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Stability domains in barrier island dune systems

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Abstract

Early ecological descriptions of barrier island dune landscapes recognized the importance of biogeomorphic feedbacks and thresholds. However, these dynamics have not been formally linked to complexity theory. In this article, I develop models of dune landscape phase states, or stability domains, based on a synthesis of these prior studies and statistical analyses. Data for these analyses were obtained from compositional and topographic sampling along Sapelo Island, Georgia and South Core Banks, North Carolina. These undeveloped barrier islands are at opposite ends of a regional meteorological gradient in storm-forced overwash disturbance along the southeastern US Atlantic coast. The topography and plant functional group abundances on each island were supportive of earlier studies noting the propensity for distinct self-organizing biogeomorphic feedbacks to emerge along barrier coasts. On South Core Banks, where storm forcings of overwash are more frequent, the recovery processes initiated by burial-tolerant species may reduce topographic resistance to overwash exposure and contagion. On Sapelo Island, a greater abundance of dune-building and burial-intolerant swale species may confer a higher topographic roughness and more resistance to overwash exposure and contagion. Conceptually, the biogeomorphic modifications of overwash forcings on each island perpetuate the habitat conditions and dominant dune plant species in a weak positive feedback. To provide more empirical evidence for these models, I tested a suite of hypotheses built from the premise that the biogeomorphic interactions on each island engender unique landscape patterns. These patterns originate in each island's distinctive coupling of extrinsic overwash disturbance processes with intrinsic plant-mediated topographic modification. Via this premise, the properties proposed for each domain model were subsequently supported, through: (1) the structure of compositional variance along principal coordinate ordination axes; (2) differences in biotopographic thresholds measured in cross sections; and (3) the distinctive elevational boundaries and spatial scales over which elevation exerted its influence on species diversity. These two domain models can be used as conceptual templates for the development of dune computational simulations.

Keywords: Stability domains; Attractors; Barrier islands; Dunes; Disturbance; Complex adaptive systems

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1. Introduction

Complex adaptive systems theory holds that ecological systems may exhibit a range of assembly states because of non-linear interactions among their

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components (Perry, 1995; Levin, 1999). These states may be self-entailing, whereby their organizational interactions confer stability across a bounded region of space and time. A variety of synonyms have been used to describe these dynamically favorable configurations of components, including stability domains, phase states, multiple (or alternative) stable states, or attractors (Vale, 1982; Carpenter, 2001; Gunderson, 2000; Li, 2002). The stability implicit in these assembly states has two facets (Holling, 1973). One is equilibrium in design, reflecting the persistence of function within the bounds of a single stability domain following perturbation. The other is a non-equilibrium measure of the magnitude of perturbation that can be absorbed by a system before it shifts to another stability domain.

Stability domains have been described for a variety of environments, including shallow lakes, rangelands, longleaf pine forests, and coral reefs (Nystrom and Folke, 2001; Scheffer et al., 2001; Dent et al., 2002; Gunderson and Pritchard, 2002). With increases in grazing intensity and fire suppression, a rangeland may flip from a grass-dominated to a woody shrub-dominated stability domain. Shallow lakes may shift between an oligotrophic and eutrophic stability domain in response to changes in nutrient input, sediment loading, or food-web dynamics. These descriptions of stability domains, as are many in the ecology literature, focus on shifts between domains through time. Two perspectives have been invoked to explain these temporal shifts. The first assumes a constant environment with changes in population parameters. The second focuses on changes in environmental variables. Recent interest in the effects of ecosystem engineers (Lawton, 1994; Jones et al., 1997) recognizes that these two perspectives are intertwined. Changing population abundances can change interactions with environmental fluxes and thereby drive flips between stability domains (Chapin et al., 1997; Beisner et al., 2003).

These domain shifts and their underlying mechanisms can also be anticipated in a spatial context. This geographic conceptualization underpins Holling's (1992) textural discontinuity hypothesis, which posits that the fabric of ecological space is lumpy. The distribution of processes, patterns, and populations should reflect a discontinuous texture as it organizes into stability domains. To an extent, the field of macroecology (Brown, 1995; Maurer, 1999) addresses these patterns, whereby power laws can be used to denote breaks in the organizational structure of the underlying domains (Milne, 1998). However, more detailed spatial models of stability domains are needed (Wiens, 1989). A spatial view of stability domains is relevant given that disturbance, as a fundamental agent shaping diversity and stability in ecological systems, is as equally a spatial phenomena as it is a temporal event.

Our understanding of stability domains might also benefit from a closer look at the dynamics of dune systems. Although dunes and dune plants were central to the development of some of the central ideas in ecology (Cowles, 1899; Sprugel, 1980), these landscapes have been overlooked relative to their potential to contribute to complexity theory. When compared to other systems in which stability domains are described, dune systems are similarly 'fast' and sensitive (Hansom, 2001). Positive feedbacks are a ubiquitous structuring agent (Wilson and Agnew, 1992). Moreover, vegetation is slaved to the underlying dynamics of sediment transport. Dune-building plants intercept and stabilize mobile sediments, which in turn leads to more plant growth, sediment capture, and stabilization. This feedback ultimately leads to the emergence of dune landforms. Once in place, dune landforms mediate the incremental and episodic movement of sediments, and shape the expression of environmental gradients that influence neighboring species. In this sense, dune plant species can be conceptualized as ecosystem engineers or driver species (Walker, 1995) in that their topography-modifying characteristics have indirect influences on the occurrence of other plant species (Bruno, 2000; Stachowicz, 2001; Bruno et al., 2003).

In this paper, I develop models of dune stability domains. Dunes, like other landscapes, represent self-organizing systems that may exist in a number of different phases where macroscopic behavior can differ dramatically (Li, 2002). The models I present are manifestations of the larger barrier island process-form morphologies that organize and emerge in response to geographic variability in tidal flux and wave energy along maritime coasts (Williams and Leatherman, 1993). For dune modelers, vegetation is increasingly recognized as a critical element shaping the morphology and dynamics of dune landscapes (Rastetter, 1991; Baas, 2002). Presently, however, there is a dearth of suitable attractor descriptions with respect to both dune morphology and vegetation pattern (Baas, 2002). Such descriptions are required to develop simulation-based studies. For computational modeling in general, there is a need for more open-ended, exploratory investigations (Boero et al., 2004, p. 107), echoing Phillips' (2004) concern that our ability to measure and compute has outstripped our mental models of what we should be measuring. The qualitative descriptions and quantitative evidence for the two domain models developed in this study are initial steps to address this need.

2. Background

2.1. Barrier island process-form morphologies

Sandy coasts are recognized for their sensitivity to geomorphic, biological, and meteorologic inputs and their propensity to self-organize (Riggs, 1976; Forbes et al., 1995; Werner, 1999). Along the large-scale gradients of wave and tidal energy of coastal embayments, sandy barrier islands may organize into two distinctive process-form morphologies (Hayes, 1979, 1994). These morphologies are well developed along the Georgia Bight of the southeastern US Atlantic coast. Mixed-energy mesotidal island morphologies develop toward the center of this broad embayment (Fig. 1). These short, squat landforms are the outcome of nearshore processes driven by high tidal ranges and low wave energies, conditions typical of protected positions within the concave interior of coastal bights. Overwash, the inland forcing of surge and sediments during coastal storms, is infrequent. Wave energy from storms may be deflected into extensive networks of tidal inlets that bound islands (Sexton and Hayes, 1991).

Along the North Carolina perimeter of the Georgia Bight, long, linear, wave-dominated microtidal barrier islands emerge (Fig. 2). These morphologies are the summation of nearshore processes driven by high wave energy and low tidal ranges. Overwash, as a means of dissipating wave energy, is potentially more frequent. This is due to a gradient of increased exposure to winter extratropical cyclones with increased latitude along the US Atlantic seaboard, resulting in a strong geographic continuum of potential overwash exposure from Georgia to North Carolina (Dolan and Davis, 1992; Davis et al., 1993). Topography on each of these two morphologies reflects these storm inputs. The microtidal islands of North Carolina's Outer Banks have a low relief profile characterized by a single fronting line of foredunes and extensive backbarrier overwash flats. Once these foredunes are breached, overwash can easily propagate across interior locations. Mixed-energy mesotidal islands along the Georgia coast are often characterized by dune ridge-and-swale topography (Oertel and Larsen, 1976). This augmented topographic roughness limits the incursion of storm surge, directing overwash laterally toward tidal inlets.

