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The persistence and conversion of coastal foredune and swale vegetation community distributions 63 years later

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Abstract

Vegetation shifts can directly alter habitat dynamics and indirectly impact habitat stability relative to disturbance response. Barrier island dune habitats exhibit spatiotemporally dynamic topography that is affected by vegetation. However, vegetation distribution data can be rare and vegetation persistence is largely unknown such that species turnover over in communities can occur unnoticed. This is true despite concerns and documented cases of woody encroachment related to climate change in these ecogeomorphic habitats where physical stability to resist storm erosion varies with vegetation distribution and density. In 1956 and 1957, the vegetation of Island Beach State Park, NJ, was mapped as a permanent record for subsequent ecological study. In June 2020, we remapped the vegetation of 5.4 of 17 km north to south, seaward of the thicket community boundary. We maintained the same classification system as the historic record, physically mapping vegetation patches via GPS. We quantified changes in thicket, heather, and grass community distribution between the two time periods. Habitat persistence and conversion varied in the 63 years. Heath communities saw 80%–97% habitat loss in conversion to woody thicket. Conversely, thicket community distribution drastically increased, replacing heath where it was previously prevalent. This represents the first known documented instances of woody encroachment for *Morella pensylvanica*. When they did not expand, thicket communities receded landward or underwent turnover to an invasive species. Woody species of interest for dune stabilization occupied areas of similar habitat characteristics. Dune vegetation distribution persistence from 1957 to 2020 was relatively consistent and stable with the exception of heath habitat conversion. Barrier island stability is directly related to vegetation stability such that understanding where community shifts might occur over time can aid in managing and modeling efforts surrounding these dynamic ecogeomorphic habitats.

KEYWORDS

Ammophila breviligulata, barrier island, habitat stability, invasive species, *Morella* and *Myrica*, plant community shift, shrub communities, vegetation distribution, vegetation mapping, vegetation turnover, woody shrub encroachment

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INTRODUCTION

Vegetation shifts can alter community dynamics and structure, in turn affecting topography and disturbance response in ecogeomorphic systems (Fei et al., 2014; Viles et al., 2008). Ecogeomorphic habitats maintain a reciprocal coupling between topographic, geomorphological, and biological processes (Corenblit et al., 2015; Viles et al., 2008). These habitats provide invaluable ecosystem services (Corenblit et al., 2015; Elko et al., 2016; Feagin et al., 2010; Zinnert et al., 2019), which can change with habitat alteration (Janssen et al., 2020; Verhagen et al., 2018). Habitat alteration is expected to increase disproportionately in ecogeomorphic systems given their vulnerability to climate change (IPCC, 2019). For example, increased disturbances will create more opportunities for invasive species establishment (Charbonneau et al., 2020; Fei et al., 2014) and changing temperatures can and have begun to shift community extents (Goldstein et al., 2018; Huang et al., 2018; Zinnert et al., 2011, 2019). Shifting vegetation composition and functional diversity can alert managers to altered susceptibility to future stressors and change (Díaz & Cabido, 2001; García-Mora et al., 1999).

Baseline distribution data are needed to recognize and monitor vegetation community shifts, but are typically not consistently available (Austin, 2002; Austin et al., 2006; Sperandii et al., 2018). Landscape- and habitat-level species distribution data can be rare and invaluable (e.g., Charbonneau et al., 2020; Jackson & Nordstrom, 2019; Martin, 1959). Field surveys (e.g., topographic, vegetation distribution) can be difficult to collect consistently through time, but often do not include vegetation given that mapping techniques in ecogeomorphic habitats are often more geologically focused (Jackson & Nordstrom, 2019; Moore, 2000). Remote vegetation indices (e.g., normalized difference vegetation index, enhanced vegetation index) can be used to infer vegetation distribution where in situ field distributions are missing, but often at too low of a resolution for examining community shifts (Sciandrello et al., 2015; Silleos et al., 2006). Similarly, where vegetation distribution data exist, it must often be necessarily localized to repeat measures of transects over time, as opposed to habitat level (Álvarez-Molina et al., 2012; Charbonneau, 2019; Kuiters et al., 2009; Sperandii et al., 2018). As a result, vegetation community shifts can go unnoticed until a related ecogeomorphic change occurs such as the shifting of a high-barrier island dune system to a low-barrier island dune system (Durán Vinent & Moore, 2014).

Vegetation community distributions in dune habitats are a classic example of succession with implications for storm response. Typically, stress-tolerant grass communities oceanward give way to less stress-tolerant shrub and woody species inland (Cowles, 1899; Maun, 2009). High abiotic stress associated with proximity to the ocean selects for only a handful of species worldwide, which can build and stabilize foredunes as the most oceanward parallel dune ridge (Maun, 2009). Foredune community shifts are of heightened concern given that species vary in their dune-building and stabilizing abilities, ultimately affecting storm response and growth relative to sea level rise (Charbonneau, 2019; Charbonneau et al., 2017; Elko et al., 2019; Hacker et al., 2019). The establishment of dune-building grasses, such as American beach grass (*Ammophila breviligulata*), can facilitate the establishment of less stress-tolerant species and the formation of belted habitat gradients moving inland (Cowles, 1899; Martin, 1959; Maun, 2009).

More sensitive dune species and habitats also play important ecological roles (Griffiths, 2006). Heath habitat, dominated by beach heather (*Hudsonia tomentosa*) in the Mid-Atlantic United States, is a sensitive species that impacts soil hydrology, nutrient availability, and ectomycorrhizal status (Massicotte et al., 2010; Nelson et al., 2011; Skaradek & Miller, 2009; Smith et al., 2004). Heath can create suitable habitat for woody plants, which typically do not survive closer to the ocean (Cowles, 1899; Oosting, 1945; Sharp & Hawk, 1977), and can contribute to natural and managed dune stabilization (Miller, 2002; Miller et al., 2008; Nordstrom et al., 2000; Sharp & Hawk, 1977; Uva, 2003; Wang et al., 2012). Shrubs, like northern bayberry (*Morella pensylvanica*) and beach plum (*Prunus maritima*), can directly and indirectly increase habitat stability, which has created commercial interest in planting these species for managed dune stabilization efforts (Sharp & Hawk, 1977; Shumway, 2000; Wang et al., 2012). However, warming temperatures associated with climate change can increase woody seedling success, causing nonlinear habitat shifts to shrubland from woody encroachment with associated consequences on habitat structure and storm response (Huang et al., 2018; Zinnert et al., 2011, 2016, 2019). Barrier island habitats are highly connected such that management actions on one habitat can positively or negatively impact another (Álvarez-Molina et al., 2012; Díaz & Cabido, 2001; García-Mora et al., 1999).

