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Invited review

Interdependence of geomorphic and ecologic resilience properties in a geographic context

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ABSTRACT

Ecology and geomorphology recognize the dynamic aspects of resistance and resilience. However, formal resilience theory in ecology has tended to deemphasize the geomorphic habitat template. Conversely, landscape sensitivity and state-and-transition models in geomorphology downweight mechanisms of biotic adaptation operative in fluctuating, spatially explicit environments. Adding to the interdisciplinary challenge of understanding complex biogeomorphic systems is that environmental heterogeneity and overlapping gradients of disturbance complicate inference of the geographic patterns of resistance and resilience. We develop a conceptual model for comparing the resilience properties among barrier dunes. The model illustrates how adaptive cycles and panarchies, the formal building blocks of resilience recognized in ecology, can be expressed as a set of hierarchically nested geomorphic and ecological metrics. The variance structure of these data is proposed as a means to delineate different kinds and levels of resilience. Specifically, it is the dimensionality of these data and how geomorphic and ecological variables load on the first and succeeding axes that facilitates the delineation of resistance and resilience. The construction of dune topographic state space from observations among different barrier islands is proposed as a way to measure the interdependence of geomorphic and ecological resilience properties.

Contents

1. Introduction: the pluralistic nature of resilience

Accompanying coastal morphological responses to sea level rise and changes in wave climate (Johnson et al., 2015) are the effects of dune plants. Although restricted to the narrow border between terrestrial and marine habitats, dune vegetation is linearly extensive at global extents and can have a significant influence on dune geomorphic processes (Durán and Moore, 2013; Corenblit et al., 2015; Keijsers et al., 2016). Through their adaptations to harsh physical gradients and biotic interactions (Ehrenfeld, 1990; Franks, 2003; Feagin and Wu, 2007), dune plants exert a degree of control over topography, sediment budgets, and the impacts of storm surges and overwash. In this article, we describe how dune vegetation generates resilience and propose a methodology to measure and compare its interdependent geomorphic and ecological components from a spatially explicit, geographic perspective.

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Although less familiar to geomorphologists, formal resilience theory as it has developed in ecology has proliferated across academic disciplines (Westman, 1978; Gunderson et al., 2009; Sundstrom et al., 2016). Although a constructive difference, or pluralism, about how resilience can be defined persists, its meanings has evolved in ecology in a fundamentally cohesive way (Grimm and Wissel, 1997; Desjardins et al., 2015). As a fusion of older concepts from systems theory and ecology (Holling, 1973), resilience theory invokes two kinds of resilience (Holling, 1996; Gunderson, 2000; Donohue et al., 2013, 2016; Standish et al., 2014; Martinez et al., 2017; Table 1). Engineering resilience is resistance to a change or perturbation and recovery around a single, global equilibrium. This resistance component of resilience is derived from more traditional engineering and economic ideas about stability (Holling, 1996). Ecological resilience is the magnitude of disturbance that a system can absorb before the system reorganizes its structure by altering the variables and processes that control behavior. It denotes the potential for recovery around another set of interactions rather than a return to the original state. As resistance, engineering resilience focuses on constancy and predictability. By contrast, ecological resilience focuses on change and unpredictability, attributes related to adaptation and evolutionary design (Holling, 1996). While tempting to conceive of these two types of resilience as independent, they have a degree of collinearity. Ecological systems can have both resilience properties simultaneously (Donohue et al., 2013). They can exhibit varying degrees of resistance to disturbance at the same time they can be resilient in the sense of having the capacity to reorganize into another state if thresholds are exceeded.

Geomorphic concepts similar to these from resilience theory are found in landscape sensitivity (Brunsden and Thornes, 1979; Schumm, 1979; Thomas and Allison, 1993; Brunsden, 2001; Phillips, 2006, 2009). Like resilience theory, landscape sensitivity encompasses the propensities of a geomorphic system to recover from disturbance as well as the propensity for change in state (Downs and Gregory, 1995; Fryirs, 2017). Multiple resilience properties can be operative at once. Phillips (2009) and Phillips and Van Dyke (2016) identify resistance and resilience as two of four properties of change in geomorphic systems. Resistance in this framework refers to intrinsic properties that counter geomorphic expressions of power from floods, wind, or gravity. Resilience is the ability of the geomorphic system to recover from disturbance and the degrees of freedom to absorb or adjust to disturbance. Through the variable expression of thresholds, the impacts of physical disturbances can be filtered and disproportionately attenuated rather than amplified in some geomorphic circumstances. In other cases, small, short-lived inputs to abiotically defined systems can produce disproportionately large and long-lived changes (Phillips and Van Dyke, 2016).

Resilience ideas are also invoked in the application of state-and-transition models (STMs; see review by Phillips and Van Dyke, 2017). State and transition models track changes among singular, qualitative geomorphic and biogeomorphic states. They align with ideas about resilience in ecology through their recognition of multiple scales of causality, threshold responses, and changes of state (Bestelmeyer et al., 2011). Yet despite these ties to ecology, STMs, like landscape sensitivity, do not place as much emphasis on accounting for how organisms and the systems they are embedded in can simultaneously be adapted and resistant as well as resilient and adaptable. Given the ubiquity of biotic influences on earth surface systems, geomorphic conceptions of resilience are partial insofar as they do not incorporate the mechanisms surrounding the emergence and influence of organismal adaptation. In other words, to more fully comprehend resilience from a geomorphic perspective necessitates recognition of biotic adaptations and how they arise through their historical interaction with the environment and other organisms. Plants and other life forms in biogeomorphic systems have the potential to exhibit over time and space different adaptations to physiological and physical constraints. Organisms can evolve a range of trait attributes that can in turn modulate their effect on their local geomorphic context.

Biogeomorphic resilience, as we expand upon it in this article, is an integration of these overlapping geomorphic, ecological, evolutionary, and geographic perspectives (Wohl et al., 2014; Corenblit et al., 2015; Eichel et al., 2016). It can be summarized as the resilience properties generated by the functional capacity of organisms to shape biogeomorphic variability arising from disturbances such that the biogeomorphic conditions and processes that shape these capacities persist. Over the past two decades, a wide variety of animals, plants, and biotic crusts have been shown to resist and redirect what were formerly considered abiotic geomorphic processes (Butler, 1995; Kinast et al., 2013; Viles, 2012). Organism-mediated feedbacks between sediment mobility, landform geometry, and functional traits of plants can confer resistance to disturbance and also facilitate the emergence of self-organizing resilience properties that mold thresholds to change. With changes in the frequency, magnitude, or timing of the historically prevalent disturbance regime, the potential exists for biotic as well as abiotic components to reorganize around a new set of feedbacks. As the primary example for this article, biogeomorphic resilience along barrier island dunes has been postulated to emerge out of feedbacks that select for and canalize interactions between plant functional abundances and these dune processes and forms (Stallins, 2005; Wolner et al., 2013; Durán and Moore, 2015). These feedbacks influence the resistance to disturbances as well as the range of variability exhibited by a dune system before it changes to another state, or stability domain.

Given this foundation, two issues need to be addressed in order to develop a more integrative conceptualization of resilience for coastal vegetated dunes. First, current conceptualizations of barrier dune resilience (e.g., Stallins, 2005; Wolner et al., 2013; Durán and Moore, 2015) generalize the interdependency of its geomorphic and ecological components. Nor do they offer a mechanistic, quantitative descriptions of how the dual aspects of resilience (i.e., engineering and ecological resilience) emerge, coexist, and vary geographically. Ways to tease apart this multidimensional character of barrier island resilience have been suggested (Berry et al., 2014). However, multidimensionality as we employ it here denotes that resilience properties can be partitioned as separate but not necessarily independent axes of resistance and of resilience in statistical space (Donohue et al., 2013). These axes also correlate with parameters in a way that facilitates identification of how the

Table 1
Resilience terms adapted from Gunderson et al., 2009; Allen et al., 2014; Angeler et al., 2014; and Donohue et al., 2016. Phillips and Van Dyke (2016) provided analogous definitions from a more geomorphic perspective.

Adaptive capacity	Variability and turnover in ecological pattern and processes that can promote ecological resilience under changing and/or novel environmental conditions.
Adaptive cycle	Sequence of change accounting for cycles of growth, collapse, and reorganization in complex systems.
Bistability	Potential expression of one or more stability domains or states within the same range of conditions.
Ecological resilience	The magnitude of disturbance that a system can absorb before the system changes its structure by altering the variables and processes that control behavior.
Engineering resilience	In ecology, recovery time of structural and functional attributes to predisturbance conditions, referred to as resistance in this paper.
Resistance	In geomorphology, the ratio of some system variable measured after, compared to before, some perturbation.
Panarchy	Set of hierarchically nested and linked adaptive cycles that determines resilience.
Regime shift	Nonlinear change or shift between stability domains and the panarchies that comprise them. Tipping points and critical transitions are often used in an analogous manner.
Stability domains	Range of structure and function over which a system exhibits resistance and the resilience that emerges from it, as often represented by a ball and cup diagram. A stability domain is also defined by a panarchy and the adaptive cycles that comprise it.

geomorphic and ecological contributions to resilience properties differ. Ecologists and geomorphologists have advocated for a multidimensional approach to resilience (Desjardins et al., 2015; Donohue et al., 2013, 2016; Phillips and Van Dyke, 2016). Yet it frequently becomes collapsed into a singular property. Resilience, in a more rigorous characterization, would quantitatively convey how resistance and resilience covary alongshore and between coastal strands in terms of geomorphic and ecological variables.

Second, the current perspectives on barrier dune resilience have not been expressed in terms of adaptive cycles and panarchies, the formal building blocks of resilience theory (Allen et al., 2014). Adaptive cycles and panarchies can be detected through the distribution of a small set of organisms and the abiotic resources and conditions that sustain them (Holling, 1992; Allen et al., 2006; Nash et al., 2014). Discontinuities in these biotic and abiotic variables can in turn be used to infer resilience properties (Allen et al., 2014; Angeler et al., 2016). What makes these building blocks of resilience particularly useful is that they incorporate the adaptive (i.e., genotypic and epigenetic adaptation) and plastic (i.e., phenotypic plasticity) propensities of biota and their role in modulating abiotic fluxes of sediment and water. While geomorphic processes can be sustained by gravity and forces generated by chemical and physical thermodynamics, adaptation encoded in the interaction among their genotype, phenotype, and environment can also modify the organization of geomorphic systems. Given the ubiquity of the recursive interaction between organisms and their environment, the geomorphic and biological components of resistance and resilience cannot be analyzed separately. As an illustration of this coupling, some plant taxa may promote their fitness and abundance through the acquisition of traits that modify their environment to resist a geomorphic disturbance. Other plant species may promote their fitness and abundance by acquiring traits that lower resistance to this same geomorphic disturbance. Thus the selection of traits promoting the abundance of a plant species can take place through their constructive as well as destructive structural impacts on landforms. Conversely, the recovery and abundance of vegetation may be promoted in situations where landforms are destroyed, as with disturbance-dependent species. Recovery and abundance can be promoted for other species as landforms develop during disturbance-free intervals. Adaptive cycles and panarchies incorporate these kinds of cyclical trends in growth and destruction to explain how resilience properties emerge. They account for an additional causal dynamic shaping resilience: biotic adaptation in light of fluctuations in geomorphic landforms and processes.

To address these two issues, we conceptualize how adaptive cycles and panarchies vary geographically in response to the heterogeneous geomorphic and ecological conditions expressed along sandy barrier island coasts. We qualify how the resilience properties tied to this heterogeneity are reflected in the underlying distribution of dune plant species abundances, their functional traits, topographic conditions, and responses to overwash-forcing events. In this conceptual model, we describe methods to disentangle resistance and ecological resilience. We argue how the structure of data in statistical space (e.g., Prager and Reiners, 2009) can be used to track resilience properties and to compare the relative importance of resistance and resilience from geomorphic and ecological points of view.

