

# SOIL AND VEGETATION PATTERNS IN BARRIER-ISLAND DUNE ENVIRONMENTS

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**Abstract:** Plant species distributions often have been attributed to landform characteristics or their associated geomorphic processes. This complicates interpretation of vegetation patterns in that geomorphic processes shape, and are shaped by, landforms. To characterize the biogeographic impacts of this interaction, I used principal components analysis (PCA) to examine hypotheses regarding the structure of variation among soil properties in active barrier-island dune systems. Dune soils and vegetation were sampled on two well-recognized barrier-island morphologies. On low-profile, wave-dominated microtidal barrier islands (South Core Banks, North Carolina) frequent overwash exerts a greater control on the distribution of soil properties. On mixed-energy mesotidal barrier islands (Sapelo Island, Georgia), overwash is less frequent, and the distribution of soil properties is shaped by a complex dune topography. Nontrivial principal components on both islands captured an equivalent amount of variance in the soil data. However, there were inter-island differences in the dimensionality of these nontrivial principal components, and differences in the distribution of variance and factor loadings. Suites of topography-modifying species, unique to each island, were uniform in the strength of their individual correlation with local edaphic variability. I posit that soil variance structure is a useful criterion to distinguish the relative influence on vegetation patterns of soil properties expressed through landforms (Sapelo Island) versus sediment transport processes (South Core Banks). [Key words: dune vegetation, barrier islands, principal components analysis (PCA), overwash.]

## INTRODUCTION

Sediment mobility is one of the most important geomorphic processes in relation to the regulation of plant compositional patterns (Parker and Bendix, 1996). Along sandy coastal strands, sediment mobility shapes the chemical and physical properties of dune soils (Gerrard, 1992) and the subsequent development of dune landforms (Gares et al., 1979). As such, sediment mobility has a dual role in its regulation of dune vegetation patterns. It regulates plant compositional patterns through its role as a geomorphic-disturbance agent, and through the edaphic characteristics expressed along landforms (Swanson et al., 1988; Hayden et al., 1995; Martínez et al., 1997).

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Most studies of dune vegetation patterns typically have stressed the influence of one or the other of these two structuring agents (Ehrenfeld, 1990). For example, position along a landform regulates vegetation patterns by constraining the availability of soil moisture and the input of salt spray nutrients (Oosting and Billings, 1942; Stalter, 1974; van der Valk, 1974; Barbour, 1978). Conversely, the sediment mobility that shapes these landforms regulates vegetation patterns through disturbance from overwash and eolian processes (Schroeder et al., 1979; Moreno-Casasola 1986; Costa et al., 1996).

This dichotomy of structuring agents is, to an extent, problematic in that it is often difficult to distinguish between the relative influence on vegetation patterns of the environmental characteristics expressed along a given landform, versus the dynamic geomorphic processes associated with landform development (Parker and Bendix, 1996). As first articulated in studies of riparian vegetation, plant species distributions are a product of both geomorphic processes and landform characteristics. Along riparian corridors, variability in substrate textures regulates riparian vegetation patterns by engendering differences in moisture availability and by the likelihood of flood exposure and disturbance associated with each textural class (McBride and Strahan, 1984; Hupp and Osterkamp, 1985; Harris, 1987). In their review of geomorphic influences on vegetation, Parker and Bendix (1996) recognized that these two interpretative positions are equally valid, since the relationship between geomorphic processes and landforms is axiomatic. However, they have advocated the need for more studies that seek to disentangle the biogeographic impacts of geomorphic processes from the patterning of species along landform-mediated environmental gradients.

Barrier-island dune systems are dynamic environments well suited for contrasting the relative influence on vegetation of geomorphic processes and landform characteristics. Two barrier-island morphologic types are widely recognized (Hayes, 1979; Fisher, 1982; Williams and Leatherman, 1993; Trenhaile, 1997). Episodic, overland transport of sediments during storm-driven overwash is common to low-profile, wave-dominated microtidal barrier-island morphologies. By contrast, overwash is infrequent and spatially restricted on mixed-energy mesotidal barriers, where longer intervals between disturbance and incremental sand transport foster a greater topographic complexity. Numerous coastal studies emphasize that barrier islands behave as sensitive biogeomorphic systems, rather than a collection of independent components (Riggs, 1976; Cleary and Hosier, 1979; Godfrey et al., 1979; Odum et al., 1987; Rastetter, 1991). On each of these two barrier-island types, geomorphic processes shape, and are shaped by, landforms and their accompanying vegetation.

The purpose of this study is to characterize the quantitative differences in soil-data structure and soil-vegetation relationships originating from the distinctive process-form setting of each morphology. I investigate three questions: (1) Are the soil properties expressed on each island significantly different? (2) Do barrier-island morphologies exhibit differences in the structure of variation among soil properties? (3) Does this edaphic variability differ in its correlation with vegetation cover on each morphology? For maritime dune soils in general, organic matter often increases, whereas pH and particle size commonly decrease as one moves inland.

