. amarum* had intermediate abundances, and *S. patens* was least abundant, but this depended on the island (Figure 1b) (also see Hacker et al., 2019 for vegetation patterns). The northern islands generally had more *A. breviligulata* and *P. amarum* compared with the southern islands, which had more *U. paniculata*. Average tiller densities did not change over the course of one year for any of the dune grass species (Figure 3g,h; *U. paniculata* *p* = 0.935, *P. amarum* *p* = 0.124, *A. breviligulata* *p* = 0.255, and *S. patens* *p* = 0.325).

Regression models, hierarchical partitioning, and controls on foredune morphology

Regression models and hierarchical partitioning analyses showed correlations between foredune morphology and several explanatory variables (beach sand supply, beach morphology, and changes in dune grass density, particularly *A. breviligulata* density), but the relative importance of these factors and the strength of the correlations depended on the foredune morphology metric considered (Figure 5, Table 1). For the foredune morphology variables as a group, SCR (range: 20.4%–45.3%) and beach morphology (31.2%–69.9%) variables made up the greatest proportion of overall variance explained compared with that of the dune grass variables (9.7%–28.2%) (Figure 5; Appendix S1: Table S2).

The top model for foredune height showed positive correlations with multidecadal SCR and an interaction

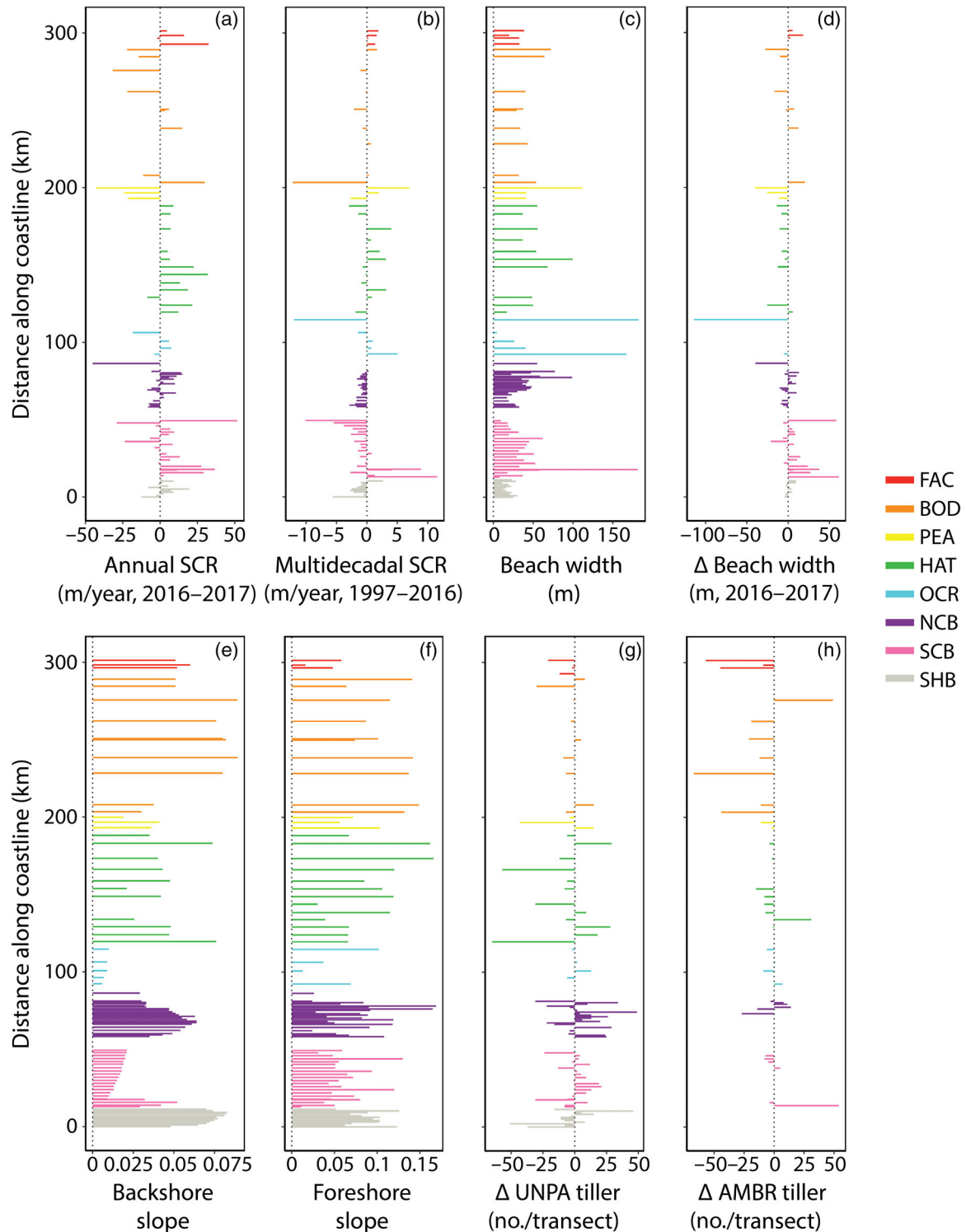


FIGURE 3 Beach sand supply, beach geomorphology, and vegetation density explanatory variables from 2016 to 2017 (unless otherwise indicated), with distance (in kilometers) along the coastline from the southwestern-most transect. Beach geomorphology variables were calculated as shown in Figure 2. (a) Annual shoreline change rate (SCR; in meters per year), (b) multidecadal SCR (in meters per year). See text for calculation details. (c) Beach width (in meters), (d) change in beach width (in meters), (e) backshore slope, (f) foreshore slope, (g) change in *Uniola paniculata* (UNPA) tiller number, (h) change in *Ammophila breviligulata* (AMBR) tiller number. Abbreviations as described in Figure 1.

between beach width and backshore slope, but negative correlations with backshore slope and beach width (Figure 5, Table 1). In the next best model (but not a top

model due to its Δ AIC > 4), foredune height was positively correlated with multidecadal SCR and beach width, and negatively correlated with change in *A. breviligulata* tiller

