Crossing Scales: The Complexity of Barrier-Island Processes for Predicting Future Change

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Barrier islands are heavily influenced by external drivers such as sea-level rise, storm-related disturbances, and other complex factors that affect net sediment exchange. Numerous ecological processes (e.g., dispersal, competition, and facilitation) interact with these drivers and ultimately influence barrier-island state change and therefore stability. Our synthesis of physical and ecological processes controlling barrier-island function highlights the importance of incorporating ecological factors into predictive models of barrier-island state change. We present a conceptual framework that outlines how local-scale processes contribute to broadscale patterns of barrier-island function. We have also identified specific, scale-dependent drivers and cross-scale interactions that lead to different topographic states, which vary in species composition, and generate contrasts in function between and within individual islands. This multidimensional continuum of topographic states ultimately determines island resilience in response to climate change.

Keywords: biogeomorphologic feedback, disturbance, ecosystem engineers, state change

Barrier systems serve as sensitive sentinels of global climate change because physical and ecological processes are coupled to both atmospheric and oceanic drivers (Arkema et al. 2013). Coastal barrier systems constitute 10%–15% of coastlines globally and occur on all continents except Antarctica (Stutz and Pilkey 2001). They are the frontline ecosystem that protects mainland human infrastructure and areas of great economic value (Arkema et al. 2013) from coastal storms and sea-level rise. Twenty-five years after Hayden and colleagues (1991) first introduced the concept of island state change for the Virginia Coast Reserve (VCR), a protected barrier island–lagoon system along the Atlantic coast, significant advancements in modeling highly dynamic environments have been made (Hayden et al. 1991, Rastetter 1991, Durán a`nd Moore 2013, Bel and Ashkenazy 2014). However, despite our understanding of the physical processes shaping these landscapes, most studies or models of barrier islands do not adequately incorporate ecological processes (Zinnert et al. 2016a).

Historically, ecological research on barrier islands has focused on answering fundamental scientific questions at local scales (Ehrenfeld 1990). As our understanding of barrier-island ecology has grown, so has recognition that these systems are highly complex and dynamic across time and space (Stallins and Parker 2003). Islands exhibit a range of ecosystem states (e.g., dunes, grassland, and shrubland) as a result of nonlinear interactions among many individual components (e.g., sediment or vegetation; Holling 1992, Stallins 2005, McGlathery et al. 2013), which will be discussed later in detail. The recognition and study of ecosystems as complex systems have been ongoing for approximately 40 years (Holling 1973) and are at the heart of ecological hierarchy theory and landscape ecology (e.g., Allen TFH and Starr 1982, Urban et al. 1987). Only recently has the wider scientific community embraced broadscale ecology to view biological, geophysical, and social phenomena at multiple spatial and temporal scales (Allen CR and Holling 2010, Nash et al. 2014, Sorrano et al. 2014). Ecosystems are strongly influenced by both abiotic and biotic variables that operate across multiple scales (Urban et al. 1987); these cross-scale interactions must be considered when predicting or interpreting ecosystem state change.

The objective of this synthesis review article is to highlight how ecological processes interact with broadscale physical (i.e., geomorphological) processes, to discuss the complexity of these interactions across scales, and to better frame the challenge of making generalizations and testing hypotheses in coastal barrier ecosystems. We approach our synthesis with the goal of building on the understanding of barrier-island state change as first described by Hayden and colleagues (1991). Using barrier islands of the VCR as a model system, we provide a framework for conceptualizing

interactions among abiotic and biotic processes, emergent patterns that arise, and broadscale changes in island geomorphology that result from cross-scale interactions (Young et al. 2007). We summarize important biological controls on barrier-island evolution and demonstrate the relationship to topographic "state" configurations extending beyond the dune to the interior using results from previously published studies. As islands develop, these configurations interact with local-scale physical or ecological processes and broadscale island shape and size, which leads to contrasting ecosystem function among islands, ultimately determining the response to sea-level rise and storm intensity.

Predicting barrier-island state change is a fundamental requirement for coastal management and conservation with current sea-level rise threatening these landscapes and adjacent ecosystems (Hayden et al. 1991, McGlathery et al. 2013). Climate change is expected to cause more intense storms, rising sea level, and changes in plant-species composition. The continued existence of barrier-island landforms and the value of the ecosystem service they provide will depend on the degree to which islands can maintain elevation above sea level (Durán Vinent and Moore 2015).

Cross-scale interactions: The complexity of predicting island state change

The Virginia Coast Reserve was established as a biosphere reserve and a National Science Foundation long-term ecological research (LTER) site in the late 1980s (Hayden et al. 1991). Since establishment, barrier-island upland area has declined dramatically because of sea-level rise (3.8 to 4.0 millimeters per year), whereas increased woody vegetation and frequent transitions of vegetative states have occurred on many islands (Young et al. 2007, Zinnert et al. 2016b). Even as barrier islands respond to sea-level rise, vegetation is an important functional component of coastal systems that affects geomorphological change by trapping sediment and promoting organic matter deposition, both of which are critical processes for shaping coastal landscapes (Rastetter 1991).

The ISLAND model by Rastetter (1991) was one of the first models to integrate abiotic controls (e.g., groundwater, salinity, and sediment) on biotic processes (i.e., the growth and survival of hypothetical plant functional types) in barrier-island landscapes demonstrating that large-scale processes are integral, dynamic parts of the system and not extrinsic controlling factors. Recent work on barrier-island modeling has demonstrated the importance of dune height and other geomorpological features (i.e., beach width and height) that are relevant to coastal vulnerability and related to shoreline change (Durán and Moore 2015, Gutierrez et al. 2015, Plant et al. 2016). These models have also shown bimodality in dune height (Durán and Moore 2015) and that threshold conditions exist that can influence the rate of erosion of barrier islands (Gutierrez et al. 2015, Plant et al. 2016). For example, sections of barrier islands that have high erosion rates are typically narrow, have low dunes, and

experience more overwash (Houser et al. 2008, Gutierrez et al. 2015). Elevation is an important determinant in vegetation cover (Young et al. 2011, Lentz et al. 2016), and vegetative cover type influences overall barrier-island response to sea-level rise (Lentz et al. 2016). In barrier uplands, vegetation influences sediment-supply transfer processes by trapping and stabilizing sand (reviewed in Feagin et al. 2015).

Sediment trapping can create new substrate for further colonization by plants or cause a change in elevation resulting in a vegetative state change at the local scale. Local-scale processes can be separated as occurring within two distinct geomorphological units: dunes and swales, the relative positions of which affect barrier-island shape and size (figure 1). Vegetation growth influences sediment-transfer processes by stabilizing sand in different dune morphologies (Durán Vinent and Moore 2015). As islands develop, feedback between vegetation and sediment influences vegetation cover type at the broad scale, leading to contrasting ecosystem function and resilience among islands (Young et al. 2007, Durán Vinent and Moore 2015). Linking local and broadscale processes (i.e., drivers and response variables) will transform our understanding of system response to climate change by focusing on the interactions of mechanisms operating at different spatial scales (figure 2).