2.2. Complexity in barrier island dune systems

These macroscale barrier island morphologies can be conceptualized as stability domains. During the

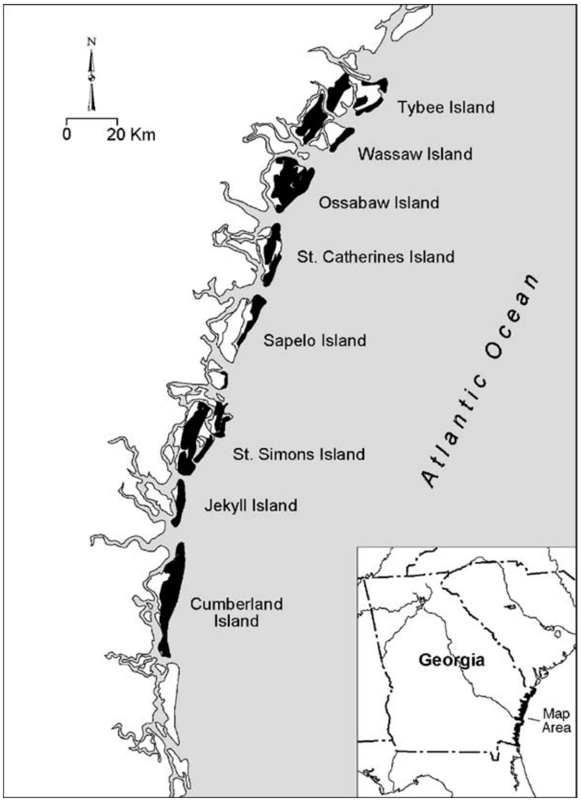

Fig. 1. Mixed-energy mesotidal barrier island morphologies of the Georgia coast.

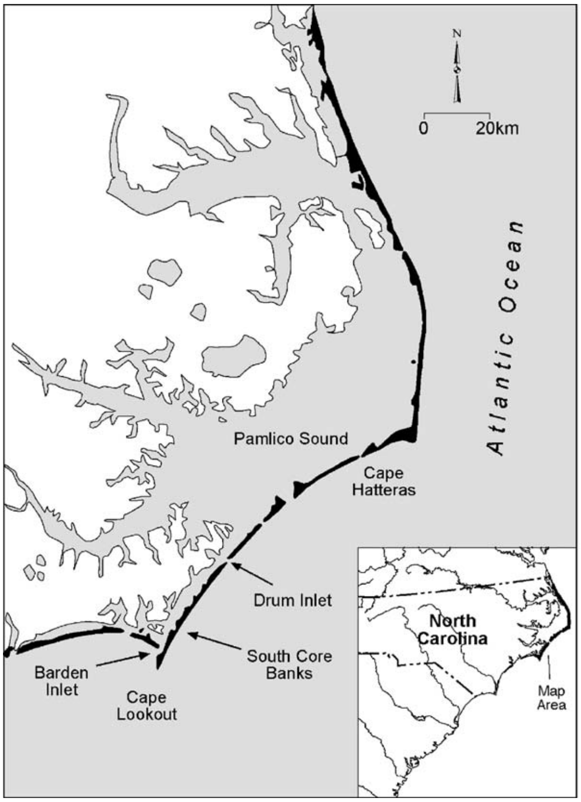

Fig. 2. Wave-dominated microtidal barrier island morphologies of the North Carolina coast.

1970s and 1980s, numerous coastal scholars suggested that barrier island dune plants, topography, and disturbance exhibit what we would now consider complex system dynamics (Table 1). Godfrey et al. (1979) related how the growth form of a common coastal grass, *Spartina patens* var. monogyna, can reinforce overwash exposure by stabilizing overwash sediments, thereby indirectly minimizing vertical dune development. By binding sediments in place, *Spartina patens* limits the availability of sediments for more efficient dune-building species. This contributes to the maintenance of a low, flat overwash-prone topography, in effect reproducing the conditions for which this species is adapted. Godfrey (1977) suggested that large-scale breaks in coastal dune physiography along the US east coast correlate with shifts in the distribution and abundance of dune plant species that differentially modify topography and overwash contagion. Barrier island dune topographic development and its influence upon the patterning of overwash exposures and vegetation responses were further explicated by Odum et al. (1987) and Rastetter (1991). Odum et al. (1987) detailed how the biogeomorphic components of barrier island dune systems, when altered by the construction of artificial dunes, may either resist or reinforce overwash exposure. Rastetter described how dune plant species

Table 1
Facets of complexity expressed in earlier barrier island dune studies

Cowles (1899)	Positive feedbacks between plants and substrates Sensitive, rapid responsiveness of dune systems Dune plant growth forms and their association with dune topography Convergence of growth form among different dune systems
Godfrey (1977), Godfrey et al. (1979), Hosier and Cleary (1977)	Regional classification of dune physiography based on dune plant abundances and their adaptations to overwash Feedbacks between vegetation, topography, and overwash in a geographic context
Hayes (1979); Williams and Leatherman (1993)	Barrier islands as emergent phenomena Classification of barrier islands into process-form types Distribution of barrier island types in response to local and regional-scale nearshore variables
Odum et al. (1987); Rastetter (1991)	Sensitive, rapid responsiveness of dune systems Interactive spatial structure of dune systems Facilitation of species coexistence through topographic habitat-modification Biogeomorphic modulation of overwash disturbance processes Modeling of dune biogeomorphic dynamics Resistance and resilience as criteria for two-fold classification of barrier island dune dynamics

shape and are shaped by complex environmental gradients that create the distinctive zonation of species along maritime shores. These works posit that overwash, like fire, is a contagious disturbance process, the extent and duration of which are dynamically determined by the interaction of the disturbance with the spatial configuration of the landscape (see Peterson, 2002).

Mechanisms for these dynamics are linked to dune plant growth form. Distinctive growth form attributes among dune plants can be readily linked to their specific responses to sediment burial and to their subsequent effects upon topography (Ehrenfeld, 1990). Sand movement and plant burial exert a strong influence on dune plant community composition (Moreno-Casasola, 1986; Maun and Perumal, 1999). Burial of plants is a selective force in sand dunes, acting as a filter that eliminates species when burial exceeds their threshold of survival (Maun, 2004; Kent et al., 2001). However, burial can also result in increased growth and vigor in many species. This in turn directs the type of topographic development that can occur. Based upon the response-effects encapsulated in growth form, three dune plant functional types can be identified along coastal strands: dune builders, burial-tolerant stabilizers, and burial-intolerant stabilizers (Hosier, 1973; Woodhouse, 1982; Ehrenfeld, 1990). Dune builders have upright growth habits that produce rapid vertical accumulation near the margins of vegetation. Their positive growth responses to burial and slow lateral spread produce the steep dune slopes typical of foredunes. Burial-tolerant stabilizers also have positive growth responses to burial, but their decumbent growth forms do not promote vertical dune development. Instead, an extensive network of horizontal rhizomes stabilizes substrates [“guerilla” growth forms (Harper, 1977; Fahrig et al., 1994)]. These species are well adapted to overwash. The third group, burial-intolerant stabilizers, comprises inland-ranging species that colonize protected mesic dunal swales. These species have negative growth responses to burial. Their dense compact growth form facilitates intense resource use by pre-empting a site (“phalanx” growth forms, Harper, 1977; Fahrig et al., 1994), thus effectively binding substrates. A fourth group of coastal dune plants can be categorized as passenger species (Walker, 1995), those entrained taxa with no strong or direct functional role in modifying topography.