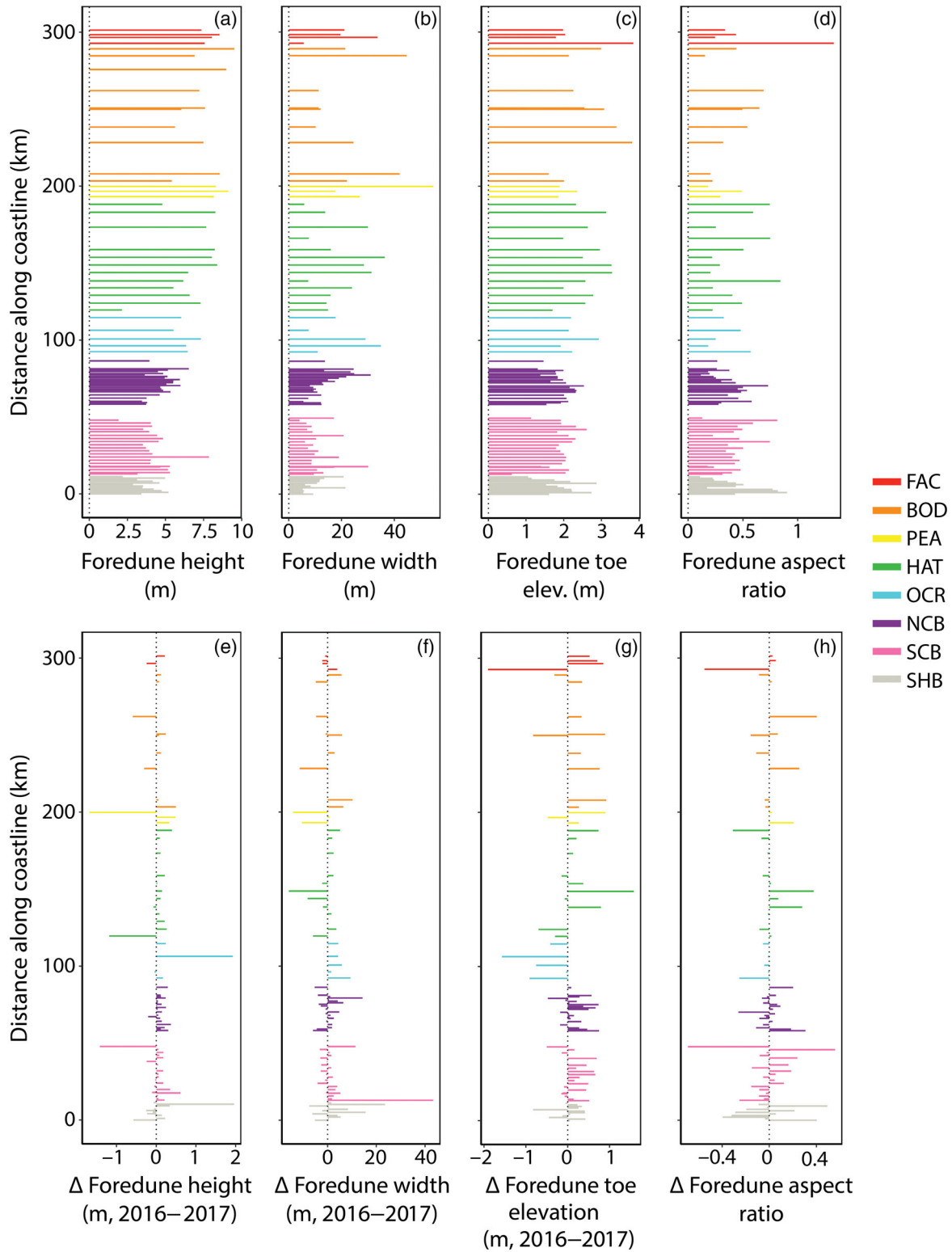


FIGURE 4 Foredune morphology response variables (Figure 2) from 2016 to 2017, with distance (in kilometers) along the coastline from the southwestern-most transect.

density. Hierarchical partitioning showed that multidecadal SCR, beach width, combined dune grass density, and change in *A. breviligulata* tiller density comprised 40.6%, 20.3%, 11.1%, and 9.2% of explained variance in foredune height, respectively (Figure 5; Appendix S1: Table S2).

Top models for foredune width showed positive correlations with both SCR metrics, beach width, and foreshore slope, and a