The importance of dune-building processes

Among the most important links between biological and physical forcing factors on barrier islands is the effect of dune-building grasses on landform stability (Godfrey and Godfrey 1976). The composition of sediments plays an important role in the rate of sediment erosion and thresholds for the onset of different modes of erosion. Vegetation stabilizes dunes and alters the physical properties of sediment in two distinct ways: by adding an extensive root system and by altering sediment structure (reviewed in Feagin et al. 2015). The dune topography on barrier islands is influenced by the interplay between vegetation and sand transported by prevailing winds. Sand accumulates around plants, which reduces local surface wind below the canopy surface, forming small hills (Hesp 2002). These embryonic dunes may grow and merge depending on sand supply and the growth characteristics of plant species (Hesp 2002).

Many coastal grasses respond to sand burial by vertically elongating following deposition (Emery and Rudgers 2014); however, different species affect topography in various ways. For example, *Ammophila breviligulata* and *Uniola paniculata* are stimulated to grow by sand burial, thereby facilitating further deposition and creating a dune-building feedback (van der Stoel et al. 2002). Although both species are stimulated by burial, the species differ in the way they vegetatively propagate. *Ammophila breviligulata* produces a network of horizontal rhizomes to stabilize substrates (guerilla strategy), and *U. paniculata* exhibits a dense compact growth form that binds substrates (phalanx strategy; Stallins 2005). The effect of the different strategies is seen in the types of dunes formed (ridge versus hummock; Stallins and Parker 2003). Species
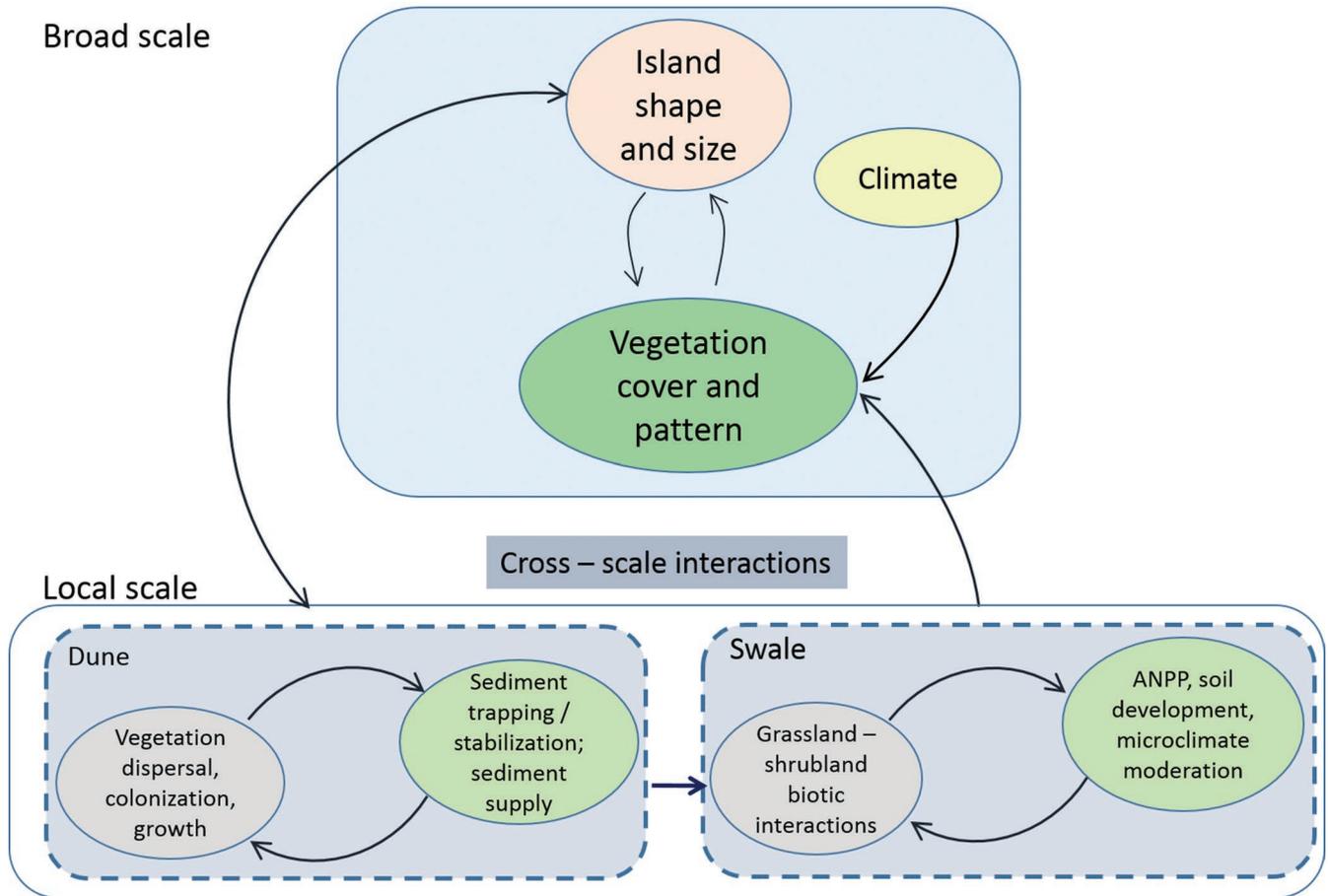
Figure 1. A geographic and ecological framework for cross-scale interactions between vegetation and sediments that influence barrier-island shape and size. Within dunes, interactions between vegetation and sediments determine dune morphology. The resulting dune types affect physical disturbance and determine community patterns in the swale. The interactions between swale grasses and shrub seedling establishment lead to shrub thicket development and associated increases in aboveground net primary productivity, soil C and N, and microclimate moderation. As islands develop, different configurations of dune–swale topography feed back with island shape and size and ultimately determine island response to sea-level rise and storm intensity. Design inspired by Heffernan and colleagues (2014).

that support dune building may be classified as "ecosystem engineers" because the induced change in ecosystem structure affects all subsequent aspects of ecosystem development and adjacent systems (Stallins 2005).

Dune–swale interactions

Unlike other temperate communities (e.g., terrestrial forests), where changes in plant-species composition occur over hundreds of meters in elevation because of changes in mesoclimate, the effects of elevation in coastal ecosystems can be observed over just a few centimeters and are primarily related to disturbance (Young et al. 2011). An adequate supply of sediment and the presence of dune-building grasses can transform narrow, flat, sparsely vegetated islands with frequent overwash to topographically complex, heavily vegetated islands (Durán Vinent and Moore 2015). Over decades and in conjunction with prevailing patterns of aeolian and surge-driven sediment transport, these dominant,

dune-building species create ecological–topographic feedback, which we discuss later. This feedback results in barrier islands differing in vegetation type and topographic features on islands with regressive shorelines. Dune-building processes are important for interior swale development and provide the first line of defense for protection against disturbance.

