JON ANTHONY STALLINS
Barrier Island Morphology and Dune Vegetation Pattern and Process in the Georgia Bight
(Under the Direction ALBERT J. PARKER)

Vegetation patterns reflect the interplay of two processes: the imposition of site factors along gradients and disturbance exposure and recovery. I investigated how these processes interact to generate patterns in dune plant species composition, diversity, and soil-vegetation relationships on two barrier islands in the Georgia Bight: South Core Banks, North Carolina, a frequently storm-overwashed barrier island, and Sapelo Island, Georgia, an infrequently overwashed barrier. A single transverse compositional gradient characterized South Core versus two intersecting gradients on Sapelo. Dune ridge-and-swale topography on Sapelo restricts the spread of overwash, thus disturbance-structured vegetation adjoins the prominent transverse vegetation zonation expressed along gradients. On South Core, topography reinforces the spread of disturbance across the landscape, thus folding disturbance and transverse vegetation zonation into a single overlapping gradient. These contrasting gradient structures contributed to Sapelo's higher longitudinal and transverse compositional variability.

Biogeomorphic feedback and threshold processes that mold compositional patterns decouple disturbance exposure and effect on Sapelo, while this coupling is reinforced on South Core. The Intermediate Disturbance Hypothesis (IDH) presupposes a geographically-consistent direct coupling between disturbance exposure and effect, and thus was applicable at the landscape-scale only on South Core. Here, disturbance is frequent, and biogeomorphic processes reinforced an inhibition-structuring of diversity patterns. On Sapelo, diversity patterns did not conform to IDH, largely due to a decrease in the spatial scale of the processes regulating species patterns. The Dynamic Equilibrium Model (DEM) was a more robust framework for examining the geographic patterns of species diversity in this study given its ability to incorporate direct and indirect structuring effects of disturbance, and changes in the scale expression of diversity patterns.

Infrequent overwash enhanced edaphic organization on Sapelo, while frequent overwash dampened edaphic organization on South Core. Relatively stronger associations between soil and total vegetation cover were expressed on Sapelo, however, this may not necessarily be due to edaphic organization. Individual species on both islands were responsive to variability in edaphic properties. This association between the dominant dune-building and sediment-stabilizing taxa and edaphic variability on both islands reinforces their importance as regulators of topography and the spread of disturbance.

INDEX WORDS: Barrier islands, Biogeomorphology, Dune Vegetation, Disturbance, Gradient zonation, Feedbacks, Thresholds, Intermediate Disturbance Hypothesis, Dynamic Equilibrium Model.

BARRIER ISLAND MORPHOLOGY AND DUNE VEGETATION PATTERN AND PROCESS IN THE GEORGIA BIGHT

by

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CHAPTER 1

INTRODUCTION

Vegetation studies in coastal sand dunes have played an important role in the articulation of fundamental concepts in ecology and biogeography. Cowles (1899) described the patterns of succession on the sand dunes around Lake Michigan, and emphasized a dynamic nature of vegetation change that had not been recognized by earlier botanists. Clements (1916) used these same dune systems as a setting to illustrate his concepts of succession. Although his ideas about climax and plant species self-directed development (the 'superorganismal' concept) have been discredited, Clements work has its modern counterpart in systems ecology, where emergent properties are thought to result from the organization of internal components (Huston, 1994).

The landscape-scale study of vegetated coastal dune systems, particularly in the United States, is limited to habitats in the Great Lakes region, the Atlantic/Gulf coast, and stretches of sandy coastlines along the Pacific shore. For early field botanists—and for researchers today—the ecological and geomorphic complexity contained within dune systems (Lichter, 1998; Sherman and Bauer, 1993), and to an extent their restricted distribution, may have limited their study. As such, there has been greater research emphasis in the more accessible temperate forest habitats of North America. By shifting to temperate forests, ecological views that suggested notions of holism and equifinality were replaced by ones that stressed reductionist mechanisms and disequilibrium between vegetation and environment (Watt, 1947; Egler, 1954). In temperate forests, geomorphic processes, climatic variability, and vegetation operate on different temporal scales, and thus preempt any operative definition of an end state (Vale, 1988; Sprugel, 1991)

More recently, environmental scholars have described the existence of multiple stable states in geomorphic and ecological systems. Multiple stable states are potential configurations of abiotic and biotic components that confer system resistance and resilience, which in concert act to conserve landscape structure and function (Wu and Loucks, Odum et al., 1987; Allison and Thomas, 1993). Evidence for and deliberation on the documentation of multiple stable states has evolved from studies in rangelands (Westoby, 1989; Laycock, 1991; Tausch, 1993), as well as riparian (Baker and Walford, 1995), and forested habitats (Vale, 1982). Environmental scholars are also becoming increasingly aware that biogeographic patterns arise from a more complex interplay, one in which feedbacks mediate interactions between external forcings and local abiotic and biotic factors. This interplay is postulated to drive the shifts, or changes, from one state to another (Malanson *et al*., 1990; Perry, 1995; Malanson, 1999). This systems viewpoint, often referred to as self-organization, or biocomplexity, has reinserted the concept of directionality into vegetation dynamics. Vegetation as a passive template upon which environmental factors are subjected upon is being replaced with a more dynamic view, in which both vegetation and environment exhibit reciprocity in their interactions. These interactions may confer directionality to the evolution of landscape patterns (Phillips, 1999).

Vegetated coastal dune systems are an ideal setting to complement our current understanding of vegetation pattern and process, which has for the most part been influenced by the scales invoked in studies of temperate forests. In coastal vegetated dunes, potential disparities in temporal scaling are minimized. Ecological and geomorphic processes interact over relatively short temporal scales, and thus minimize the disequilibrium in the vegetation-environment relationship (Rastetter, 1991). Process-form relationships between vegetation pattern and disturbance agents are rapidly equilibrating. Furthermore, feedbacks are ubiquitous and responsive in these environments. Sandy coastal landscapes behave as a sensitive biogeomorphic system, rather than a collection of independent components (Rastetter, 1991). For example, vegetation cover induces incremental sediment deposition which ultimately shapes dune landforms; these landforms, in turn, regulate the storage and movement of sediments and the environmental conditions influencing vegetation cover. As such, the patterns of sediment mobility become a key variable in regulating vegetation patterns, a characteristic shared with other biogeomorphic environments (Parker and Bendix, 1996).

Two divergent conceptual frames have been deployed historically to explicate vegetation patterns in coastal settings. Many authors have stressed the effects of overwash disturbance on dune vegetation patterns (Figure 1.1). Overwash, the transport of large volumes of sediment from the beach face to interior location during hurricanes and winter storms, clears patches of ground

Figure 1.1. Repeat photos of overwash effects on South Core Banks, North Carolina. Top photo was taken August 1998. Bottom photo was taken in October 1998, one month after the passage of a tropical storm. Photographs were taken at the same island location, but at different perspectives. Both photographs by author.

and triggers vegetation recovery sequences (Godfrey and Godfrey, 1976). Regional variation in overwash frequency and vegetation responses also shapes barrier island physiography (Godfrey, 1976). Overwash physiography includes a number of identifiable shoreline and vegetation patterns that suggest a cyclic pattern of overwash (Hosier and Cleary, 1977). Woody shrub expansion may increase in the absence of storm overwash (Schroeder *et al*., 1979; Young *et al*., 1995). More recently, Hayden *et al*. (1995), working on low profile, frequently overwashed barrier islands of the Virginia Coastal Long Term Ecological Research site, found that dune vegetation pattern covaried with land surface elevation. They posited that elevation dictates exposure to overwash events and imposes spatial variability in the depth to fresh and salt water. However, most studies of coastal dune vegetation over the past century have emphasized environmental gradients over overwash disturbance as predominant influences on dune vegetation pattern (Figure 2.1). The striking zonation of dune species along coastal environmental gradients was the stimulus for Cowles (1899) work along Lake Michigan. Numerous studies consistently identify salt spray exposure, incremental sediment mobility, and soil moisture as primary factors regulating dune vegetation patterns in the absence of disturbance (Oosting and Billings, 1942; Oosting, 1945; van der Valk, 1974; Barbour, 1978; Moreno-Casasola, 1986; Hesp, 1991). Maun and Perumal (1999) suggest that sand burial is more important than salt spray as a control of species occurrence. Wilson and Sykes (1999) state that salt spray and incremental burial vary in their relative importance depending upon island position.

These conceptual frames need not be viewed as mutually exclusive. Vegetation patterns across a landscape reflect the interplay of disturbance patch dynamics (Pickett and White, 1985) and local gradients of energy, moisture, and nutrients (Whittaker, 1970). It has been recognized that the relative importance of these two structuring processes varies geographically and is scale dependent (Veblen, 1985; Peet, 1992). Furthermore, disturbances overlay environmental gradients, both influencing and being influenced by those gradients (Harmon *et al*., 1983; White, 1987). The interaction of extrinsic and intrinsic controls in regulating biogeographic patterns has received little study, especially in coastal habitats. Several studies that consider this interaction are evident in the literature. Martinez *et al*. (1997) acknowledge that the mobility of dune substrates regulates local resource availability, while also acting as a disturbance agent. Costa *et al*. (1996) found that

Figure 2.1. Repeat photos of transverse zonation along local environmental gradients on Sapelo Island, Georgia. Top photo was taken in 1996. Bottom photo was taken in October 1999. Both photographs by author.

edaphic variables were significant in explaining the regional contrasts in vegetation zonation along a shore disturbance gradient encompassing 700 km of the Brazilian coast. Based upon a comparison of barrier islands in the Outer Banks of North Carolina and Massachusetts, Godfrey *et al*. (1979) suggested that each island's distinctive physiography was shaped by geographic variation in the biogeomorphic feedbacks between vegetation and overwash frequency.

The objectives of this dissertation are to examine dune vegetation patterns for two southeastern Atlantic coast barrier islands that differ dramatically in their spatial and temporal scale forcings of sediment mobility. Episodic, massive overland transport of sediments during storm-driven overwash is common to wave-dominated microtidal barrier island morphologies of North Carolina. The sum of biogeomorphic feedbacks and thresholds operating on this type of landscape maintains a low morphologic resistance to overwash, and a composition with a high resiliency to burial. By contrast, incremental processes of sediment transport predominate on mixed-energy mesotidal barriers of the Georgia coast, where overwash is infrequent and spatially restricted. The sum of biogeomorphic feedbacks operating on this landscape increases morphologic resistance to overwash, while fostering a composition that has a lower resiliency to recover from such an event.

My overarching objective is to document how these disparate geomorphic environments influence compositional patterns, species diversity, and the relationship between substrates and vegetation. These objectives are addressed in separate chapters. Chapter 1 serves as a literature review and introduction to my research objectives. Chapter 2 addresses compositional variability on my study islands. In this chapter, I articulate a conceptual synthesis that seeks to describe how feedback and threshold responses regulate the hierarchical arrangement of system components, and shape the spatial expression of compositional patterns. My third chapter compares species diversity patterns between islands. In this chapter, I examine the relevancy of two models of plant species diversity, the Intermediate Disturbance Hypothesis (Loucks, 1970; Grime, 1973; Connell, 1978) and the Dynamic Equilibrium Model (Huston, 1979, 1994), in light of my results. I discuss how feedback and threshold behaviors in biogeomorphic systems may complicate established assumptions about disturbance exposure, effects, and the regulation of diversity. My fourth chapter investigates whether dune soils differ in their association with species cover between islands. I detail how regionally distinctive pedogenic and geomorphic processes shape the relationship between dune soils and species cover on my two study islands. An overview of my findings are presented in Chapter 5. In this closing chapter, I provide a conceptual model of a landscape sensitivity gradient that synthesizes my findings from previous chapters.

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CHAPTER 2

DUNE PLANT COMPOSITIONAL PATTERNS IN TWO BARRIER ISLAND GEOMORPHIC ENVIRONMENTS

Overview

Vegetation patterns reflect the interplay of two processes: the imposition of site factors that control local gradients and disturbance events that trigger vegetation recovery sequences. I investigate how these processes interact to generate patterns in longitudinal (along-island) compositional variability and transverse (across-island) gradient structure on two barrier island morphologies of the Georgia Bight. Topographic and cover data were sampled within strip transects aligned perpendicular to the shoreline at study sites parsed along a frequently storm-overwashed microtidal (South Core Banks, North Carolina) and an infrequently overwashed mesotidal (Sapelo Island, Georgia) barrier island. Site-level non-metric multidimensional scaling (NMS) and analysis of similarity revealed divergence in island compositions, and a greater longitudinal compositional variability on Sapelo. Multi-response permutation procedure comparisons of transect species turnover and transverse zonation also revealed significant differences between islands. Sapelo had a higher species turnover, and a greater transverse zonation. NMS plots of quadrat-level species clusters indicate that a single dominant transverse species gradient characterizes South Core versus two spatially intersecting vegetation gradients for Sapelo. The high morphologic resistance of the dune ridge-and-swale topography on Sapelo restricts the spread of overwash disturbance, and thus incorporates disturbance-structured vegetation as an adjoining zone along the transverse sequence of vegetation responding to local maritime environmental gradients. By contrast, on South Core, the low morphologic resistance of topography reinforces the spread of disturbance across the landscape, thus folding disturbance and transverse vegetation zonation into a single overlapping gradient. These contrasting gradient

structures contribute to the higher longitudinal and transverse compositional variability evidenced on Sapelo. The biogeomorphic feedback and threshold behaviors that mold morphologic resistance and species distributions on Sapelo act to decouple disturbance exposure and effect, and enhance a fine-scale differentiation of compositional patterns. On South Core, a reinforced coupling between disturbance exposure and effect augments a broad-scale regularity of compositional patterns.

Introduction

Vegetation patterns across a landscape reflect the interplay of two structuring processes: 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). It has been recognized that the relative importance of these two structuring processes varies geographically and is scale-dependent (Veblen, 1985; Peet, 1992). Furthermore, disturbances overlay environmental gradients, both influencing and being influenced by those gradients (Harmon *et al*., 1983; White, 1987; Reice, 1994). Environmental scholars have begun to recognize that biogeographic patterns arise from a complex interplay, one in which feedbacks mediate interactions between external forcings and local abiotic and biotic factors (Urban and Shugart, 1992; Allison and Thomas, 1993; Baker, 1995; Parker and Bendix, 1996; Malanson, 1999).

Vegetation patterns across a landscape also reflect their geomorphic setting. Geomorphic setting regulates vegetation patterns, either through the direct effects of landforms or indirectly by controlling the spatial arrangement and rates of geomorphic processes (Swanson, 1988; Parker and Bendix, 1996). In the temperate forests where the interplay of site factors and disturbance has been most intensively scrutinized (Watt, 1947; Loucks, 1970), vegetation may vary continuously and rapidly, while landforms sometimes vary episodically or relatively slowly. For studies seeking to establish linkages between vegetation and environment, this disparity in temporal scaling complicates interpretations of compositional pattern (Sprugel, 1991; Urban and Shugart, 1992; Phillips, 1995a). In contrast, coastal environments afford more resolution in the inference of process from pattern. Within vegetated dune systems, ecological and geomorphic processes interact over relatively short temporal scales, and thus minimize the disequilibrium in the vegetation-environment relationship (Rastetter, 1991). Here, the process-form relationship between disturbance agents and vegetation pattern is rapidly equilibrating.

Surprisingly, there are few recent studies of dune vegetation that quantify compositional variability in relation to disturbance regime and site factors. Barrier islands of the southeastern U.S. Atlantic coast are ideal for investigating these linkages. Regional contrasts in wave and tidal energy along the margin of the Georgia Bight foster a continuum of morphologies that differ in their temporal and spatial expression of sediment mobility and landform genesis. Overwash, in which large volumes of sediment and salt water are transported overland during cyclonic storms, is frequent to wave-dominated microtidal barrier island morphologies. By contrast, mixed-energy mesotidal barrier island morphologies are characterized by incremental processes of sediment transport. Overwash is rare except where land is newly formed and without dunes, or severely eroded. Distinctive biogeomorphic responses, incorporating locale-specific feedbacks and thresholds, characterize each morphology.

In this study, I examine the contrasts in compositional and topographic pattern expressed on these two barrier island morphologies. I investigate how biogeomorphic feedbacks and thresholds are linked to the emergence of compositional pattern across multiple scales. The specific questions I address are: 1) What are the differences between island morphologies in their dune topography and species compositions? 2) How do species vary in their arrangement along the transverse environmental gradients of each island morphology? 3) Does dune vegetation exhibit significant differences in longitudinal (along-island) and transverse (across-island) compositional variability between island morphologies? The first research question is largely descriptive and serves to outline the broad topographic and floristic differences between island morphologies. My second research question details the spatial arrangement of individual species along the transverse environmental gradient of each island morphology. In the analyses addressing my third research question, I decompose transverse compositional variability into two components, species turnover and transverse zonation. By scrutiny of these topographic and compositional patterns, I hope to amplify, expand, and possibly generalize biogeomorphic concepts developed in other landscape settings.

Background

Most studies of coastal dune vegetation over the past century have emphasized transverse environmental gradients as influences on dune vegetation pattern. These studies consistently identify transverse environmental gradients of salt spray exposure, incremental sediment mobility, and soil moisture as primary factors distinguishing dune vegetation (Oosting and Billings, 1942; Oosting, 1945; van der Valk, 1974; Barbour, 1978; Moreno-Casasola, 1986; Hesp, 1991; Wilson and Sykes, 1999). Maun and Perumal (1999) suggest that sand burial is more important than salt spray as a control of species occurrence. In response to these overlapping physical gradients, dune vegetation often develops its characteristic compositional zonation parallel to the shoreline. Several authors have addressed the effects of overwash disturbance on dune vegetation patterns (Godfrey, 1976; Hosier and Cleary, 1977; Cleary and Hosier, 1979; Godfrey *et al.*, 1979; Schroeder *et al.*, 1979; Zaremba and Leatherman, 1986). More recently, Hayden *et al*. (1995), working on low profile, frequently overwashed barrier islands of the Virginia Coastal Long Term Ecological Research site, found that dune vegetation pattern covaried with land surface elevation. They posited that elevation dictates exposure to overwash events and imposes spatial variability in the depth to fresh and salt water.

Several studies that consider compositional sorting along a coastal disturbance gradient are evident in the literature. In the Outer Banks of North Carolina, Odum *et al*. (1987) observed increased transverse zonation with construction of artificial foredunes. By dramatically decreasing shore disturbance frequencies, woody shrubs and herbaceous species usually restricted to the broad back-shore setting were able to colonize within the narrow protected areas behind the constructed dune line. Hesp (1988) observed an increase in the width of the vegetated foredune zone as wave-energy increased along an unmanaged coastal dune strand of southeastern Australia. This study cited increased salt spray exposure as a potential causative agent, but did not address the concomitant role of vegetation-landform feedbacks. Barbour *et al*. (1987), in a study of dune vegetation patterns along the Gulf of Mexico, observed regional variation in composition that was correlated with sand particle size and topographic roughness. An index of disturbance, based on historic hurricane landfalls for each sampled beach, yielded no insights into regional compositional variability. However, they noted that the role of disturbance as a control of compositional pattern was weakened by the high spatial variability in the location of hurricane landfalls across the study area. More recently, Costa *et al*. (1996) found that elevation, sand particle size, and pH were significant variables in explaining the regional contrasts in vegetation zonation along a shore disturbance gradient encompassing 700 km of the Brazilian coast. Godfrey *et al*. (1979) suggested that regionally distinctive barrier island physiographies are shaped by species distributions and geographic variation in the biogeomorphic feedbacks between vegetation and overwash frequency and magnitude. Their conclusions were drawn from a comparison of a barrier island in the Outer Banks of North Carolina and in Massachusetts.

Central to this study is the pronounced morphometric variability in barrier islands that develops along the Georgia Bight (Figure 2.1). Coastal landform studies (Hayes, 1979; Williams and Leatherman, 1993) have established that embayments in coastal plain shorelines exhibit a continuum of morphologies around their margin. Entrances to bights are characterized by wave-dominated features, with tide-dominated features toward the center. On microtidal coasts along the margin of embayments, barrier islands are long and linear, as exemplified by the Outer Banks of North Carolina (Figure 2.2). On mesotidal coasts at the center of bights, barrier islands are short and wide with numerous tidal inlets, as exemplified along the coast of Georgia (Figure 2.3). These contrasts in island morphology, coupled with climatological gradients of increased exposure to extratropical cyclones with increased latitude over eastern North America in the winter season (Davis *et al*.,1993), yield a strong geographic continuum of disturbance regimes along the southeastern U.S. Atlantic coast (Mather *et al.*, 1964; Fox and Davis, 1976; Riggs, 1976; Hayes, 1979; Godfrey *et al.*, 1979; Williams and Leatherman, 1993).

Striking biogeomorphic feedbacks develop among islands along this morphometric and climatological gradient (Godfrey 1976; Godfrey,1977). Storms and waves are the agents that mobilize sediments on the microtidal barrier island of the Outer Banks. Here, even mild winter

Figure 2.1. Barrier island morphologies of the Georgia Bight.

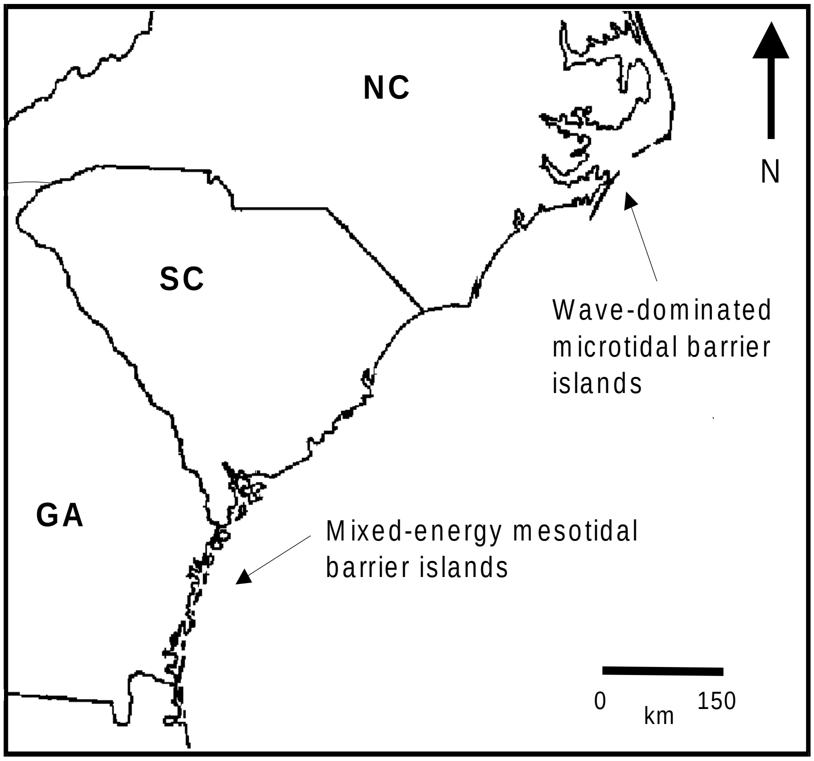

NC
SC
GA
N
Wave-dominated microtidal barrier islands
Mixed-energy mesotidal barrier islands
0
km
150

Figure 2.2. Wave-dominated microtidal barrier island morphologies of the Outer Banks of North Carolina.

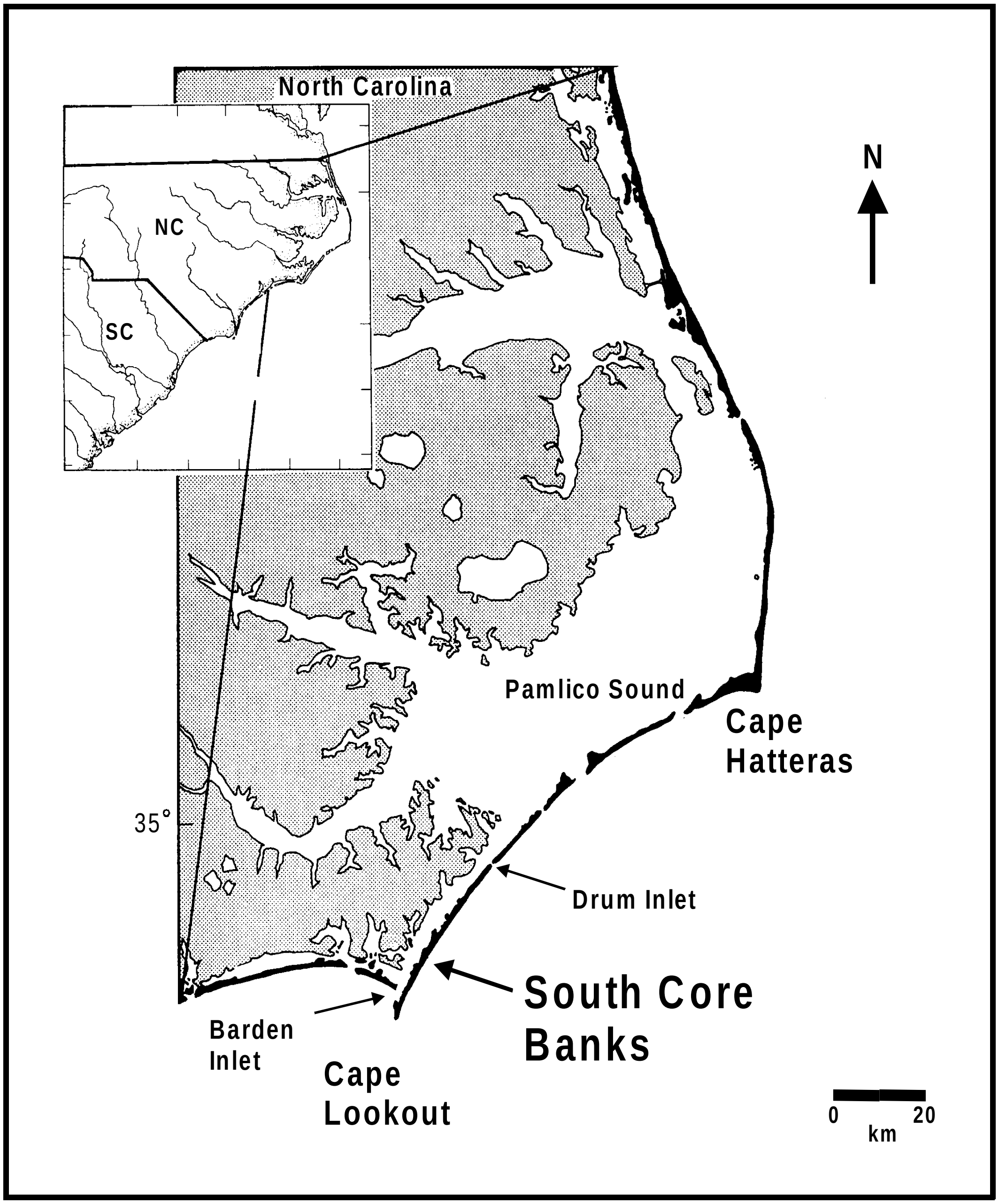
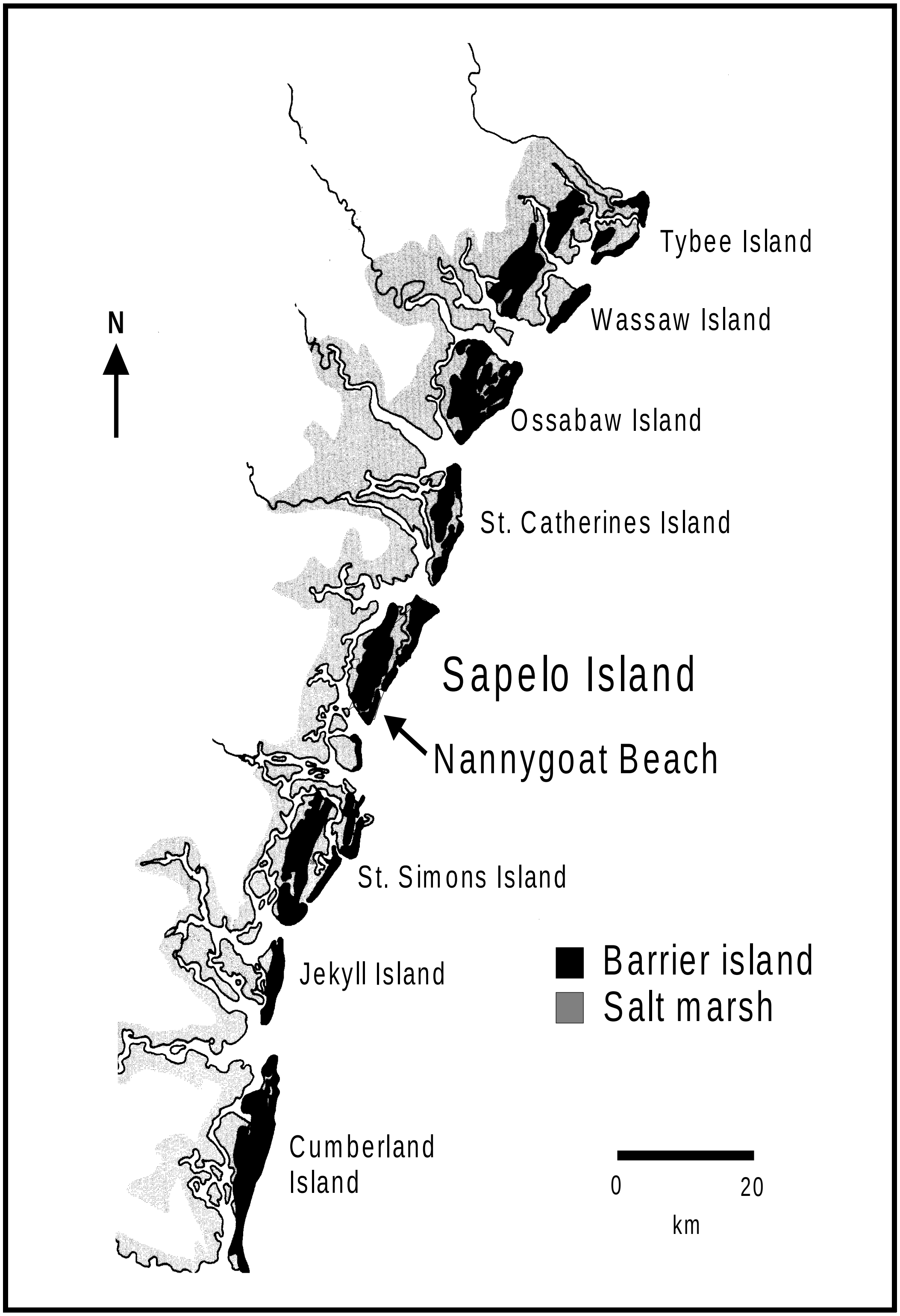

North Carolina
NC
SC
N
Pamlico Sound
Cape Hatteras
35°
Drum Inlet
South Core Banks
Barden Inlet
Cape Lookout
0
20
km

Figure 2.3. Mixed-enegy mesotidal barrier islands of the Georgia coast.