2.3. Barrier island dune stability domains

Intrinsic population processes may interact with periodic extrinsic fluctuations so as to reinforce or dampen their occurrence (Orland, 2003). I posit that dune plants and dune topography have a propensity to dampen or reinforce the historically prevalent patterns of surface sediment mobility in such a way as to become self-entailing systems. These stability domains are maintained by their mutually reinforcing interactions between a small set of plant species, sediment transport processes, and dune landforms. By responding to their environment, dune plants simultaneously modify that environment through their propensity to alter topography, resulting in a recursive interaction of organisms and the environment (see Odling-Smee et al., 2003; Lewontin, 2000). In this manner, the prevailing patterns of aeolian and overwash-driven sediment transport become encoded and reinforced in the abundance and spatial pattern of vegetation and topography. As detailed below, the sum of these lower-level biogeomorphic feedbacks have the effect of lowering the topographic resistance to overwash in one domain, and increasing topographic resistance in the other.

On the wave-dominated microtidal barrier island morphologies of the Outer Banks, dunes are often low and discontinuous. Wave energy from passing storms is dissipated as overwash across the island surface. After overwash deposition, the mobility of sediments is mediated by burial-tolerant taxa, chiefly the rhizomatous perennial *Spartina patens*. *Spartina patens* is not an efficient dune builder (Woodhouse, 1982), but its high tolerance to burial and extensive horizontal network of rhizomes permits it to recover rapidly following overwash and effectively bind deposited sediments. *Hydrocotyle bonariensis* has similar functional attributes (Hosier, 1973). Once sediments are stabilized by these burial-tolerant species, or sequestered through the formation of deflation lags (wind-sorted pavements of overwash-deposited coarse particles that armor the surface), their availability to form protective foredunes is limited (Godfrey and Godfrey, 1976; Woodhouse et al., 1976). In this manner, disturbance-dependent species promote their abundance by contributing to a low relief topography that reinforces exposure to future overwash in a positive feedback (Godfrey et al., 1979).

Positive feedback here implies the perpetuation of a low resistance landscape, and not a runaway 'snowball effect' also associated with positive feedback. A similar effect is seen in fire-tolerant forests: with an increasing abundance of tree species that depend upon fire and have characteristics that promote the occurrence and spread of fire, the likelihood of extensive fire disturbance increases.

The dune plant functional abundances on mixed-energy mesotidal islands may similarly attenuate geomorphic processes and landforms to promote the development of habitat conditions for which they are adapted. Along the barrier islands of the Georgia coast, an extensive dune ridge-and-swale topography may develop when sediment is abundant. Numerous models of dune ridge formation emphasize the role of vegetation (Taylor and Stone, 1996). Positive relief generated by dune-building taxa, and the stabilization of intervening low swales by burial-intolerant woody shrubs and grass species maintains elevational contrasts. This topographic roughness acts as a barrier to the spread of overwash into backshore dune habitats. In this manner, ridge and swale plant species reinforce their presence in the landscape by contributing to a high-relief topography that dampens overwash exposure and perpetuates the relatively undisturbed habitat conditions for which they are competitively superior.

3. Study area

To build a stronger empirical basis for the evidence synthesized from these earlier dune studies, I sampled plant cover and topography on two barrier island morphologies at either end of a geographic gradient of overwash disturbance spanning the Georgia Bight. The two islands, South Core Banks, North Carolina, and Sapelo Island, Georgia are largely undeveloped. Sampling on the group of islands comprising Sapelo was confined to the 5 km of the southernmost Holocene island to minimize the confounding influence of multiple tidal inlets. Overwash occurs on Sapelo but is infrequent and spatially restricted (Deery and Howard, 1977). South Core Banks, part of Cape Lookout National Seashore, is a retreating Holocene barrier with a greater frequency of overwash. Return intervals for the winter extra-tropical storms capable of generating overwash are approximately 10 years for the mid-Atlanta coast (Dolan and Davis, 1992).

A total of five sites were sampled along the south-to-north axis of each island during June through August of 1999. Each site expressed a distinctive dune physiography as detected though aerial photographs and field reconnaissance. Sites on both islands ranged from recently overwashed to protected. Three randomly positioned strip transects (at a minimum of 20 m intervening distance) were nested within each of the five sites. Each transect began at the high water mark, the point along the seaward base of the primary foredunes where dune vegetation first occurs. Transects extended inland through dune habitats to the first occurrence of extensive cover of the inland woody shrub *Myrica cerifera*. *M. cerifera* invades backshore herbaceous habitats in the absence of overwash (Young et al., 1995). Vegetation data were collected within contiguous 1 m × 2 m quadrats aligned perpendicular to the centerline of each transect. Within each quadrat, a 2 m point-frame sampler aligned perpendicular to the transect was used to measure species presence at 10 cm intervals. A total of 1082 quadrats were sampled on Sapelo, and 1139 on South Core. Point-frame hits in each quadrat were summed for individual species and expressed as percent absolute cover at quadrat, transect, site, and island scales. The presence of any species off transect but within a site was recorded. Several genera were indistinguishable in the field and were lumped into species complexes. Plant identification and nomenclature follows Radford et al. (1968).

4. Analyses

4.1. Framework

Statistical analyses of field data were framed within three hypotheses. These hypotheses were built from the premise that each domain manifests a unique interaction of extrinsic disturbance and intrinsic gradient zonation, the two prominent paradigms broadly invoked by ecologists and biogeographers to explain vegetation patterns (Harmon et al., 1983; White, 1987). A few studies have explicitly assessed vegetation patterns as an interaction of disturbance patch dynamics and gradient zonation (Myster, 2001; van Coller et al., 2000). However, I posit that the interaction between the two are a hallmark of complex adaptive systems, and the macroscale statistical properties of the vegetation patterns that result can be used to develop hypotheses based in complexity theory. By framing complexity as an interaction of disturbance patch dynamics and gradient zonation, a more tactical hypothesis-oriented framework for conducting exploratory fieldwork can be deployed.

This operational formalization follows the landscape antagonistic principle articulated by Li (2000, p. 33). Endogenic (originating inside the landscape) and exogenic (originating outside the landscape) processes are often antagonistic, and for landscape development to occur, they must roughly balance each other out. Similarly, Perry (1995) states that system dynamics must involve not only internal interactions, but also modification of external forces such that they reinforce, or at least do not overwhelm, internally generated order. As such, the compositional statistical properties my hypotheses investigate originate not only through internal processes related to the plant-mediated formation of topography and the subsequent emergence of environmental gradients, but also through the effects these intrinsic processes have on extrinsic forcings of overwash.

4.2. Variance structure

Some landscapes tend to absorb and damp the spread of disturbances, while other landscapes magnify them, with process reinforcing structure in each case (Perry, 1995). I hypothesized that the propensity for island-domains to damp disturbance exposure (Sapelo) or reinforce it (South Core Banks) are a consequence of the interactions between extrinsic and intrinsic processes. On South Core Banks, disturbance and gradient zonation reinforce one another, resulting in an overlay of these two structuring agents. In other words, overwash penetrates inland over the same surfaces from which the intrinsic recovery processes originate (Fig. 3). On Sapelo, where plant-mediated topography has the effect of dampening the occurrence and inland penetration of overwash, disturbance processes and gradient zonation should be more disjunct (Fig. 4). Ridge-and-swale topography acts to deflect overwash alongshore, thereby creating a mosaic of vegetation in which disturbed areas are proximal to habitats of greater topographic roughness.

Principal components analysis (PCO) was employed as a visualization tool and quantitative technique to test these hypotheses. PCO is a distance-based, non-parametric ordination technique well suited for ecological data having large numbers of zero values. Like PCA, PCO is also metric (eigenvalue) technique. The largest percentage of explained variance loads on the first axis, with subsequent axes capturing decreasing percentages of this variance. I used PCO to extract the variance from the compositional data for each of the five island sites. By examining the distribution of variance among PCO axes, inferences can be made as to the extent of overlay or disjunct structure between disturbance processes and gradient zonation. On South Core

Fig. 3. Disturbance processes and subsequent recovery overlay one another on South Core Banks. In the left photo, *Myrica cerifera*, a woody shrub typical of stabilized habitats occurs within Spartina patens, a disturbance-dependent burial-intolerant stabilizer. Effects of overwash disturbance (right).

