The Influence of Complex Systems Interactions on Barrier Island Dune Vegetation Pattern and Process

J. Anthony Stallins* and Albert J. Parker**

*Department of Geography, Florida State University
**Department of Geography, University of Georgia

Studies of dune vegetation patterns have emphasized two structuring agents: local environmental gradients that shape the prominent zonation of coastal plant species, and disturbance patches initiated by overwash during coastal storms. For dune systems of two barrier islands in the Georgia Bight, we investigate how the interplay of these two conceptual frames generate patterns in (1) longitudinal (along-shore) and transverse (across-shore) compositional variability and (2) the arrangement of species along transverse gradients. We describe how this interplay constitutes a complex biogeomorphic system in which disturbance and recovery along gradients reinforce one another in positive feedback. Topographic and cover data were sampled within strip transects aligned perpendicular to the shoreline at study sites along a frequently storm-overwashed microtidal (South Core Banks, North Carolina) and an infrequently overwashed mesotidal (Sapelo Island, Georgia) barrier island. Multiresponse permutation procedures revealed that Sapelo has significantly greater transect-level longitudinal and transverse compositional variability. Nonmetric multidimensional scaling indicated that a single dominant transverse species gradient characterizes South Core, versus two spatially intersecting vegetation gradients for Sapelo. On South Core, reduced relief promoted by plant species of horizontally extensive growth forms reinforces the spread of overwash events across the landscape, thus overlaying disturbance and recovery gradients. Species-mediated dune topographic roughness on Sapelo buffers the dune vegetation from potential stand-wide disturbances, thereby juxtaposing disturbance and recovery gradients to a greater extent. We discuss the benefit of incorporating a complex adaptive-systems framework into the reductionist methodologies invoked in field-based biogeographical studies. *Key Words: barrier islands, complex adaptive systems, dune vegetation, overwash.*

Two conceptual frames have been historically invoked to explicate vegetation patterns: the imposition of site factors that control local gradients of energy, moisture, and nutrients (Gleason 1926; Whittaker 1970) and disturbance events that clear patches of ground and trigger vegetation recovery sequences (Pickett and White 1985). While often invoked separately, these two conceptual frames need not be viewed as mutually exclusive. Biogeographic patterns across a landscape reflect the interplay of disturbance patch dynamics and gradient zonation. Disturbances overlay environmental gradients, both influencing and being influenced by those gradients (Harmon, Bratton, and White 1983; White 1987). Moreover, the relative importance of these two structuring agents is scale-dependent, varying in time and across geographic space (Peet 1992). Plant community patterns emerge from an interaction of externally forced disturbance and the local abiotic and biotic factors expressed along physical gradients (Parker 1993; Reice 1994).

In this article, we work from the premise that feedbacks between disturbance and gradient zonation are a defining characteristic of complex adaptive systems. Complex adaptive systems theory (Levin 1998; Malanson 1999; Maurer 1999) and its counterpart, developmental systems theory (Oyama, Griffiths, and Gray 2001), abjure dichotomous causal frames. They presume parity in the structuring agency contributed by intrinsic and extrinsic factors and avoid drawing out distinctions as to how individual causal factors shape patterns. While material fluxes underlying complex adaptive systems have received considerable attention (Jørgensen and Müller 2000), subsequent effects on biogeographic patterns have been sparingly articulated despite the recognition of potential theoretical insight (Milne 1998).

Barrier-island dune systems afford a compelling setting to observe how the recursive, self-organizing behavior of complex adaptive systems molds biogeographic patterns. Biogeomorphic environments are characterized by a network of feedbacks among vegetation, landforms, and sediment mobility (Parker and Bendix 1996). On barrier islands, these interactions constitute a sensitive biogeomorphic system, rather than a collection of independent components (Riggs 1976; Rastetter 1991; Hansom 2001). Over relatively short temporal scales, dune plant species promote sediment deposition, which ultimately shapes dune

landforms. Dune landforms, in turn, influence sediment mobility, the spatial pattern and frequency of disturbance events, and the structure of physical gradients influencing vegetation cover (Swanson et al. 1988; Stallins 2001).

Surprisingly, few recent studies of dune vegetation quantify compositional patterns as an interaction of disturbance regime and site factors (Ehrenfeld 1990). Well-documented barrier-island morphologies of the southeastern U.S. Atlantic coast are ideal for investigating these linkages. Overwash, in which large volumes of sediment and salt water are transported overland during cyclonic storms, occurs frequently in wave-dominated microtidal barrier-island morphologies. By contrast, sediment transport on mixed-energy mesotidal barrier-island morphologies is more strongly influenced by tidal inlets. Along-shore erosion and deposition is incremental. Overwash is rare except where land is newly formed and without dunes, or severely eroded.

The purpose of our article is to suggest how complex systems interactions mold barrier-island dune-plant species patterns and processes for these two contrasting geomorphic settings. We present conceptual models of complex adaptive systems for two barrierisland morphologies of the Georgia Bight and address two specific questions: (1) Do barrier-island dune vegetation patterns exhibit contrasts in orientation, with transverse, or cross-island, compositional variability more prominent on an infrequently disturbed island and longitudinal, or along-shore, structure more evident on a frequently disturbed island? (2) How do species vary in their arrangement along the transverse environmental gradients of each island morphology? By basing our hypotheses about compositional variability on either patch dynamics or gradient structuring, our questions seek to resolve how these conceptual frames, independent of each other, correspond to species patterns for each barrier island morphology. The extent to which the predictions of these two conceptual frames fall short of observed patterns will provide insight as to how complex adaptive systems mold the distribution of dune plant species. We close with a discussion of how a complex adaptive systems framework, in which disturbance and gradient zonation are linked, may challenge some of the assumptions underlying the characterization of disturbance regimes.

Our research questions do not purport to prove the complex adaptive systems models presented for each island morphology. Indeed, "proving" any complex adaptive system is difficult, given its ontogenetic character (Bak 1996; Ulanowicz 1997). Following Baker (1996) and Phillips (1999c), our geographical inquiry is as much novel hypothesis formulation as it is empirical substantiation.

Background

Most studies of coastal dune vegetation over the past century have consistently identified transverse environmental gradients of salt spray exposure, incremental sediment mobility, and soil moisture as primary factors distinguishing dune vegetation (Oosting and Billings 1942; van der Valk 1974; Barbour 1978; Moreno-Casasola 1986; Hesp 1991). In response to these overlapping physical gradients, dune vegetation often develops its characteristic compositional zonation parallel to the shoreline. Other authors have emphasized the effects of overwash disturbance on dune vegetation patterns (Schroeder, Hayden, and Dolan 1979; Zaremba and Leatherman 1986; Roman and Nordstrom 1988). Exposure to frequent and extensive overwash events rearranges transverse structure and establishes in its place a mosaic of along-shore disturbed patches that vary in age and composition.

A number of conceptual and field-based studies recognize that disturbance-related patch dynamics and the zonation imposed by harsh physical gradients are not mutually exclusive structuring agents. Overwash disturbance and recovery along local physical gradients interact to mold broad-scale geographic trends in dune physiography and vegetation patterns (Godfrey 1977; Godfrey, Leatherman, and Zaremba 1979; Costa, Cordazzo, and Seeliger 1996; Martínez, Moreno-Casasola, and Vázquez 1997). On the Outer Banks of North Carolina, Odum, Smith, and Dolan (1987) observed increased transverse vegetation zonation with construction of artificial fore-dunes, which dramatically decreased shore disturbance frequencies. More recently, Hayden and colleagues (1995), working on low-profile, frequently overwashed barrier islands, described how land surface elevation structures vegetation pattern by dictating potential exposure to overwash events, while also imposing spatial variability in the depth to freshwater.

