


# Connectivity in coastal systems: Barrier island vegetation influences upland migration in a changing climate

Julie C. Zinnert<sup>1</sup>  | Stephen M. Via<sup>2</sup> | Benjamin P. Nettleton<sup>1</sup> | Philip A. Tuley<sup>1</sup> |  
Laura J. Moore<sup>3</sup> | Jon Anthony Stallins<sup>4</sup>

<sup>1</sup>Virginia Commonwealth University,  
Richmond, Virginia

<sup>2</sup>Norfolk State University, Norfolk, Virginia

<sup>3</sup>University of North Carolina, Chapel Hill,  
North Carolina

<sup>4</sup>University of Kentucky, Lexington,  
Kentucky

## Correspondence

Julie C. Zinnert, Virginia Commonwealth  
University, 1000 West Cary Street,  
Richmond, VA 23284.  
Email: jczinnert@vcu.edu

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## Abstract

Due to their position at the land–sea interface, barrier islands are vulnerable to both oceanic and atmospheric climate change-related drivers. In response to relative sea-level rise, barrier islands tend to migrate landward via overwash processes which deposit sediment onto the backbarrier marsh, thus maintaining elevation above sea level. In this paper, we assess the importance of interior upland vegetation and sediment transport (from upland to marsh) on the movement of the marsh–upland boundary in a transgressive barrier system along the mid-Atlantic Coast. We hypothesize that recent woody expansion is altering the rate of marsh to upland conversion. Using Landsat imagery over a 32 year time period (1984–2016), we quantify transitions between land cover (bare, grassland, woody vegetation, and marsh) and the marsh–upland boundary. We find that the Virginia Barrier Islands have both gains and losses in backbarrier marsh and upland, with 19% net loss from the system during the timeframe of the study and increased variance in marsh to upland conversion. This is consistent with recent work indicating a shift toward increasing rates of landward barrier island migration. Despite a net loss of upland area, macroclimatic winter warming resulted in 41% increase in woody vegetation in protected, low-elevation areas, introducing new ecological scenarios that increase resistance to sediment movement from upland to marsh. Our analysis demonstrates how the interplay between elevation and interior island vegetative cover influences landward migration of the boundary between upland and marsh (a previously underappreciated indicator that an island is migrating), and thus, the importance of including ecological processes in the island interior into coastal modeling of barrier island migration and sediment movement across the barrier landscape.

## KEYWORDS

barrier island migration, coastal system, dune, Landsat, macroclimate, sea-level rise, woody expansion

## 1 | INTRODUCTION

Barrier islands are highly vulnerable to global climate change because of the tight coupling among island ecological processes, geomorphological processes, and oceanic/atmospheric drivers of disturbance (e.g., hurricanes, nor'easters, sea-level rise) (Arkema

et al., 2013; Zinnert, Stallins, Brantley, & Young, 2017). The processes which maintain these islands are being disrupted by rising sea level and increased storm intensity and frequency (FitzGerald et al., 2018). Barrier island systems are the front to >20,000 km or ~10% of coastline globally (Stutz & Pilkey, 2011). Thirty percent of these barrier islands are along the US Atlantic and Gulf Coasts, one of the

most anthropogenically developed coastlines in the world. Coastal barrier islands provide numerous ecosystem services which are economically critical to local communities (Seabloom, Ruggiero, Hacker, Mull, & Zarnetske, 2013; Spalding et al., 2014), protecting millions of residents and billions of dollars in real estate and assets (Arkema et al., 2013) on the mainland.

Several recent studies have indicated accelerating relative sea-level rise (RSLR) along the coastal mid-Atlantic region (Ezer, Atkinson, Corlett, & Blanco, 2013; Sallenger, Doran, & Howd, 2012). Barrier islands are comprised of multiple connected habitat types that may influence resistance to storms, the effects of which are worsened by sea-level rise (Woodruff, Irish, & Camargo, 2013). Barrier beaches protect the mainland from storms, dissipate wave energy, and act as sediment (specifically sand) reserves. Backbarrier wetlands also contribute to storm buffering and wave energy dissipation while acting as filters, improving water quality, capturing sediment, and natural engineers of coastal defenses (Arkema et al., 2013; Wilson & Fischetti, 2010; Zhang & Leatherman, 2011). Barrier island upland ecosystems (referred to as upland in this paper) consist of multiple community types that are not tidally influenced and may include dune/swale complex, grassland, shrubland, and maritime forest, and have received little attention relative to the backbarrier counterparts (i.e., saltmarsh, tidal flat) (Feagin, Smith, et al., 2010; Zinnert et al., 2016). Barrier islands are extremely dynamic as major changes in geomorphology and vegetation composition can occur over a wide range of spatiotemporal scales in response to winds, waves, tides, and extreme storm events (e.g., Cleary & Hosier, 1979; Feagin, Smith, et al., 2010; Godfrey, Leatherman, & Zaremba, 1979; Roman & Nordstrom, 1988; Zinnert et al., 2017). Barrier islands respond to long-term presses, like RSLR, by migrating landward, often through sediment transport onto the fringe marsh platform via overwash (Deaton, Hein, & Kirwan, 2017; Hayden, Santos, Shao, & Kochel, 1995; Héquette & Ruz, 1991) or drowning in place if the rate of RSLR is rapid and sediments are not available (e.g., Miselis & Lorenzo-Trueba, 2017; Moore, List, Williams, & Stolper, 2010). Migration via overwash results in islands maintaining elevation above sea level, demonstrating the importance of coupled ecosystems (i.e., upland and marsh).