Major shifts in plant community assemblages in barrier systems have been attributed to biogeomorphic processes (Battaglia et al. 2007, Young et al. 2007, Vallés et al. 2011). Along the Atlantic and Gulf coasts, major plant shifts have occurred because of range expansion in woody shrubs (Battaglia et al. 2007, Young et al. 2007). The dominant woody species on Atlantic barrier islands, *Morella cerifera* (formerly *Myrica cerifera*), forms a symbiotic relationship with the nitrogen-fixing bacterium *Frankia*, which allows for increased growth in an otherwise nitrogen-limited environment (Young 1992, Knapp et al. 2008, Brantley
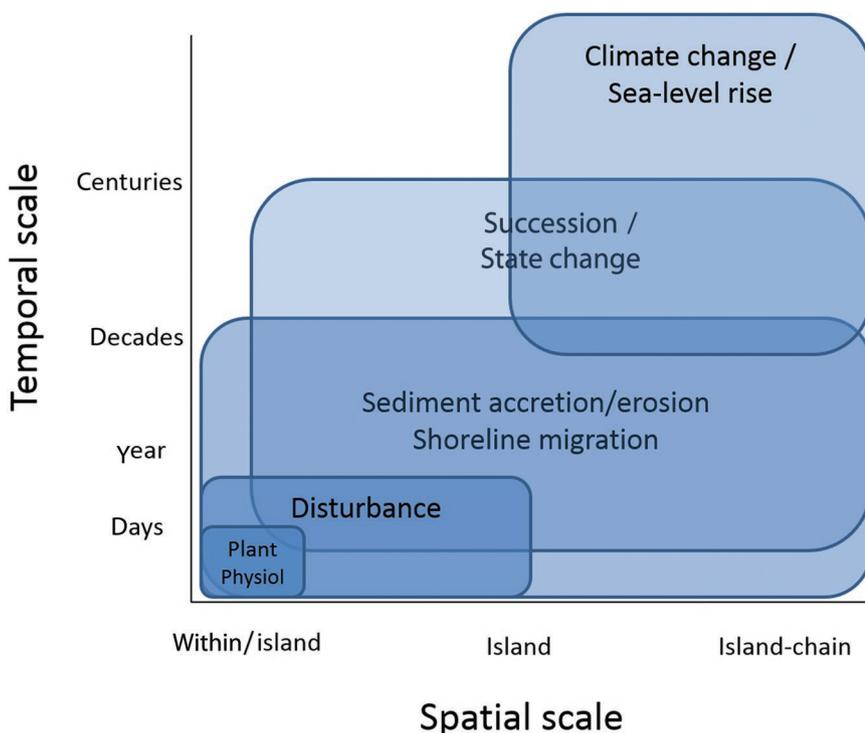
Figure 2. Important abiotic and biotic processes shape barrier islands in space and time. The significant area of overlap indicates cross-scale interactions. Plant physiological responses operate at small spatial-temporal scales but are influenced by larger-scale factors of disturbance, sediment movement, and climate change. Plant succession and state change overlap in space and time with abiotic factors.

and Young 2010). At the VCR, woody cover (primarily *M. cerifera*) has increased by 40% over 27 years (Zinnert et al. 2016b). Dune ridges may enable the establishment of woody vegetation by reducing the abiotic disturbance to the interior island because many woody species found in barrier islands are salt sensitive (Ehrenfeld 1990). Increased woody vegetation affects barrier-island response to storms and sea-level rise. In the short term, woody vegetation provides stability by protecting coastal communities from hurricane damage (Claudino-Sales et al. 2008, Arkema et al. 2013, US Army Corps of Engineers 2013); however, the physical stabilization of sediments and the resulting barrier to overwash create resistance to island migration with sea-level rise. The interplay between local-scale dune growth and upland vegetation is influenced by biotic processes that are often overlooked because of the strong physical forces shaping barrier islands.

Key biological controls on plant communities

Plant communities on barrier islands vary considerably, but some general patterns can be observed that are strongly related to island geomorphology (table 1). Controls on plant communities in any system can be conceptualized as a series of three environmental filters that reduce the overall potential species pool (Lambers et al. 1998). The first and coarsest of these filters is the dispersal of propagules from the regional species pool. The arrival of viable plant propagules is the antecedent control over all other community processes on barrier islands. The three primary modes of dispersal that affect barrier-island community composition are wind, water, and animal dispersal (Ehrenfeld 1990). The relative geographic isolation of barrier islands makes specialized dispersal mechanisms particularly important in shaping community composition, but the relative importance of these three modes of dispersal to a specific island depends on a complex combination of regional, landscape, and island-level drivers (Ehrenfeld 1990, Young et al. 2007).

Dispersal. Community structure is often strongly linked to dispersal rates, which are dependent on both landscape characteristics and disturbance type and frequency. At the island scale, frequent storm exposure and long shorelines increase the probability of water-borne seed deposition from floating vegetation debris (i.e., wrack). Rapid recolonization and high vegetation density have been observed in overwash zones after major storms because of water-borne dispersal (Snyder and Boss 2002), and higher species richness may occur in low-elevation, frequently disturbed overwash zones compared with undisturbed areas (Brantley et al. 2014). Moving inland, water dispersal becomes less important as colonization and recruitment become dependent on disturbances, such as wind throw and gap formation, that open new habitats for incoming propagules (Crawford and Young 1998). In these relatively stable communities, more localized disturbance opens new habitat and promotes the recruitment of certain propagules, especially fleshy-fruited species that tend to be dispersed by birds (Crawford and Young 1998). These conditions tend to favor the recruitment of long-lived species, including perennial grasses and woody species.

Avian dispersal is one of the most important dispersal mechanisms and is neither random nor homogenous across space and time. Islands with an abundance of woody vegetation, such as *M. cerifera*, provide perches and are an important food source for migrating birds (Mabey et al. 1993). As a result, islands with existing patches of woody cover are often characterized by the increased dispersal of additional fleshy-fruited plant species reinforcing the recruitment of woody plants (table 1; Shiflett and Young 2010). Avian dispersal is strongly related to island size, both for introducing woody species to barrier islands (Shiflett and Young 2010) and maintaining genetic diversity within established

Table 1. Hypothesized abiotic and biotic characteristics of the regions of barrier-island state space.

	High positive relief	Resisting	Reinforcing	Low and negative relief
Disturbance				
Overwash frequency	Very low	Low, attenuated by vegetation feedback	High, attenuated by vegetation feedback	High
Resilience	Very high resistance–low resilience	High resistance–high resilience	Low resistance–high resilience	Very low resistance–low resilience
Landforms	High single dune ridges	Multiple dune and ridges	Relatively flat, low topography	Minimal relief or negative topography
Relative exchange with adjacent systems				
Local sediment budget	Surplus	Low net gain	High net gain	Deficit
Nutrients	Increasing terrestrial inputs	Terrestrial and marine inputs	Terrestrial and marine inputs	Increasing marine inputs
Biological characteristics				
Dominant life history	r-selected	K-selected	K- and r-selected	r-selected
Dominant plant functional type	Dune-building grasses	Dune-building grasses; burial-intolerant stabilizers; woody species	Dune-building grasses and burial-tolerant stabilizers	Burial-tolerant stabilizers
Structuring process	Niche (species sorting based on dispersal mechanism and stress tolerance)	Niche (species sorting based on competition)	Niche/neutral (less species sorting approaching a random distribution)	Niche (species sorting based on dispersal mechanism and stress tolerance)
Species richness	Low	Low to high (depending on woody species)	High/very patchy	Low/few dominants
Woody cover	Low (<5% island area)[a]	High (>10% island area) [1]	Low	Absent or low
Woody species richness	Low (3–4)[b]	High (>10)[2]	Low/few dominants	Absent or low
ANPP	Low (<350 g per m^2)[c]	High (>500 g per m^2)[3]	Low to high	Low

Abbreviations: ANPP = annual net primary productivity. [a] Zinnert et al. 2016b. [b] McCaffrey and Dueser 1990. [c] Knapp et al. 2008.

populations (Erickson et al. 2004). As island size and woody cover increase, productivity and suitability of island habitat (i.e., food and cover) also increase (table 1).