These more integrative dune studies, however, do not fully address the role of positive feedbacks as an important organizing force (DeAngelis, Post, and Travis 1986; Perry 1995; Ulanowicz 1997). Complex adaptive system properties emerge when vegetation-induced sedimentation changes the nature of the vegetation that can be supported across a landform or when successional changes in vegetation alter its contribution to sedimentation (Bendix and Hupp 2000). With self-organization, topography and the species that shape the topography may be maintained in a positive feedback (Wilson and Agnew 1992).

Coastal landform studies have established that embayments in coastal plain shorelines exhibit a range of

morphologies around their margin (Hayes 1979, 1994; Davis and Hayes 1984). On microtidal coasts along the margin of the Georgia Bight, barrier islands are long and linear, as exemplified by the Outer Banks of North Carolina. On mesotidal coasts at the center of embayments, barrier islands are short and wide, with a characteristic "drumstick" shape, as exemplified by the Sea Islands along the coast of Georgia and South Carolina. These contrasts in island morphology are coupled with climatological gradients of increased exposure to extratropical cyclones with increased latitude in the winter season (Mather, Adams, and Yoshioka 1964; Davis, Dolan, and Demme 1993). As a result, shore disturbance exposure varies dramatically along the southeastern U.S. Atlantic coast (Williams and Leatherman 1993). Islands in the Outer Banks are frequently buffeted by winter storms (particularly nor'easters). Topography and vegetation are strongly influenced by overwash events. By contrast, on the Georgia and South Carolina coasts, cyclonic events that generate overwash are less frequent.

We posit that the dune habitats of these two barrier-island morphologies exhibit self-organizing properties and exemplify distinctive complex adaptive systems. Biogeomorphic interactions dominant on each island morphology may modify external disturbance such that they reinforce an internally generated order, a hallmark of complex adaptive systems (Levin 1998). Our inference of these self-organizing interactions is drawn from field-based studies (Hosier 1973; Godfrey 1977; Godfrey, Leatherman, and Zaremba 1979), from computer simulations (Rastetter 1991), and from theoretical and applied ecology. Dominant species may modify variability in disturbance exposure to enhance survivability (Kay 2000; Therriault and Kolasa 2000; and see the self-disturbance hypothesis of Bascompte and Rodriguez 2000). It has also been suggested that barrier islands may organize into two distinct process-forms at larger, island-level scales (see Carter and Orford 1991 in Phillips 1999a).

On each barrier-island morphology, landform-mediated environmental gradients, overwash, and species abundances may reinforce one another in a positive feedback. For the wave-dominated microtidal barrier islands of the Outer Banks, dunes are often low and discontinuous (Figure 1). Extensive barrier flats develop, in part, because burial-tolerant plant species recolonize overwash sediments and prevent excessive loss of sand by deflation (Godfrey and Godfrey 1976). Once sediments are stabilized by the horizontally extensive rhizome networks of burial-tolerant plants, or sequestered through the formation of a shell lag layer on the surface, they are unavailable to form protective foredunes (Woodhouse, Seneca, and Broome 1976). In this manner, disturbance-dependent species mediate their abundance by contributing to a low-relief topography that reinforces exposure to future overwash in a positive feedback (Godfrey, Leatherman, and Zaremba 1979; see Figure 2).

By contrast, overland sediment mobility in the mixed-energy mesotidal barrier islands of Georgia is strongly controlled by incremental transport processes. In the absence of overwash, an extensive dune ridge-and-swale topography may develop (Figure 3). Numerous models of dune ridge formation emphasize the role of vegetation (Taylor and Stone 1996). Elevational contrasts are maintained by positive relief generated by dune-building taxa and stabilization of intervening low swales by burial-intolerant woody shrubs and grass species. This topographic roughness acts as a barrier to the spread of overwash into backshore dune habitats. Wave energy from

Figure 1. Barrier flats of wave-dominated microtidal barrier islands of the Outer Banks (north end).
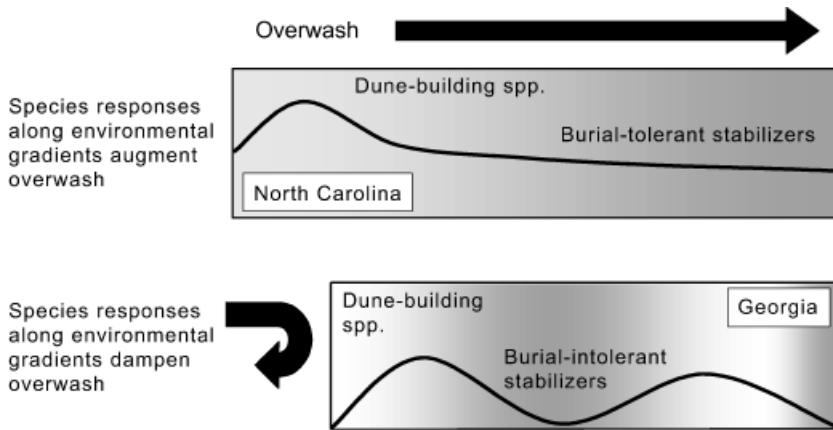
Figure 2. Models of complex systems interactions for two barrier island morphologies. Disturbance (overwash) and gradient zonation (represented by shading) reinforce one another in a positive feedback but with differing impacts on the patterning of disturbance. Based on Godfrey and Godfrey (1976) and Godfrey, Leatherman, and Zaremba (1979).

storms may be deflected into extensive networks of tidal inlets that bound islands (Sexton and Hayes 1991). 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 habitat conditions for which they are competitively superior. For both island morphologies, the abundant topography-modifying species may function as "ecosystem engineers," in that they may regulate habitat heterogeneity and species coexistence (Jones, Lawton, and Shachak 1997; Stachowicz 2001).

To address how the predictions of patch dynamics and gradient zonation, under an assumption of noninteraction, correspond to observed dune-plant compositional variability, we deployed compositional and topographic surveys on two barrier morphologies in the Georgia Bight. We hypothesized that where disturbances are infrequent and limited in area, environmental gradients should mold vegetation patterns. Similarly, as disturbance events increase in frequency and extent, patch dynamics should obscure the sorting effects of local environmental gradients. The extent to which patch dynamics and gradient zonation predict longitudinal and transverse compositional variability will facilitate inference of how their self-organizing interaction shapes dune vegetation pattern and process.

Study Region

We intensively sampled vegetation cover across the range of dune physiographies for two largely undeveloped barrier islands: the wave-dominated microtidal barrier of South Core Banks, North Carolina, and the mixed-energy mesotidal barrier of Sapelo Island, Georgia (Figure 4). Sapelo Island is a complex of several islands. Because a large, immobile Pleistocene core characterizes many of the island complexes of the Georgia and South Carolina coast, these islands may be referred to as "sea islands." Sapelo Island is a sea island surrounded by the