negative correlation with change in *A. breviligulata* density (Figure 5, Table 1). Hierarchical partitioning showed that beach width,

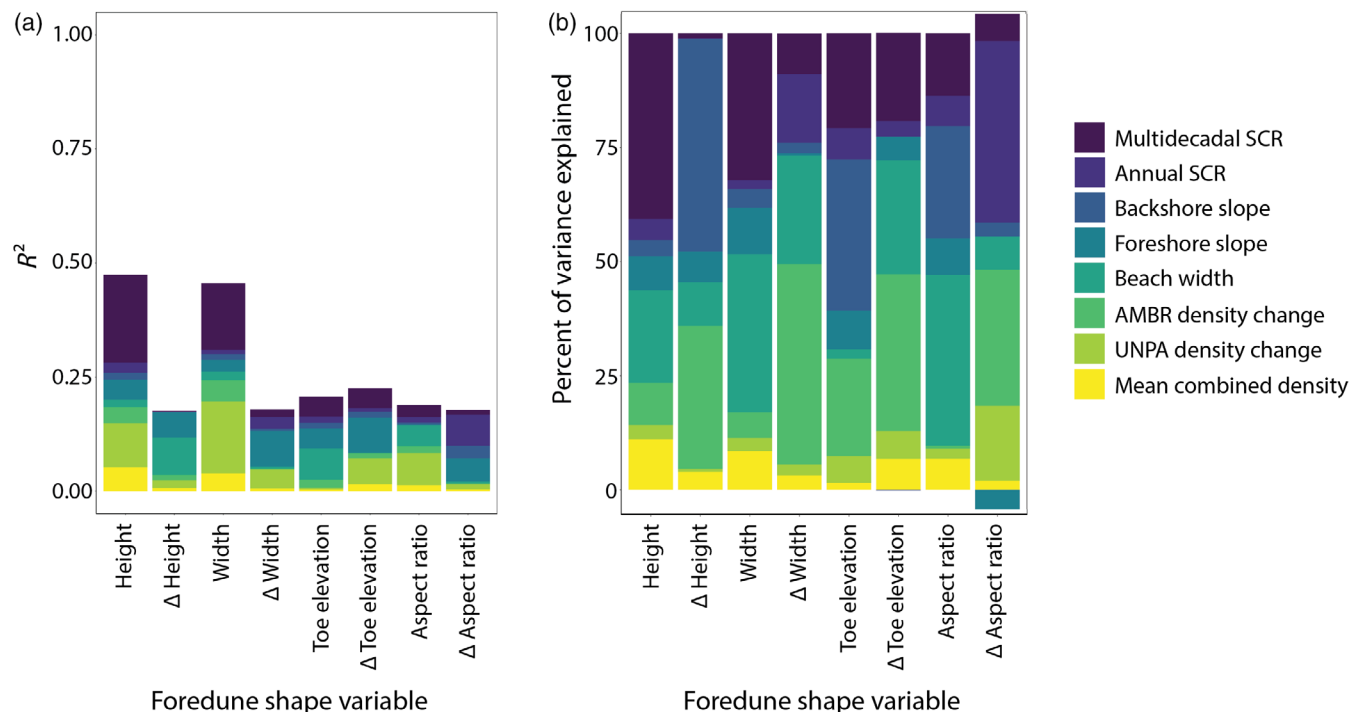


FIGURE 5 Results of hierarchical partitioning analyses. (a) Independent contribution (R^2) of each explanatory variable (SCR and beach morphology [shades of blue] and dune grass [shades of green to yellow]) for each foredune morphology response variable. (b) Variation (in %) explained by the same explanatory variables for each foredune morphology response variable. Abbreviations as described in Figure 1. SCR, shoreline change rate.