We begin by providing a more detailed review of ecological concepts from resilience theory and by reiterating some of its similarities and differences to ideas about resilience in geomorphology. We then summarize the existing stability domain model of barrier dune resilience and reinterpret it in terms of adaptive cycles and panarchies. This reinterpretation is then used to hypothesize how dune biogeomorphic resilience properties can be distributed along a barrier island in more quantifiable, geographic detail. To get to this point though, we additionally have to show how dune ecological and geomorphic metrics can be chosen so that they track adaptive cycle and panarchical structure. Through these tasks, we show how resilience is best understood as something more than a binary in which it is either present or absent. To speak of a biogeomorphic system as resilient or not is misleading, as the presence of a system indicates a persistence of form and function in itself, a resistance to degradation, from which ecological resilience properties can emerge. Interpretations of resilience must account for this complexity.

Indirectly, the conceptual and methodological outlooks developed in this article propose a compromise to debates over how geomorphic versus ecological processes contribute to coastal dune resilience. Some scholars view dune resilience as driven more by geomorphic and meteorological variables that constrain baseline sediment availability, storm impacts, and dune recovery (Houser et al., 2008; Houser, 2013). Other scholars see dune resilience as arising from ecological relationships (Godfrey and Godfrey, 1973; Odum et al., 1987; Stallins, 2005) because dune plants actively shape and are shaped by geomorphic processes and landforms (e.g., Parker and Bendix, 1996; Swanson et al., 1988; Corenblit et al., 2015). But even in this ecology-driven perspective on dune resilience, the mechanisms to explain biological assembly and adaptation are underdeveloped. The attention to mechanism has been replaced by appeals to traditional interpretations of historical and place-based contingency as explanations for qualitative and categorical differences in species abundances and topography among locations with different disturbance regimes. By examining the larger multivariate state space defined by geomorphic properties and by assessing how vegetation shapes space through the iterative, cyclical, adaptationist mechanisms postulated in resilience theory, more nuance can be acquired as to how geomorphic and ecological components of resistance and resilience relate to one another.

2. Resilience theory

2.1. Adaptive cycles and panarchies

Resilience properties arise through the scalar compartmentalization of ecological interactions into adaptive cycles and panarchies (Allen and Holling, 2010; Allen et al., 2014). An individual adaptive cycle demarcates a sequence of environmental and ecological change. As a successional sequence, it proceeds from resource exploitation and rapid growth, to a slower accumulation of structure and biomass, followed by collapse and the potential for reorganization and continued cycling (Fig. 1). A wide variety of terrestrial and aquatic ecological systems have been characterized in terms of adaptive cycles (Gunderson et al., 2002; Walker et al., 2006; Nash et al., 2014; Angeler et al., 2015a, 2015b). In many of these examples, seasonal or multiyear environmentally driven oscillations in species abundances and cyclical

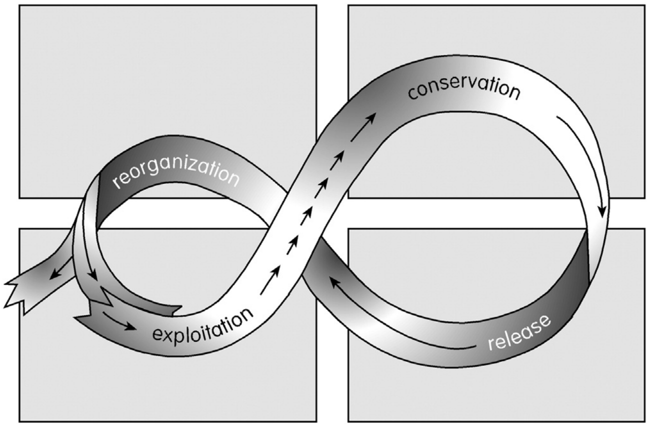

Fig. 1. The four stages of an adaptive cycle. Shorter, closely spaced arrows indicate slowly changing conditions. Longer arrows represent more rapidly changing conditions. In reorganization, the cycle may repeat itself, or it can reconfigure into another cyclical dynamic. The exit arrow on the left represents this potential for reconfiguration. Adapted from Gunderson and Holling (2002).

disturbance are used to define an adaptive cycle (Allen et al., 2014; Stallins et al., 2015).

Holling (1973) invoked the fluctuation of forest vegetation, insect pest outbreaks, and fire disturbance in his original example of an adaptive cycle. It can be generalized into four categories. The reorganization phase of an adaptive cycle begins after disturbance. This initial recovery has low connectivity among abiotic and biotic variables, sensitivity to initial conditions, and a high potential for novelty. In the exploitation phase, ecological development commences. Seeds and plant fragments from the past or from distant sources germinate, and surviving residual vegetation is released. Because connectedness is low, external variability exerts a strong selective influence on biota. Competition for resources begins to increase in the transition to the conservation phase. Connectivity increases, and ecological capital in the form of biomass or other attributes begins to accumulate. These relationships modulate externally driven variability while also reinforcing the abundance of the organisms with functional roles that shape this variability. While this control may be strong, it increasingly operates over a narrower range of conditions. In the release phase, the system has become brittle and subject to disruption. Accumulated capital is released from its bound state, connections are broken and the feedback regulatory control weakens.

The ecological processes underlying these four phases of an adaptive cycle (conservation, release, reorganization, and exploitation) maintain a system within a given structural and functional range. That is, the system exhibits a range of resilience properties as it progresses through these phases. It has the potential to control its structure and function within a bounded region of environmental variability while still allowing for periodic release and reorganization (Desjardins et al., 2015). At the point of reorganization following the release of accumulated capital, the adaptive cycle can repeat itself; or it can reorganize around a new set of cyclical relationships and thus exhibit its defining property of adaptivity.

As with landscape sensitivity and STMs (Brunsden and Thornes, 1979; Thomas, 2001; Bestelmeyer et al., 2011), resilience theory recognizes the importance of cross-scalar dynamics. For resilience properties to develop and persist, adaptive cycles must operate across a range of temporal and spatial extents. Adaptive cycles, each with their own growth and release dynamics, link across scales to form a panarchy (Gunderson and Holling, 2002; Allen and Holling, 2010). The adaptive cycles comprising a panarchy are not stages that replace one another. Instead, they coexist. The resilience properties of a panarchy arise through the linkages among its hierarchically nested adaptive cycles. The higher the number of adaptive cycles in a panarchy, the greater its overall resilience. With more adaptive cycles, the range of variability in structure and function is more deeply entrained.

These cross-scaled linkages between adaptive cycles can be retained, or 'remembered', through biotic legacies, residuals, and other kinds of ecological memory (Peterson, 2002; Allen et al., 2016; Johnstone et al., 2016). Adaptive cycles can also 'revolt' or break apart from a panarchy. This occurs when environmental (i.e., geomorphic) or ecological changes interrupt one or more adaptive cycles. As referenced in resilience theory by these terms, remember and revolt mechanisms provide a panarchy with the capacity to adapt and restructure in new and potentially resilient ways. This mechanistic property, adaptive capacity, distinguishes resilience theory from other formal paradigms that associate landscape structure and function with resilience, including hierarchy theory, landscape sensitivity, and STMs.

Scholars working in resilience theory have proposed ways to track resilience properties through the detection of discontinuities in ecological attributes (Peterson et al., 1998; Nash et al., 2014). These gaps reflect the different operational scales of adaptive cycles and the panarchies they form (Holling, 1992; Allen et al., 2014). Body mass in animals has been the primary attribute employed to document this discontinuous structure (Allen et al., 2006; Sundstrom et al., 2012). However, other attributes may also be diagnostic. Plant life history strategies expressed as morphological, biomechanical, physiological, and phenological functional attributes (sensu Violle et al., 2007) may also reflect discontinuous structure. Far less has been said by ecologists and biogeographers working in resilience theory about how geomorphic characteristics related to the construction of habitat might also exhibit discontinuous structure. Topography, insofar as it reflects biological influences, should likewise exhibit discontinuities indicative of changing resilience properties (Durán and Moore, 2013; Phillips, 2016).

2.2. Current models of barrier dune biogeomorphic resilience

Although the invocation of resilience in barrier dune studies has oversimplified its complexity, these investigations do highlight a critical relationship for a more formal treatment of dune biogeomorphic resilience: the impact vegetation has on dune sediment storage and mobility (Durán and Moore, 2013; Silva et al., 2016; Mendoza et al., 2017). Common dune grass species have been designated as ecosystem engineers (Jones et al., 1997; Corenblit et al., 2011). Their positive growth response to sand burial, in tandem with functional differences in how their rooting and canopy strategies respectively bind and trap sediments, gives rise to different types of dune topography (Feagin et al., 2015). These biogenic topographies, in turn, modulate exposure to overwash, a disturbance agent that mobilizes dune sediments originating from meteorological and tidal forcings. In this way, coastal dune plants may indirectly shape the resources, conditions, and flows of matter and energy that influence their persistence as well as that of other biological and geomorphic components of the landscape. Given this capacity to influence landscape structure and function, common dune grasses are considered driver (Walker, 1992; Peterson et al., 1998) or foundational species (Angelini et al., 2011). They construct niches for themselves as well as for other organisms (Corenblit et al., 2009).

At least two states, or stability domains (e.g., Gunderson, 2000), have been postulated for barrier island dunes (Godfrey and Godfrey, 1973; Odum et al., 1987; Stallins, 2005; Wolner et al., 2013; Brantley et al., 2014; Durán and Moore, 2015). The contributors to this generalized domain model all postulate, to varying degrees and with slightly different terminology, that a small set of driver species in each dune stability domain engenders resilience through the modification of topography. Contrasts among these investigators arise in how they subdivide the number of plant functional groups. Durán and Moore (2015) modeled resilience through a single functional group, dune-building plants. The other recent studies considered a larger number of plant functional groups. They posited that the ecological interactions of dune plant functional groups and how they adapt and respond to overwash disturbance are more integral for resilience properties.

These interacting functional groups correspond to two categories of adaptive strategies associated with their geomorphic context: avoidance and tolerance sensu Puijalon et al. (2011). Their strategies can modulate overwash variability across a landscape, either by lowering resistance to it and making it more regular (as in an overwash-reinforcing stability domain) or by resisting its occurrence (as in an overwash-resisting stability domain; Fig. 2). In each domain, plant adaptations exert an influence on external variability by shaping topographic recovery in a way that reinforces the conditions and overwash exposures for which they are better adapted. Through the historical coupling of erosional and depositional conditions, dune plant species have evolved functional traits and species-specific strategies to survive related to how they partition growth-limiting resources (Bermúdez and Retuerto, 2014; Ciccarelli, 2015). Rooting patterns reflective of the acquisition of nutrients and/or water have been shown to contribute to the functional differentiation of dune plants (Stubbs and Bastow Wilson, 2004; Wolner et al., 2013).