Figure 3. Ridge-and-swale topography along a mixed-energy mesotidal barrier island on the Georgia coast.
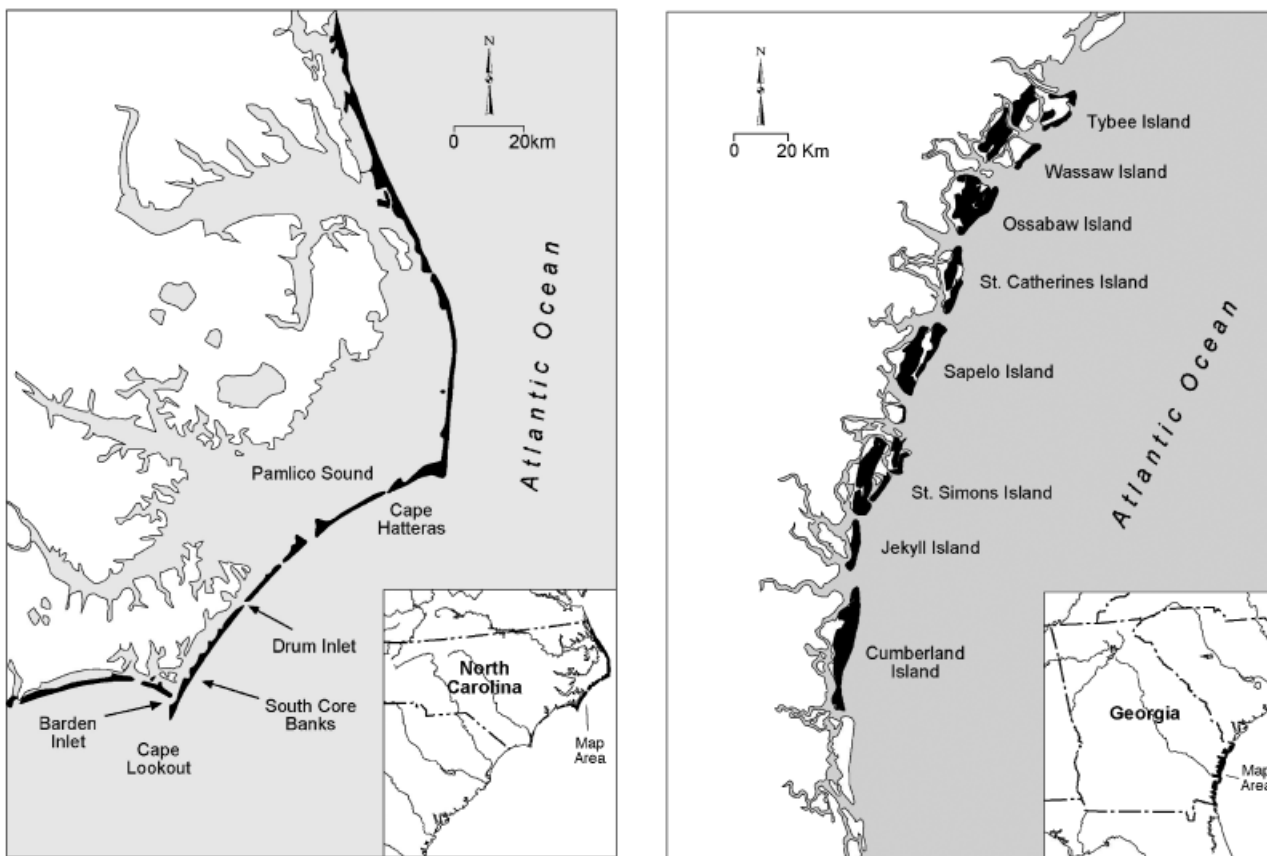
Figure 4. Study islands and coastal morphology. Pleistocene-aged sea island of Sapelo Island, Georgia and surrounding Holocene barrier islands (mixed–energy mesotidal barrier-island coast), and South Core Banks, North Carolina (wave-dominated microtidal barrier-island coast).

smaller, more mobile barrier islands of Blackbeard, Cabretta, and Nannygoat (see Walker and Coleman 1987). In order to minimize the confounding influence of multiple tidal inlets on Sapelo, we confined our sampling to the 5 km of Nannygoat Beach, the southernmost Holocene barrier island. On Nannygoat Beach, overwash is infrequent and restricted to the south end (Deery and Howard 1977). By sampling this smaller, more mobile barrier of the Sapelo complex, we effectively constrain the comparative nature of our study to single barrier-island landforms bounded by tidal inlets. South Core Banks is a retreating Holocene barrier. Overwash increases in frequency and intensity from south to north along-shore. Sampling here covered a much larger extent (35 km) than on Sapelo.

Regional uniformity in temperature and precipitation regime, especially in the growing season, greatly diminishes the potential confounding effect of regional macroclimatic sorting on species composition. As a consequence of climatic uniformity (Stalter and Odum 1993), the dune flora on these barrier islands is potentially similar along the latitudinal breadth of our study region, with the same major species evident throughout the region (Godfrey 1976; Duncan and Duncan 1987). General climatic factors may contribute little to interisland variability when compared to dune microenvironmental factors, such as incidence of salt spray, substrate mobility, and exposure (Barbour and Johnson 1977).

Geographic variation in island orientation and local beach and dune sediment budgets introduces considerable dune topographic variability within barrier-island morphologies (Godfrey 1977; Psuty 1988). Consequently, the purpose of our study was not to provide a template for all islands of a given morphology. Rather, we examined the biogeographic effects of complex systems interactions in two different geomorphic settings of potentially similar species pools.

Methods

Field Sampling

Aerial photographs and field reconnaissance suggested that five sites should be sampled on each island to capture the range of dune physiographies (Figure 5). By sampling the range of dune physiographies on each island, we
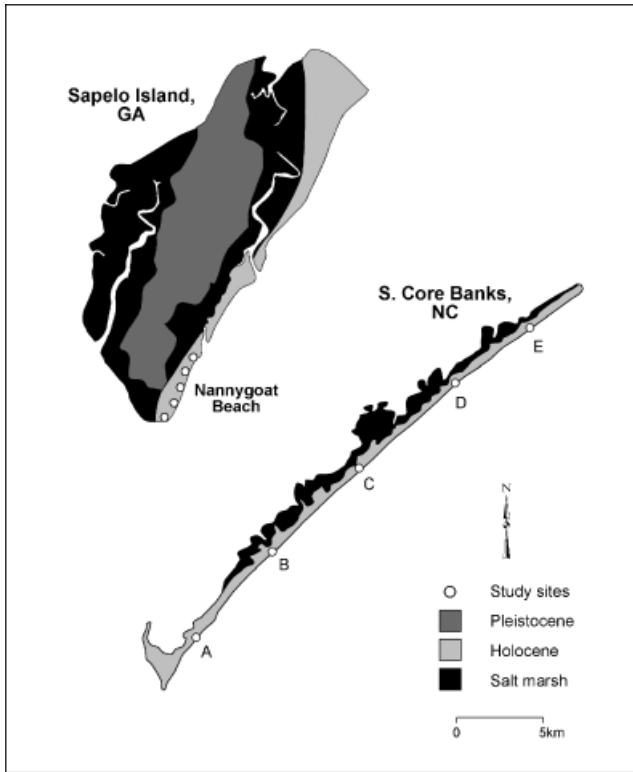
Figure 5. Location of sampling sites along each study island.

effectively captured a large portion of the temporal variability in species abundances and topography expected on each island. For many dynamic processes, space and time are largely interchangeable (Levin 1998): the variation observed across sites on each island at any one time will eventually be seen in time. Nested within each of the five sites (A through E) along the south-to-north axis of each island were three strip transects. Each transect was aligned perpendicular to the tide line in order to capture the compositional variation along the transverse gradient of exposure to oceanic inputs. At each site, the starting point for an initial transect was randomly placed along the seaward edge of vegetation at the base of the primary foredunes. This seaward vegetation line corresponds to the high-water mark. The high-water mark accurately reflects the position of frequent maximum high-water levels (Morton and Speed 1998). Starting points for the two adjacent parallel transects were randomly positioned at a minimum of 20 m distance from the central transect. Each transect began at the high-water mark and extended inland through herbaceous vegetation to the first occurrence of extensive woody shrub cover. Sampling was conducted in June, July, and August 1999.