Leaching and pH typically decrease with decreased particle size (Ehrenfeld, 1990; Hesp, 1991). I expect each morphology to show distinctive departures from these generalized cross-island edaphic gradients. My central hypothesis is that the landforms and sediment transport processes characterizing each morphology should confer differences in the extent to which its soil variables covary. On wave-dominated barrier islands, the distribution of soil properties is more actively shaped by overwash processes that mobilize sediments. Storm-deposited sediments show considerable variability in their pH, organic matter, and particle size (Nyman et al., 1995). Nearshore sediments deposited during overwash can originate from the ocean or bay side of an island given changes in wind direction during cyclonic storms (Godfrey and Godfrey, 1976). As such, the sedimentologic processes associated with overwash should interrupt and dampen the consistent covariation of soil variables along cross-island gradients. On mixed-energy mesotidal islands, landforms more directly shape the distribution of soil properties. With the reduction in overwash, incremental sediment mobility and plant species have longer intervals to interact and build dunes. Consequently, a suite of soil variables, sorted by position along dune landform and reinforced by vegetation (Wilson and Agnew, 1992), can develop. Soil properties in this setting should exhibit a more consistent covariation across these topographic contrasts.

## STUDY AREA

Broad regional contrasts in nearshore environments within the Georgia Bight of the southeastern U.S. Atlantic coast (Hayes, 1994) provide an ideal setting to contrast soil-vegetation patterns on different barrier-island morphologies. Overwash events, in which large volumes of sediment and saltwater are transported overland during cyclonic storms, are frequent on the wave-dominated microtidal barrier islands of North Carolina (Fig. 1). Once deposited, the mobility of overwash sediments is mediated by *Spartina patens*, and by the formation of surface shell lags. *Spartina patens*, a rhizomatous perennial, has a high tolerance to burial that permits it to recover and stabilize a portion of overwash sediment that would otherwise be directly diverted for dune reestablishment. Deflation of fine sand-sized particles from unstabilized sediments leaves behind a coarse lag of surface shell debris and coarse sand. The formation of this residual surface eventually terminates deflation by covering the remainder of surficial sand, thus curtailing sand transport into dunes (Godfrey, 1976). The sediment-stabilizing adaptations of *Spartina patens*, and the sequestering of dune sediments under deflation lags, maintains a relatively weaker morphologic resistance to overwash during coastal storms by perpetuating low-relief overwash topography. Return intervals for winter cyclones capable of generating overwash are approximately 10 years for the mid-Atlantic coast (Dolan and Davis, 1992).

By contrast, mixed-energy mesotidal barrier islands of Georgia (Fig. 2) are characterized by more incremental processes of sediment transport. Large tidal ranges restrict the effects of storm surge and overwash to the duration of high tides (Godfrey, 1976). Abundant tidal inlets along this barrier coast also serve as natural safety

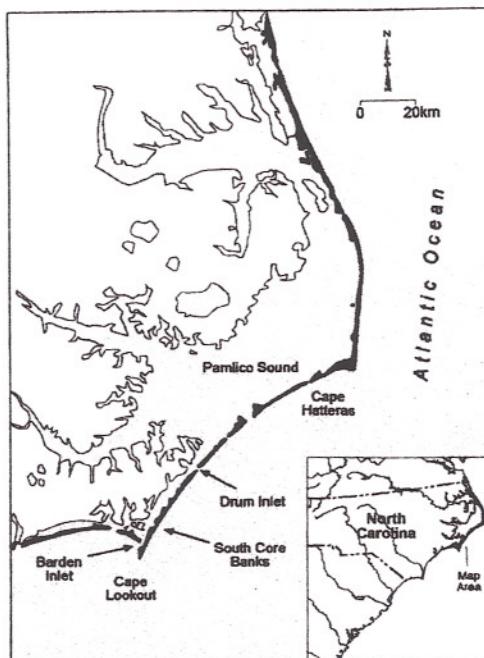
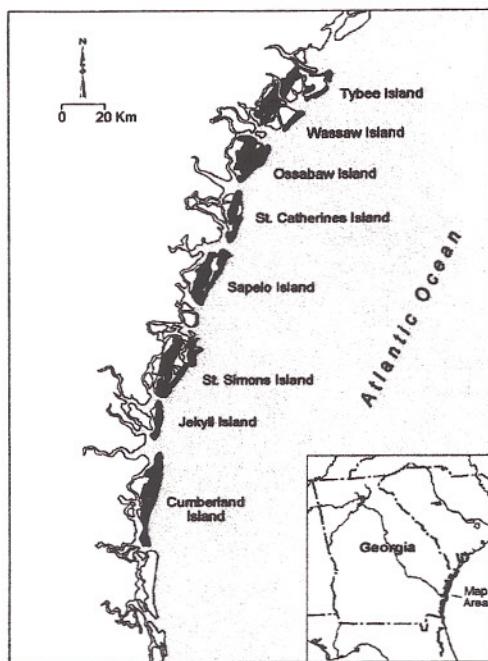


Fig. 1. Wave-dominated microtidal barrier islands of the North Carolina coast.

valves that dampen overwash during periods of infrequent storm surge (Sexton and Hayes, 1991). During quiescent intervals, extensive vegetated dune ridges may accrete parallel to the shoreline given an abundant supply of sediment (Oertel and Larsen, 1976; Taylor and Stone, 1996). Dune-building species augment topographic relief by vertical accretion, while swale species bind and stabilize sediments at low elevations. The high topographic roughness of this landscape acts to increase morphologic resistance to infrequent storm surges. No overwash return intervals are available for the Georgia coast; however, the reduced wave-heights at the center of the Georgia Bight, and the paucity of intense coastal winter storms (Mather et al., 1964; Whittaker and Horn, 1984) curtail the frequency of high storm surges.