The objectives of this study were to (1) quantify vegetation persistence versus conversion over 63 years, from 1957 (Martin, 1959) to 2020 at the habitat-level surrounding grass, shrub, and heath dune communities and (2) define the habitat of woody species of interest, *M. pensylvanica* and beach plum (*P. maritima*) for dune stabilization. To date, woody encroachment has been observed in southern wax myrtle (*M. cerifera*) in Virginia and south in the United States, but to our knowledge has not been documented as occurring in *M. pensylvanica* (Huang et al., 2018; Zinnert et al., 2011,

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2016, 2019). Understanding vegetation persistence is necessary for better predicting how barrier island habitats may change over time relative to daily and episodic stressors.

MATERIALS AND METHODS

Study site

Island Beach State Park (IBSP), NJ, is a 17-km Mid-Atlantic sandy shore barrier island sheltering Barnegat Bay. It is a medium grain microtidal environment with total annual precipitation of 127 cm (NJ Gov, 2022). It represents one of the few undeveloped barrier island stretches in the Mid-Atlantic, and the largest undeveloped NJ barrier island reserve and one of the largest in the United States. The park vegetation was extensively mapped between 1956 and 1957 to "provide a permanent record of the vegetation of IBSP in its pre-park-development condition and a descriptive point-of-reference for subsequent ecological study" (Martin, 1959). The park has never undergone beach nourishment and development since this survey has been minimal. The park is divided into a northern and southern natural area and middle recreation area (Figure 1).

Habitats east of the road span partially or fully developed barrier island dune successional gradients containing foredune, swale, secondary, gray or tertiary dune, and/or maritime forest (Maun, 2009). The foredunes are dominated by native *A. breviligulata* or invasive Asiatic sand sedge (*Carex kobomugi*) with few exceptions where poison ivy (*Toxicodendron radicans*) is prevalent (Charbonneau et al., 2017). Invasive *C. kobomugi* arrived in the United States in 1929 at IBSP, and in 1957, *C. kobomugi* was contained to "one exceptionally stable dune" (Martin, 1959; Small, 1954; Wootton et al., 2005). However, it has since spread to multiple

