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# Biotic Characteristics of Managed and Unmanaged Coastal Dunes in the Outer Banks, North Carolina

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# BIOTIC CHARACTERISTICS OF MANAGED AND UNMANAGED COASTAL DUNES IN THE OUTER BANKS, NORTH CAROLINA

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

by

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**Abstract**

BIOTIC CHARACTERISTICS OF COASTAL DUNES ACROSS A SPECTRUM OF MANAGEMENT IN THE OUTER BANKS, NORTH CAROLINA

By Andrew Eugene White, Bachelor of Art

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

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

Under future climate change and sea level rise scenarios, Natural and Nature-Based Features (e.g., dunes) that protect coastal habitat and infrastructure will be exposed to increased wave energy and storm surge. Understanding how these forces will impact coastal dunes is necessary for their continued use as protective features. Coastal dunes develop through feedback between vegetation and sediment deposition, a process complicated by species-specific growth rates and responses to burial. Wave flume studies have tested the effects of dune vegetation on erosion and found multiple plant organs across several functional types to be important for resisting erosion. Although dune building and erosion are known to be mediated by dune vegetation, the amount and distribution of plant belowground biomass within a dune represents a knowledge gap in coastal ecology and geomorphology. Our objectives were to quantify the belowground structure (e.g., plant roots, belowground stems and rhizomes) and aboveground composition of dunes across a range of management styles. To do so, we utilized a geological sampling method (e.g., vibracoring) to sample belowground biomass at depths greater than those represented in the literature across the dune profile at several sites representing multiple management histories. Our study occurred on foredunes of the Outer Banks, North Carolina, a net-erosional barrier island chain with varying levels of human development and management.

Sites ranged from an unmanaged, undeveloped dune backed by shrub thicket to a dune constructed and planted with *Ammophila breviligulata* following a beach nourishment in 2017. Living belowground biomass was highly variable across sites and did not exhibit differences between managed and unmanaged dunes or among depths within 90 cm of the sediment surface. Elevation was a significant predictor of living belowground biomass, fine root surface area, soil organic matter content, living cover and species richness. Plant community differences between management histories and among dune positions and sites occurred with larger sampling frequency (e.g. whole dune multiple transect survey) but were not present when considering plant community at coring plots only. The dune face at managed sites was dominated by *Ammophila breviligulata*, likely as a result of planting efforts by local managers. We also found a strong relationship between total living cover and living belowground biomass at coring plots, a finding that may prove useful in future estimates of living belowground biomass. These results underscore the importance of geomorphology on dune plant communities, with effects on species that may influence erosion resistance. Our findings will be incorporated into future numerical models used to predict dune response to sea-level rise and storms in order to better understand and manage dunes as natural protective features with climate change.

## Introduction

Natural and Nature-Based Features (NNBFs) are infrastructure designed to mimic or incorporate natural biological and geomorphological features for the purpose of protecting property and established infrastructure from damaging weather events and climatic changes (Bridges et al., 2015). In coastal communities, NNBFs (e.g., living shorelines, oyster reefs, mangrove forests, etc.) are increasingly popular and replacing hard structures like sea walls, ripraps and groins (Sutton-Grier et al., 2018), which can have unintended negative consequences for local and regional sediment transport and ecology (Firth et al., 2014; Martinez et al., 2019). Sand dunes are common coastal NNBFs and widely considered the first line of defense against storms (Charbonneau, 2015; Sigren et al., 2018). Predicting the functional role and future of dunes is a priority as coastal populations grow, sea levels rise and storms increase in frequency and intensity (Church et al., 2013; Neumann et al., 2015; Salgado and Martinez, 2017).

Sand dunes are more adaptable than hard structures due to natural feedbacks between sediment and vegetation. Common dune plants (e.g., *Uniola paniculata*, *Ammophila breviligulata*, *Cakile edentula*) respond positively to burial by sand (Zhang and Maun, 1992; Harris et al., 2017; Hacker et al., 2019), a regular occurrence due to the near-constant movement of sediment by currents, tides, waves and wind. When partially buried, ecosystem engineering dune plants extend stems and roots, allocate biomass aboveground and vegetatively expand with rhizomes and stolons (Perumal and Maun, 2006; Gilbert and Ripley, 2008; Brown and Zinnert, 2018). As burial occurs, dunes increase in volume with an assumed increase in biomass belowground. The burial-vegetation growth feedback also allows dunes to “repair” themselves following erosion provided enough sediment, living vegetation and time between disturbance events. Vegetated dunes are thus adaptable and dynamic structures, responding to the forces of the coastal environment. This process, however, is mediated by positive and negative species interactions that affect the amount of above- and belowground biomass within a dune (Brown et al., 2018).

Sediment availability is an important factor for dune building processes. Beach nourishment and dune construction are common practices that widen beaches and supplement the supply of sediment in areas where dunes have been destroyed by development or erosion (Elko et al., 2021). Sediment from offshore sources is pumped onshore and graded to create a wide, shallow-sloping beach (Kana and Kaczkowski, 2012). Sand is often piled in the backshore and planted with vegetation to create an artificial dune (Wootton et al., 2016; Rogers and Nash, 2003). These constructed dunes are supported with sand fencing and planted with dune grasses to capture aeolian (i.e., wind-blown) sediment deposits with the intention of increasing protection through dune growth (Jackson and Nordstrom, 2011; Swann et al., 2015). Here, we define management as practices intended to stabilize or grow a dune. These include beach nourishment, planting dune vegetation and installing sand fencing.

Physical characteristics of dunes (i.e., width, height, volume, distance between primary and secondary dune ridges) are correlated with dune resistance to erosion (Pries et al., 2008). A dune without vegetation; however, is a mound of unconsolidated sand; more dynamic than a hard structure but lacking the internal or external structure and support provided by dune vegetation. During storms and high-surf events, aboveground biomass (e.g., leaves, stems and stolons) of vegetation in the backshore and on the dune slows wave run-up and reduces the erosive power of waves that collide with the dune toe (Feagin et al., 2019). This may decrease beach and dune erosion and allow for wave-transported sediment accumulation during a storm, and aeolian sediment accumulation during and following a storm. When high waves erode the beach and dune, belowground biomass (e.g., roots, belowground stems and rhizomes) holds sediment in place and, when exposed, slows wave run-up and collision (Feagin et al., 2019).

Although physical erosion resistance by dune vegetation has been demonstrated in wave flume experiments, modeling efforts, and large-scale remote sensing studies, the amount and structure of belowground biomass are poorly understood aspects of dune systems (Ajedegba et al., 2019; Feagin et al., 2019). The current understanding of dune belowground composition documents that most roots occur in the top 30cm of soil (Conn and Day, 1993; Stevenson and Day, 1996). A gap in the literature exists regarding belowground structure and biomass across the dune profile (e.g., toe, face, crest, back) in dunes with various management histories. Conceptually, belowground structure is described as an internal lattice of roots, belowground stems and rhizomes that grow with successively deposited layers of wind-blown and wave-transported sediment (Maun, 2009; Feagin et al., 2015). As dune plants are buried by sand, they grow vertically into this new deposition, sending out roots and rhizomes horizontally. Over time this feedback of sediment accretion and plant growth may result in an extensive belowground structure capable of resisting erosion. The majority of belowground measurements focus on biomass in the top 30-60 cm of soil and are collected using pit excavation or small, manually collected (auger, slide hammer, etc.) cores (Conn and Day, 1993; Stevenson and Day, 1996; Lane et al., 2008; Charbonneau et al., 2016). Using a belowground sampling method novel to ecological studies (i.e. vibracoring), we were able to sample belowground biomass to a greater depth (>90 cm), thus providing us with more thorough sampling of belowground structure within dunes. Our objectives were to characterize aboveground composition and belowground biomass structure across the dune profile among dunes varying in management history. Because natural dunes are built by vegetation growing in conjunction with aeolian and marine sediment deposition, we hypothesized that less managed dunes would have more belowground biomass, more complex root structure, and higher species richness compared to actively managed dunes.

## Methods

### *Study locations*

Study sites occurred along a ~35 km stretch of beach in the Outer Banks of North Carolina and represented coastal dunes with various management histories (Figure 1a). From least to most managed, the sites were: Pine Island Undeveloped (PIV-U), Field Research Facility North (FRF-N), Field Research Facility South (FRF-S), Hillcrest Beach (HBV), Pine Island Residential (PIV-R), Bonnett Street (BSV) and Duck Residential (DRV). PIV-U in Corolla, NC near the Pine Island Audubon Donal C. O'Brien, Jr. Sanctuary was undeveloped at the time of sampling and had never been planted or nourished. FRF-N and FRF-S are located within the United States Army Corps of Engineers Field Research Facility in Duck, NC. These sites have not been actively managed since being constructed between the 1930s - 1950s (Dolan, 1986). HBV, adjacent to the Hillcrest Beach Access in Southern Shores, NC, is not actively managed, although property owners adjacent to this semi-public beach-access utilize sand fencing and privately conducted planting.