Physiological limitations. Dispersal to an island is balanced by extinction rates, and the interplay between these processes ultimately determines long-term community composition (MacArthur and Wilson 1963). Physiological filters determine the germination and establishment success of viable seeds. Barrier-island environments are characterized by steep physical gradients (Ehrenfeld 1990, Young et al. 2011). Although the effects of these gradients have been extensively studied on extant plant communities, few studies have specifically documented the effects of physical stresses on the success rates of plant propagules. Among the most important of these physical stresses are high wind and wave energy, saline sea spray, lack of fresh water, and extremely low levels of soil nutrients (Art et al. 1974, Maun 2009, Young et al. 2011). Distance to shoreline and elevation above sea level play a crucial role in reducing exposure to these stresses and reducing the frequency of exposure to severe disturbances such as storm overwash (Young et al. 2011). Although higher inland sites are characterized by less exposure to disturbance, there are trade-offs. Higher elevation reduces the likelihood of exposure to saltwater flooding but increases the distance to fresh groundwater, which limits the

diversity, growth, and cover on inland dunes (Maun 2009, Young et al. 2011).

Nutrient dynamics are one of the more complex drivers of vegetation distribution, diversity, and productivity and affect the physiological success of species across barrier islands from strand to dune to inland habitats (Art et al. 1974). On the strand and in young foredunes, sand may have nearly undetectable levels of key nutrients such as nitrogen, phosphorus, and potassium, as well as many necessary trace minerals (Art et al. 1974, Day et al. 2004, Brantley and Young 2010). Soil nutrient concentrations generally increase inland, but this trend is affected by soil age, site history, and community composition (Brantley and Young 2010). In some cases, nutrient stress may increase in inland habitats because many plant species benefit from the micronutrients delivered by sea spray and the nutrients rapidly leached out of sandy soils, especially on interior dunes, making nutrient-use efficiency an important characteristic of barrier-island vegetation (Art et al. 1974, Day et al. 2004). Adaptation to nutrient stress takes varied forms, including physiological adaptations such as nitrogen fixation (Bond 1951, Brantley and Young 2010) and morphological adaptations such as evergreeness and specialized rooting strategies (Ehrenfeld 1990).

Biotic interactions. The third and final filter controlling community assemblage comes from biotic interactions. On

Figure 3. A configuration of dune topographic states and their relationship with plant functional types. **MWH** *is mean high water line (after Stallins 2005).*

may intensify, and diversity may decline (Pennings and Calloway 1992, Maun 2009, Brantley et al. 2014). Perhaps the most abundant resource, light, on the strand may become a major limiting factor for inland plants.

Community assemblage on barrier islands depends on a complex suite of drivers that span scales from the microclimate of individual plants to the region. These drivers are often the same as geomorphic drivers such as island size, shape, and position, sediment supply, and climate. Although complex, some clear patterns in community structure tend to emerge across island domains, and community characteristics tend to vary consistently by island state (table 1).

Ecological–topographic feedback in barrier-dune state space

Although ecological factors across a range of scales shape plant communities (figure 2), plant communities also modulate abiotic components of the landscape (figure 1; Chapin et al. 1997, Corenblit et al. 2011). Through impacts on topography, dune plants shape their habitat and can reinforce persistence in the landscape in a positive feedback. Dynamics that confer this persistence of system structure and function define its resilience. In this article, we define *resilience* as the amount of disturbance that a system can absorb while still remaining within the same state (Scheffer et al. 2015). A stretch of coast may exhibit multiple topographic "state" configurations arising from the relationship between vegetation and elevation (Hayden et al. 1991, Stallins 2005). These configurations interact with local-scale physical or ecological processes and broadscale island shape and size to generate contrasts in ecosystem function between and within individual islands and ultimately shape properties of the barrier-island landscape.

Stability domains. Two resilient states, known as *stability domains* (Gunderson 2000), have been identified in results from models that include one species of vegetation and physical processes associated with high-water events for barrier-island dunes (figure 3; Dúran Vinent and Moore 2015, Goldstein and Moore 2016). They develop out of feedback among dune vegetation, topography, and overwash disturbance. The concept of stability domains is based on work by Godfrey and Godfrey (1976), as was later refined by Stallins (2005). Analogs of these barrier-dune stability domains and their ecological relationships were

accreting shorelines or after disturbance, highly specialized dispersers tolerant of the harsh physical stresses represent early successional, or pioneer, species. These species are often quickly replaced by more generalist species and communities may resemble old fields. Like old field communities on the mainland, these communities are transient as competition for resources increases and more competitive species are introduced (Snyder and Boss 2002, Miller et al. 2009, Brantley et al. 2014). Inland plants experience a less stressful maritime physical environment, and in some cases, positive interactions between species (i.e., facilitation) can become an important influence on community composition (He et al. 2013). Biotic interactions among coastal grasses, especially facilitation in high-stress dune environments, can promote species co-existence (Zarnetske et al. 2013) and influence dune-building processes. However, in the most undisturbed sites with stable communities, competition between species

(a) Disturbance-resisting domain
(Sapelo A)

3.9 m

0.0 m
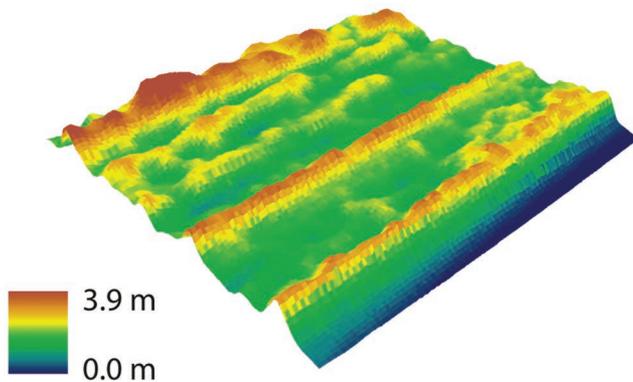
(b) Disturbance-reinforcing domain
(S.Core Banks B)