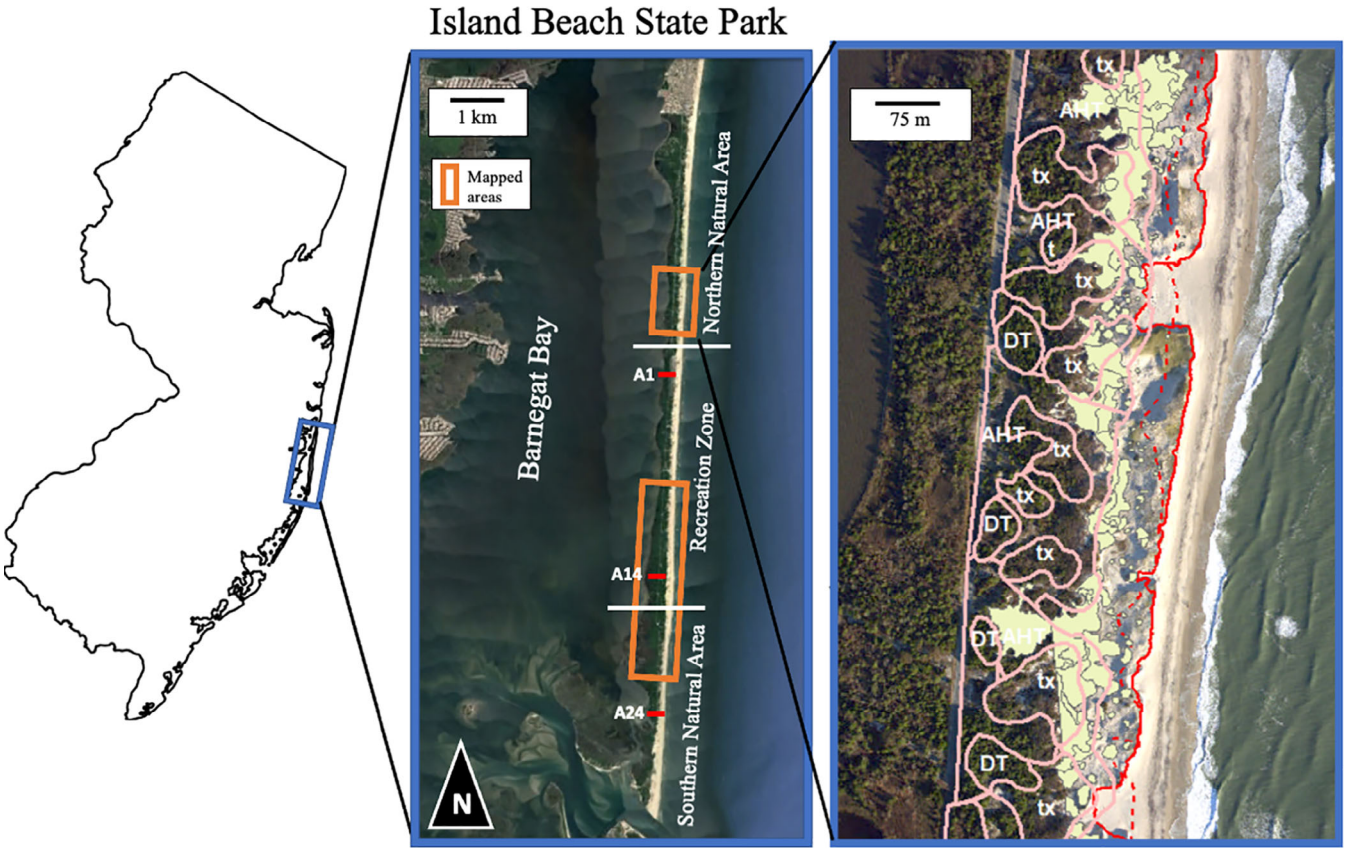


FIGURE 1 Mapped dune habitats of Island Beach State Park, NJ. We collected data from a north (≈1400 north to south) and south (≈4000 m latitudinally, A9 to A20) mapped area denoted with orange boxes. There are 24 beach access foot paths (A1–24; red line denoting A1, A14 and A24) through the dunes. The right image shows a subset of the mapping effort from the north mapped area. Mapping consisted of delineating distinct vegetation patches (yellow polygons) and polylines to compare to mapping data from 1957 (Martin, 1959). We digitized the mapping data from Martin (1959), represented by the pink outlines. These polygons are labeled per his patch categorization designations, which guided his and our subsequent mapping efforts. Here, t and tx denote low xeric thicket, DT represents low dune thicket, and AHT denotes dunegrass-beach heather-high thicket; the full list of Martin's habitat and vegetation classifications are in Appendix S1. The dashed and solid red line represent the foredune crest in 1957 and 2020, respectively.

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foredune and swale areas all over the park (Charbonneau et al., 2017, 2020). Numerous named as well as unnamed storms have impacted IBSP since 1957, most notably, the Ash Wednesday Storm in March 1962 (Dolan & Davis, 1992) and Hurricane Sandy in October 2012 (Charbonneau et al., 2017; Doran et al., 2013).

Martin 1957 vegetation survey

Some knowledge of relevant details of the methodology of the Martin survey (Martin, 1959), conducted from 1956 through 1957 (referred to as 1957 throughout), is necessary to understand how our survey complements it. Aerial images were used to create a georeferenced map of natural and manmade features to define structural vegetation types as grassland, marsh, herb–shrub mixture, thicket, or woodland, further refined to specific vegetation species and growth forms (Martin, 1959). Vegetation extents were delineated as distinct polygon patches on foot or from clear vantage points where boundaries were visibly observable and referenced to landmarks. Martin delineated a linear boundary between the foredune and beach, but did not explicitly define it or how it was mapped; from this context, we assume this boundary represents the foredune crest (Martin, 1959). More details on the methods of this survey are available in Appendix S1.

Vegetation resurvey

Our goal was to remap vegetation east of the low and high thicket community boundary (referred to as thicket boundary) following Martin (1959). We assumed that these areas would be less impacted by edge effects since they are buffered from the road and paths by forest and thicket communities (Jørgensen & Kollmann, 2009). In June 2020, using ESRI ArcMap on a Trimble GeoExplorer GeoXH 7000 (±10-cm accuracy), we remapped 5.4 km, north to south, 1400 and 4000 m in the northern natural area (referred to as the north-mapped area) and recreation area from beach access path A9 to A20 (referred to as the south-mapped area), respectively (Figure 1). We did not map vegetation patches within 50 m of a beach path as some of these paths did not exist in 1957, and in general, paths likely support increased changes in topography and invasive establishment (Barone et al., 2014; Charbonneau et al., 2020; Jørgensen & Kollmann, 2009).

We mapped the thicket community boundary as polylines and monospecific and heterospecific vegetation patches (i.e., polygons) east of it, noting all nonannual species present (Silberhorn, 1999). We defined vegetation as part of the same patch if it was within 1 m of the closest conspecific (Charbonneau et al., 2017). Most patches were monocultures. For mixed assemblages, we defined a dominant species if it had >50% representation or cover in the mapped area visually. In the foredune, we explicitly mapped vegetation patches that were not *A. breviligulata* given it encompassed 82% of dunegrass community then and remains similarly dominant now (Charbonneau et al., 2017; Martin, 1959). Lastly, we used the most recently mapped extent of *C. kobomugi*, surveyed 2018 (Charbonneau et al., 2020), to examine in which habitats invasions have occurred.

We classified all patches ex situ to align with the definitions in Martin (1959) for herbaceous (*Ammophila*, A; and Heather, Ht) and herb–shrub thicket mixtures (low thicket communities: low-xeric thicket, tx; and low-dune thicket, Dt; Appendix S1). All *M. pensylvanica*-dominated patches are low-xeric thicket (tx) that lack domination by highbush blueberry (*Vaccinium corymbosum*) compared with low-mesic thicket (tm; Martin, 1959). All *P. maritima*-dominated patches are classified as low-dune thicket (Dt). In 1957, approximately half of the existing heath habitat (*H. tomentosa* dominated) was concentrated in our north-mapped area (Martin, 1959); there could have been heath west of our mapped impenetrable thicket boundary, but these instances are considered negligible given they are rare and small in area as indicated by observing the developed canopy aerially (Wright et al., 2014).

Spatial processing and analysis

To ensure spatial accuracy when comparing across the two survey times, we georeferenced the survey map presented in Martin (1959, pp. 5–6; Figure 2) following Favretto (2012) and created shapefiles of the vegetation of interest from the georeferenced map. We processed these data to extract the following:

1. Vegetation habitat areas (in square meters) and width (in meters east to west), both times
2. 2020 Vegetation patch elevations
3. 2020 *M. pensylvanica* and *P. maritima* due east
   a. crest elevation
   b. distance to the crest
   c. distance to the ocean

where distance to the crest and ocean is measured from patch centroids and as quantified characteristics represent numerous biotic and abiotic factors influencing vegetation distributions in coastal dune ecosystems (Cowles, 1899; Martin, 1959; Maun, 2009; Young et al., 2011), where crest elevation is a metric of sheltering. All geospatial analyses