Fig. 4. Ridge-and-swale topography on Sapelo (left). The resulting high topographic roughness lessens the likelihood of overwash spreading into backbarrier locations. Where overwash does occur, it is limited to the fronting dunes and thus proximal to, or adjoining, gradient sequences of vegetation. Right photograph shows Site A on Sapelo, an area where overwash occurs. Disturbance vegetation is in the foreground, and undisturbed gradient zonation landward.

Banks, it was expected that most of the variance in the data would load on the first axis. Because disturbance processes and gradient zonation overlay and reinforce one another in this setting, the first PCO axis should capture the sum of foredune-to-backshore compositional change. In terms of explained variance, there should be a sharp break, or elbow, between the first and second PCO axes.

On Sapelo, variance should be shared among more axes. In this domain setting, disturbance exposure and intrinsic recovery processes are disjunct and decoupled from each other. Consequently, the variance within the data set should not be as readily summarized along a single axis. The dampening of disturbance through increased topographic roughness would also have the effect of folding in secondary gradients, further lessening the extraction of variance on the first axis. In this island-domain, there should be less of a break in explained variance between first and second axis. An earlier analysis of the compositional variance structure on Sapelo suggested that disturbance species and the dune-to-inland gradient sequence of vegetation load more separately across multiple axes (Stallins and Parker, 2003).

Ecological meaningful variance can be partitioned across multiple axes in metric ordination. This complicates the assumption that one can infer a distinctive ecological interpretation for individual axes. For this reason, variance structure was scrutinized as an aggregate variable, thereby avoiding more forced and noisy scatterplot interpretations of species and quadrat axis scores. To accomplish this, scree plots were used to summarize the percentage of variance extracted along the first five PCO axes. Multi-response permutation procedures (MRPP) were then used to test for significant island differences in the variance structure postulated for each island domain. MRPP non-parametrically measures the extent to which two or more multivariate data sets differ based on comparisons of the observed and permutated average within-group distance among samples (McCune and Grace, 2002). MRPP employs an effect size statistic (A) to gauge whether statistical significance reflected in p values is robust or an artifact of within-group variability no different from random expectation. This statistic typically ranges from 0 to 1. Values converging upon zero indicate that the heterogeneity within groups equals expectation by chance. Values approaching 1 indicate that all items within groups are identical and the heterogeneity within groups is greater than random expectation. Statistical significance in conjunction with high A values is indicative of stronger group differences. With ecological data, an A value of 0.3 is fairly high. All MRPP significance tests were conducted at the 0.05 significance level using PC-Ord Version 4.04 (McCune and Mefford, 1999). Sorenson (also know as Bray-Curtis) coefficients were employed as the distance metric. PCO was performed using MVSP software (Kovatch Computing Services, 1999) using Bray-Curtis distances.

4.3. Biotopographic thresholds

Elevation strongly controls overwash disturbance exposure (Hayden et al., 1995). In turn, dune plants modulate disturbance through their propensity to modify elevational contours during recovery. Cross-sectional topographic profiles constructed from total station surveys along each transect were assessed for their potential to resist the inland penetration of overwash. This was accomplished by comparing the elevational position of each island's vegetated quadrats relative to high water mark datum. This datum accurately reflects the position of frequent maximum high-water levels due to storm and tidal forcings (Morton and Speed, 1998). Where quadrat elevations were significantly lower than the high water mark elevation, it was expected that overwash could easily propagate into backshore dune habitats, a hypothesis applied to South Core Banks. On Sapelo, where biotopographic resistance to the inland penetration of overwash was hypothesized to be higher, there should be a significantly greater presence of vegetation above the high water mark datum. MRPP was used to test for significant differences between islands in the number of vegetated quadrats above and below this datum.

4.4. *Divergence of diversity controls*

Dynamics in complex earth surface systems exhibit, in a general sense, two trends: a convergence or divergence in landscape patterns (Phillips, 1999). Some patterns diversify through time and space; others show more of a bounded convergence. Such phenomena have been demonstrated for coastal landscapes (Phillips, 1999). I hypothesized that a distinctive divergence or convergence in the pattern and elevational control of species diversity should emerge in each island-domain. To test this hypothesis, Spearman's non-parametric correlation coefficients for elevation and species diversity were assessed at the island and site scales.

On Sapelo, where disturbance is more divorced from gradient zonation, elevation should not be as strongly correlated with species diversity. Once uncoupled from any island-scale elevational controls of disturbance exposure (via a greater topographic roughness), diversity should show more variability in its correlation with elevation among sites. Other more localized abiotic and biotic controls should constrain diversity, resulting in an overall weaker island-scale correlation with elevation. By contrast, on South Core, elevation and diversity should show a stronger correlation among sites. Because disturbance and gradient zonation are more strongly coupled, elevation should regulate diversity patterns over larger spatial scales. Diversity was calculated as the Shannon–Weiner index for all of the quadrats on each island. Input values were the number of point frame hits for each species within the quadrat sampling frame. Only vegetated quadrats were correlated with elevation.

4.5. *Compositional patterns*

An additional fourth hypothesis posed the more general question as to how the number and cover of species within each dune plant biogeomorphic functional group (dune builders, burial-intolerant stabilizers, and burial-tolerant stabilizers) would reflect the stability domain interactions synthesized from previous studies. As a consequence of climatic uniformity, it was expected that the dune flora on these barrier islands would show a high degree of similarity (Duncan and Duncan, 1987). Regional uniformities in temperature and precipitation regime across the coastal zone of the Georgia Bight greatly diminish any regional macroclimatic sorting on species composition (Stalter and Odum, 1993). However, microenvironmental factors, especially substrate mobility, may exert more influence than climate on the local abundance of species (Barbour and Johnson, 1977). As the two islands differ in the extent that substrate mobility is predominantly incremental versus episodic, I also expected to find a measurable degree of difference between islands in their plant functional group signatures.

I anticipated a higher total species cover of dune-builders, distributed evenly amongst the species comprising this group on Sapelo. Dune-building in this setting restricts the expression and contagion of episodic overwash disturbance. With a fronting line of foredunes, inland dune habitats are protected and the incremental modes of sediment transport required for dune building are promoted. Analogously, burial-intolerant stabilizers should also have a higher, more evenly distributed cover on Sapelo. These species stabilize swale habitats between intervening dunes. The abundance of burial-tolerant stabilizers on South Core would follow a similar logic. Species in this functional group bind overwash sediments and minimize dune-building.

Table 2
Absolute species cover for plant functional groups by site, South Core Banks, North Carolina

Species and species complexes		South Core, NC sites[a]					
		A	B	C	D	E	Total
Dune builders							
Ammophila brevigulata Fernald	P				0.2	4.9	1.1
Panicum amarum Ell.	P			OT	0.1	4.7	1.0
Sporobolus virginicus (L.) Kunth	P				OT		
Uniola paniculata L.	P	20.1	18.7	20.8	21.6	5.4	16.9
Burial-tolerant stabilizers							
Ditrichum pallidum	P	4.1	22.9	14.0	0.1		8.4
Hydrocotyle bonariensis Lam.	P	6.2	4.2	6.1	9.6	8.4	6.8
Spartina patens (Aiton) Muhl.	P	14.1	5.8	7.0	18.8	28.7	15.0
Burial-intolerant stabilizers							
Andropogon spp.	P	0.5	0.1	0.4			0.2
Muhlenbergia filipes M.A. Curtis	P	2.3	1.2	0.8	0.1		0.9
Myrica cerifera L.	P	1.3	0.5	1.7	0.8	0.9	1.0
Phyla nodiflora (L.) Greene	P	0.1					<0.1
Selected passenger species							
Cenchrus spp.	P	0.4					0.1
Commelina erecta L.	P	<0.1	0.8	1.4	0.2	0.3	0.6
Conyza canadensis L. Cronq.	A	1.6	1.8	1.9	1.2	0.1	1.3
Croton punctatus Jacquin	P	0.1				OT	< 0.1
Cynanchum angustifolium Pers	P	0.2	0.5	2.0	0.1	<0.1	0.6
Diodia teres Walter	A	0.3	0.1	0.3	0.8	<0.1	0.3
Eragrostis spp.	P	0.8	0.7	0.7	0.1		0.4
Fimbristylis spp.	P	0.3	0.2	<0.1			0.1
Gnaphalium purpureum L.	A		<0.1				<0.1
Heterotheca subaxillaris (Lam.)	A	5.5	8.3	6.2	4.1		4.8
Oenothera humifusa Nuttall	P	1.5	5.8	5.5	1.0	0.1	2.8
Solidago spp.	P	3.4	5.4	0.8	0.5	OT	2.0
Triplasis purpurea (Walter) Chapman	A	3.0	1.3	0.9	0.4		1.1

P: perennial; A: annual; OT: on site but off transect.