Barrier island migration over time is dependent on factors such as geologic context, storm frequency and intensity, topography, and sediment availability (e.g., Miselis et al., 2016; Nebel, Trembanis, & Barber, 2012; Wernette et al., 2018). However, sub-island scale processes can influence overall patterns of island response to RSLR due to topographic-vegetation interactions (e.g., Durán & Moore, 2015; Roman & Nordstrom, 1988; Stallins & Corenblit, 2018). The stabilization of sediment is influenced by vegetation with plant roots reducing erosion and aerial stems and leaves intercepting aeolian-transported sediments (Feagin et al., 2015; Silva Martínez, Odériz, Mendoza, & Feagin, 2016). Interactions between vegetation cover and elevation may play an important role in influencing the amount and frequency of sediment washing onto the marsh (Stallins & Corenblit, 2018; Zinnert et al., 2017), a process important for marsh persistence (Walters,

Moore, Vinent, Fagherazzi, & Mariotti, 2014). Dune/swale vegetation creates feedbacks with island topography and influences the disturbance frequency and severity that interior ecological communities experience. (Miller, Gornish, & Buckley, 2010; Roman & Nordstrom, 1988; Stallins, 2005; Stallins & Parker, 2003). Following the work of Stallins (2005), Vinent and Moore (2015) showed that feedbacks between vegetation and topography can lead to the coexistence of low and high states, and demonstrated the coexistence of low and high dune states across the Virginia Coast Reserve (VCR). Zinnert et al. (2017) also demonstrated that two stability domains (disturbance-reinforcing and disturbance-resisting) exist across the mid-Atlantic barrier island landscape. When dunes are low, a higher frequency of disturbance leads to reduced interior island vegetation, the presence of species tolerant to burial and high salinity, and little to no woody cover (disturbance-reinforcing; Figure 1). Conversely, dune building grasses that interact with sediment transport processes to build extensive dune ridges (e.g., *Ammophila breviligulata*) create higher topography and greater topographic roughness that resist overwash. This allows for the development of higher woody vegetation cover in swales (Figure 1).

Predictions for coastal response to sea-level rise often involves an assumption that the system will remain in equilibrium (Zhang, Douglas, & Leatherman, 2004). However, the changing macroclimatic conditions (i.e., temperature, rainfall) have resulted in foundation plant species replacement along coastlines, which will impact island geomorphology and stability (Goldstein et al., 2018; Osland et al., 2016; Zinnert et al., 2016). Increasing temperatures and atmospheric CO<sub>2</sub> have been implicated in woody species (often shrubs) expansion into grassland and marsh in several coastal systems (Battaglia, Denslow, & Hargis, 2007; Bond & Midgley, 2000; Lucas & Carter, 2010; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014; Stevens, Lehmann, Murphy, & Durigan, 2017). Across the Virginia Barrier Islands (VBI), this has occurred in the form of the rapid expansion of a few woody species and reduction in diversity of upland grasses and forbs due to increased winter temperatures (Huang, Zinnert, Wood, Young, & D'Odorico, 2018; Thompson, Zinnert, & Young, 2017). Woody expansion has occurred in protected, low-elevation areas despite landscape losses in upland area that are attributed to the combined effects of erosion and RSLR (Entwistle, Mora, & Knight, 2018; Irish et al., 2010; Zinnert et al., 2016). Such expansion may impact sediment flux and the trajectory of migration in a transgressive system.

Understanding connectivity of sediment via the transport of sediment across multiple habitat types on barrier islands is essential in improving future predictions of coastal response to climate change, especially given the various drivers that can alter the system. Recently, it was demonstrated that connection between the upland and backbarrier environment plays as an important in the maintenance of barrier island-marsh systems (Walters et al., 2014), and is an innovative framework for assessing barrier system stability over the past 150 years (Deaton et al., 2017) and sediment mobility during storms (Houser, Hapke, & Hamilton, 2008). Here, we fill a knowledge gap by extending the framework of coupled ecosystems identified in previous

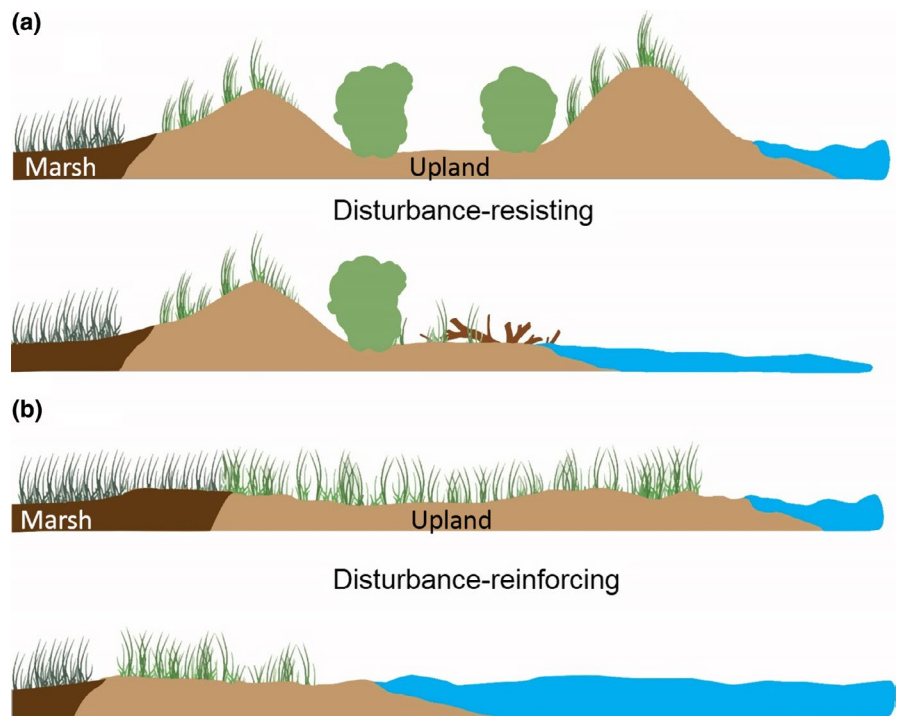
work by considering how upland vegetation affects the conversion of backbarrier marsh into barrier island upland along the VBI. In our regional analysis, we quantify transitions between ecosystem states (e.g., bare, grassland, woody, marsh, ocean) from Landsat imagery at two different spatial scales (island and sub-island) during a time of increased RSLR (1984–2016). We focus on barrier islands and backbarrier marsh. We hypothesize that recent woody expansion is altering the rate of marsh to upland conversion (i.e., this normally occurs through burial of marsh by sediment delivered via overwash, a process which occurs during island migration), thus affecting connectivity of these habitats. We also demonstrate the importance of sub-island scale processes for understanding overall island change.