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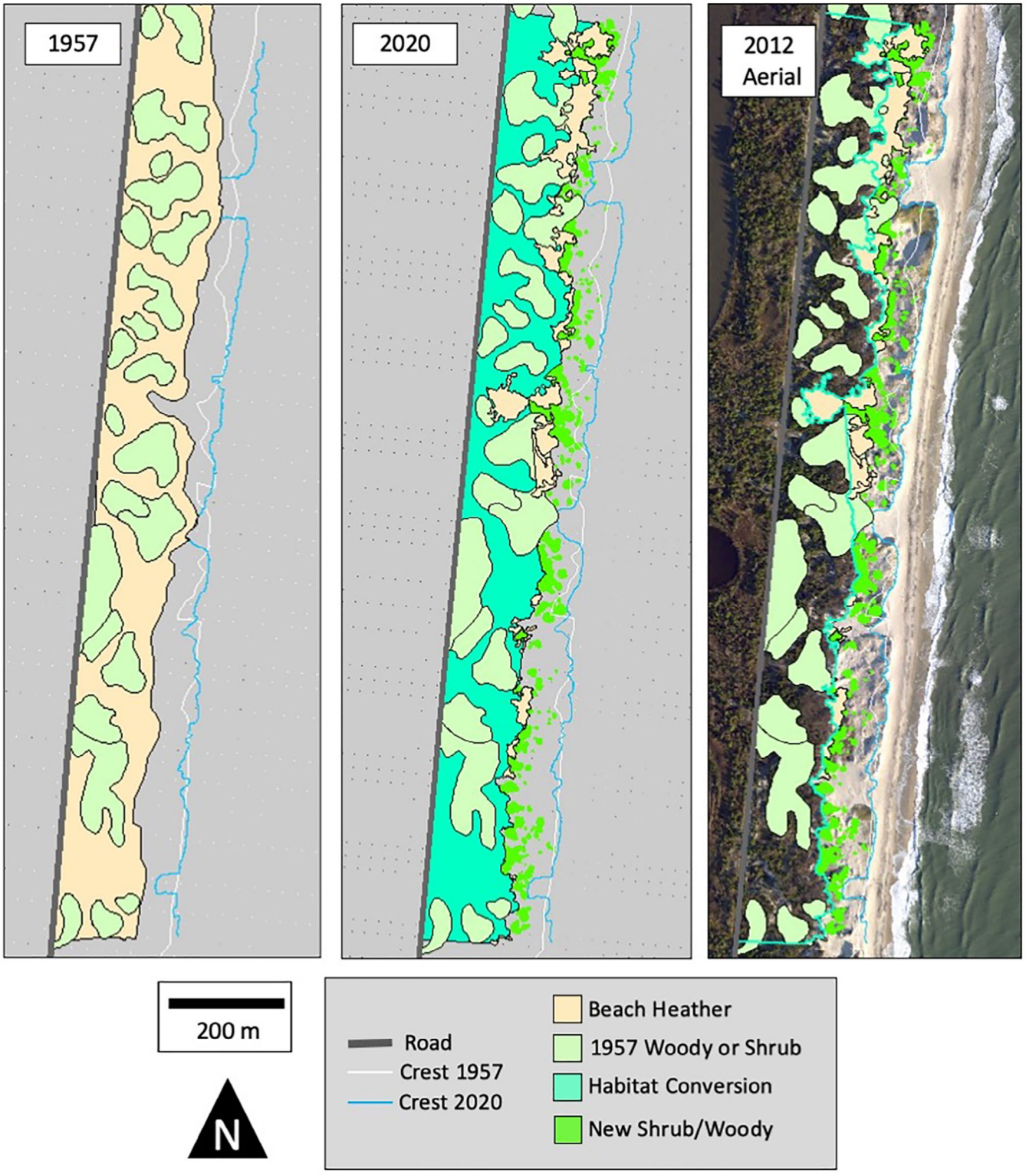


FIGURE 2 Island Beach State Park heath habitat. Heath habitat delineated by Martin (1959) was largely concentrated in the north-mapped area, but by 2020, most of that habitat (≈80%) has been converted to thicket shrub or woody habitat. Woody and shrub habitat has expanded seaward into grassland foredune habitat where *Ammophila* was only previously found (lime green). Note the dense canopy in the aerial (2012), which was previously heath.

were conducted using ArcGIS 10.8 (Environmental Systems Research Institute, 2019). Specific details of spatial processing and data extraction are provided in Appendix S1. Only areas mapped in the same manner in both surveys are compared and we did not attempt to make assumptions regarding when or why changes

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occurred between surveys as this would be purely speculative given the time gap and lack of IBSP elevation data before 2000. For example, we examined thicket habitat boundary recession and expansion by examining east to west thicket habitat width only in the south-mapped area, as this is where there was a clear thicket boundary at both survey times. All means are reported ±SE.

Our analyses largely focus on how the thicket community expanse has changed in area and location. We examine if monoculture patch or woody plant size, a proxy for age (Jørgensen & Kollmann, 2009), varies with distance to the crest via linear regression. To assess whether thicket habitat area differed in the two surveys, in the south-mapped area, we performed a Wilcoxon signed rank test comparing thicket area within access stretches at the two time periods. To examine whether thicket habitat width has changed over the 63 years, we employed an individual mixed model with a nested spatial autocorrelation structure (Charbonneau et al., 2017; Qian et al., 2010); here we test whether thicket transect width, measured every meter as the east to west road to thicket boundary in each north to south beach access stretch (south-mapped area), differs with survey time and beach access as categorical independent variables. In this analysis, beach access is included to account for locally varying abiotic conditions latitudinally (Houser et al., 2008). We used the same model structure to examine if nonoverlapping thicket habitat widths (only present one survey time) categorized as gained versus lost varied if over the 63 years, the foredune habitat underwent recession or progradation, based on crest location; here we necessarily exclude beach access stretches that only had foredune recession (A18–A20) and/or very unbalanced sample sizes between loss and gain (A10, A14, and A16) as including these accesses caused loss of degrees of freedom. All tests are two-tailed with $\alpha = 0.05$ performed with JMP Pro 15.0. Lastly, to try to understand when vegetation shifts might have occurred, we looked through historical Landsat images in Google Earth, which span 1995 to present.