Within the Georgia Bight, a regional uniformity in temperature and precipitation regime, especially in the growing season, greatly diminishes any regional macroclimatic sorting on species composition. General climatic factors likely contribute little to inter-island variability when compared to dune microenvironmental factors, such as incidence of sediment mobility and salt spray (Barbour and Johnson, 1977). As a consequence of climatic uniformity, the dune flora is similar along the latitudinal breadth of the study region, with the same major species evident throughout the region (Duncan and Duncan, 1987).



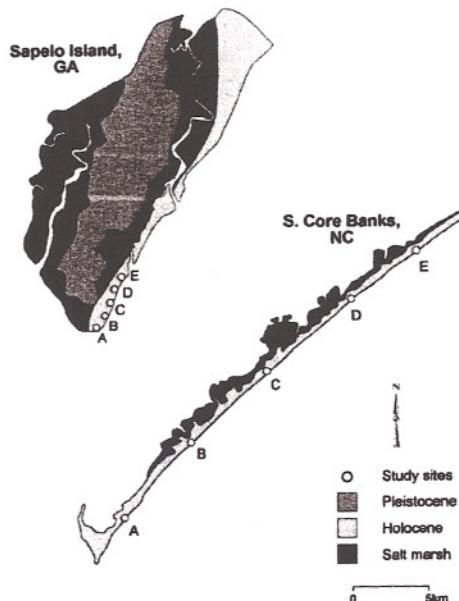
**Fig. 2.** Mixed energy mesotidal barrier islands of the Georgia coast.

## METHODS

### *Field Sampling*

Two largely undeveloped islands were selected for soil and vegetation sampling (Fig. 3): South Core Banks, North Carolina (Cape Lookout National Seashore), and Sapelo Island, Georgia (Georgia Department of Natural Resources). Sapelo is a geologic complex of several individual barrier islands (Mathews et al., 1980). To confine my comparison to individual barrier islands bounded by tidal inlets, I restricted sampling on Sapelo to the 5 km of the southernmost Holocene island. Disturbed patches initiated by storms are infrequent on Sapelo. Along the 35-km coastline of South Core, overwash is more frequent, with its importance increasing along-island from south to north.

Five sites, each containing three randomly positioned strip transects, were randomly positioned along the north-south axis of each island (Fig. 3). In order to capture the compositional and edaphic variation along a gradient of exposure to oceanic inputs, each transect began at the seaward base of the primary foredunes and extended inland across dune habitats. Transects were terminated at the first occurrence of extensive stabilized inland vegetation, as indicated by dense growth of the woody shrub *Myrica cerifera*. This endpoint provided a systematic criterion for establishing transect length on my study islands, given their differing dune hab-



**Fig. 3.** Study islands and site locations.

itat widths. The seaward starting points of each transect corresponded to the high-water mark. The high-water mark accurately reflects the position of frequent maximum high-water levels (Morton and Speed, 1998). At meter intervals along each transect, I sampled vegetation cover with a 2-m point-frame sampler deployed within a 1 × 2 m quadrat straddling the centerline of each transect. To maintain comparable sampling intensities between islands, the longer distances to stabilized vegetation on South Core Banks required that quadrats be sampled systematically in 2-m intervals. Point-frame hits were summed for individual species and expressed as percent absolute and relative cover for each quadrat. Soil samples were collected at 10-cm depth among the vegetated landforms (primary and secondary foredunes, wet and dry swales, overwash and interdunal flats) of each transect. The distances between successive soil collection points on a transect did not exceed 10 m on Sapelo and 20 m on South Core. In addition, a total station was employed to construct topographic profiles for each transect. Plant identification and nomenclature follows Radford et al. (1968) and Duncan and Duncan (1987). Species of several genera were indistinguishable in the field and were lumped into species complexes.

#### Laboratory Methods

For each quadrat soil sample, I determined its pH, particle-size distributions, and percent content by weight for organic matter and carbonate. Soil pH was measured with a hand held, electronic pH-meter (U.S. Department of Agriculture, 1992). Wet

and dry sieving was used to determine the percent contribution of particle sizes in four classes: silt and clay ( $<0.0625$  mm), very fine to fine sand ( $<0.25$  and  $>0.0625$  mm), very coarse to medium sand ( $<2$  and  $>0.25$  mm), and granules plus coarser-grained inorganic material ( $>2$  mm). Soil organic matter, as a proxy for soil nutrient status, was measured using loss on ignition (Dean, 1974). A HCl digest was employed to determine percent content by weight of calcium carbonate.

### *Data Analysis*

To test for significant island difference in individual soil variables, I used multiresponse permutation procedures (MRPP). MRPP is a nonparametric, distance-based test of group differences (Biondini et al., 1991). In distance-based statistics, similarities between observations are summarized by calculating their relative distance in variable space. MRPP tests for group differences by comparing observed and permuted average within-group distances. As such, MRPP tests for significant island differences based on the collective distribution of quadrat-level soil properties rather than island means. Probability values for MRPP express the likelihood of getting an average group distance as extreme or more extreme than observed, given a distribution of all possible distances. MRPP also calculates a within-group homogeneity statistic ( $A$ ) that can be used to gauge whether observed between-group differences are useful, and not the result of random variation within groups. This statistic ranges from -1 to 1, with values greater than 0 indicating within-group agreement greater than expected from random variation. All MRPP significance tests were conducted at the .05 significance level in PC-Ord Version 4.04 (McCune and Mefford, 1999).