[a] Overwash increases in frequency from Site A to E.

Therefore, a higher cover (evenly distributed among the constituent species of this group) would be expected to enhance the reproduction of the habitat conditions for these species.

5. Results

5.1. Compositional patterns

Eighty-eight dune plant species and species complexes were identified on Sapelo. Seventy-eight species and species complexes were recorded on South Core Banks. Total percent cover of vegetation was higher on South Core (71% versus 52%). In all, both islands shared 43 species. These shared species comprised 96% of the total absolute species cover on Sapelo, and 78% of the total absolute species cover on South Core Banks. Based on percent absolute species cover and growth form, eleven species were identified as having a strong influence upon dune topography and placed into the aforementioned functional groups: burial-intolerant stabilizers (four spp.), burial-tolerant stabilizers (three spp.), and dune builders (four spp.) (Tables 2 and 3). These driver species were dominantly perennials typical of dune environments. Most of the species on each island were passenger species (Fig. 5). These were chiefly ruderals from upland environments, annuals that have reduced persistence, or species that were rarely

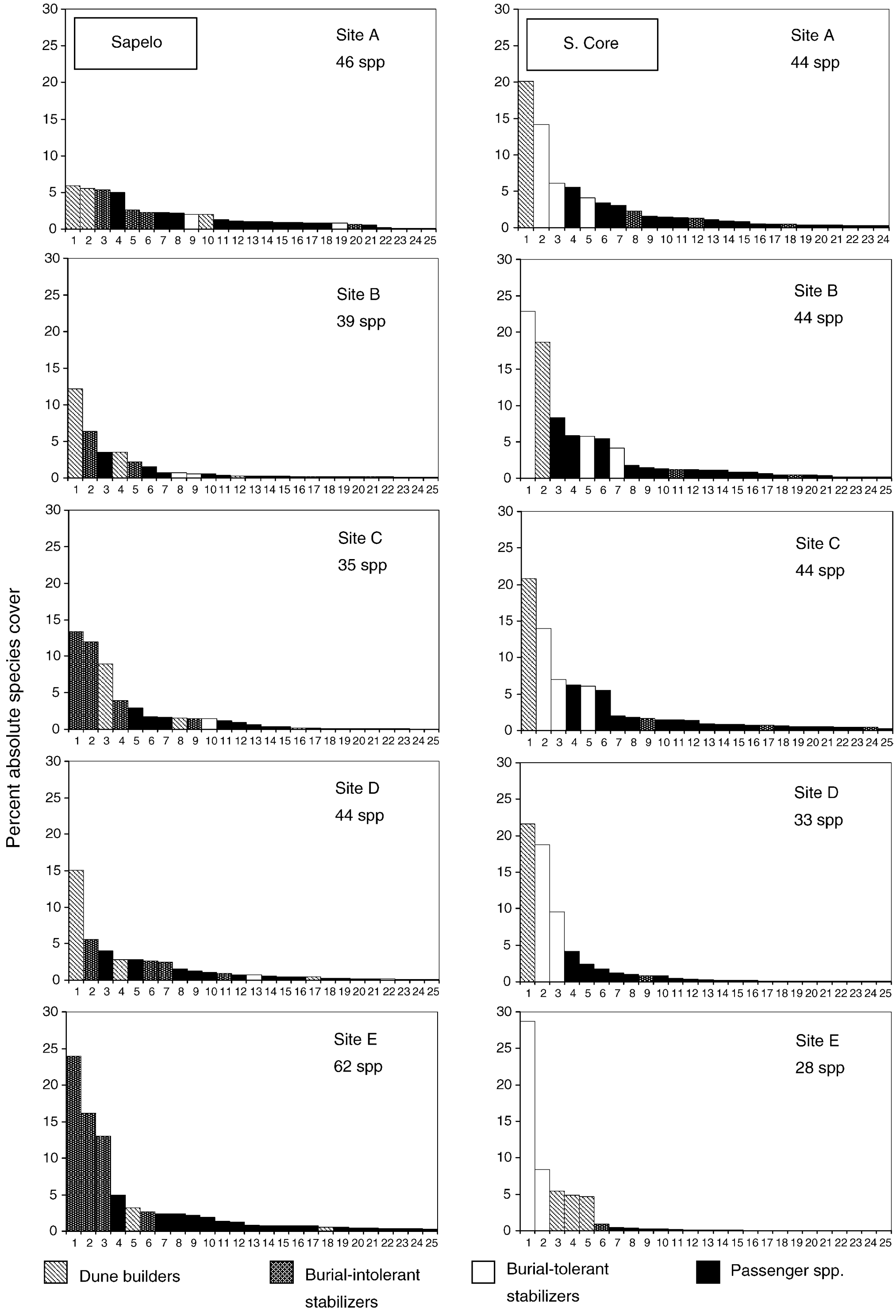
Percent absolute species cover
Sapelo
Site A
46 spp
S. Core
Site A
44 spp
Site B
39 spp
Site B
44 spp
Site C
35 spp
Site C
44 spp
Site D
44 spp
Site D
33 spp
Site E
62 spp
Site E
28 spp
0
5
10
15
20
25
30
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
Dune builders
Burial-intolerant stabilizers
Burial-tolerant stabilizers
Passenger spp.

Table 3
Absolute species cover for plant functional groups by site, Sapelo Island, Georgia

Species and species complexes		Sapelo Island, GA sites[a]					
		A	B	C	D	E	Total
Dune-builders							
Ammophila breviguIata Fernald	P						
Panicum amarum Ell.	P	5.6	3.6	1.5	2.8	0.6	2.9
Sporobolus virginicus (L.) Kunth	P	2.0	0.3	0.2	0.5		0.6
Uniola paniculata L.	P	5.9	12.2	9.0	15.1	3.2	9.5
Burial-tolerant stabilizers							
Ditrichum pallidum	P						
Hydrocotyle bonariensis Lam.	P	2.0	0.7	1.4	0.7	<0.1	1.0
Spartina patens (Aiton) Muhl.	P	0.8	0.5		0.2	<0.1	0.3
Burial-intolerant stabilizers							
Andropogon spp.	P	2.6	0.2	1.4	2.7	2.7	1.9
Muhlenbergia filipes M.A. Curtis	P	2.3	6.3	3.9	0.9	13.0	4.9
Myrica cerifera L.	P	0.6	0.2	11.9	2.5	23.9	7.2
Phyla nodiflora (L.) Greene	P	5.4	2.2	13.4	5.6	16.2	8.2
Selected passenger species							
Cenchrus spp.	P	0.5	0.1	3.0	2.8	4.9	2.2
Commelina erecta L.	P						
Conyza canadensis L. Cronq.	A	1.0	0.2	<0.1	0.7	0.2	0.4
Croton punctatus Jacquin	P	0.9	3.6	1.2	4.0	0.8	2.2
Cynanchum angustifolium Pers	P						
Diodia teres Walter	A						
Eragrostis spp.	P	5.0	OT	0.1		<0.1	1.0
Fimbristylis spp.	P	1.3	<0.1	0.9	1.6	2.4	1.2
Gnaphalium purpureum L.	A	2.2	0.1	0.1	0.2	0.7	0.7
Heterotheca subaxillaris (Lam.)	A	2.2	0.8	1.7	1.1	0.1	1.2
Oenothera humifusa Nuttall	P	< 0.1	0.4	0.4	0.1	0.4	0.2
Solidago spp.	P						
Triplasis purpurea (Walter) Chapman	A	1.0	1.5	1.7	1.3	1.3	1.4

P: perennial; A: annual; OT: on site but off transect.
[a] Overwash is infrequent at all sites except Site A.

encountered. The total absolute cover of passenger species was similar on each island (Sapelo 15%; South Core Banks 20%).