4.0 m

−0.2 m
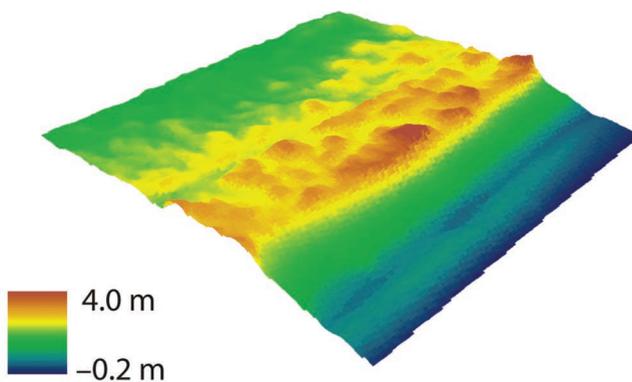
Figure 4. The representative domain topographies of barrier-island dunes. The vertical scale is exaggerated. (a) Sapelo A, an example of the overwash-resisting domain; plot size = 111 meters (m) × 111 m. (b) South Core Banks B, an example of the overwash-reinforcing domain; plot size = 161 m × 161 m. The island locations and detailed methods are provided in Monge and Stallins (2016).

identified in a range of other systems throughout the early 2000s (Folke et al. 2004). In our framework for each stability domain that includes the dune–swale complex, topography-modifying plants adapt to overwash disturbance by minimizing variability, either by making disturbance more regular or by limiting it. However, along barrier coasts where topographies and plant functional types are intermediate of these domain configurations, bistability at the local scale may develop (figure 3; Dúran Vinent and Moore 2015, Zinnert et al. 2016a).

On a disturbance-reinforcing barrier-island site, the greater richness and abundance of species such as *Spartina*

patens maintain low, flat topography and increase the likelihood of future overwash (figure 4). *Spartina patens* does not build dunes but recovers quickly following burial during overwash to bind sediments in place with its laterally extensive rhizomes. With frequent overwash events, burial-tolerant stabilizers such as *S. patens* may decrease resistance to future overwash exposure through effects on topography (table 1). Sites in the reinforcing domain may be characterized by either niche or neutral community-assemblage rules as physiological stress diminishes and wind-borne annual plants dominate new dispersal in some habitats, especially older, protected swales where plant communities tend to resemble those of old fields (Brantley et al. 2014). Conversely, on disturbance-resisting islands, dominant plant species promote dune and swale topography and reduce overwash disturbance (figure 4). Dune-grass species that augment the vertical development of dunes, including *Uniola paniculata*, and highly competitive, bird-dispersed woody species that stabilize protected microhabitats (e.g., swales) enhance greater topographic roughness to resist overwash (table 1).

The elevations over which these domains develop do not span the full range of dune elevations exhibited along barrier coasts. Therefore, not all dune systems may exhibit this resilience-generating feedback. The predominant source of variability for barrier dunes is topographic relief, positive and negative (figure 5). One must consider that resilience is a multidimensional concept (Donohue et al. 2013, 2016) that invokes resistance to perturbations, as well as the resilience to recover from them once they occur. Domain states maintain a balance of resistance and resilience, whereas positive- and negative-relief regions of state space do not.

Sites with high positive relief are characterized by a high single dune ridge dominated by dune-building grasses but low species richness. These sites have a surplus of sediment and the potential for more than one line of dunes. There is little woody cover directly on the dunes, but it may colonize protected areas behind the dunes (table 1). High dune ridges offer resistance to storm disturbance and minimize overwash frequency. These sites have low resilience because they have low to no cover of burial-tolerant stabilizers in the landscape (figure 3). By strongly resisting incursions of overwash, these sites are more likely to erode over time. With significant erosion or catastrophic events, these sites can convert to negative relief (discussed below). Disturbance-resistant domains have higher resilience than high positive-relief sites because they are not as resistant to overwash. Their lower elevations permit the occasional overwash event (Houser et al. 2008) to maintain disturbance-adapted species in the landscape. The resilience to recover from perturbations and maintain system structure and function is greater.

Conversely, sites with negative topographic relief result from significant erosion. These areas are dominated by species adapted for water-borne dispersal and physiological tolerance to stress. Because of high overwash frequency, burial-tolerant stabilizing species dominate (i.e., *S. patens*),

(a) Positive relief (Canaveral B)

(b) Negative relief (Parramore D)

5.2 m
0.2 m

1.9 m
0.3 m
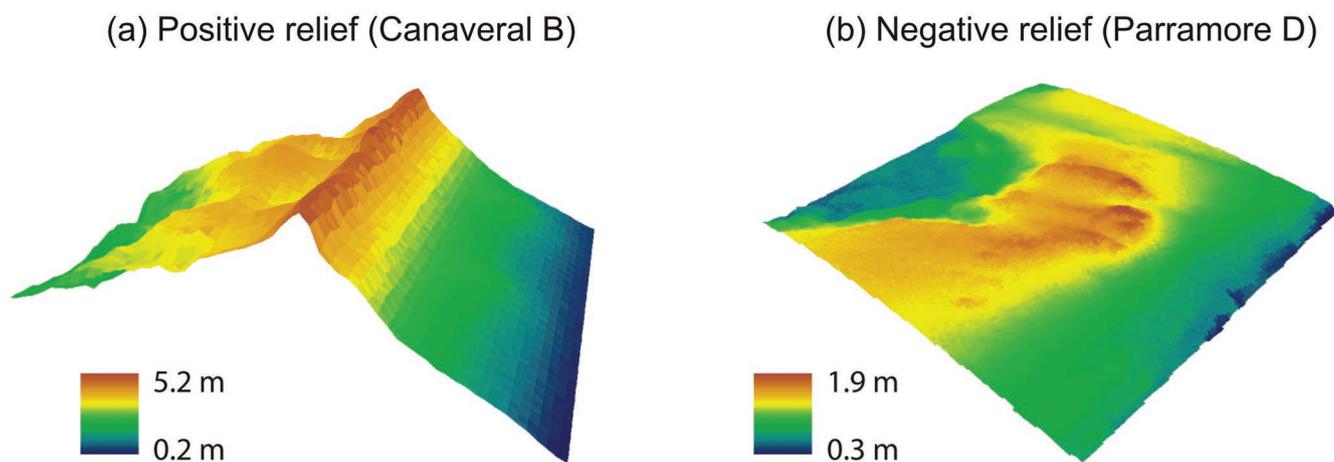
Figure 5. Topographies representing variability in barrier-island dunes. The vertical scale is exaggerated. (a) A high positive relief of plot B on Cape Canaveral; plot size = 62 meters (m) × 62 m. (b) A negative relief of plot D on Parramore Island; plot size = 184 m × 184 m. The island locations and detailed methods are provided in Monge and Stallins (2016).

and woody species are low to absent, resulting in low diversity (table 1). Negative relief sites have a very low resistance to overwash. Disturbance is frequent, and sediment supply is limited, thereby interrupting the development of positive topographic relief that could increase resistance. Disturbance-reinforcing domains acquire a greater cover of burial-tolerant dune plant species. This augments topographic resistance enough to allow feedback between plants and sediment mobility to augment resilience. Depending on the frequency of extreme disturbance events, these sites may convert to disturbance-reinforcing domain if dune-building grasses can establish enough cover. The type of transition between states may be gradual or abrupt depending on their initial location in state space (Monge and Stallins 2016) and the frequency or intensity of strong disturbance events.