BSV is located on the small undeveloped dune immediately south of the Bonnett Street Beach Access walkway in Nags Head, NC. This site is actively managed through implementation of sand fencing and planting as well as the use of Christmas trees to stabilize sediment on the dune toe. The PIV-R in Corolla, NC is a privately owned property abutting a large beachfront rental home <1 km north of PIV-U. The site is bisected by a wooden beach access walkway and the owner has implemented sand fencing and regular planting to maintain and grow the dune there.  The most managed site in the study is DRV in Duck, NC. This dune was constructed following a beach nourishment in 2017. *Ammophila breviligulata* was planted on top of the constructed dune and sand fencing was used to capture and retain sediment, although the dune toe and face, and its sand fencing, were destroyed during several storm events that occurred between its construction and our sampling.

Dr. Nicholas Cohn with the U.S. Army Engineer Research and Development Center, Coastal Hydraulics Laboratory derived dune growth measurements (e.g. dune retreat, dune growth, elevation change) at each site using topographic data from the Coastal Lidar and Radar Imaging System (CLARIS; Spore and Brodie, 2017; Cohn et al., 2021; Figure S1). These values represent net dune growth between 2012 and 2020. Measurements at some sites were unavailable due to a lack of usable data on the dune face, crest and back.

*Belowground sampling*

Vibracores were collected in September and December 2020 by the Coastal Geology Lab at the Virginia Institute of Marine Science (VIMS). Cores were collected along a single transect at each site from the dune toe, face, crest and back (Figure 1b) where the topography of the dune allowed for safe operation of the vibracore equipment. Two cores were collected at each plot along the transect: one core for sedimentary analysis by the Coastal Geology Lab at VIMS and one core for ecological analysis at VCU. Cores ranged in length from 82-191 cm. Variability in core depth was due to differences in site sediments and buried obstructio ns (coarse sediment, buried sand fencing, etc.). All analyses of belowground variables were carried out with the first 90 cm of core to standardize analyses.

Cores were kept at 4 °C and processed within 1.5 weeks to prevent root degradation. Cores were bisected longitudinally using 14-gauge swivel head electric shears. The top of the aluminum core was removed and segmented into 30 cm sections from the soil surface. Each section was separated, bagged and frozen until further processing occurred. To separate belowground biomass, core sections were wet sieved using stacked 3.36 mm, 1 mm, 0.5 mm mesh-size sieves. Living belowground biomass included roots, rhizomes and belowground stems that were still flexible and did not exhibit signs of decomposition. All other biotic material was collected as non-living biomass (e.g., twigs, seeds, wrack). Within the living belowground biomass component, live roots were separated from other belowground structures (rhizomes, belowground-stems) and scanned using an Epson Perfection V800 Photo electric scanner calibrated for image analysis with WinRhizo™ by Regent Instruments (Regent Instruments Inc, Quebec City, Quebec, Canada). Images were analyzed using WinRhizo™ Pro 2019a (Regent Instruments Inc, Quebec City, Quebec, Canada) to quantify root surface area by diameter size class. Fine roots were defined as roots of $< 1$ mm diameter (Freschet and Roumet, 2017). All living and non-living belowground biomass was oven-dried at 60 °C for 72 hours and weighed. Soil organic matter content was quantified by loss on ignition of sediment samples with roots removed. Samples (1 g) were baked in a muffle furnace at 550 °C for 5 hours and reweighed to calculate soil organic matter content (%).

*Aboveground sampling*

Vegetation surveys were conducted during summer 2021. At each coring site, vegetation survey transects were established adjacent to the original coring transect at ~5-15 m intervals, depending on length of the dune. Some sites were bound by property lines and beach access walkways (PIV-R and DRV) and thus accommodated only narrowly spaced transects. Plots (0.25 $m^2$) were established along transects at ~5 m intervals from the dune toe (roughly in-line with the furthest seaward coring plot at each site) across the dune profile, over the crest. Species composition was assessed and percent cover, stem count and height were collected for each species within each plot. Percent cover of bare ground and dead plant material was also estimated in each plot. Aboveground biomass (within a 0.1 x 1 m quadrat) was collected adjacent to all coring sites except DRV where permission was not granted to harvest plants. Aboveground biomass was oven-dried at 60 °C for 72 hours and weighed.

*Statistical Analysis*

To meet assumptions of normality and homogeneity of variance for analyses, the following variables were transformed: non-living belowground biomass, living belowground biomass, fine root surface area, species richness were cube-root transformed; soil organic matter content and aboveground living biomass were square-root transformed, and living cover was log-transformed. Differences in living belowground biomass and fine root surface area by depth (30 cm, 60 cm, 90 cm) were analyzed with Analysis of Covariance (ANCOVA) with elevation as a covariate. Differences in fine root surface area among root diameter classes was also analyzed using ANCOVA. ANCOVA was used to detect differences in biomass, root surface area, species richness, and living cover, which were analyzed by management history (unmanaged- PIV-U, FRF-S, FRF-N vs. managed- HBV, BSV, PIV-R, DRV) with elevation as a covariate, but no difference was found. Thus, variables were analyzed by site using ANCOVA with elevation as a covariate. Species richness and total living cover were analyzed at coring locations only and with the full dune vegetation survey plots. Site × elevation interactions were tested for each variable and removed from the model when not significant. Post-hoc tests for significant site × elevation interactions were analyzed with t-test pairwise comparison of slopes.

Significant differences among sites were analyzed with Tukey Honest Significant Differences post-hoc test or a Sidak pot-hoc test as appropriate. Simple linear regressions were used to assess relationships between living cover or aboveground biomass and belowground biomass at coring plots. An alpha value $\alpha = 0.05$ was used for all univariate statistical analyses which were carried out in R Studio version 4.1.0.

Importance values were calculated at each dune position within each site using data collected during the whole-dune vegetation surveys. Relative density (stem count within the 0.25 $m^2$ plot), relative percent cover, and relative frequency were used to calculate the importance value of each species present. These were used to determine the dominant species across the dune profiles at each site based on multiple characteristics that influence sediment dynamics.

Multiple Response Permutation Procedure (MRPP; using Bray-Curtis Distance) was used to determine multivariate differences among dune positions, sites and management histories for species composition at coring plot and whole-dune vegetation survey plots. Post-hoc multiple pairwise comparisons were assessed for significance with a Bonferonni corrected alpha value based on the number of comparisons. Differences in whole-dune vegetation survey species composition were visualized with Non-Metric Multidimensional Scaling (NMS) ordination (McCune and Grace, 2002). All multivariate analyses were performed in PC-ORD version 7.

**Results**

*Internal Belowground Structure*

When pooled across sites, there were no differences in living biomass among depth classes, although variability increased with depth (30 cm: 81 ± 19 g $m^{-2}$; 60 cm: 137 ± 40 g $m^{-2}$; 90 cm: 110 ± 46 g $m^{-2}$, $p = 0.43$). Fine roots (< 1 mm diameter) comprised ~80% of total root surface area in all samples ($F_{9,827}$ = 135.44, p < 0.001) and surface area was greatest at 31-60 cm depth ($F_{2, 827}$ = 6.88, p = 0.001; Figure 2).

Living biomass increased with elevation (i.e., highest at crest plots, $F_{1, 17}$ = 7.32, p = 0.015; Figure 3) and was variable across sites, ranging from 67 ± 42 g $m^2$ at BSV to 1171 ± 291 g $m^2$ at FRF-S ($F_{6, 17}$ = 7.09, p < 0.001). Non-living belowground biomass also increased with elevation ($F_{1, 17}$ = 34.68, p < 0.001; Figure S2), but did not differ among sites (p = 0.15) or show any relationship with living belowground biomass (p = 0.08). Fine root surface area was highest at FRF-S with no differences among the other sites ($F_{6, 17}$ = 6.78, p < 0.001, Figure S3). Soil organic matter content was low, ranging from 0.18 ± 0.08% at FRF-N to 0.58 ± 0.22% at DRV. There was a significant site by elevation interaction ($F_{6, 11}$ = 6.18, p = 0.0047), with DRV ($\beta$ = -0.39, $r^2$ = 0.86) differing from FRF-N ($\beta$ = 0.02, $r^2$ = 0.06) and PIV-U ($\beta$ = 0.04, $r^2$ = 0.88).

*Above and Belowground Structure*

Total living cover significantly predicted living belowground biomass ($r^2$ = 0.67, p < 0.001), whereas there was a weak, positive relationship between aboveground and living belowground biomass ($r^2$ = 0.20, p = 0.049; Figure 4). Aboveground biomass from coring plots was similar across all sites (p = 0.59) and did not change with elevation (p = 0.43).

*Vegetation Cover by Sampling Effort*

At coring plots only, there were no differences in total living cover among sites (p = 0.08) due to high variability, but elevation was a significant covariate with the highest cover typically occurring at the crest ($F_{1, 19}$ = 5.12, p = 0.04). Species richness differed by site ($F_{6, 16}$ = 4.71, p =

0.006) with HBV exhibiting the highest number of species (5.0 ± 0.0). There were no differences among all other sites.

When sampling effort included multiple transects across the entire dune, significant differences arose among sites for total living cover ($F_{6, 140} = 3.62$, $p = 0.002$), which increased with elevation ($F_{3, 140} = 47.3$, $p < 0.001$, Figure 5). The lowest cover occurred at DRV and the highest at FRF-S. Likewise, when including the full dune plots, species richness differed among sites ($F_{6, 140} = 5.73$, $p < 0.001$) and increased with elevation ($F_{3, 140} = 72.7$, $p < 0.0001$). Species richness was highest at FRF-S, HBV, and BSV (Figure S4) and was a significant predictor of total living cover ($r^2 = 0.76$, $p < 0.001$).