As hypothesized, even with the large overlap in species occurrence, the abundance of dune builders, burial-tolerant stabilizers, and burial-intolerant stabilizers differed among islands. South Core had the higher cover of two burial-tolerant stabilizers, *Spartina patens* and *Hydrocotyle bonariensis*, species adapted to frequent overwash (Table 2). An assemblage of burial-tolerant mosses, comprised chiefly of the genera Ditrichum, was found only on South Core. In sand dune habitats, bryophytes stabilize potentially mobile sediments (Martínez and Maun, 1999). These three burial-tolerant stabilizers comprised nearly half (30%) of the total absolute cover (71%) of the island. *Uniola paniculata*, a common dune-building species of the southeastern United States, was the dominant dune-building species. The three other dune-building species were present; however, only one, *Panicum amarum*, had a cover value >1%. The four species

Fig. 5. Species rank abundance by plant functional groups for island sites. Overwash was confined to Site A on Sapelo. On South Core, overwash increases in frequency from Site A to Site E. Passenger species make up the bulk of species richness on each island. Site richness values record the number of species encountered along transect as well within the boundaries of each site. Diversity expressed as the Shannon–Weiner index.

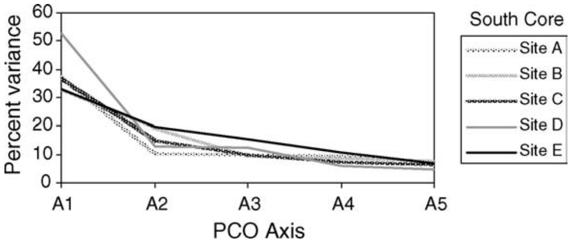

Fig. 6. Scree plots for South Core Banks. Site ordinations varied in the number of quadrats and species present: Site A (40/212; B 38/223); C (40/210); D (29/150); and E (23/162).

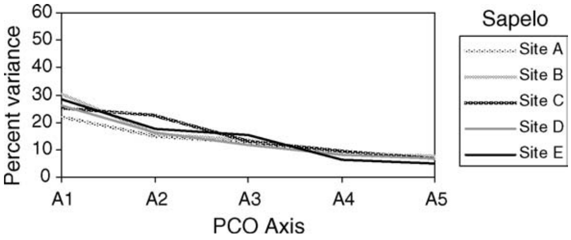

Fig. 7. Scree plot for Sapelo Island. Site ordinations varied in the number of quadrats and species present: Site A (35/180); B (30/209); C (27/208); D (31/253); and E (47/177).

designated as burial-intolerant stabilizers were infrequent on South Core. Only two, *Muhlenbergia filipes* and *M. cerifera*, had cover values >1%. The bulk of species richness was contributed by passenger species that colonized disturbed patches on stabilized overwash flats (63 spp).

Sapelo dune habitats were dominated by burial-intolerant stabilizers, comprising 22% of the total absolute species cover for the island (Table 3). All four species in this functional group (*M. filipes*, *Phyla nodiflora*, *Andropogon* spp., and *M. cerifera*) were abundant in the low-lying swales between dune ridges. Sapelo was also characterized by a higher cover of *P. amarum* and *Sporobolus virginicus*. These two dune-building species often initiate primary foredune recovery (Woodhouse, 1982). Of the three burial-tolerant stabilizers, only *H. bonariensis*, had a cover >1%. *S. patens* was present but sparse. Passenger species also comprised the bulk of species richness on Sapelo (70 spp). These species were ruderals, vines and herb species associated with *M. cerifera* thickets, and forbs in open swales.

Table 4
Position of all quadrats with vegetation relative to the high water mark datum

Island	Site	Number of vegetated quadrats	Percent below or equal to HWM datum	Percent above HWM datum
Sapelo	A	154	51.3	48.7
	B	156	16.0	84.0
	C	186	11.3	88.7
	D	213	28.6	71.4
	E	149	32.2	67.8
	Island	858	27.3	72.7
South Core Banks	A	184	62.5	37.5
	B	214	94.9	5.1
	C	161	95.7	4.3
	D	118	70.3	29.7
	E	118	78.8	21.2
	Island	795	82.9	17.1

5.2. Variance structure

As hypothesized, the first PCO axis extracted a larger amount of variance among South Core sites (median = 37.4%) when compared to Sapelo (26.1%). The scree plot for South Core indicated a distinct break between the first and second PCO axis (Fig. 6). On Sapelo, the elbow was less pronounced, and the percent variance extracted was distributed more evenly across the first five axes (Fig. 7). MRPP indicated that the differences in island variance structure were statistically significant ($A = 0.23$, $p < 0.01$) across the first five PCO axes.

5.3. Biotopographic thresholds

Sapelo had a much higher number of vegetated quadrats above the higher water mark (73%) compared to South Core (17%) (Table 4). Site-level MRPP indicated that this difference between islands was significant ($A = 0.35$; $p < 0.01$). More qualitatively, the geometry of the plant-mediated dune topography on South Core suggested that with the breaching of the fronting dune line, overwash would spread into backshore habitats (Fig. 8). By contrast, on Sapelo, biotopographic thresholds were better developed as a consequence of its more prominent ridge-and-swale topography.

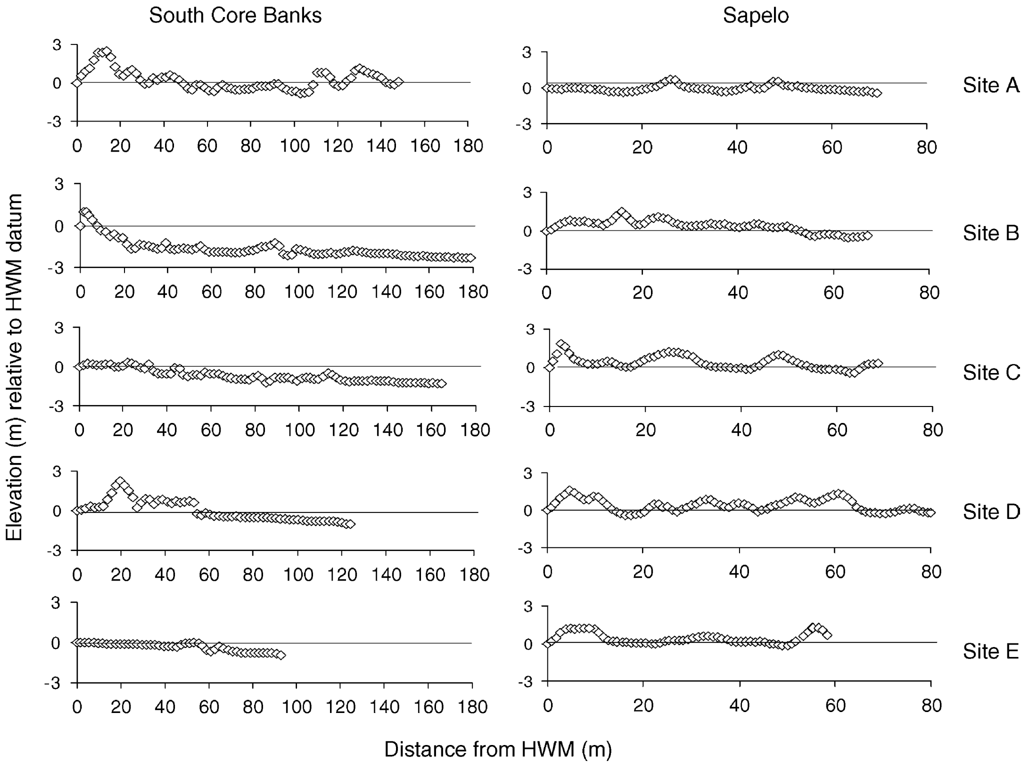

Fig. 8. Topographic profiles for representative transects from each island. Elevation and point frame measurements were spaced at 1-m intervals along transects on Sapelo. To maintain comparable sampling intensities between islands, the longer distances to stabilized vegetation on South Core Banks required that point-frame sampling be spaced at 2-m intervals. Scaling of horizontal axis for each island tends to deemphasize island differences in topographic roughness.