Specific to their impacts on topography, burial-tolerant stabilizers are in general more physiologically tolerant of saturated soils, exposure to salt water, and burial by sediment. Their growth forms may have a more turf-like horizontal mat of roots and rhizomes. Dune-building

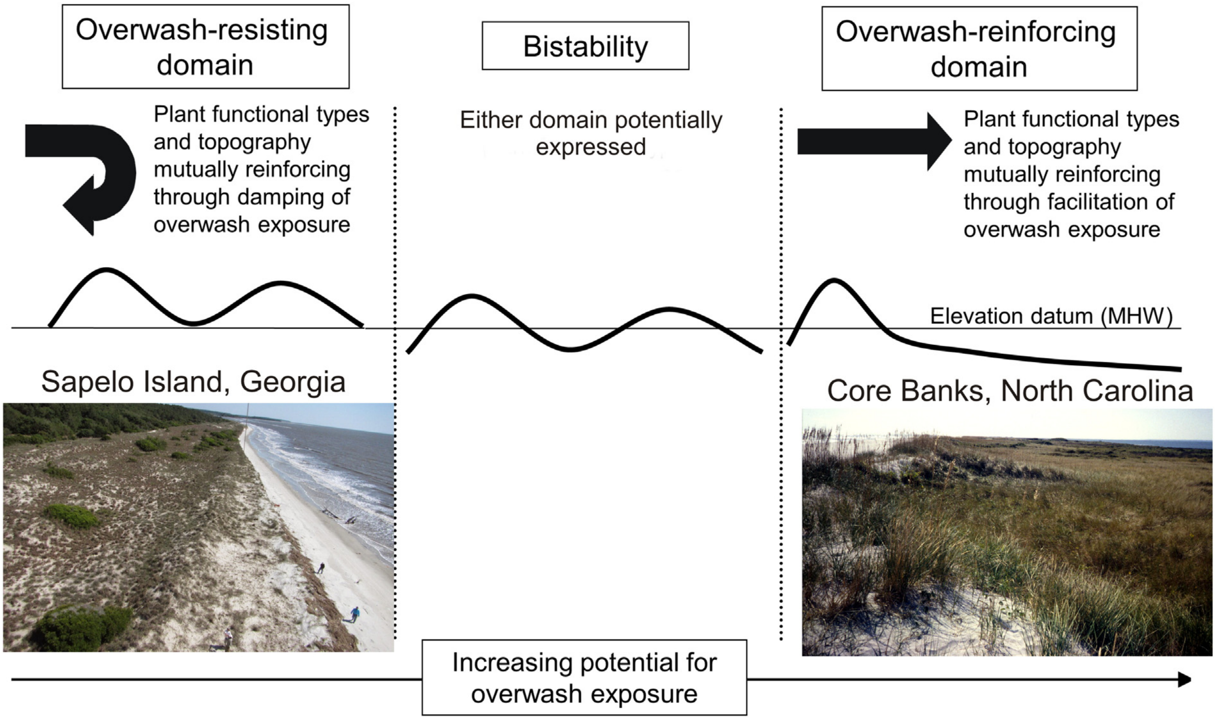

Fig. 2. Generalized two-state stability domain model with bistability. Stability domains have been identified in a range of terrestrial and marine systems (Gunderson, 2000; Folke et al., 2004). Bistability indicates the potential expression of either domain under the same conditions. However, bistable landscapes may exhibit less ecological resilience and exhibit more turnover due to conditions that have a propensity to be more intermediate of both domains. MHW: mean high water mark.

plants have more upright growth forms and a vertically elongated root system. Their positive growth responses to burial promotes vertical dune development. Burial-intolerant stabilizers are inland herbaceous and woody species that can establish in dune habitats when foredunes ameliorate harsh physical environmental gradients. Some inland grass taxa, for example, can colonize stabilized dune habitats. These plants bind sediments and stabilize topography but are not as adapted to recover from burial by sediment or exposure to high salinities. Although maritime dune plant taxa around the world could be expected to exhibit similar functional traits, plant functional design may be more variable (Doing, 1985; Mahdavi and Bergmeier, 2016). Similar fitness may evolve in the same environment out of alternative functional designs as a result of complex interactions and trade-offs among traits (Bermúdez and Retuerto, 2013). Biotic interactions between dune plants and climate can also play a role in the expression of functional traits and which plant species drive topographic modification (Emery and Rudgers, 2014; Brown, 2016; Harris et al., 2017).

The resilience that develops in each stability domain shown in Fig. 2 arises from different landscape-scale positive feedbacks. These landscape-scale positive feedbacks differ because of geographic contrasts in sediment availability, the coupling of seasonal erosional and depositional intervals, the frequency of exposure to overwash-forcing events, and in the local abundance of the aforementioned plant functional traits that modify topography in response to these conditions. For the overwash-reinforcing dune stability domain in Fig. 2, sediment budgets are less strongly positive and overwash forcing event frequency is relatively higher. Consequently, under these prevailing historic geomorphic conditions, a greater richness and evenness of burial-tolerant stabilizer driver species, typically dune grasses, can develop. Following burial from overwash, the growth of laterally extensive rhizomes of this functional type binds sediments in place. This limits the sediment available for grasses that build high dunes. The low topographic resistance that results increases the likelihood of exposure to overwash. With frequent overwash-forcing events, a positive landscape-scale feedback can develop out of the abundances of burial-adapted species and their maintenance of a low, flat topography.

By contrast, for the disturbance-resisting stability domain shown in Fig. 2 sediment budgets are historically more strongly positive and overwash-forcing event frequencies are lower. In these coastal contexts, the dominant plant driver species promote dune ridge and swale landforms and greater topographic resistance. Here, the positive feedbacks between vegetation and topography resists overwash contagion. A higher richness and evenness of dune-building grasses as well as burial-intolerant species that colonize interior low swales promote their persistence by stabilizing sediments and augmenting topographic roughness in a landscape-scale positive feedback that resists and redirects overwash.

As this two-state model evolved, it was recognized that these feedbacks and their domain states likely vary within an individual island and among adjacent islands (Stallins, 2005; Zinnert et al., 2016a). An entire island may not correspond to one or the other of these two domain models and the kinds of resilience they confer. Stretches of coast can be bistable (Fig. 2; Stallins, 2005, p. 426; Durán and Moore, 2015; Goldstein and Moore, 2016). With bistability, the disturbance-resisting or the disturbance-reinforcing domain can be expressed under the same conditions. However, these bistable 'mid-domain' states may exhibit a propensity for more transient dynamics because of their greater overlap in external conditions (Savage et al., 2000; Stallins, 2005, p. 426). Turnover among domain states may be higher than where external conditions are less similar.

Detecting these complex biogeomorphic dynamics have been hampered in part by the lack of an analytical framework that can accommodate this multidimensional, geographically explicit view of resilience. As we describe next, adaptive cycles and panarchies provide a means to do this (e.g., Nash et al., 2014). Modeling, simulation, and field-based studies have substantiated the potential resilience associated with complex feedbacks among dune plants and topography on barrier islands. But these investigation have been restricted to small stretches of coast and individual islands. They tend to downweight the full potential range of coastal variability. A geographically comparative framework, spanning the boundary conditions under which dune biogeomorphic interactions arise, would permit more inferences as to how resilience properties are (and are not) expressed along barrier island coasts.

2.3. Biogeomorphic adaptive cycles

The fluvial biogeomorphic successional model of Corenblit et al. (2007, 2009) provides an entry point for expressing the domain model of dune resilience in terms of adaptive cycles and panarchies. Corenblit's model is conveniently organized around couplings of endogenous and exogenous drivers that generate windows in time and space for new system dynamics to develop, proceeding from diaspore dispersal, recruitment, and the establishment and initiation of topographic modification, to the emergence of strong vegetation-induced feedbacks on geomorphic processes (i.e., a 'feedback window'; Eichel et al., 2016). The general outline of Corenblit's model is intact in this translation of it to a formal adaptive cycle framework, but with some minor departures. These were required to accentuate the cyclical aspects of resilience and to accommodate the conundrum of where to delineate the influence of abiotic and biotic phenomena on the highly interactive surfaces of dunes (Dietrich and Perron, 2006). Microbes and biofilms can stabilize substrates and modify topography in the absence of vascular plants (Viles, 2012), thus any division between abiotic and biotic influences is more a matter of scale and organism of interest.

Corenblit's biogeomorphic model of succession has four phases. Each can be considered an adaptive cycle associated with different time- and space-limited ecosystem structures, functions, and feedbacks (Corenblit et al., 2007). An adaptive cycle approximating Corenblit's geomorphic phase (Table 2; Fig. 3) encompasses the deposition and erosion of substrate suitable for plant colonization and the potential formation of the basic habitat template. Marine and geomorphic conditions are largely responsible for determining whether exposed habitat persists long enough for dune plant diaspores to accumulate or whether it is destroyed. The presence of stable terrestrial habitat with physicochemical properties suitable for colonization along with the availability of diaspores form the link to higher adaptive cycles. The revolt mechanism, the causality that would break this linkage, is the absence of these habitat-forming and colonizing conditions. Revolt may occur because of erosion, constraints on local sediment availability, or the absence of diaspores. Environmental variability spanned in this cycle ranges widely, from low elevations where geomorphic conditions are dominated by inundation to unvegetated high elevations where sediments have accumulated through aeolian processes.

The pioneer adaptive cycle spans the exploitation of suitable habitat by plant diaspores and the potential for continued cycling as individual plants grow and mature. Predictability in geomorphic conditions that shape habitat and disturbance regime favors success of pioneer plants and thus the degree they will be able to bind sediment and begin to modify topography in their immediate vicinity as individuals (e.g., Feagin et al., 2005). While this window of opportunity (Balke et al., 2014) for plant establishment can initiate biogeomorphic feedbacks, the overall influence of vegetation on geomorphic processes across the larger landscape remains weak in this adaptive cycle. However, when individual plants persist long enough to initiate sediment trapping and locally modify topography that reinforces their abundance in a form of ecological memory, linkages to a higher adaptive cycle can develop. The revolt mechanism is unsuccessful colonization and substrate destabilization. Failure of vegetation to persist may be caused by the harsh physical environment or by the absence of locally-adaptive plant traits. The variability in this adaptive cycle spans suitable terrestrial habitat lacking vegetation to the local topographic changes induced by plants colonizing new substrate.

Our division between the pioneer and the biogeomorphic adaptive cycles differs slightly from Corenblit's model. Our division here is based on Feagin et al.'s (2005) distinction in the scale at which dune plants and topography influence one another. In our pioneer adaptive cycle local biogeomorphic effects are expressed by individual plants in response to their local neighborhood. With enhanced sediment trapping and the expansion of dune landforms and plant populations in our biogeomorphic adaptive cycle, strong geomorphic-biotic interactions emerge beyond the level of individual plants and their local neighborhood. Consequently, biogeomorphic processes such as wind or water transport of sediments become more constrained by the global history and spatial patterning of the entire community. Interspecific biotic interactions also increase in overall importance and can include indirect as well as direct effects (e.g., Miller, 1994; Feagin and Wu, 2007). Cyclical dynamics increasingly become organized around seasonal expansions and contractions of vegetation cover in the biogeomorphic adaptive cycle. This can be attributable to the alteration of erosional and depositional condition associated with winter and summer wave regimes as well as with extratropical and tropical storms. After these potentially destructive events, the recovery of vegetation and landforms are dependent on the local species pool and the availability of diaspores, as well as the adaptations of plants to recolonize and persist in disturbed areas. When this recovery fails, it may lead to the revolt, or demise, of plant-landform feedbacks and a reversion to a lower adaptive cycle.

In the ecological adaptive cycle, niche construction (sensu Odling-Smee et al., 2003) by topography-modifying plants exerts its greatest impact on other organisms. By transforming topography at one location to suit its habitat requirements, dominant dune plant species can alter pedogenesis, salt spray exposure, the rates of sediment erosion and deposition, and the availability of nutrients and water for other types of vegetation at a distance away (Feagin and Wu, 2007). These landform effects not only construct new habitats for other organisms (Bruno et al., 2003) they also shape the outcome of biotic interactions, which may be either positive or negative depending upon spatial extent and the geometry of the landscape (Rastetter, 1991, p. 373; Corenblit et al., 2018–this issue). Subsequently, ecological and evolutionary selection is for the dune plant functional types that engineer predictable flows of matter and energy and promote a more spatially interacting assemblage of plant abundances and geomorphic processes and landforms emerges.

As a result, the landscape-scale positive feedbacks of stability domains emerge in this adaptive cycle. They correspond to those of

Table 2
Dune biogeomorphic adaptive cycles; the smaller temporal and spatial extents of the lowermost adaptive cycles are embedded in the broader temporal and spatial extents of the adaptive cycles above them.