## 2 | MATERIALS AND METHODS

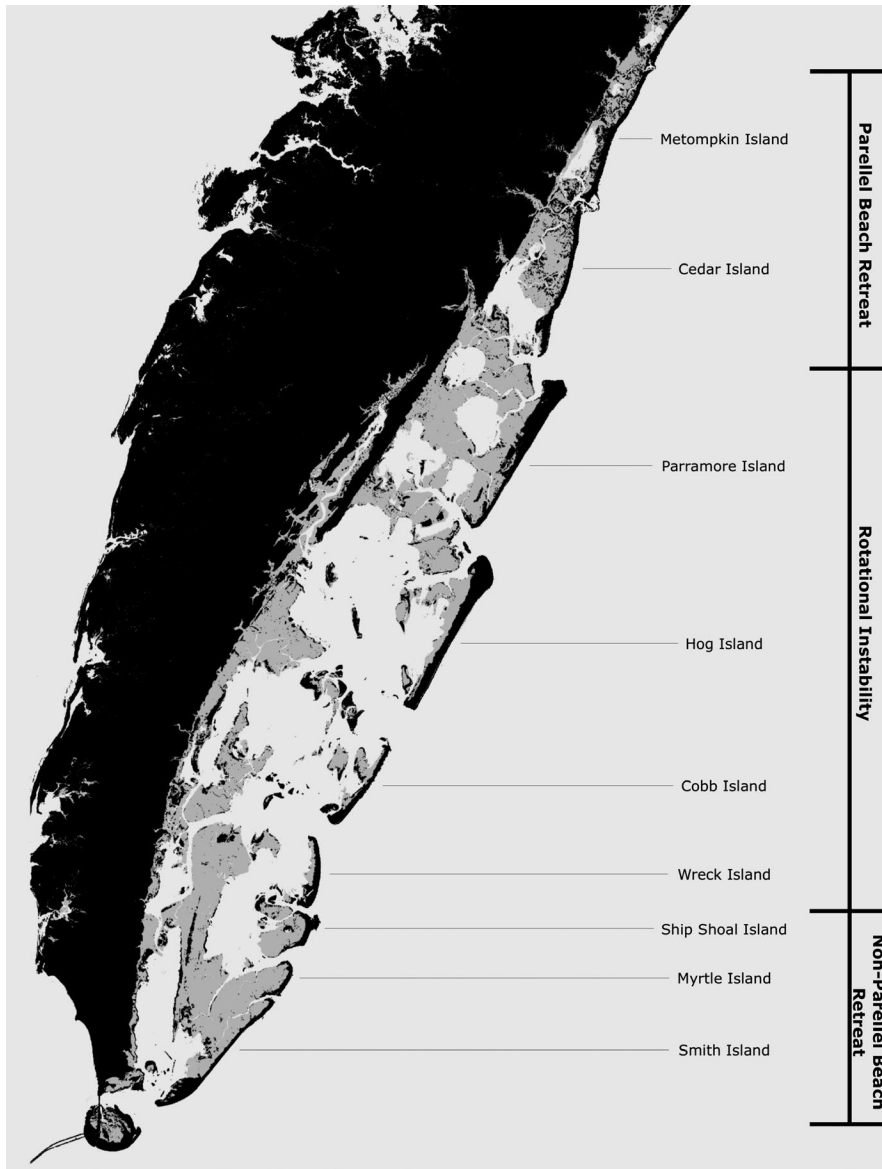
The VBI are part of the VCR, a Long-Term Ecological Research site and are within the Atlantic northeast hotspot of RSLR (Sallenger et al., 2012). The VCR was established in 1970 by the Nature Conservancy and consists of >15 islands, marshes, sand bars, and bays. The VCR is >14,000 ha and has been largely free of direct anthropogenic development and habitation since the 1930s, making this the largest undeveloped barrier system along the US Atlantic Coast. This provides a unique opportunity to study barrier island response to RSLR in the near absence of direct human alteration. Our study included nine undeveloped islands from Metompkin Island to Smith Island (Figure 2). Analysis was specific to barrier islands and associated backbarrier marsh (Figure S1). The VBI have been classified into three geomorphic groups based on historical migration patterns from 1852 to 1974: parallel beach retreat, rotational instability, and non-parallel

beach retreat (Leatherman, Rice, & Goldsmith, 1982). Parallel beach retreat islands occur in the north and are sediment starved due to the spit formation on southern Assateague Island, which alters the local wave climate and therefore longshore sediment transport gradients. Rotational instability islands occur in the middle of the island chain; each island alternately experiences erosion at one end and deposition on the other, as the islands retreat landward overall. The southern, non-parallel beach retreat islands have undergone changes in shape, with each island exhibiting a different response as landward retreat progresses. Due to its unique circular shape and location at the mouth of the Chesapeake Bay, southernmost Fisherman Island was excluded from analysis. Net longshore sediment transport along the oceanside of the VBI is southward, largely due to tropical and extratropical storms and the rate of RSLR along the VCR has been ~5.7 mm/year over the last 40 years (2018).

To assess transitions in ecosystem states (bare, grassland, woody, marsh, and ocean), we obtained Landsat TM5 and seven satellite images from the USGS Global Visualization Viewer for the following dates: September 21, 1984, September 12, 1998, August 12, 2011, and September 12, 2016. Cloud-free images were chosen from available dates within the growing season and at similar tide levels to minimize uncertainties due to heterogeneous natural conditions. Each image file was radiometrically corrected using ENVI 4.7 and predefined ENVI settings for Landsat calibration. Atmospheric correction was done to retrieve surface reflectance with ENVI quick atmospheric correction (QUAC). QUAC is a scene-based empirical approach used for the removal of atmospheric effects based on the radiance values of the scene and provides suitable reflectance spectra even when imagery does not have proper wavelength or radiometric calibration or when solar illumination intensity is unknown



**FIGURE 1** Conceptual model of barrier island response to relative sea-level rise (RSLR)/disturbance. Disturbance-resisting landscapes with greater topographic variability and vegetative diversity result in higher rates of shoreline erosion and little to no marsh to upland conversion (a). Disturbance-reinforcing landscapes have lower topographic relief, sparse vegetation, and experience higher rates of transition in landscape type (e.g., marsh to upland conversion; b)



**FIGURE 2** Map of the Virginia Barrier Islands along the eastern side of the DelMarVa Peninsula. The islands we focus in this study are labeled with classifications from Leatherman, Rice, and Goldsmith (1982). Black represents upland and gray represents marsh

(Agrawal, Sarup, & Bhopal, 2011). All Landsat scenes were subset to the VBI.