multidecadal SCR, and foreshore slope comprised the greatest proportion of explained variance in foredune width (34.7%, 32.2%, and 10.1%, respectively) (Figure 5; Appendix S1: Table S2).

Top models for foredune toe elevation showed positive correlations with backshore slope (33.0% explained variance) and multidecadal SCR (20.8% explained variance), and negative correlations with a change in *A. breviligulata* tiller density (21.3% explained variance) (Figure 5, Table 1; Appendix S1: Table S2). Finally, models for foredune aspect ratio were less strong overall, but showed negative correlations with multidecadal SCR (13.7% explained variance) and beach width (37.4% explained variance), and positive correlations with backshore slope (24.6% explained variance) (Figure 5, Table 1; Appendix S1: Table S2). In one of our models (but not a top model due to its Δ AIC > 4), foredune aspect ratio was negatively correlated with mean *A. breviligulata* density.

By contrast, our second analysis showed that for the group of foredune morphology change variables, dune grass variables (range: 34.9%–49.5%) and beach morphology (14.6%–63.0%) metrics comprised the greatest proportion of explained variance compared with that of the SCR variables (1.2%–45.9%) (Figure 5, Table 1; Appendix S1: Table S2). The proportion of unexplained variance in our hierarchical partitioning models was also higher for the foredune

morphology change metrics (Figure 5a). Regression models showed that foredune height change was positively correlated with a change in *A. breviligulata* tiller density and negatively correlated with backshore slope (Figure 5, Table 1). In addition, backshore slope, change in *A. breviligulata* tiller density, and beach width comprised 46.7%, 31.3%, and 9.6% of variation in foredune height change (Figure 5; Appendix S1: Table S2). For foredune width change, both top models showed a positive relationship with annual SCR and change in *A. breviligulata* tiller density, and one model showed a positive correlation with beach width while the other showed a positive correlation with backshore slope (Figure 5, Table 1). However, the only significant term in these models was the change in *A. breviligulata* tiller density. Hierarchical partitioning showed that the change in *A. breviligulata* tiller density, beach width, and annual SCR comprised 43.9%, 23.8%, and 15% of explained variance, respectively (Figure 5; Appendix S1: Table S2). Top models for foredune toe elevation change showed negative correlations with a change in *A. breviligulata* tiller density (34.3% explained variance), multidecadal SCR (19.3% explained variance), and backshore slope (not a significant term in the model), and a positive correlation with beach width (25.0% explained variance) (Figure 5, Table 1; Appendix S1: Table S2). Foredune aspect ratio change was negatively correlated with annual SCR

TABLE 1 Results from linear regression analyses showing top models for each response variable.