N
Tybee Island
Wassaw Island
Ossabaw Island
St. Catherines Island
Sapelo Island
Nannygoat Beach
St. Simons Island
Jekyll Island
Cumberland
Island
■ Barrier island
▨ Salt marsh
0
20
km

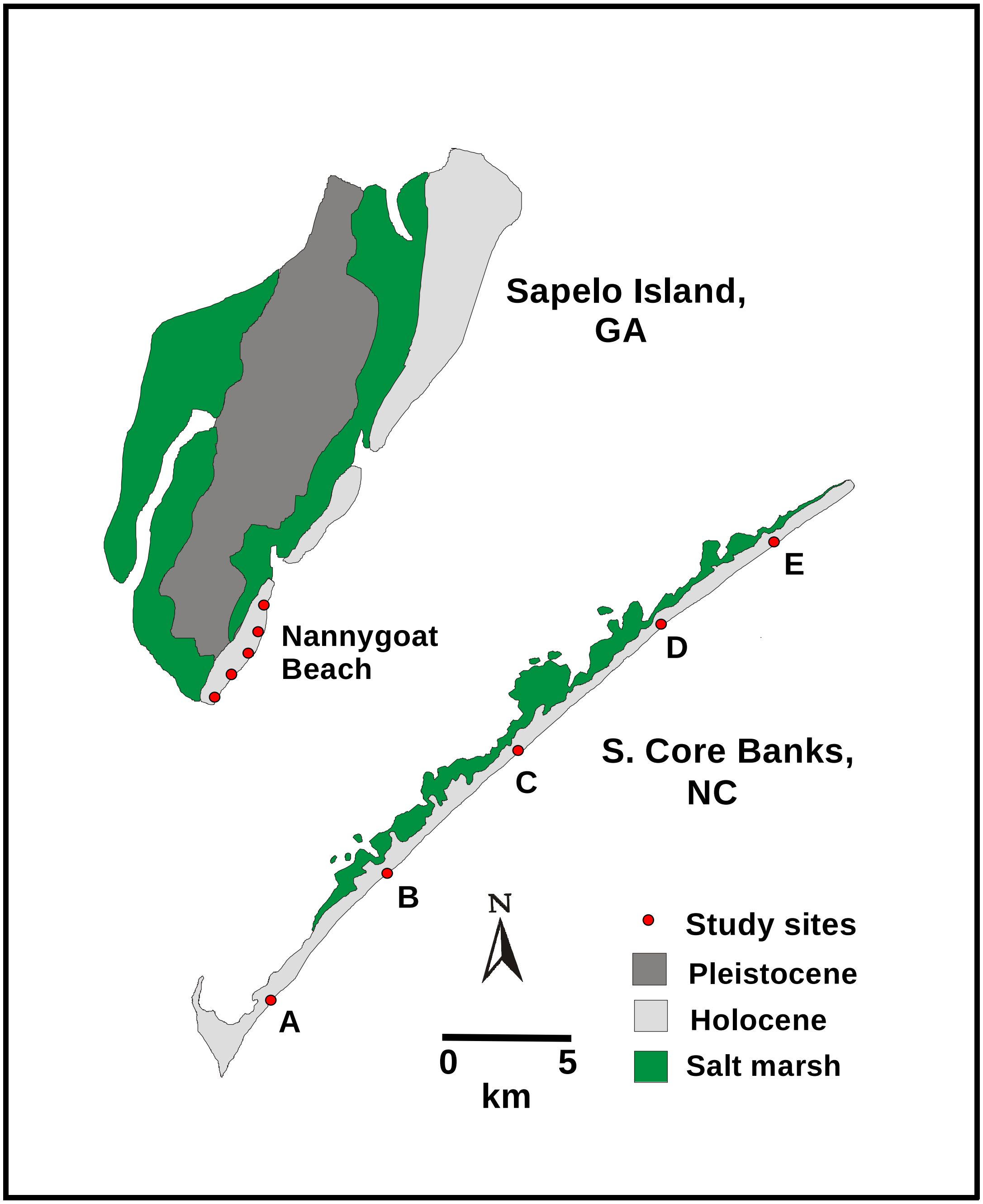
storms or offshore hurricanes can produce overwash (Hosier, 1973). Once deposited, the mobility of overwash sediments is mediated by the presence of *Spartina patens*, an abundant grass species. This rhizomatous perennial has a high tolerance to burial that permits it to recover and stabilize overwash deposits quickly. Through these adaptations, *Spartina patens* mediates a suite of biogeomorphic feedback and thresholds. *Spartina patens* reinforces overwash events by perpetuating a flat topography and by stabilizing a portion of the sediments that would otherwise be directly diverted for dune reestablishment. These effects also confer a degree of resistance to future overwash events, largely through the slightly elevated position of overwash sediments, as does the eventual reestablishment of a single protective primary foredune ridge (Hosier, 1973; Hosier and Cleary, 1977). However, the balance of biogeomorphic feedbacks and thresholds operating on this type of landscape confers a low morphologic resistance to overwash, and a composition with a high resiliency to burial (Odum *et al.*, 1987). In consequence, the presence of a flat overwash topography and *Spartina patens* are reinforced in a positive feedback (*sensu* Wilson and Agnew, 1992).

By contrast, overwash is infrequent on the Georgia coast (Deery and Howard, 1977). The dynamics of the mesotidal barrier islands of Georgia are strongly controlled by tides and tidal inlets (Hayes, 1979; Fenster and Dolan, 1996). At the island scale, large tidal ranges restrict the effects of storm surge and overwash to the duration of high tides (Godfrey, 1976). Tidal inlets serve as natural safety valves that dampen overwash during periods of infrequent high storm surge (Riggs,1976; Sexton and Hayes, 1991). These tidal inlets also influence the patterns of local-scale sediment mobility. Given an abundant supply of dune and beach sediments in these low wave energy environments, extensive beach ridges may accrete parallel to the shoreline (Oertel and Larson, 1976; Psuty, 1988). Beach ridges (or dune ridges when they occur at more inland positions) are topographic features implying local controls on shoreline dynamics. Numerous models of dune ridge formation emphasize the role of positive feedbacks between vegetation cover and aeolian deposition in their formation and stability (Taylor and Stone, 1996). In this positive feedback process, the accumulation of sand stimulates plant growth. This, in turn, increases sand entrapment, fostering continued plant growth and an increase in elevation relative to areas where dune species are absent (Woodhouse, 1982). With changes in local sediment budgets, beach ridges may be interrupted, truncated by erosion, or exhibit changes in their orientation (Taylor and Stone, 1996). The potential expression of this hummocky dune ridge-and-swale topography increases morphologic resistance to overwash. The sum of biogeomorphic feedbacks operating on this landscape increases morphologic resistance to overwash through the formation of dune ridges, while fostering a composition in low wet swales that has a lower resiliency to recover from such an event. As such, ridge-and-swale topography and the dune species that foster this topography are maintained in a positive feedback (*sensu* Wilson and Agnew, 1992).

Study Area

Two islands were selected for study: the wave-dominated microtidal barrier of South Core Banks, North Carolina, and Sapelo Island, Georgia, a mixed-energy mesotidal barrier (Figure 2.4). These island are largely undeveloped, with limited emplacement of dune or shore stabilization structures. Sapelo Island, Georgia is a mesotidal complex of Holocene and Pleistocene barriers. Several smaller Holocene islands are retreating inland and welding to the Pliestocene core. I confined my sampling to the 5 km of Nannygoat Beach on the southernmost Holocene island so as to minimize the confounding influence of multiple tidal inlets. Here, overwash is infrequent and restricted to a small area on the south end of the island. South Core Banks, part of Cape Lookout National Seashore (CLNS), is a retreating Holocene barrier. Overwash increases in frequency and intensity from south to north along this microtidal island. Sampling here covered a much larger extent (35 km) in comparison to Sapelo. Although CLNS permits vehicular traffic along a small controlled-access road along the length of the entire island, development is minimal in comparison to the closest suitable islands in Cape Hatteras National Seashore. I avoided sampling in areas that evidenced impacts of recreational use. Prior to my field sampling (from south to north) in June through August of 1998, the last hurricanes to affect South Core were Hurricanes Bertha (Category 2) and Hurricane Fran (Category 3) in 1996. These storms made landfall on the North Carolina coast below CLNP, which only received minor overwash (National Park Service

Figure 2.4. Study island morphologies and approximate location of study sites.


Sapelo Island,
GA
Nannygoat
Beach
S. Core Banks,
NC
A
B
C
D
E
N
0
5
km
Study sites
Pleistocene
Holocene
Salt marsh

personnel, personal communication). The last intense hurricane to strike the Georgia coast was one of a series of storms in the 1890's (Pielke, 1997).

Regional uniformity in temperature and precipitation regime, especially in the growing season, greatly diminish the potential confounding effect of regional macroclimatic sorting on species composition. The humid subtropical climate of the southeastern coast is characterized by mild winters, and a long summer season of hot and humid conditions. Mean July temperatures for Cape Hatteras, NC, and Jacksonville, FL, are 26° C and 28° C, respectively. Mean January temperatures range from 8° C at Cape Hatteras, NC, to 14° C at Jacksonville, FL. Annual precipitation totals are uniform along this stretch of coast, with a precipitation maximum in summer and early autumn (Stalter and Odum, 1993). As a consequence of climatic uniformity, the dune flora on these barrier islands is similar along the latitudinal breadth of my study region, with the same major species evident throughout the region (Duncan and Duncan, 1987; Stalter and Odum, 1993). General climatic factors may contribute little to inter-island variability when compared to dune microenvironmental factors, such as incidence of salt spray, substrate mobility, and exposure (Barbour and Johnson, 1977).

Considerable topographic variability within barrier island morphologies and dune systems develops from geographic variation in local beach and dune sediment budgets and island orientation (Hosier, 1973; Godfrey, 1977; Psuty,1988; Ehrenfeld, 1990; Sherman and Bauer, 1993). Consequently, the purpose of my study is not to provide a template for all islands of a given morphology, but to examine the effects of disparate geomorphic settings on potentially similar species pools.

Methods

Field sampling

Five sites (A through E), each containing three strip transects, were parsed along the south to north axis of each island. Each transect was placed perpendicular to the tide line in order to capture the compositional variation along a gradient of exposure to oceanic inputs. At each site, the starting point for an initial transect was randomly positioned 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). Two more transect starting points were randomly positioned parallel to the first at a minimum of twenty meters distance. Each transect began at the high water mark, and extended inland through the width of dunal microhabitats (primary and secondary foredunes, overwash flats, interdunal flats, and wet swales) to the first occurrence of extensive thickets of the woody shrub species *Myrica cerifera*. *Myrica cerifera* invades herbaceous habitats as disturbance intensity and frequency are reduced (Young *et al.*, 1995).

Vegetation data were collected within a 1 x 2-m quadrat straddling the centerline of each transect. Within each quadrat, a 2-m point-frame sampler, also aligned perpendicular to the transect, was used to measure species presence at 10 cm intervals, for a total of 20 observations per paired quadrats. To maintain comparable sampling intensities between islands, the longer distances to stabilized vegetation on South Core Banks required that quadrats be systematically parsed in intervals of every other quadrat. In this manner, I expected to collect species cover and topographic data for approximately 75 quadrats along the transects of each island, and roughly 1000 quadrats per island. Point-frame hits in each quadrat were summed for individual species and expressed as percent absolute cover. The presence of a species off-transect but within the area confined by the perimeters of my transects was also recorded. These species and species complexes are referred to as ‘off-transect’ species. A total station was employed to survey elevation and distance relative to the mean high water mark for all quadrats. Plant identification and nomenclature follows Radford *et al.* (1968) and Duncan and Duncan (1987). Several genera were indistinguishable in the field and were lumped into species complexes. These complexes are composed of species that hybridize, or exhibit morphologic variation in diagnostic traits that are not readily discernible in the field. Voucher specimens were collected for each species and are available from the author upon request.

Data Analysis

Dune topography and species composition

For each of the fifteen transects per island, I calculated two topographic measurements, primary foredune height and dune habitat width. Primary foredunes are the fronting line of dunes. Where this fronting line of dunes was poorly developed, I used the maximum elevation within the first 10 meters landward of the high water mark as my dune height. To test for significant differences between islands in these topographic measurements, I used multiresponse permutation procedures (MRPP). MRPP is a non-parametric, distance-based test of group differences. The strategy of MRPP is to compare the average within-group distance with the average distance that would have resulted from all other possible combinations of the data. As such, MRPP tests for differences based on the collective distribution of data for each group rather than their respective means (Biondini *et al*., 1991). However, to simplify the underlying patterns contributing to group differences, I rely upon group means and standard deviations when applicable, as well as more detailed descriptions of the intra-group distributions. All MRRP tests were conducted at the 0.05 significance level in PC-ORD Version 4.04 (McCune and Mefford, 1999). To evaluate the inter-island differences in dune relief qualitatively, I constructed topographic cross-sections for a selected transect from each site.

To quantify the compositional differences between island morphologies, I first aggregated quadrat absolute cover values to their respective transect abundances. Each species occurring along a transect was classified according to life history (annual or perennial) and island affinity (shared or unique). For each transect, I summed percent absolute cover in these four compositional categories. MRPP was used to test for significant differences between islands in these compositional categories as well as transect-level percent bare ground and percent absolute cover for dominant taxa.

Transverse compositional gradients

I used non-metric multidimensional scaling (NMS) and hierarchical agglomerative clustering to plot species along the transverse environmental gradients for each island morphology. NMS 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. Distances between samples (quadrats) in their NMS ordination space optimally represent their similarities in variable (species) space (Kenkel and Orloci, 1986). Metric ordination techniques such as detrended correspondence analysis (DCA) may distort relationships among the data due to detrending and the rescaling of first axis scores (Minchin, 1987; Wartenberg, 1987). NMS has been shown to be superior to DCA as a means of recovering compositional community variation along environmental gradients, especially at high levels of species turnover (Kenkel and Orloci, 1986; Minchin 1987; Clarke, 1993).

In this first NMS ordination, my samples were the quadrats from each island, and the variables describing them were their respective species percent absolute cover values. Quadrats from both islands were pooled into one data set and relativized so that each quadrat had a total cover of 1. This sample relativization made observational units more equitable in species abundance (Gauch, 1984), and enhanced the capture of broad compositional similarities between groups of quadrats. No species were deleted since such deletions are unnecessary in NMS (Clarke and Warwick, 1994). Sorenson's distance was used to calculate sample similarities. Sorenson's coefficient gives less weight to outliers, and is the recommended distance coefficient for use in NMS analyses (Minchin, 1987; Clarke and Warwick, 1994; McCune and Mefford, 1999). In NMS, rotation of axes can be used to enhance interpretability (Legendre and Legendre, 1998; Clarke, 1993). I employed varimax rotation of my NMS quadrat scores in order to maximize the expression of compositional variability on the first and subsequent axes. I originally reasoned that this would align the shared compositional components of each island's transverse gradient along the first axis. All NMS ordinations were performed in PC-ORD Version 4.04 (McCune and Mefford, 1999).

In NMS, the final stress value is one of the criteria used to select an optimal solution. Minimizing stress can be achieved by increasing the number of dimensions, or axes, used to plot the sample units. A very high-dimension solution will have minimal stress, but will be difficult to interpret. When selecting a final solution, additional dimensions are considered useful only if they reduce the final stress by 5 units or more (on a scale of 1-100) (McCune and Mefford, 1999). An optimal NMS solution should be a parsiminous representation of distance and similarity within a final dimensionality that optimizes trend-seeking or pattern recognition (Dale, 1975; Kenkel and Orloci, 1986).

Hierarchical agglomerative clustering was used to classify the same relativized pooled quadrat data set. Hierarchical clustering starts with each quadrat in a separate cluster and, based on species cover, combines relatively homogeneous groups of quadrats into a user-specified number of clusters. Ward's Method and Euclidean squared distances were selected as the cluster method and the distance measure. Ward's method is recommended as a general-purpose group linkage-method (McCune and Mefford, 1999). Quadrats were grouped by their cluster membership, whereupon I calculated a cluster centroid based on the NMS axis scores for member quadrats. Hierarchical clustering was performed with SPSS Version 8.0.

To contrast the importance of transverse environmental gradients as correlates of species composition on each island, I calculated Spearman's rank correlation coefficients for quadrat NMS axis scores and their elevation and distances relative to the mean high water mark. I originally hypothesized that elevation and distance were likely to emerge as stronger correlates of vegetation pattern on South Core. Here, frequent overwash should impose a perpetual nonequilibrium state between vegetation and environment. At overwash-vulnerable positions, the inhibitory effects of frequent disturbance should restrict composition to species adapted to frequent burial. By contrast, at positions where overwash is less frequent, the inhibitory effects of overwash are reduced enough to allow more compositional adjustment, but still sufficiently frequent to constrain composition to a narrow range of species. Therefore, compositional contrasts at equivalent distances or elevations should be minimal. In this manner, disturbance is an environmental characteristic that maintains a spatially predictable assemblage of vegetation by constraining the species that can occur at a given elevation or distance relative to the high water mark (Bendix,1998; Harmon et al., 1983). On Sapelo, disturbed patches initiated by storms are infrequent and spatially restricted. In terms of vegetation dynamics theory, protection from disturbance allows compositional adjustment to site conditions. This permits expression of local competitive outcomes and a species-driven sorting along topographic and edaphic variables. In the absence of the inhibitory effects of frequent disturbance, compositional contrasts among sites at a given value of elevation or distance from mean high water should be strong.

Longitudinal compositional variability

I originally hypothesized that longitudinal compositional variability would be more evident 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 habitats that occur along transects. 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 along the length of the island. To assess longitudinal compositional variability, I employed NMS and analysis of similarity (ANOSIM). I used NMS to plot each site's cover data in species space so that their separating distances were qualitative measures of their compositional similarity. The average between-site distance for each island provides an estimate of the longitudinal compositional variability. This NMS was performed on a data set of the site-level absolute species cover for both islands. Because of the smaller size of this data set, it was feasible to perform multiple runs (n = 40) in order to lessen the likelihood of local minima. Local minima are non-optimal solutions to stress reduction that arise from the iteration of an initially arbitrary starting configuration of samples. The smaller data set also permitted Monte Carlo significance testing to determine if reductions in stress exceed those achieved by randomization of the data. No standardizations were employed, and final axis solutions were unrotated.

I used ANOSIM to examine in greater detail the compositional separation between islands and among the sites parsed along each island's longitudinal axis. ANOSIM is a non-parametric, distance-based test of group differences that employs ranked within-group and between-group measures of similarity. The test statistic, R, typically ranges from 0 to 1. R approaches 1 if all samples within groups are more similar to each other than any samples from different groups. R is approximately zero when the null hypothesis of no difference among groups cannot be rejected. In my first analysis, I compared my two island groups, each comprised of their 15 transect samples. The resulting R value indicates the degree of compositional similarity between islands. On the second level of analysis, longitudinal contrasts across islands were emphasized. Each island was tested separately, and groups were defined as the single sites (each with three transect samples). In this case, R values for each island indicate the degree of its longitudinal compositional variability.

For each ANOSIM, I used species absolute cover for individual transects as the within-group metric. Sorenson's distances were employed as measures of similarity. ANOSIM was performed in PRIMER 4.0 (Plymouth Marine Laboratory, 1997).

ANOSIM applies rank distances, as a means to assess group differences. MRPP assesses group differences based on distance measures of similarity alone. In this analysis, ANOSIM was employed to compare compositional groups because it retains sensitivity to the heterogeneity common in ecological data sets, and the results it provides are more similar in theory to NMS (McCune and Mefford, 1999).

Transverse compositional variability

Beta diversity, or species turnover, is a measure of species replacement along an environmental gradient (Whittaker, 1972). In this study, beta diversity measures the replacement of species in moving along the individual quadrats of a transect. Beta diversity expresses the degree to which habitats have been partitioned by species (Wilson and Shmida, 1984). To test for significant differences between islands in their species turnover, I employed MRPP as the analytical tool and transect-level beta diversity as the test metric. I calculated the Wilson-Shmida index (Bt) of beta diversity for all transects using quadrat-level species presence-absence data. I originally hypothesized significant differences between islands in their transect beta diversities. Infrequent overwash on Sapelo should lead to a finer scale partitioning of habitat and subsequently higher beta diversities in comparison to South Core.

Transverse zonation captures the range of distinctive quadrat compositions expressed along each transect. Whereas beta diversity measures species turnover along contiguous quadrats based on presence-absence data, transverse zonation collapses non-adjoining quadrats of similar species cover to convey the non-repeating range of compositions across a transect. To test for significant differences between islands in their along-island transverse zonation, I employed MRPP as the analytical tool and the standard deviations of the first NMS quadrat axis positions, grouped by transect, as my test metric. Individual transect standard deviations were calculated from the rotated axes scores of my quadrat-level NMS. High transect standard deviations indicate that quadrats span a broad range of compositions. This indicates that vegetation along these transects has more compositional zonation in the transverse direction. Low standard deviations among transects indicate a discrete clustering of quadrats along a narrow portion of the first axis. This suggests that each transect spans a relatively homogeneous patch or a repeating sequence of similar compositional types, with an overall lower zonation in the transverse direction. I originally hypothesized that Sapelo should have a larger standard deviation along the first axis of the island-level NMS. I reasoned that this would ensue from the greater along-island expression of local site factors in the absence of overwash, and the subsequent longitudinal repetition of transverse zonational units. By contrast, I reasoned that transects from North Carolina barrier islands should have smaller standard deviations for NMS axis position. Here, overwash is frequent, and individual transects were expected to track over homogeneous overwash patches, each of different age and a distinctive species assemblage.

Results

Dune topography

Cross-sections indicated strong departures in topography between and within my two study islands (Figures 2.5 and 2.6). On South Core, a simplified overwash topography was well-developed. These topographic profiles suggested that the loss of the fronting foredunes would perpetuate disturbance across the downsloping area in their lee. 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 (Figure 2.7). South Core cross-sections and field observations were in agreement with dune process-form morphologies proposed by Cleary and Hosier (1979). Their analysis linked dune physiography with cyclic patterns of overwash and recovery on the North Carolina barrier coast. At Site A, the large primary and secondary foredunes dampen 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. These dune morphologies suggested a time interval since the last overwash event of sufficient duration to permit the

Figure 2.5. Topographic cross-sections for representative transects from each site on South Core Banks, North Carolina. 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.

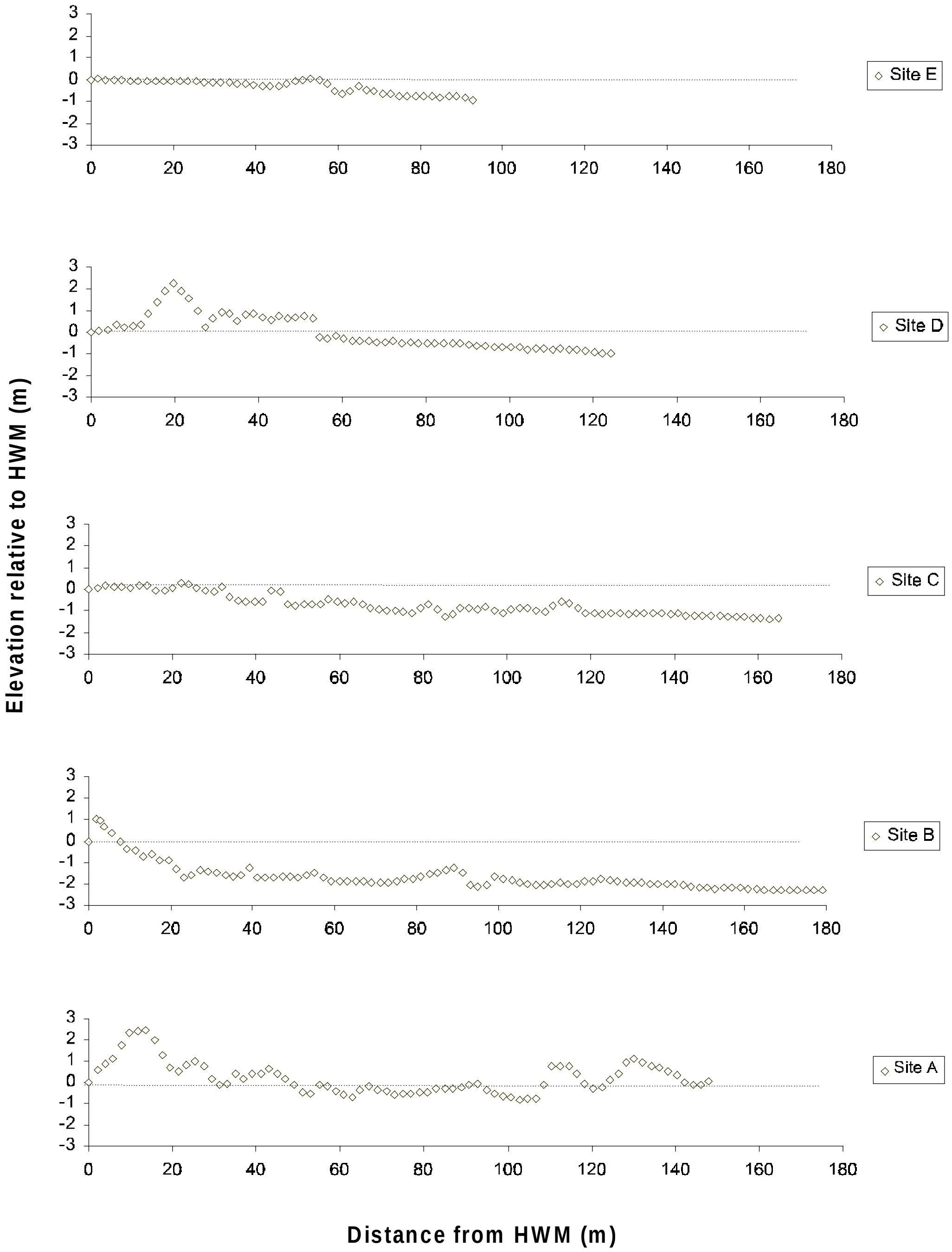

Site E
Site D
Site C
Site B
Site A
3
2
1
0
-1
-2
-3
0
20
40
60
80
100
120
140
160
180
Elevation relative to HWM (m)
Distance from HWM (m)

Figure 2.6. 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.