Corenblit's phase of biogeomorphic succession	Adaptive cycling process	Causality that links to other adaptive cycles (remember mechanism)	Causality that breaks potential linkage (revolt mechanism)
Ecological	Disturbance cycling: landscape-scale entrainment of plants, topography, and sediment mobility in response to local frequency of overwash forcing events	Selection for the dune plants that engineer predictable flows of matter and energy through landscape in response to overwash	Unpredictable flows when this entrainment fails
Biogeomorphic	Seasonal cycling: expansion and contraction of plant biomass and dune landforms in response to seasonal climate and changes in wave and wind energy	Recovery and persistence of plant species that reinforce their abundance via the landforms they engineer	Loss of landform and potential local source regions for plants that shape this topography
Pioneer	Colonization cycling: plant colonization, initial topographic modification by vascular plants	Enhancement of local substrate stability and habitat quality with plant colonization	Unsuccessful recruitment, failure to persist through life cycle, remobilization of substrate
Geomorphic	Sediment cycling: sediment accumulation above water level	Terrestrial habitat suitable for plant establishment	Terrestrial habitat unsuitable for plant establishment

the existing dune biogeomorphic domain models shown in Fig. 2. Dunes with a greater abundance of burial-tolerant stabilizers would make exposure to overwash more predictable in terms of its regularity (the disturbance-reinforcing domain). Dunes with more burial-intolerant stabilizers would make overwash more predictable through its suppression (the disturbance-resisting domain). In the ecological adaptive cycle, variance in ecological and geomorphic conditions narrows to a range that confers persistence of the feedbacks characteristic of each domain. The richness and evenness (i.e., diversity) of plant functional types, as defined by their responses to sediment mobility and effects on topography, contribute to this narrowing (e.g., Hooper et al., 2005). These biotic metrics, along with topographic ones, make it possible to measure and discriminate among resilience properties.

2.4. Dune biogeomorphic panarchies and their measurement

In a panarchy for a disturbance-reinforcing stretch of barrier dune coast, the nestedness of these four adaptive cycles generates resilience properties by reinforcing overwash exposure (Fig. 4). In a panarchy for a disturbance-resisting stretch of barrier dune coast, the nested linkages among these adaptive cycles generates resilience properties by increased topographic resistance to overwash (Fig. 5). In both panarchies, resilience does not emerge *sui generis*. Instead, it arises from the interactions remembered and reinforced across the linkages among adaptive cycles. Each panarchy maintains system structure by canalizing a range of variability in geomorphic and biotic conditions that evolves in response to disturbance. Although structurally similar, these two panarchies culminate in different landscape-scale positive feedbacks in their ecological adaptive cycles. Through coupled cycles of sediment flux, colonization windows, and landscape-scale positive feedbacks, the larger system evolves the propensity to reinforce and tolerate overwash in meteorological and sedimentological contexts where it is common and resist or dampen it where it is more unlikely to occur.

This panarchical framework is more in agreement with studies of dune morphodynamics that stress the importance of the coupling of periods of sediment erosion and deposition with negative and positive plant growth responses across scales as a means to understand dune responses to high water events (Houser et al., 2015; Hapke et al., 2016; Angnuureng et al., 2017; Goldstein et al., 2017; Walker et al., 2017). As components of a coastal disturbance regime, storm sequence and intensity would influence which adaptive cycles develop, persist, and form links to other adaptive cycles. As compared to the existing domain models of barrier island dune resilience, this panarchical approach in Fig. 4 and Fig. 5 provides more mechanistic detail as to how resilience properties would be sensitive to the timing of storm events shaping cycles of dune growth and erosion from the microsite up to landscape extents. The development of a panarchy with high ecological resilience (i.e., one with several adaptive cycles) would hinge on how the historic frequency and intensity of storm events and their impacts coincide in space and time. If coastal storms increase in frequency and intensity under climate change, barrier dune resilience could be expected to change because of potential modifications in the emergence of windows of opportunity for habitat stabilization, plant colonization, and for the landscape-scale positive feedbacks that emerge out of them. Shifts in the timing of disturbance and recovery sequences, in how they overlap in space and in the abundances of plant response functional types, will determine whether the linkages between adaptive cycles will be remembered and reinforced or broken. However, this variability in panarchical structure could also be expected across any individual island. Because of the inherent environmental heterogeneity of barrier island dune strands, the emergence and connectivity among adaptive cycles may even vary to the extent that both panarchies can occur along different stretches of the same island. At the other extreme, a

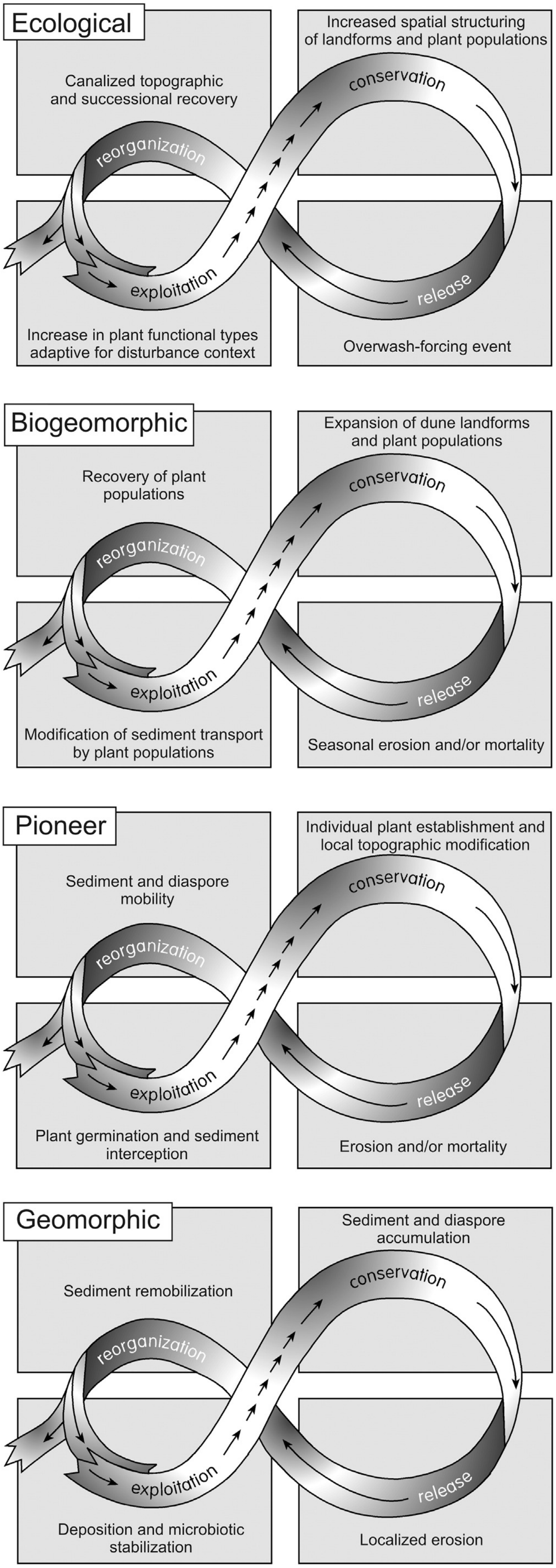

Fig. 3. Adaptive cycles approximating the phases of biogeomorphic succession proposed by Corenblit et al. (2007, 2009).

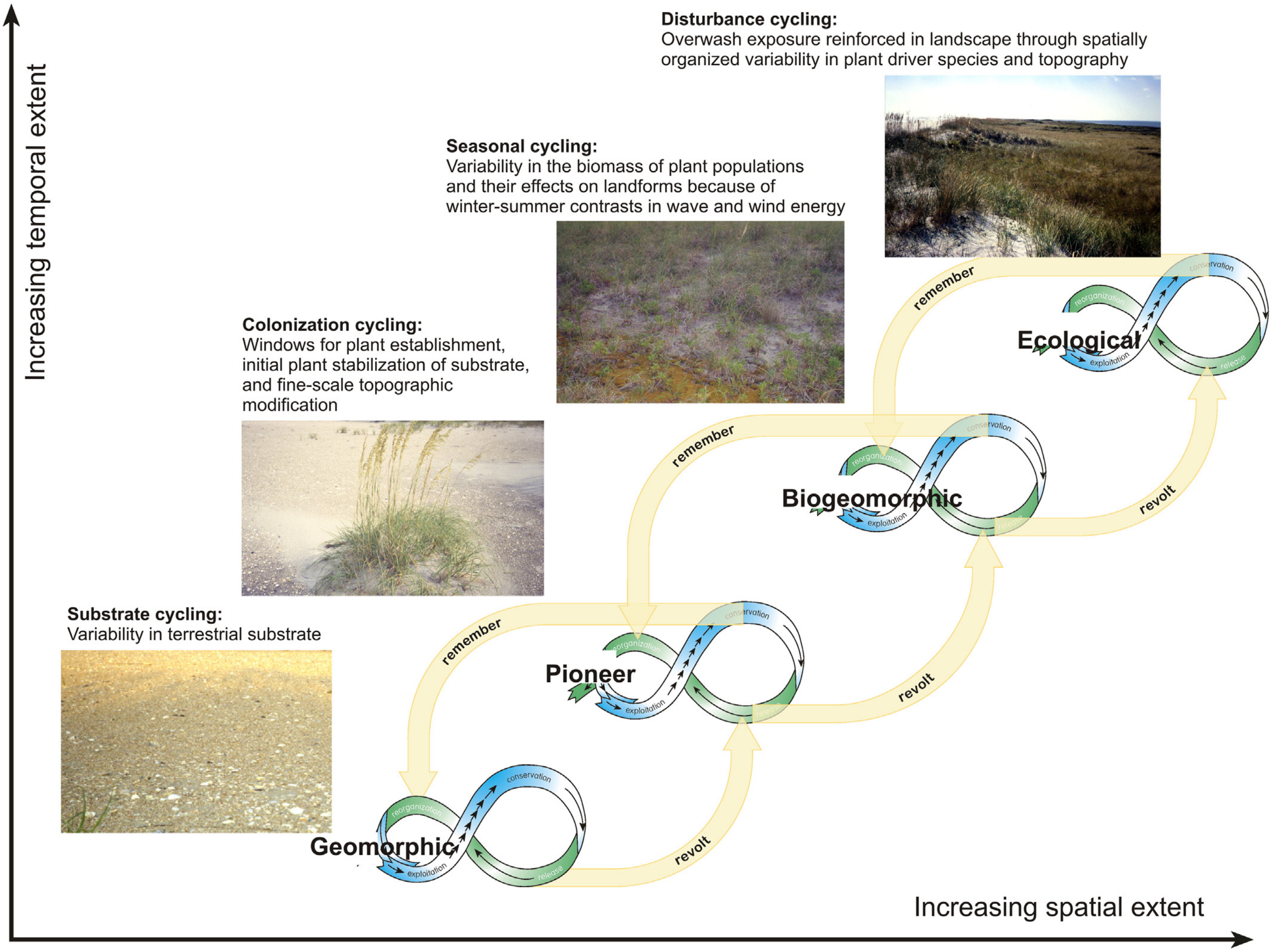

Fig. 4. Linkages among the adaptive cycles of a panarchy for an overwash-reinforcing barrier island stability domain. Based on Allen et al. (2014).

coastal barrier landform may consist of a single adaptive cycle if elevation is extremely low and vegetation or other biotic influences are minimal.