Response variable	Linear model	AIC	ΔAIC	df	R ²
Foredune height	$[\ln(\text{DuneHt})] = 0.087[\text{Multi_SCR}]^{***} - 9.707$ $[\text{Backshore_slope}]^{***} - 0.011[\text{Beach_width}]^{**} + 0.381$ $[\text{Beach_width}:\text{Backshore_slope}]^{***} + 1.962^{***}$	-5.06	0	63	0.49
<i>Foredune height</i>	<i>$[\ln(\text{DuneHt})] = 0.099[\text{Multi_SCR}]^{***} - 0.010[\text{AMBR_chg}]^{***}$</i> <i>$+ 0.003[\text{Beach_width}] + 0.005[\text{AMBR_chg}:\text{Multi_SCR}]^*$</i> <i>$+ 1.582^{***}$</i>	<i>1.58</i>	<i>6.64</i>	<i>64</i>	<i>0.44</i>
Foredune width	$[\ln(\text{DuneWidth})] = 0.104[\text{Multi_SCR}]^{**} - 0.008[\text{AMBR_chg}]^*$ $+ 2.094[\text{Foreshore_slope}] + 0.009[\text{Beach_width}]^{**}$ $+ 2.083^{***}$	82	0	63	0.40
Foredune width	$[\ln(\text{DuneWidth})] = 0.109[\text{Multi_SCR}]^{**} + 2.681$ $[\text{Foreshore_slope}]^\dagger + 0.009[\text{Beach_width}]^* + 2.080^{***}$	84.23	2.23	64	0.36
Foredune width	$[\ln(\text{DuneWidth})] = 0.163[\text{Multi_SCR}]^{***} + 2.633$ $[\text{Foreshore_slope}]^\dagger + 2.449^{***}$	85.42	3.42	68	0.28
Foredune toe elevation	$[\ln(\text{DuneToeElev})] = -0.003[\text{AMBR_chg}]^\dagger + 2.314$ $[\text{Backshore_slope}]^* + 0.66^{***}$	-24.64	0	67	0.13
Foredune toe elevation	$[\ln(\text{DuneToeElev})] = 0.025[\text{Multi_SCR}]^\dagger - 0.003$ $[\text{AMBR_chg}]^\dagger + 2.494[\text{Backshore_slope}]^* + 0.666^{***}$	-24.36	0.28	65	0.17
Foredune height change	$[\ln(\text{DuneHtChg})] = 0.003[\text{AMBR_chg}] - 2.424$ $[\text{Backshore_slope}]^* + 0.194^{**}$	-9.02	0	66	0.12
Foredune height change	$[\ln(\text{DuneHtChg})] = -2.851[\text{Backshore_slope}]^* + 0.205^{**}$	-8.38	0.64	67	0.08
Foredune width change	$\text{DuneWidthChg} = 0.082[\text{Annual_SCR}] + 0.108[\text{AMBR_chg}]^*$ $+ 0.039[\text{Beach_width}] + 2.289$	414.31	0	64	0.14
Foredune width change	$\text{DuneWidthChg} = 0.079[\text{Annual_SCR}] + 0.102[\text{AMBR_chg}]^*$ $+ 12.148[\text{Backshore_slope}] + 0.212$	416.29	1.98	64	0.11
Foredune toe elevation change	$[(\text{DuneToeElevChg} + 2)^2 - 1]/2 = -0.222[\text{Multi_SCR}]^{**}$ $- 0.026[\text{AMBR_chg}]^{**} + 0.019[\text{Beach_width}]^{**} + 1.01^{**}$	193.21	0	67	0.22
Foredune toe elevation change	$[(\text{DuneToeElevChg} + 2)^2 - 1]/2 = -0.023[\text{AMBR_chg}]^{**}$ $- 1.526[\text{Backshore_slope}] + 1.979$	196.89	3.68	66	0.10
Foredune aspect ratio	$[\ln(\text{DuneAspectRatio})] = 4.299[\text{Backshore_slope}]^\dagger - 0.064$ $[\text{Multi_SCR}]^* - 1.165^{***}$	78.08	0	66	0.12
Foredune aspect ratio	$[\ln(\text{DuneAspectRatio})] = 2.554[\text{Backshore_slope}] - 0.008$ $[\text{Beach_width}]^{**} - 0.769^{***}$	79.12	1.04	66	0.15
<i>Foredune aspect ratio</i>	<i>$[\ln(\text{DuneAspectRatio})] = -0.009[\text{Beach_width}]^{**} - 0.110$</i> <i>$[\ln(\text{mean_AMBR} + 1)]^\dagger - 0.528^{***}$</i>	<i>85.01</i>	<i>6.93</i>	<i>67</i>	<i>0.17</i>
Foredune aspect ratio change	$[\text{DuneAspectRatioChg}] = -0.004[\text{Annual_SCR}]^* - 0.003$ $[\text{AMBR_chg}]^\dagger + 0.009$	-42.12	0	68	0.12
Foredune aspect ratio change	$[\text{DuneAspectRatioChg}] = -0.004[\text{Annual_SCR}]^* + 0.017$	-41.24	0.88	69	0.08

Note: Top models were chosen using ΔAIC within 4 (except see below). Explanatory variables included together in models were uncorrelated with Pearson correlation coefficient <|0.6|. Significance codes for explanatory variables are: ****p* < 0.001, ***p* < 0.01, **p* < 0.05, and †*p* < 0.1. Response variable transformations were applied following Shapiro–Wilk tests for normality and residual investigations. Transects adjacent to inlets and capes were removed prior to analysis (*n* = 15; see Appendix S1: Table S1), with 75 transects remaining for the analysis. The two models in italics do not fit the top model criteria (ΔAIC within 4) but were included due to their high R² values (relative to top models) and to show significant relationships between the variables.