The reinforcement of stability domains by plant functional types. In barrier-dune stability domains, dune plants shape the environment to reinforce a resilient configuration of topography and plant functional type abundances. Plant engineer species with strong functional roles related to topography can be conceived as driver or foundation species. They can be contrasted with passenger or stochastic species (Peterson et al. 1998, Angelini et al. 2011), plants whose roles may be weaker or more indirect for persistence of system structure and state. In barrier islands, three groups of driver species can be defined on the basis of their functional role in responding to sediment burial and shaping topography: burial-intolerant species, burial-tolerant stabilizers, and dune-builders. The evenness and richness of these driver species vary along shore in tandem with the prevailing overwash disturbance regime (figure 6; Stallins 2005). Via their modification on topography, the local assemblage of plant functional types respond to the prevailing disturbance regimes in a way that promotes conditions for their persistence (Corenblit et al. 2011).

The challenge to comprehending the mechanistic responses to sea-level rise and future storm inputs is that physical and biotic processes in these domains operate across a range of scales (figure 2). The concept of ecological topology (Prager and Reiners 2009) recognizes that there are different ways to represent space other than in explicitly geographic terms. Over the past two decades, resilience properties have been inferred from state space approaches that track system dynamic properties in time and space (Anderson et al. 2008, Scheffer et al. 2015). Because dunes reflect a topographic signature of their vegetation, mapping the diversity of topographies within an island or across multiple islands provides insight into the underlying properties of distinct regions of topography and the level of resilience they may exhibit. This state space captures the range of topographies that can develop under the permutations of vegetation composition, geomorphic context, and disturbance. It documents what topographies are possible out of all of these combinations. From this, one can further characterize the degree a particular assemblage of plant functional types, ecosystem properties and topography can self-organize in response to the dynamism of inputs and controls along sandy barrier coasts (table 1).

Examples from mid-Atlantic barrier islands. Based on a multivariate classification of lidar-derived dune topographies from six barrier islands along the southeastern United States, plots from an individual island can exhibit topographies indicative of both stability domains (figure 7). Plots near the center of topographic state space may represent more bistable topographies (Stallins 2005, p. 426 and figure 12). There, elevations and plant functional abundances that reinforce topographic development may not simultaneously reinforce or resist disturbance, leading to a bistable state in which one or the other domain would be expressed.
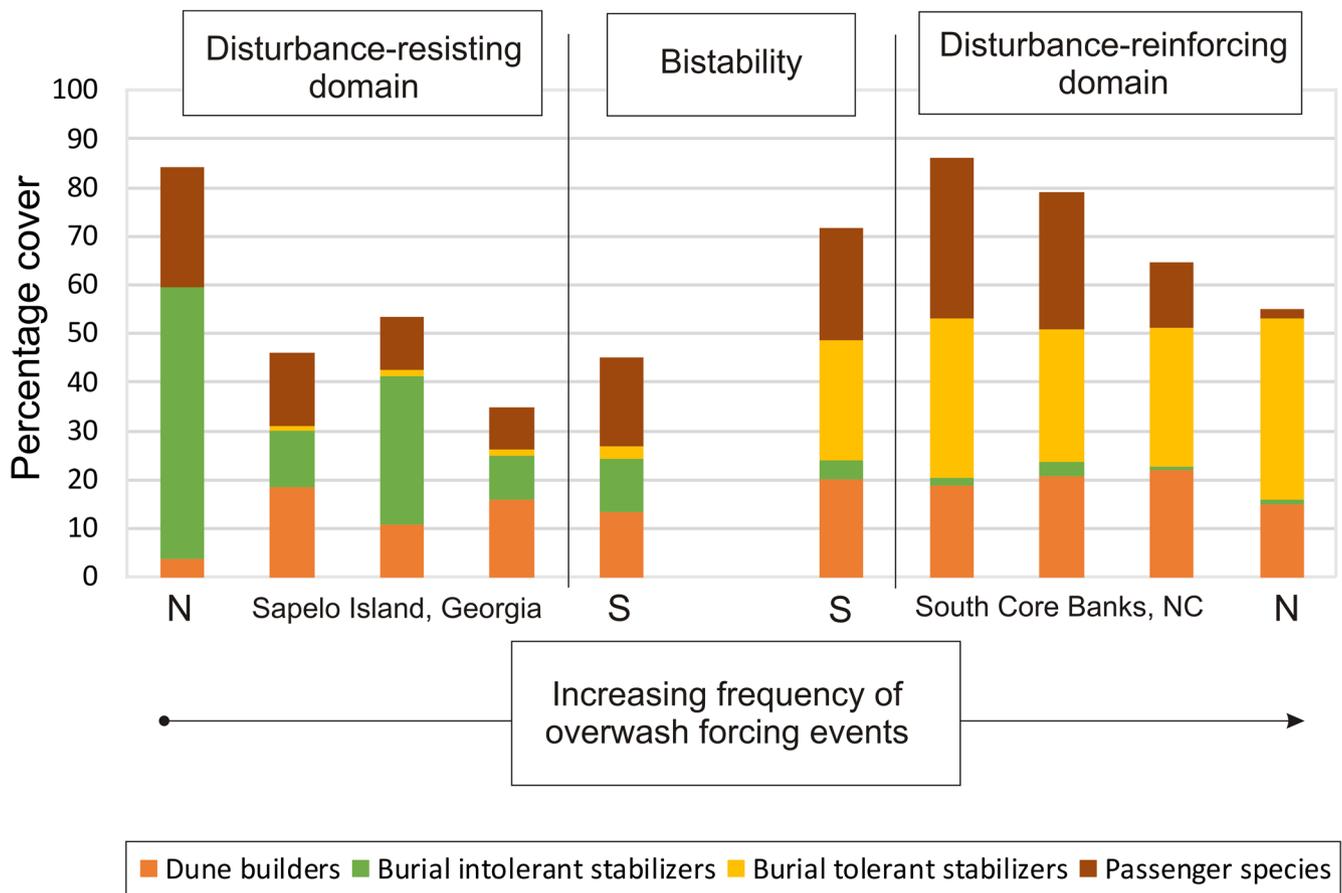
Figure 6. The distribution of plant functional type abundances spanning a regional macroclimatic and north-to-south within-island overwash disturbance exposure gradient. Each column represents a site within the island. Sapelo Island, Georgia, has a greater cover and richness of dune-building species and burial-intolerant plants that contribute to its ridge and swale topography. South Core Banks, North Carolina, has many of the same dune plants, but their functional abundances differ in response to exposure to more frequent potential overwash-forcing events. A greater abundance and richness of burial-tolerant stabilizers and dune-building species contribute to feedback that can reinforce overwash contagion. The island sites, data, and methods are provided in Stallins (2005).