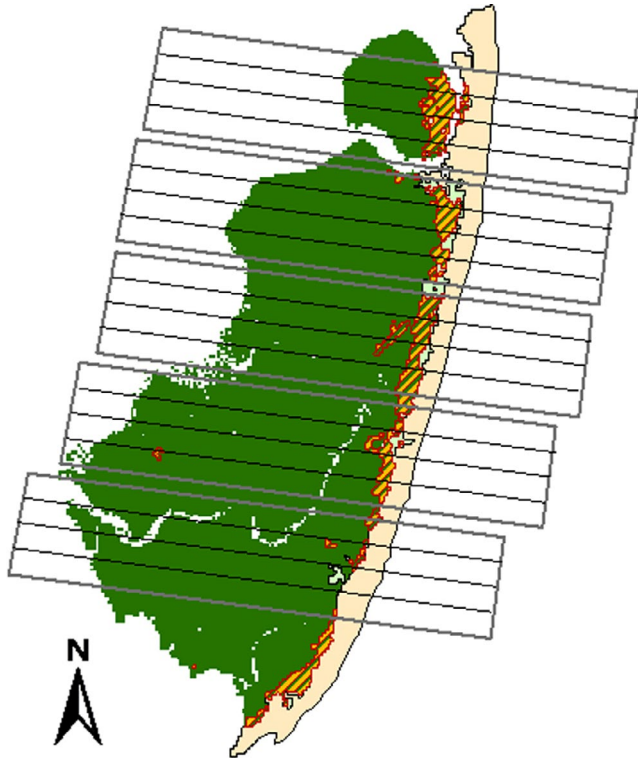
Classifications of land use and cover were carried out as in Zinnert et al. (2016) and included five classes: woody, grassland, sand/bare, water, and marsh. The bare class includes low vegetative cover as found on beaches and dunes, with relatively high amounts of sand exposed in a 30 m pixel. Regions of interest (ROI) were selected for each classification type within each scene based on georectified aerial photography, field-surveyed vegetation using a Trimble Geo-XT GPS unit, known vegetation sampling locations established in 1989 (Young, 1992), and corresponding 1–4 m spatial resolution hyperspectral imagery from 2000 to 2008 (Aguilar, Zinnert, Polo, & Young, 2012; Young et al., 2007). In November 2017, we conducted a visual aerial survey to confirm established woody vegetation identified in 2016 imagery. After ROIs were selected, supervised classifications using Landsat bands 1, 2, 3, 4, 5, and 7 were performed using the maximum likelihood

methodology. Classified scenes were exported to ArcGIS 10.4.1 (ESRI, CA). The total upland area was calculated by merging the following classes: bare sand, woody, and grassland. Upland water (interior ponds) was not included as it was absent or less than 8 ha in the total area during any given time.

## 2.1 | Analysis of land cover change

Changes in land cover classes over the entire timeframe and between years were quantified by overlaying the class of interest from the initial year (e.g., 1984 marsh) and the class of interest from a different year (e.g., 1998 upland). An intersect was performed and overlapping areas were summed for each pairwise comparison of cover classes. To account for variation in geographic characteristics within individual islands, each island was subdivided into ~1 km long shapefiles that span the width of the island. We calculated the total class area (ha) for each time period and class changes between

time periods for whole islands and each island subsection. Within the 1 km subsections, ArcGIS was used to draw three cross-island transects, perpendicular to the shoreline that divided the 1 km subsection into equal thirds. We used these transects to calculate the distance of marsh to upland conversion (i.e., how far into the marsh the upland moved; Figure 3). Fore-dune elevation is a potential metric for protection from overwash and movement of sediment. For



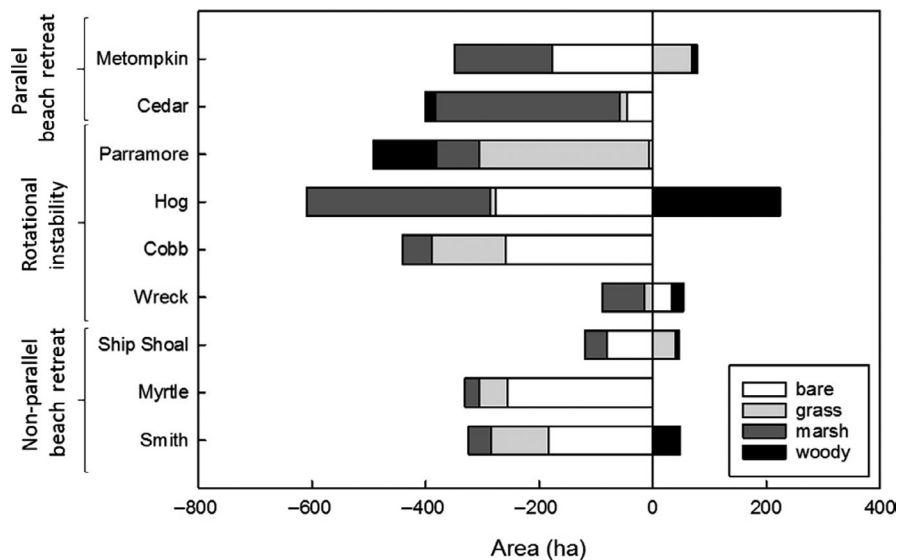
**FIGURE 3** Cedar Island, VA showing 1 km subplots (boxed frames) and the three transects within in each subplot are used for measurements. Green represents 1998 marsh, beige represents 1998 upland, and orange cross-hatching represents marsh to upland conversion between 1998 and 2011

each aforementioned transect, fore-dune elevation in 1998 was determined using the fore-dune elevation dataset of Oster and Moore (2009), which was created by extracting fore-dune crest elevation from LiDAR data along transects spaced at 10 m increments along the shoreline.

Nonlinear regression was used to predict 1998 marsh to upland change (distance in meters) using 1998 dune elevation (m). Multiple regression was used to determine if the distance between the marsh–upland boundary in 1998 and 2011 (representing marsh to upland conversion) was related to 1998 dune elevation and vegetation parameters (e.g., 1998 woody area, 1998 % woody cover, 1998 grass area, and 1998 % grass cover) within 1 km subsections. Dune elevation was log transformed to meet normality assumptions. Model fits were determined using the Akaike information criterion (Akaike, 1974). Levene's test was used to test for unequal variance in rates of marsh to upland conversion over time. The Wilcoxon test was used to determine if rates of marsh to upland conversion differed based on geomorphic classifications of Leatherman et al. (1982) over time. To examine how upland composition across an island has changed, we conducted one principal components analysis (PCA) of upland area (i.e., grass, woody, bare) across the 1 km subsections over the entire timeframe. Multi-response permutation procedure was used to detect significant differences among years (McCune & Grace, 2002) using a Bonferonni corrected *p*-value.