A 2-m point-frame sampler, aligned perpendicular to the centerline of the transect, was used to measure species presence. Point-frame measures were spaced at 1-m intervals along transects on Sapelo. To maintain compar-

able 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. Each point-frame sample consisted of twenty observations of species presence, with 10-cm intervals between observations. Presence was summed for individual species and expressed as percent absolute cover for each point-frame sample. The presence of any species off-transect but within a site was recorded. A total station was employed to survey elevation and distance relative to the mean high-water mark for each point-frame sample. Plant identification and nomenclature follows Radford, Ahles, and Bell (1968). Several species were indistinguishable in the field and were recorded as genera.

Species Cover and Dune Topography

Absolute cover for each species was aggregated to the point-frame, transect, and site levels. To test for broad compositional differences between islands, we employed multiresponse permutation procedures (MRPP) as the analytical tool and a pooled-island dataset of transect-level species covers as our test metric. MRPP is a nonparametric, distance-based test of group differences that we employed in a manner analogous to one-way analysis of variance (Biondini, Mielke, and Redente 1991). The strategy of MRPP is to compare an observed mean within-group distance among sample points with the mean within-group distance that would have resulted from all other possible combinations of group membership. As such, MRPP tests for differences among two or more groups based on the collective variability of data for each group, rather than their respective means. MRPP was also employed to test for significant differences between islands in transect-level absolute species cover for individual species, primary foredune height, and dune habitat width. Where the fronting line of dunes was poorly developed, we designated the maximum elevation within the first 10 m landward of the high-water mark as dune height. To evaluate qualitative differences in dune relief, we constructed topographic cross-sections for a representative transect from each site.

In MRPP, the test statistic T summarizes the agreement between the observed and permutated mean within group distances. While the associated p value is useful for evaluating how likely an observed clustering is to be due to chance, a description of the effect size that is independent of the sample size is also needed. The within-group homogeneity statistic (A) gauges whether observed between-group differences are useful, rather than the result of random variation within groups. A ranges from −1 to 1. Values less than zero indicate that groups are no

more different than expected by chance. A value from 0 to 1 indicates group differences greater than expected due to chance. For multivariate MRPP tests, distances were based on Sørensen's coefficient of similarity. Univariate MRPP tests employ Euclidean distances as the distance metric. Sørensen's distance matrices were rank-transformed in order to lessen the loss of sensitivity of our distance measure with heterogeneous datasets. MRPP on ranked distances rather than raw distances is more similar to analysis of similarity (ANOSIM) and analogous, in theory, to nonmetric multidimensional scaling. All MRRP tests were conducted at the 0.05 significance level in PC-ORD Version 4.04 (McCune and Mefford 1999).

Longitudinal Compositional Variability

Dune species compositional variability was examined in two orientations, transverse, or cross-island, and longitudinal, or along-shore. We employed a null hypothesis that disturbance and gradient zonation do not interact on each island. Compositional variability on Sapelo should correspond to the patterns predicated by gradient zonation, as is typically invoked in infrequently disturbed settings. Patterns of compositional variability on South Core, by contrast, should correspond to the tenets of patch dynamics. By comparing observed patterns of compositional variability to null hypotheses framed around this dualistic causal framework, we can infer general relationships about how complex adaptive systems shape biogeographic patterns.

We originally hypothesized that longitudinal compositional variability would be greater on South Core Banks, whereas Sapelo would reflect more uniformity among sites. This logic ensues from the protected nature of the dune vegetation on Sapelo, where infrequent disturbance permits greater species sorting in the array of protected habitats that occur along transects. As a result, transverse zonation of the vegetation should be prominent, with similar zonational sequences repeated longitudinally. Conversely, exposure to frequent and extensive overwash events on South Core Banks would tend to obliterate transverse structure and establish in its place a mosaic of disturbed patches that vary in age and composition along the length of the island. To assess longitudinal compositional variability, we performed two MRPP tests, one for each island. Groups in each MRPP were defined as sites (five per island), consisting of three transects and their absolute species cover values. Higher values of A and significant small (more negative) T values indicate greater longitudinal compositional variability.

Nonmetric multidimensional scaling (NMDS) was used to detail among-site compositional variability.

NMDS is a distance-based ordination method that iteratively minimizes the stress between ecological similarity among sample units and the representation of that distance in multidimensional ordination space. In this first NMDS ordination, our samples were the sites from each island, and the variables describing them were their respective species percent absolute cover values. The resulting NMDS plot arranges sites such that their separating distances provide an island-scale measure of compositional variability. No species were deleted, since such deletions are unnecessary in NMDS (Clarke and Warwick 1994). Sørensen's distance was used to calculate sample similarities. Sørensen's coefficient gives less weight to outliers, and is the recommended distance coefficient for use in NMDS analyses (McCune and Mefford 1999). Because of the small size of this dataset, it was feasible to perform multiple runs ($n = 40$) in order to lessen the likelihood of local minima. Local minima are nonoptimal solutions to stress reduction that arise from the iteration of an initially arbitrary starting configuration. Monte Carlo tests were employed to determine whether reductions in stress were significantly greater than those achieved by randomization of the data. All NMDS ordinations were performed in PC-ORD Version 4.04.

Transverse Compositional Variability

Beta diversity, or species turnover, is a measure of species replacement along an environmental gradient. In this study, beta diversity measures the replacement of species in point-frame samples along a transect. To test for significant differences between islands in their species turnover, we employed MRPP as the analytical tool and a pooled island dataset of transect-level beta diversity as the test metric. We calculated the Wilson-Shmida index (Bt) of beta diversity (Wilson and Shmida 1984) for all transects using point-frame species presence-absence data. We hypothesized that infrequent overwash on Sapelo should lead to a finer-scale gradient partitioning of habitat and, consequently, to higher beta diversities in comparison to South Core.

Transverse Gradient Structure

NMDS and hierarchical agglomerative clustering were used to plot species along the transverse environmental gradients for each island morphology. In this second NMDS ordination, our observations were the point-frame samples from each island (Sapelo = 1082; South Core = 1139), and the variables describing them were their respective species percent absolute cover. Point-frame samples from both islands were pooled into one

dataset and relativized so that each had a total cover of 1. This sample relativization made observational units more equitable in species abundance and enhanced the capture of broad compositional similarities between groups of point-frame samples. Sørensen's distance was used to calculate sample similarities. In NMDS, rotation of axes can be used to enhance interpretability (Legendre and Legendre 1998). We employed varimax rotation of our NMDS point-frame scores in order to maximize the expression of compositional variability on the first axis. We originally reasoned that this would align the shared compositional components of each island's transverse gradient along the first axis. Because of the large size of this dataset, three runs were performed to guard against a local-minimum solution.

Hierarchical agglomerative clustering was used to classify the same relativized pooled point-frame dataset. Ward's Method was selected as the cluster method. Euclidean squared distance was selected as our similarity coefficient. Point-frame samples were grouped by their cluster membership, whereupon we calculated a cluster centroid based on the NMDS axis scores. Hierarchical clustering was performed with SPSS Version 8.0.

Results

Dune Topography and Species Composition

The major topographic differences between islands reflected those generally attributable to the geomorphic setting (Johnson et al. 1974; Oertel and Larsen 1976; Hosier and Cleary 1977). Overwash profiles were well expressed on South Core. Cross-sections suggested that the loss of the fronting foredunes would perpetuate disturbance across the downsloping area in their lee (Figure 6). Mean transect primary foredune height declined incrementally along-island from a maximum of 2.4 ± 0.1 m above the high-water mark at site A, the southernmost site, to the absence of a primary foredune at site E, the northernmost sampled location. At site A, the large primary and secondary foredunes dampened overwash effects, as evidenced by the observed lack of overwash fans and wrack debris at this location. Single dune ridges were well expressed at mid-island sites B and C. Absent and scattered dunes at sites D and E on the north end of the island were indicative of recent or frequent overwash.