RESULTS

Species encountered

The 2020 vegetation encountered and mapped can be found in Table 1. It was not possible to map landward of the low thicket boundary, which was impenetrably dense and largely heavily underlain with *T. radicans*. This impenetrable boundary was predominantly *M. pensylvanica* laced with *T. radicans* and *Parthenocissus quinquefolia* defined by Martin (1959) as low thicket. In 1957, *T. radicans* patches were only found in the swale and thicket communities (Martin, 1959), but in 2020 were found in the foredune up to the crest or on the downwind slope in multiple instances in the south-mapped area. Diversity was generally low, with a maximum of five perennial or woody species, not including annuals, in heath or shrub habitat.

Heath habitat

In the north-mapped area, the habitat space including or dominated by *H. tomentosa* (Ht or AHt as per Martin, 1959) has shrunk considerably (Figure 2). In 1957,

TABLE 1 Vegetation species encountered and mapped at Island Beach State Park in 2020.

Predominant habitat	Vegetation type	Common name	Scientific name
Foredune or secondary dune	Herbaceous	American beach grass	*Ammophila breviligulata*
		Asiatic sand sedge	*Carex kobomugi*[a]
		Beach pea	*Lathyrus japonicus*
		Poison ivy	*Toxicodendron radicans*
		Purple sand grass	*Triplasis purpurea*
	Herbaceous vine	Virginia creeper	*Parthenocissus quinquefolia*
Heath	Heath	Beach heather	*Hudsonia tomentosa*
Thicket	Shrub	Northern bayberry	*Morella pensylvanica*
		Beach plum	*Prunus maritima*
Maritime forest	Tree	American holly	*Ilex opaca*
		Eastern red cedar	*Juniperus virginiana*
	Shrub	Lowbush blueberry	*Vaccinium angustifolium*

Note: Many additional species were identified, but not included in the mapping effort, such as annuals and other species that are common, but do not define a habitat type (Martin, 1959). Similarly, *A. breviligulata* stands were not explicitly mapped, but used to distinguish habitat bounds.
[a]Invasive species status.

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H. tomentosa covered 110,822 m^2 in a large continuous patch, excluding 20 patches of low and high thicket species (t, tm, DT, and tx) within this heath expanse. By 2020, this area had experienced an 80% reduction split into 15 discontinuous patches. Of the 20% of habitat space remaining, 55% of it was *H. tomentosa* at both time periods (11,831 m^2), and 20% (4302 m^2) and 25% (5295 m^2) are newly colonized heath habitat expanded into previously *A. breviligulata* habitat or low thicket community space, respectively (Figure 2 and Table 2). Visually examining the heath coverage and woody canopy, we can see that the heath habitat had largely been replaced with woody species by 2010 (Appendix S1: Figure S1).

In the south-mapped area, habitat including or dominated by *H. tomentosa* has almost fully disappeared (Figures 1 and 2). In 1957, *H. tomentosa* covered 72,289 m^2 in 23 discontinuous patches seaward of the high and low thicket communities. By 2020, only 3 of the 23 patches

TABLE 2 Changes in heath and woody/thicket habitat (in square meters) from 1957 to 2020.

		Total area				
Mapped area	**Habitat**	**1957**	**2020**	**Lost**	**Stable**	**New**
North	Heath	110,822	21,428	89,394	11,831	9597
	Woody	77,777	175,789	5198	2489	173,300
South	Heath	72,289	9909	70,360	1937	7972
	Woody	490,625	451,328	32,112	443,143	7185

Note: "Stable" represents areas that were the same habitat in both time periods. "New" and "Lost" habitats represent turnover to and from a habitat, respectively.