5.4. Divergence of diversity controls

Elevation had a stronger, negative correlation with species diversity on South Core Banks ($r_s = -0.5$, $p < 0.01$) (Fig. 9). This relationship was

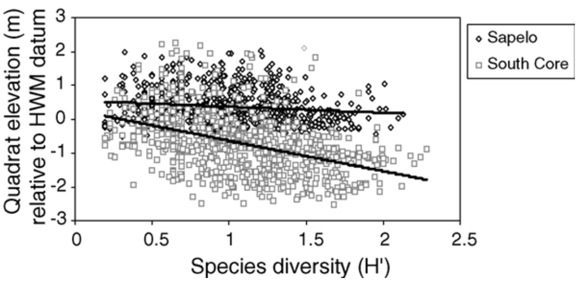

Fig. 9. Scatterplot of species diversity (Shannon–Weiner index)and elevation with linear trendlines. Sapelo ($r_s = -0.1$, $p < 0.01$) South Core ($r_s = -0.5$, $p < 0.01$). Total number of quadrats with alpha greater than zero: Sapelo = 858, South Core = 795.

Table 5
Correlation of quadrat species diversity (Shannon–Weiner index) with elevation relative to high water mark datum

Location	Site	Number of quadrats	Spearman's correlation coefficient	*p*-value
Sapelo	A	154	−0.25	<0.01
	B	156	−0.13	0.12
	C	186	0.18	0.01
	D	213	−0.18	<0.01
	E	149	0.05	0.58
	Island	858	−0.12	<0.01
South Core Banks	A	184	−0.22	<0.01
	B	214	−0.43	<0.01
	C	161	−0.51	<0.01
	D	118	−0.51	<0.01
	E	118	−0.28	<0.01
	Island	795	−0.48	<0.01

weak but significant across Sapelo ($r_s = -0.1$, $p < 0.01$). Site-level correlations also exhibited this trend (Table 5). On Sapelo, these values were weak, hovering around zero, and often insignificant. On South Core Banks they were uniformly significant, ranging from −0.2 to −0.5, a narrower spread of values when compared to Sapelo (−0.3 to 0.2). Correlations at the transect-level followed these trends.

6. Discussion

The distinctive functional identity and relative abundances of biogeomorphic plant functional types on each island supported the domain dynamics inferred from earlier studies. On South Core, the relatively higher cover values among species designated as burial-tolerant stabilizers should act to reinforce the persistence of a low, flat topography. Conversely, on Sapelo, the greater cover of dune builders and burial-intolerant swale species should augment topographic roughness and dampen the inland contagion of overwash. Cross-sectional profiles conveyed the potential for overwash to spread into backshore habitats with the breaching of dunes on South Core. More topographic resistance, due to increased topographic roughness and elevational positions above the high water mark, characterized Sapelo profiles.

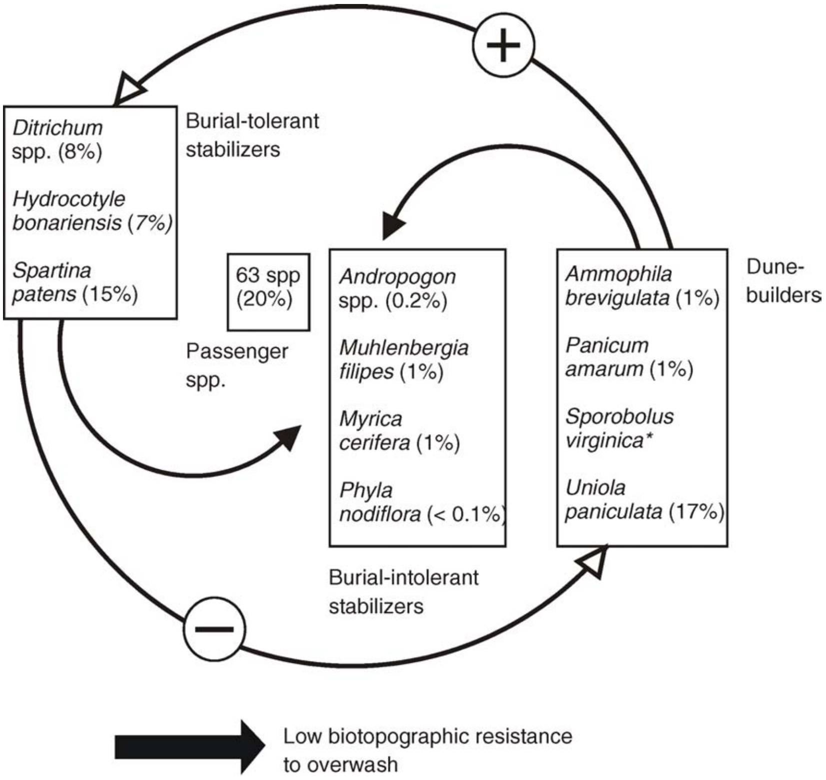

Fig. 10. Dune stability domain model for a wave-dominated microtidal barrier island dune system (South Core Banks, North Carolina). Species and topography reproduce each other by reinforcement of disturbance and intrinsic recovery processes. Following overwash, the growth forms of burial-tolerant stabilizers bind sediments in place and contribute to a low, flat topography. These species exert a damping influence (negative feedback) on dune-builder functional group abundance and evenness by sequestering sediments needed for vertical dune growth. Because of their reduced impacts upon topography, dune-building species indirectly lower the resistance to future overwash, thereby promoting the abundance of burial-tolerant stabilizers in a weak positive feedback. Passenger species colonize stabilize surfaces in the intervals between overwash exposure. Note the lower redundancy in dune-building species. Percentages represent absolute species cover. Asterisk denotes species encountered off transect but within a site.

The results of deductive analyses were also supportive of the dynamics hypothesized for each domain. Percent variance loaded more strongly on the first axis in the island-domain of South Core Banks, the expected outcome if disturbance patch dynamics and gradient zonation overlay one another. Variance structure on Sapelo was more indicative of a landscape geometry in which disturbance processes and gradient zonation are more segregated. Domain dynamics were also supported in the thresholds properties quantified in cross sections. Biotopographic resistance to overwash was greater on South Core relative to Sapelo. The propensity of each island-domain to modify disturbance exposure was also evident in the association between species diversity and elevation. Sapelo had weaker and more divergent correlative relationships between species diversity and elevation at island, site, and transect scales. Conversely, on South Core, these correlations were stronger, more significant, and expressed within a smaller range of values. Species and topography also reproduced one another within differing elevational ranges, at more protected locations above the high water mark on Sapelo, and at more exposed positions below the high water mark on South Core.

Based on these field observations, statistical properties, as well as earlier foreshadowing of complex systems dynamics in barrier island dunes, two formal stability domain models can be synthesized (Figs. 10 and 11). In these domains, the