A more complex dune-and-swale morphology was prevalent on Sapelo. Topography ranged from protective parallel dune ridges and swales (sites B, C, and D) to a more exposed, flat terrain (sites A and E). Primary foredune height varied from 1.6 ± 0.01 m relative to mean high water at site D to the absence of a primary foredune at site A. The low relief at site A developed from the accretional conditions at the southern terminus of the island (Welch, Remillard, and Alberts 1992). Rapid accretion engenders a progradation of the shoreline and maintains a low topography of frequently overwashed incipient dune ridges toward the seaward edge of the transects. Erosional retreat of the fronting line of dunes at
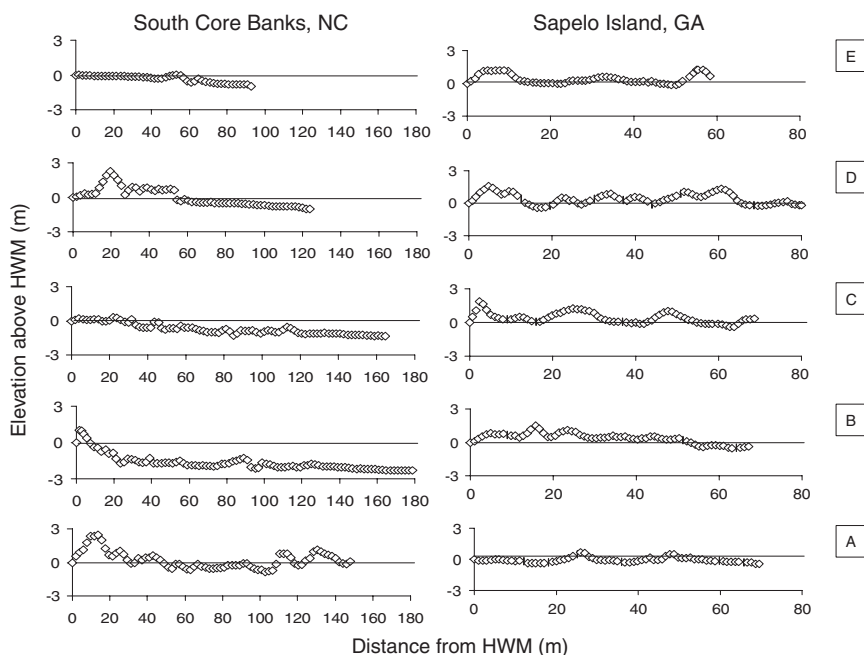
Figure 6. Topographic cross-sections for representative transects from each site on South Core Banks, North Carolina (left) and Sapelo Island, Georgia (right). Zero represents high-water-mark datum. Diamonds indicate individual quadrats. Sites are arranged from A (south) to E (north).

Table 1. MRPP Results for Compositional and Topographic Comparisons

Test Metric	Grouped By	T	p	A
Species composition and dune topography				
Absolute species cover	Island	-16.4	<0.001	0.40
Andropogon spp	Island	-5.8	0.001	0.17
Hydrocotyle bonariensis	Island	-15.0	<0.001	0.48
Muhlenbergia filipes	Island	-6.2	0.001	0.18
Myrica cerifera	Island	-3.5	0.01	0.12
Panicum amarum	Island	-4.3	0.005	0.13
Spartina patens	Island	-14.3	<0.001	0.46
Uniola paniculata	Island	-6.8	<0.001	0.20
Primary foredune height	Island	-1.0	0.14	0.03
Dune habitat width	Island	-13.6	<0.001	0.45
Longitudinal compositional variability				
Absolute species cover—Sapelo	Site	-5.6	<0.001	0.64
Absolute species cover—South Core	Site	-5.9	<0.001	0.66
Transverse compositional variability				
Beta diversity	Island	-3.1	0.02	0.09

site E juxtaposed dune and inland-ranging habitats and fostered a low hummocky topography. The position of dune vegetation relative to the high-water mark on Sapelo suggested a higher degree of morphologic resistance to overwash when compared to South Core. Seventy percent of the point-frame samples on Sapelo were positioned above the high-water mark. By contrast, 78 percent of the point-frame samples on South Core were located below the high-water mark, indicating a greater susceptibility to the inland penetration of overwash across downsloping dune habitats.

Mean dune habitat width on Sapelo (70 ± 8 m) was roughly half that on South Core (140 ± 38 m). MRPP confirmed that dune habitat width was significantly different between islands ($T = -13.60$, $A = 0.45$, $p < 0.01$). Differences in transect-level primary foredune height were nonsignificant ($T = -0.97$, $A = 0.03$, $p = 0.14$).

Differences between islands in point-frame sampling intensities were nonsignificant ($T = -0.81$; $A = 0.002$; $p = 0.33$). Eighty-eight species and species complexes were encountered on Sapelo, and seventy-five on South Core. Total percent absolute cover on Sapelo was 52 percent, as compared to 71 percent on South Core. MRPP of pooled-island transect-level species cover indicated significantly different island compositions (Table 1). However, 43 species out of a total of 120 were found on both islands. These shared species comprised 96 percent of total absolute species cover on Sapelo, and 78 percent of the total absolute cover on South Core. The absolute cover of species found only on Sapelo was lower (Sapelo = 2 percent; Core = 15 percent) but was derived from a larger number of species (Sapelo = 45, Core = 32).

Sapelo had more off-transect species when compared to South Core (Sapelo = 16, Core = 4).

MRPP of transect-level absolute species cover for *Uniola paniculata*, the most abundant species on both islands, indicated significant island differences for this common foredune species in the Georgia Bight. *Uniola paniculata* attained a higher cover on South Core (Sapelo = 9 percent, Core = 17 percent; Figure 7). MRPP detected significant differences in the transect-level cover of two other shared species. Frequent and extensive burial from overwash on South Core favored the increased abundance of *Spartina patens,* which commonly co-occurred with *Hydrocotyle bonariensis.* The moss *Ditrichum* spp. and *Solidago* spp. were abundant on South Core but absent from Sapelo. *Solidago* is a gap colonizer (Lee 1995), abundant on older overwash flats. Mosses are burial-tolerant and are important sediment stabilizers in temperate dunes (Martínez and Maun 1999). Significant differences for individual species with higher absolute covers on Sapelo included those for the woody shrub *Myrica cerifera* and the dune-initiating species *Panicum amarum.* A greater areal extent of wet swales on Sapelo contributed to higher absolute cover for the herbaceous species *Muhlenbergia filipes, Phyla nodiflora,* and *Andropogon* spp.