Because resilience reflects resistance as well as ecological resilience, the task of measuring each of them via their expression in adaptive cycles and panarchies requires a combination of metrics. Tracking resilience properties with a single measure or summary value, or expressing resilience as a present or absent quality, misses the dynamism that defines it (Barros et al., 2016; Wohl, 2016). Topography reflects the interaction of numerous (and not entirely independent) processes that can each be summarized with different metrics and at different levels of measurement. Biota can also be summarized in terms of multiple metrics as well as different levels of measurement. To delineate resistance and ecological resilience, we followed an ontological specification of resilience metrics developed in ecology (Wardwell et al., 2008; Sundstrom et al., 2012, 2014). We selected metrics with the goal of optimizing the extraction of the geomorphic as well as the ecological components of resilience properties expressed across barrier dunes (Fig. 6). Levels of measurement spanned presence-absence versus interval, absolute versus relativized, and whether the metrics represented discrete (patch) or continuous (gradient) phenomena. Use of multiple data types has been shown to enhance the capture of landscape characteristics (Fig. 7; McGarigal and Cushman, 2005; Lausch et al., 2015). Most real landscapes fall somewhere between patch and gradient models of landscape structure (Wagner and Fortin, 2005; Coller et al., 2000). Studies that gauge the vulnerability of the coast only through alongshore point or line-based measurement of primary foredune elevation (e.g., Hapke et al., 2013; Long et al., 2014) are gauging resilience, but more so as resistance, a correlate of ecological resilience (Donohue et al., 2013; Desjardins et al., 2015, p. 151.). Point and line-based measures alone would not encompass the elements of ecological resilience that would be embedded in more area-based patch and gradient characterizations of pattern. Spatial elements quantified in areal units are an important component of ecological resilience (Cumming, 2011; Allen et al., 2016; Cumming et al., 2016).

As a metric for the geomorphic adaptive cycle, elevation above oceanic influences would be a key indicator of resilience properties. Elevation determines the tempo of sediment mobility and whether a stretch of sandy coast is high enough to serve as a barrier and offer some resistance to wave energy. Windows of opportunity for plant recruitment can emerge only above a given elevational threshold. In the pioneer adaptive cycle, the success of plants that germinate on these bare, mobile substrates often depends on their propensity to modify the immediate topography around their base and engineer their local geomorphic context. Given the sensitivity of dune surfaces to the presence of plants, newly established vegetation should leave behind a topographic signature. Consequently, beginning in the pioneer adaptive cycle, metrics for the frequency distribution of elevations (i.e., average elevation, maximum elevation) could be expected to begin to deviate from what would characterize an uncolonized stretch of coast (Fig. 7A). Vegetation presence or absence can also be a metric for resilience for the geomorphic adaptive cycle, as the presence of

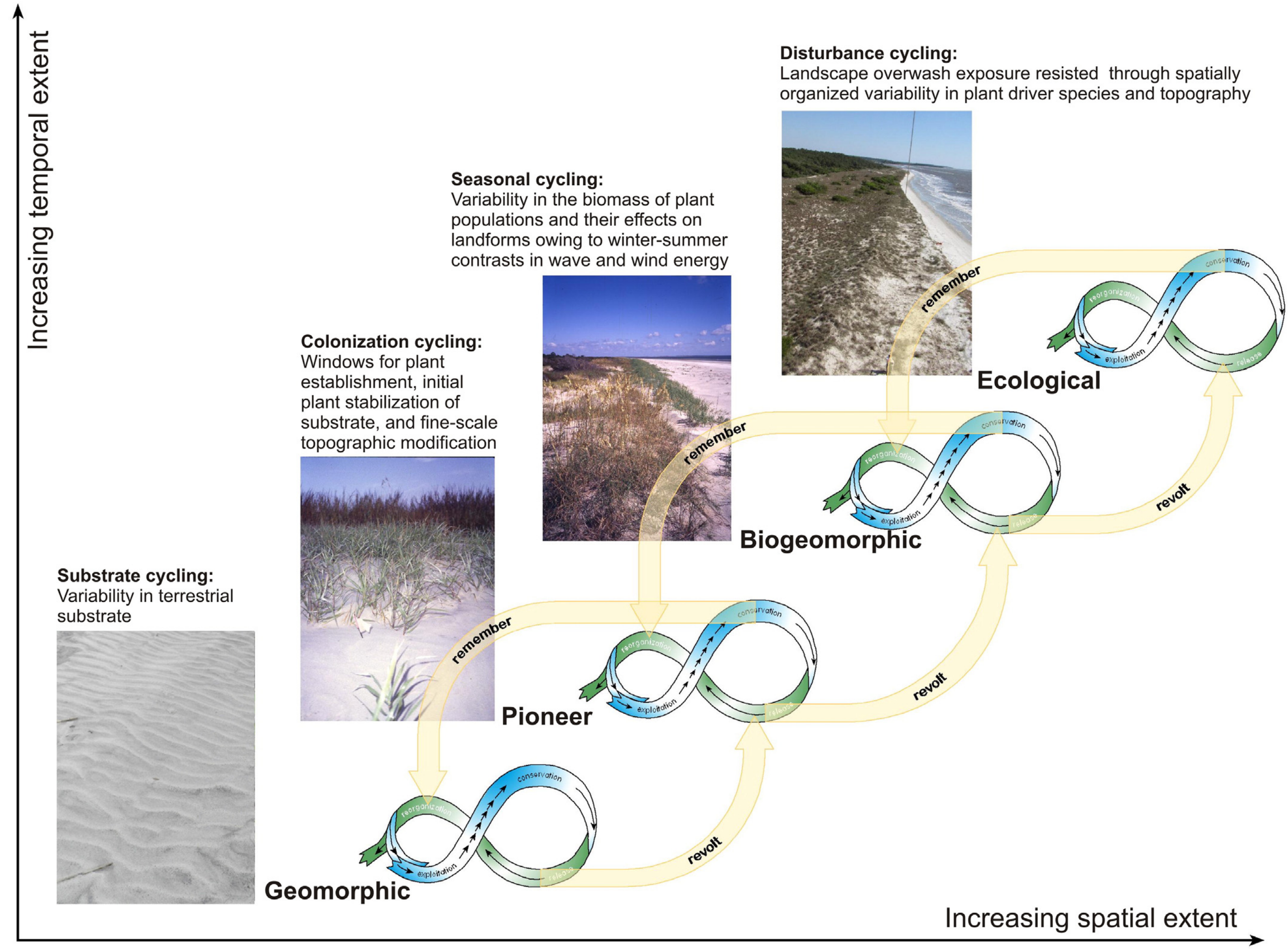

Fig. 5. Linkages among the adaptive cycles of a panarchy for an overwash-resisting barrier island stability domain. Based on Allen et al. (2014).

plants, particularly those with strong sediment-stabilizing functions, would augment the development of resilience properties.

The greatest accumulation of topographic structure via vegetation occurs in the biogeomorphic adaptive cycle. In this cycle, metrics for the patch structure of elevation can be employed to capture the expanding reciprocative influence of vegetation and topography on one another. The areal patterning of elevation, in addition to its use as an absolute value in centimeters or meters to summarize resilience properties in lower adaptive cycles, provides additional information about the potential process-responses of vegetation to overwash forcings, sediment mobility, and salt spray exposure. The patch structure of elevation can be summarized in landscape indices, such as those generated in the software program FRAGSTATS (Fig. 7B). These indices can quantify the shape and arrangement of discrete patches of elevation within an interval range (i.e., 1 to 2 m, 2 to 3 m) in terms relativized to plot size. These can then be used to infer their relationships to resilience (Allen et al., 2016). For example, more circular, lobe-like, across-island patches would suggest conditions of frequent overwash and the potential for vegetation adaptation to this disturbance agent. As ecological metrics for the biogeomorphic adaptive cycle, plants can be categorized as to whether they are driver or passenger species based on their functional traits (Walker, 1992). An increasing number and cover of driver species (versus passenger species, like, ruderal annuals) is suggestive of an increasing diversity of plant functional roles associated with specific strategies for topographic modification and a growing capacity to self-organize an adaptive response to overwash forcing events. An increasing number and cover of passenger species would also reflect the expanding indirect impacts of driver species on substrate stabilization and habitat availability.

Resilience in the ecological adaptive cycle is more attributable to the explicit spatial configuration of topography and vegetation in light of the prevailing overwash disturbance regime (Monge and Stallins, 2016). Spatial interactions have been shown to confine the range of conditions over which bistability can develop (Staal et al., 2016). To capture the spatial resilience signal embedded in the landscape-scale abiotic-biotic positive feedbacks of this adaptive cycle, metrics are needed that summarize landscape connectivity and represent how continuous elevational surface properties vary (i.e., McGarigal et al., 2009; Ryu and Sherman, 2014). The skewness and kurtosis of elevations at a dune site is one way to summarize the distributional properties of elevation (Bertoldi et al., 2011). Dune and beach widths over which these elevations are expressed are also relevant (Plant and Stockdon, 2012; Gutierrez et al., 2015). Quantifying the spatial autocorrelation structure of elevation (i.e., how point elevations are correlated with each other across a range of separating distances, or lags) is another (Walker et al., 2013; Scown et al., 2015). Differences in spatial autocorrelation structure (Fig. 7C) have been shown to track changes in resilience properties (e.g., Scheffer et al., 2015). Shifts or breaks in the skewness of elevation observations may also indicate changes in resilience properties (Guttal and Jayaprakash, 2009; Eby et al., 2017).

The association of spatial structure with resilience properties has other precedents. The spatial patterns of vegetation and patches of bare ground in semiarid range and grassland systems (i.e., its arrangement into repeating spots, gaps, and strips), has been shown to indicate

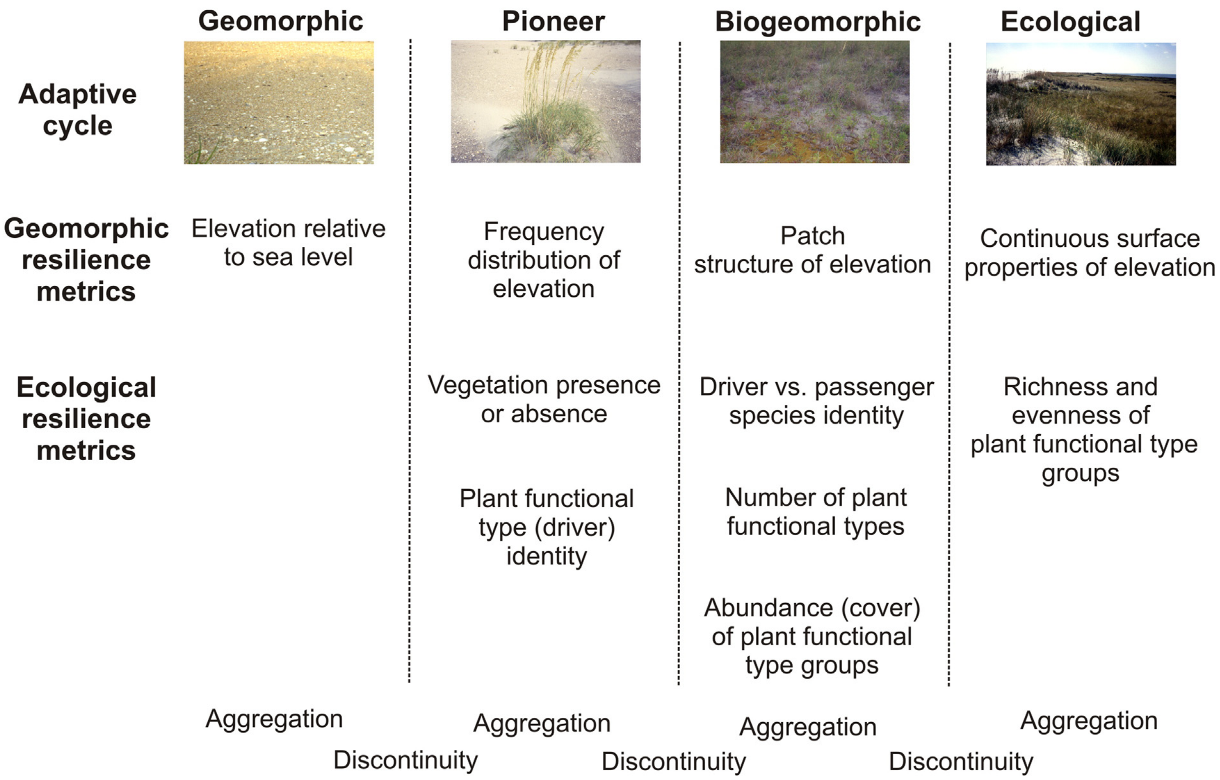

Fig. 6. Nested ecological and geomorphic resilience metrics for biogeomorphic adaptive cycles. Modeled after Sundstrom et al. (2012, 2014). These metrics are cross-scaled; i.e., the metrics for the higher adaptive cycles contain those in lower adaptive cycles.