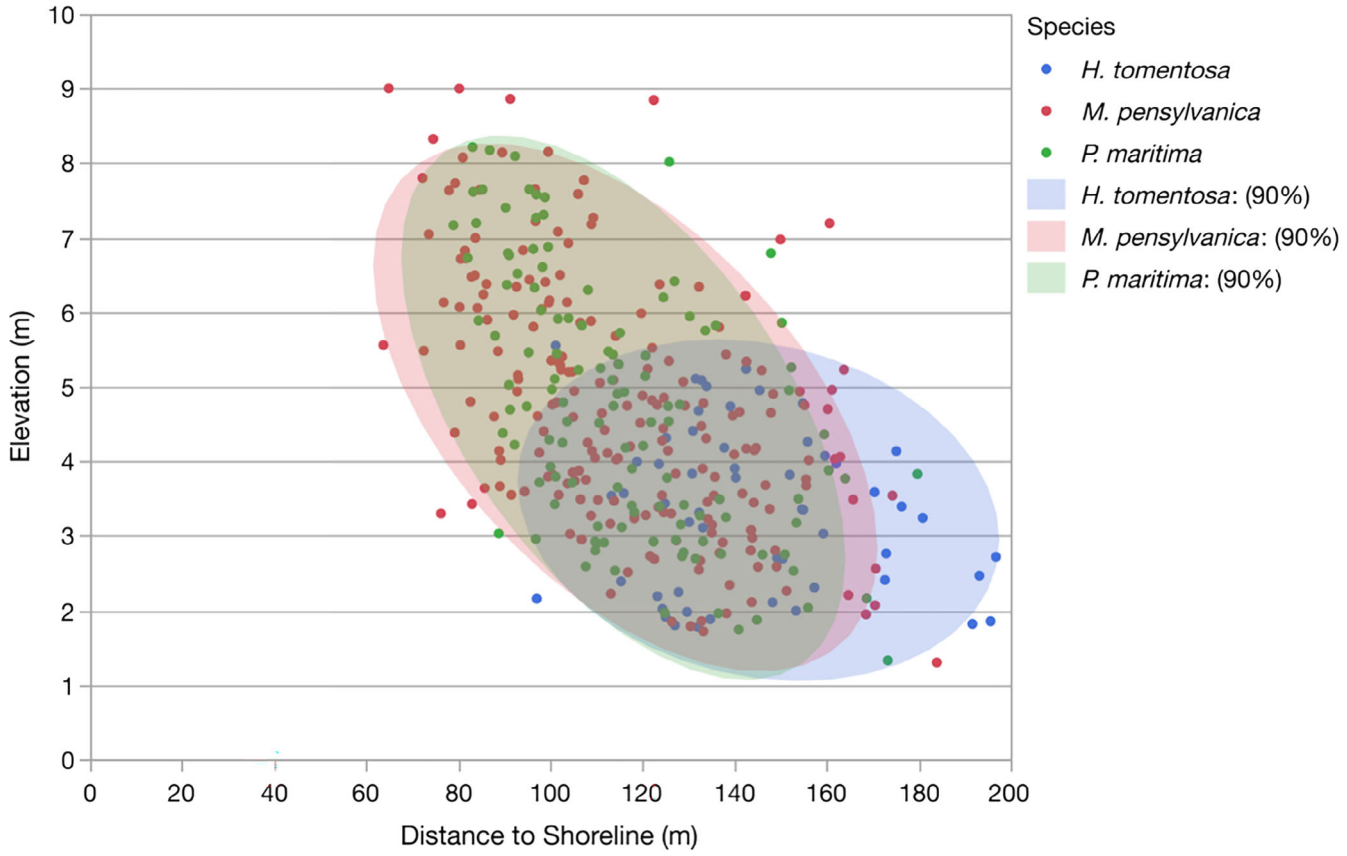


FIGURE 3 Habitat space for thicket species of interest *Morella pensylvanica* and *Prunus maritima*, and *Hudsonia tomentosa* at Island Beach State Park in 2020. Habitat spaces for *M. pensylvanica* and *P. maritima* represent the most oceanward extents for each species as there were individuals further inland in *Toxicodendron radicans*-infested dense thicket. Ellipsoids represent normal bivariate density ellipse encompassing 90% of habitat area. There is more than 50% overlap between the three species.

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remained, representing a 97% reduction in past heath habitat, all of which has become thicket community. In 2020, there was 9909 m^2 of *H. tomentosa*, where 7972 m^2 of this is new habitat that since 1957 (Martin, 1959) has replaced *Ammophila*, thicket, or *V. corymbosum* habitat (Table 2).

The loss of heath habitat in both mapped areas equates to an 87% loss of habitat space across the mapped landscape. A total of 159,756 m^2 previously heath habitat has been converted to shrub or woody thicket community in the 63 years. See Figure 3 for the range of habitat space that *H. tomentosa* was found in with regard to elevation ($\bar{x} = 3.34 \pm 0.14$ m) and distance to the ocean ($\bar{x} = 145 \pm 3.26$ m).

Woody shrub species of interest

In general, *M. pensylvanica* was more prevalent than *P. maritima*, but the two species occupied the same habitat space/conditions (Figure 3, Table 3). They were equally sheltered regarding crest elevation due east; mean elevation differences were $\bar{x} = 0.76 \pm 0.08$ m and $\bar{x} = -2.05 \pm 0.12$ m for instances where the plant location was taller ($n = 93$) or shorter ($n = 233$) than the crest, respectively (Appendix S1: Figure S2). We encountered one or both species in 359 instances, 58 of which were mixed assemblage patches. In more than 50% of the mixed patches, the species were codominant ($n = 36$) or *M. pensylvanica*-dominated ($n = 18$). Patch size was unrelated to patch distance to the crest ($p = 0.76$; Appendix S1: Figure S3). Approximately half of the *M. pensylvanica* and *P. maritima* ($n = 164$) encountered in 2020 in the north ($n = 95$) and south ($n = 74$) mapped areas were established prior to 1957 in areas that were previously *Ammophila* grassland habitat.

In the north-mapped area, woody species have expanded considerably since 1957, replacing 89,394 m^2 of previously heath habitat (Table 2; Appendix S1: Figure S1), while in the south-mapped area, despite 125 new shrub and woody thicket patches east of the thicket boundary, this habitat has shrunk (Figure 4); this result remains true when we exclude (Wilcoxon signed rank; $\bar{x}_{1957} = 44{,}602 \pm 1646\ m^2$, $\bar{x}_{2020} = 40{,}286 \pm 1646\ m^2$, $S = -24.0$, $p = 0.03$) or include the area of the 125 new patches in the analysis ($\bar{x}_{2020} = 41{,}030 \pm 1448\ m^2$, $S = 24.0$, $p = 0.03$). Thicket habitat width varied between beach access stretches ($F_{10,219} = 1.97$, $p = 0.04$), but did not vary between the two survey times ($F_{1,1} = 0.03$, $p = 0.88$; Figure 4; Appendix S1). Similarly, spatial overlap in thicket and woody habitat per beach access stretch was $\bar{x} = 85.9\% \pm 3.13\%$ and in total 443,143 m^2 of the 490,625 m^2 of the 1957 thicket or woody habitat remains today (Table 2). Maximum and mean new thicket patch size was 890 m^2 and $65.5 \pm 10.5\ m^2$, respectively (Figure 4).

Despite less total thicket area in 2020, the habitat did prograde seaward over the years, as 23,074 m^2 encroached into *Ammophila* habitat. This gain was offset by 61,880 m^2 of thicket loss in recession west such that habitat width lost and gained were equivalent across beach access stretches ($F_{4,18} = 0.81$, $p = 0.54$) with variability surrounding if habitat width was lost or gained in the accesses that could be included in the test (Appendix S1). Habitat width change (east–west recession and encroachment) was the loss or gain of 23.4 ± 0.43 m or 0.33 m/year. In general, Landsat images show that the longitudinal location of the habitat boundary oscillated yearly and appears to recess with storm occurrence and prograde during temporal stretches of relative calm (Appendix S1: Figure S4). In the north-mapped area, existing thicket patches appear to have expanded radially, but a lack of a clear thicket boundary in 1957 (Martin, 1959) precluded further analyses (Appendix S1: Figure S1).

TABLE 3 Habitat characteristics of *Morella pensylvanica* and *Prunus maritima*.

Measure	*M. pensylvanica*	*P. maritima*
N	210	120
Elevation (m)		
Minimum	1.30	1.32
Maximum	9.00	8.21
Mean ± SD	4.72 ± 0.12	4.72 ± 0.16
Distance to the ocean (m)		
Minimum	63.77	78.97
Maximum	183.95	179.76
Mean ± SD	116.31 ± 1.80	115.87 ± 2.05
Distance to crest (m)		
Minimum	1.89	2.70
Maximum	108.37	99.38
Mean ± SD	36.91 ± 1.55	36.51 ± 1.87

Note: Data are only shown for instances of a monoculture of the species or mixed assemblage when one species was dominant.