Longitudinal Compositional Variability

A two-dimensional final solution was selected for our site-level NMDS. Monte Carlo randomizations ($n = 40$) indicated a significant reduction in stress ($p = 0.02$) for this dimensionality. The separation of islands in the
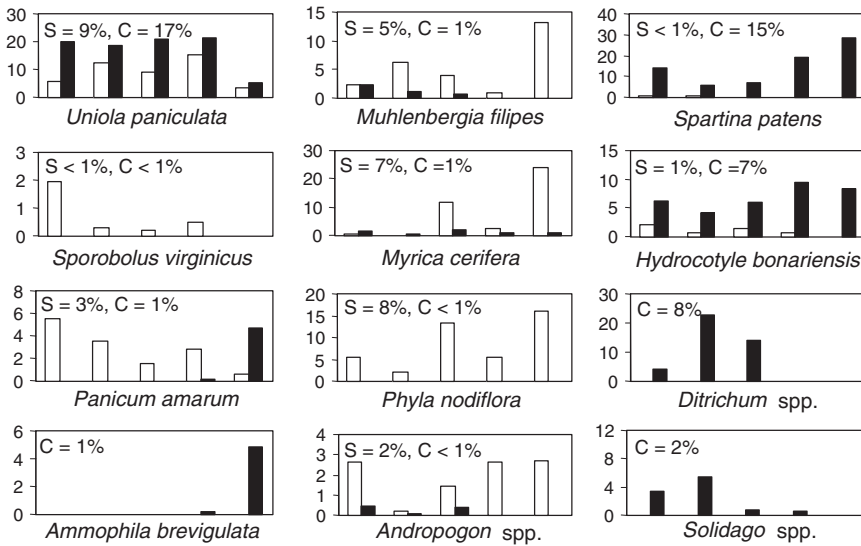
Figure 7. Percent absolute species cover by site and function for each island (Sapelo = white bars; South Core Banks = black bars). Sites are arranged from A (south) to E (north) left to right across x axis. Total island absolute species cover is noted by letters above bar graphs (Sapelo = S; South Core Banks = C). Note that the only occurrence on South Core of *Sporobolus virginicus* was off-transect individual (site D), and the only occurrence of *Phyla nodiflora* on South Core was a single on-transect individual (site A).

NMDS plot corroborated their strong compositional divergence (Figure 8). Individual island MRPP tests indicated that compositional differences between sites were significant for both Sapelo and South Core Banks. Similar *A* and *T* statistics indicate a shared compositional variance structure between and within sites for each island. However, this equivalence in longitudinal compositional variability does not take into account the geographic extent of dune habitats sampled on each island. As such, Sapelo has a greater longitudinal compositional variability, given the smaller island extent.

Transverse Compositional Variability

MRPP revealed significant differences between islands in their transverse compositional variability, as measured by the Wilson-Shmida index of beta diversity. In agree-
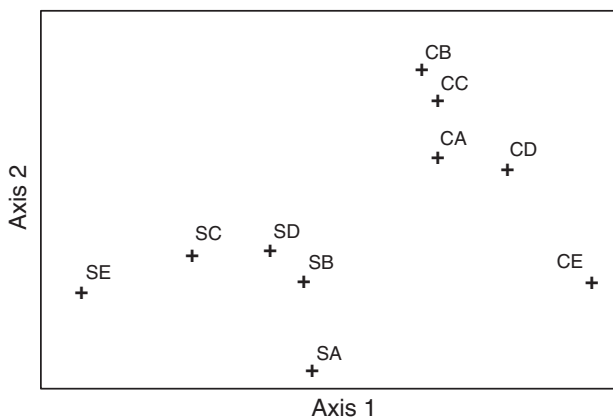
Figure 8. NMDS plot of site composition by island. First letter designates island (Sapelo = S; South Core Banks = C); second letter indicates site. Distance between sites is indicative of their compositional similarity.

ment with our initial hypothesis for species turnover, mean transect beta diversity was higher on Sapelo (Sapelo t = 7.1 $\pm$ 1.4; Core Bt = 5.6 $\pm$ 1.5)

Transverse Gradient Structure

Our hierarchical cluster solution identified sixteen species groupings. We ran an additional hierarchical cluster analysis on one of these groups that was particularly heterogeneous in order to refine its membership. The refinement delineated five additional species clusters, for a total of twenty. Species clusters were classified into four habitat categories (Table 2). The first category consisted of the foredune-builder *Uniola paniculata*, and several common foredune species (*Croton punctatus, Heterotheca subaxillaris,* and *Hydrocotyle bonariensis*). Our second category included more inland-ranging species, often forming a dense and persistent ground cover or canopy that inhibits the establishment of other species. These burial-intolerant stabilizers (*Andropogon* spp, *Phyla nodiflora, Muhlenbergia filipes,* and *Myrica cerifera*) were more abundant on Sapelo. The third compositional category included perennial species common to stabilizing disturbed areas, particularly overwash flats. These transitional species have no direct role in dune-forming processes, but are moderately tolerant of sediment mobility and burial (*Ditrichum* spp., *Eragrostis* spp., *Solidago* spp., and *Oenothera humifusa*). The fourth category was composed of taxa abundant in geomorphically disturbed areas in which dune development was lacking or incipient (*Ammophila brevigulata, Cenchrus* spp., *Panicum amarum, Spartina patens, Hydrocotyle bonariensis,* and *Sporobolus virginicus*). While *Ammophila brevigulata* is a major dune-building species on more northern coasts, its

Table 2. Cluster Groups Arranged by Habitat Categories

Habitat Category	Cluster ID	Cluster Description
Primary and secondary foredunes	CROTP	*Croton punctatus*
	HET	*Heterotheca subaxillaris*
	HYDB-UNI	*Hydrocotyle bonariensis* and *Uniola paniculata*
	UNI	*Uniola paniculata*
	UNI-HET	*Uniola paniculata* and *Heterotheca subaxillaris*
	UNI-TRIP	*Uniola paniculata* and *Triplasis purpurea*
Stabilized swales and protected microsites	AND	*Andropogon* spp.
	PHYLA	*Phyla nodiflora*
	MUHL	*Muhlenbergia filipes*
	MYR	*Myrica cerifera*
Transitional habitats, chiefly vegetated overwash flats	DITR	*Ditrichum* spp.
	ERG	*Eragrostis* spp.
	SOLD	*Solidago* spp.
	OEN	*Oenothera humifusa*
Disturbed areas characterized by frequent overwash or high aeolian sediment mobility.	AMMO	*Ammophila brevigulata*
	CENC	*Cenchrus* spp.
	PAN	*Panicum amarum*
	SPARP	*Spartina patens*
	SPARP-HYDB	*Spartina patens* and *Hydrocotyle bonariensis*
Dunes lacking or incipient.	SPOR	*Sporobolus virginicus*

sparse on South Core was confined to frequently overwashed sites D and E, where it was associated with small, incipient dunes.

Three NMDS runs on pooled point-frame cover data generated a similar sequence of stress reduction in each, decreasing the likelihood of a suboptimal local minima. Furthermore, reductions in stress after three dimensions were less than five units, signaling that a three-dimensional solution was optimal (McCune and Mefford 1999). Plots of cluster centroids based on NMDS coordinates indicated that each barrier-island morphology had a distinctive transverse compositional structure (Figure 9). Two axes of compositional variation were evident on Sapelo, forming a t-shaped gradient. Disturbance species sorted along a stability gradient on the first axis, ranging from *Spartina patens* in highly unstable habitats to the more inland-distributed *Cenchrus* spp. The species clusters along the prominent compositional gradient for axis 2 on Sapelo demarcated a zoned sequence of dune-to-inland distributed vegetation typically associated along coastal transverse environmental gradients: a *Uniola paniculata*-dominated foredune zone, a transitional mid-island zone, and a rear assemblage of stabilized species. By contrast, South Core Banks exhibited one dominant

vegetation gradient that ran diagonally across both axes. Disturbance species and the dune-to-inland gradient sequence of vegetation were superimposed upon each other. Three broad zones of species were identifiable along the diagonal of the South Core NMDS axes: a seaward *Uniola paniculata* zone, a mid-island transitional zone, and an assemblage of disturbance and stabilized species.

Discussion

Species Composition

The strong separation of island sites in our NMDS plot confirmed that distinctive island compositions were expressed. However, there was a strong distributional overlap between islands. Forty-three species shared by Sapelo and South Core Banks contributed 96 percent and 78 percent, respectively, of the total species cover for each island. As such, island setting did not appear to affect colonization for shared species, but it did affect their relative success.