resilience properties as well as the proximity of an approaching change in state (Rietkerk et al., 2004; Scheffer et al., 2009). This pattern-process approach to gauge resilience properties in semiarid contexts can be readily transferred to barrier dune coasts. Although our examples here are not quantitative, along stretches of Cape Canaveral, Florida, high positive relief along a narrow single fronting dune may be indicative of high resistance but low ecological resilience (Fig. 8A; Monge and Stallins, 2016). Along this infrequently overwashed coast, few overwash-adapted burial-tolerant stabilizers would persist to facilitate recovery after an overwash event. On Sapelo Island, Georgia (Fig. 8B), slightly lower mean elevations along parallel dune ridge and swale topography would confer less resistance. Topographic and vegetation patterns may contribute to more ecological resilience through a less than full attenuation of overwash and the consequent maintenance of disturbance-dependent plant species in the landscape. For South Core Banks (Fig. 8C), cross-shore topographic patterns are indicative of less resistance, but vegetation can still maintain relatively high ecological resilience through topographic and biotic patterns that reinforce overwash contagion. On Parramore Island, Virginia (Fig. 8D), low elevations and the erosion of sediment during inundation leaves behind topographic highs or 'pimples' (Hayden et al., 1995) that have little resistance or ecological resilience. In each of these four photos, the patterns of topography and vegetation are approximations of their different relative levels of resilience properties.

Plant functional type diversity has been underutilized as biotic metric to distinguish resilience properties (e.g., Allen et al., 2005; Angeler et al., 2014; Angelini et al., 2015). In the ecological adaptive cycle, functional diversity would reflect the propensity for biogeomorphic feedbacks to maximize resilience by either reinforcing or resisting overwash according to the domain model. Specifically, the richness and evenness aspects of plant functional diversity relate to the number and redundancy of the growth form strategies employed by dominant topography-modifying driver species. Ecological resilience may be greater where the overall diversity of plant topographic responses (e.g., response diversity; Elmqvist et al., 2003) is less than its potential maximum. Functional redundancy at these locations would be high only in some, but not all, plant functional groups. These abundant plant functional groups would be those that set up the feedbacks that either resist or reinforce overwash for a particular geographic location. Observable ecological resilience may actually be lower where richness and evenness of all plant functional type groups is at a peak (Angeler et al., 2013). Here, such a broad overlap of functional types may be more indicative of a bistable state, where either domain dynamic could persist under the same general conditions.

3. The distribution of resilience properties: a single island model

As a result of inherent environmental heterogeneity, entire barrier islands cannot have uniform resilience properties. Marine and geomorphic conditions that shape dune surface elevations, exposure to overwash, and sediment supply vary continuously along shore. Shoreline orientation can change within an island, giving rise to transitions between erosional to depositional conditions. Just as overwash disturbance gradients that can be regional in response to extratropical and tropical storm tracks, within a single island there can be newly emergent, frequently overwashed depositional areas as well as high primary foredunes that resist incursions of overwash into back barrier habitats. Then, as barrier islands approach their limits near tidal inlets, dune resilience properties have to diminish to zero as colonizable terrestrial substrate disappears entirely. Biogeographic factors such as the availability of diaspores and the composition of local species pools could also be expected to vary alongshore. Within-island trends in historical shoreline retreat and advance would set the stage for what type of vegetation is present along the fronting dunes. With all of this heterogeneity in vegetation and geomorphic context, the number of adaptive cycles and the kind of panarchy they comprise could be expected to vary along a single island and accordingly so would alongshore resilience properties.

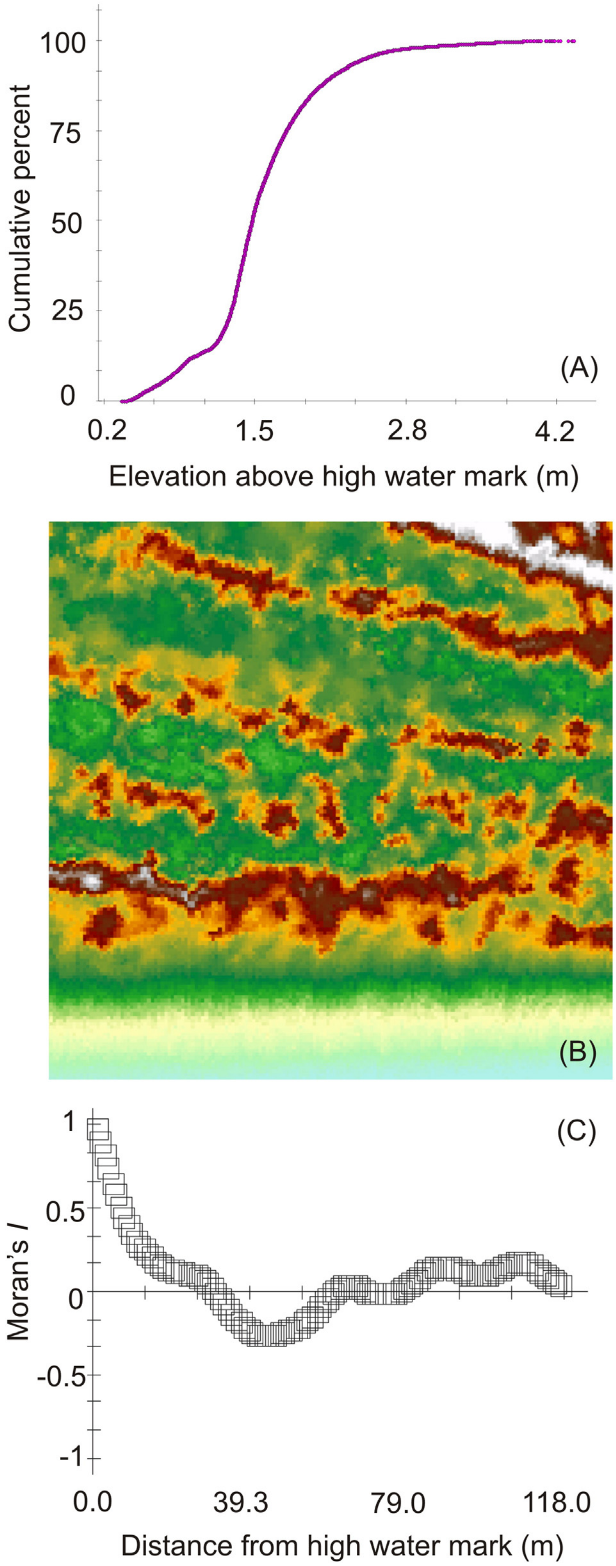

Fig. 7. The different representations and measurement levels for barrier island dune elevation and their association with resilience in adaptive cycles: (A) the frequency distribution of elevations in the geomorphic and pioneer adaptive cycle establishes engineering resilience; (B) the patch structure of similarly ranged elevation intervals in the biogeomorphic adaptive cycle reflects a growing balance of engineering and ecological resilience; and (C) spatial correlograms for elevation track changes in ecological resilience in the ecological adaptive cycle. Moran's *I* measures direction and strength of the correlation of elevations over a range of distance intervals. Direction is constrained to the shore perpendicular direction in this correlogram. All data derived from a 1-m elevation raster derived from airborne LIDAR for Kiawah Island, South Carolina.

Fig. 8. Patterns of topography and vegetation in dune systems on four barrier islands associated with differing levels of resistance and resilience: (A) Cape Canaveral, Florida; (B) Sapelo Island, Georgia; (C) South Core Banks, North Carolina; (D) Parramore Island, Virginia.

In this geographic, developmental view of resilience (Fig. 9) abiotic and biotic heterogeneity is reflected in the way resilience properties, via the adaptive cycles and panarchies that comprise them, vary over space (Scheffer et al., 2001; van Nes and Scheffer, 2005; Bel et al., 2012; Srinivasan and Kumar, 2015). Along an island, changes in the number of linked adaptive cycles would manifest as changes in resilience properties and the metrics that measure them. For example, increasingly frequent or high-magnitude overwash for a segment of coast on an island may overwhelm the local capacity of adaptive cycle feedbacks and lead to sharper transitions in resilience metrics alongshore. Where a new domain (i.e., a new panarchy) appears on an island, geomorphic or ecological conditions may have crossed a tipping point, such as on the south end of Sapelo Island in Fig. 9. Here, the dunes

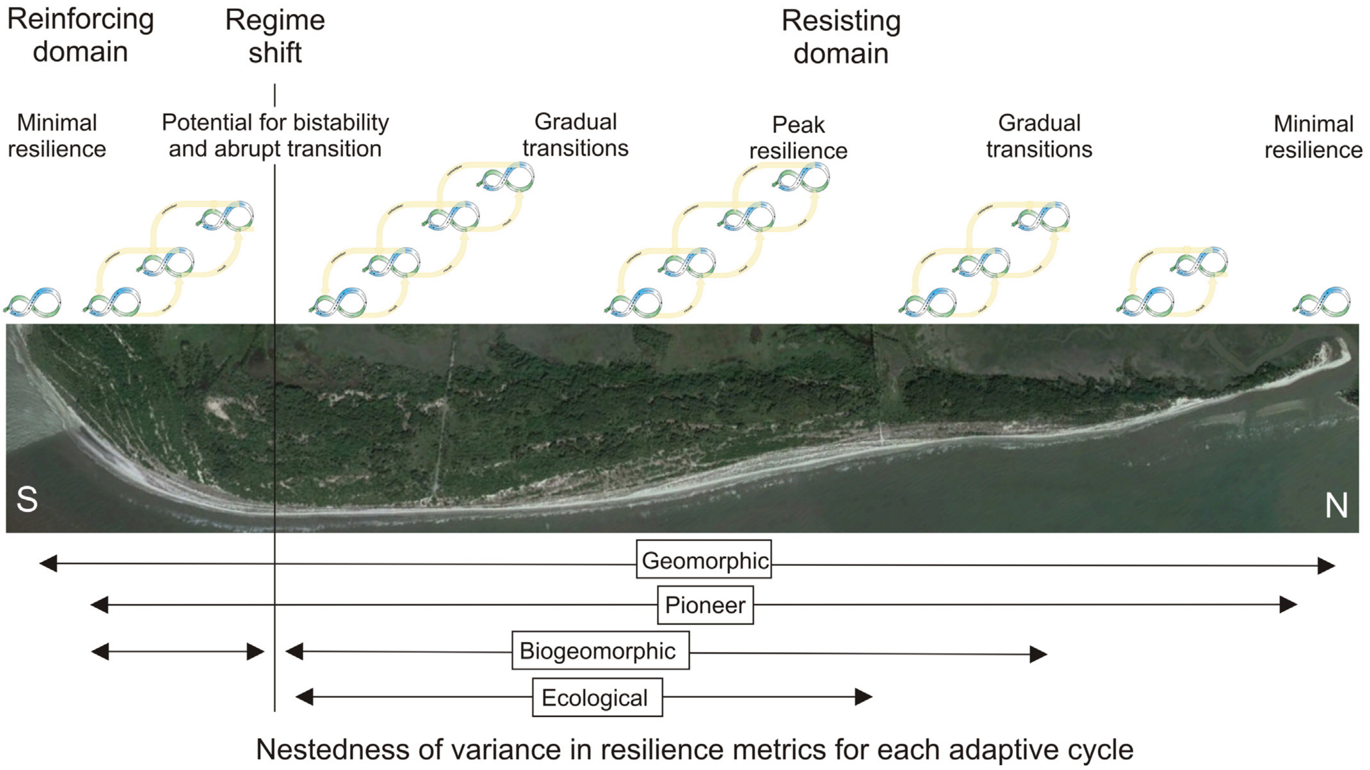

Fig. 9. Conceptual distribution of resilience along a barrier island dune system (Sapelo Island, Georgia). Number of adaptive cycles indicates relative level of resilience. Accretional, low elevation conditions promote more frequent overwash-forcing events on the south end of the island. However, resilience drops to a minimum at both ends of the island as overwash increases as an edge effect where the island disappears under the water.

have undergone a more abrupt discontinuous shift typifying a regime change (Scheffer et al., 2015). Near these regime changes, bistability may also develop (Durán and Moore, 2015).