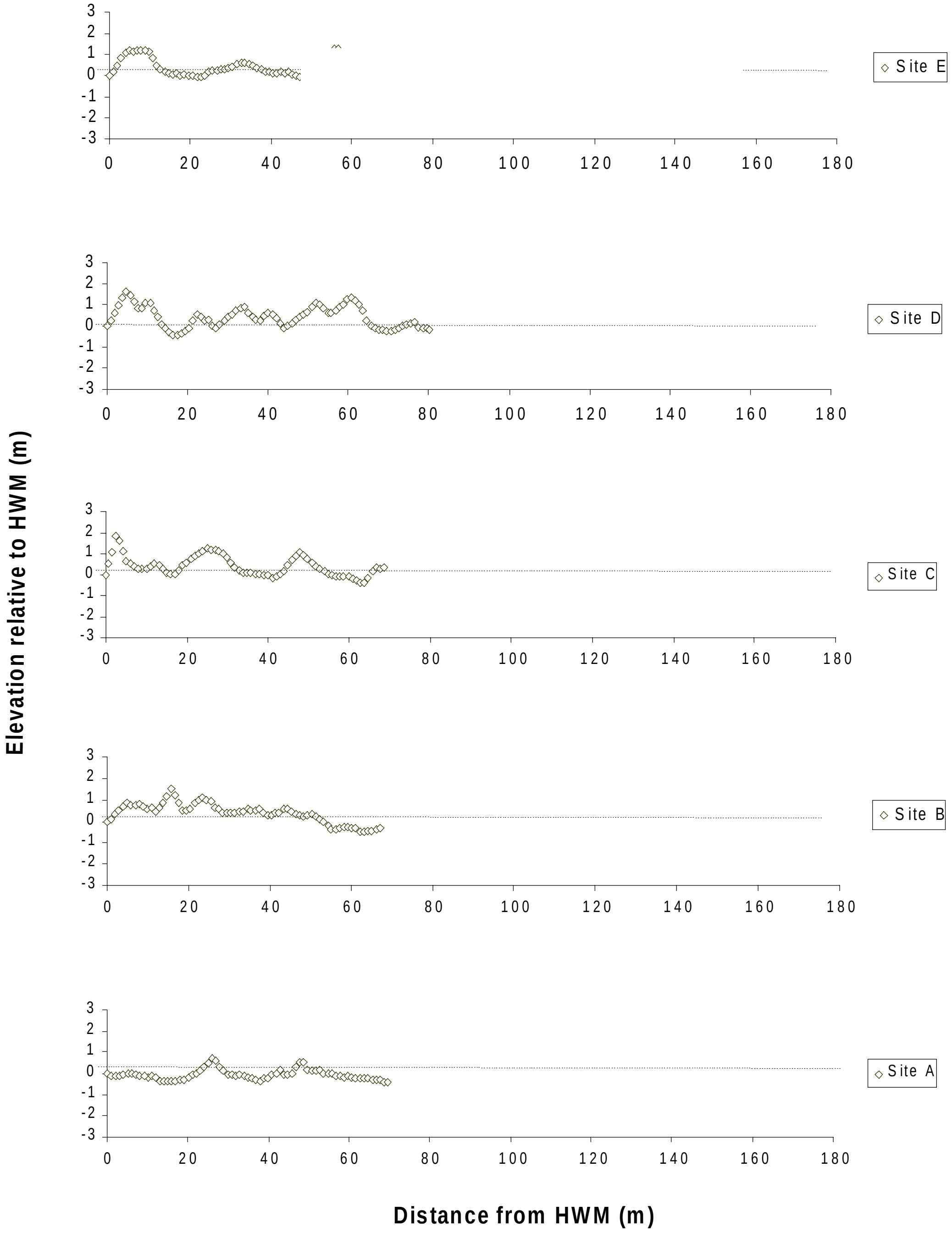
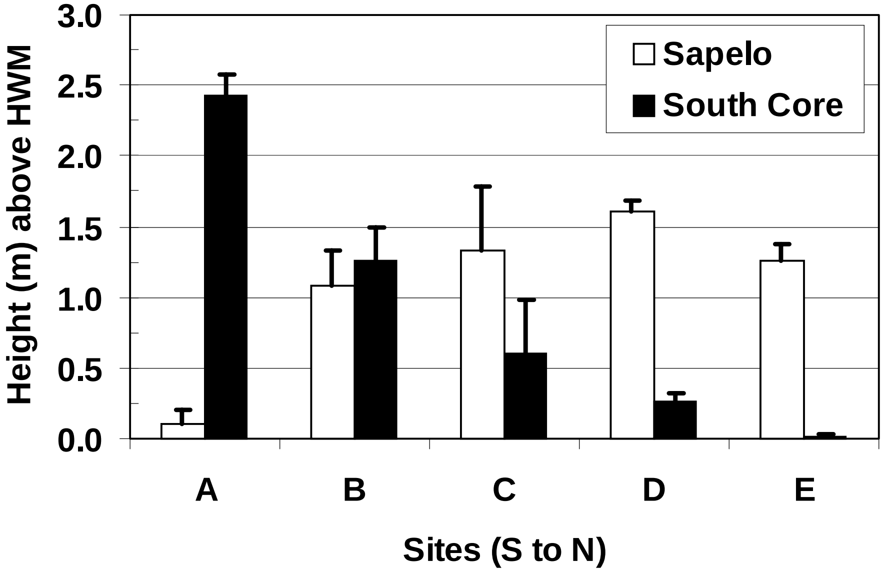

Elevation relative to HWM (m)
Distance from HWM (m)
Site E
Site D
Site C
Site B
Site A
3
2
1
0
-1
-2
-3
0
20
40
60
80
100
120
140
160
180

Figure 2.7. Mean transect primary foredune height by site for each study island. Error bars denote standard deviation (n = 3).


3.0
2.5
2.0
1.5
1.0
0.5
0.0
Height (m) above HWM
☐ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

reestablishment of the fronting dune ridge. The absent and scattered dunes at Site E on the north end of the island suggested recent or chronic overwash.

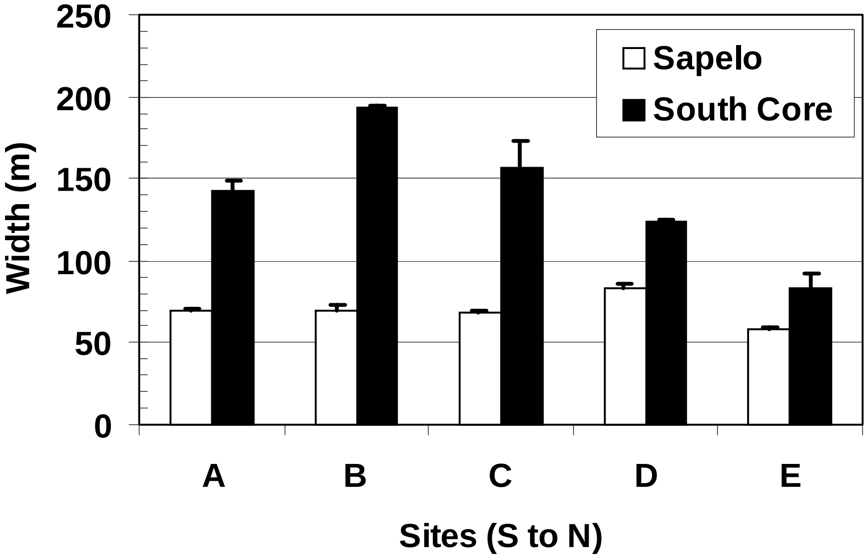
Dune morphology on Sapelo was more complex. Topography ranged from protective parallel dune ridges and swales to a more exposed, flat, hummocky terrain. Mean transect primary foredune height varied from 1.6 ± 0.01 m relative to mean high water at Site D, to the absence of a primary foredune at Site A. At the southernmost Site A, a low hummocky terrain developed from the accretional conditions at the southern terminus of the island (Welch *et al*., 1992). Here, rapid accretion engenders a seaward progradation of the shoreline, and maintains a low topography of distantly spaced incipient dune ridges that are frequently overwashed. In comparison to South Core, these profiles suggested a higher degree of morphologic resistance to overwash, with a weaker tendency to perpetuate overwash across the landscape. Although they suggested erosional conditions, the scarped dune profiles at sites B through D would also act as a barrier shielding the back barrier dune environment from overwash and other maritime inputs.

A striking difference developed between islands in the position of the dune habitats relative to the high water mark datum. On South Core, 78% of the sampled quadrats were located below the high water mark, comprising 85% of the total absolute species cover. In contrast, the majority of the vegetation is positioned above the high water mark on Sapelo. Here, 70% of the total quadrats were above this datum, comprising 62% of the total absolute species cover. Dune habitat widths also diverged between islands (Figure 2.8). Mean dune habitat width on Sapelo (70 ± 8 m) was roughly half of South Core (140 ± 38 m). MRPP of topographic variables confirmed that dune habitat width was significantly different between islands ($T = -13.60$, $p < 0.01$; [Appendix 2.1]). Dune habitat widths averaged 70 ± 8 m on Sapelo, and 140 ± 38 m on South Core. The two islands showed no significant differences in transect primary foredune heights ($T = -0.97$, $p = 0.14$).

Species composition

Differences between islands in their total quadrat sampling intensities were non-significant (Sap = 1082, Core = 1139; $T = -0.08$, $p = 0.33$ [Appendix 2.2]). Based on quadrat cover data

Figure 2.8. Mean dune habitat width by site for each study island. Error bars denote standard deviation (n = 3).


250
200
150
100
50
0
Width (m)
☐ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

aggregated to the transect-level (n = 15), my study islands were significantly different in their percent bare ground (T = -5.08, p < 0.001) (Figure 2.9; [Appendix 2.3]).

Including off-transect species, 43 species out of a total 120 were shared by both islands (Appendix 2.4). Sapelo had a total of 35 shared species on-transect, while South Core had 36. These on-transect shared species comprised 50% of total percent absolute cover on Sapelo, and 56% on South Core (Figure 2.10). MRPP revealed no significant differences between islands in their transect-level cover for all shared species; however, there were numerous significant differences for individual species (Figure 2.11). Sapelo had a significantly higher absolute cover of the woody species *Myrica cerifera* (7%) (T = -3.47, p = 0.01) and a low cover of *Spartina patens* (< 1%) (T = -14.26, p < 0.001). This relationship was reversed on South Core (*M. cerifera* = 1%; *S. patens* = 15%). The most abundant and consistent species cover for both islands was *Uniola paniculata,* the common foredune species of the southeastern United States. Its total cover was significantly higher on South Core (Sap = 9%, C = 17%) (T = -6.83, p < 0.001). Other significant differences in island composition among shared species reflected the greater areal extent of wet swales on Sapelo, where the herbaceous species *Muhlenbergia filipes, Phyla nodiflora, Andropogon* spp., *Fimbristylis* spp. attained a higher cover. On South Core, frequent and extensive burial from overwash favored the increased abundance of *Hydrocotyle bonariensis,* which commonly co-occurred with *Spartina patens* under these conditions.

The number of unique species, including off-transect species, was higher on Sapelo (S = 45, C = 32). However, both islands shared a similar number of unique on-transect species (S = 29, C = 28). MRPP revealed significant differences between islands in their transect-level cover for unique species (T = -7.64, p < 0.001). These unique species comprised more of the total percent absolute cover on South Core (S = 2%, C = 15% [Appendices 2.5 and 2.6]). Important unique species on South Core included *Ditrichum pallidium, Solidago spp., Ammophila brevigulata,* and *Strophostyles helvola*. *Ditrichum pallidium* is a bryophyte that formed a dense ground cover on protected dune aspects and on interdune flats on South Core (Godfrey and Godfrey, 1976). The perennial *Solidago* spp. is a gap colonizer (Lee, 1993) that occurred mainly on older overwash flats on the southern end of South Core. *Ammophila brevigulata* is a rhizomatous perennial whose southernmost occurrence is in North Carolina (Duncan and Duncan, 1987). *Strophostyles helvola*

Figure 2.9. Percent bare ground by site.

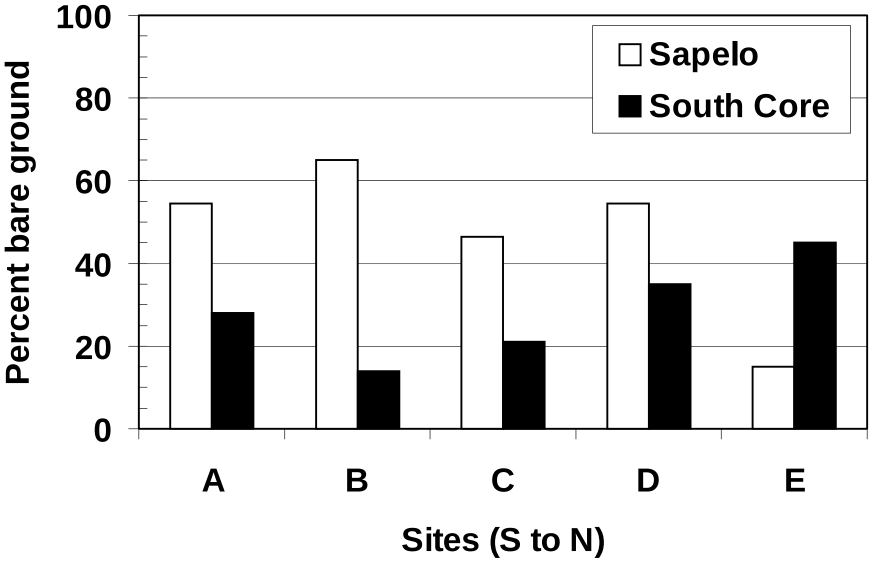
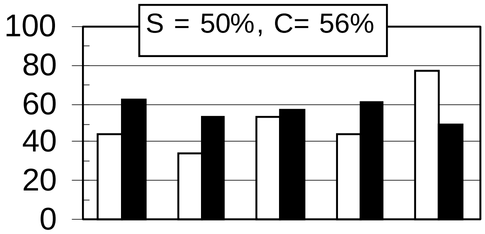
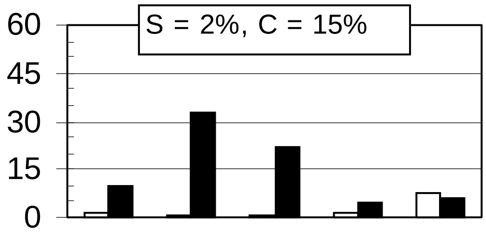

100
80
60
40
20
0
Percent bare ground
☐ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

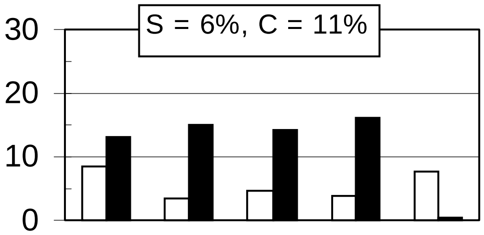
Figure 2.10. Percent absolute cover for life history and island affinity compositional categories by site. Light-shaded bars indicate cover percentages for Sapelo, dark-shaded bars represent South Core Banks. Numbers in text boxes indicate total island percent absolute cover by category. (Note: * = MRPP significantly different at p < .05).



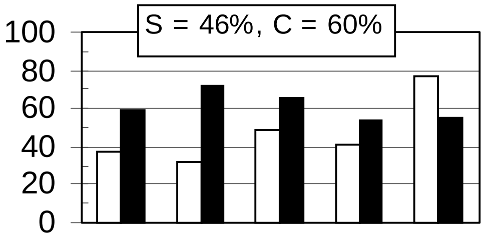
Cover shared spp.



Cover unique spp.*

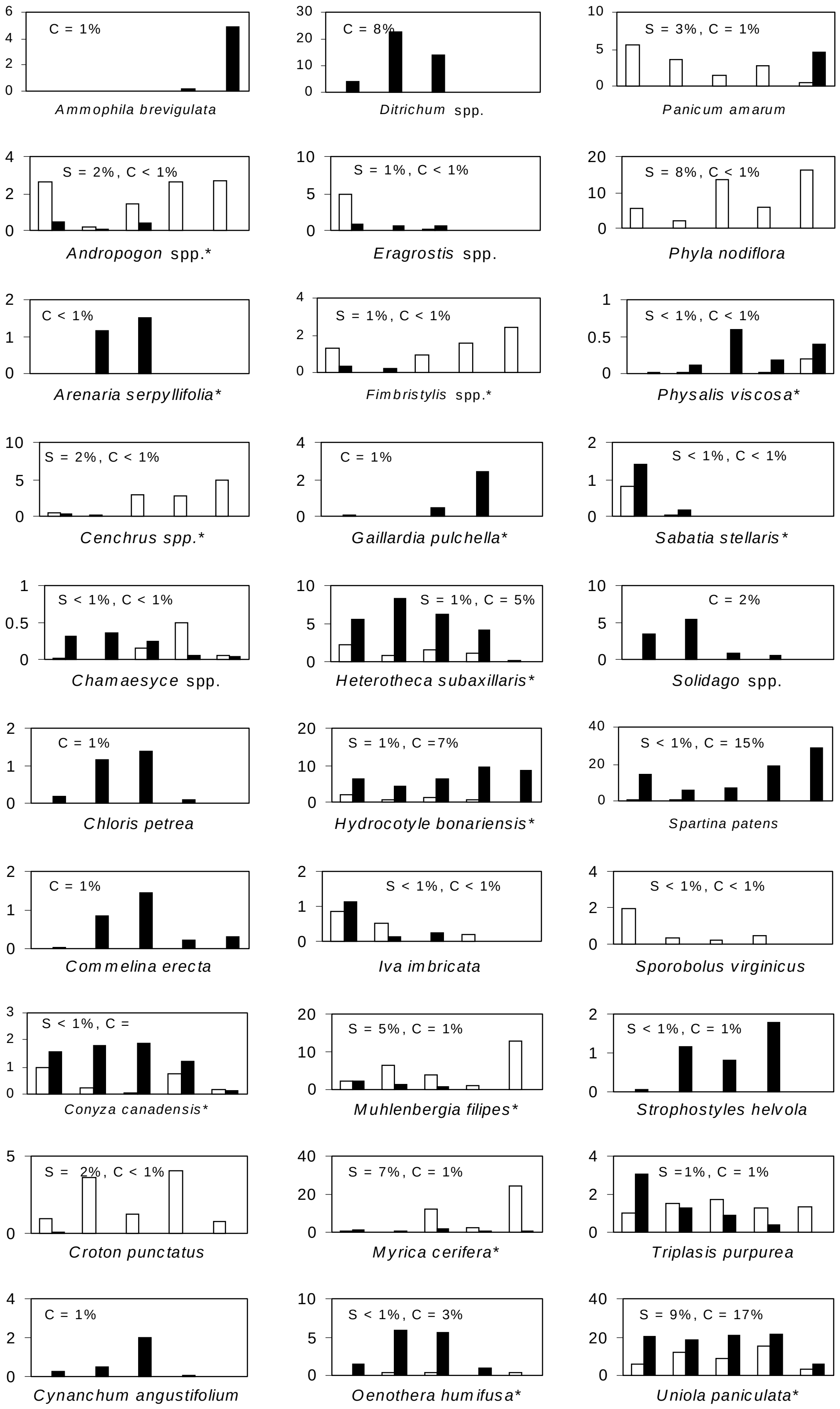


Cover annuals*



Cover perennials*

Figure 2.11. Percent absolute cover for dominant shared and unique-island species by site. Light-shaded bars indicate Sapelo percent cover and dark-shaded bars indicate South Core Banks percent cover. Numbers indicate total island percent absolute cover. (Note: * = MRPP significantly different at $p < .05$).


0 2 4 6
C = 1%
Ammophila brevigulata
0 10 20 30
C = 8%
Ditrichum spp.
0 5 10
S = 3%, C = 1%
Panicum amarum
0 2 4
S = 2%, C < 1%
Andropogon spp.*
0 5 10
S = 1%, C < 1%
Eragrostis spp.
0 10 20
S = 8%, C < 1%
Phyla nodiflora
0 1 2
C < 1%
Arenaria serpyllifolia*
0 2 4
S = 1%, C < 1%
Fimbristylis spp.*
0 0.5 1
S < 1%, C < 1%
Physalis viscosa*
0 5 10
S = 2%, C < 1%
Cenchrus spp.*
0 2 4
C = 1%
Gaillardia pulchella*
0 1 2
S < 1%, C < 1%
Sabatia stellaris*
0 0.5 1
S < 1%, C < 1%
Chamaesyce spp.
0 5 10
S = 1%, C = 5%
Heterotheca subaxillaris*
0 5 10
C = 2%
Solidago spp.
0 1 2
C = 1%
Chloris petrea
0 10 20
S = 1%, C =7%
Hydrocotyle bonariensis*
0 20 40
S < 1%, C = 15%
Spartina patens
0 1 2
C = 1%
Commelina erecta
0 1 2
S < 1%, C < 1%
Iva imbricata
0 2 4
S < 1%, C < 1%
Sporobolus virginicus
0 1 2 3
S < 1%, C =
Conyza canadensis*
0 10 20
S = 5%, C = 1%
Muhlenbergia filipes*
0 1 2
S < 1%, C = 1%
Strophostyles helvola
0 5
S = 2%, C < 1%
Croton punctatus
0 20 40
S = 7%, C = 1%
Myrica cerifera*
0 2 4
S =1%, C = 1%
Triplasis purpurea
0 2 4
C = 1%
Cynanchum angustifolium
0 5 10
S < 1%, C = 3%
Oenothera humifusa*
0 20 40
S = 9%, C = 17%
Uniola paniculata*

is a common trailing legume that increases in abundance on dunes in the early stage of stability (Oosting, 1945). Sapelo had more unique species, but many of these were isolated individuals that did not contribute sizeably to total species cover. The most abundant unique species on Sapelo included *Phyla nodiflora*, a decumbent perennial abundant in the sandy soils of open wet swales.

Sapelo and South Core were significantly different in their percent absolute cover of perennial species (T = -5.07, p < 0.01). South Core had a higher percent absolute cover of perennials (S = 46%, C = 60%), the most abundant life history category on both islands. Annuals also showed a significant difference between islands (T = -7.45, p < 0.001). South Core had a higher percent absolute cover of annual species (S = 6%, C = 11%).

There were strong differences between islands in their within-island distributions of species cover based on compositional categories of life history and island affinity. Unique species cover differed markedly. Site E had the highest site cover of unique species on Sapelo. On South Core, the cover of unique species showed a dramatic peak mid-island at Sites B and C. Within-island distributions of annual cover also differed markedly between islands, and were similar to those observed for unique species. Sites A and E, the two sites adjacent to tidal inlets on Sapelo, had the highest island cover of annual species. On South Core, the cover of annual species had a very pronounced peak at mid-island sites B and C.

Each island expressed distinctive within-island distributions of individual species in response to the local geomorphic setting. On Site A of Sapelo, low dunes and frequent overwash encouraged the establishment of species tolerant of burial and sediment mobility (*Panicum amarum*, *Sporobolus virginicus, Iva imbricata*). Here, shoreline accretion fostered a chronosequence in which low fronting dunes graded into wet swales. Several wet swale species peaked in cover here *(Sabatia stellaris, Rumex hastalus, Juncus marginatus, Juncus megacephalus*). The shared annual *Strophostyles helvola* had one occurrence on Sapelo, as an off-transect individual at Site A. This species was very abundant on South Core. At Sites B and D on Sapelo, wet swale species decreased in abundance. Vegetation was sparse, especially along broad interdunal flats that characterized these sites. *Croton punctatus,* a dune perennial abundant only on Sapelo, had peaks in cover at each of these sites. At sites C and E, mature dune ridges and swales were well-expressed, and *Myrica cerifera, Andropogon* spp. and *Phyla nodiflora* increased in abundance. Additionally, local erosion at Site E has juxtaposed dunal habitats with inland soils and vegetation. Several inland-ranging ruderal species peaked in cover at Site E (*Cnidoscolus stimulosus, Cenchrus* spp., *Opuntia pusilla, Cyperus* spp., *Paspalum* spp., *Eupatorium* spp., *and Stenotaphrum* spp.).

The distribution of individual species on South Core was also regulated by contrasting geomorphic processes and topography among sites. *Spartina patens* and *Hydrocotyle bonariensis* increased in abundance in parallel with increasing overwash disturbance from south to north. At Site A, increased topographic complexity enhanced the coexistence of dune species (including *Iva imbricata*) and wet swale species (*Sabatia stellaris, Juncus marginatus, Juncus roemerianus*). In general, wet swales on South Core supported assemblages of species associated with more brackish conditions (*Juncus roemerianus*, *Spartina patens*). *Phyla nodiflora* was an abundant shared species on Sapelo, but was restricted to a single individual on South Core at Site A. At Sites B and C, the perennial *Solidago* spp. and the bryophyte *Ditrichum pallidium* attained their highest covers, as well as the annuals forbs *Arenaria serpyllifolia* and *Conyza canadensis*, and the perennials *Chloris petrea* and *Commelina erecta.* At Sites D and E, *Solidago* spp. declined in cover, and *Spartina patens* and *Hydrocotyle bonariensis* formed the dense maritime grassland that characterized this site. Two species had localized peaks at Site D on South Core, *Strophostyles helvola* and *Gaillardia pulchella*. *Ammophila brevigulata* and *Panicum amarum*, dune grasses well-adapted to burial, peaked in cover at the recently overwashed sites D and E on South Core. The dune grass *Uniola paniculata* was less abundant at Site E on South Core, where disturbance was too frequent to favor this dune-forming perennial.

Hierarchical clustering

My hierarchical cluster solution identified sixteen species groupings (Table 2.1). I ran an additional hierarchical cluster analysis on one of these groups which was particularly heterogeneous in order to refine its membership. The refinement delineated five additional species clusters. Species clusters may be broadly associated with four habitat categories. The first habitat category was composed of taxa that were frequent in overwashed and geomorphically unstable areas (*Ammophila brevigulata, Panicum amarum, Spartina patens, Sporobolus virginicus,*

Table 2.1. Species clusters and quadrat membership.