To ascertain the degree to which each barrier morphology exhibited differences in the covariation of soil properties, I performed a standardized principal components analysis (PCA) on the quadrat-level soil data for each island. PCA is an eigenvalue (metric) technique that is particularly well suited to the summary of environmental variables through the reduction of dimensionality (Gauch, 1984). PCA requires an assumption of multivariate normality, but for descriptive purposes, larger departures from ideal data structures are tolerable (Grieg-Smith, 1980). Prior to ordination, soil variables were square-root transformed to minimize departures from normality (Zar, 1999). I compared eigenvalues for each principal component to a broken-stick eigenvalue to determine if the captured variance summarized more information than expected by chance. Broken-stick eigenvalues have been shown to be a robust method for selection of nontrivial components in PCA. Principal components are considered useful, or nontrivial, if their eigenvalue exceeds that of their broken-stick counterpart (Jackson, 1993; Legendre and Légonde, 1998). I hypothesized that less-frequent overwash disturbance on Sapelo should foster a greater consistency in the covariation of edaphic properties. In the absence of frequent overwash, eolian sorting should separate well-sorted fine dune sand from coarser, low-elevation sediments (Friedman, 1978). As vegetation sorts along this topographic variability in particle size, it also differentially modifies the pedogenic properties (pH, organic matter) of these elevational habitats (Wilson and Agnew, 1992). This should maintain sharp elevational contrasts among soil properties, but

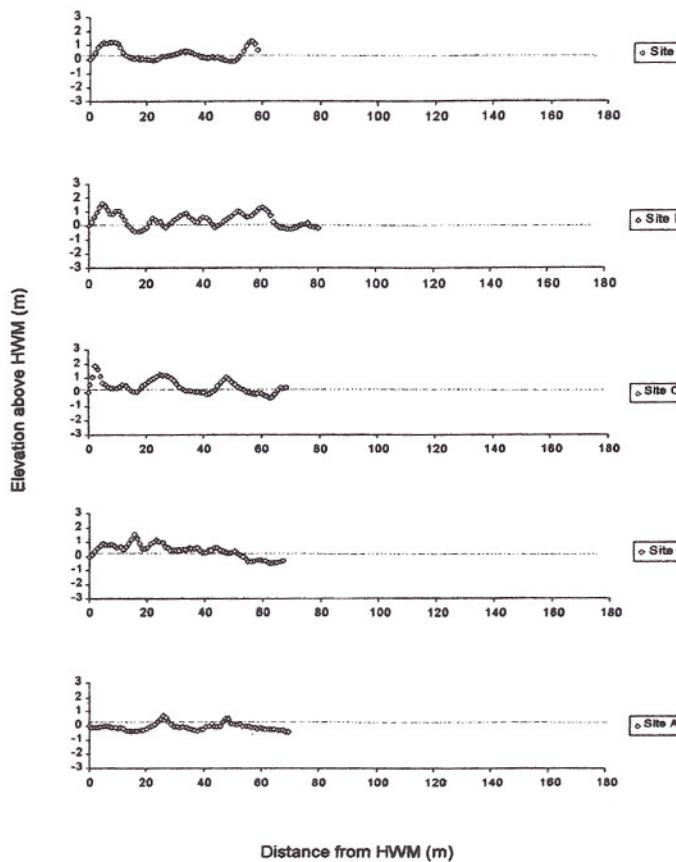
contribute to a greater overall consistency in the covariation among soil properties when summed across habitats. In terms of PCA, soil variables on Sapelo should exhibit a higher multicollinearity. I expected that a larger portion of the variance in the soil data can be summarized in a lower dimensionality, and that interpretable, nontrivial factor loadings of soil variables will be concentrated on a lower dimension principal component. For South Core, I hypothesized that overwash should interrupt and dampen the covariation of edaphic properties. Frequent overwash should reduce particle-size sorting, and limit the pedogenic modification of substrates by vegetation. Less multicollinearity among measured soil variables should necessitate a higher dimensionality, with factor loadings dispersed across several principal components. PCA tests were performed in PC-Ord Version 4.04. Sapelo had only two quadrats with particles larger than 2 mm; this textural class was deleted from the PCA.

To determine the strength of the multivariate association between the suite of soil variables and the sum of vegetation cover for each island, I employed Mantel tests (Legendre and Legendre, 1998). For each island, I performed one-tailed Mantel tests for relative species cover and quadrat soil variables. Monte Carlo tests ( $n = 999$ ) were employed to determine the significance of this multivariate correlation. Mantel tests were conducted in R Package Version 4.0 (Legendre and Casgrain, 1999). Bivariate Spearman's correlation coefficients were employed to assess how individual species cover covaried with edaphic variability expressed on nontrivial principal components. I examined this relationship for species occurring in 15 or more of the quadrats from each island. These species were classified as sediment-stabilizers or dune-builders (Godfrey and Godfrey, 1976; Woodhouse, 1982). Dune-building taxa promote and maintain prominent foredunes. Sediment-stabilizers bind and trap sand without forming dunes. I used nontrivial principal components, rather than the quadrat soil variables, for bivariate correlations because my intent was to examine individual species responses to soil variance structure. Correlations between species and quadrat soil variables would not allow me to parsimoniously infer how differences in the interrelationships among soil variables were associated with vegetation.