At coring plots only, there were no differences in species composition between management histories (p = 0.16), among dune positions (p = 0.25), or across sites (p = 0.16). When including sampling along the entire dune, management history (T = -12.11, p < 0.001), dune position (T = -12.91, p < 0.001; Table S1), and site (T = -17.82, p < 0.001; Table S2) had significant effects on species composition. Differences in species composition between management histories were visualized with NMS (stress = 15.3, Figure S6). Managed dunes had less variation in species composition than unmanaged ones.

*Dune Species Composition*

43% of full dune vegetation survey plots had species richness >1 with only 3% of these plots occurring on the dune toe. Toe plots at all sites were dominated by 1-2 species, typically the annual forb *Cakile edentula*, or a dominant dune grass (e.g., *Spartina patens*, *Uniola paniculata*, *Ammophila breviligulata*; Table 1). These dominant dune grasses and *Panicum amarum* were common on the dune face across sites. Managed sites (which are frequently planted) tended to be dominated by *Ammophila breviligulata*. The plant community at FRF-S was unique relative to other sites on the dune face where the shrub *Iva imbricata* and the invasive sedge *Carex kobomugi* dominated. At the dune crest, forbs and lianas emerged as dominant species across sites (Table 1).

## Discussion

In the coming decades, coastal areas will be subjected to stronger and more frequent storms and rising sea levels (Church and White, 2011). Quantifying how plant biomass is distributed in dunes is vital to adapting coastal NNBFs to a changing climate. Previous research in coastal dunes focused on the effects of succession and species on belowground biomass (Conn and Day, 1993; Charbonneau et al., 2016), but a knowledge gap remains about belowground composition and structure across dunes varying in management history. Utilizing a novel method for sampling belowground biomass in coastal sand dunes (i.e., vibracoring), our findings reveal that living belowground biomass is distributed in similar amounts up to 90 cm and elevation is important for the distribution of belowground biomass and aboveground cover within a dune, regardless of management history or location.

Multiple biotic factors (e.g., belowground biomass, vegetation cover, species richness) were greatest at higher elevation plots on the dune face, crest and back. We found that total living cover was a significant predictor of living belowground biomass across dunes, which can aid in rapid assessment. Species composition differed between managed dunes relative to those not actively managed in >5 years, likely influenced by plantings, but across sites, plant communities were composed of multiple interacting species. Our hypothesis that managed dunes would have less belowground biomass than unmanaged dunes was not supported due to high variability across sites and management styles; however, this may be constrained by sample size. Further, species composition influences belowground biomass (Conn and Day, 1993; Charbonneau et al., 2016; Walker and Zinnert, 2022) and high variability in cover and biomass among coring plots may mask management and site differences.

The amount and composition of dune belowground biomass is an important feature of NNBFs, as it plays a role in erosion prevention and recovery (Feagin et al., 2015; Bryant et al., 2019; De Battisti and Griffin, 2020). Our results that biomass did not differ within the top 90 cm of sediment contrasts previous findings (Conn and Day, 1993) which have constrained sampling to 30 cm from the sediment surface (Stevenson and Day, 1996; Nordstrom et al., 2018). The importance of biomass >30 cm within a dune is relevant for post-storm recovery of foredunes as well as during-storm erosion resistance. Depending on the extent of erosion, belowground biomass can be exposed at depths commensurate with the height of an escarpment. Following a storm event, this exposed biomass, as well as vegetation landward of the escarpment, acts as a reservoir of living plant material capable of vegetatively growing (e.g., rhizomes) and reproducing in response to deposition from slumping and avalanching sediment from the dune itself, or aeolian sediment deposition from the beach (Hesp and Martinez, 2007). With adequate sediment supply and low disturbance frequency, dune vegetation at the edge of an escarpment colonizes sediment and facilitates the recovery of the dune. Although sediment supply is a prerequisite for post-storm recovery, this process is mediated by species-specific differences in burial response and lateral growth, both of which are influenced by species composition. For example, rhizome length varies by species, with *Ammophila breviligulata* exhibiting longer rhizomes than the common dune grasses *Uniola paniculata*, *Panicum amarum* and *Spartina patens* (Walker and Zinnert, 2022). Lateral growth rates also vary among species. *Uniola* *paniculata* rhizomes can grow between 0.6 - 1.8 m $yr^{-1}$ and exhibit high variability in response to sediment supply (Hester and Mendelssohn, 1991), whereas *Ammophila breviligulata* rhizome growth rates can be as high as 2 - 3 m $yr^{-1}$ (Woodhouse et al., 1977).

The importance of elevation for multiple biotic variables (e.g., living and non-living belowground biomass, soil organic matter, total living cover and species richness) highlights the close coupling between geomorphology and plant biology. Elevation, distance from shoreline and beach slope determine the extent of wave run-up and collision at the dune (Pries et al., 2008). This control on wave forces exposes plants at lower elevations (primarily pioneer species and dune grasses; Snyder and Boss, 2002; Lonard and Judd, 2011) to more frequent disturbance, altering the plant community and successional stage (Ehrenfeld, 1990). At our study sites, bare sediment, low vegetative cover and the presence of pioneer species like *Cakile edentula* at the dune toe typify early-successional stages (Table 1). Increased cover, species richness and the presence of lianas and shrubs at the dune crest/back indicate longer periods of post-disturbance stability and later successional stages (Ehrenfeld, 1990), even among managed sites.

Complexity and spatial heterogeneity in aboveground community composition has consequences for belowground structure. Species differ in belowground allocation and structure (Charbonneau et al., 2017; de Battisti and Griffin, 2020; Walker and Zinnert, 2022), resource acquisition (Reijers et al., 2020), disturbance response (Brown and Zinnert, 2018; Lee, 1995) and competitive/facilitative interactions (Harris et al., 2017; Brown et al., 2018), which ultimately determine the functional role of belowground dune composition and erosion resistance (Feagin et al., 2019). Species composition was spatially variable from site to site and across the dune profile. Planting within the last 5 years at managed sites (BSV, PIV-R, DRV) were evident through abundance of *Ammophila breviligulata*, often resulting in large nearly-monocultural patches on the dune. *Ammophila breviligulata* was less common on the dune face at unmanaged sites, where the common dune grasses *Uniola paniculata*, *Spartina patens* and *Panicum amarum* were dominant. FRF-S, an accretionary, unmanaged site (Brodie et al., 2019) was dominated by the invasive *Carex kobomugi* and the dune building shrub *Iva imbricata* (Woodhouse, 1982). Unmanaged sites also exhibited dominance by lianas at the crest, a pattern we did not observe at the managed sites. This pattern may be an artifact of erosion and recovery of the dune face. Following severe erosion, seral-stage lianas commonly found in the dune back and swale (e.g. *Vitis labrusca*, *Smilax bona-nox*, *Parthenocissus quinquefolia*, *Lonicera japonica*) occupy a new position at a dune crest created by the loss of seaward dune volume and this process can contribute to sudden transitions between dune plant communities across the dune profile. Plant communities can also experience sudden transitions where elevation-mediated gradients in stressor exposure and resource availability exist across a dune (Young et al., 2011).

Elevation affects water table depth from the sediment surface (Vick and Young, 2011; Smith and Day, 2017), creating niches of moisture availability on a dune occupied by different species and functional types (Hester and Mendelssohn, 1989; Bissett et al., 2014). Species that share habitat on the dune toe and face generally differ in belowground biomass amount and composition. For example, annual forbs generally have lower belowground biomass and little to no rhizomes compared to perennial grasses (de Battisti and Griffin, 2020). These dominant dune grasses, although similar in functional form (e.g. *Ammophila breviligulata, Spartina patens, Uniola paniculata*), exhibit differences in belowground traits (i.e., average root diameter, rhizome length and number, root tensile strength; Walker and Zinnert, 2022). Higher species richness at >50% of our plots suggests interspecific interactions within 0.25 $m^2$ plots occur across the face, crest and back of dunes which influences variation in above and belowground biomass (Franks and Peterson, 2003; Harris et al., 2017; Brown et al., 2018). Because these interactions can alter the amount of above- and belowground biomass dune species produce, they may have consequences for modeling and predicting erosion resistance.

Our study shows that species composition varies within a narrow range, influencing the distribution of biomass and fine root surface area within a dune (Walker and Zinnert, 2022). One site (FRF-S) had extremely high belowground biomass and fine root surface area due to high cover of *Carex kobomugi.* This site was an outlier in both the amount of belowground biomass present and the presence of invasive *Carex kobomugi*. Non-native *Carex kobomugi,* has higher root:shoot ratio and biomass than native *Ammophila breviligulata* (Charbonneau et al., 2016). New Jersey foredunes dominated by *Carex kobomugi* experienced lower erosion rates during Hurricane Sandy, a finding attributed to the high amounts of belowground biomass produced by the species (Charbonneau et al., 2016). Although erosion resistance by an invasive species with more belowground biomass than natives may be attractive to coastal managers and homeowners, care must be taken when weighing the multiple ecosystem services provided by non-native dune vegetation (Wootton et al., 2005). Non-native and invasive species typically out-compete native species, reducing native plant richness and negatively impacting native biota (Wootton et al., 2005; Ceradini & Chalfoun, 2017).