### 3 | RESULTS

Over the timeframe of this study, RSLR was ~172 mm (2018). At the regional scale, there was a total loss of 19.1% (~2550 ha) of island and backbarrier marsh from the system (Figure S1). The majority of this loss occurred in upland area (11.8%; ~1581 ha) with a 7.3% (~970 ha) loss of back barrier marsh (Table S1; Figure 4) from 1984 to 2016. Patterns of upland communities were highly variable over



**FIGURE 4** Net change in ecosystem state from 1984 to 2016 along the Virginia Barrier Islands

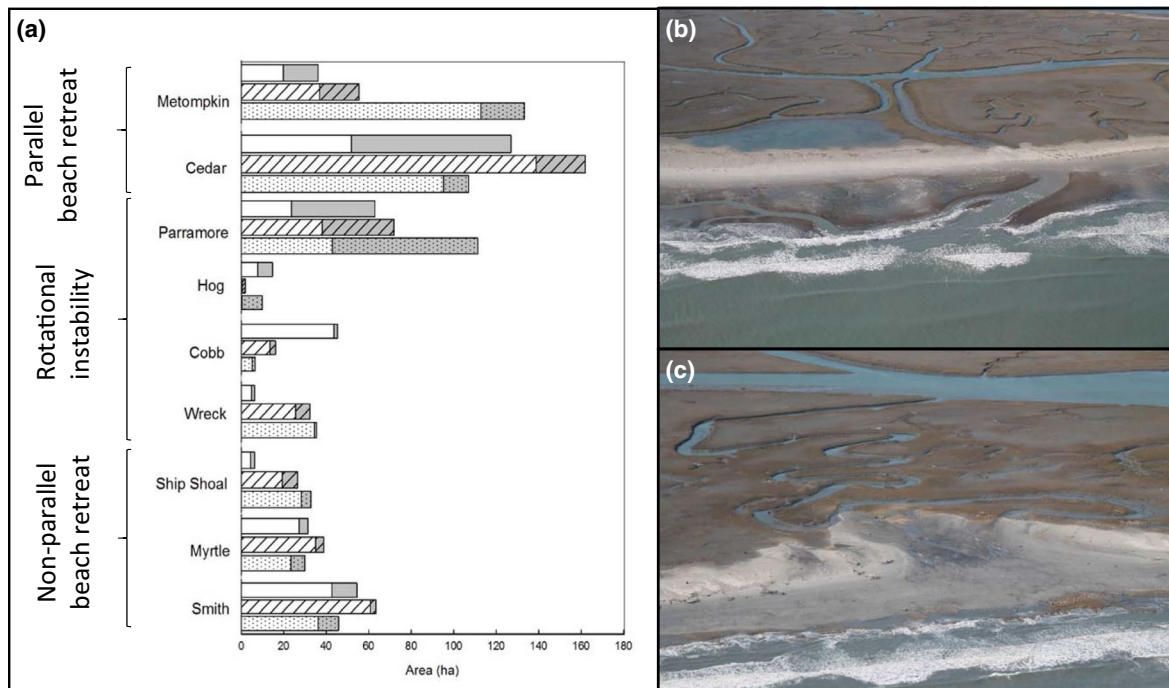
the timeframe, with gains and losses in bare, grassland, and woody states (Figure S2). There were no obvious patterns in gains or losses from our data based on historical geomorphic classification of Leatherman et al. (1982). Despite the reductions in land area, several islands still saw large expansions of woody cover (483 ha across the system). Ship Shoal did not have any woody vegetation until 2016 and Myrtle was the only island with no woody cover during the entire study period.

### 3.1 | Marsh to upland conversion

Over 1,300 ha of backbarrier marsh converted to barrier island upland between 1984 and 2016 (Figure 4; Table S2), an indication of overwash deposition that became colonized by upland vegetation. This exceeds total marsh loss (−970 ha), indicating that new marsh is being formed. In addition, 719 ha of upland converted to marsh during the same timeframe, compensating for over half of marsh converted to upland. There were no apparent patterns of upland to marsh conversion, but the highest amount occurred from 1984 to 1998 (Table S3). Of marsh converted to upland, parallel retreat islands (Metompkin and Cedar) had the highest percent relative to the 1984 total island area (upland and marsh) (Table S2). Parramore (a rotational island) had a large area of marsh to upland conversion, but this was minimal relative to the size of the island (8.1%).