Habitat category	Cluster ID	Cluster description	Number of quadrats	
			Sapelo	South Core
Disturbance	AMMO-PAN	*Ammophila brevigulata* and *Panicum amarum*	0	15
		Sand-binding species adapted to burial		
	CENC	*Cenchrus* spp.	47	0
		Unstable, sparsely vegetated interdunal flats		
	SPARP-HYDB	*Spartina patens* and *Hydrocotyle bonariensis*	6	205
		Areas of recent or active overwash		
	SPARP	*Spartina patens*	23	39
		Areas of recent or active overwash		
	SPOR	*Sporobolus virginicus*	22	0
		Sand-binding species adapted to rapid burial.		
	PAN	*Panicum amarum*	63	21
		Sand-binding species adapted to rapid burial.		
Dune	CROTP	*Croton punctatus*	64	0
		Dry swales, hummocky dunes, interdunal flats		
	UNI	*Uniola paniculata*	69	114
		Highly exposed, steep foredunes.		
	UNI-HET	*Uniola paniculata* and *Heterotheca subaxillaris*	170	251
		Stable dunes		
	UNI-TRIP	*Uniola paniculata* and *Triplasis purpurea*	104	38
		Unstable dunal flats.		
	HYDB-UNI	*Hydrocotyle bonariensis* and *Uniola paniculata*	15	53
		Less-exposed dunes		
	HET	*Heterotheca subaxillaris*	16	42
		Stabilized dunes, overwash flats, interdunal flats		
Transitional	AND	*Andropogon* spp.	33	1
		Low areas in interdunal flats, wet swales.		
	DITR	*Ditrichum pallidium*	1	120

		Bryophyte common on sandy, stabilized surfaces		
	ERG	*Eragrostis* spp.	23	3
		Sandy wet swales.		
	OEN	*Oenothera humifusa*	3	39
		Stabilized dunes and overwash flats.		
	SOLD	*Solidago* spp.	0	11
		Inactive overwash areas		
Stabilized	PHYLA	*Phyla nodiflora*	251	1
		Perennial ground cover at protected sites.		
	MYR	*Myrica cerifera*	65	2
		Woody shrub. Protected sites and wet swales		
	MUHL	*Muhlenbergia filipes* and *Myrica cerifera*	52	2
		Protected sites, wet swales		
		Total quadrats	1027	957

Cenchrus spp., and *Hydrocotyle bonariensis*). A second category, consisting of dune species (*Croton punctatus, Uniola paniculata, Heterotheca subaxillaris, Hydrocotyle bonariensis*), was also abundant where substrates were unstable. These species exhibit a weaker tendency to invade gaps immediately after disturbance. *Hydrocotyle bonariensis* exhibits a high degree of phenotypic plasticity that permits it to be maintained under a variety of environmental conditions (Costa *et al*., 1996). The third compositional category consisted of species from transitional habitats. These species were perennials that had no direct role in dune-forming processes (*Andropogon* spp., *Ditrichum pallidium*, *Eragrostis* spp., *Oenothera humifusa*, and *Solidago* spp.). My fourth category of species clusters differed from the transitional taxa in that they were well-established, often forming a dense and persistent ground cover or canopy that would inhibit the establishment of other species. These stabilized species (*Phyla nodiflora*, *Muhlenbergia filipes*, and *Myrica cerifera*) were abundant on Sapelo. The bryophyte *Ditrichum pallidium* was classified as transitional rather than stabilized because it was frequently associated with other species in this category. Mosses are important sediment stabilizers in temperate dunes (Birse *et al.*, 1957; Martínez and Maun, 1999)

Quadrat counts for species clusters in each of these four habitat categories varied considerably between study islands. *Panicum amarum* was the most abundant species cluster in the disturbance category for Sapelo. *Cenchrus* spp., a wide-ranging perennial, was also abundant on the unstable, sparsely vegetated interdunal flats on Sapelo. In contrast, *Spartina patens*/*Hydrocotyle bonariensis* was the dominant disturbance species cluster on South Core. The most abundant species cluster on both islands in the dune category, which encompassed primary and secondary foredunes, was *Uniola paniculata*/*Heterotheca subaxillaris*. For South Core, *Ditrichum pallidium* was the most abundant transitional species. This bryophyte was absent on *Sapelo,* where *Andropogon* spp. was the most abundant species cluster in the transitional category. On Sapelo, *Phyla nodiflora* was the dominant species in stabilized habitats. Stabilized species were weakly represented in the cluster analysis for South Core, given their overall lower abundance.

Transverse compositional gradients

Three runs with random starting configurations were performed in my pooled quadrat NMS. In each, a similar sequence of stress reduction was generated, thus decreasing the likelihood of a suboptimal local minima. Reductions in stress after three dimensions were less than 5 units, signaling that a three-dimensional solution was optimal. The high final stress value (18.4) was expected, given the large number of vegetated quadrats (S = 1027, C = 957) and species (93).

NMS plots of cluster centroids indicated that each barrier island morphology had a distinctive compositional structure that developed in response to island environmental conditions (Figure 2.12). Two distinct axes of compositional variation were evident on Sapelo. 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. Spearman's rank order correlation coefficients (r_s) for Axis 1 quadrat scores were significant but weak for elevation ($r_s = -0.173$, $p < 0.01$) and distance ($r_s = -0.103$, $p < 0.01$) relative to the high water mark (Table 2.2). The species clusters that formed the prominent compositional gradient along Axis 2 on Sapelo outlined the zoned sequence of strandline-to-inland vegetation typically associated along coastal transverse environmental gradients. On this second axis, species were more responsive to sorting along elevational ($r_s = -0.45$, $p < 0.01$) and distance ($r_s = 0.23$, $p < 0.01$) gradients. By contrast, South Core Banks exhibited one prominent vegetation gradient that ran diagonally across both axes. Axis 1 correlations for elevation ($r_s = -0.34$, $p < 0.01$) and distance ($r_s = 0.390$, $p < 0.01$) were stronger compared to those on Sapelo for this stability gradient. Axis 2 correlations increased in strength relative to Axis 1, as was observed on Sapelo. However, the influence of elevation on Axis 2 was comparable ($r_s = -0.41$, $p < 0.01$) to Sapelo. Distance was the stronger correlate for South Core on this axis ($r_s = 0.46$, $p < 0.01$). Three broad zones of species were associated with Axis 2 on both islands: a *Uniola paniculata*-dominated foredune zone, a transitional mid-island zone, and a rear assemblage of disturbance (South Core) or stabilized species (Sapelo).

Scale variation in Spearman's correlation coefficients diverged markedly between islands. At the site and transect-levels of analysis, quadrat compositions and their elevation and distance from the high water mark were stronger and more consistently distributed on South Core. These

Figure 2.12. Non-metric multidimensional scaling of species clusters.

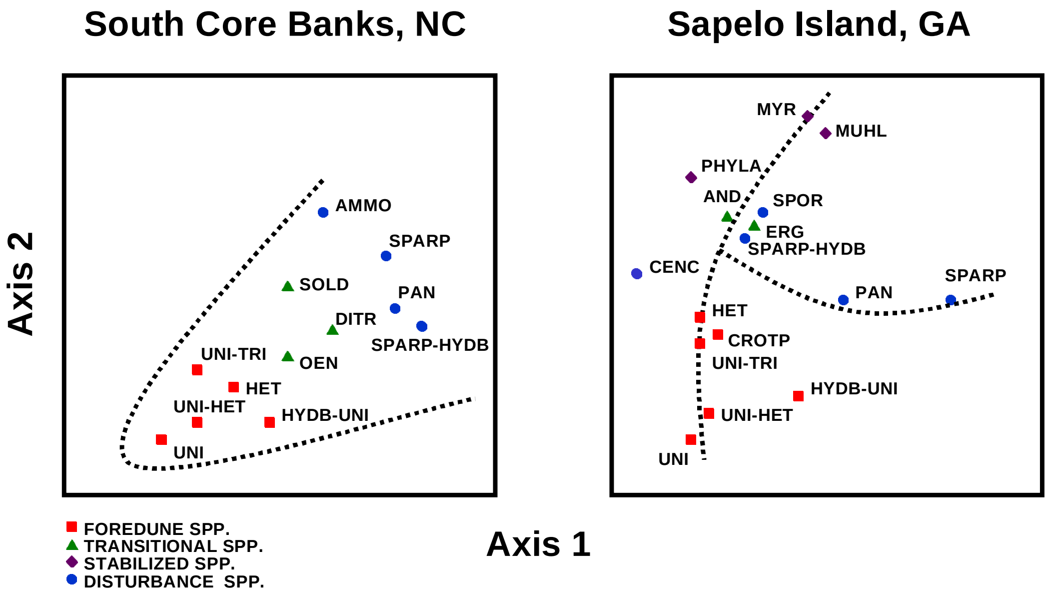

South Core Banks, NC
Sapelo Island, GA
Axis 2
Axis 1
AMMO
SPARP
SOLD
PAN
DITR
SPARP-HYDB
UNI-TRI
OEN
HET
UNI-HET
HYDB-UNI
UNI
MYR
MUHL
PHYLA
AND
SPOR
ERG
SPARP-HYDB
CENC
PAN
SPARP
HET
CROTP
UNI-TRI
HYDB-UNI
UNI-HET
UNI
■ FOREDUNE SPP.
▲ TRANSITIONAL SPP.
◆ STABILIZED SPP.
● DISTURBANCE SPP.

Table 2.2. Spearman's correlation coefficients for species cover with elevation and distance relative to the high water mark. (Bold-faced coefficients significantly different $p < 0.05$)

	Sapelo						South Core				
	AXIS 1		AXIS 2				AXIS 1		AXIS 2		
	ELEV	DIST	ELEV	DIST	ELEV-DIST		ELEV	DIST	ELEV	DIST	ELEV-DIST
Transect											
SAT1	**-0.27**	0.17	**-0.76**	**0.42**	**-0.37**	CAT1	**-0.70**	**0.30**	**-0.73**	**0.52**	**-0.25**
SAT2	**0.31**	-0.21	**-0.62**	**0.33**	**-0.26**	CAT2	**-0.74**	**0.30**	**-0.86**	**0.50**	**-0.33**
SAT3	-0.03	-0.22	**-0.64**	0.09	-0.10	CAT3	**-0.68**	**0.38**	**-0.77**	**0.63**	**-0.69**
SBT1	**0.27**	**-0.44**	**-0.43**	0.14	**-0.44**	CBT1	**-0.76**	**0.69**	**-0.81**	**0.71**	**-0.91**
SBT2	-0.16	0.09	**-0.59**	**0.56**	**-0.71**	CBT2	**-0.75**	**0.61**	**-0.69**	**0.53**	**-0.87**
SBT3	**-0.39**	**0.46**	**-0.73**	**0.64**	**-0.84**	CBT3	**-0.66**	**0.55**	**-0.65**	**0.50**	**-0.92**
SCT1	-0.16	-0.07	-0.19	-0.15	-0.01	CCT1	**-0.86**	**0.81**	**-0.81**	**0.82**	**-0.92**
SCT2	**-0.46**	-0.13	**-0.67**	**0.27**	0.17	CCT2	**-0.76**	**0.66**	**-0.76**	**0.65**	**-0.93**
SCT3	**-0.43**	-0.06	**-0.74**	**0.57**	**-0.52**	CCT3	**-0.73**	**0.65**	**-0.67**	**0.65**	**-0.82**
SDT1	**0.35**	**-0.63**	-0.06	**0.52**	**-0.25**	CDT1	**-0.75**	**0.76**	**-0.70**	**0.70**	**-0.98**
SDT2	0.10	**-0.24**	**-0.28**	**0.46**	**-0.42**	CDT2	**-0.71**	**0.75**	**-0.84**	**0.86**	**-0.97**
SDT3	**0.47**	**-0.40**	**-0.40**	**0.52**	-0.17	CDT3	**-0.55**	**0.67**	**-0.81**	**0.90**	**-0.89**
SET1	**-0.28**	0.22	-0.22	0.22	-0.15	CET1	**-0.38**	**0.33**	-0.16	0.05	**-0.44**
SET2	**-0.56**	**0.37**	**-0.60**	**0.43**	**-0.71**	CET2	-0.04	**0.31**	**-0.29**	0.01	**-0.62**
SET3	**-0.60**	0.18	**-0.63**	-0.05	**-0.27**	CET3	**-0.35**	0.24	-0.04	-0.04	**-0.90**
Site											
SA	0.02	-0.12	**-0.62**	**0.28**	**-0.21**	CA	**-0.66**	**0.30**	**-0.76**	**0.53**	**-0.45**
SB	-0.07	0.01	**-0.57**	**0.44**	**-0.62**	CB	**-0.64**	**0.61**	**-0.65**	**0.57**	**-0.82**
SC	**-0.39**	-0.09	**-0.47**	**0.24**	-0.12	CC	**-0.64**	**0.74**	**-0.61**	**0.73**	**-0.76**
SD	**0.30**	**-0.42**	**-0.27**	**0.50**	**-0.29**	CD	**-0.70**	**0.77**	**-0.76**	**0.82**	**-0.91**
SE	**-0.52**	**0.24**	**-0.54**	**0.20**	**-0.33**	CE	**-0.31**	**0.34**	**-0.19**	0.05	**-0.73**
Island											
Sapelo	**-0.17**	**-0.10**	**-0.45**	**0.23**	**-0.29**	S0. Core	**-0.34**	**0.39**	**-0.41**	**0.46**	**-0.63**

correlations were weaker and less consistent on Sapelo, with no pronounced longitudinal trend at either level of analysis.

Longitudinal compositional variability

A two-dimensional final solution was selected for my site-level NMS (final stress = 1.575). Monte Carlo randomizations (n = 40) indicated a significant reduction in stress ($p = 0.02$) for this dimensionality. The separation of island groups in the NMS plot indicated a strong departure between islands in composition (Figure 2.13). Analysis of similarity between islands corroborated this separation ($R = 0.82$, $p < 0.01$). Analyses of similarity within each island indicated no strong comparative departures in site longitudinal compositional variability. Sapelo had only a slightly higher R value ($R = 0.88$, $p < 0.01$) than South Core ($R = 0.86$, $p < 0.01$). The site-level NMS plot also confirmed that Sapelo had only slightly more longitudinal compositional variability. Average NMS relative distance between any two sites for Sapelo was 0.83 in comparison to 0.78 for South Core. However, this near equivalence in longitudinal compositional variability does not take into account the geographic extent of dune habitats on each island. As such, Sapelo has a greater longitudinal compositional variability given this island's smaller geographic extent of dune habitats.

Transverse compositional variability

MRPP revealed significant differences between islands for each of my two measures of transverse compositional variability. The Wilson-Shmida index of beta diversity was significantly different between islands ($T = -3.08$, $p = 0.02$ [Appendix 2.7]). In agreement with my initial hypothesis for species turnover, mean transect beta diversity was higher on Sapelo (Sap Bt = 7.1 ± 1.4; Core Bt = 5.6 ± 1.5 [Figure 2.14]). The distinctive compositional gradients evident in my NMS plots of species clusters suggested that the second axis, rather than the first, represented the prominent sequence of the transverse strandline-to-inland compositional variability I sought to measure. Therefore, I conducted an additional MRPP test using my second axis standard deviations as the test metric. Sapelo exhibited significantly higher standard deviations on the second axis, thus indicating a greater along-island transverse zonation ($T = -14.88$ $p < 0.001$ [Fig.

Figure 2.13. NMS plot of site-level species cover. S = Sapelo and C = S. Core Banks. Individual sites are designated by the letters A through E, with Site A the southernmost study site on an island, and site E the northernmost.

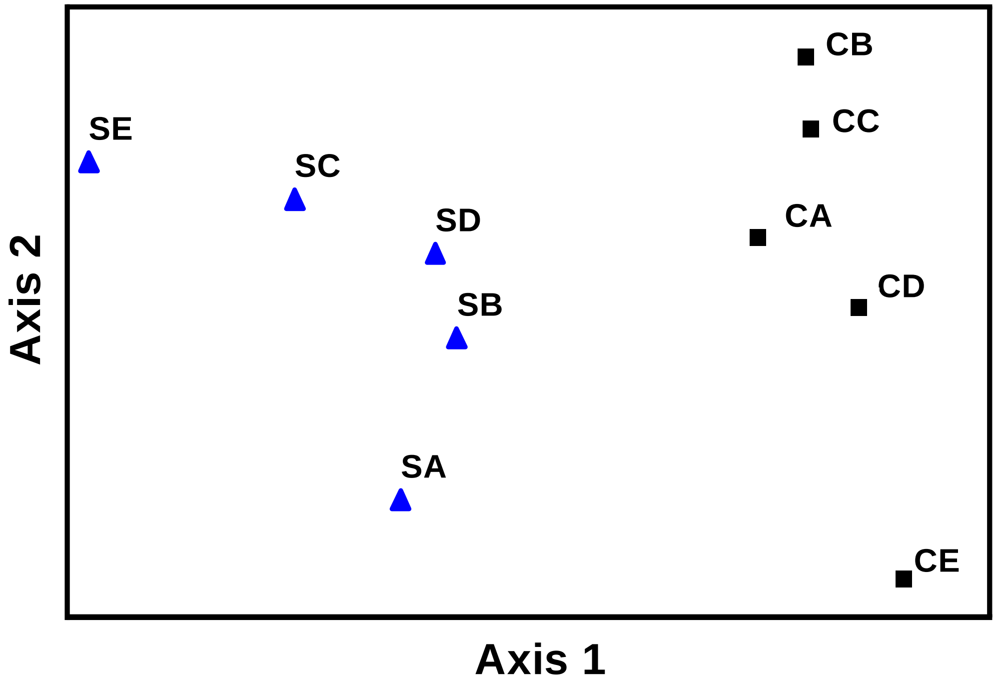
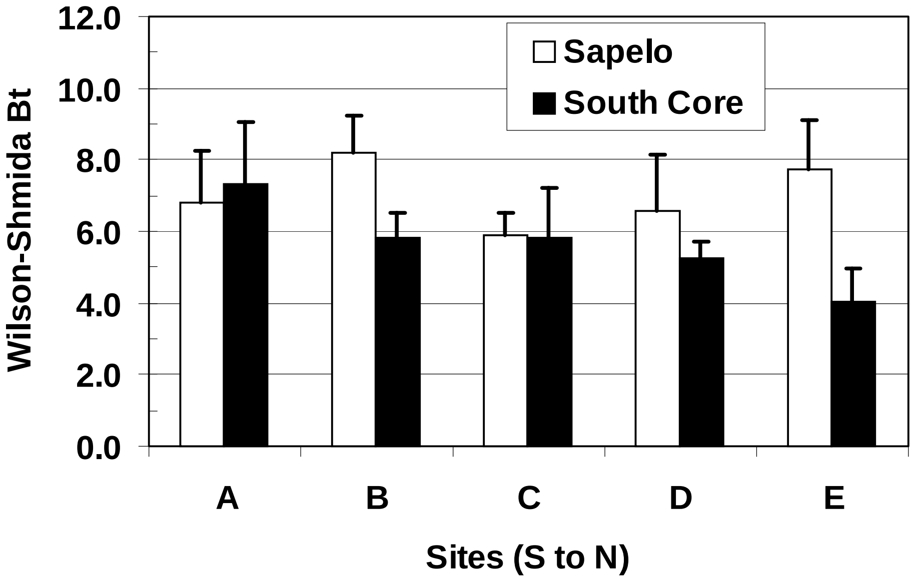

CB
CC
SE
SC
SD
CA
CD
SB
SA
CE
Axis 2
Axis 1

Figure 2.14. Mean transect beta diversity by site for each island. Error bars denote standard deviation (n = 3).


12.0
10.0
8.0
6.0
4.0
2.0
0.0
Wilson-Shmida Bt
☐ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

2.15; Appendix 2.7]). For the first axis, which represented the stability gradient along which disturbance species sorted, South Core exhibited significantly higher transect standard deviations (T = -9.69, p < 0.001 [Fig. 2.15; Appendix 2.6]).

Discussion

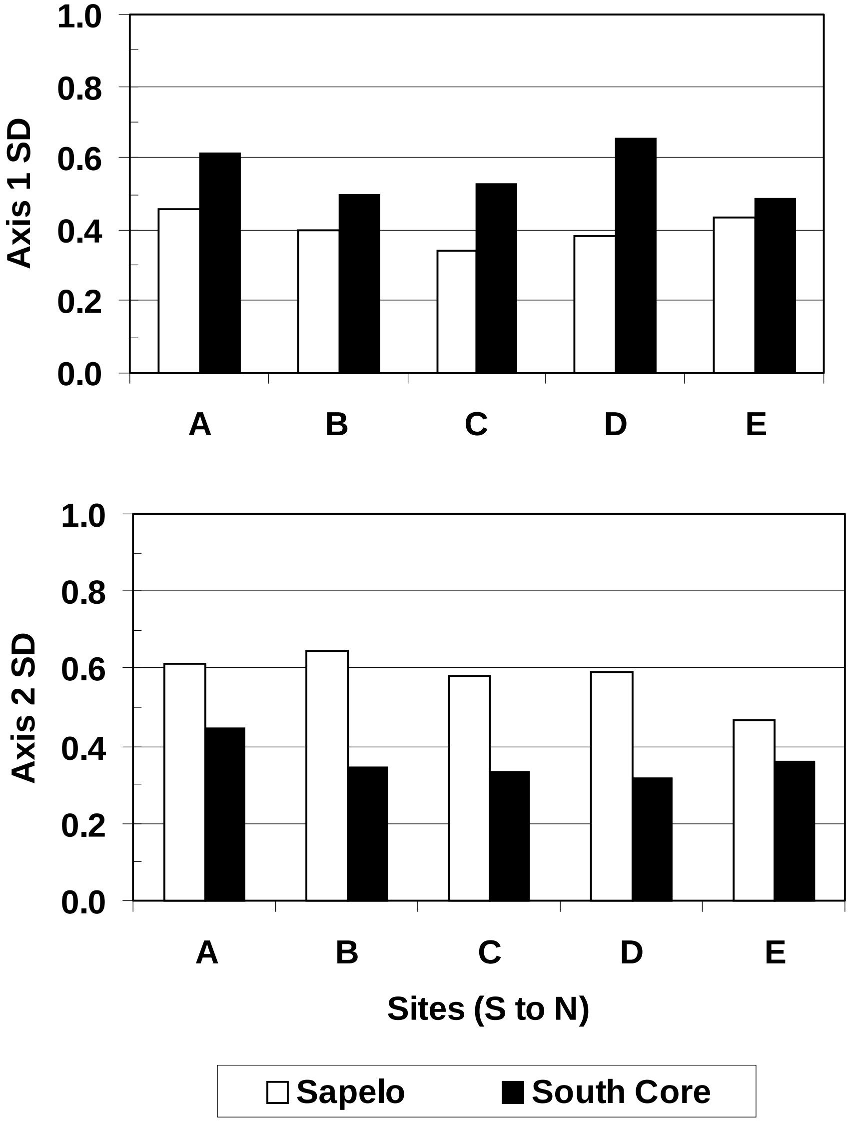
Topography and species composition

The major topographic differences between islands reflected those generally attributable to the geomorphic setting (Godfrey and Godfrey, 1973; Stalter, 1974; Oertel and Larsen, 1976; Hayes 1994). A hummocky dune-and-ridge topography was prevalent on Sapelo, while overwash profiles were well-expressed on South Core.

The strong separation in my NMS plot of island sites confirmed that distinctive island compositions were expressed, despite the strong potential overlap of species distributions along the latitudinal breadth of my study region. There was divergence between islands in their species abundances and distributions for both individual species and compositional categories based on life history and island affinity. In general, broad compositional differences between islands developed from their differences in disturbance regime, with a strong separation of islands along a woody-herbaceous axis. On South Core, where large overwash patches are frequent and common, the burial-adapted herbaceous species *Spartina patens* and *Hydrocotyle bonariensis* had a higher percent absolute cover. As the importance of large gaps decreased on Sapelo, species that have growth strategies to replace or inhibit species within gaps, such as the woody shrub *Myrica cerifera, Phyla nodiflora,* and the bunch grass *Muhlenbergia filipes* increased in cover. These three species formed a dense cover in the wet swales they colonized on Sapelo. Several studies note that woody shrubs such as *Myrica cerifera* increase in importance with the cessation of overwash (Schroeder *et al*., 1979; Fahrig *et al*., 1993; Stalter and Odum, 1993; Young *et al*., 1995; Crawford and Young, 1998).

The decreased importance of *Spartina patens* on Sapelo may be the result of decreased overwash and the outcome of its competitive interactions with dune-building species. Cattelino *et*

Figure 2.15. NMS Axis 1 and Axis 2 mean standard deviations for transects by island sites.


1.0
0.8
0.6
0.4
0.2
0.0
Axis 1 SD
A
B
C
D
E
1.0
0.8
0.6
0.4
0.2
0.0
Axis 2 SD
A
B
C
D
E
Sites (S to N)
□ Sapelo
■ South Core

al. (1979) described an analogous scenario for forested habitats, in which a disturbance-dependent tree species was lost from the landscape following the cessation of the disturbance agent that was essential to its occurrence. On Sapelo, *Spartina patens* peaked in cover at Site A, the only site that receives overwash. *Spartina patens* occurred on three other sites on Sapelo, but its cover was still less than 1% of the island total. A similar decrease in *Spartina patens* has been described for barriers of the United States northern Atlantic coast where overwash is infrequent (Godfrey *et al*., 1979). On these northern barriers, *Spartina patens* exhibited a weaker ability to regrow through overwash when compared to frequently overwash islands such as South Core Banks. Mortality and decreased regrowth of *Spartina patens* following overwash on these northern barriers encouraged sand deflation, and the establishment of *Ammophila brevigulata,* which replaces *Uniola paniculata* as the common dune building species at this latitude. In general, *Spartina patens* is not an effective dune builder. It is often replaced by species better adapted to high, exposed conditions, such as *Uniola paniculata. Panicum amarum* and *Sporobolus virginicus,* two burial-adapted perennial grasses that increased in abundance on Sapelo, are also more efficient in trapping wind-blown sediments and establishing foredunes in comparison to *Spartina patens* (Woodhouse, 1982). These two species may also have contributed to the reduced cover of *Spartina patens* on Sapelo. Interspecific competition is an important factor that affects the abundance of species across dune habitats (Silander and Antonovics, 1982)

South Core's higher cover of perennials may reflect its higher rates of sediment mobility. In coastal habitats where sand burial is frequent, perennial species are more abundant than annuals (Fahrig *et al*., 1993). Perennial cover on Sapelo surpassed that of South Core's only at Site E. At this northernmost site on Sapelo, erosional shoreline conditions increased the cover of perennials common to more inland habitats. Interestingly, two abundant, unique perennial species, *Phyla nodiflora* on Sapelo and the bryophyte *Ditrichum pallidum* on South Core, formed low, dense ground covers. Despite their taxonomic differences, both species may have a similar function in their ability to stabilize sediments.

Fahrig *et al*. (1994) state that annual cover increases from areas of low to moderate disturbance frequencies, but then decreases as disturbance frequencies continue to increase. The distribution of annuals on South Core supports this finding in that annual cover increased at sites protected from overwash. Most annual species show little ability to recover from burial (Hosier, 1973). Furthermore, barrier island dune seed bank development and persistence increase with decreasing disturbance frequency (Looney and Gibson, 1995). On the mid-island sites B and C of South Core, the protection from overwash afforded by a fronting dune ridge may have enhanced the establishment and successful germination of annual species (*Chamaesyce* spp., *Arenaria serpyllifolia*, *Heterotheca subaxillaris, Strophostyles helvola*, *Conyza canadensis)*. *Spartina patens,* by stabilizing and sequestering overwash sediment may directly facilitate annual species by providing a stable habitat for their successful establishment. (Hacker and Gaines, 1997; Jones *et al*., 1997). On Sapelo, sediment mobility may be too low to support germination of annual species except where local shoreline dynamics have increased sediment mobility. Moderate overwash at Site A on Sapelo may have indirectly facilitated the establishment of annual species by providing fresh substrate for colonization by annual species. The accretion-mediated chronosequence of dune habitats at Site A on Sapelo may enhance the availability of regeneration niches (Grubb, 1977) for annual species. Recently formed wet swales at this site are only partially colonized with *Myrica cerifera*, thus competitive displacement from this woody shrub species is relaxed for annuals dispersing to or germinating in these moist sandy habitats. At Site E on Sapelo, erosion has truncated the dune ridge-and-swale system, and increased sediment mobility. Ruderal annuals (*Eupatorium* spp., *Gnapthalium purpureum*, *Vulpina octoflora*) have established in this disturbed, nearshore habitat.