Disturbance also affects biomass allocation within and among species. Following sediment burial, *Ammophila breviligulata* decreases aboveground and increases belowground allocation, whereas *Spartina patens* and *Uniola paniculata* exhibit the opposite response (Brown and Zinnert, 2018). Species-specific disturbance responses also vary with distance from the shoreline and elevation. Following simulated loss of aboveground biomass, dune grasses

(*Elytrigia juncea* and *Ammophila arenaria*) recovered at different rates based on position across the beach-dune profile (Reijers et al., 2020).

The strong relationship observed in our study between total vegetative cover and living belowground biomass has potential implications for coastal management, modeling and predicting erosion resistance. Aboveground biomass as a predictor of living belowground biomass did not perform as well as total living cover, likely due to different resource allocation strategies and diverse plant communities in the region (Simpson et al., 2019; Walker and Zinnert, 2022). Our finding that site differences in cover, species richness and management effects on composition arose with increasing sampling frequency demonstrates the need for increased belowground sampling to >60cm depths across a range of dunes. The relationship between aboveground cover and belowground biomass coupled with site differences in total cover when analyzed across the full dune suggest that belowground biomass may exhibit site and/or management differences with additional sampling. Aboveground percent cover can be easily quantified via remote sensing and data analysis technologies (i.e., affordable unmanned aerial vehicles (UAVs), LiDAR, machine learning) that allow for rapid, relatively inexpensive surveys of vegetation (Laporte-Fauret et al., 2020). These methods are also less invasive as they do not require the deployment of machinery or people directly onto a dune, reducing trauma on the aboveground and belowground organs of dune vegetation. Future research investigating relationships between remote estimations of cover and belowground biomass can provide quick and inexpensive tools for assessing the protective function of different dunes.

**Conclusions**

Under future climate change scenarios, protective coastal NNBFs will be subjected to rising sea levels and more frequent and intense storms. Our study is an important step toward characterizing managed and unmanaged dunes in a region that experiences dune and beach erosion and increasing rates of sea level rise. Using vibracoring as a novel sampling method, we collected belowground biomass at depths greater than those sampled in the literature and demonstrated that biomass did not differ within 90 cm of the sediment surface. Living belowground biomass was highly variable by site with few differences among sites, and no difference between managed and unmanaged dunes. Elevation had a significant effect on multiple above and belowground variables (e.g. fine root surface area, soil organic matter content, total living cover and species richness), likely as a result of niche segregation along a gradient of abiotic stressors (e.g. aeolian deposition, depth to water table, salinity3) and varying stages of succession across a dune profile in response to erosion and recovery. Analyses of plant community differences between management histories and among dune positions and sites were affected by sampling effort, a finding that speaks to the importance of high variability in living cover and species composition and the intensive sampling required to account for this variability. We also found that total living cover is a strong predictor of living belowground biomass, a relationship that may be used to rapidly estimate living belowground biomass in the future. These findings will be incorporated into numerical models predicting dune growth and erosion in collaboration with the U.S. Army Corps of Engineers, Engineer Research and Development Center and Virginia Institute of Marine Science. Modeling, expanded sampling of belowground biomass patterns and continued surveillance of dune plant community changes will be necessary to understand how these systems respond to sea level rise and climate change in order to maintain the ecosystem services they provide.

## Figures

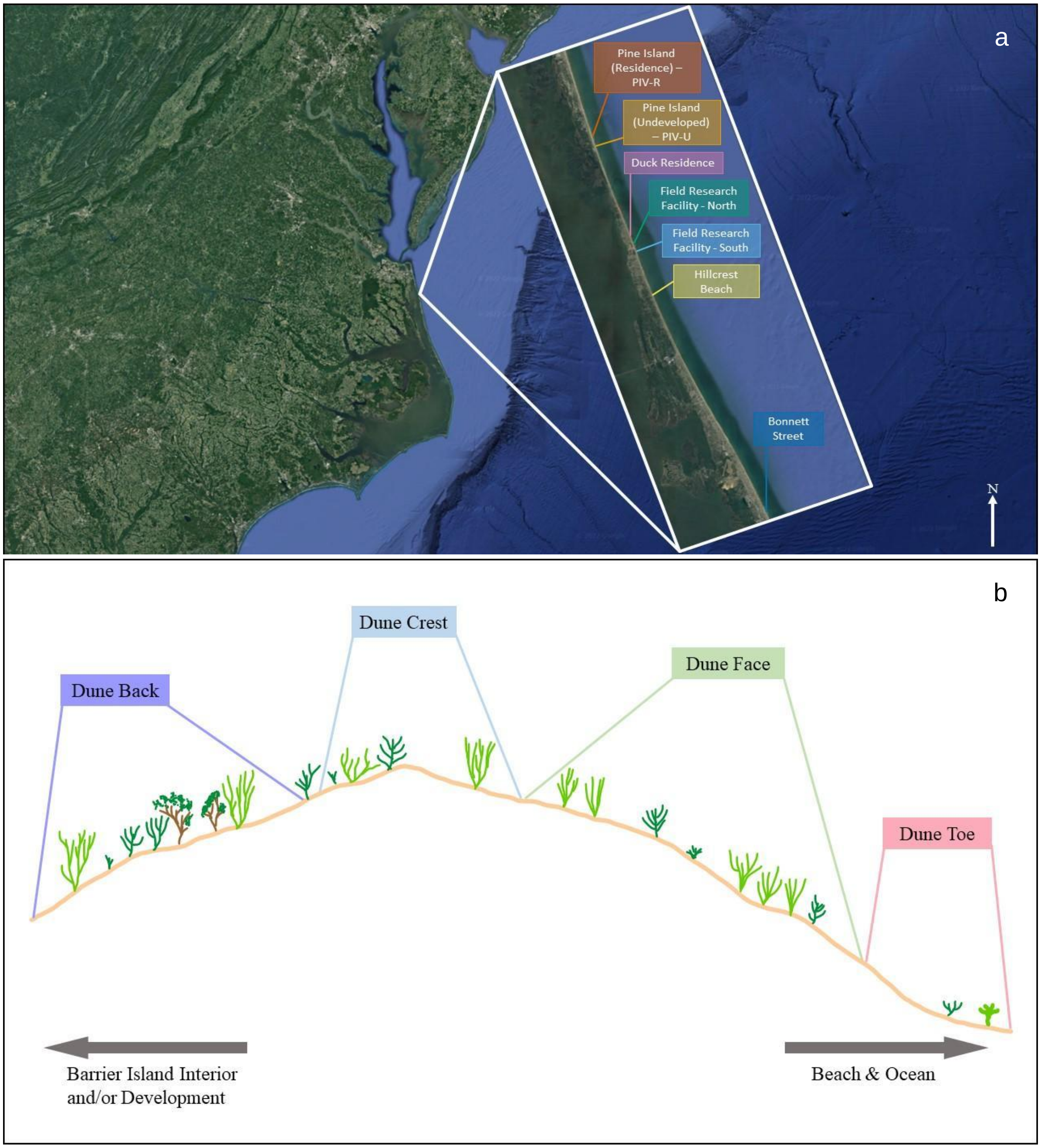


Figure 1a) The Outer Banks of North Carolina. From least- to most-managed the sites are as follows: Pine Island (Undeveloped) (PIV-U), Field Research Facility - North (FRF-N), Field Research Facility - South (FRF-S), Hillcrest Beach (HBV), Bonnet Street (BSV), Pine Island (Residence) (PIV-R), Duck Residential (DRV). 1b) Conceptual diagram of a hypothetical dune profile showing the dune toe, face, crest and back.