Abbreviations: AIC, Akaike information criterion; AMBR, *Ammophila breviligulata*; SCR, shoreline change rate.

(39.8% explained variance) and a change in *A. breviligulata* tiller density (29.8% explained variance) and positively related to a change in *U. paniculata* density (16.8% explained variance, although not significant in regression models) (Figure 5, Table 1; Appendix S1: Table S2).

DISCUSSION

Our analyses support the role of beach sand supply, beach morphology, and vegetation density as significant factors shaping foredune morphology in US Central

Atlantic coast dunes, but the relative importance of these variables varied depending on the foredune morphology metric considered. Overall, we found that taller and wider foredunes were positively associated with increased beach sand supply (measured as multidecadal SCR) and wider beaches (Figure 5, Table 1; Appendix S1: Table S2), as reported in previous studies from dunes around the world (e.g., Biel et al., 2019; de Vries et al., 2012; Hesp & Smyth, 2016; Keijsers et al., 2014; Sherman & Bauer, 1993; Short & Hesp, 1982; van Puijenbroek et al., 2017), but vegetation density also played a role. Combined dune grass density was associated with taller and wider foredunes and explained a similar amount of variability (~10%; Figure 5b; Appendix S1: Table S2) to that in Pacific Northwest dunes (Biel et al., 2019). Moreover, as with Biel et al. (2019), an annual change in dune grass density explained a greater proportion of variance in changes in foredune morphology than beach sand supply and beach morphology metrics. There were also species-specific differences: *A. breviligulata* density was more important in shaping foredune morphology than *U. paniculata*, particularly with respect to increases in foredune width. Even though beach sand supply had the largest effect on foredune morphology, our results reinforce those of other studies that detail the importance of vegetation and the biophysical feedback it serves to generate (Biel et al., 2019; Cheng et al., 2019; Garzon et al., 2021; Keijsers et al., 2016; Zarnetske et al., 2012, 2015).

Our statistical models best predicted foredune height and foredune width compared with foredune toe elevation, foredune aspect ratio, or any of the foredune change metrics. In particular, most of the foredune change models had low R^2 values, which is unsurprising given that little change occurred in foredune morphology and associated explanatory variables over the short, one-year time period (Figures 3 and 4). In comparison, for Pacific Northwest coastal dunes, Zarnetske et al. (2015) found stronger support for foredune morphology change models, likely because of the longer, decadal timescales used in their study and the high sand delivery to those beaches and dunes. By contrast, the NC Outer Banks are characterized by lower average SCRs and lower vegetation densities than the Pacific Northwest (Figures 3 and 4; Hacker et al., 2012, 2019), in addition to more frequent storm events and prevalent destructive forces, leading to pervasive overwash and erosion (Hovenga et al., 2021). To better understand the factors that control changes in foredune morphology over time, additional years of field measurements will be needed to establish a longer-term dataset.

Relationships between beach sand supply, beach morphology, and foredune morphology

In this study, we examined the relative contribution of beach sand supply, beach morphology, and dune grass density and species in shaping foredune morphology along the NC Outer Banks. Our regression models and hierarchical partitioning results suggest that beach sand supply and beach morphology metrics together comprise most of the explained variation in foredune morphology across our study region. In particular, foredune morphology is strongly related to SCR and beach width, both factors that influence sand supply to foredunes (Biel et al., 2019; Farris & List, 2007) and vary regionally across our study sites. Foredunes along Cape Hatteras and northward, where multidecadal SCR values were more positive and beaches were typically wider, tended to be taller and wider, while dunes to the south where SCRs were often negative were shorter and narrower (Figures 3b and 4a,b). Besides differences in absolute height and width, we also observed a continuum in foredune shape from high-aspect-ratio dunes (height more equivalent to width) to low-aspect-ratio dunes (height less than width) (Figure 4d; Appendix S1: Figure S1). Foredune aspect ratio was negatively related to both multidecadal SCR and beach width (Table 1; Appendix S1: Table S2), indicating that dunes in areas with higher positive SCRs (prograding shorelines) and therefore wider beaches had lower aspect ratios; at our field sites, these were relatively high volume dunes that were much wider than tall and gently sloping. Likewise, in areas where SCRs were neutral or negative, and beaches were narrow, foredunes tended to have high aspect ratios and steeper slopes. The factors important to the differences in the absolute height and width of foredunes, as well as their aspect ratio, have been considered in a handful of other empirical studies in different regions of the world (Bauer & Davidson-Arnott, 2002; Biel et al., 2019; Short & Hesp, 1982). These studies show that, in general, taller and wider dunes are typically found on wider beaches, although incident wind direction can alter this pattern. Field and modeling studies have demonstrated that this finding may be explained by longer fetch lengths, and therefore, greater potential sand flux (Duran & Moore, 2013; Hesp & Smyth, 2016; Short & Hesp, 1982). Wider beaches allow for sand transport to the dune to occur for a longer period of time before dune topography steers the wind above the beach, reducing sand transport. In addition, wider beaches can absorb more wave energy than narrower beaches and typically have higher rates of embryo dune growth, all of which

contribute to less foredune erosion during storm events (van Puijenbroek et al., 2017).