Differences in species abundances between islands may reflect the filtering effects of disturbance regime (Denslow 1980). On South Core, where large overwash patches are common, the herbaceous species *Spartina patens* and *Hydrocotyle bonariensis* had a higher percent absolute cover. Both species are ineffective dune-builders but are well adapted to recolonize large patches following overwash deposition (Hosier 1973). Because large overwash patches are infrequent on Sapelo, species that colonize small gaps in vegetation cover are more abundant. The woody shrub *Myrica cerifera, Phyla nodiflora*, and the bunch grass *Muhlenbergia filipes* invade and stabilize wet swale habitats and may preempt the establishment of other species (Young, Shao, and Porter 1995). *Panicum amarum* and *Sporobolus virginicus,* two abundant perennial grasses on Sapelo, colonize unstable substrates near the high-water mark and initiate dune regrowth (Woodhouse 1982).

Longitudinal and Transverse Compositional Variability

The study islands had roughly equivalent statistical measures of longitudinal compositional variability. Yet, given the smaller geographic extent of sampling on Sapelo, variability in the longitudinal orientation exceeded that of South Core. Increased geomorphic instability adjacent to tidal inlets on Sapelo augmented its along-island compositional variability. Accretion at site A and erosion at site E on Sapelo engendered larger compositional separation among island sites.
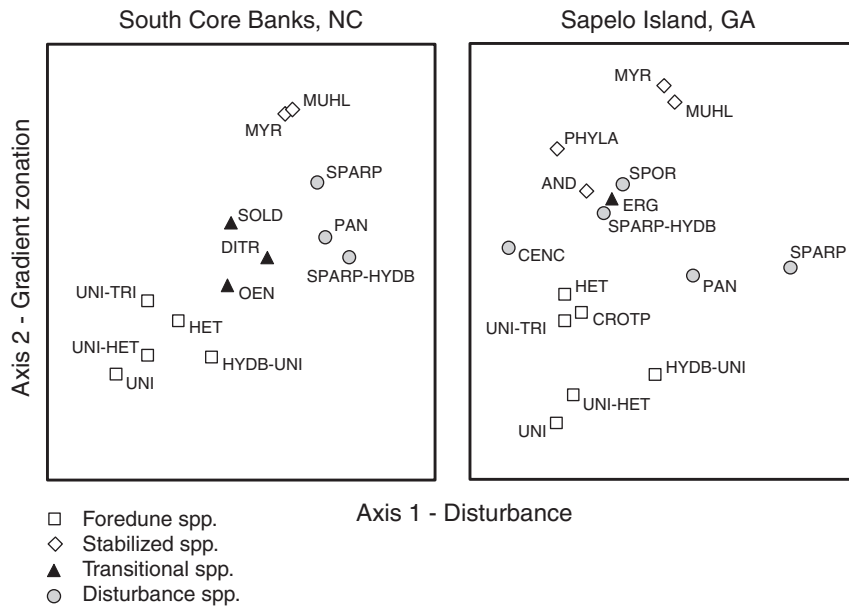
Figure 9. NMDS plots of point-frame compositional data arranged by cluster categories (see Table 2 for species abbreviations). South Core Banks exhibited one prominent transverse gradient aligned across both axes 1 and 2, suggesting that disturbance species and the foredune-to-inland sequence of vegetation were superimposed upon one another. A more intersecting gradient geometry characterized Sapelo, as disturbance species sorted out along axis 1 and the zoned foredune-to-inland vegetation sequence was more closely associated with axis 2.

As hypothesized, our measure of transverse compositional variability was greater on Sapelo. A higher habitat heterogeneity, attributable to Sapelo's more complex topography (or topodiversity; see Phillips 1999b) facilitated the coexistence of wet swale and dune species. While the dense canopy of the late-successional species *Myrica cerifera* could be expected to lower the number of co-occurring species in wet swales, these woody shrubs actually supported numerous vine species (*Ampelopsis arborea, Mikania scandens, Smilax spp., Vitis spp.,* and *Melothria pendula*). In this case, habitat heterogeneity augmented species coexistence indirectly, through species architecture, more than directly, through topography. Moreover, senescence of older thickets of *Myrica cerifera* opened gaps that permitted the establishment of ruderal species (*Eupatorium* and *Cirsium* spp), herbaceous wet swale species, or tree seedlings (Crawford and Young 1998). Local shoreline movement also augmented species turnover (Doing 1985). On Sapelo, beta diversity increased with both the erosional compression of shoreline habitats (site E) and their accretional expansion (site A). These differences in transverse compositional variability are all the more striking when one considers the smaller mean dune-habitat widths on Sapelo versus those on South Core.

Transverse Gradient Structure

A three-dimensional NMDS solution and clustering of point-frame species cover from our pooled-island dataset revealed distinctive transverse compositional gradients for each island. Axis 1, which maximized compositional variability as a result of varimax rotation, outlined a geomorphic disturbance gradient. Axis 2 represented a strandline-to-inland zonation typical of coastal dune vegetation. South Core Banks exhibited one prominent gradient of composition arrayed diagonally across both NMDS axes. By contrast, Sapelo exhibited two distinct compositional gradients that intersect in a T-shaped pattern, with distinct articulation of traditional transverse zonation (axis 2) as well as a geomorphic disturbance gradient (axis 1). Malanson and Butler (1991) described a similar T-shaped arrangement of species with the same axis interpretations for a riparian system.

Topographic profiles for South Core, with their single fronting dune and point-frame elevations well below the high-water mark, suggest that the loss of the fronting foredunes would perpetuate disturbance across the downsloping area in their lee. Consequently, disturbance structuring and the zoned sequence of strandline-to-inland vegetation typically associated with coastal transverse gradients overlay each other to form one prominent vegetation gradient along both the first and the second NMDS axes. In contrast, Sapelo cross-sections suggest a higher morphologic resistance to overwash, with a weaker tendency to perpetuate overwash inland, given their increased topographic roughness and elevations above the high-water mark. In the field, we observed that disturbance from overwash and from higher rates of incremental sediment mobility were confined largely to the front of transects and, to a lesser extent, the sparsely vegetated interdunal flats in interior locations. As a result, disturbance structuring is spatially decoupled from the dominant transverse zonation. Consequently, two discrete

Table 3. Spearman's Correlation Coefficients for Point-Frame NMDS Axis Scores with Elevation and Distance

	Axis 1 (Disturbance-Structured)		Axis 2 (Gradient Zonation)	
	Elevation	Distance	Elevation	Distance
South Core	− 0.34	0.39	− 0.41	0.46
Sapelo	− 0.17	− 0.10	− 0.45	0.23

Note: All correlations are significant at $p < 0.05$. Elevation and distance measured in meters relative to high water mark.

NMDS axes were expressed on Sapelo: a smaller spatial-scale gap-based disturbance gradient along axis 1 and the arrangement of zoned transverse compositions along the environmental gradients expressed by axis 2. Spearman's correlations of NMDS point-frame scores with elevation and distance relative to the high-water mark support this interpretation. Elevation and distance correlations are weaker for the first axes on both islands, as would be expected if this axis represents a stability gradient spanning unstable to stable habitats (Table 3).

Complex Adaptive Systems, Pattern, and Process

A complex systems framework was supported, in that our initial hypothesis of noninteraction between overwash disturbance (South Core Banks) and gradient zonation (Sapelo) afforded only partial explanation of compositional variability. Observed compositional patterns corresponded to our initial hypotheses only for the transverse orientation on Sapelo, where gradient zonation was defined as the operative structuring agent. However, gradient zonation could not account for the greater-than-predicted longitudinal compositional variability on Sapelo. While history—in the form of inherited topography—shapes subsequent development on each island, its outcome on Sapelo may be to diversify along-shore compositional variability. Consistently expressed transverse sequences of similar vegetation are not strongly repeated along-island, because intrinsic biogeomorphic processes that shape topography are highly variable from site to site in the absence of frequent overwash.