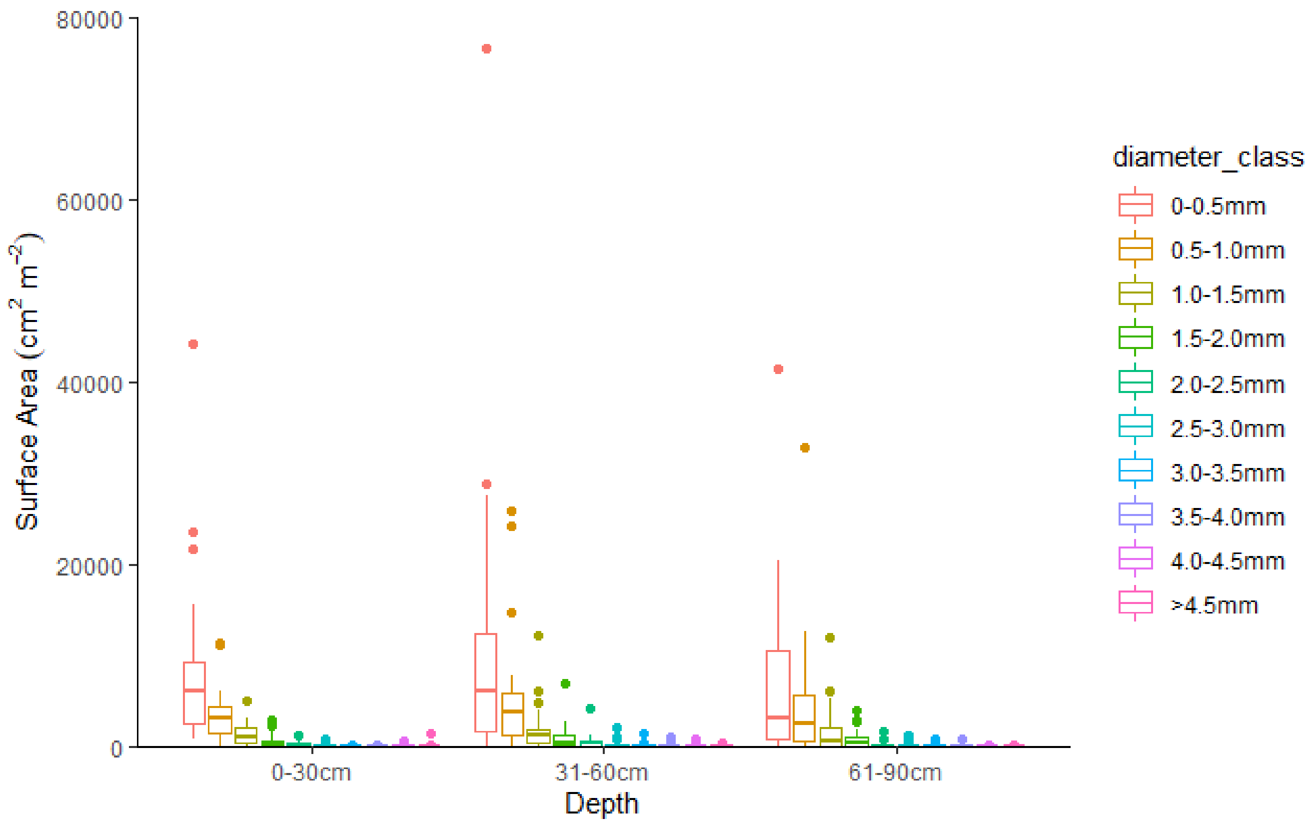

Figure 2) Distribution of root surface area across root diameter classes and depths. Highest surface area occurred in the finest diameter class.

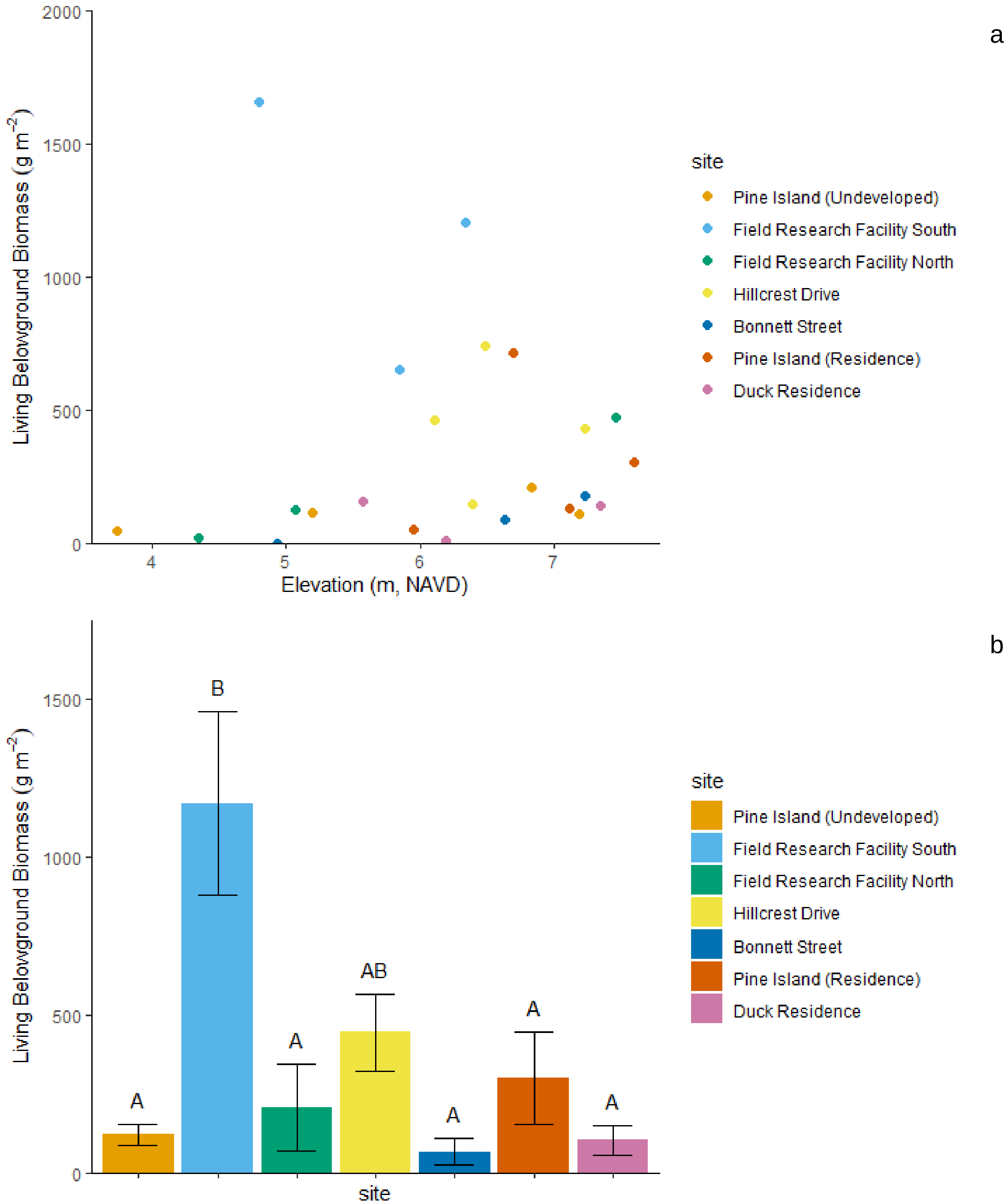


Figure 3a) Relationship between elevation and living belowground biomass across all sites. Sites that share a letter are not significantly different ($p < 0.05$). Sites are arranged left to right from least to most managed. 3b) Living belowground biomass ± standard error.

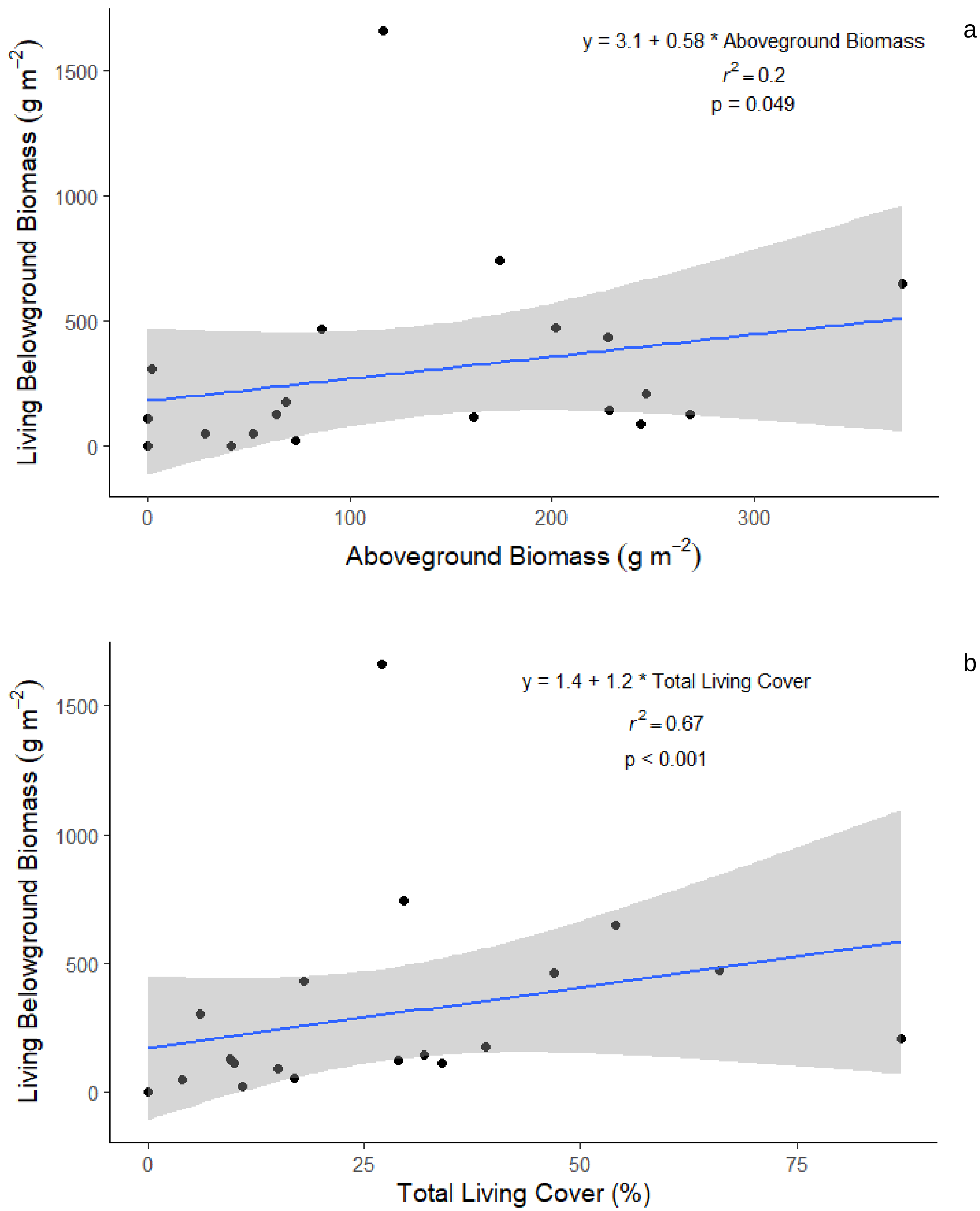


Figure 4a) Simple linear regression between aboveground biomass and living belowground biomass, and 4b) total living cover and living belowground biomass across all sites.