As with annual species, the within-island distribution of unique species on each island paralleled opposing trends in sediment stabilization. The higher cover of unique species on South Core was confined largely to sites B and C where overwash frequency and sediment mobility declined. *Ditrichum pallidium* and *Solidago* spp. have colonized the older overwash deposits at these sites. These two unique species peaked in cover as the two dominant disturbance species on the island*, Spartina patens* and *Hydrocotyle bonariensis,* declined. The genus *Ditrichum* has a high tolerance for burial (Martínez and Maun, 1999) and may act as secondary stabilizer after *Spartina patens*. On Sapelo, unique species were observed to peak in cover in association with the erosional conditions and increased sediment mobility at Site E. Unique species also showed a secondary peak in cover at Sites A and D. Site A may have supported more unique species through increased sediment mobility associated with moderate frequencies of overwash. Site D is the located near a disturbed, frequently-used hiking trail that cuts through the dunes. Species dispersal along this corridor may have augmented the cover of several unique ruderal species encountered at this site (Rodgers, 1999).

Transverse compositional gradients

NMS of quadrat-level data revealed distinctive compositional gradients for each island. Sapelo exhibited two distinct compositional gradients that intersect as part of a larger cross-shaped gradient structure. South Core Banks exhibited one prominent vegetation gradient that ran diagonally across both axes. These gradients may develop from the way in which each island's topography constrains the spread of disturbance across the landscape (Swanson *et al.,* 1988). Turner *et al*. (1993) note that recovery from disturbance may be influenced by the spatial extent of disturbance, which in turn may feedback to the disturbance regime. Topographic profiles for South Core, with their single fronting dune and quadrat 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 second NMS 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, I observed that disturbance from overwash and from higher rates of incremental sediment mobility was confined largely to the front of transects, and to a lesser extent, on the sparsely vegetated interdunal flats in interior locations. As a result, disturbance structuring is spatially decoupled from the dominant transverse zonation. Consequently, two discrete NMS axes are 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 NMS quadrat 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. On the second axis, which captured the predominant transverse zonation on each island, frequent and spatially extensive overwash on South Core generated a stronger correlative relationship with distance, largely through the structural and temporal regularity imposed by this disturbance agent. However, correlation coefficients for elevation were nearly equivalent between islands along this axis, which is in contrast to my original hypothesis. This may reflect the geographically variable importance of elevation, as an autogenic control of composition largely through depth to water table on Sapelo, and as an allogenic control on South Core that determines potential exposure to overwash.

Transverse compositional variability

As hypothesized, transect species turnover was greater on the high resistance-landscape of Sapelo. This reflected the high spatial, or habitat, heterogeneity (Huston, 1994; Rosenzweig, 1995) associated with Sapelo's more complex topography. Greater topographic contrasts facilitated the coexistence of wet swale species at low elevations and the dune species at drier, elevated habitats. Elevational contrasts may have enhanced species turnover by engendering more diversity among hydrologically-defined niches (Silvertown *et al.*, 1999). Several authors have emphasized the role of topography and water table dynamics in shaping compositional patterns in coastal settings (Hayden *et al.*, 1995; Martinez *et al.*, 1997). Phillips (1999a) outlines a systems-oriented relationship in which topographic complexity, or 'topodiversity', may promote an increase in hydrodiversity and species diversity. Shoreline movement also influenced species turnover (Doing,1985; Ehrenfeld, 1990). On Sapelo, beta diversity increased with both the erosional compression of shoreline habitats (Site E) and their accretional expansion (Site A). The higher transect species turnover on Sapelo was also promoted by the assemblage of species accompanying *Myrica cerifera* in wet swale habitats. Mature *Myrica cerifera* shrubs supported a number of vine (*Ampelopsis arborea, Mikania scandens, Smilax spp., Vitis spp., Melothria pendula)* and understory (*Phyla nodiflora, Parietaria floridana)* species. Senescence of older thickets of *Myrica cerifera* (Crawford and Young, 1998) permitted the establishment of ruderal species

(*Eupatorium* and *Cirsium* spp), and gaps may allow the reestablishment of wet swale species or tree seedlings.

In agreement with my initial hypothesis, Sapelo transects spanned a larger range of compositions. However, the second axis, rather than the first, captured the transverse compositional variability that was compared with MRPP. On Sapelo, the repetition of topographically-constrained compositional units along ridges and swales could be expected to collapse non-overlapping quadrat compositions to a narrow portion of the axis. However, the aforementioned dynamics in *Myrica cerifera* thickets, and the associated interstitial and gap species, may introduce enough compositional variability to have widened transect standard deviations on Sapelo. By contrast, the low profile topography upon which overwash dissipates on South Core contributed to its smaller transverse zonation. The high frequency of spatially superimposed disturbance patches, and the harsh environmental gradients associated with a higher frequency of extratropical storm exposure, may have collapsed quadrat compositions along transects to a smaller portion of the NMS axis.

Longitudinal compositional variability

ANOSIM indicated that each island had a roughly equivalent longitudinal compositional variability. However, Sapelo has a higher compositional variability given its smaller geographic extent of dune habitats. Longitudinal compositional variability increased on Sapelo largely because of increased sediment mobility adjacent to tidal inlets. At Sites A and E on Sapelo, erosion and accretion contributed to novel compositions that fostered larger compositional separation among island sites. Without the compositional separation contributed by these sites, overall longitudinal variability would have been less on Sapelo. Similarly, Site E on South Core may contribute disproportionately to longitudinal compositional variability expressed along-island. At this site, frequent or recent overwash fostered a depauperate cover consisting primarily of *Spartina patens*.

Conceptual synthesis

An overriding conceptual question remains: how has a disproportionately high amount of compositional variability developed within the smaller habitat width and island length on Sapelo? On each of my study islands, topography-forming processes, operative in the intervals between overwash, may feed back to the disturbance regime by differentially regulating the spread of disturbance. This has the effect of regulating the geometry of the interaction between disturbance and environmental gradients, ranging along a continuum from overlap on South Core, to spatial disjunction on Sapelo. This has a dramatic effect upon the spatial-scale expression of compositional patterns, as more fine-scale patterns are folded into a smaller area on Sapelo. This may be evident in the hierarchical structuring of the environmental variables unique to each island (Wu and Loucks, 1995; Meentemeyer, 1989). South Core represents a landscape with a strong hierarchical structuring of variables. Here elevation constrains the expression of local site factors (including feedback processes between vegetation and landform) through exposure to frequent overwash. Given that the cyclones that cause overwash act on a regional scale, elevation similarly constrains local site factors over a large geographic area. Only after overwash, during patch regeneration, does this hierarchical constraint lessen. The resulting biogeomorphic responses mediated by *Spartina patens*, however, perpetuates a state of low resistance to overwash. Given frequent disturbance exposure, the hierarchical alignment of variables is reset. This, in turn, promotes an island-scale regularity in topography and species composition. On Sapelo, longer intervals between disturbance contribute to a greater expression of non-hierarchical relationships among environmental variables. Elevation, as a predisposing factor in the exposure to overwash, does not constrain local site processes over a wide geographic area. A comparable, but less regular compositional variability arises on Sapelo because local processes, acting on a finer spatial scale, are operational and arise independent of any large-scale external forcings from cyclonic events. Species composition on each island reflects the interaction of environmental influences, including feedbacks and thresholds, operating at varied spatial scales (Bendix, 1994)

Both study islands may be self-organizing systems in that structure and processes mutually reinforce each other in positive feedbacks (Urban and Shugart, 1992; Perry, 1995; Malanson 1999, Werner, 1999). Although employed as a conceptual tool, self-organization is of value in this study in that it distinguishes between different modes of landscape development and patterns (Phillips,1995b, 1999b). Sapelo and South Core may comprise end points on a coastal gradient of landscape sensitivity as outlined by Carter and Orford (1991) and Malanson (1999). A high morphologic resistance to overwash on Sapelo results in a divergence of landscape patterns by promoting a greater expression of autogenic biogeomorphic processes. Across Sapelo, there was a high local-scale variability in topography and composition. Even with the smaller sampling interval and extent employed, there were more off-transect species when compared to South Core (Sap = 16 , Core = 4 [Appendices 2.5 and 2.6]). Correlations of NMS quadrat scores with elevation and distance exhibited a high variability even among transects within an individual site (Table 2.2). On Sapelo, the lower absolute cover of unique species (S = 2%; C = 15%) was attained by a larger number of these species (S = 45, C = 32). This suggests that environmental conditions are sufficiently differentiated to support a larger proportion of the available unique species. As a result, the geographically small extent of Sapelo developed a higher beta diversity, transverse zonation, and longitudinal compositional variability when compared to the 35 km of sampled dune habitat on South Core. On South Core, *Spartina patens* regulates its continued presence in the landscape by maintaining an overwash topography that perpetuates the conditions for which it is competitively superior, while also dampening externally-generated overwash so that there is a enough resistance within the system to prevent catastrophic loss of landscape structure and function. In this manner, internal processes modify external forces such that they reinforce an internally generated order, a quality exhibited by systems exhibiting self-organized criticality (Perry, 1995 Malanson, 1999). On South Core, frequent overwash and the cyclical recovery process constrain topographic and compositional patterns to a narrow range over a larger geographic area.

Conclusions

Barrier islands are useful settings to investigate how compositional patterns and the processes creating them change as a function of scale. The strong compositional differences between the two distinctive barrier island morphologies in this study were molded by the feedbacks between the prevailing overwash disturbance regime on each island, and the effects of niche-constructing species on the regulation of the spatial and temporal patterns of sediment mobility. Compositional variability, chiefly the variability of annuals and island-unique species, was initiated by increased sediment mobility on Sapelo, especially near tidal inlets. Increased sediment mobility may have augmented the availability of habitat for the recruitment of annual and unique species otherwise competitively excluded in these infrequently overwashed landscapes. The absence of massive sediment mobility associated with overwash on Sapelo also permitted the species-mediated formation of a complex ridge-and-swale topography. This topography imposed more spatial variability in plant-water relations, facilitated species coexistence by narrowing specialization to preferred elevational habitats, and thus contributed to the higher compositional variability observed on Sapelo. For the more frequently overwashed landscape of South Core, compositional variability was associated with decreasing sediment mobility. Decreased sediment mobility may enhance the recruitment or germination success of annual or unique species, given the highly unstable substrates in this landscape. *Spartina patens* and *Ditrichum pallidium* may facilitate this compositional variability by stabilizing overwash deposits for the successful colonization of sites by species poorly adapted to high sediment mobility.

To a certain extent, my initial hypotheses were simplified in that they assumed a linear relationship between disturbance frequency, and its exposure and subsequent effects. Although two of my three original hypotheses regarding compositional variability were supported in my results, I suggest that a more complex relationship, one in which recovery may dampen or reinforce the effects of disturbance regime, offers a more satisfying explanation for the observed patterns in compositional variability. The species-mediated formation of dune ridge-and-swale topography on Sapelo dampens disturbance exposure, fosters a divergence in the interactions between species and sediment mobility, and thus contributes to the expression of a large amount of compositional variability within a given geographic area. On South Core, the sand-binding function of *Spartina patens* maintains a simplified topography that reinforces overwash effects, fosters a landscape convergence in the interactions between species and sediment mobility, and thus contributes to the expression of a smaller amount of compositional variability over a given area.

Landform, vegetation and sediment mobility cannot be considered independent factors when examining compositional patterns in highly responsive geomorphic systems, such as coastal sandy barriers. During intervals between disturbance events, gradient reorganization through biogeomorphic feedbacks may change the way in which the landscape responds to the next external event, in the manner outlined by Schumm (1973, 1979) for complex responses in fluvial systems. Furthermore, the two biogeomorphic settings in this study, a wave-dominated microtidal barrier island and a mixed-energy mesotidal barrier island, may represent stable states (Baker, 1995) perpetuated by locale-specific feedback and threshold interactions between the existing disturbance regime and recovery along environmental gradients. In this study, two biogeomorphic systems exhibiting morphologic differences in their resistance to disturbance, and in their species resilience following disturbance, had distinctive differences in species composition and distribution, as well as in the strength of hierarchical influences on spatial-scale organization.

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CHAPTER 3

DUNE PLANT SPECIES DIVERSITY IN TWO BARRIER ISLAND GEOMORPHIC ENVIRONMENTS

Overview

I investigate the interplay of disturbance and environmental gradients in shaping dune plant species diversity patterns on for two barrier islands of the Georgia Bight. Topographic and cover data were sampled within strip transects aligned perpendicular to the shoreline at study sites parsed along a frequently storm-overwashed microtidal (South Core Banks, North Carolina) and an infrequently overwashed mesotidal (Sapelo Island, Georgia) barrier island. Non-parametric comparisons (MRPP) of transect-level alpha diversity and species richness revealed no significant differences between islands despite strong differences in disturbance regime. Primary foredune height was significantly positively correlated with species richness and alpha diversity on South Core Banks, while this relationship was not significant on Sapelo. On South Core, successional inhibition and the biogeomorphic processes that reinforce this inhibition maintain a regularity in the distributional variation in along-shore species diversity. Sapelo represents a landscape in which directionality in compositional sorting and reinforcing biogeomorphic processes interact to foster a fine-scale differentiation of landscape patterns of species diversity. I posit that the relevancy of the Intermediate Disturbance Hypothesis is weak when comparing diversities along a disturbance gradient. Biogeomorphic feedbacks and threshold processes, operating in the intervals between disturbance, change responses to extrinsic disturbance, and introduce non-linearities in the relationship between disturbance exposure and effects. The Dynamic Equilibrium Model is a more robust framework given its incorporation of scale effects, and its independence from any delineation of a geographically-fixed intermediate-level of disturbance frequency or magnitude.

Introduction

Patterns of plant species diversity in numerous upland environments have been subject to intense scrutiny (Loucks, 1970, Connell, 1978; Huston, 1979) but surprisingly neglected on barrier island coasts (Ehrenfeld, 1990). Barrier islands are elongate, essentially shore parallel landforms composed chiefly of unconsolidated sediments. A morphologic spectrum of these highly mobile—and ultimately ephemeral—sand bodies is well-expressed within the Georgia Bight of the southeastern Atlantic coast of the United States. Although contrasts between these islands in their morphology and geomorphic processes are well-documented (Hayes, 1994), these differences have not been extended to biogeographic patterns of plant species diversity.

The geomorphic-meteorologic agents that structure the morphologies of these barrier island dune systems have strong linkages to vegetation. During quiescent intervals, sediments are incrementally transported by wind or wave action. Dune vegetation may trap and bind these sediments to construct dune landforms. By contrast, high wave energy and storm surge can result in the massive remobilization of these sediments during topography-simplifying overwash events. Overwash, the transport of large volumes of sediment from the beach face to interior locations during hurricanes and winter storms, clears patches of ground and triggers vegetation recovery sequences (Hosier, 1973; Schroeder *et al.*, 1979; Hayden *et al.*, 1995).

The life history adaptations of the common coastal dune plant species are shaped by this dynamism in sediment mobility. On barrier island dune systems, the process-form relationship between vegetation pattern and disturbance agents is rapidly equilibrating. Ecological and geomorphic processes interact over relatively short temporal scales, and thus minimize the disequilibrium in the vegetation-environment relationship (Rastetter, 1991). This is in strong contrast to temperate forests, where the vegetation-environment relationship has been well-studies (Watt, 1947; Loucks, 1970). In these environments, vegetation may vary continuously and rapidly, while geomorphic processes and landforms often vary episodically and relatively slowly. This disparity in temporal scaling complicates process interpretations of species pattern (Sprugel, 1991; Urban and Shugart, 1992; Phillips, 1995). By comparison, coastal dune environments afford more resolution in the inference of process from pattern. Feedback and threshold responses between vegetation and geomorphic processes and landforms are discernible over short time intervals. These landscapes behave as a sensitive biogeomorphic system, rather than a collection of independent components (Rastetter, 1991).

Surprisingly, there are few recent studies of dune vegetation that quantify species diversity. Barrier islands of the southeastern U.S. Atlantic coast are ideal for investigating the biogeomorphic patterning of dune plant species diversity. Regional contrasts in wave and tidal energy along the margin of the Georgia Bight foster a continuum of morphologies that differ in their temporal and spatial-scale expression of sediment mobility and landform genesis. Overwash, in which large volumes of sediment and salt water are transported overland during cyclonic storms, is frequent to wave-dominated microtidal barrier island morphologies of North Carolina. By contrast, mixed energy mesotidal barrier island morphologies of Georgia and South Carolina are characterized by incremental processes of sediment transport. Overwash is rare except where land is newly formed and without dunes, or severely eroded. Distinctive biogeomorphic responses, incorporating locale-specific feedbacks and thresholds characterize each morphology.

In this study, I examine the contrasts in topography and species diversity expressed on these two barrier island morphologies. I investigate how biogeomorphic feedbacks and threshold responses are linked to the emergence of diversity patterns across geographic scales. My specific research questions are: 1) Do significant differences in dune plant species diversity develop between two barrier islands differing in their exposure to storm-generated overwash? 2) How do these diversity patterns covary with dune topography? I examine the influence of dune topography through topographic cross-sections and two descriptors, primary foredune height and topographic roughness. Additionally, I examine my results in light of two diversity models, the Intermediate Disturbance Hypothesis (IDH; Loucks, 1970; Grime, 1973; Connell, 1978) and the Dynamic Equilibrium Model (DEM; Huston, 1979, 1994). The application and intent of IDH is a subject of debate (Collins and Glenn, 1997); however, DEM has received little attention despite its origin in a similar conceptual design: the species present at a given location are determined by the interaction of disturbance frequency and the population dynamics of competitively dominant species.

This study is unique in that it examines how biogeomorphic processes contribute to the patterning of species diversity. Few studies have addressed how regionally distinctive biogeomorphic feedbacks and threshold processes influence diversity patterns. In coastal dune settings, these biogeomorphic processes interact with disturbance regimes and mold environmental gradients, two well-recognized influences on the expression of species diversity. Coastal environments, in general, afford a compelling opportunity to amplify, expand, and possibly generalize biogeomorphic concepts developed in other environments (Swanson *et al*., 1988; Parker and Bendix, 1996) notably riparian settings (Hupp, 1982; Baker, 1990; Bornette and Amoros, 1996; Bendix, 1997).

Background

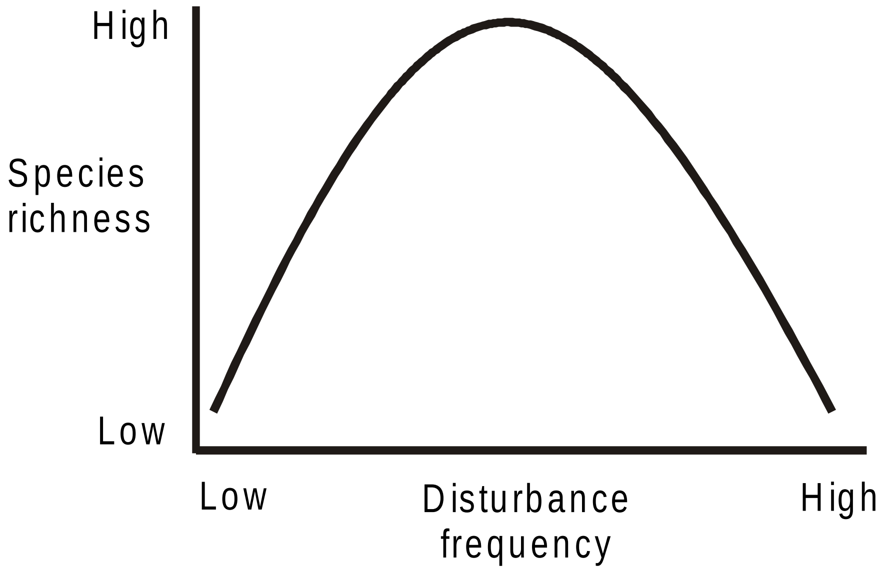
Species diversity is an attribute of plant communities that exhibits patterning through successional time and across environmental gradients (Huston, 1994; Tilman and Pacula, 1993). Landscape-scale studies of species diversity have typically invoked two broad paradigms to explain observed patterns: disturbance patch dynamics (Pickett and White, 1985) and the sorting of species along environmental gradients (Gleason, 1926; Whittaker, 1970). Overwash is a landscape-scale disturbance agent in maritime coastal settings. Overwash shapes vegetation dynamics through massive burial by sediment and exposure to salt water, the differential species adaptations to these inputs, and, more indirectly, through the rearrangement of topography (Godfrey, 1976; Hosier and Cleary, 1977; Cleary and Hosier, 1979; Godfrey *et al.,* 1979; Schroeder *et al*., 1979; Zaremba and Leatherman, 1986). Hayden *et al*. (1995) found that dune vegetation pattern covaried with land surface elevation. They posit that elevation dictates exposure to overwash events and imposes spatial variability in the depth to fresh and salt water. Based on their studies of low profile, frequently overwashed barrier islands of the Virginia coast, species diversity decreased as overwash probability increased. However, Odum *et al*. (1987) observed a lowered species diversity on a barrier island landscape as a result of the construction of a large artificial primary foredune in the Outer Banks of North Carolina. This alteration of topography decreased overwash frequencies and permitted the expansion of woody shrubs that subsequently lowered species diversity by excluding herbaceous plants.

A dramatic pattern of diversity on coastal landscapes is the zonation of species along environmental gradients. These patterns stimulated the pioneering ecological work of Cowles (1899) on the coastal dunes of Lake Michigan. Most studies of coastal dune vegetation over the past century have emphasized transverse environmental gradients as influences on dune vegetation pattern. These studies consistently identify physical gradients of salt spray exposure, incremental sediment mobility, and soil moisture as primary factors distinguishing dune vegetation (Oosting and Billings, 1942; Oosting, 1945; van der Valk, 1974; Barbour, 1978; Moreno-Casasola, 1986; Hesp, 1991; Martínez *et al*., 1997; Wilson and Sykes, 1999). Maun and Perumal (1999) suggest that sand burial is more important than salt spray as a control of species distributions. In response to these overlapping physical gradients, dune vegetation may develop a transverse zonation parallel to the shoreline. This zonation is a complex mosaic of microenvironments and fluctuating species assemblages delimited by varying degrees of sediment mobility, salt spray exposure, and inundation due to erosional exposure of the water table (Martínez *et al*., 1997).

Diversity models

The Intermediate Disturbance Hypothesis holds that species diversity within habitats will be maximized at intermediate frequencies or intensities of disturbance because competitive exclusion will be balanced by destruction of the competitive dominants (Figure 3.1). IDH postulates a similar relationship between habitats or patches. Across a landscape where patch creation is asynchronous, to the extent that patches of different age coexist, diversity at the larger scale is maximized at an intermediate frequency of patch formation (Abugov, 1982). Although it is beyond the scope of this paper to review IDH in detail, several recent articles merit attention, largely for their recognition of factors that complicate the IDH. Hubbell *et al.* (1999) concluded that compositional variability within disturbance gaps in a tropical forest was weakened by recruitment limitation to the extent that local variation in tree diversity did not correspond to that predicted by IDH. Bendix (1997) noted that the correspondence of maximum species diversity with intermediate disturbance magnitudes varied according to the diversity metric employed. Numerous studies have found departures in the correspondence of intermediate frequencies of disturbance with maximum species richness or diversity (Baker, 1990; Collins *et al*., 1995; Bornette and

Figure 3.1. A generalized version of the Intermediate Disturbance Hypothesis.


High
Species richness
Low
Low
Disturbance frequency
High

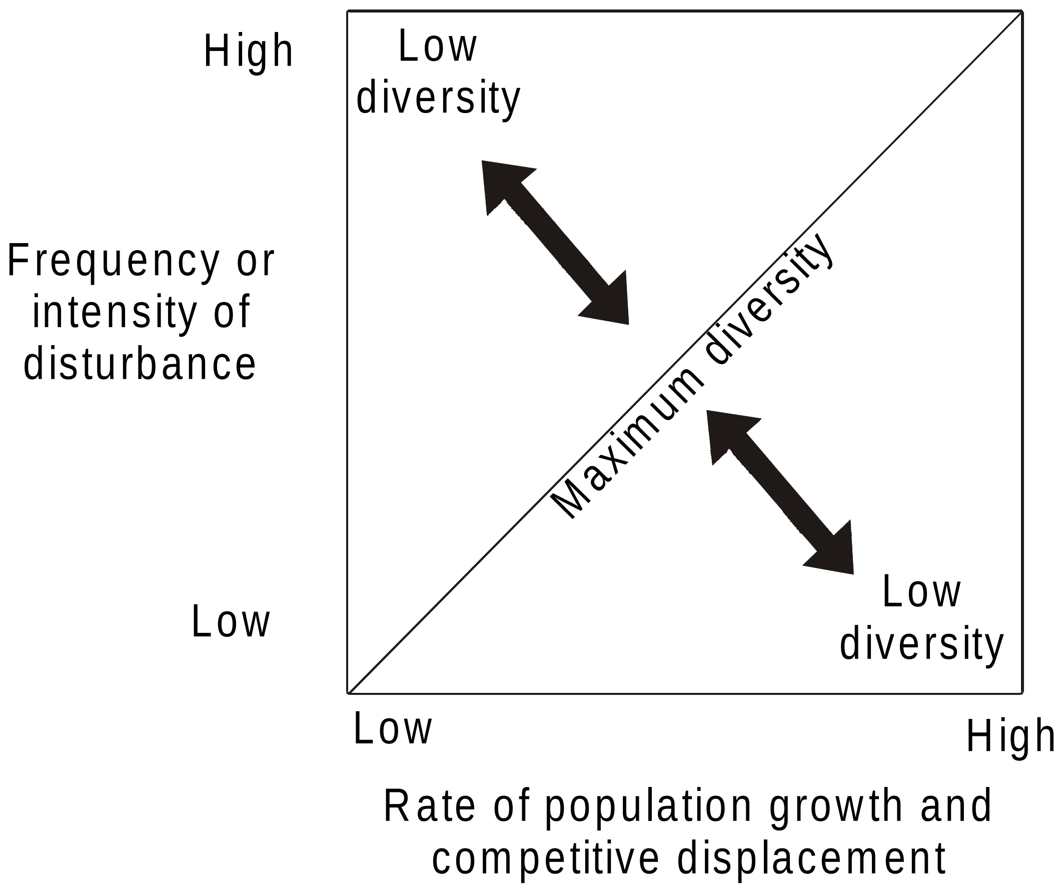
Amoros, 1996; Trebino *et al*., 1996). Furthermore, the scale at which IDH should be applied, as either a within-patch or between-patch conceptual frame, is a source of contention among environmental scholars (Collins and Glenn, 1997; Wilson, 1994).

By contrast, the Dynamic Equilibrium Model, an extension of IDH, has received comparatively minor attention (but see Death, 1995; Pollock *et al*., 1998). DEM assumes a dynamic equilibrium between disturbance frequency and competitive displacement (Figure 3.2). This dynamism is introduced by the assumption that the rate at which competitive dominants exclude earlier successional species is variable. High and low growth or replacement rates for competitive dominants, in concert with disturbance frequency, determine the timing of competitive exclusion and resulting diversity patterns. DEM describes how different disturbance frequencies can have the same level of diversity given differences in the rate of competitive displacement. Most important, DEM does not require delineation of an intermediate level of disturbance. An intermediate level of disturbance may have very different diversities depending upon the rate of competitive displacement. DEM also makes assumptions on the spatial-scale controls of species diversity. Diversity is reduced by local patch-scale processes, either the physiological failure of populations to recover from high frequencies of disturbance, or from high rates of competitive displacement among interacting species. Diversity is most likely to be maximized under conditions when the influence of these local processes is relaxed, and landscape-scale processes (habitat heterogeneity, dispersal, size of species pool) are operative.

Study Area

Central to this study is the pronounced morphometric variability in barrier islands that develops along the Georgia Bight (Figure 2.1). Entrances to bights are characterized by wave-dominated features, with tide-dominated features toward the center. On microtidal coasts along the margin of embayments, barrier islands are long and linear, as exemplified by the Outer Banks of North Carolina (Figure 2.2). On mesotidal coasts at the center of bights, barrier islands are short and wide with numerous tidal inlets, as exemplified along the coast of Georgia (Figure 2.3).