Most beaches along the NC coastline are 20–60 m wide with a handful of exceptions near island inlets and capes, where beach width can exceed 150 m (and dune growth is complicated by high shoreline curvature and associated changes in local wind forcing conditions) or where beaches are more severely eroded (Figure 3c). For this reason, unlike research on the Pacific Northwest coast (Biel et al., 2019; Hacker et al., 2012; Ruggiero et al., 2016, 2018; Zarnetske et al., 2015), beaches in this study area are not wide enough to test the Psuty (1986) conceptual model. The model hypothesizes that on rapidly prograding beaches at the extreme end of positive SCR and beach width, multiple short and wide foredunes will develop over time. Psuty (1986) also posited that foredune development is enhanced (increased height) under slightly negative beach sand supply, but high dune sand supply. Our data on the NC coast do not fully support this hypothesis, as we observed taller dunes in areas with relatively higher multidecadal SCR and thus greater sand supply to the beach and dune.

Relationships between vegetation density and foredune morphology

We next asked, do the dune grass species *A. breviligulata* and *U. paniculata* affect foredune morphology in species-specific ways, and if so, how? Vegetation density variables played a lesser, but still significant role in shaping foredune morphology compared with sand supply and beach morphology metrics, and the role of vegetation differed between species. For example, our finding that an increase in *A. breviligulata* density was more strongly associated with foredune height and width, and their annual changes, than other dune grass species supports previous experimental research showing that, in general, *A. breviligulata* builds dunes of similar height, but greater width, compared with *U. paniculata* or a combination of *U. paniculata* and *P. amarum* (Woodhouse et al., 1977). Moreover, our results are similar to findings in the Pacific Northwest where *A. breviligulata* tends to form wider foredunes and *A. arenaria* tends to build taller foredunes (Biel et al., 2019; Hacker et al., 2012; Zarnetske et al., 2012, 2015). This widening of foredunes is likely the result of the growth form of *A. breviligulata*, which includes dense, clumped shoots coupled with horizontally growing rhizomes that spread seaward at the foredune toe (Biel et al., 2019; Hacker et al., 2012, 2019). Interestingly, we also found that an increase in *A. breviligulata* density was negatively correlated with the elevation of the

foredune toe (Appendix S1: Table S2). The rapid lateral spread of *A. breviligulata* (~2–3 m/year; Woodhouse et al., 1977) coupled with high sand supply to dunes would likely result in sand accretion in the seaward direction, ultimately producing lower dune toe elevations and wider dunes overall. Furthermore, an increase in *A. breviligulata* density was negatively correlated with a change in foredune aspect ratio, supporting the hypothesis that this beachgrass builds wider, gently sloping, low-aspect-ratio dunes. In contrast, an increase in *U. paniculata* density was positively correlated with narrower and steeper foredunes, a possible result of less lateral spread but more vertical growth of *U. paniculata* rhizomes compared with those of *A. breviligulata* (Hacker et al., 2019; Woodhouse et al., 1977).

The species-specific differences in foredune morphology that we document here also support the functional morphological characteristics of the different grass species as documented previously. In the same study region, Hacker et al. (2019) found that, for a given area, *A. breviligulata*, *U. paniculata*, and *P. amarum* had similar plant densities, but varied in shoot density, with *A. breviligulata* having almost double the number of shoots per plant. As a result, when *A. breviligulata* grows in a monoculture, it accretes ~42% more sand in a given area (measured over a one-year period) compared with the other two species. Our results are also consistent with those of Hacker et al. (2019), showing that, in field settings, other morphological differences in these grasses, including the height and weight of the shoots (e.g., *U. paniculata* had taller and heavier shoots than *A. breviligulata*, *P. amarum*, or *S. patens*), are unlikely to be as important to sand accretion as shoot density and growth form. This finding is also supported by flow studies with vegetation (Charbonneau et al., 2021; ChenChen et al., 2018; Cheng et al., 2019; Hesp et al., 2019; Zarnetske et al., 2012).