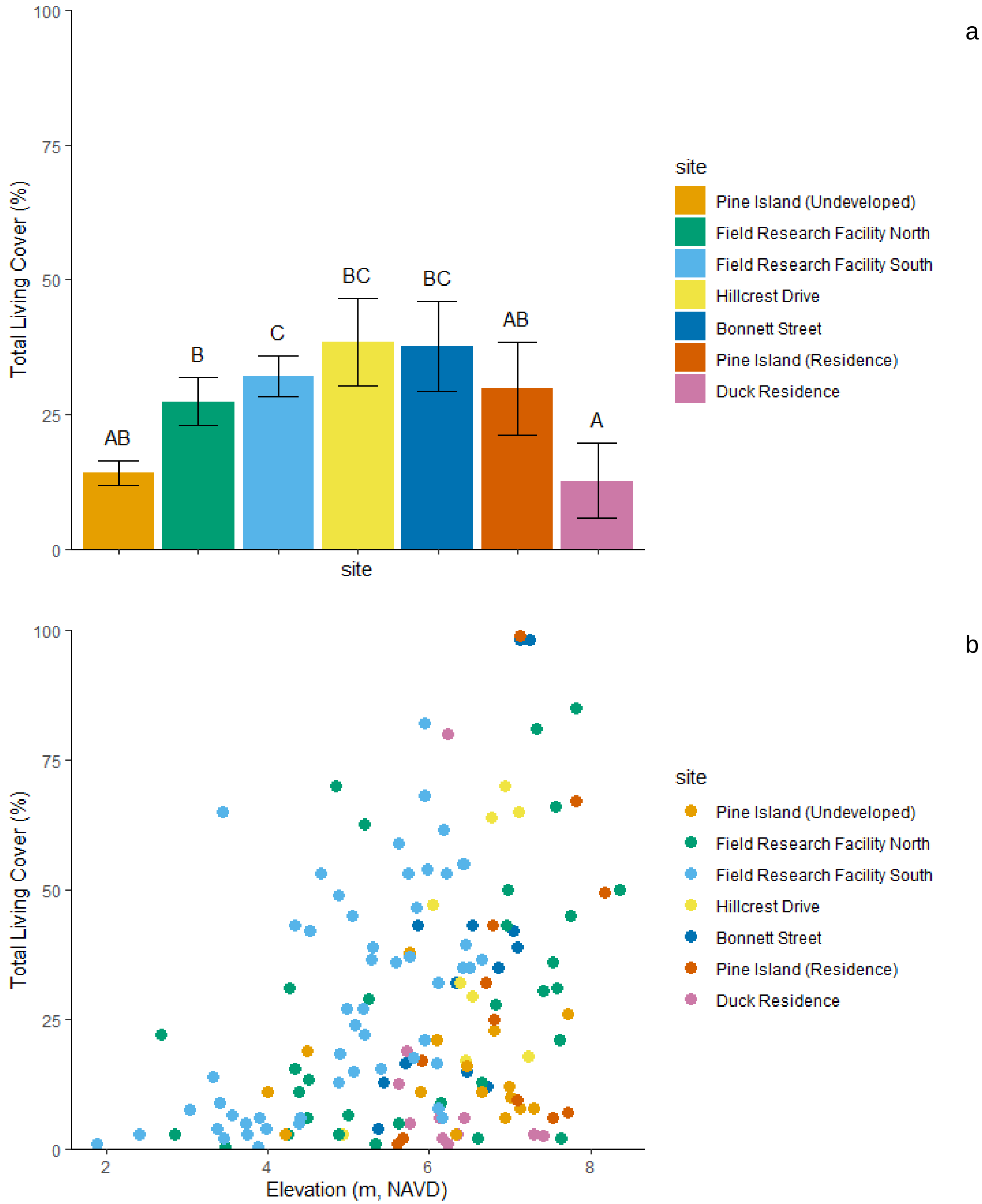


Figure 5a) Total living cover ± standard error. Sites that share a letter are not significantly different ($p < 0.05$). Sites are arranged left to right from least to most managed. 5b) Relationship between total living cover and elevation.

Table 1. Dominant species at each dune position within each site based on Importance Values (in parentheses). Letters denote plant functional type (G: graminoid, F: forb, L: liana, S: shrub). Sites are arranged top to bottom from least to most managed.

| Site | Toe | Face | Crest |
|---|---|---|---|
| Pine Island - Undeveloped | G ~ *Uniola paniculata* (300) | G ~ *Uniola paniculata* (82)<br>G ~ *Panicum amarum* (77)<br>F ~ *Oenothera humifousa* (62) | L ~ *Vitis labrusca* (143)<br>G ~ *Ammophila breviligulata* (62)<br>F ~ *Solidago sempervirens* (50) |
| Field Research Facility - South | F ~ *Cakile edentula* (251)<br>G ~ *Spartina patens* (49) | S ~ *Iva imbricata* (78)<br>G ~ *Carex kobomugi* (69)<br>G ~ *Panicum amarum* (51) | S ~ *Iva imbricata* (57)<br>G ~ *Spartina patens* (55)<br>G ~ *Uniola paniculata* (35) |
| Field Research Facility - North | F ~ *Cakile edentula* (300) | G ~ *Panicum amarum* (120)<br>G ~ *Spartina patens* (54)<br>G ~ *Uniola paniculata* (51) | G ~ *Spartina patens* (129)<br>L ~ *Smilax bona-nox* (66)<br>L ~ *Parthenocissus quinquefolia* (37) |
| Hillcrest Beach | G ~ *Uniola paniculata* (300) | G ~ *Panicum amarum* (71)<br>G ~ *Uniola paniculata* (56)<br>G ~ *Spartina patens* (40) | L ~ *Parthenocissus quinquefolia* (79)<br>L ~ *Lonicera japonica* (73)<br>L ~ *Smilax bona-nox* (52) |
| Bonnett Street | G ~ *Ammophila breviligulata* (300) | G ~ *Ammophila breviligulata* (66)<br>G ~ *Panicum amarum* (56)<br>F ~ *Heterotheca subaxillaris* (42) | G ~ *Spartina patens* (86)<br>F ~ *Heterotheca subaxillaris* (68)<br>F ~ *Solidago sempervirens* (28) |
| Pine Island Residential | | G ~ *Ammophila breviligulata* (243)<br>F ~ *Cakile edentula* (57) | G ~ *Ammophila breviligulata* (102)<br>S ~ *Iva imbricata* (90)<br>F ~ *Heterotheca subaxillaris* (47) |
| Duck Residential | G ~ *Ammophila breviligulata* (170)<br>F ~ *Conyza canadensis* (130) | G ~ *Ammophila breviligulata* (183)<br>G ~ *Panicum amarum* (100)<br>F ~ *Cakile edentula* (17) | G ~ *Ammophila breviligulata* (154)<br>G ~ *Spartina patens* (74)<br>F ~ *Heterotheca subaxillaris* (48) |

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**Vita**

Andrew Eugene White was born in Heidelberg, Germany to David and Angie White in 1994. His family moved to Fort Monroe, Virginia in 1996 where he first saw the Chesapeake Bay, sandy beaches and dunes. Andrew lived in Newport News, followed by Toano, Virginia, the town he calls home. In 2013, he graduated from Warhill Highschool in Lightfoot, Virginia before pursuing a Bachelor of Arts Degree in English Literature and Language at Virginia Tech, receiving his B.A. in 2017. Unsatisfied with job opportunities available in Richmond, Virginia, Andrew began taking classes at J. Sargent Reynolds Community College and working in fiscal administration on Virginia Commonwealth University's Medical Campus of Virginia. During this time, he also became a Virginia Master Naturalist with the Riverine Chapter of the Virginia Master Naturalists, with whom he also volunteered as an Audio-Visual Technician and basic training committee member. In 2019, Andrew began volunteering in Dr. Julie Zinnert's Coastal Plant Ecology Lab at VCU, where he enrolled as a Master Student for the Spring 2020 semester. That summer he was given the opportunity to work as a research intern at the U.S. Army Engineer Research and Design Center and Coastal Hydraulics Laboratory at the Field Research Facility in Duck, North Carolina. He continued this internship under the mentorship of Dr. Nicholas Cohn through 2021. Andrew will complete his Master's Degree in the summer of 2022 and will pursue a career that allows him as much outdoor time as possible.