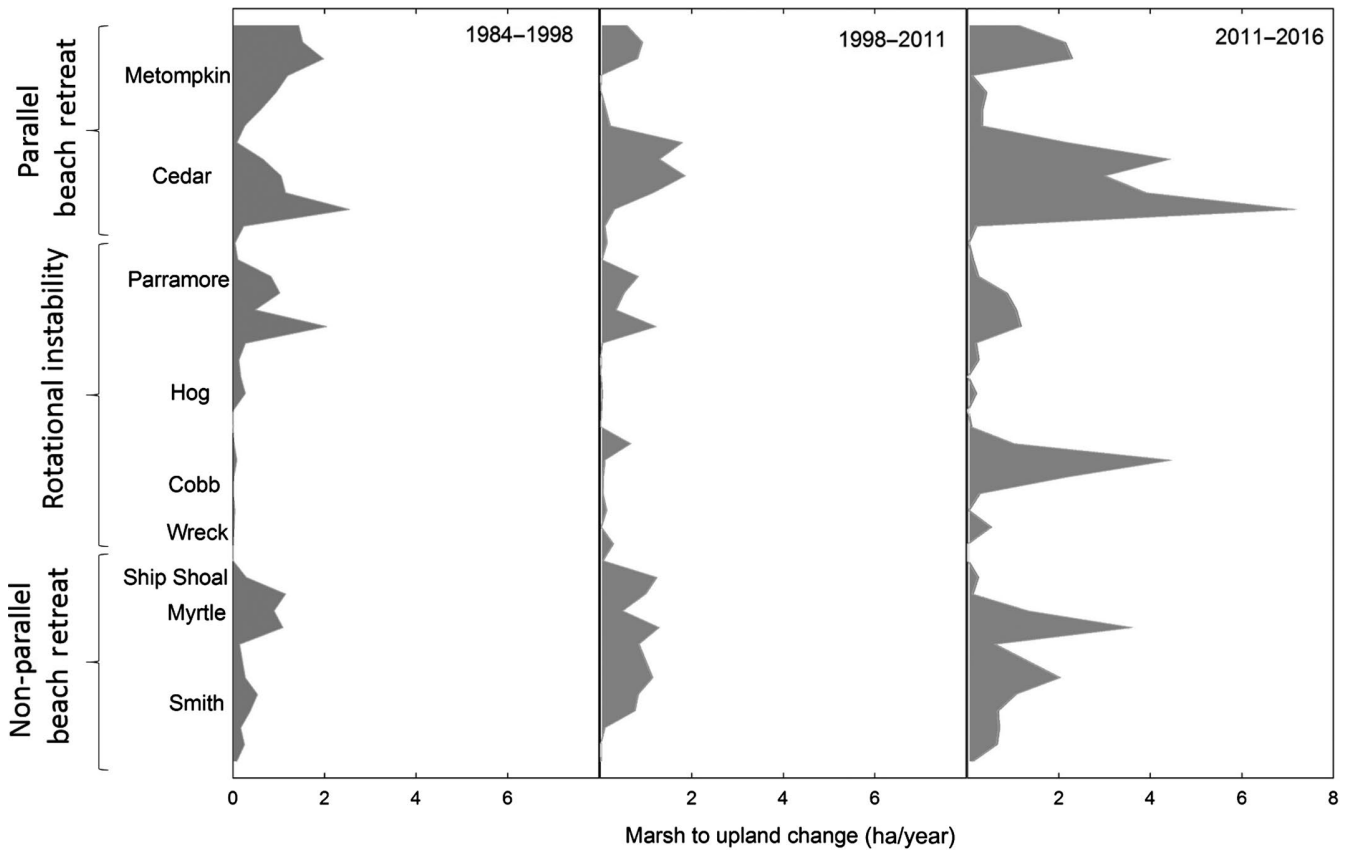
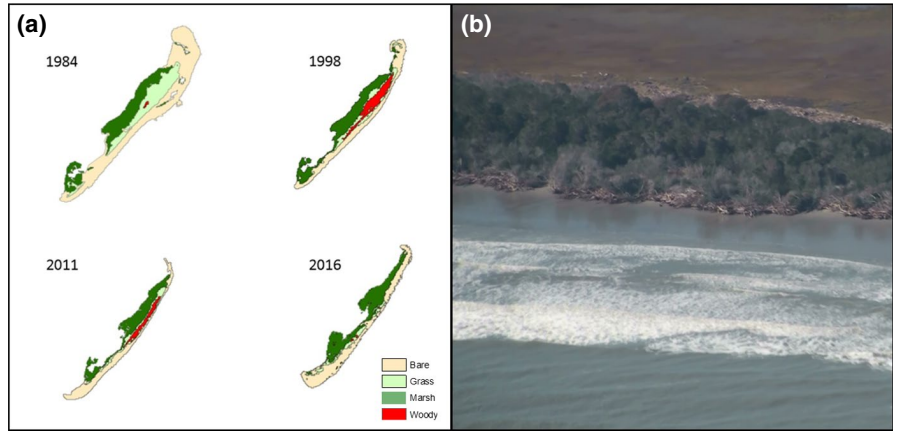
The northern islands had a higher percentage of conversion into grassland vegetation compared to the southern islands

(Figure 5). Across all islands, ~12 ha of woody vegetation established in area that was once marsh; the majority of this (11.1 ha) occurred in 2016 on upland that was once marsh in 1984. The rate of marsh conversion into upland increased in the last 5 years (67 ha/year) relative to the entire time period (~41 ha/year). Evidence of this rapid conversion is seen in the exposure of marsh peat and former marsh tidal channels on the ocean side of several islands (Figure 5; Figure S1). Prior to this study period, Cobb Island exhibited drumstick morphology (i.e., similarity in shape to a chicken leg; Hayes, 1979) with minimal shoreline migration. During the first time period of this study, woody vegetation rapidly expanded seaward (concurrent with shoreline progradation) and alongshore on Cobb Island (2.3 ha in 1984 to 80.8 ha in 1998; a rate of 5.6 ha/year), but marsh–upland migration rates remained low (<1.6 ha/year). After 1998, extensive shoreline erosion occurred. Marsh to upland conversion rates (mostly bare) increased rapidly between 2011 and 2016 (11.1 ha/year) once waves eroded upland sediment and woody vegetation into the sea leading to the loss of >375 ha of island upland (Figure 6). Relative to the 1984 size of the island, the rate of marsh to upland conversion was minimal (7.5%, Table S2). Conversely, rates of marsh to upland conversion on Ship Shoal decreased in the most recent time period and woody vegetation established for the first time by 2016. Hog Island remained relatively stable during the study period, with extensive woody vegetation and little to no marsh to upland conversion (Tables S1 and S2). Upland area loss (primarily bare) over the timeframe (~63 ha), suggests a modest amount of shoreline erosion.



**FIGURE 5** (a) Marsh conversion to bare (white) or grass (light gray) between 1984 and 1998 (no hatching), 1998 and 2011 (cross-hatching), and 2011 and 2016 (dots). (b) Former marsh tidal channels are exposed on the oceanside of Myrtle Island—November 2017. (c) Cobb Island overwash into marsh and exposure of marsh peat in deepest part of overwash channel—November 2017

**FIGURE 6** (a) Landsat TM-derived classifications showing change in woody cover, grassland, and bare sand from 1984 to 2016 on Cobb Island. Red represents woody cover, light green represents grassland, beige represents sand, and dark green represents salt marsh. (b) Photo of extensive woody vegetation on the oceanside of Cobb Island and lack of sandy beach taken after Hurricane Sandy in 2012. Photo credit: John Porter