In terms of vegetation dynamics theory, exposure to frequent and extensive overwash on South Core Banks should impose a more nonequilibrating relationship between vegetation and environment. As such, I expected weaker correlations between species cover and edaphic variables in this setting. Overwash processes should inhibit and obscure compositional adjustment to the edaphic variability expressed along environmental gradients. On Sapelo, protection from disturbance allows compositional adjustment to site conditions. This facilitates expression of a species-driven sorting along the edaphic gradients associated with the island's prominent dune ridge-and-swale topography. Consequently, I expected stronger correlations between species cover and edaphic variables in this geomorphic environment.

## RESULTS

Cross-sections documented the prevalence of a dune-and-ridge topography on Sapelo (Fig. 4), and a simplified overwash topography on South Core (Fig. 5). Mean



**Fig. 4.** Topographic cross-sections for representative transects from each site on Sapelo Island, Georgia. Dashed line represents high-water-mark datum. Diamonds indicate individual quadrats. Site A is the southernmost site on the island, and Site E is the northernmost.

dune habitat widths on Sapelo ( $70 \pm 8$  m) were roughly half those of South Core ( $140 \pm 38$  m). Shared species, those taxa encountered along transects of both islands, comprised 96% of the total absolute species cover on Sapelo, and 79% of the total absolute cover on South Core. The most abundant species cover for both islands was *Uniola paniculata*, the common dune-building species of the southeastern United States. South Core supported a higher absolute cover of two overwash adapted species, *Spartina patens* and *Hydrocotyle bonariensis*, and an assemblage of mosses, comprised chiefly of the genera *Ditrichum* and *Barbula*. These mosses were found only on South Core, where they formed a low, dense ground cover on older stabilized overwash flats. Mosses exhibit a high resiliency to sand burial, and are prominent in succession following the destruction of established vegetation (Scott, 1982; Longton, 1992; Martínez and Maun, 1999). Sapelo was characterized by a higher cover of the woody shrub *Myrica cerifera*, and the herbaceous species

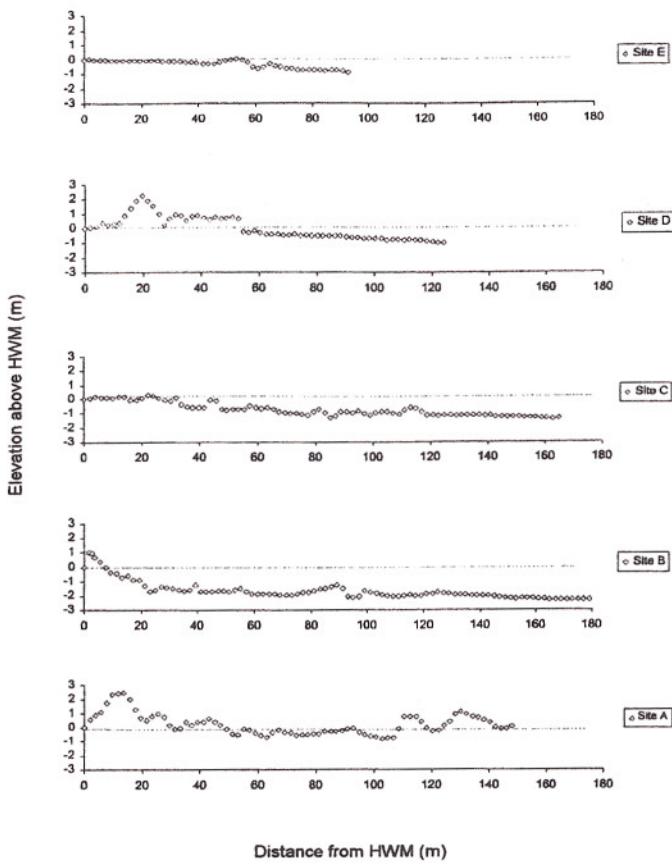


Fig. 5. Topographic cross-sections for representative transects from each site on Sapelo Island, Georgia.

*Muhlenbergia filipes*. These two species typically stabilize low, wet swale habitats (Duncan and Duncan, 1987). Dune-building species, such as *Panicum amarum* and *Sporobolus virginica* also were more abundant on Sapelo.