Although the models that considered factors important to foredune morphology change had lower explanatory power, the finding that a one-year change in foredune morphometrics was correlated to *A. breviligulata* density was somewhat surprising. The Outer Banks and Shackleford Banks experience highly variable annual SCRs (Figure 3a,b) and frequent disturbances from hurricanes (Hovenga et al., 2021); therefore, we expected that physical factors would mostly dominate as controlling factors and that there would be a lag between erosion or deposition events and the growth response of vegetation. For example, Zarnetske et al. (2015) found that invasive *A. breviligulata* on dunes in northern Oregon and southern Washington, which experience mostly positive SCRs, explained more of the variation in increases in dune height and width at decadal timescales (~50%–75% depending on the metric) compared with interannual timescales (~20%–40%). Measurements at

decadal timescales are less susceptible to antecedent conditions, which could have also influenced the general lack of changes in foredune morphology that we observed over the one-year time period. However, despite these differences, it is interesting to note that the variance explained by vegetation at annual timescales is similar between our study and Zarnetske et al. (2015) and demonstrates that *A. breviligulata* is able to spread and accrete sand relatively quickly, especially under positive beach sand supply conditions.

Potential implications of changes in vegetation and SCR on foredune morphology

Understanding the relative influence of beach sand supply, beach morphology, and vegetation on coastal dune evolution is critical as future climate change may mediate these factors, likely influencing foredune morphology, and in turn, dune ecosystem services. One potential impact of climate change on dune morphology that has been overlooked is that of possible range shifts in dune grass species, particularly along the US Central Atlantic coast. A literature survey conducted by Goldstein et al. (2018) showed that the southern range limit of *A. breviligulata* is Cape Fear, NC, while the northern range limit of *U. paniculata* is Assateague Island in VA and Maryland (a likely result of their differing physiological tolerance). Based on comparisons in the literature, they also found a slight northward range expansion in *U. paniculata*, possibly associated with recent warming trends (range shifts for *A. breviligulata* were inconclusive). A glasshouse study by Harris et al. (2017) found that physiological (electron transport rate) and morphological (relative growth rate, biomass) vigor of *A. breviligulata* diminished when planted in mixture with *U. paniculata*, while *U. paniculata* performance was unaffected by the presence of *A. breviligulata*. Taken together, these findings indicate that there is a possibility that *U. paniculata* could outcompete and displace *A. breviligulata* in parts of its current range as a result of climate change induced warming, which could, in turn, have implications for foredune morphology along the US Central Atlantic coast. A northward shift in *U. paniculata* abundance could eventually alter foredune morphology through biophysical feedbacks, resulting in the possibility that wider, low-aspect-ratio *A. breviligulata* dominated dunes could be replaced by narrower, higher aspect ratio *U. paniculata* dominated dunes. For example, at our field sites, *A. breviligulata* was typically associated with taller foredunes, but this result was confounded by latitudinal trends in beach sand supply and our finding that *A. breviligulata* density change

was negatively correlated with foredune height. While foredune height could be affected by shifts in dune grass dominance, previous experimental work in NC dunes showed that *U. paniculata* and *A. breviligulata* built dunes of similar height (Woodhouse et al., 1977), suggesting that foredune width and aspect ratio are more likely to be affected. If shifts in dune grass distributions lead to changes in foredune morphology over time, there could be consequences for the protective services that foredunes can provide against storm wave run-up and inundation. For example, model simulations by Itzkin et al. (2021) suggest that low-aspect-ratio dunes are more resistant to volumetric erosion during long-duration but low-intensity storms, while high aspect ratio dunes are more protective during short-duration, high-intensity storms. Morphological differences in foredune shape, which may be reinforced over time by dune grass species-specific feedbacks, can have important implications for coastal vulnerability; thus, additional studies are needed to determine the possible impacts of species range shifts on foredune morphology and ecosystem services.

Our findings demonstrate the interactive roles of beach sand supply and dune grass functional morphology in dune building processes on vulnerable Atlantic coast barrier islands. Understanding how dunes are modified by geologic and climate processes, as well as human-induced changes, will allow us to better predict how their ecosystem services are likely to change in the future. Further observations, experimental manipulations, and modeling efforts are needed to understand how dune vegetation will respond to climate change and what the consequences will be for foredune evolution.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Jay et al., 2022) are available from the EDI Data Portal: <https://doi.org/10.6073/pasta/59770602ba34230815f31f55da5c61e5>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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