Figure 3.2. A generalized version of the Dynamic Equilibrium Model.


High
Low diversity
Frequency or intensity of disturbance
Maximum diversity
Low
Low diversity
Low
High
Rate of population growth and competitive displacement

These contrasts in island morphology, coupled with climatological gradients of increased exposure to extratropical cyclones with increased latitude in the winter season (Davis *et al.*,1993), yield a strong geographic continuum of disturbance regimes along the southeastern U.S. Atlantic coast (Mather *et al.*, 1964; Fox and Davis, 1976; Riggs, 1976; Hayes, 1979; Godfrey *et al.*, 1979; Williams and Leatherman, 1993).

Striking biogeomorphic feedbacks develop among islands along this morphometric and climatological gradient (Godfrey 1976). Storms and waves are the agents that mobilize sediments on the microtidal barrier island of the Outer Banks of North Carolina. Here, even mild winter storms or offshore hurricanes can produce overwash (Hosier, 1973). Once deposited, the mobility of overwash sediments is mediated by the presence of the gap species *Spartina patens.* This rhizomatous perennial has a high tolerance to burial that permits it to recover and stabilize overwash deposits quickly. As such, *Spartina patens* reinforces overwash events by perpetuating a flat topography and by stabilizing a portion of the sediments that would otherwise be directly diverted for dune reestablishment. The slightly elevated position of overwash deposits increase the resistance of the landscape to overwash, as does the potential recovery of a single protective dune ridge (Hosier, 1973; Hosier and Cleary, 1977). However, the sum of biogeomorphic feedbacks operating on this type of landscape maintain a low morphologic resistance to overwash, and a composition with a high resiliency to burial (Odum *et al.*, 1987). In consequence, the presence of a flat overwash topography and *Spartina patens* are reinforced in a positive feedback (*sensu* Wilson and Agnew, 1992). Cyclical patterns of overwash and recovery have been documented for barrier islands of the North Carolina coast (Cleary and Hosier, 1979).

By contrast, sediment mobility on the mixed-energy mesotidal barrier islands of Georgia is strongly controlled by tides and tidal inlets (Hayes,1979; Fenster and Dolan, 1996). At the island scale, large tidal ranges restrict the effects of storm surge and overwash to the duration of high tides (Godfrey, 1977). Tidal inlets serve as natural safety valves that dampen overwash during periods of infrequent high storm surge (Riggs,1976; Sexton and Hayes, 1991). These tidal inlets also influence the patterns of local-scale sediment mobility. Given an abundant supply of sediment and low wave energy, extensive beach ridges may accrete parallel to the shoreline (Oertel and Larson, 1976; Hayes, 1994). Beach ridges (or dune ridges when they occur at more inland positions) are topographic features implying local controls on shoreline dynamics. Numerous models of dune ridge formation emphasize the role of positive feedbacks between vegetation cover and aeolian deposition in their formation and stability (Taylor and Stone, 1996). In this positive feedback process, the accumulation of sand stimulates plant growth. This in turn increases sand entrapment, fostering continued plant growth, and an increase in elevation relative to areas where dune species are absent (Woodhouse, 1982). With changes in local sediment budgets, beach ridges may be interrupted, truncated by erosion, or exhibit changes in their orientation (Taylor and Stone, 1996). Most importantly, elevational contrasts along ridge-and-swale topography are maintained by dune-building species at higher elevation, while wet swale species bind and anchor sediments at low elevations. In sum, the biogeomorphic processes operating on this landscape increase morphologic resistance to overwash (Odum *et al.*, 1987), and perpetuate the dune ridge-and-swale topography and vegetation in a positive feedback (*sensu* Wilson and Agnew, 1992)

Two islands were selected for study: the wave-dominated microtidal barrier of South Core Banks, North Carolina, and Sapelo Island, Georgia, a mixed-energy mesotidal barrier (Figure 2.4). These island are largely undeveloped, with limited emplacement of dune or shore stabilization structures. I confined my sampling on Sapelo to the 5 km of Nannygoat Beach on the southernmost Holocene island so as to minimize the confounding influence of multiple tidal inlets. Here, overwash is infrequent (Deery and Howard, 1977) and restricted to a small area on the south end of the island. South Core Banks, part of Cape Lookout National Seashore (CLNS), is a retreating Holocene barrier. Overwash increases in frequency and intensity from south to north along this microtidal island. Sampling here covered a much larger extent (35 km) in comparison to Sapelo. Although CLNS permits vehicular traffic along a small controlled-access road along the length of the entire island, development is minimal in comparison to the closest suitable islands in Cape Hatteras National Seashore. I avoided sampling in areas that evidenced impacts of recreational use. Prior to my field sampling in June through August of 1998, the last hurricanes to affect South Core were Hurricane Bertha (Category 2) and Hurricane Fran (Category 3) in 1996. These storm made landfall on the North Carolina coast below CLNP, which only received minor overwash (National Park Service personnel, personal communication). The last intense hurricane to strike the Georgia coast was among a series of storms in the 1890's (Pielke, 1997).

Regional uniformity in temperature and precipitation regime, especially in the growing season, greatly diminish the potential confounding effect of regional macroclimatic sorting on species composition. As a consequence of climatic uniformity, the dune flora on these barrier islands is similar along the latitudinal breadth of my study region, with the same major species evident throughout the region (Duncan and Duncan, 1987; Stalter and Odum, 1993). However, these general climatic factors contribute little to inter-island variability when compared to dune microenvironmental factors, such as topography, incidence of salt spray, substrate mobility, and exposure (Barbour and Johnson, 1977). Within the Georgia Bight, there is considerable topographic variability within the dune systems of individual islands, even within a single morphologic type. This develops from geographic variability in local beach and dune sediment budgets, prevailing winds, and island orientation (Hosier, 1973; Godfrey, 1977; Psuty,1988; Ehrenfeld, 1990). Consequently, the purpose of my study is not to provide a template for all islands of a given morphology, but to examine the effects of disparate geomorphic settings on potentially similar species pools.

Methods

Field sampling

Five sites, each containing three randomly-positioned strip transects, were parsed along the north-south axis of each island. In order to capture the compositional variation along a gradient of exposure to oceanic inputs, each transect began at the high water mark and extended inland through the width of dunal microhabitats to the first occurrence of extensive thickets of the woody shrub *Myrica cerifera*. *Myrica cerifera* invades herbaceous habitats as disturbance intensity and frequency are reduced (Young *et al.*, 1995). Vegetation data were collected within a 1 x 2-m quadrat aligned perpendicular to the centerline of each transect. Within each quadrat, a 2-m point-frame sampler, also aligned perpendicular to the transect, was used to measure species presence at 10 cm intervals, for a total of 20 observations per paired quadrats. To maintain comparable sampling intensities between islands, the longer distances to stabilized vegetation on

South Core Banks required that quadrats be systematically parsed in intervals of every other quadrat. In this manner, I expected to collect species cover and topographic data for approximately 75 quadrats along the transects of each island, and roughly 1000 quadrats per island. The point-frame hits in each quadrat were summed for individual species and expressed as percent absolute cover. The presence of a species off-transect but within-site was also recorded. A total station was employed to survey elevation and distance relative to the mean high water mark for all quadrats. Plant identification and nomenclature follows Radford *et al.* (1968) and Duncan and Duncan (1987). Several genera were indistinguishable in the field and were lumped into species complexes. These complexes are composed of species that hybridize, or exhibit morphologic variation in diagnostic traits that are not readily discernible in the field.

Data analysis

Dune topography and island composition

Two components of topography were selected for analysis, primary foredune height and transect roughness. For each of the fifteen transects per island, I defined their primary foredune height as the maximum surveyed elevation within the first 10 meters landward of my datum, the high water mark. Topographic roughness is the sum of the absolute values of elevational changes between sequential quadrats of a transect. Higher values for topographic roughness indicate more elevational contrasts and a higher habitat heterogeneity along a transect. To test for significant differences between islands in these topographic metrics, I used multi-response permutation procedures (MRPP). MRPP is a non-parametric, distance-based test of group differences. The strategy of MRPP is to compare the average within-group distance with the average distance that would have resulted from all other possible combinations of the data. As such, MRPP tests for differences based on the collective distribution of data for each group rather than their respective means (Biondini *et al*., 1991). All MRRP tests were conducted at the 0.05 significance level in PC-ORD Version 4.04 (McCune and Mefford, 1999). MRPP tests were also employed to test for significant differences between islands in dune habitat width, as expressed in the length of each transect. To evaluate the inter-island differences in dune relief further, I constructed topographic cross-sections for a selected transect from each site.

Species diversity

The primary objective of this study is to examine the differences in dune plant species diversity for two barrier island landscapes along a regional gradient of shore disturbance. To assess species diversity at the island-level and for transects (n = 15 per island), I calculated two commonly applied species diversity metrics, species richness and alpha diversity. Species richness in this study is the total number of species and species complexes per level of analysis. Alpha diversity is a measure of local site diversity (Whittaker, 1972). For my alpha diversity metric, I selected the Shannon-Weiner index. This index incorporates measures of species richness and evenness of representation. The Shannon-Weiner function (H′) is calculated from the equation:

$$H' = -\sum p_i \ln p_i$$

where p_i is the proportion of the individuals found in the *i*th species (Magurran, 1988). To calculate the Shannon-Weiner index for each sampling point along a transect, I used frequency data based on the total number of point frame hits for each species in my paired quadrats. H' usually ranges from 1.5 to 3.5 and rarely surpass 4.5. Species richness and alpha diversity are often correlated (Magurran, 1988).

I originally hypothesized significant differences between islands in their transect species richness and alpha diversities. Infrequent overwash disturbance on Sapelo should lead to increased competitive displacement of herbaceous wet swale species by the woody shrub *Myrica cerifera* and consequently lower species richness and alpha diversities. To test this hypothesis, I employed MRPP as the analytical tool and my two transect-level measures of species diversity, the Shannon-Weiner index of alpha diversity and species richness, as test metrics.

A second objective of this study is to detail how topography covaries with the distribution of species diversity. To ascertain how my diversity measures and topographic variables covary, I employed Spearman's non-parametric rank order correlation coefficients. I originally hypothesized that topographic variables and species diversity would be more strongly correlated on South Core. Frequent overwash here should confer a stronger correlation because of the topography's role in predisposing a site to exposure to maritime inputs and overwash.

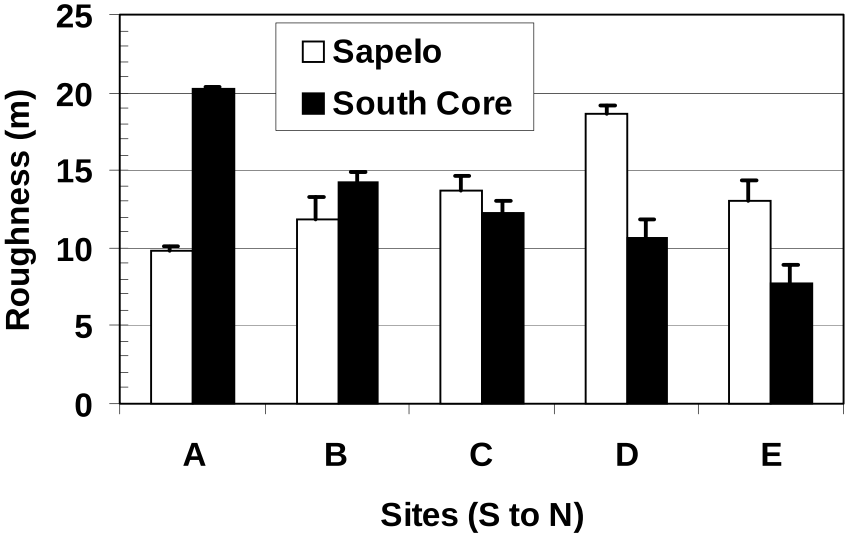
Results

Dune topography

Cross-sections indicated strong departures in topography between and within my two study islands (Figure 2.5 and 2.6). These contrasts reflected those generally attributed to the geomorphic setting of each morphology (Godfrey and Godfrey, 1973; Stalter, 1974; Johnson *et al.*, 1974; Oertel and Larsen, 1976; Hayes 1994) On South Core, a simplified overwash topography was well-developed. Mean transect primary foredune height declined incrementally along-island from a maximum of 2.4 ± .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 (Figure 2.7). Transect roughness followed a similar trend: higher topographic roughness was observed at Site A (20.2 ± .1 m) and generally decreased northward to Site E (7.7 ± 1.2 m) (Figure 3.3). Spearman's correlation coefficients indicated that primary foredune height and topographic roughness have a significant positive association on South Core ($r_s = .95$, $p < 0.001$). South Core cross-sections and field observations were in agreement with dune process-form morphologies proposed by Cleary and Hosier (1979). Their analysis linked dune physiography with cyclic patterns of overwash and recovery on the North Carolina barrier coast. At Site A, the large primary and secondary foredunes dampen 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. These dune morphologies suggest a time interval since the last overwash event of sufficient duration to permit the reestablishment of the fronting dune ridge. The low, discontinuous dunes and overwash deposits at Site E on the north end of the island suggest recent or chronic overwash.

Dune morphology on Sapelo was more complex. Topography ranged from protective parallel dune ridges and swales to a more exposed flat hummocky terrain. Mean transect dune height varied from 1.6 m relative to mean high water at Site D, to the absence of a primary foredune at Site A. As expressed at the southernmost Site A, this low hummocky terrain developed from the accretional conditions that characterize the south end of Sapelo (Welch *et al.*, 1992). Here, rapid accretion engenders a seaward progradation of the shoreline, and maintains a low topography of

Figure 3.3. Mean transect topographic roughness by site for each island. Error bars denote standard deviation (n = 3).


25
20
15
10
5
0
Roughness (m)
☐ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

distantly-spaced incipient dune ridges that are frequently overwashed. Topographic roughness was a minimum at this site (9.8 ± .4 m), and peaked mid-island at Site D (18.6 ± .5m).

Two other topographic differences were evident between islands. Mean dune habitat width on Sapelo (70 ± 8 m) was roughly half of that on South Core (140 ± 38 m) (Figure 2.8). A pronounced departure in the position of the dune habitats relative to the high water mark datum also developed between islands. Vegetation position relative to the high water mark datum on South Core suggested that the loss of the fronting foredunes would perpetuate disturbance across downsloping back-barrier environments. In contrast, vegetation was positioned above the high water mark on Sapelo. These profiles reflected a higher morphologic resistance to the potential spread of overwash on Sapelo. Although they suggested erosional conditions, the scarped dune profiles at sites B through D on Sapelo would also act as a threshold or barrier shielding the adjacent inland from maritime inputs.

MRPP of topographic variables confirmed that only dune habitat width was significantly different between islands ($T = -13.60$, $p < 0.01$; [Appendix 3.1]). Island groups showed no significant differences in transect primary foredune heights ($T = -0.97$, $p = 0.14$) or topographic roughness ($T = 0.58$, $p = 0.66$).

Island composition

Transect sampling intensities were similar for each island (Sap = 1082, Core = 1139; $T = -0.08$, $p = 0.33$ [Appendix 2.2]). Based on quadrat cover data aggregated to the transect, my study islands were significantly different in their percentage of bare ground ($T =-5.08$, $p < 0.001$; [Appendix 2.3]), with Sapelo having a higher percentage of bare ground (S = 48%, C = 29%) (Figure 2.9).

Islands were similar in their cover of shared species. 43 species out of a total 120 were shared by both islands inclusive of off-transect species (Appendix 2.4). On Sapelo, shared species comprised 50% of the total vegetation cover (52%), and 56% of the total vegetation cover (71%) on South Core (Figure 2.10). The total number of unique species, including off-transect occurrences, was higher on Sapelo (S =45, C = 32). These unique species comprised more of the total ground cover on South Core (S = 2%, C = 15% [Appendix 2.5 and 2.6]).

Island-level species diversity

Based on quadrat-level data, Sapelo had a slightly higher alpha diversity (2.80) than South Core (2.57). However, there were stronger contrasts in total island species richness. A total of 88 species and species complexes were encountered across all sites on Sapelo. 75 species and species complexes were identified across all sites on South Core. Based on botanical surveys on Sapelo housed at the University of Georgia Marine Institute, the National Park Service (1977) at Cape Lookout National Park, and Duncan (1982), the delineation of species complexes from genera into their potentially-occurring constituent species increased the total number of species on Sapelo to 99 and on South Core to 83. These island-level diversity and richness values included off-transect species.

Transect-level species diversity and richness

There were no large departures along island in alpha diversity, as based upon the mean transect alpha diversity for each site (Figure 3.4). Total species richness was more variable (Figure 3.5). Along-island departures in both of these metrics occurred at sites adjacent to tidal inlets (Sites A and E). At these sites, sediment mobility and disturbance was observed to increased due to local shoreline accretion or erosion. For Site A, mean transect alpha diversity was the highest of any site across both islands (H′ = 2.70 ± 0.07; Spp. = 46). The accretionary conditions at this site foster low fronting dunes, which permit moderate overwash near the seaward edge, and create extensive wet swale habitats in the landward direction that have not been invaded by the woody shrub *Myrica cerifera*. Alpha diversity was enhanced by an increase in the number and frequency (expressed as cover) of disturbance species (*Sporobolus virginicus, Panicum amarum, Cyperus esculentes, Cyperus polystachos*), wet swale species that are potentially shaded out by *Myrica cerifera* (*Juncus marginatus*, *Juncus megacephalus*, *Sabatia stellaris, Andropogon* spp. *Rumex hastalus*, *Gnapthalium purpureum*), and strandline taxa (*Atriplex arenaria, Salicornia europaea)*. At the northern end of the island, erosional conditions predominated. Species richness here was the highest of any site across both islands (Spp. = 62), with a moderate level of mean transect alpha diversity (H′ = 2.31 ± 0.13). This elevated species richness was associated with local sediment remobilization and the destabilization of dunes, which created gaps in *Myrica*

Figure 3.4. Mean transect alpha diversity (Shannon-Weiner H′) by site for each island. Error bars denote standard deviation (n = 3).

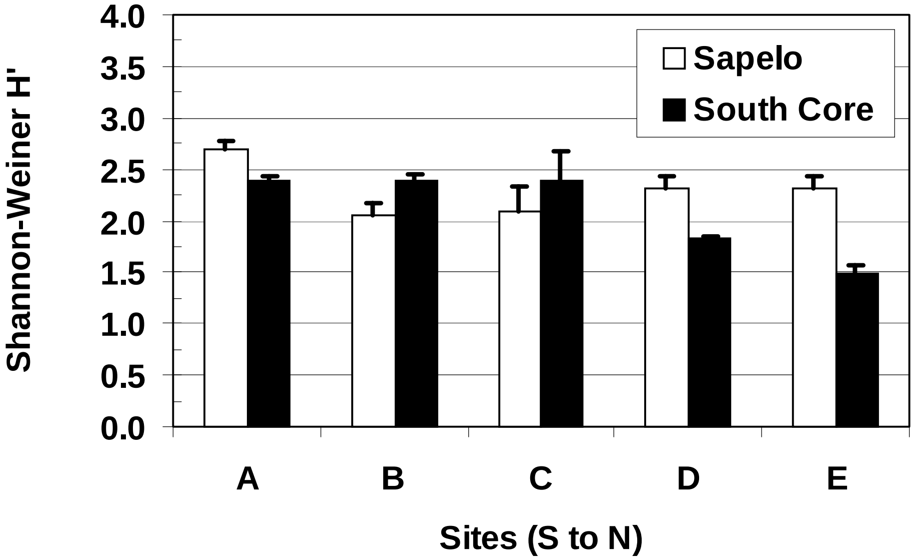
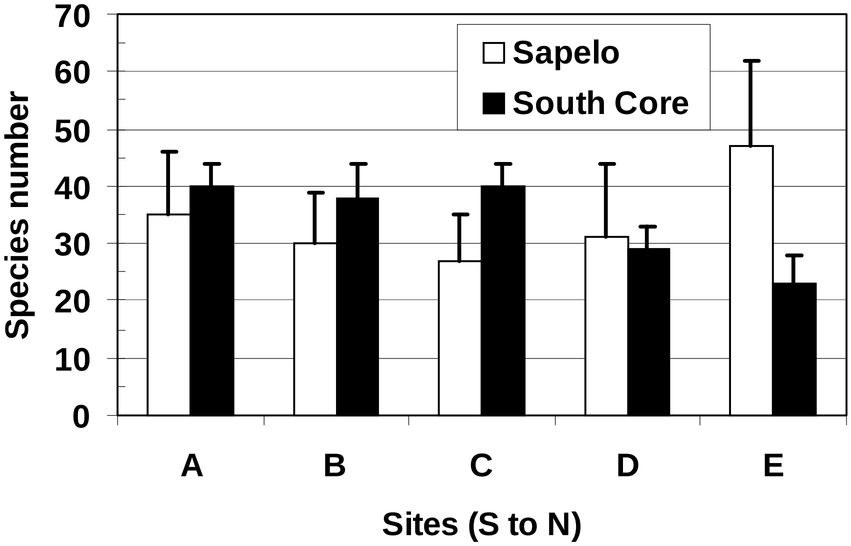

Shannon-Weiner H'
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
□ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

Figure 3.5. Mean transect species richness by site for each island. Error bars denote off-transect species.


70
60
50
40
30
20
10
0
Species number
□ Sapelo
■ South Core
A
B
C
D
E
Sites (S to N)

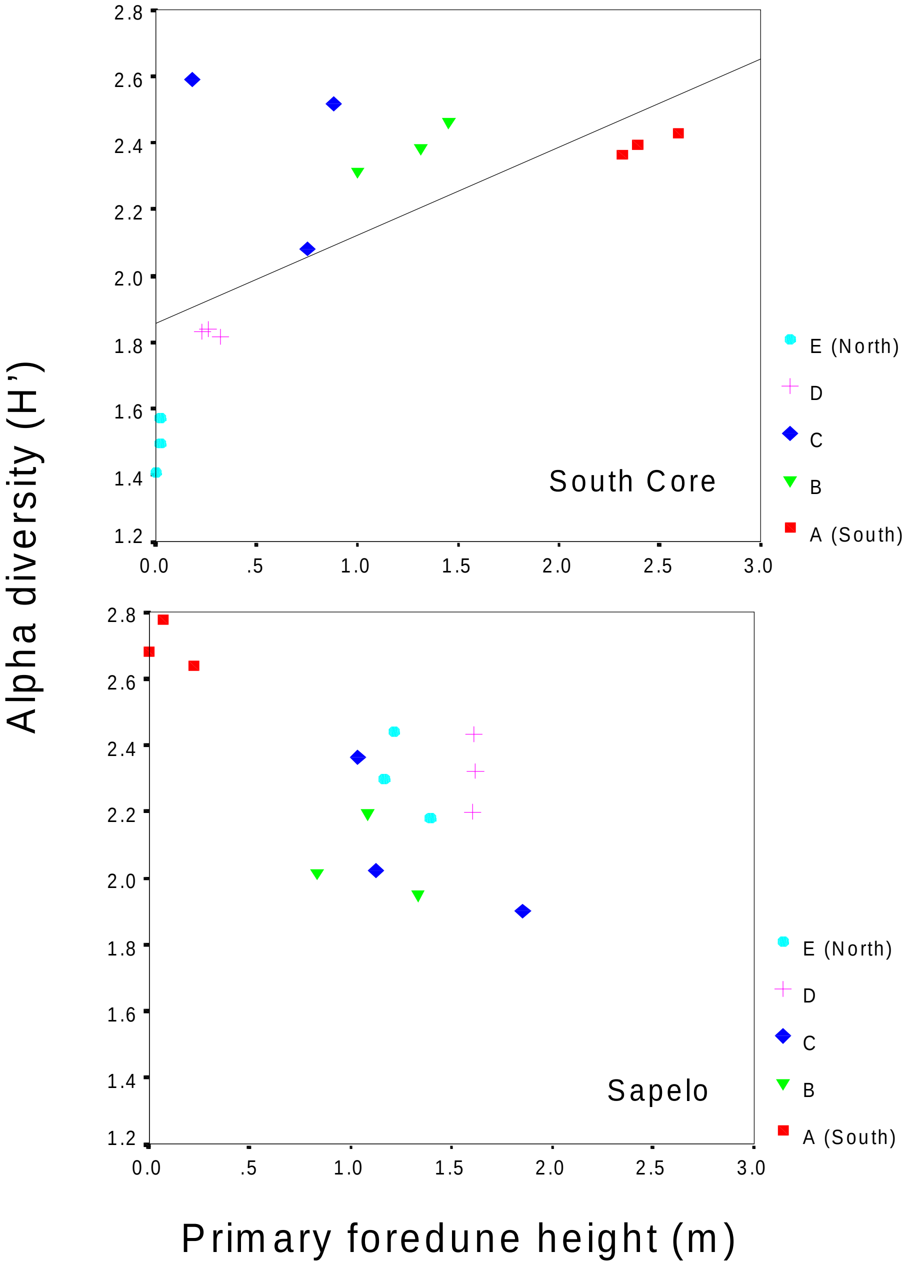
cerifera thickets that permitted the establishment of ruderal species (*Cnidoscolus stimulosus, Cenchrus* spp. *Opuntia pusilla, Cyperus* spp.*, Paspalum* spp.*, Eupatorium* spp.*, and Stenotaphrum* spp.*, Vulpina octoflora*, *Cirsium* spp). Erosion here also increased species richness by compressing dune habitats: species from wet swales (*Andropogon* spp., *Muhlenbergia filipes, Myrica cerifera, Phyla nodiflora*), inland shrub species (*Pinus* spp., *Bumelia tenax*, *Xanthoxylum clava-herculis*, *Ilex vomitoria*), and interstitial species associated with *Myrica cerifera* thickets coexisted at the site. These interstitial taxa were dominantly vines (*Ampelopsis arborea*, *Mikania scandens, Smilax* spp.*, Vitis* spp.*, Melothria pendula)* and understory species (*Phyla nodiflora, Parietaria floridana*). Mid-island sites on Sapelo had lower species richness counts, ranging from a low of 35 species at Site C to 44 at Site D. Species diversity was lowest at Site B (H′ = 2.05 ± 0.13) and Site C (H′ = 2.10 ± 0.24), while Site D (H′ = 2.32 ± 0.12) is comparable to Site E in its mean transect alpha diversity. These mid-island sites showed a decrease in the number of unique species that contributed to the high species richness and alpha diversity associated with Sites A and E. The site-level NMS plot presented in the previous chapter confirmed the distinctive compositions that developed in association with increased sediment mobility at Site A and E on Sapelo (Figure 2.13).

South Core had mean transect alpha diversities comparable to Sapelo. Alpha diversity and species richness decreased in tandem with increasing overwash disturbance from south to north on South Core. Species richness followed a similar trend, but is more equitably distributed across sites when compared to alpha diversity. Site A had the highest primary foredunes and topographic roughness of any site on both islands. A topographically-mediated coexistence of dune (including *Iva imbricata*, *Croton punctatus*) and wet swale *(Sabatia stellaris*, *Juncus marginatus, Juncus roemerianus*) species at this site generated a high within-island mean transect alpha diversity (H′ = 2.39 ± 0.03) and total species richness (Spp. = 44). Rareness among wet swale species (*Scleria* spp., *Cladonia* spp.*, Centella asiatica*) and in the understory of *Myrica cerifera* (*Phyla nodiflora Parietaria floridiana*) contributed in part to this richness. Sites B and C had the same number of species as Site A, and comparable alpha diversities. However, this diversity was expressed on profiles with lower dune heights, decreased topographic roughness, and a history of more recent overwash when compared to Site A.