A total of 140 quadrat soil samples from Sapelo and 136 from South Core were collected and analyzed. Sapelo soil textures were well sorted and dominated by fine to very fine sands (Fig. 6). Only two quadrats contained particles larger than 2 mm, each with a content less than 1%. By contrast, particles larger than 2 mm were more abundant ( $2\% \pm 4\%$ ) on South Core. South Core soils were characterized by a range of textural classes, of which very coarse to medium sand and fine to very fine sands were predominant. Silt-clay content was higher on South Core, as were pH and carbonates. MRPP confirmed significant differences between islands in all but one of these soil variables, organic matter, which averaged less than 1% for both islands (Table 1). Organic matter content is typically low in vegetated dunes (Ehren-

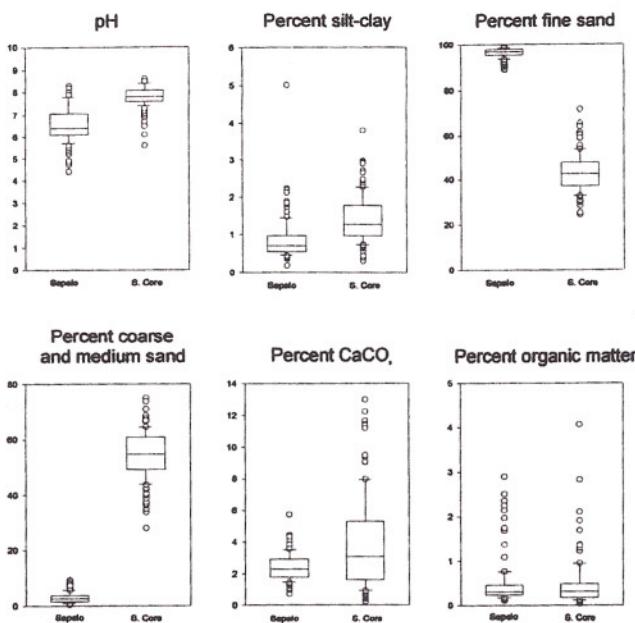
**Table 1.** Mean Quadrat Soil Properties by Site

Island/site	pH*	Percent silt and clay*	Percent fine to very fine sand*	Percent coarse to medium sand*	Percent carbonate*	Percent organic matter
<b>Sapelo</b>						
A	7.2 ± 0.5	1.1 ± 0.9	96.8 ± 1.4	2.1 ± 1.2	3.5 ± 0.8	0.3 ± 0.2
B	6.6 ± 0.7	0.6 ± 0.2	96.4 ± 1.3	3.0 ± 1.3	2.2 ± 0.6	0.3 ± 0.2
C	6.2 ± 0.6	0.9 ± 0.4	94.6 ± 2.5	4.5 ± 2.2	2.0 ± 0.5	0.5 ± 0.5
D	6.8 ± 0.6	0.6 ± 0.2	97.3 ± 1.7	2.1 ± 1.6	2.1 ± 0.6	0.3 ± 0.2
E	6.0 ± 0.9	1.1 ± 0.5	96.2 ± 2.1	2.7 ± 1.9	2.2 ± 0.8	0.8 ± 0.8
<b>South core</b>						
A	7.6 ± 0.7	1.3 ± 0.5	40.6 ± 6.8	58.0 ± 6.9	2.2 ± 1.3	0.5 ± 0.6
B	7.7 ± 0.5	1.5 ± 0.6	40.9 ± 7.4	53.7 ± 7.8	5.1 ± 3.7	0.6 ± 0.7
C	7.8 ± 0.3	1.6 ± 0.7	44.3 ± 7.0	52.6 ± 7.5	4.6 ± 2.6	0.5 ± 0.3
D	8.0 ± 0.4	1.4 ± 0.5	42.0 ± 9.4	56.0 ± 9.0	4.7 ± 2.5	0.3 ± 0.3
E	7.9 ± 0.3	1.3 ± 0.7	46.8 ± 10.0	51.1 ± 9.3	2.4 ± 2.1	0.3 ± 0.5
<b>MRPP</b>						
A value	0.25	0.14	0.81	0.80	0.08	0.003
p	<.001	<.001	<.001	<.001	<.001	.31

\*Significantly different MRPP at  $p < .05$ .

feld, 1990). All inter-island edaphic differences resulted from greater within-group agreement than expected by chance.

PCA revealed contrasts between islands in the dimensionality of their soil descriptors and the distribution of captured variance and factor loadings. Broken-stick eigenvalues for Sapelo indicated that only the first principal component (PC1) resolutely captured more variance (51%) than that expected by chance (Table 2). Factor loadings for this component indicated that pH and percent fine to very fine sands were inversely associated with organic matter and very coarse to medium sand. PC3 on Sapelo was categorized as trivial given the near equivalence between observed and broken-stick eigenvalues. On South Core, the second and third principal components captured a larger percentage of sample variance than predicted by the broken-stick null model (Table 3). PC2 captured 32% of the sample variance after extraction of the trivial variance associated with PC1. Factor loadings for this component also expressed an inverse relationship between pH and organic matter. Yet in contrast to Sapelo, strong particle-size loadings were not associated with this component's variability in pH and organic matter. Instead, particle sizes loaded more strongly on PC3 for South Core. PC3 captured 22% of the sample variance, and expressed a strong inverse relationship between the particles larger than 2 mm and the coarse to medium sand fraction.



**Fig. 6.** Box plots for untransformed soil variables by island. Box boundaries indicate the 25th and 75th percentiles. Whiskers above and below the box indicate the 10th and 90th percentiles. Outlying samples are denoted by circles.