We posit that the variance structure among the nested geomorphic and ecological resilience metrics summarized in Fig. 9 can be used to distinguish resistance and ecological resilience. As geomorphic and pioneer adaptive cycles are a foundation for much of the island, the resilience metrics that characterize these lower adaptive cycles (absolute measures of elevation and elevational patch structure) should summarize most of the variability in topography. These metrics convey the base resistance properties derived from the elevations of dune landforms. Within the elevational boundary conditions of these 'defensive' lower adaptive cycles, however, emerges the ecological resilience promoted in the higher 'offensive' adaptive cycles. Because of their nestedness within these boundary conditions, the biogeomorphic and the ecological adaptive cycles should summarize a smaller amount of the overall variance. Their contribution to ecological resilience could be expected to develop within a middle range of elevations, given the constraints on adaptation imposed when resistance to geomorphic disturbance is very high or low. The relative patch structure of elevation and vegetation as well as the continuous spatial metrics like spatial autocorrelation would be the only viable way to distinguish this ecologically selected variance. Once expressed, ecological resilience and the resistance expressed in lower adaptive cycles should reinforce each other through top-down and bottom-up controls.

4. Comparing biogeomorphic resilience: a multiple island model

Because resilience properties are embedded in the relationships among the metrics used to measure them (Donohue et al., 2013, 2016), comparing the structure (or topology) of data from multiple islands—and for multiple sites among individual islands—would facilitate discrimination of resistance from resilience and the relative contribution of geomorphic and ecological phenomena. Ordination is a way to partition variance on successive axes, or dimensions. It is commonly used to group and compare observations based on measures of resilience (Andersen et al., 2009). Nonmetric, multidimensional scaling and principal coordinates analysis are non-parametric ordination techniques that reduce the dimensionality of multivariate data and make the direct comparison of similarity among observations tractable. We propose that the dimensionality of the ordination solution and how variables load on significant axes of variation make it possible to quantitatively delineate and assess the distribution of resilience properties. First and lower dimension axes of an ordination of our proposed resilience metrics should capture the variance associated with lower adaptive cycles and the resistance components of resilience. Within the variance spanning these lower adaptive cycles (i.e., the geomorphic and the pioneer adaptive cycles) are the boundary conditions from which the higher adaptive cycles emerge (Fig. 10). Subsequently, higher dimension axes in an ordination should extract variance associated with ecological resilience. These axes would be more associated with the specific metrics that contribute to the domain feedbacks that maximize ecological resilience in the biogeomorphic and ecological adaptive cycles.

Barrineau et al. (2016) have already suggested how the variance structure derived from ordination can reveal distinct multiscale dune topographic variation associated with different process-form regimes and evolutionary stages. Resilience properties could similarly be visualized as regions along different axis positions in this ordination state space, as has been done in Monge and Stallins (2016; Fig. 11A, B). State space is a demarcation of the range of conditions under which a dynamic phenomenon develops, from those that are favored, and more likely, to those that are less persistent and unlikely to occur (Baas and Nield, 2010; Berry et al., 2014; Inkpen and Hall, 2016). Specific regions in state space can be associated with different resilience properties. If the first axis in state space captures the resistance components of resilience generated by the lower adaptive cycles, this dimension should correspond to a gradient from high-elevation positive relief to

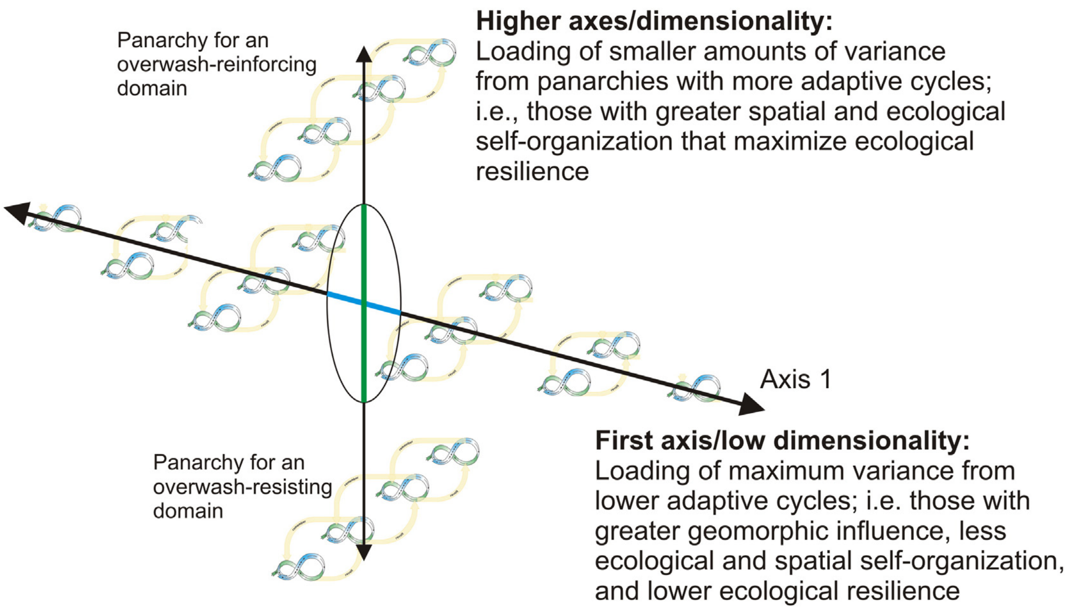

Fig. 10. Variance structure of resilience properties for the barrier island shown in Fig. 9. The green ellipse axis demarcates less dynamically favored configurations of topography and vegetation associated with ecological resilience. The blue ellipse axis demarcates the overlap in elevational and geomorphic conditions associated with the bistability that can develop between overwash-resisting and overwash-reinforcing domains.

low-elevation relief. Where positive relief is high along a single fronting foredune, resistance would be at a maximum. Even with increased erosion at its seaward dune edge, inland dune habitats would remain protected and may even increase in cover of woody vegetation (Zinnert et al., 2016b). Thus, the ecological resilience to recover if overtopped and maintain the same set of feedbacks is low, as overwash-adapted vegetation is likely to be outcompeted by more inland plant taxa and lost from the landscape during long periods without overwash disturbance. Where relief is low on the other end of this elevational gradient, resistance is at a minimum. Negative or remnant dune relief, such as pimples, may develop. Greater resistance to maritime inputs (i.e., higher elevations and fronting dunes) is needed to stabilize habitat and topography enough to promote the emergence of biogeomorphic and ecological interactions that facilitate resilient responses to disturbance.

In this way, where the ecological resilience of higher adaptive cycles evolves the capacity to either recover from disturbance or undergo a threshold change to another domain state is neither at the high nor the low end of the elevational gradient of resistance. These domain dynamics require an intermediate level of resistance. With too much resistance (i.e., high elevations), these feedbacks may not develop, as overwash is required to maintain disturbance-dependent plant functional types in the landscape so they can initiate topographic recovery. Too little resistance (i.e., low elevations) likewise prohibits the persistence of biogeomorphic feedbacks that are self-organizing and promote ecological resilience. Regions in state space between these inferred domains may be more likely to correspond to bistable landscapes. In sum, when a wide range of coastal conditions are characterized via different topographic metrics, the resilience properties that can develop in this state space range from where there is high and low resistance, to more intermediate resistance conditions with a propensity for bistability, and to domains states that maximize ecological resilience.

Visualizing resilience properties in state space with ordination would not be without its challenges. For one, testing the hypotheses we have presented here would be sensitive to sampling extent and resolution. The dimensionality and variance structure of a set of dune metrics would vary according to where and over what kind of coastal conditions the observations were taken from. A small subset of islands may not capture the full range of the dynamical properties of resilience. To understand resilience properties using a state space approach, observations across different types of barrier islands would be needed. Moreover, explanations for the variance summarized in an ordination may not neatly parse onto individual axes (Gauch, 1982). Other methods for reducing complex multidimensional data sets, such as geodesic ordination techniques like Isomap (Tenenbaum et al., 2000; Mahecha et al., 2007) may be useful. Networks may also be a productive way to define state space in a way that avoids some of the issues related to high dimensionality and its interpretability (Phillips et al., 2015).

5. Summary

Spatial and temporal perspectives on resilience differ (Dakos et al., 2010; Allen et al., 2016). In time-based studies, resilience properties are affiliated with the ability to withstand disturbances represented as shocks that are instantaneous, isolated, and noninteracting. Transitions between domain states can be sharp and abrupt. However, on the long, linear dune strands of barrier islands, resilience properties may be more variable (e.g., van Nes and Scheffer, 2005; Scheffer and van Nes, 2007). Erosion and deposition vary along dune coasts in association with the potential adaptive responses of dune plants. Through conceptual representation of this heterogeneity in terms of adaptive cycles and their potential to assemble into panarchies, we have shown how resilience properties could be expected to vary alongshore. Gradual as well as abrupt discontinuities in resilience properties may occur even within the same island.