The greater compositional variability overall on Sapelo may be attributed to the more spatially disjunct geometry there between disturbance species and the zoned sequence of strandline-to-inland species when compared to South Core. We posit that complex systems interactions may increase compositional variability by decoupling disturbance from gradient zonation. This would have the effect of folding more habitat heterogeneity and potential stochasticity related to plant establishment into a given area. These interactions between disturbance and

gradient zonation have larger theoretical importance than suggested here (see Collins, Glenn, and Gibson 1995; Hubbell et al. 1999), as compositional variability is very similar to the concept of species diversity.

Disturbance regimes may prove difficult to quantify under natural conditions (Pollock, Naiman, and Hanley 1998; Parker, Parker, and McCay 2001) because of complex systems interactions that emerge along disturbance gradients (Holling 1992). Disturbance gradients may be partitioned into a set of spatially organized domains, each characterized by distinctive interactions amongst structuring processes and forms (Holling 1992; Montgomery 1999; Reif 1999; Thompson et al. 2001). We suggest that this compartmentalization may foster more nonlinearity in the relationship between forcing-event frequency and disturbance exposure (Figure 10). Intrinsic processes (species sorting along environmental gradients, modification of topography) operative in the intervals between extrinsic forcing events may modulate subsequent disturbance exposure. The more widely invoked linear relationship does not address these potential complex adaptive systems interactions and how they may augment or dampen disturbance exposure. In a complex adaptive system framework, increases in forcing-event frequency result in disproportionately greater disturbance exposure. As a result, the nonlinear model is similar to the concept of complex responses in [bio]geomorphic systems (see Schumm 1973) in which a broad-scale forcing of disturbance may not have the same effects along the length of the disturbance gradient (Bendix 1998). Characterizations of disturbance regime should consider a complex systems approach in which the
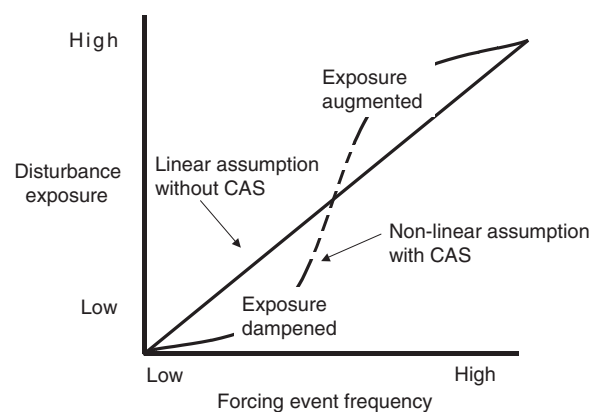
Figure 10. Potential influence of complex systems interactions on disturbance exposure. In a nonlinear interaction between forcing-event frequency and disturbance exposure, species may either dampen or augment disturbance exposure to enhance survivability. Assumptions of a linear relationship overlook these complex systems interactions, thus potentially complicating characterization of disturbance regimes.

organizational relationships between heterogeneity, intrinsic dynamics, and external perturbation are articulated (Bascompte and Rodriguez 2000).

For other islands in the Georgia Bight, orientation relative to prevailing winds and local-scale controls on sediment budgets may superimpose smaller-scale variability in potential overwash (Godfrey 1977; Psuty 1988). This would have the effect of embedding considerably more intricacy in the distribution of dune plants than that which be attributed to the macroscale meteorologic disturbance gradient extending across coastal Georgia and the Carolinas. We also suggest that the degree of nonlinearity and linearity in the relationship between forcing-event frequency and disturbance exposure may be a function of the responsiveness of the system under study. Coastal dunes, riparian systems, and similarly responsive biogeomorphic environments may better approximate nonlinearity in the relationship between forcing-event frequency and disturbance exposure.

Conclusions

We have outlined a complex interplay between disturbance and environmental gradients, one in which plant-species abundances, landform-mediated physical gradients, and disturbance regimes interact and influence biogeographical patterns. The relationships between these structuring agents, rather than any measure of their relative causal importance, may better explain observed patterns in dune-plant compositional variability. This study re-emphasizes that landforms, sediment mobility, and vegetation cannot be considered independent factors when examining compositional patterns in highly responsive biogeomorphic systems (Bendix and Hupp 2000).

Biogeographers, in particular, have yet to exploit the full potential of systems thinking such relationships entail, despite a long history of conceptual systems schemata (Graf and Gober 1992; Gregory 2000). The dearth of systems approaches among biogeographers may be, in part, a reflection of the reductionism embraced by physical geographers at large (Bauer, Veblen, and Winkler 1999), but it may also be a lingering apprehension of Clementsian ideas about plant succession. This hesitancy is not surprising, given that Clement's deterministic view of ecological succession has been countered with evidence that there are no consistent community or ecosystem level patterns in succession (Egler 1954, Vale 1988, Sprugel 1991; Johnson and Mayeux 1992). Whether attributed to a Clementsian determinism or to the indeterminacy of these critical, nonequilibrial views, the process of successional assembly continues to be contested (Baker and Walford 1995).

However, it is now recognized that Clementsian ideas about successional assembly have their modern counterpart in complex adaptive systems theory (Huston 1994; Chapin et al. 1997) and its earlier analog, multiple stable states (Holling 1973; Gunderson 2000; and see Vale 1982). In a complex adaptive system, a recursive self-organization may confer directionality—a convergence or divergence—in the evolution of landscape patterns (Phillips 1999a). Yet this directionality does not necessarily constrain succession to the inexorable self-regulating determinism of Clementsian succession. On the contrary, complex adaptive systems theory encompasses determinism and contingency and integrates equilibrium, multiple equilibrium, and nonequilibrium perspectives (Wu and Loucks 1995; Savage, Sawhill, and Askenazi 2000).

The dune systems in this study may behave as two stable states, each a resilient assemblage of plant-species compositions and topographies that emerge under high and low levels of shore disturbance. Savage, Sawhill, and Askenazi (2000) describe a similar bifurcation in disturbance responses and composition in a simulation of forest dynamics. Along a disturbance gradient, low levels of fire disturbance converged to a stable state, which dampened extrinsic disturbance in a landscape dominated by late-successional species. High levels of disturbance led to a stable state characterized by frequent large disturbances and a composition that oscillated between early and late successional species. While we recognize that further sampling is needed to verify the existence of stable states in barrier-islands dune systems, it does not obviate the rationale of our study: to ascertain how complex systems interactions influence dune-plant biogeographic patterns.

Hypotheses drawn from systems-oriented relationships among disturbance, gradient structure, and compositional variability may be a productive line of inquiry for refining our understanding of plant distributions and disturbance regimes. However, for geographers, adopting a methodological view that incorporates the potential range of systems organization requires broadening the definition of the term "system," which has come to be misleadingly associated only with Clementsian ideas of community assembly (Oyama 2001). Complex adaptive systems promote a richer strategic vision by encouraging researchers to make more intelligent and flexible "tactical" use of reductionist field-based strategies (Brown 1995; Oyama, Griffiths, and Gray 2001) in order to elucidate the controls of biogeographic patterns.

Acknowledgments

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Correspondence: Department of Geography, Florida State University, Tallahassee, FL 32306-2190, e-mail: jstallin@mailer.fsu.edu (Stallins); Department of Geography, University of Georgia, Athens, GA 30602, e-mail: ajparker@arches.uga.edu (Parker).