Because a variety of geomorphic conditions can be expressed along a stretch of coastline, there is a heterogeneous distribution of resilience and underlying patterns in topography and vegetation. Resilience can vary between islands and within islands, because topographies range from more persistent, resilient states to those that are bistable or transitory. Barrier islands function in a complex and multidimensional framework and both net sediment exchange and influence of vegetation operate at local scales (Durán Vinent and Moore 2015, Zinnert et al. 2016a). Island wide generalizations are useful, but do not account for variations in local resilience and may oversimplify highly dynamic biotic and physical interactions that shape the heterogeneous barrier-island landscape including plant functional type distribution and resulting feedback (Hayden et al. 1991, Stallins and Parker 2003, Stallins 2005, Young et al. 2007, Brantley et al. 2014, Zinnert et al. 2016a). For example, on Parramore Island, topography varies enough such that one of the island sites shown in figure 5 is more similar to

topographies from another region of state space. This particular site has a topography that resists overwash, which is frequent and spatially extensive on other sites of the island (figure 8).

Linking models to ecological mechanisms: Multiple states of equilibrium

The concept that barrier islands can exist in a range of states has been driving long-term research at the Virginia Coast Reserve for nearly three decades and continues to be an important foundation of the research at the VCR (Hayden et al. 1991, McGlathery et al. 2013, Durán Vinent and Moore 2015, Zinnert et al. 2016b). As previously discussed, islands may exist within a broad, multidimensional range of states depending on the relative influence of the various drivers and ecological processes (Hayden et al. 1991, Beisner et al. 2003, Houser 2012). A subset of these potential states may be considered resilient if a significant disturbance or set of disturbances is needed to move the system to an alternate
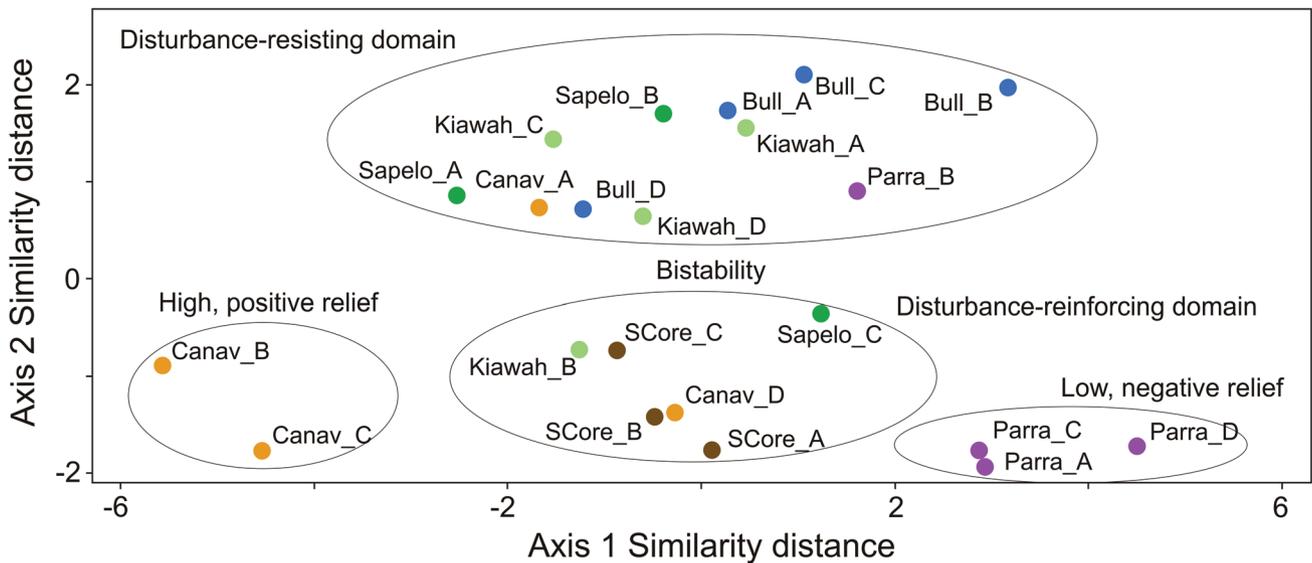
Figure 7. The ordination-derived topographic state space for three-dimensional dune topographic variables extracted from airborne lidar data for six barrier islands along the US Atlantic coast: Cape Canaveral, Florida; Sapelo Island, Georgia; Bull Island, South Carolina; Kiawah Island, South Carolina; South Core Banks, North Carolina; and Parramore Island, Virginia. The letters A, B, C, and D designate the dune topographies sampled from north to south, respectively, on each island. The first and second axes captured 59% and 21% of the variance, respectively. The variables included descriptive elevation statistics, landscape indices for patch structure of similarly ranged elevations, and the unidirectional spatial autocorrelation structure of elevation. The separation of sites in state space reflects their multivariate topographic similarity as measured in units of Euclidean distance. The island locations and detailed methods are provided in Monge and Stallins (2016).

state (Beisner et al. 2003). However, there is no truly stable equilibrium state for a barrier island because external forces, in the form of sediment and vegetation inputs, are constantly needed to maintain island integrity in these inherently unstable systems (figure 9). For simplicity, the multiple complex drivers can be distilled into two surrogate characteristics that represent abiotic (physical) and biotic (ecological) influences. Respectively, these are net sediment supply and influence of vegetation on island stability. These two properties set boundary conditions within which specific topographies and resilience properties can develop.

The role of disturbance. Disturbance is key to understanding transitions among regions in state space. With disturbance, a section of coast can be "pushed" from one region in state space to another, with increases or decreases in resilience. Disturbance can be a single, acute "pulse," such as a major coastal storm, or a longer-lasting, chronic "press," such as sea-level rise or a gradual change in longshore currents that affects sediment supply (Hayden et al. 1991, Oertel and Overman 2004). For example, a severe coastal storm may flatten dunes, cause severe local erosion, expose terrestrial plant communities to saltwater intrusion, and/or destabilize biophysical processes driving dune building and maintenance (Davis and Dolan 1992, Snyder and Boss 2002, Claudino-Sales et al. 2008, Houser et al. 2008, McBride et al. 2013).

These changes may be of sufficient magnitude to cause a shift of a coastal strand or an entire island toward a less resilient position in state space dominated by low- and negative-relief topographies. Recovery to a resilient, disturbance-reinforcing state would be contingent on whether or not the altered plant community (both surviving members of the predisturbance community and new colonizers) can self-organize in tandem with available sediment. In many cases, storms may deposit large amounts of new sand or move sand from one area to another, providing new substrate for the establishment of new dunes and other communities (Oertel and Overman 2004, McBride et al. 2013).