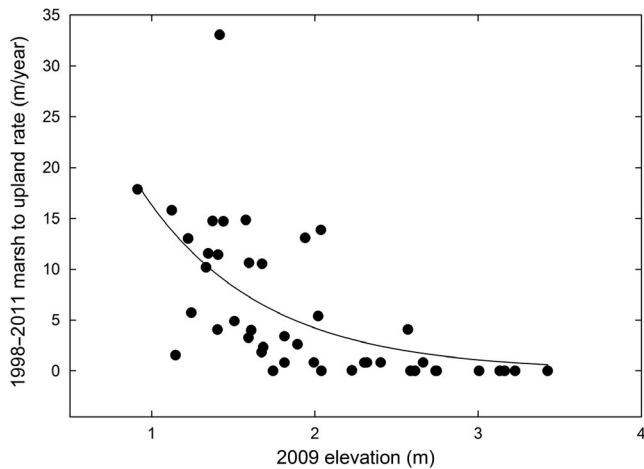


**FIGURE 7** Marsh to upland conversion rate in 1 km island subsections along the Virginia Coast Reserve

### 3.2 | Sub-island scale

Sub-island scale observations reveal that rates are not uniform within an island (Figure 7). Using 1 km subsections, rates of marsh to upland conversion ranged from 0 to 7.16 ha/year and varied over time with the greatest variability observed between 2011 and 2016 ( $F = 14.2, p < 0.0001$ ). Parallel retreat island segments had the fastest rate of marsh to upland conversion across all years (1984-1998:  $\chi^2 = 16.5, p < 0.001$ ; 1998-2011:  $\chi^2 = 8.4, p = 0.015$ ;

2011-2016:  $\chi^2 = 10.4, p = 0.005$ ; Table S3). Rotational islands did not conform to the historical patterns of movement, potentially indicating a shift in the system. For example, the northern portion of Parramore Island represents a disturbance-resisting regime characterized by a dune/swale complex, higher foredune elevation (1.6–2.0 m), and extensive woody cover. This area experienced shoreline erosion over the entire 32 year timeframe with little marsh to upland migration. Conversely, the southern portion of Parramore Island has been rapidly migrating, with large transitions



**FIGURE 8** Scatterplot of 1 km island subsection foredune elevations from Oster and Moore (2009) and the marsh to upland migration rates between 1998 and 2011

of marsh to upland over the entire timeframe, lower foredune elevation (1.1–1.6 m), and a general lack of woody cover.

Our empirical data suggest a dune elevation threshold (close to 2.5 m) above which upland does not convert to marsh (Figure 8), likely because higher elevations are more resistant to overwash during storms (and therefore to migration of the island landform), which is an important contributor to the conversion process. Although elevation is an important predictor of marsh to upland conversion within 1 km subsections between 1998 and 2011 ( $r^2 = 0.39$ ,  $p < 0.0001$ ), we found that inclusion of vegetation cover improved model fits and change in % woody cover + elevation was the most parsimonious model when considering data from the barrier island chain ( $R^2 = 0.475$ ,  $p < 0.001$ , Table 1). Inclusion of woody vegetation (i.e., % woody cover or woody area) was important in the top four out of five models (Table 1). The large spatiotemporal extent of our data lends confidence to our overall finding that including woody vegetation cover data improves the predictability of resistance to overwash, and through this process woody vegetation affects barrier island migration.

Due to variability in change over the study period, PCA was used to assess the multivariate changes in upland cover within each island transect over the entire timeframe. As shown in Figure 9, 84.4% of

variance was explained by the first two axes. Locations on individual islands became more similar to one another as seen in the clustering that has occurred over 1984–2016 ( $T = -6.72$ ,  $p < 0.0001$ ). This suggests a homogenization of cover in subsections across the landscape due to woody expansion (axis 1) and reduction in grass (axis 1) and bare (axis 2). The overlap of transects from different islands demonstrates that individual islands are composed of multiple habitat types.

## 4 | DISCUSSION

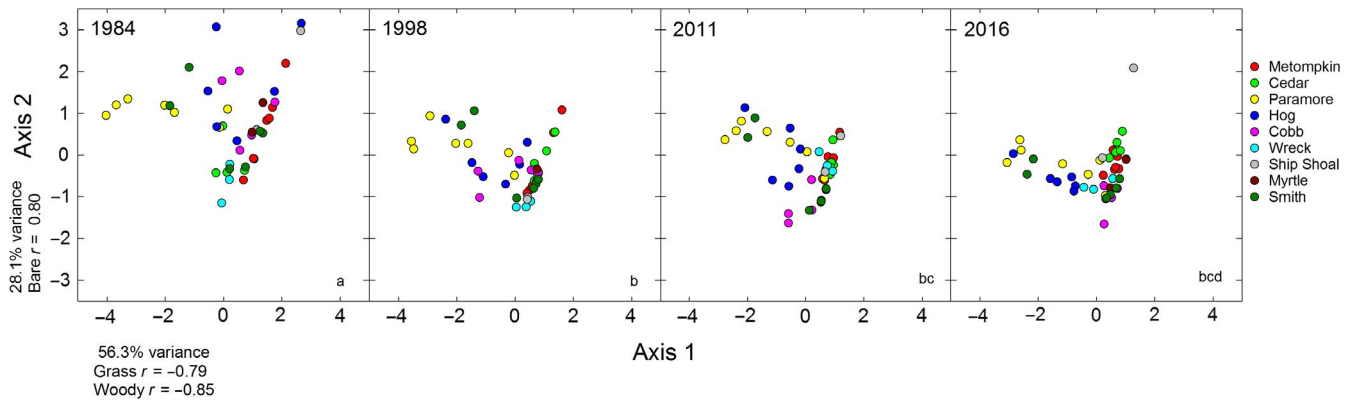
Our regional analysis of the VBIs shows that the system is transgressing landward with increased rate and variability, and that some areas have begun to experience marsh to upland transition only in recent years (2011–2016). Losses in total upland (–1580 ha) and marsh area (–970 ha) over the 32 year time period, along with the expansion of woody vegetation (483 ha) are consistent with trends seen on other Atlantic and Gulf of Mexico barrier islands (Lucas & Carter, 2010; Morton, 2008). We demonstrate the importance of connectivity—and lack of connectivity—between barrier island upland (e.g., bare, woody, grass) and marsh and the importance of woody vegetation. Higher elevations and the cover of woody vegetation appear to sever connectivity and reduce the rate of marsh to upland conversion by reducing delivery of sediment onto the marsh via overwash. Our data suggest that through this reduction in connectivity by recent expansion of woody vegetation into available habitat may alter patterns of island migration in the future by temporarily limiting overwash processes.