**Appendix**

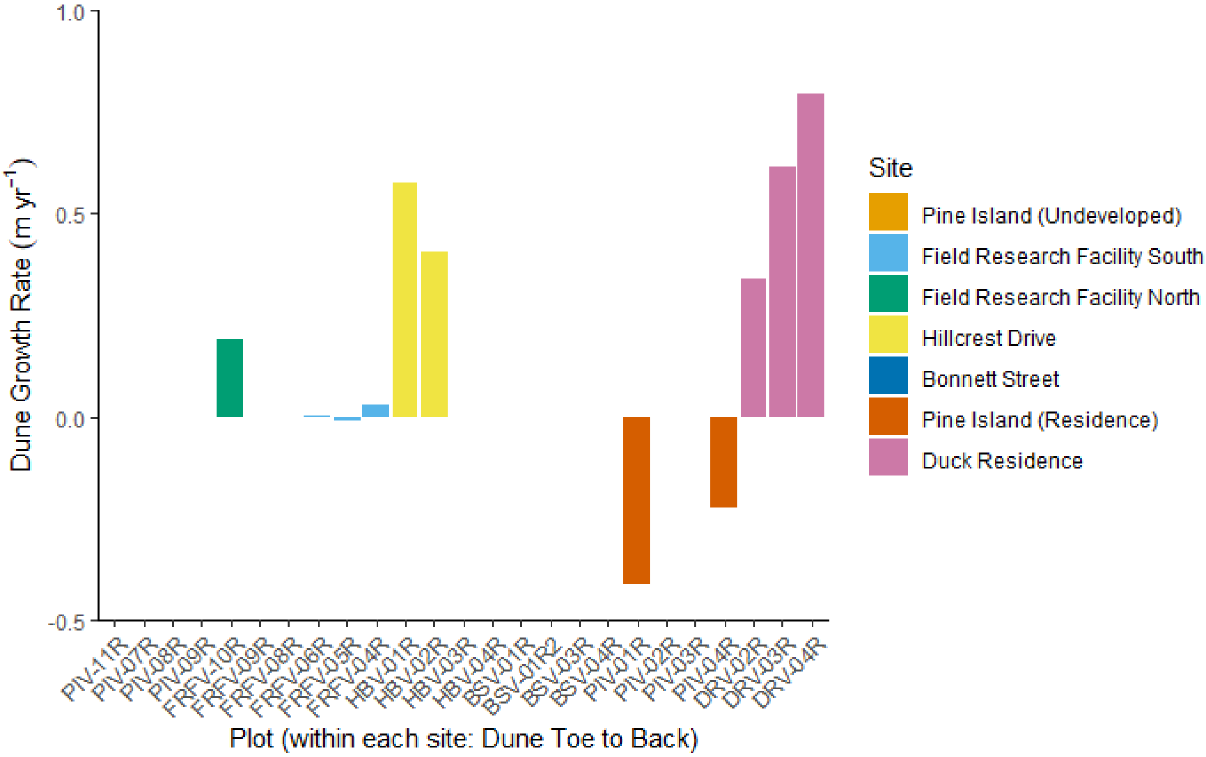


Figure S1. Net accretion and erosion at coring sites. Sites are arranged left to right from least to most managed. Plots within each site are arranged left to right from dune toe to dune crest/back. Measurements at some sites were unavailable due to a lack of usable data on the dune face, crest and back.

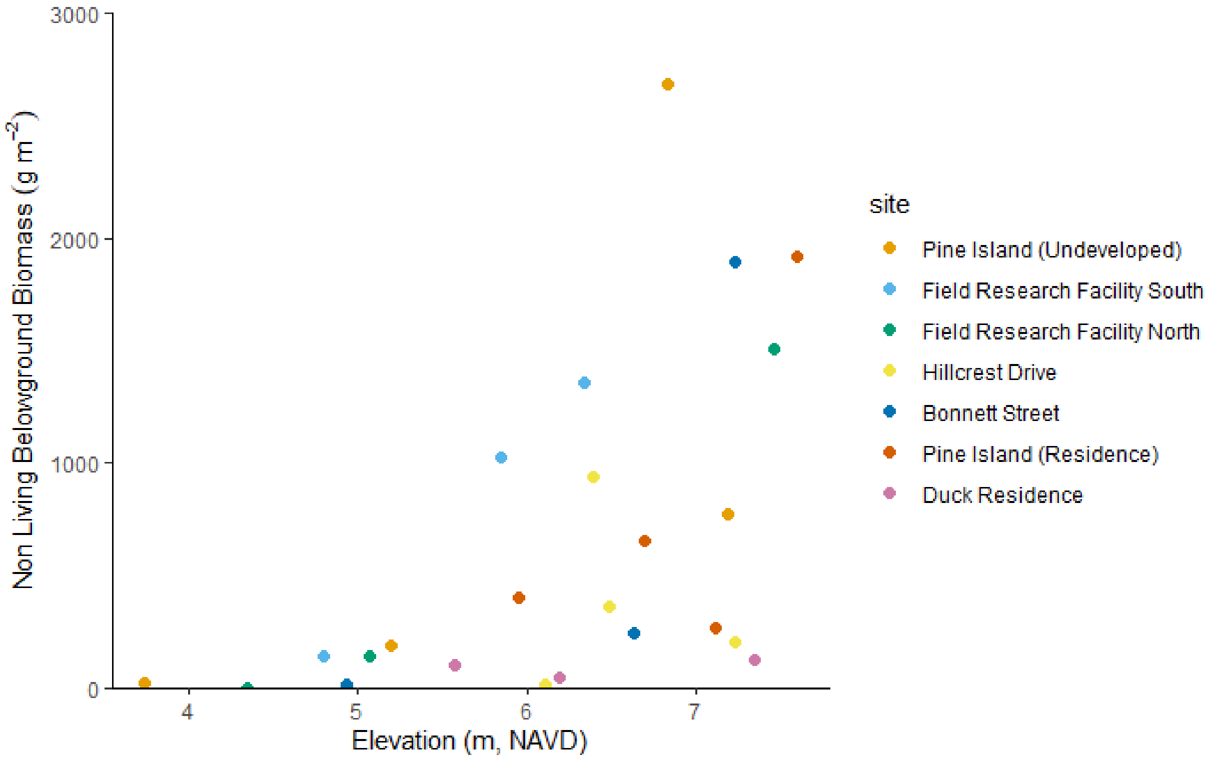


Figure S2. The relationship between non-living biomass and elevation across all sites.

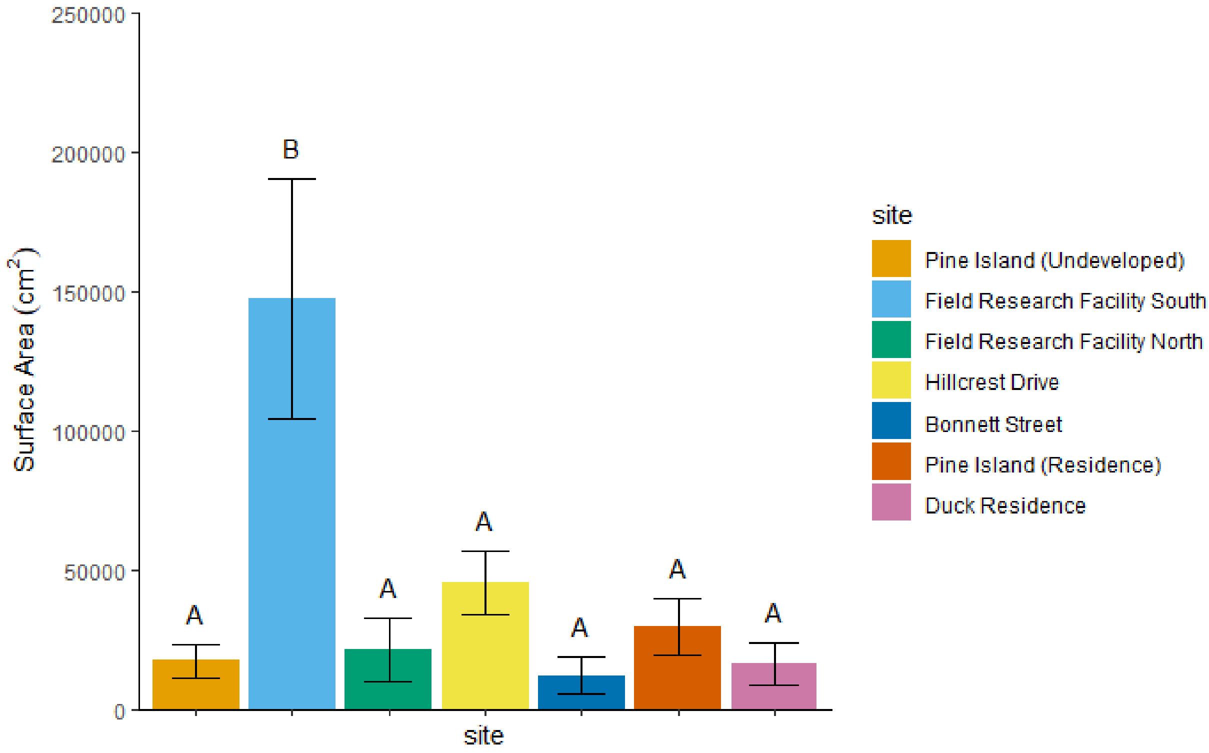


Figure S3. Mean fine root (<1mm diameter) surface area ± standard error. Sites that share a letter are not significantly different ($p < 0.05$). Sites are arranged left to right from least to most managed.