Mantel tests indicated significant but similarly weak correlations between soil variables and species cover on each island. Sapelo had only a slightly higher Mantel multivariate correlation ( $r_s = .14, p < .05$ ) in comparison to South Core ( $r_s = .04, p < .05$ ). However, individual species on both islands were significantly correlated with nontrivial principal components (Table 4). Many of these taxa were driver species (Walker, 1992; Jones et al., 1997; Bruno, 2000) in that their interaction with sediment mobility molds each island's characteristic topography. On Sapelo, bivariate correlations of individual species with PC1 revealed a prominent separation of species along a gradient of pH, particle size, and organic matter. Negative correlations for dune-building species (chiefly *Uniola paniculata* and *Panicum amarum*) indicated their affinity for high pH, low organic content, well-sorted fine sands that characterize dune landforms (Fig. 7). Sediment-stabilizing species (*Myrica cerifera*, *Muhlenbergia filipes*) had stronger positive correlations with this component, thus reflecting these species' proclivities for the coarser, low pH, high organic matter soils characteristic of low wet swale landforms. Of note, the trivial second principal component on Sapelo had several weakly significant correlations with species cover. This suggests that ecologically meaningful variance may have been partitioned among the first two axes. However, the larger amount of captured variance on PC1 underscored its importance.

In support of the distribution of broken-stick eigenvalue comparisons for South Core, none of the species had significant correlations with the trivial first principal

**Table 2.** Principal Components Analysis of Sapelo Soil Variables

	Eigenvalue	Broken-stick eigenvalue	Percent of variance	PC1 <sup>a</sup>	PC2	PC3
Axis						
1	3.08	2.45	51.31			
2	1.38	1.45	22.92			
3	0.96	0.95	15.93			
4	0.41	0.62	6.83			
pH				-0.445	0.241	0.389
Silt and clay				0.373	-0.462	0.324
Fine to very fine sand				-0.481	-0.331	-0.365
Coarse to medium sand				0.419	0.499	0.304
Carbonate				-0.235	-0.433	0.693
Organic matter				0.447	-0.427	-0.196

<sup>a</sup>Nontrivial principal component.

**Table 3.** Principal Components Analysis of South Core Soil Variables

	Eigenvalue	Broken-stick eigenvalue	Percentage of variance	PC1	PC2 <sup>a</sup>	PC3 <sup>a</sup>
Axis						
1	2.55	2.59	36.45			
2	2.26	1.59	32.33			
3	1.51	1.09	21.50			
4	0.32	0.76	4.52			
pH				0.039	-0.570	0.289
Silt and clay				-0.404	0.412	0.083
Fine to very fine sand				0.472	0.323	0.320
Coarse to medium sand				-0.314	-0.341	-0.558
Granules				-0.394	0.037	0.583
Carbonate				-0.519	-0.182	0.295
Organic matter				-0.299	0.501	-0.263

<sup>a</sup>Nontrivial principal component.

component. Correlation coefficients for individual species with the first nontrivial component, PC2, evidenced a separation of species along a gradient of pH and organic matter. As on Sapelo, dune-building species here (exclusively *Uniola paniculata*) were associated with high pH and low organic matter soils. Sediment-sta-

**Table 4.** Spearman's Rank Correlation Coefficients for Species Cover and Principal Components

Island/species	Landform functionality <sup>a</sup>	Number of quadrats	PC1	PC2	PC3
<b>Sapelo</b>					
<i>Andropogon</i> spp.	S	16	0.13	-0.13	0.02
<i>Cenchrus</i> spp.	S	16	-0.01	0.00	-0.12
<i>Croton punctatus</i>	S	18	-0.19*	0.17*	-0.05
<i>Fimbristylis</i> spp.	S	19	0.04	-0.26*	-0.13
<i>Muhlenbergia</i> spp. <sup>b</sup>	S	22	0.42*	-0.19*	0.02
<i>Myrica cerifera</i> <sup>b</sup>	S	21	0.33*	-0.19*	-0.03
<i>Panicum amarum</i> <sup>b</sup>	D	29	-0.21*	0.19*	0.10
<i>Phyla nodiflora</i>	S	52	0.20*	-0.13	-0.07
<i>Uniola paniculata</i> <sup>b</sup>	D	71	-0.27*	0.37*	-0.17*
<b>South core</b>					
<i>Ditrichum</i> spp. <sup>b</sup>	S	22	-0.08	0.42*	0.25*
<i>Heterotheca subaxillaris</i>	S	49	-0.07	0.25*	0.05
<i>Hydrocotyle bonariensis</i> <sup>b</sup>	S	62	-0.05	0.28*	-0.14
<i>Oenothera humifusa</i>	S	37	0.08	0.21*	0.17
<i>Solidago sempervirens</i>	S	23	0.10	0.28*	0.12
<i>Spartina patens</i> <sup>b</sup>	S	61	-0.05	0.25*	0.06
<i>Uniola paniculata</i> <sup>b</sup>	D	81	0.10	-0.55*	-0.10

<sup>a</sup>S = sediment stabilizer; D = dune builder.

<sup>b</sup>Driver species.

\*Significant at  $p < .05$ .

bilizing herbaceous species (chiefly *Spartina patens*, *Hydrocotyle bonariensis*, and the assemblage of moss species) attained its highest cover in soils with lower pH and higher organic matter content. Mosses also were the only species significantly correlated with the other nontrivial component, PC3. Factor loadings for particles larger than 2 mm (chiefly abraded shell fragments) were associated with an increasing cover of these taxa.