We have also presented an ontology of dune geomorphic and ecological resilience metrics to facilitate the identification of engineering and ecological resilience. The construction of dune topographic state space from these metrics (Fig. 11A) was proposed as a strategy to operationalize the characterization of coastal resilience properties. Airborne LIDAR can provide the high-resolution elevational data necessary to derive dune topographic metrics at different levels of measurement and with varying degrees of spatial explicitness (Baas and Nield, 2010; Hugenholtz et al., 2012). Photography from unmanned aerial vehicles and structure-from-motion software also make it possible to derive observation-rich elevation models in a more customized manner (Mancini et al., 2013; Vautier et al., 2016; Hortobágyi et al., 2017). With these data, dune topographies from across a large set of islands could be characterized in terms of geomorphic resilience metrics and ordinated to reveal their correspondence with the conceptual model of state space presented here (e.g., Monge and Stallins, 2016). Then, to test

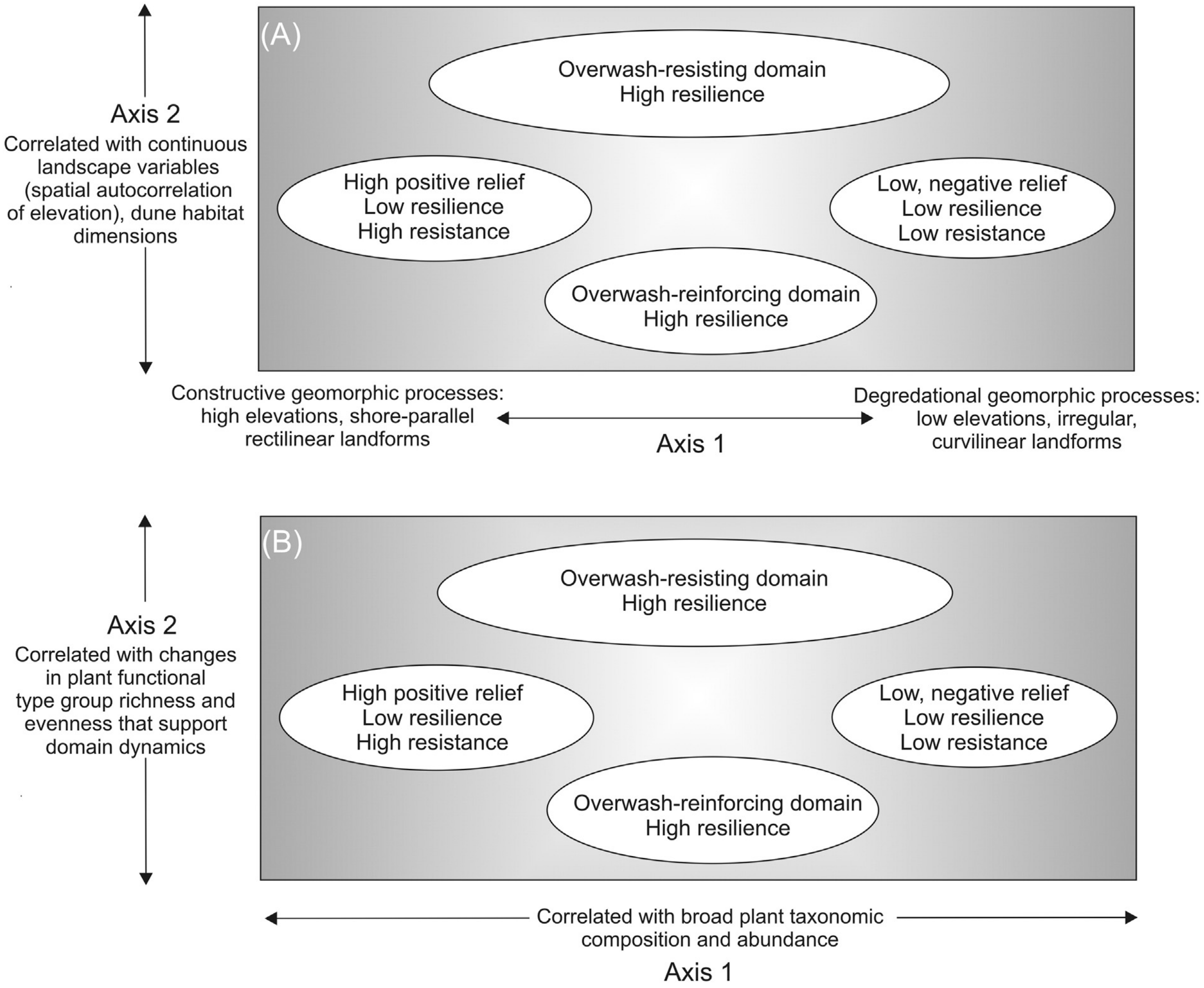

Fig. 11. Conceptualization of state space for barrier island dunes. The horizontal first axis (i.e., dimension) maximizes variance in engineering resilience for lower-order adaptive cycles where geomorphic processes predominate. The vertical second axis captures variance in ecological resilience for higher-order adaptive cycles where spatially integrated biogeomorphic interactions emerge at landscape extents. (A) Geomorphic variables correlated with these axes. (B) Ecological variables correlated with these axes. Lighter-colored region in center indicates where bistability as well as abrupt threshold transitions may develop (based on Monge and Stallins, 2016).

this model, specific island sites within regions of state space could be selected and sampled in the field to make finer-grain ecological and topographic observations (e.g., Albert et al., 2010). This stratified sampling of state space would be useful for refining, selecting, and testing hypotheses about how plant functional type abundances, richness, and evenness vary in relation to topography (Fig. 11B). Our data-driven state space approach is compatible with field-based research. They each have the shared goal of understanding how the variety of topographies that dune system can manifest within a gradient of exposure to disturbance is related to the proportional abundances of life history strategies and related morphological and biomechanical traits of a pool of species.

With more insight into these relationships, it may be feasible to determine under what general conditions dunes are more likely to develop self-organizing feedbacks characterizing peak ecological resilience (Fig. 12), a goal desired for the longer-term management and restoration of ecosystem services (Nordstrom et al., 2011; Lithgow et al., 2013; Angeler et al., 2016; Elko et al., 2016). At peak ecological resilience, dunes are more likely to exhibit the adaptive capacity for self-repair and recovery, an advantage over traditional shoreline engineering approaches (Spalding et al., 2014; Masselink and van Heteren, 2014; Feagin et al., 2015). Still, in other coastal settings, the strategy may be one of simply maximizing resistance without regard to underlying ecological organization and mode of development of the dunes (Nordstrom, 1990). Investigations of how invasive dune grasses greatly modify topography (e.g., Buell et al., 1995; Zarnetske et al., 2012) illustrate the sensitivity of coastal biogeomorphic systems to biotic factors and the feasibility of the intentional modification of plant functional type abundances to develop specific resilience properties. Finally, the conciliatory position on these approaches to resilience is that the geomorphic processes that control the availability of habitat and the potential for plant colonization form the foundation for more ecologically derived resilience to emerge. Geomorphic setting contributes to the resilience template in the form of resistance, and habitat engineering by dune plants fosters a narrower range of self-reinforcing geomorphic and ecological variability. Geomorphic and geological context may constrain whether an island is present or not and whether it is resistant to maritime inputs to the extent that plants can colonize stabilized substrates and persist. But it is only through ecological processes that peak ecological resilience develops.

Neither geomorphologists nor ecologists would disagree with the idea that the effects of dune vegetation on topographic variability would be expected to differ from what geomorphic processes would do acting in isolation. As we have shown, geographic context gives rise to different biotic adaptive strategies and more complex ways in which this topographic variability is expressed (Table 3). The question about resilience is how the convergence and divergence of states recognized by geomorphologists prioritizing geomorphic variables corresponds with the convergence and divergence of states recognized by ecologists prioritizing ecological variables. What resistance and resilience are for landforms is not necessarily what is resistant and resilient for biota when adaptive propensities or organisms are

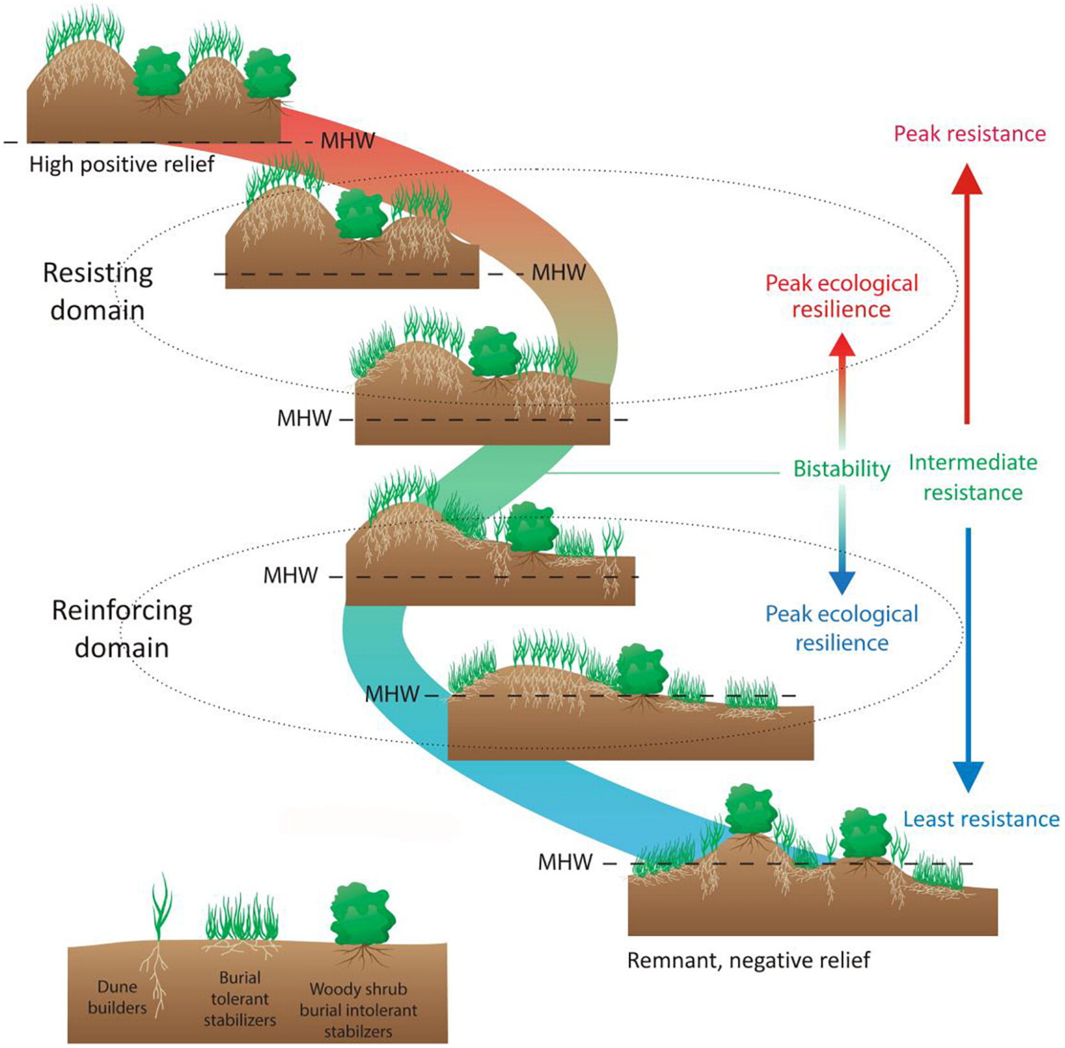

Fig. 12. Potential range of dynamical conditions and resilience properties embedded in a biogeomorphic system. See Monge and Stallins (2016) and Zinnert et al. (2017) for more detail.

taken into account. Arguments can be made that biota diversify geomorphic states as a way of generating the novelty in environment that can lead to new selection opportunities. Arguments can also be made that biota narrow the range of geomorphic states as a way of fostering predictability.

Biotic influences on coastal dune topography should also include those filtered through the command and control strategies humans implement through sea walls, beach nourishment, groins, and artificial dunes. While not discussed in this article, these human practices of variance engineering are also relevant for assessing dune resilience properties (e.g., Berry et al., 2014; Lazarus et al., 2016; Tarolli and Sofia, 2016; Arkema et al., 2017). A state space mapping of the anthropogenic as well as the more natural permutations of barrier dune topographies and their vegetation is necessary for an improved understanding of the resilience properties of these complex biogeomorphic systems.

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Table 3
The major difference between geomorphic and ecological resilience properties is in how they formalize and incorporate biotic adaptive strategies. Through adaptation, organisms can modify resistance and resilience in ways not directly accounted for in geomorphic conceptions of resilience. Organisms can promote resistance and resilience by modulating landform resistance and resilience in different ways depending upon context.

Biogeomorphic resilience		
Geomorphic lineage: landscape sensitivity and state-and-transition models	Ecological lineage: resilience theory	
Landform resilience: Recovery of landform from perturbation (no biotic adaptive strategy)	Biotic resilience: Recovery of biota from perturbation may reinforce or attenuate recovery of landform based on contextual biotic adaptive strategies	Ecological adaptive cycle Biogeomorphic adaptive cycle
Landform resistance: Absorption of perturbation by landform (no biotic adaptive strategy)	Biotic resistance: Absorption of perturbations by biota may reinforce or attenuate landform resistance based on contextual biotic adaptive strategies	Pioneer adaptive cycle Geomorphic adaptive cycle

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