Invasive establishment

Invasive *C. kobomugi* now shares habitat space with both *M. pensylvanica* and *P. maritima*. In the most southern expanse of the south-mapped area (accesses A18–A20; Figures 1 and 4), both *M. pensylvanica* and *P. maritima* support *C. kobomugi* in their understory.

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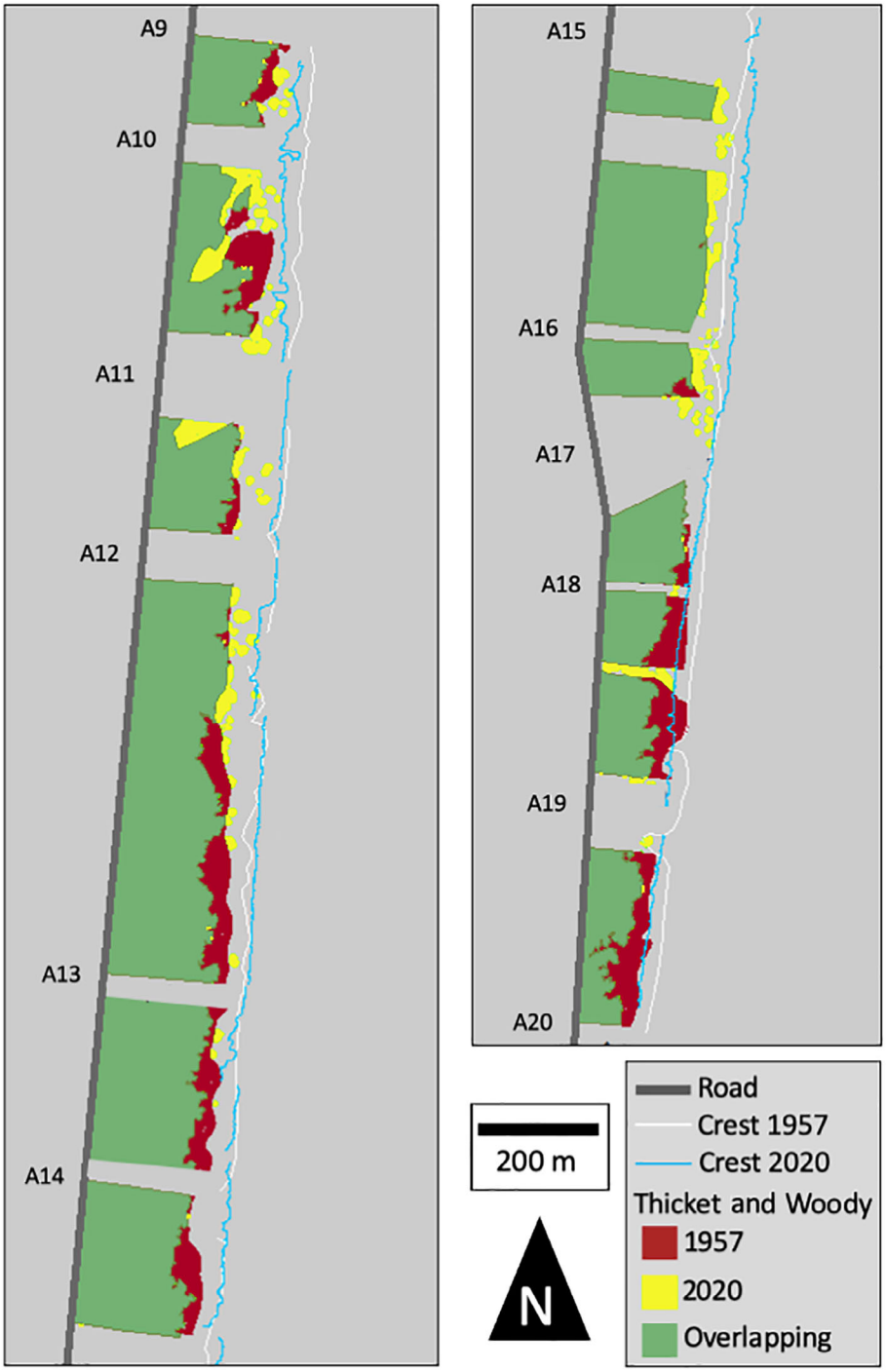


FIGURE 4 Woody and shrub thicket and maritime forest communities east of the park road 1957 as surveyed by Martin (1959) compared with 2020 in the south-mapped area from beach access paths 9–20 (denoted). An access stretch is the latitudinal span between paths denoted by the number of the southern bookending path. Dark green areas represent habitat present in both surveys. Red areas denote where the shrub thicket habitat boundary has receded since 1957. Lime green areas denote seaward expansion of the shrub thicket habitat boundary, since 1957 into *Ammophila* foredune habitat amounting to 23,074 m^2.

These access stretches lost a combined 24,582 m^2 of thicket community since 1957 and *C. kobomugi* and *A. breviligulata* have separately come to occupy 50% of this space each (≈12,000 m^2); these are also the only three access stretches where there was no seaward thicket expansion, only recession (Figure 4). This space is now the foredune, but was previously swale or secondary dune habitat in 1957 (Martin, 1959). Thicket loss cannot be compared with *C. kobomugi* extent in other parts of the south-mapped area. In the north-mapped

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area in 2020, *C. kobomugi* was present in the dunes and backdunes; we did not map its full distribution as this was most recently done in 2008, where it was predominantly exclusively contained to the foredune (Wootton et al., 2005).