Species diversity and richness at sites B and C on South Core reflected an increased abundance of annual species (*Chamaesyce* spp., *Arenaria serpyllifolia, Ambrosia artemisiifolia, Heterotheca subaxillaris, Conyza canadensis, Spenopholis obtusa, Trichostema dichotomum)* and two perennial species (*Chloris petrea* and *Commelina erecta)*. At these sites, two locally abundant species unique to South Core, *Ditrichum pallidium* and *Solidago* spp., have colonized older overwash deposits. Along-island, these two species peaked in abundance at the expense of *Spartina patens* cover. *Ditrichum pallidium* cooccurred with many of the annual and perennial species that contributed to the higher species diversity at these sites B and C were associated at the quadrat level with the moss *Ditrichum pallidium*. Declines in diversity metrics were observed for Site D (H′ = 1.8 ± 0.1; Spp. = 33) and Site E (H′ = 1.5 ± 0.1; Spp. = 28) in response to increasing overwash. At Sites D and E, *Solidago* spp. and *Ditrichum pallidium* declined in cover, and a maritime grassland dominated by the overwash-adapted species *Spartina patens* and *Hydrocotyle bonariensis* developed. The site-level NMS plot presented in the previous chapter confirmed a compositional separation of sites D and E from their southern counterparts (Figure 2.13).

MRPP of transect-level species diversity and species richness confirmed that there were no significant differences between islands in these diversity metrics (H′: T = -0.85, p = 0.15; Spp.: T = -0.22; p = 0.28); [Appendix 3.2]). In addition, MRPP of site-level species diversity and species richness, inclusive of off-transect species, was also non-significant (H′: T = -0.36, p = 0.41; Spp.: T = 0.33; p = 0.52); [Appendix 3.3]). Among the fifteen transects of each study island, there was a significant positive correlation between species richness and alpha diversity, which was more weakly expressed on Sapelo (Sap $r_s = 0.57$, $p = 0.03$; Core $r_s = 0.77$, $p < 0.001$). Spearman’s correlation coefficents revealed a high degree of multicollinearity between primary foredune height and topographic roughness on each island (Sap: $r_s = 0.88$, $p < 0.001$; Core: $r_s = 0.95$, $p < 0.001$), and I thus examine only primary foredune height as my topographic variable. The association of primary foredune height with alpha diversity was weakly non-significant and negative ($r_s = -0.49$, $p = 0.07$) on Sapelo, while this relationship was significant and positive on South Core Banks ($r_s = 0.65$, $p = 0.009$). As expected, species richness exhibited a similar trend (Sap: $r_s = -0.23$, $p = 0.40$; Core: $r_s = 0.73$ $p = 0.002$). I employed scatterplots and trendlines to summarize these correlative relationships for alpha diversity and primary foredune height (Figure 3.6). A prominent

Figure 3.6. Scatterplot of alpha diversity (Shannon-Weiner H′) and transect primary foredune height by island.


Alpha diversity (H')
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
0.0
.5
1.0
1.5
2.0
2.5
3.0
South Core
E (North)
D
C
B
A (South)
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
0.0
.5
1.0
1.5
2.0
2.5
3.0
Sapelo
E (North)
D
C
B
A (South)
Primary foredune height (m)

along-shore sequential trend of increasing alpha diversity with increasing dune heights is apparent on South Core. The along-shore structuring of alpha diversity and dune height is weak on Sapelo, but lowered dune heights show a tendency for increased levels of alpha diversity.

Discussion

I originally hypothesized that Sapelo would have reduced diversity given the longer intervals for competitive displacement by the colonizing shrub *Myrica cerifera*. To the contrary, there were no significant differences in transect-level dune plant species diversity between islands, despite strong differences in disturbance regime. At the island-level, Sapelo had a higher alpha diversity and species richness, but these island contrasts are relatively small. The lower island-level measures for species richness for South Core are in agreement with Hesp (1988), who observed a decrease in species richness as wave-energy increased along a coastal strand of southeastern Australia.

Similarity in species diversity between islands may reflect the compensatory effects of species that regulate topography and shape species coexistence. Recent studies have documented the importance of species that engineer topographies and regulate ecosystem properties (Jones *et al*., 1994, 1997; Chapin *et al*., 1997). By modifying or creating habitats, or by regulating resource use, these niche-constructing species may indirectly facilitate the coexistence of species and thus augment species diversity (Hacker and Gaines, 1997). For example, *Juncus gerardi*, a salt marsh species, has been shown to increase species diversity by ameliorating soil conditions that inhibit the establishment of other species (Hacker and Bertness, 1999). On South Core, *Spartina patens* may provide the initial stabilization of overwash sediments that permits the eventual germination and colonization of other species, particularly annuals. Most annual species on South Core show little ability to recover from overwash burial (Hosier, 1973). For sites A, B, and C, peaks in the number and cover of annual species in part contributed to their higher species diversity (Figure 2.10 and Appendices 2.4-2.6). The importance of annuals and unique species declined as overwash increased at the lower-diversity sites D and E (Figure 2.10 and Appendices 2.4-2.6). Although

Spartina patens is reduced at sites B and C, another stabilizing species peaked in cover, the bryophyte *Ditrichum pallidium.* This low-growing moss species is functionally similar to *Spartina patens* in that it has a high resilience to burial (Martínez and Maun, 1999). This may allow it to act as a secondary stabilizer to promote the successful germination of annual species in the same manner as *Spartina patens*.

On Sapelo, species coexistence is engineered by dune-building species (*Uniola paniculata*) and species that stabilize low, wet swales (*Myrica cerifera* and *Muhlenbergia filipes*). By maintaining elevational contrasts and their very distinctive habitat conditions in a positive feedback (*sensu* Wilson and Agnew, 1992), species coexistence is enhanced. On Sapelo, foredune ridges were separated by swales that were rich in inland species, including tree seedlings, that ordinarily would not be able to survive if fully exposed to salt spray or the high sand mobility at elevated or seaward positions. In this manner, the high topographic roughness expressed along the dune ridge-and-swale landforms at Site D may have contributed to a diversity of habitats at this location, and its augmented species richness. Peaks in diversity were confined to sites A and E, where dune ridge-and-swale topography co-occurred with topographies presently influenced by shoreline accretion or erosion. These shifts in shoreline position increased sediment mobility, and may have enhanced the local availability of regeneration niches (Grubb, 1977) for the increased number and cover of annual and unique species.

To a large extent, diversity patterns in this study were molded by the distinctive erosional and accretional sediment patterns that shaped the physiography of each island (Eleuterius, 1979; Clark, 1986). On Sapelo, this sediment mobility was confined to areas adjacent to tidal inlets. High diversities were fostered by accretion (Site A), and by moderate rates of erosion (Site E). On South Core, sediment mobility was more uniformly distributed over the landscape. Erosion and accretion are intertwined in the cyclical process of overwash and dune recovery (Hosier and Cleary, 1977). Where erosional conditions have led to breaching of the fronting dunes and permitted the inland deposition of overwash sediments, plant mortality reduced diversity (Sites D and E). As sediments stabilized following overwash and recovery of a protective dune line, diversity increased (Sites A-C). This suggests that decreasing sediment mobility, associated with a reduction in overwash disturbance, enhances species diversity on South Core, while an inverse relationship is expressed on Sapelo. As such, disturbance does not determine diversity; instead, it creates the opportunities for recolonization that more directly generates the patterns of diversity (Reice, 1994). These findings adds more detail to conclusions by Hayden *et al*. (1995), who noted that increasing overwash disturbance was linked to lower species diversity for a frequently-overwashed barrier island. My results suggest that an increase in overwash frequency on the infrequently overwashed landscape of Sapelo may increase species diversity. Thus the effect of disturbance on dune plant species diversity depends more upon whether or not the prevailing disturbance regime approximates that historically characteristic of a site (Denslow, 1980).

In agreement with my initial hypothesis, a significant positive correlation between primary foredune height and high species diversity was expressed on South Core. Furthermore, this correlation paralleled the along-island disturbance gradient. To a large degree, these results reflected the contrasting importance of inhibition (Egler, 1954) versus directional (or Clementsian) models of plant succession (Baker, 1995), and their geographic expression along each island. Frequent disturbance on South Core constrains patch formation to early successional stages relative to Sapelo, and thus inhibits compositional sorting derived from competitive exclusion. On the simplified topography of South Core, this fosters the strong correlative relationship between recovering dune height and alpha diversity, one that varies geographically in tandem with time since last disturbance. On Sapelo, the development of a dune-and-ridge topography during the longer intervals between disturbance increases topographic complexity. In consequence, there is more topographically-mediated diversity in habitats, and potentially more directional sorting of vegetation through time along these topographic gradients. This, in effect, decouples the co-developmental linkage among disturbance, dune height, and vegetation recovery. Therefore, diversity and the fronting dune height show a weak association along-island. The unique biogeomorphic feedback and threshold responses that develop on each island may act to perpetuate these patterns. The low resistance landscape of South Core reinforces overwash and inhibition structuring, while on Sapelo, high morphologic resistance dampens overwash and may permit more directional sorting of vegetation. Nevertheless, I caution that separating disturbance effects from the feedbacks that may reinforce or dampen them is problematic.

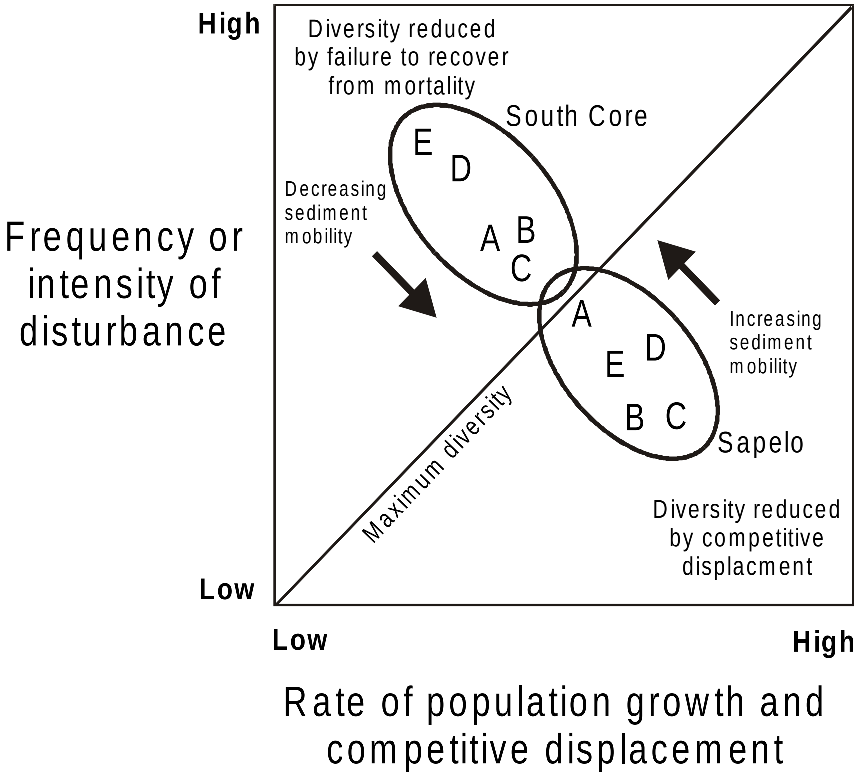
The explanatory effectiveness of IDH varied within islands. On South Core, a systematic, along-island asynchrony in disturbance exposure roughly approximated a geographic expression of IDH. Alpha diversity showed a weak peak mid-island at sites C and B, where dune topographies suggested an intermediate time interval since the last overwash event. Similar systematic, linear responses have been observed in tallgrass prairie (Collins, 1992) and riparian environments (Bendix, 1997). IDH was clearly an ineffective concept for explaining between-patch diversity patterns on Sapelo. Here, IDH bears no obvious systematic spatial expression among the sites investigated for both alpha diversity and species richness. As a between-site concept for examining diversity patterns, IDH may be more applicable to environments such as South Core, where asynchronous and frequent disturbance promoted a geographic consistency in diversity patterning. The between-patch application of IDH fails on Sapelo, in part because an intermediate level of disturbance cannot be geographically defined at the scale applied in this study. These findings underscore the dependence of IDH upon the scales encompassed by the research design (Bendix, 1997).

However, consideration of scaling effects imposed by methodological design alone overlooks an equally important relationship in assessing the application of IDH: changes in the spatial and temporal-scale expression of processes controlling diversity may be regulated by the ecological components of the system under study. A potential weakness of IDH is its assumption of a strongly coupled responses between disturbance, recovery, and diversity along a disturbance gradient. In this study, comparing diversity along a regional gradient in shore disturbance is complicated by the fact that biogeomorphic feedbacks and threshold processes, operating in the intervals between infrequent disturbance, may change the responses to extrinsic disturbance, and introduce intrinsic processes that regulate diversity patterns on different spatial and temporal scales. IDH addresses only extrinsic disturbance, and does not incorporate intrinsic processes (Shiel,1999), or their subsequent modification of disturbance. The self-organizing properties exhibited by biogeomorphic systems suggests that the geographic delineation of an intermediate level of disturbance frequency or magnitude is likely to be more variable in time and space than previously assumed.

In this manner, IDH structuring is weakened by complex responses along disturbance gradients. As outlined by Schumm (1973, 1979) for complex responses in fluvial systems, the existence of thresholds and feedback responses in [bio]geomorphic systems ultimately determines the effects of a disturbance event. The application of disturbance along a disturbance gradient will not have the same result everywhere, especially as the system to which the disturbance is applied is itself changing through time. On Sapelo, during the longer intervals between disturbance, diversity may not necessarily be dramatically reduced by the increasing competitive dominance of *Myrica cerifera,* as I originally hypothesized. Instead, processes operating at temporal and spatial scales other than those encompassed by overwash more directly constrain the expression of diversity. Incremental transport of sediment shapes dune ridge-and-swale topography, and the subsequent coexistence of species according to elevational contrasts. *Myrica cerifera* may competitively displace more diminutive herbaceous wet swale species, but these shrubs also increase diversity through their role as host to interstitial vines and understory species. Additionally, intrinsic patch dynamics associated with the senescence of older *Myrica cerifera* thickets (Crawford and Young, 1998) may increase species diversity through the establishment of ruderal species, forbs common to wet swale habitats, or woody seedlings of coastal tree species in newly-formed gaps.

DEM can be qualitatively employed to illustrate how contrasting frequencies of disturbance can foster equivalent species diversities given differing rates of competitive displacement (Figure 3.7). Sapelo had a lower disturbance frequency and a higher rate of competitive displacement, as inferred from the increased abundance of competitively dominant species that can colonize low sites in the absence of frequent overwash *(Muhlenbergia filipes, Myrica cerifera*). Lower diversities at Sites B and C are associated with increased cover of these *k*-selected species. Higher diversities at sites A and E reflect the lessening of local competitive pressures, and an increasing importance of sediment mobility and the availability of regeneration niches as controls of diversity. By contrast, South Core has a higher frequency of disturbance and a lower rate of competitive displacement. In this setting, mortality from overwash constrains the expression of diversity. At sites D and E, diversity is reduced by failure of local populations to recover from frequent or recently imposed overwash. *Spartina patens* was the dominant species at these sites. With reduction in overwash at Sites A, B, and C on South Core, and the concomitant stabilization of

Figure 3.7. A generalized model of the Dynamic Equilibrium Model for site alpha diversity on South Core Banks, North Carolina and Sapelo Island, Georgia. Site A is the southernmost site on each island, Site E is the northernmost.


High
Diversity reduced by failure to recover from mortality
South Core
E
D
Decreasing sediment mobility
A
B
C
Frequency or intensity of disturbance
A
E
D
Increasing sediment mobility
B
C
Sapelo
Maximum diversity
Diversity reduced by competitive displacment
Low
Low
High
Rate of population growth and competitive displacement

sediments, species diversity is enhanced by the potential dispersal or germination of species. DEM also provides a better template for framing spatial controls of diversity. On Sapelo, diversity may be reduced by the local expression of competitive outcomes. The potential augmentation of diversity near tidal inlets (Sites A and E) is a function of larger-scale processes, such as dispersal, size of the species pool, or habitat heterogeneity. Habitat heterogeneity is often cited as a factor that influences species richness and diversity (Nichols *et al*., 1998; Burnett *et al*., 1998). On South Core, diversity patterns are constrained locally by the physiological inability of most populations to recover from high frequencies of disturbance. On South Core, decreased sediment mobility fosters development of regeneration niches that may potentially augment diversity through these same larger scale processes for Sites A, B, and C. As noted by Bendix (1997) and Baker (1990), diversity is constrained not only by time since disturbance, but also by the length of time for dispersal, and the location of potential colonizer sources areas in the landscape.

Conclusions

No significant overall differences in dune plant species diversity developed between two barrier islands differing in their exposure to storm-generated overwash. Different temporal and spatial forcings of sediment mobility on each island, and the biogeomorphic feedbacks and thresholds that may maintain or dampen sediment mobility, contributed to the observed equivalency in species diversity. In terms of species diversity per unit area, Sapelo was by far the more diverse dune habitat, given its smaller dimensions. On South Core, successional inhibition, and the biogeomorphic processes that reinforce this inhibition, maintain a regularity in the distributional pattern of along-shore species diversity that is strongly correlated to primary foredune height. Sapelo represents a landscape characterized by greater directionality in compositional sorting, and in the biogeomorphic reinforcement of this sorting. This fostered a fine-spatial scale differentiation of landscape patterns of species diversity that was less strongly correlated to the topographic metrics applied in this study.

Discrepancies between disturbance exposure and expression of effects may develop along disturbance gradients from the self-organizing properties of biogeomorphic systems. As a result, any intermediate level of disturbance may be more variable geographically, and more species-dependent, than previously assumed. It is surprising that IDH remains so widely invoked given its assumptions of linear process and response. Its appeal lies in its simplicity, and in its validity in environments where inhibition of patch dynamics maintains a regularity in composition at a scale that facilitates observation and measurement. IDH, however, erroneously assumes a geographically consistent, direct relationship between disturbance exposure and effect. As such, it is a circular argument, one that limits insight into the interplay of extrinsic and intrinsic controls of species diversity patterns (Huston, 1994). Mechanisms controlling species diversity in response to disturbance are not the same as those affecting post-disturbance succession (Collins and Glenn, 1997). In this manner, biogeomorphic feedback and threshold behaviors, recolonization (Glenn and Collins, 1992; Reice, 1994) and species adaptations (Bendix, 1999) intercede in shaping disturbance effects following exposure. I suggest that the Dynamic Equilibrium Model is a more robust conceptual tool for framing diversity patterns on both of my study islands, given that it defines an ‘intermediate’ frequency of disturbance exposure independently of its effects on species diversity. The Dynamic Equilibrium Model has greater flexibility in framing geographic variability in disturbance regime, species adaptations, and the scaling of controls of diversity.

Vegetated environments where there is a rapid equilibration of process and form may be ideal for examining how species diversity is shaped by species interactions that in turn regulate the environmental conditions that support this diversity. On each island in this study, the expression of diversity was constrained not only by disturbance, but also by the biogeomorphic responses to disturbance that regulated topography. I suggest that future research in barrier island dune habitats and along riparian corridors evaluate the relative contribution of biogeomorphic feedbacks and threshold responses, rather than rates of disturbance or vegetation recovery along gradients alone, as the agents that mold landscape patterns of species diversity.

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CHAPTER 4

DUNE SOIL AND VEGETATION PATTERNS IN TWO BARRIER ISLAND GEOMORPHIC ENVIRONMENTS

Overview

I compare key edaphic variables and the strength of the association between these edaphic variables and species cover for the dune habitats of two geomorphically distinctive barrier island morphologies in the Georgia Bight. Vegetation and soils were sampled within strip transects aligned perpendicular to the shoreline at study sites parsed along a frequently storm-overwashed microtidal (South Core Banks, North Carolina) and an infrequently overwashed mesotidal (Sapelo Island, Georgia) barrier island. Non-parametric tests of island differences (MRPP) indicated strong significant differences between islands in particle size, pH, and carbonate content, while organic matter was not significantly different. PCA and broken-stick eigenvalue assessment of variance in the soil data of each island revealed differences in the dimensionality of nontrivial principal components, and their captured variance. I suggest that these differences in underlying data structure reflect increased edaphic organization among soil variables on Sapelo, while frequent overwash dampens edaphic organization on South Core. Mantel tests indicated that Sapelo had relatively stronger associations between soil parameters and vegetation cover. However, these stronger associations may not necessarily be the result of greater edaphic organization. Frequent overwash on South Core precluded a strong organization among individual soil variables, but species correlations were shown to be as responsive to variability in edaphic properties as on Sapelo. These significant correlations between edaphic variability and the dune-building and sediment-stabilizing taxa on both islands reinforces the importance of these species as biotic engineers of topographically-defined habitats.

Introduction

Coastal dune habitats are dynamic biogeomorphic settings. Sediment mobility shapes the physical and chemical properties of dune soils (Gerrard, 1992) and the accompanying patterns of landforms and vegetation (Maun and Perumal, 1999; Moreno-Casasola, 1986; Martínez *et al.*, 1997). Over large geographic scales, sediment mobility has been used as a criterion to categorize barrier islands (Hayes, 1979; Zaremba and Leatherman, 1986). Two broad barrier island morphologies have been well documented along passive continental coastlines, based largely upon their contrasts in the geomorphic agents that mobilize sediments (Fisher, 1982). Episodic, overland transport of sediments during storm-driven overwash is common to wave-dominated microtidal barrier island morphologies. By contrast, incremental processes of sediment transport predominate on mixed-energy mesotidal barriers, where overwash is infrequent and spatially restricted.

To date, few studies have described differences in dune soil characteristics, and their association with plant species patterns, for these two barrier island morphologies. Well-documented contrasts in barrier island morphology within the Georgia Bight provide an ideal setting to examine these relationships. Overwash deposition in dune habitats on the wave-dominated microtidal barrier islands of the Outer Banks of North Carolina resets pedogenic development to an earlier stage (Hosier, 1973). By contrast, infrequent disturbance in the dune habitats of the mixed-energy mesotidal barrier islands of Georgia may enhance pedogenic development given the longer intervals without massive deposition of overwash. Dune pedogenic development in this study does not imply a horizonation of the soil profile as manifested over long temporal scales (*sensu* Walker *et al*., 1981), but instead the extent to which individual edaphic properties covary in the absence of overwash disturbance. This covariance, as a measure of edaphic interaction or organization, should be more fully expressed on Sapelo. Here, dune ridge and swale formation should reinforce the sorting and interaction among key edaphic variables.

In this paper, I examine the relationships between soil properties, the extent of their organization, and their correlation with species cover for two geomorphically distinctive barrier island environments. My first research objective is to characterize differences in dune soils between island morphologies. I investigate these questions: 1) Are there significant differences in measured soil properties between island morphologies? 2) Do barrier island morphologies exhibit differences in the degree of interaction, or organization, among these edaphic variables? My second research objective addresses variation in the strength of the soil-vegetation relationship between island morphologies. The specific question I investigate is: 1) Do soil properties differ in their correlation with vegetation cover on different barrier island morphologies? I examine this last question in light of the dichotomy of mechanisms, pedogenic versus geomorphic, that regulate edaphic organization and variability on each island. I expect that geomorphic inputs from frequent overwash in the Outer Banks of North Carolina should engender a distribution of patches of differing ages along-island that interrupts and dampens the organization and subsequent influence of soil properties on compositional patterns. By contrast, less frequent overwash disturbance of the mesotidal barriers along the Georgia coast, permits greater compositional sorting and pedogenic development along local environmental gradients. I expect that this setting should enhance the correlation and variability among key edaphic properties such as pH and particle size, and engender a stronger association between soil and species cover.

Background

Most studies of coastal dune vegetation have stressed the importance of sediments as an autogenic and an allogenic regulator of compositional patterns. Martínez *et al.* (1997) noted that the mobility of dune sediment regulates both local resource availability, while also acting as a disturbance agent. Autogenic regulation of dune compositional patterns is exemplified in the prominent transverse (across-island) edaphic gradients that typify sandy coastal strands. Sediment mobility, particle size, and pH typically decrease away from the strandline (Hesp, 1991; Moreno-Casasola, 1986). The concentration of the major limiting nutrients in barrier island dune systems is positively correlated with organic matter, which increases with increasing distance from the strandline (Ranwell, 1972; Ehrenfeld, 1990). Leaching of these nutrients increases with increased particle size (Hesp, 1991). These transverse edaphic variables interact to shape autogenic compositional patterns, through their distribution as a function of distance inland, and as a function of elevation and the protectivity afforded by dune profiles. Low protected dune microhabitats abate harsh maritime gradients, and shape environmental conditions that may approximate more inland locations. By contrast, the allogenic regulation of compositional patterns, in association with periodic cyclonic forcings of overwash, exposes dune species to mechanical injury over an extensive land area, and obscures the influence of distance and microhabitat-regulation of edaphic and compositional patterns. With the deposition of fresh substrate during overwash, pedogenic development is reset. In these high-energy coastal environments, patterns of sediment mobility associated with overwash exert relatively more control on landscape compositional patterns (Hosier and Cleary, 1977; Godfrey *et al.*, 1979).

Study Area

Central to this study is the pronounced morphometric variability in barrier islands that develops along the Georgia Bight (Figure 2.1). On microtidal coasts along the margin of bights, or embayments, barrier islands are long and linear, as exemplified by the Outer Banks of North Carolina (Figure 2.2). On mesotidal coasts at the center of bights, barrier islands are short and wide with numerous tidal inlets, as exemplified along the coast of Georgia (Figure 2.3). These contrasts in island morphology, coupled with climatological gradients of increased exposure to extratropical cyclones with increased latitude in the winter season (Davis *et al.*,1993), yield a strong geographic continuum of disturbance regimes along the southeastern U.S. Atlantic coast (Mather *et al.*, 1964; Fox and Davis, 1976; Riggs, 1976; Hayes, 1979; Godfrey *et al.*, 1979; Williams and Leatherman, 1993).

Striking biogeomorphic feedbacks develop among islands along this morphometric and climatological gradient (Godfrey 1976). Storms and waves are the agents that mobilize sediments on the microtidal barrier island of the Outer Banks of North Carolina. Here, even mild winter storms or offshore hurricanes can produce overwash (Hosier, 1973). Once deposited, the mobility of overwash sediments is mediated by the presence of the gap species *Spartina patens*, and by the formation of a shell lag. *Spartina patens*, a rhizomatous perennial, has a high tolerance to burial that permits it to recover and stabilize overwash deposits quickly. As such, *Spartina patens* reinforces overwash events by perpetuating a flat topography and by stabilizing a portion of the sediments that would otherwise be directly diverted for dune reestablishment. In the intervals between disturbance, deflation of fine sand-sized particles 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 (Hosier, 1973).

By contrast, sediment mobility on the mixed-energy mesotidal barrier islands of Georgia is strongly controlled by tidal inlets (Hayes,1979; Fenster and Dolan, 1996). Tidal inlets serve as natural safety valves that dampen overwash during periods of infrequent high storm surge (Riggs,1976; Sexton and Hayes, 1991). These tidal inlets also influence the patterns of local-scale sediment mobility. Given an abundant supply of sediment and low wave energy, extensive beach ridges may accrete parallel to the shoreline (Oertel and Larson, 1976; Hayes, 1994). Beach ridges (or dune ridges when they occur at more inland positions) are topographic features implying local controls on shoreline dynamics. Numerous models of dune ridge formation emphasize the role of positive feedbacks between vegetation cover and aeolian deposition in their formation and stability (Taylor and Stone, 1996). In this positive feedback process, the accumulation of sand stimulates plant growth. This in turn increases sand entrapment, fostering continued plant growth, and an increase in elevation relative to areas where dune species are absent (Woodhouse, 1982).