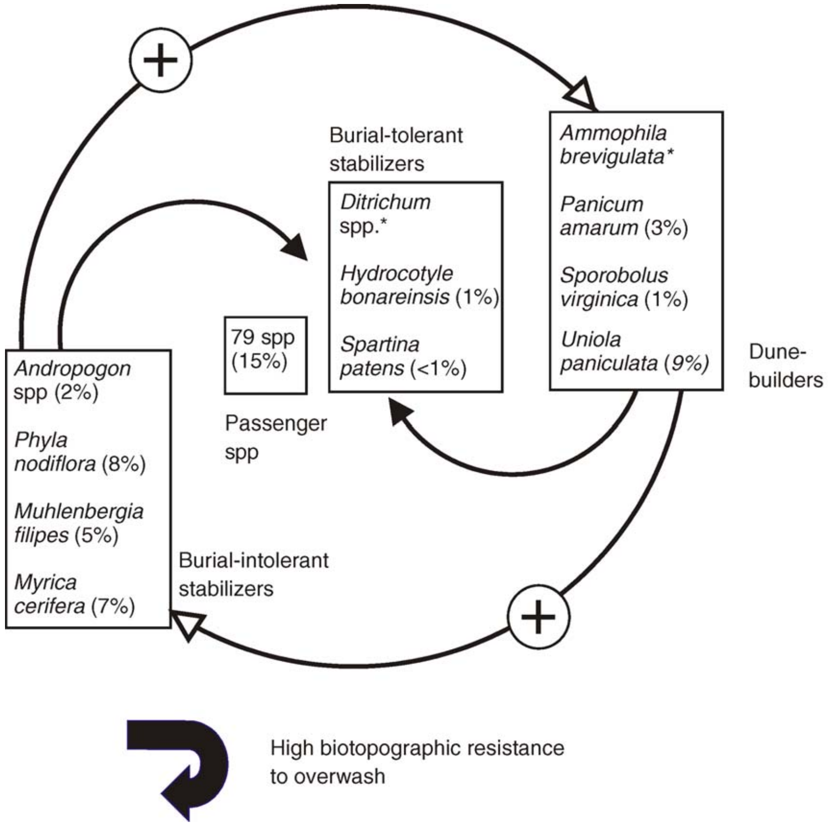

Fig. 11. Dune stability domain model for a mixed-energy mesotidal barrier island dune system (Sapelo Island, Georgia). Species and topography reproduce each other by decoupling disturbance from intrinsic processes. A high evenness in dune-building and burial-intolerant species reinforce their abundance along dune ridge-and-swale topography through positive feedbacks. Dune-builders elevate ridge surfaces, while the phalanx growth forms of burial-intolerant stabilizers anchor sediments in the intervening low-elevation swales. The resulting topographic roughness damps inland overwash exposure and reinforces the incremental (versus episodic) modes of sediment transport that support these species and landforms. Percentages represent absolute species cover. Asterisk denotes functional species not encountered during sampling.

dynamics among plant species, sediment transport, and landforms exert some control over their own reproduction, a propensity also conceptually recognized for riparian systems (Malanson, 1993, p. 206). A general criticism of these models is that they do not capture or prove the full operational dynamism of the interactions in each domain. However, such a criticism is premature, as the intent of this field-based study was to build the details needed for attractor characterizations in formal dune landscape simulations. Such simulations can more adroitly visualize causal linkages and larger-temporal scale dynamics. One prominent modeling study has quantified generalized domain dynamics similar to the ones presented here. Using Swarm as a platform to model the dynamics of species coexistence along a gradient of fire disturbance, Savage et al. (2000) documented compositional attractors that emerge at the low and high ends of a disturbance gradient. Low levels of disturbance led to landscapes whose elements excluded fire and were dominated by fire-resistant late-successional species. High levels of disturbance led to an attractor that oscillated between domination by early successional species and large disturbances. The design of Savage et al.'s fire disturbance model drew upon a synthesis of field-based quantitative and qualitative knowledge of fire ecology.

There was one other incidental line of field evidence for the proposed domain dynamics. It concerns the relationship among plant functional type abundance, colonization potential, and relative success. Although there were sharp island differences in the relative abundance of species in each functional group, island setting did not appear to affect their colonization potential. Only two driver species (*Ammophila breviligulata* and *Ditrichum* spp.) were restricted to a single island occurrence (South Core Banks). Furthermore, many of the more numerous passenger species were common on one island-domain but restricted in distribution and abundance on the other. The point to emphasize here is the propensity for all species to occur on both islands, while differing markedly in their relative success. I speculate that this difference between colonization potential and relative abundance may also be indicative of the dynamic boundaries between island-domains. A high representative evenness and abundance (i.e. diversity) among all plant functional group could not simultaneously promote or dampen disturbance, thereby limiting the dynamic persistence of such a complete assemblage of species. Likewise, the constraint envelope of each domain may not be so tight as to preclude the colonization by all of the plant functional types. More analyses of within-island species distributions are necessary to examine this supposition.

7. Conclusion

It is difficult to cleave the extent to which patterns attributed to domain dynamics in this study can be explained by underlying variation in physical variables versus self-organization, a question posed by Levin (1998, p. 431) for complex systems in general. For example, sediment budget also shapes overwash processes. When sediment is unavailable, the frequency of overwash exposure increases (Roman and Nordstrom, 1988). Dune-building can only take place where there is a surplus of sediment (Psuty, 1988). In this light, the contrasting elevational ranges of vegetation (relative to the high water mark) in each island-domain could also be a function of sediment budget. However, one must consider that dune plants, like most organisms, are not passive in their responses to changes in their environment (Odling-Smee et al., 2003). Dune plants can modify topography irrespective of whether the sediment budget is positive or negative so as to render their environment more predictable, a central organizing strategy for adaptive agents. As posited in this study, dune plants may attenuate this unpredictability by increasing biotopographic thresholds to overwash disturbance through dune-building or by promoting low relief topography, strategies that can absorb some of the energy from overwash without catastrophic loss of landscape structure. From this same perspective, the differences in the correlations between elevation and species diversity observed on each island-domain reflect more than just a passive change in the extent of the analysis. They also reflect the propensity of dune plants to modify their environment and modify the scales at which they (and other organisms) experience it (Levin, 2000).

Sampling of a larger number of barrier islands in the Georgia Bight could add more detail to stability domain dynamics and patterns explored in this paper.

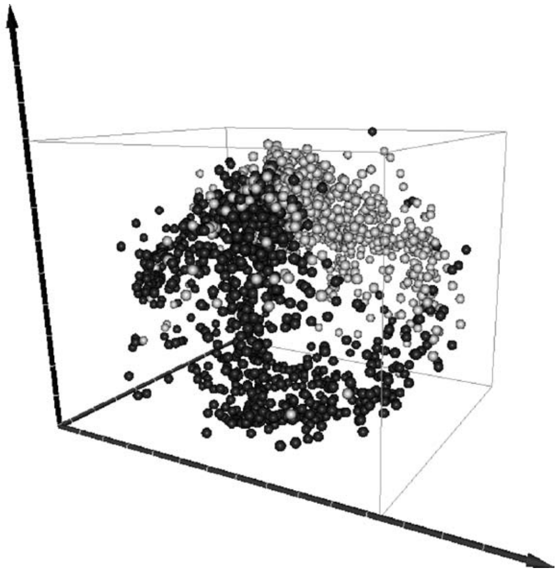

Fig. 12. Phase space demarcated by the island stability domains described in this paper. Light-colored spheres represent quadrats on Sapelo. Dark-colored spheres represent quadrats on South Core Banks. Distance between quadrats represents their compositional similarity. Ordination methods can be utilized to visualize phase space (see Anand, 2000; Malanson et al., 1990). For this plot, non-metric multidimensional scaling was utilized as the ordination method. The non-overlapping region separating the island-domains may be indicative of a dynamically unfavorable combination of species.

This approach would capture a larger phase space (see Anand, 2000; Malanson et al., 1990) over which coastal dune dynamics play out, and allow more comparisons among islands in different nearshore settings (Fig. 12). Such a broader-scale study would also illuminate how simple models of complex systems play out in the geographic contingencies of the real world (Phillips, 2001; Vale, 2003). Undoubtedly, the geographic distribution of stability domains is more complicated than presented here. For example, in addition to local sediment budget, island orientation (Godfrey, 1977), antecedent geology (Belknap and Kraft, 1985), and human impacts (Roman and Nordstrom, 1988) – all factors that influence the potential for overwash – vary considerably along the larger-scale meteorological gradient in overwash spanning the Georgia Bight. In addition, domains may change through time in response to a storm event (or lack thereof) outside of the natural range of their historic variability.

Ecological studies have utilized human impacts, nutrient cycling, and food webs as the template for stability domains. However, biogeomorphic interactions (see reviews by Parker and Bendix, 1996; Swanson et al., 1988; Bendix and Hupp, 2000) may also generate the feedbacks necessary for domain organization. The stability domain models presented in this study will hopefully provide attractor descriptions for computational simulations of dune landscapes as well as contribute to our understanding of biogeomorphic systems in general.

Acknowledgements

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