Increased variance in rates of marsh–upland conversion identified here is consistent with a shift in the system toward increasing rates of landward barrier island migration, a change that has been recognized in other recent work (Deaton et al., 2017). At the same time, the expansion of woody vegetation is creating new ecological scenarios (e.g., monotypic thickets that dominate the landscape) that have not been present historically. Prior to 2016, woody expansion dominated the mid-chain, rotational islands; this expansion is now present along the entire island chain, driven by topographic–vegetation interactions (Zinnert et al., 2017). Research on coastal system response to climate change has

Predictor	F ratio	p-value	R <sup>2</sup>	Adj R <sup>2</sup>	Akaike information criterion
% Woody + log (elevation)	18.51	<0.0001	0.475	0.449	502.62
% Woody + % grass + log (elevation)	13.48	<0.0001	0.503	0.465	502.74
Woody area + log (elevation)	17.79	<0.0001	0.465	0.439	503.44
% Woody + grass area + log (elevation)	12.81	<0.0001	0.490	0.452	503.86
% Grass + log (elevation)	17.37	<0.0001	0.459	0.432	503.93

**TABLE 1** Top five model fits for determining distance between the marsh and upland boundary (m) in 1998 and 2011





**FIGURE 9** Principal components analysis of upland cover on island transects over the four time intervals (1984, 1998, 2011, and 2016). Letters denote significant differences among years based on multi-response permutation procedure pairwise comparisons

tended to focus on the effects of RSLR; however, the recent work on mangrove migration has shown that macroclimatic drivers coupled with microclimate modification have the power to transform plant community structure, resulting in altered ecosystem services (D'Odorico et al., 2013; Gabler et al., 2017; Osland, Enwright, Day, & Doyle, 2013). Our results extend these findings to barrier island upland habitats and suggest that climate-induced range shifts (e.g., woody expansion of *Morella cerifera* in the VBI) and RSLR are leading to system homogenization.

Although woody vegetation provides coastal protection from storms (Feagin, Mukherjee, et al., 2010; U.S. Army Corps of Engineers, 2013), the expansion of dense thickets across the landscape can produce effects similar to those of coastal development, making it harder for the system to adjust to sea-level rise by restricting overwash penetration thereby limiting landward movement of islands (Enwright, Griffith, & Osland, 2016; Rogers et al., 2015), a process which is required to maintain equilibrium with rising sea level (e.g., Lorenzo-Trueba & Ashton, 2014; Moore et al., 2010). Similarly, once the foredune has been eroded, physical stabilization of sediments and resistance to sediment transport within a swale inhabited by woody vegetation can hinder, or stall, upland migration, at least until the woody vegetation has been eroded. This scenario occurred on Cobb Island where rapid expansion of *M. cerifera* created resistance to upland migration, reducing overwash of sediments until the woody vegetation was killed by wave action and lost into the ocean. Although Cobb Island now exhibits signs of landward migration, the dramatic loss of upland area (63%; through seaward erosion rather than landward movement via overwash) limits the amount of internal sediment available to sustain the island. In contrast, in low-lying disturbance-reinforcing locations (i.e., where marsh has newly converted to upland via overwash), woody vegetation does not develop, and these areas remain primarily bare (which can include sparse vegetation) or in a grassland state (Figure 1). If an overwash area recovers via aeolian deposition to an elevation at which vegetation can prosper, dune building begins (e.g., Godfrey et al., 1979; Houser et al., 2008; Vinent & Moore, 2015) and woody species may ultimately grow and expand on the landward of the dune system (e.g., Ship Shoal).

Many studies of barrier islands and coastal areas are focused at the dune scale and thus do not account for the island interior, which plays a functional role in determining resilience (i.e., the ability of the landform to maintain current function as conditions change) (Lentz et al., 2016; Zinnert et al., 2016). As we show here, plant communities beyond the dune system can modulate abiotic components of the landscape (Chapin et al., 1997; Corenblit et al., 2011; Zinnert et al., 2017) and determine island level responsiveness to variations in sea-level rise (e.g., Brenner, Moore, & Murray, 2015; Walters et al., 2014). Thus, quantifying internal island characteristics, including vegetative species composition in the island interior can provide insights on how barrier islands may evolve in the future and will improve predictions of future response to RSLR and changes in storm activity. Barrier islands represent an unusual case wherein there is a tradeoff between system resistance and resilience; more resistant systems are actually less resilient in the long-term, and more prone to catastrophic change. For barrier islands, natural system resilience to sea-level rise involves migration onto the marsh platform to maintain elevation above sea level (e.g., Leatherman, 1983; Moore et al., 2010). Extensive woody vegetation appears to delay this process.

At the sub-island scale, some islands exhibit regions with high rates of marsh-upland boundary migration along with regions where this boundary is relatively stable (e.g., Parramore, Smith). These potentially coexisting or adjacent areas of instability and stability are related to local scale factors such as vegetation and foredune elevation, which are known to be spatially and temporally dynamic. When assessing the potential for future barrier island migration, focusing only on shoreline change fails to capture the overall shift in geomorphic and ecosystem state that is occurring. For example, shoreline retreat has been documented on Cedar and Parramore islands, with rates increasing since the 1990s (Nebel et al., 2012; Richardson & McBride, 2007), but this finding alone does not distinguish whether the island itself is beginning to migrate or whether the shoreline alone is retreating. Inclusion of interior vegetative cover (primarily woody cover) in a multiple regression improved model predictions of marsh to upland conversion associated with island migration. Our analysis demonstrates the interplay between elevation and vegetation in

migration of the boundary between upland and marsh and, thus, the importance of including ecological processes in the island interior when modeling future scenarios. Finer temporal and spatial resolution along with topographic data will likely increase the predictive power of change of models (e.g., Enwright et al., 2017; Monge & Stallins, 2016).

Islands are migrating at faster rates than in the past 100 years, some are following new patterns of migration, and some are at risk of drowning or existing in new forms not previously found in this region (Fearnley, Miner, Kulp, Bohling, & Penland, 2009; Lorenzo-Trueba et al., 2014; Nebel et al., 2012; Richardson & McBride, 2007). The expansion of woody vegetation along with high dune elevation has resulted in loss of island area by limiting connectivity via landward transport of sediment, reducing marsh to upland conversion. Loss of biodiversity that occurs with woody expansion (Thompson et al., 2017) and homogenization of habitat types that we report here, will affect future resilience following disturbance (e.g., De Boeck et al., 2018). Our results complement the recent work (Deaton et al., 2017) suggesting a shift in the VBI, partly due to macroclimatic changes in species distributions. Our findings also highlight how changes in vegetation state to increased woody cover influence island response to disturbance and may limit migration of upland into marsh, at least for some time.

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## ORCID

Julie C. Zinnert  <https://orcid.org/0000-0003-2578-7236>

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## SUPPORTING INFORMATION

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