## DISCUSSION

The general inter-island differences in topography, species distributions, vegetation, and edaphic properties reflected their nearshore environment (Godfrey, 1976; Oertel and Larsen, 1976; Davis, 1994). The increased sorting and dominance of fine-grained sands on Sapelo are characteristic of this low wave energy shoreline,

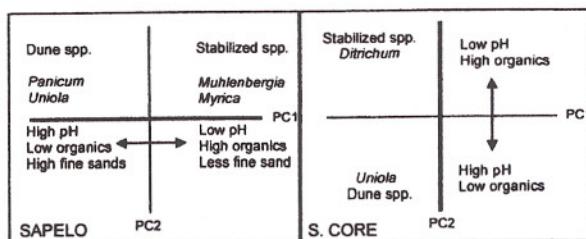


Fig. 7. Species associations with nontrivial principal components by island.

while overwash processes on South Core contributed to its poorly sorted particle sizes (Giles and Pilkey, 1965). Higher wave energies on South Core contributed to its greater soil pH through the buffering effects of locally abundant carbonates in abraded shell fragments (Hosier, 1973). Dunes in coastal Georgia typically do not contain a large percentage of carbonates owing to the inability of waves to transport and fragment shells abundant in adjacent nearshore habitats (Johnson et al., 1974). A lower mean content of silt-clay on Sapelo may reflect the rarity of overwash events of sufficient magnitude to transport and deposit suspended sediments in back-barrier environments.

Despite an equivalence in the amount of variance explained by the nontrivial components on each island (Sapelo = 53%, S. Core = 51%), there were notable differences in the underlying data structure. In agreement with my initial hypotheses, Sapelo had a lower nontrivial dimensionality that concentrated captured variance on a single component, thus suggesting a high within-island multicollinearity in edaphic characteristics and, therefore, greater covariation among soil properties. By contrast, the second and third principal components, rather than the first, were nontrivial on South Core. This indicated a reduced tendency for soil properties to covary across dune habitats on the island. My hypothesis of greater covariation among soil properties on Sapelo also was supported in that pH, organic matter, and sand particle size classes loaded on the only nontrivial principal component, PC1. As such, there may be a greater textural regulation of pH and organic matter in the protected habitats on Sapelo. By contrast, sand textural classes on South Core did not load as strongly on the same nontrivial principal component as pH and organic matter. This suggests a weaker pedogenic role for sand texture in the more frequently overwashed setting of South Core. Instead, textural classes loaded most strongly on the nontrivial third principal component. Inverse loadings for particles larger than 2 mm and coarse sand on this component may be a consequence of the eolian deflation of coarse to medium sand following overwash, and the subsequent formation of a deflation lag of large shell fragments.

Mantel correlations between the sum of vegetation cover and the suite of measured soil variables on each island were similarly weak. But more importantly, individual species on both islands were responsive to the edaphic variability expressed on nontrivial principal components. The presence of these correlations on South Core implies that more-frequent exposure to disturbance and substrate instability does not preclude a strong species responsiveness to soil properties. Following Ben-

dix (1998), disturbance in this sense is an environmental characteristic that maintains a suite of conditions and resources that constrain species abundance. For example, pH and organic matter, even in the more unstable, poorly sorted substrates of South Core, were significantly correlated with the cover of *Spartina patens* and *Ditrichum*. Insofar as I assumed a nonequilibrating relationship between vegetation and environment where overwash is frequent, compositional adjustment may be more species-specific than I initially assumed.

## CONCLUSION

Vegetation patterns, geomorphic processes, and landforms often are causally linked. Emphasis on either processes or forms as the exclusive control of vegetation restricts interpretations of pattern to a singular cause-and-effect relationship. Instead, process-form feedbacks, rather than sediment mobility or landform characteristics alone, regulate vegetation patterns (Swanson et al., 1988; Parker and Bendix, 1996). To understand how these feedbacks influence biogeographical patterns (Phillips, 1999), it becomes necessary to develop hypotheses and analytical frameworks to quantify and differentiate systems interactions.

The barrier islands in this study represent two biogeomorphic systems, each with distinctive process-form feedbacks. Compositional patterns were correlated with soil properties in both systems, but through different soil variance structures. For Sapelo Island, incremental sediment mobility and topographic complexity concentrated soil variance and factor loadings on lower dimensional axes. On South Core, frequent, episodic sediment transport processes and simplified topography dispersed soil variance and factor loadings across higher dimensional axes. Suites of topography-modifying species, unique to each island, were uniform in the strength of their individual correlation with local edaphic variability. I posit that soil variance structure is a useful criterion to distinguish the relative influence on vegetation patterns of soil properties expressed through landforms (Sapelo Island) versus sediment transport processes (South Core Banks). Given that the relative influence of processes versus forms is scale dependent, contrasts in soil-data structure may prove most useful in studies seeking to define boundary conditions for system states (Malanson et al., 1990; Montgomery, 1999).

Scaling up to include process-form interactions facilitates conceptualization of pattern emergence, yet also encourages the reductionist elucidation of the patterns and variability characterizing functionally different systems (Malanson, 1999). Biogeographers need to continue to refine their methodologies to accommodate the reductionist framework invoked in field-based studies within conceptual frames encompassing systems interactions.

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