Local vegetation type and cover can strongly influence barrier-island response to disturbance (Corenblit et al. 2011). As we previously discussed, burial-tolerant stabilizers are more resistant to overwash. In areas where parallel dunes and swales develop (resisting domain), extensive woody vegetation augments resilience (Scheffer et al. 2015) by allowing the system to absorb disturbance while remaining within the same state. However, over longer time frames, extensive woody cover blocks sediment transfer (Claudino-Sales et al. 2008) and causes extensive shoreline erosion. Conversely, grassy swales with little to no woody vegetation and disturbance-reinforcing areas with increased abundance of burial-tolerant stabilizers promote overwash and, ultimately, island migration. This has particular relevance for coastal
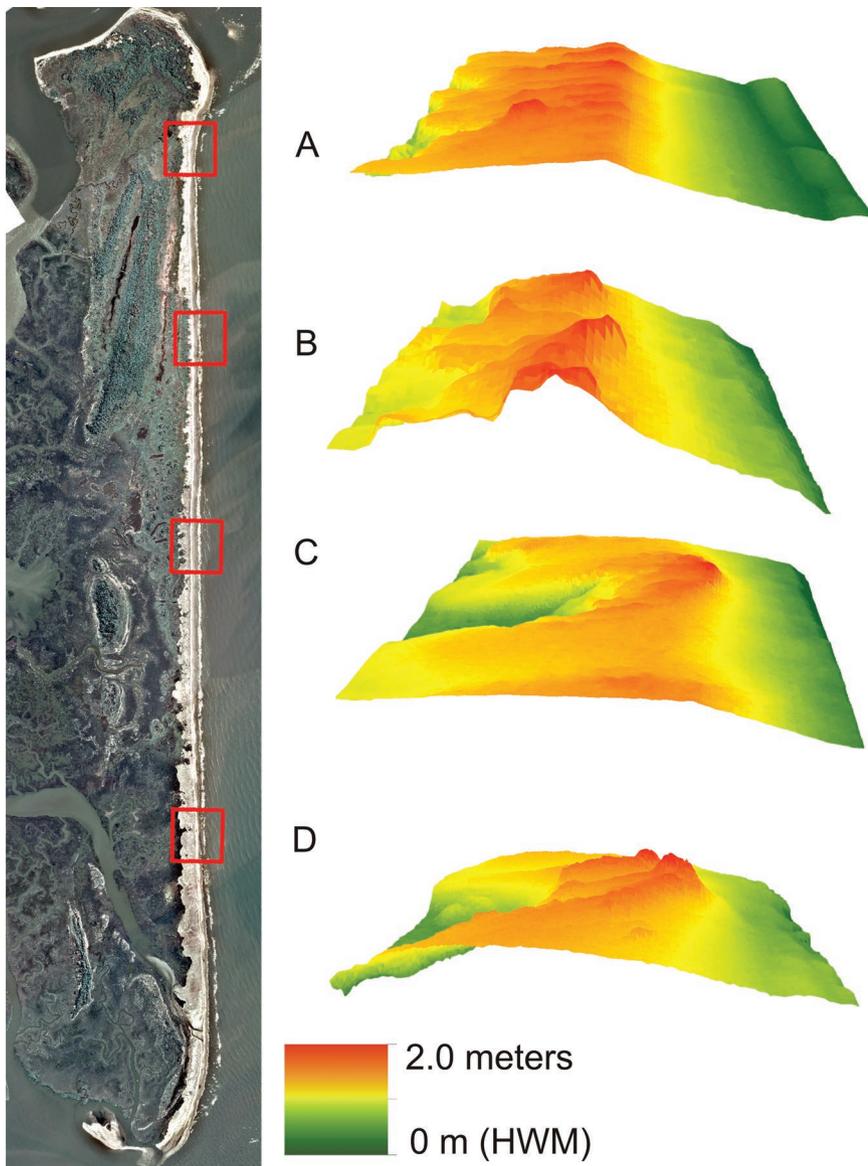
Figure 8. The dune topographies constituting state space for Parramore Island, as is shown in figure 5. The elevations are relative to the high water mark. The vertical relief has been exaggerated five times larger to bring out topographic contrasts. Site B has a topography characteristic of a disturbance-resisting domain. Sites A, C, and D are characteristic of negative relief and do not exhibit the resilience of the reinforcing domain. The areal dimensions of each site vary, although they are scaled similarly visually here: A, 140 meters (m) × 140 m; B, 73 m × 73 m; C, 153 m × 153 m; D, 185 m × 185 m. Detailed methods are provided in Monge and Stallins (2016).

plant functional roles takes many different forms (Shugart et al. 1988, Rastetter 1991, Durán Vinent and Moore 2013, Bel and Ashkenazy 2014, Plant et al. 2016). Creating models with reduced complexity (such as cellular automata) has also been suggested as a relevant tool for testing hypotheses related to vegetation or geomorphology in an ecological context (Baas and Nield 2010, Corenblit 2011). However, by mapping topographic state space using lidar from satellite or ground-based platforms, a sampling frame can be created that allows for the integration of ecological processes and encourages the inference of pattern and process. In this data-driven approach (Sagarin and Pauchard 2009), regions of topographic state space can be sampled to test hypotheses about the role of plant functional types and their influence on ecosystem properties. From the identification of discontinuities and aggregations in this state space (Nash et al. 2014), it may be possible to predict, or model, under what general conditions dunes or swales are more likely to play a self-organizing resilient function (Rastetter 1991) in wave and storm-surge attenuation, in erosion reduction, and in the longer-term maintenance of the coastal profile at larger scales.

Conclusions

The ability to predict future state change under various climate-change scenarios and to forecast changes in key ecosystem services provided by barrier systems, such as storm buffering, the support of commercial fisheries, carbon or nutrient sequestration, and wildlife habitat, is dependent on identifying the characteristics of different regions of barrier-island state space. To make these predictions both accurate and relevant for coastal conservation and management (Grimm et al. 2013), models must incorporate considerations of the spatial relationships across scales and the key aspects of ecological theory summarized herein. Barrier-island chains such as the VCR and those along the southeastern US Atlantic coast offer a range of environmental drivers that necessitate cross-scale studies in order to interpret ecosystem-level responses to climate change. Understanding physical and ecological interactions and how they affect sediment transfer processes is necessary for predicting barrier-island state change at the local

management in short-term stabilization (e.g., dune-building grasses and woody vegetation; US Army Corps of Engineers 2013) and long-term barrier-island persistence.

Identifying and quantifying the effects of key plant functional types on sediment dynamics at both local and landscape scales are crucial in predicting barrier-island resilience in the face of climate change. Incorporating abundances of key plant functional types in both dune and swale habitats is a logical step for current models in use. The modeling of

Figure 9. A hypothetical representation of the relative stability of various barrier-island domains. Resisting domains (1) can exist in multiple alternate states of stability determined by the relative influence of sediment supply and vegetation. High-relief domains (2) are influenced less directly by woody vegetation but are highly influenced by dune builders and depend on ample sediment supply. Reinforcing domains (3) are highly dependent on constant sediment supply for stability and may be characterized by increasing (shown) or decreasing vegetation influence. Negative-relief domains (4) are highly unstable and may be represented by areas where the influence of vegetation has declined, perhaps because of saltwater intrusion or another disturbance, or where vegetation has never established because of dispersal limitations and/or physiological stress. The combination of these domains ultimately determines island response to storms and sea-level rise.

scale (Durán Vinent and Moore 2015) and at broader scales. Differences in species characteristics that promote dispersal, tolerance to physical stress and disturbance, and competitive ability all have a major influence on the dynamics of barrier-island communities. State-space approaches provide a framework to initially visualize and then hypothesize and test mechanisms related to ecological influences on barrier islands. State space provides an integrated link between local-scale and broadscale processes.

Acknowledgments

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