DISCUSSION

The large loss of heath habitat supports the occurrence of woody expansion into *H. tomentosa* habitat (Figure 2). Heath to woody conversion (87%) is consistent with more sensitive species being most likely to decline compared with more robust associated species (Sciandrello et al., 2015; Sperandii et al., 2018). Heath species have been documented as capable of surviving moderate shading, but are generally sensitive, establishing and thriving in xeric full sunlight-sheltered backdune areas, almost all of which was converted in the north-mapped area (Griffiths, 2006; Moral et al., 1978; Skaradek & Miller, 2009). Examination of the available Landsat images in the north (Figure 1 & Appendix S1) suggests slow outward radiation of previously disconnected woody patches where overtopping would occur at patch edges. Woody overtopping can reduce ambient light penetration from 98% to only 7% in understories, while also drastically reducing soil and ambient temperatures (Shumway, 2000). Encroachment by nitrogen-fixers in particular, such as *M. pensylvanica*, can also alter the mycorrhizal environment (Egerton-Warburton et al., 2007; Nelson et al., 2011; Shumway, 2000), contributing to heath loss as has been observed in other heath species (Moral et al., 1978). Researchers have suggested that *H. tomentosa* may be capable of staving off competitors by producing allelopathic compounds, but drastic habitat conversion that occurred here do not support this (Skaradek & Miller, 2009).

Woody encroachment of the shrub thicket community oceanward into grassland *Ammophila* foredune habitat is inconsistent. The transgression and regression of the south thicket boundary, with respect to the shoreline, are consistent with patterns of marsh and upland decadal habitat conversion in Virginia (Zinnert et al., 2011, 2019). Differences in habitat conversion across access stretches can be indicative of different localized stress regimes (Charbonneau et al., 2017; Díaz & Cabido, 2001; García-Mora et al., 1999; Zinnert et al., 2019). For example, localized storm impact has been documented as causing thicket death and recession (Griffiths, 2006). Examination of historic Landsat images (Appendix S1: Figure S4) support the notion that past sheltered conditions allowed woody seedlings to become established in areas that would appear too stressful now with respect to shoreline distance and elevation, disconnected woody patches in what is now grassland persist in habitat that was connected thicket in 1957 (Appendix S1: Figure S4). Woody encroachment by *M. cerifera* can occur at nearly 100 m/year expansion (Huang et al., 2018; Woods et al., 2019; Zinnert et al., 2011, 2016, 2019). However, instances of encroachment by *M. pensylvanica* appear to be at a much slower pace in both the north and south (Appendix S1: Figures S1 and S4). Woody encroachment by *M. cerifera* has been linked to altered climatic factors associated with climate change (Woods et al., 2019; Zinnert et al., 2011).

Compared with *M. pensylvanica*, *P. maritima* appears less dominant or likely to become successfully established given its low prevalence. Despite shared habitat space in both survey times, *M. pensylvanica* consistently maintained greater percent cover and frequency of occurrence (Martin, 1959). The presence of *M. pensylvanica* increases the size of *P. maritima* in mixed assemblages (Uva, 2003). However, if this is occurring then it does not appear to confer an advantage that might make it outcompete *M. pensylvanica* (Skaradek & Miller, 2009). Salinity and burial tolerance likely lend to lower *P. maritima* establishment success and thus prevalence. *P. maritima* is categorized as having low salinity tolerance, compared with medium or high salinity tolerance in *M. pensylvanica* (Griffiths, 2006; Martin, 1959; Miller, 2002), which also has a more positive response to burial (Uva, 2003). Both species are documented as having greater than 50% survival success when planted as backdune bare-root-developed seedlings (Sharp & Hawk, 1977). Observed prevalence, dominance, and life histories suggest that attempting to establish *M. pensylvanica* for dune stabilization would be more successful than *P. maritima*.

M. pensylvanica was found in less sheltered areas compared with its southern equivalent, *M. cerifera*. Survivorship of rooted *M. cerifera* cuttings linearly increases with growing distance from the ocean, with survivorship at 0% and >50% when planted 92 and >170 m from the mean high tide line, respectively (Miller et al., 2008). In warmer climes, *M. cerifera* is largely restricted to mesic swales with a documented elevation range of 1.8–2.3 m above sea level (Young et al., 2011). At IBSP, *M. pensylvanica* had a much broader elevation range (1.3–9 m above sea level) and was found much closer to the ocean (64 m) than *M. cerifera* at other sites (200 m; Young et al., 2011). The observed habitat characteristics are also more extreme than previously reported for *M. pensylvanica* (Griffiths & Orians, 2003; Hauser, 2006). For example, at two beaches on Martha's Vineyard, MA, *M. pensylvanica* individuals were not found closer than 25 m from the crest (Griffiths & Orians, 2003), but at IBSP, 34% ($n = 74$) of the *M. pensylvanica* encountered was less than 25 m from

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the crest. Landsat images suggest that these individuals may be older and more established, thus more robust to short-term change (Appendix S1: Figure S4). These results suggest that *M. pensylvanica* planting efforts might be more successful for dune stabilization than attempts with *M. cerifera* in their overlapping ranges (Silberhorn, 1999; Woods et al., 2019).

CONCLUSIONS

These results in total suggest that the extent of barrier island dune vegetation communities (heath, shrub and woody thicket, and grassland) are relatively persistent over multiple decades, unless acted on by forces beyond the normal stress regime. Forces outside of the normal stress regime include (1) woody expansion in *Morella* (Huang et al., 2018; Woods et al., 2019; Zinnert et al., 2011, 2019), (2) storm events shifting topography in directions favoring plants with different life history strategies (Durán Vinent & Moore, 2014), (3) invasive species establishment (Charbonneau et al., 2020), (4) shifting community distributions latitudinally (Goldstein et al., 2018), or (5) anthropogenic habitat alterations (Elko et al., 2016; Jackson & Nordstrom, 2019). In the 63 years, habitat that was shrub and woody in 1967 largely persisted to 2020 and expanded beyond its 1957 boundaries to replace heath habitat; woody conversion of heath habitat is most prevalent in the north-mapped area. Both woody thicket species, *M. pensylvanica* and *P. maritima* are capable of surviving in less sheltered conditions than would be expected. Locally, the woody thicket community boundary either recessed landward and prograded oceanward, being replaced by or replacing foredune herbaceous *Ammophila* or its invasive sedge counterpart, respectively. Thicket community replacement by invasive establishment is most apparent in the south-mapped area. By identifying where community shifts have occurred in the past, we can better predict where they may occur and how this will impact storm response in the future (IPCC, 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Charbonneau et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.21347844.v1.

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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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