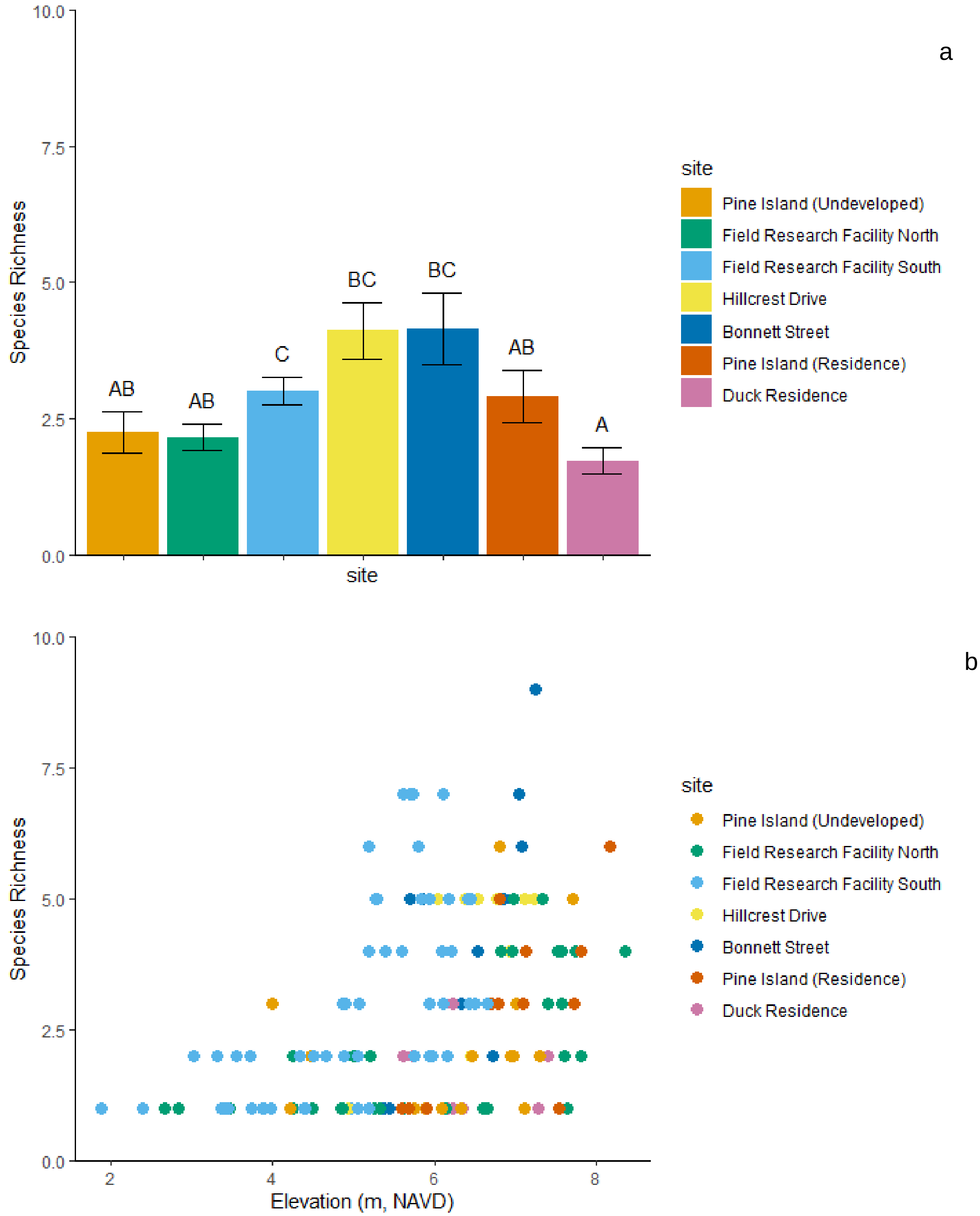


Figure S4a) Species richness ± standard error across sites. Sites that share a letter are not significantly different ($p < 0.05$). Sites are arranged left to right from least to most managed. S4b) Relationship between elevation and species richness across all sites.

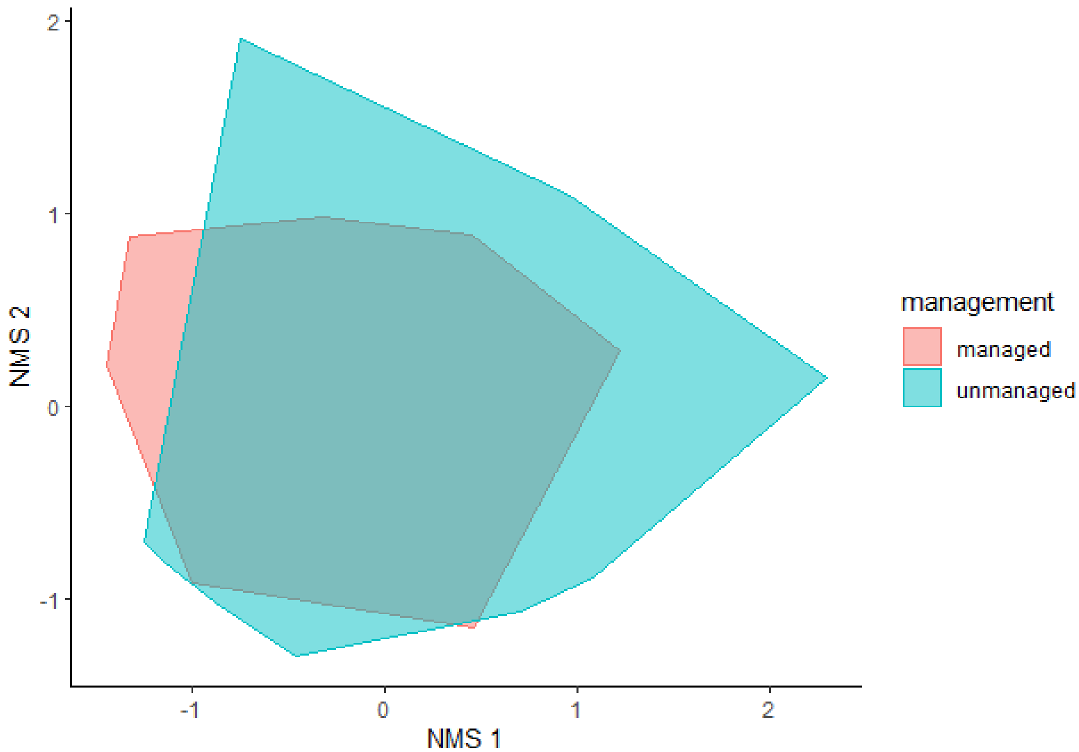


Figure S5) Differences in plant community between managed and unmanaged dunes visualized with Non-Metric Multidimensional Scaling (stress = 15.3).

Table S1. Pairwise comparison of MRPP results of species composition between dune positions across all sites. Bold indicates significant difference with a Bonferroni corrected α = 0.0083.

| Dune position comparison | T | *P* |
|---|---|---|
| **Toe — Face** | **-4.43** | **0.002** |
| **Toe — Crest** | **-7.63** | **<0.001** |
| **Toe — Back** | **-6.47** | **<0.001** |
| **Face — Crest** | **-9.93** | **<0.001** |
| **Face — Back** | **-7.91** | **<0.001** |
| **Crest — Back** | **-3.58** | **0.004** |

Table S3. Pairwise comparison of MRPP results of species composition between sites. Bold indicates significant difference with a Bonferroni corrected α = 0.0024.

| Site comparison | T | *P* |
|---|---|---|
| **BSV — FRF-S** | **-4.42** | **0.001** |
| BSV — FRF-N | -3.55 | 0.005 |
| BSV — DRV | -3.88 | 0.004 |
| BSV — HBV | -2.35 | 0.022 |
| BSV — PIV-res | -2.22 | 0.030 |
| **BSV — PIV-und** | **-4.27** | **0.001** |
| **FRF-S — FRF-N** | **-7.30** | **<0.001** |
| **FRF-S — DRV** | **-14.70** | **<0.001** |
| FRF-S — HBV | -1.94 | 0.048 |
| **FRF-S — PIV-res** | **-8.16** | **<0.001** |
| **FRF-S — PIV-und** | **-10.36** | **<0.001** |
| **FRF-N — DRV** | **-9.93** | **<0.001** |
| FRF-N — HBV | -1.55 | 0.077 |
| **FRF-N — PIV-res** | **-8.12** | **<0.001** |
| **FRF-N — PIV-und** | **-7.71** | **<0.001** |
| **DRV — HBV** | **-7.70** | **<0.001** |
| DRV — PIV-res | -3.24 | 0.009 |
| **DRV — PIV-und** | **-7.39** | **<0.001** |
| **HBV — PIV-res** | **-6.93** | **<0.001** |
| HBV — PIV-und | -3.45 | 0.005 |
| **PIV-res — PIV-und** | **-6.79** | **<0.001** |