In each of these two regionally-distinctive geomorphic settings, topographies and the species that engineer these topographies are maintained in a positive feedback (*sensu* Wilson and Agnew, 1992). The sediment-stabilizing adaptations of *Spartina patens*, and the sequestering of dune sediments under deflation lags, reinforces exposure to overwash by perpetuating a low-relief topography. The low resistance of this landscape enhances exposure to overwash, and thus perpetuates the conditions under which overwash landforms and species are expressed. In this setting, soil properties and the degree of their organization are therefore subject to periodic disruption and rearrangement from overwash deposition. By contrast, along well-developed ridge-and-swale topography, elevational contrasts are perpetuated. Dune-building species generate topographic relief by trapping wind-blown sediments, while wet swale species such as the woody shrub *Myrica cerifera* bind and anchor sediments at low elevations. The high roughness of this topography further dampens exposure to overwash events, and thus perpetuates the conditions under which this topography and the accompanying species are expressed. As a result, a suite of soil variables, sorted among distinctive topographic-vegetation habitats, can develop uninterrupted by landscape-scale disturbance.

Two islands were selected for study: the wave-dominated microtidal barrier of South Core Banks, North Carolina, and Sapelo Island, Georgia, a mixed-energy mesotidal barrier (Figure 2.4). These islands are largely undeveloped, with limited emplacement of dune or shore stabilization structures. Sapelo is a complex of individual islands (Mathews *et al*., 1980). I confined my sampling on Sapelo to the 5 km of Nannygoat Beach on the southernmost Holocene island so as to minimize the confounding influence of multiple tidal inlets. Here, overwash is infrequent (Deery and Howard, 1977) and restricted to a small area on the south end of the island. South Core Banks, part of Cape Lookout National Seashore (CLNS), is a retreating Holocene barrier. Overwash increases in frequency and intensity from south to north along this microtidal island. Numerous studies have established that the dominantly quartz sands of Georgia beaches are finer-grained, and lower in calcium carbonate when compared to the higher energy barrier environments in North Carolina (Johnson *et al*., 1974).

Methods

Field sampling

Five sites (A through E from south to north), each containing three randomly-positioned strip transects, were parsed along the north-south axis of each island. In order to capture the compositional and edaphic variation along a gradient of exposure to oceanic inputs, each transect began at the high water mark and extended inland through the width of dunal microhabitats to the first occurrence of extensive thickets of the woody shrub *Myrica cerifera*. *Myrica cerifera* invades herbaceous habitats as disturbance intensity and frequency are reduced (Young *et al.*, 1995). Vegetation cover was collected at meter intervals in a 1 x 2-m quadrat with a 2-m point-frame sampler centered perpendicular to the transect. Along this point-frame sampler, species presence was measured at 10 cm intervals, for a total of 20 observations. Point-frame hits at each transect sampling point were summed for individual species and expressed as percent absolute cover. To maintain comparable sampling intensities between islands, the longer distances to stabilized vegetation on South Core Banks required that quadrats be systematically parsed in intervals of every other meter. Soil samples were collected at 10-cm depth from each of the landforms (primary foredune, secondary foredune, wet swales, overwash flats, interdunal flats) situated along the vegetation sampling points of each transect. Because landforms varied in extent among transects, I parsed my soil sampling so that the distance between successive soil collection points on a transect did not exceed 10m on Sapelo, and 20 meters on South Core. In this manner, a total of 6-10 soil samples were collected for each of the 15 transects per island.

Laboratory methods

For each soil sample, I determined particle size distributions, pH, and percent content by weight of organic matter and carbonate. After oven-drying soil samples for 24 hours @ 95° C, wet and dry sieve analysis was used to determine particle sizes in four classes: granules plus coarser-grained material (> 2 mm), very coarse to medium sand (< 2 and > 0.25 mm), very fine to fine sand (< 0.25 and > 0.0625 mm) , and silt-clay (< .0625 mm). All particle size distributions included the potential contribution of carbonate shell fragments. Soil pH was measured with a hand held, electronic pH-meter using a 1:1 ratio to distilled water mixture following procedures in the Soil Survey Laboratory Manual (USDA, 1992). Soil organic matter, as a proxy measure of soil nutrient status, was measured using loss on ignition (LOI; Dean, 1974). In this procedure, oven-dried (24 hours @ 100°C) soil is burned in a muffle furnace for one hour at 550°C. The difference in weight between the dried and burned soil sample is used to calculate organic matter indirectly. I employed a HCl digest (1:1 dilution) of the silt and sand fraction for each sample to determine percent calcium carbonate. Samples were dried and preweighed and placed in HCl for one hour. After rinsing and drying (24 hours @ 95° C and 24 hours @ 100°C) the remaining sand fraction was reweighed to obtain an indirect measure of percent calcium carbonate.

Data analysis

To test for significant differences between islands in each of the measured soil variables, I used multiresponse permutation procedures (MRPP). MRPP is a non-parametric, distance-based test of group differences. A shortcoming of many widely used statistical tests is the lack of congruence between the geometry of the data space, which is for the most part Euclidean, and the geometry of the analysis space, which in many standard parametric and non-parametric tests is not Euclidean. Lack of congruence between the geometries of the data and analysis space can lead to errors in data interpretation (Biondini *et al.*, 1991). The strategy of MRPP is to compare the weighted average within-group soil variable distances with the average distance that would have resulted from all other possible combinations of the data. As such, MRPP tests for differences based on the collective distribution of data for each group rather than their respective means (Biondini *et al*., 1991). All MRPP significance tests were conducted at the .05 level in PC-Ord Version 4.04 (McCune and Mefford, 1999).

To ascertain the degree to which each barrier island morphology exhibited differences in edaphic organization, I used principal components analysis (PCA). 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, variables were square-root transformed to minimize departures from normality. I performed a standardized PCA on a sample-by-soil variable data matrix from each island. Each island-level PCA produced a series of ranked eigenvalues that describe the percent of sample variance captured by each axis, or principal component. The eigenvalue for each principal component was compared 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 (Jackson, 1993). Principal components are considered useful, or nontrivial, if their eigenvalue exceeds that of their broken-stick counterpart. Legendre and Legendre (1998) suggest that only those eigenvalues that are larger than the values predicted by the null broken-stick model should be selected for interpretation.

I hypothesized that overwash engenders a distribution of patches of differing ages along-island that interrupts and dampens island-scale consistency in edaphic properties and their interrelationships. By contrast, less frequent overwash disturbance should permit greater pedogenic development along local environmental gradients. I expect that this less disturbed setting should enhance the correlation between key edaphic properties. In terms of PCA, I expect that a larger portion of the variance in the soil data on Sapelo can be summarized in a lower dimensionality, and that interpretable factor loadings of soil variables will be concentrated on these lower dimension principal components. On South Core, less correlation among measure soil variables due to the rearranging influence of overwash and deflation should necessitate a higher dimensionality in order to capture the variance expressed with these samples. In sum, lower dimensionality and larger captured variance are indicative of more potential organization among edaphic variables. PCA tests were performed in PC-Ord Version 4.04 (McCune and Mefford, 1999).

To determine the strength of the association between soil properties and corresponding species cover for each island, I employed Mantel tests (Legendre and Legendre, 1998). Mantel tests evaluate the correspondence between two groups of measured variables from the same set of sample units. This multivariate technique correlates the ranked distances between sample units obtained from distance matrices calculated from each group of measured variables. For this analysis, distance matrices were calculated for quadrat soil variables and their percent relative species cover from the subset of sample points on each island in which both of these parameters were sampled. Mantel tests can accommodate both parametric and non-parametric correlation coefficients. I selected Spearman's correlation coefficients (r_s) to measure the agreement between these distance matrices for each island (Dietz, 1983). For each island, I performed Mantel tests for species cover and all of the soil variables, and for species cover and each individual soil variable. Monte Carlo tests ($n = 999$) were employed to determine the significance of this correlation. One-tailed Mantel test's were conducted in R Package Version 4.0 (Legendre and Casgrain, 1999). In terms of vegetation dynamics theory, frequent overwash on South Core should impose a perpetual nonequilibrium state between local edaphic factors and plant species composition. I hypothesized that this would result in a weaker multivariate correlation between soil variables and species cover.

By contrast, infrequent overwash on Sapelo should allow compositional adjustment to site conditions. This permits local edaphic variables to predominate in controlling species patterns. Therefore, I hypothesized that stronger correlations between soil and species cover should develop on Sapelo.

Mantel tests and my PCA results alone will not indicate whether any increased edaphic organization on Sapelo is more strongly associated with its species cover. For this reason, I also examined the bivariate correlation between individual species and axis scores from their nontrivial principal components using Spearman's rank correlation coefficients. In this manner, I addressed the degree to which individual species responded to the variability in edaphic properties expressed on nontrivial principal components. Because only a limited number of soil samples were taken, I examined this relationship only for species that were present at fifteen or more of the sampling points from which I collected my soils. I expected that infrequent overwash on Sapelo, and the edaphic organization that develop in this setting, should lead to greater species sorting along the edaphic variability captured along the first principal component. I anticipated that a larger range of correlation coefficients would characterize the relationships between species cover and the corresponding principal component axis scores for this island. Because pedogenic properties on South Core may be structured more frequently by disturbance, with consequently lower edaphic organization, species should exhibit less responsiveness to edaphic variability. I anticipated a smaller range in the sign and magnitude of my correlation coefficients in this setting. My results from this particular analysis should be viewed cautiously given the small number of soil samples, and the reduced number of species occurrences associated with those samples. Furthermore, PCA, as a tool to partition variance among several components, may not necessarily parcel variance in a way that it is ecologically meaningful.

Results

A total of 140 soils from Sapelo and 136 from South Core were collected from vegetated sample points along the transects of each island. Sapelo dune soils exhibited a high degree of sorting. Soil textures here were dominated by the fine to very fine sand fraction (mean percent sample content = 96.3 ± 2.0) (Figure. 4.1). By contrast, South Core soils were characterized by a range of textural classes, of which very coarse to medium sands (54.3 ± 8.3%) and fine to very fine sands (42.9 ± 8.3%) were the more abundant. Furthermore, particles > 2 mm were found in 55 of the 136 samples on South Core (3.8 ± 5.2%). These coarse textures were exclusively shell fragments deposited during overwash. Sapelo had only two samples with > 2mm-sized shell fragments, each with a percent content less than 1%. Surprisingly, the mean percent content of the silt-clay textural class was higher on South Core (Sapelo = 0.9 ± 0.5%; South Core = 1.4 ± 0.6). Soils on South Core also exhibited a higher mean pH (Sapelo = 6.6 ± 0.8; South Core = 7.8 ± 0.5) and percent carbonate content (Sapelo = 2.4 ± 0.8; South Core = 3.8 ± 2.8). Organic matter was predictably low in these sand-dominated environments. Mean sample content was less than 1% for both islands.

MRPP island comparisons for each soil variable, as based on sample-level data (Sapelo = 140; South Core = 136), indicated significant differences between islands for all but one variable, organic matter (Table 4.1). Sand fractions, silt-clay, pH, and carbonate content were significantly different between islands.

Principal components analysis

PCA indicated contrasts between islands in their dimensionality and captured variance. Because Sapelo had only two samples with > 2 mm sized particles, this textural class was deleted from the PCA of Sapelo soil variables. Comparison of principal component eigenvalues with their broken-stick values for Sapelo indicated that only the first principal component (PC1) captured more variance than that expected by chance (Table 4.2). PC3 had a broken stick eigenvalue slightly less than that obtained by the PCA. Given that the difference between these two values was slight, and I decided to exempt this component from my analysis. PC1 on Sapelo captured 51% of the total variance among soil samples. This component’s factor loadings indicated that pH and percent fine to very fine sands were inversely associated with organic matter and very coarse to medium sand. The results of my PCA for South Core indicated that only the second and third

Figure 4.1. Box plots for soil variables.

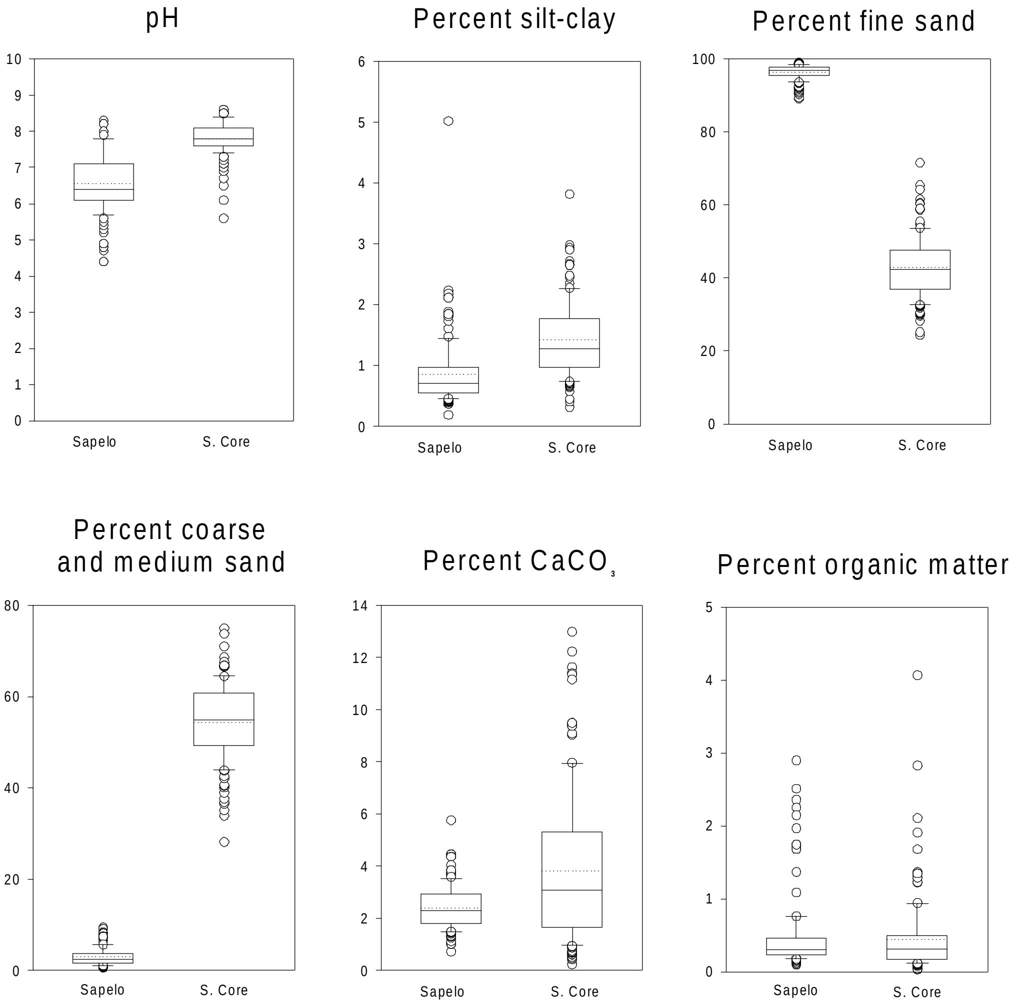

pH
10
9
8
7
6
5
4
3
2
1
0
Sapelo
S. Core
Percent silt-clay
6
5
4
3
2
1
0
Sapelo
S. Core
Percent fine sand
100
80
60
40
20
0
Sapelo
S. Core
Percent coarse and medium sand
80
60
40
20
0
Sapelo
S. Core
Percent $CaCO_3$
14
12
10
8
6
4
2
0
Sapelo
S. Core
Percent organic matter
5
4
3
2
1
0
Sapelo
S. Core

Table. 4.1. Mean soil variables by sit and MRPP statistics.

Location	pH	Percent silt-clay	Percent fine-very fine sand	Percent coarse-medium sand	Percent carbonate	Percent organic matter
Sapelo						
A	7.2 ± 0.5	1.1 ± 0.9	96.8 ± 1.4	2.1 ± 1.2	3.5 ± 0.8	0.32 ± 0.21
B	6.6 ± 0.7	0.6 ± 0.2	96.4 ± 1.3	3.0 ± 1.3	2.2 ± 0.6	0.32 ± 0.17
C	6.2 ± 0.6	0.9 ± 0.4	94.6 ± 2.5	4.5 ± 2.2	2.0 ± 0.5	0.49 ± 0.54
D	6.8 ± 0.6	0.6 ± 0.2	97.3 ± 1.7	2.1 ± 1.6	2.1 ± 0.6	0.31 ± 0.15
E	6.0 ± 0.9	1.1 ± 0.5	96.2 ± 2.1	2.7 ± 1.9	2.2 ± 0.8	0.83 ± 0.75
Island mean	6.6 ± 0.8	0.9 ± 0.5	96.3 ± 2.0	2.9 ± 1.9	2.4 ± 0.8	0.46 ± 0.48
South Core						
A	7.6 ± 0.7	1.3 ± 0.5	40.6 ± 6.8	58.0 ± 6.9	2.2 ± 1.3	0.53 ± 0.62
B	7.7 ± 0.5	1.5 ± 0.6	40.9 ± 7.4	53.7 ± 7.8	5.1 ± 3.7	0.57 ± 0.72
C	7.8 ± 0.3	1.6 ± 0.7	44.3 ± 7.0	52.6 ± 7.5	4.6 ± 2.6	0.47 ± 0.28
D	8.0 ± 0.4	1.4 ± 0.5	42.0 ± 9.4	56.0 ± 9.0	4.7 ± 2.5	0.34 ± 0.29
E	7.9 ± 0.3	1.3 ± 0.7	46.8 ± 10.0	51.1 ± 9.3	2.4 ± 2.1	0.29 ± 0.45
Island mean	7.8 ± 0.5	1.4 ± 0.6	42. 9 ± 8.3	54.4 ± 8.3	3.8 ± 2.8	0.44 ± 0.52
MRPP						
T	-98.44	-48.04	-188.51	-188.47	-27.81	-0.12
P	0.00*	0.00*	0.00*	0.00*	0.00*	0.31
Distance Sapelo	0.89	0.47	2.16	1.99	0.92	0.38
Distance Core	0.50	0.68	9.31	9.39	3.04	0.41

Note: * = MRPP significantly different at $p < .05$. Distance is mean Euclidean inter-transect distance.

Table. 4.2. PCA output for Sapelo soil variables.

Axis	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	3.08	51.31	51.31	2.45
2	1.38	22.92	74.24	1.45
3	0.96	15.93	90.17	0.95
4	0.41	6.83	97.00	0.62

	PC1	PC2	PC3	PC4
pH	-0.4453	0.2406	0.3894	0.5263
Coarse-medium sand	0.4193	0.4993	0.3038	-0.2186
Fine sand	-0.4814	-0.3309	-0.3645	-0.0174
Silt-clay	0.373	-0.4616	0.324	0.625
Carbonates in sand fraction	-0.2347	-0.4334	0.6927	-0.5261
Organics	0.4472	-0.4272	-0.1961	-0.087

principal components captured a percentage of sample variance larger than that predicted by the broken-stick null model (Table 4.3). PC2 captured 32% of the sample variance after extraction of the trivial variance associated with the first principal component. Factor loadings for this second component also expressed an inverse relationship between pHand organic matter. In contrast to Sapelo, high particle size loadings were not associated with this component's variability in pH and organic matter, with the exception of a weak loading for silt-clay. PC3 captured 22% of the sample variance, and expressed a strong inverse relationship between the particles > 2mm and the coarse sand fraction.

Mantel tests

Mantel tests indicated numerous significant but weak correlations between the soil variables and vegetation cover on each island (Table 4.4). In agreement with my initial hypothesis, Sapelo had a relatively stronger correlation ($r_s = 0.14$, $p < 0.05$) between the suite of soil variables and species cover in comparison to South Core ($r_s = 0.04$, $p < 0.05$). Each of the individual soil variables were significantly correlated with species cover on Sapelo with the exception of very coarse to medium sand, which averaged < 3% across samples. Fine sands and carbonates had low correlation coefficients, and are of little interpretive value. pH had the highest correlation with species cover on Sapelo ($r_s = 0.30$, $p < 0.05$), followed by percent organic matter ($r_s = 0.27$, $p < 0.05$). On South Core, silt-clay ($r_s = 0.21$, $p < 0.05$) and organic matter ($r_s = 0.18$, $p < 0.05$) had the highest correlations with species cover. The Mantel statistic for > 2 mm ($r_s = 0.13$, $p < 0.05$) was comparable to that for pH ($r_s = 0.12$, $p < 0.05$) for South Core.

Bivariate correlations

Bivariate Spearman's rank correlation coefficients for individual species cover and the nontrivial PC1 (variance = 51%) on Sapelo indicated a prominent separation of species along a gradient of pH, particle size, and organic matter (Table 4.5). Dune species (*Uniola paniculata*, $r_s = -0.27$, $p < 0.05$) and disturbance species exhibiting dune-building characteristics (*Panicum amarum*, $r_s = -0.21$, $p < 0.05$) had affinities for high pH, low organic content, well-sorted fine sands that characterize dune landforms (Figure 4.2). Species that stabilize low wet swales

Table. 4.3. PCA output for South Core soil variables.

Axis	Eigenvalue	% of Variance	Cum.% of Var.	Broken-stick Eigenvalue
1	2.55	36.45	36.45	2.59
2	2.26	32.33	68.77	1.59
3	1.51	21.50	90.28	1.09
4	0.32	4.52	94.79	0.76

	PC1	PC2	PC3	PC4
pH	0.0394	-0.5696	0.2888	0.5531
Granules+ (> 2mm)	-0.3941	0.0372	0.5827	-0.3753
Coarse-medium sand	-0.3137	-0.3412	-0.5581	0.0918
Fine sand	0.4719	0.3229	0.3204	0.2116
Silt-clay	-0.4047	0.4118	0.0827	0.7031
Carbonates in sand fraction	-0.5186	-0.1815	0.2952	-0.0723
Organics	-0.299	0.501	-0.2627	-0.0212

Table. 4.4. Mantel test statistics based on Spearman's correlation coefficients for soil variables and species cover for each study island.

Soil variable	Sapelo	S. Core
pH	0.30*	0.12*
Granules + (> 2 mm)		0.13*
Coarse to medium sand	0.02	0.04
Fine to very fine sand	0.06*	0.04
Silt and clay	0.22*	0.21*
Percent carbonate in sand fraction	0.12*	0.03
Organic matter	0.27*	0.18*
All soil variables	0.14*	0.04

Note: * = significant at $p < 0.05$

Table. 4.5. Bivariate Spearman's correlation coefficients for individual species cover and edaphic variability on principal components.

South Core

Species	Species Cluster Category	N	PC1	PC2*****	PC3*
Ditrichum spp.	Transitional	22	-0.08	0.42**	0.25**
Heterotheca subaxillaris	Dune	49	-0.07	0.25**	0.05
Hydrocotyle bonariensis	Dune/Disturbance	62	-0.05	0.28**	-0.14
Oenothera humifusa	Transitional	37	0.08	0.21**	0.17
Solidago sempervirens	Transitional	23	0.10	0.28**	0.12
Spartina patens	Disturbance	61	-0.05	0.25**	0.06
Uniola paniculata	Dune	81	0.10	-0.55**	-0.10

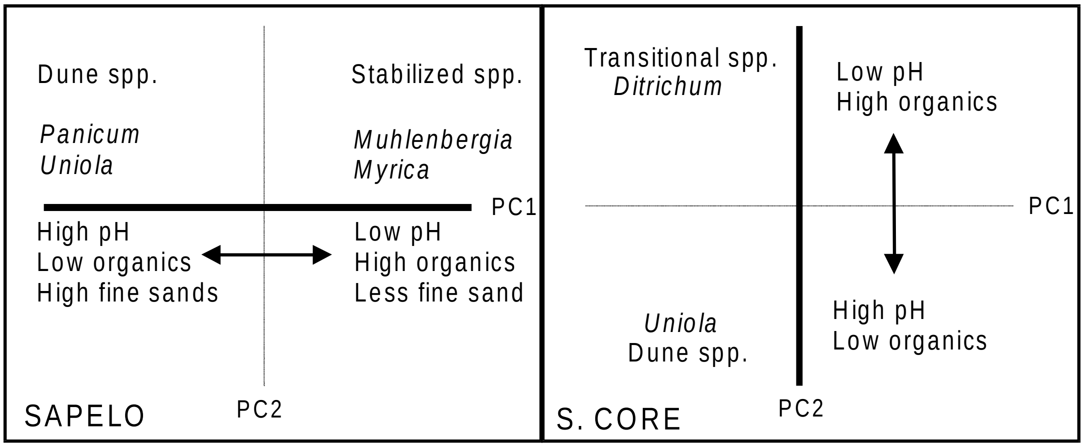
Sapelo

Species	Species Cluster Category	N	PC1*	PC2	PC3
Andropogon spp.	Transitional	16	0.13	-0.13	0.02
Cenchrus spp.	Disturbance	16	-0.01	0.00	-0.12
Croton punctatus	Dune	18	-0.19**	0.17**	-0.05
Fimbristylis spp.	Wet swale	19	0.04	-0.26**	-0.13
Muhlenbergia spp.	Stabilized	22	0.42**	-0.19**	0.02
Myrica cerifera	Stabilized	21	0.33**	-0.19**	-0.03
Panicum amarum	Disturbance	29	-0.21**	0.19**	0.10
Phyla nodiflora	Stabilized	52	0.20**	-0.13	-0.07
Uniola paniculata	Dune	71	-0.27**	0.37**	-0.17**

Note: * = Nontrivial principal component as based on broken stick eigenvalue.

** = Significant at $p < 0.05$

Figure 4.2. Species associations with predominant nontrivial principal components on each island.


Dune spp.
Stabilized spp.
Panicum
Uniola
Muhlenbergia
Myrica
PC1
High pH
Low organics
High fine sands
Low pH
High organics
Less fine sand
SAPELO
PC2
Transitional spp.
Ditrichum
Low pH
High organics
PC1
Uniola
Dune spp.
High pH
Low organics
S. CORE
PC2

(*Muhlenbergia filipes*, $r_s = 0.42$, $p < 0.05$; *Myrica cerifera*, $r_s = 0.33$, $p < 0.05$) had stronger positive correlations with this component, thus reflecting these species' proclivities for low pH, high organic matter soils. The increasing fraction of coarse sands in wet swale habitats may act to enhance leaching and the reduction of pH, especially when associated with the thick litter accumulations produced by *Myrica cerifera* in older wet swales. For South Core, Spearman's rank correlation coefficients for individual species with the nontrivial PC2 (variance = 32%) evidenced a separation of species along a gradient of pH and organic matter. Dune-building species (*Uniola paniculata*, $r_s = -0.55$, $p < 0.05$) were associated with high pH and low organic matter soils, and transitional species (*Ditrichum pallidium*, $r_s = -0.42$, $p < 0.05$) attained their highest cover in habitats of lower pH and higher organic matter. *Ditrichum pallidium* formed a dense ground cover at mid-island sites where it acts as a stabilizing agent on older overwash fans and protected dune aspects. In support of the results from my broken-stick eigenvalue comparisons, none of the species had significant correlations with my trivial first principal component. Similarly, the absence of ecological significance I attached to PC3 on South Core was supported in its lack of significant correlations with all but one of the individual species (*Ditrichum pallidium*).

Discussion

The increased sorting and dominance of fine-grained sands on Sapelo is characteristic of this low wave energy shoreline (Tanner, 1960; Giles and Pilkey, 1965). The significantly lower content of silt and clay in Sapelo dune soils was unexpected, yet the observed values could also be related to the low-energy setting. The lower silt-clay content in Sapelo dune soils may reflect the rarity of overwash events of sufficient magnitude to transport and deposit suspended sediments in back-barrier environments (Gerrard, 1992). Clay content is important for vegetation in that it enhances adsorption and potential availability of plant nutrients (Barbour *et al.*, 1999). The decreased wave energy and infrequency of high water events along this barrier coast may have also contributed to lower values of carbonate in dune sediments. Dunes in coastal Georgia typically do not contain a large percentage of carbonate due to the inability of waves to transport, fragment, and abrade the bivalve and gastropod shells that are abundant in nearshore marine habitats (Johnson *et al*., 1974). Reduced carbonate content may be linked to the significantly lower pH values because carbonates are potential buffering agents. Decaying plant material, particularly in association with litter produced by dense thickets of the woody shrub *Myrica cerifera,* may have also contributed to the lower pH values observed across samples on Sapelo.

As expected, the high-energy nearshore environment of South Core augmented the percentage of coarse-grained sands and particles > 2mm. Increased wave energy and overwash on South Core may have also fostered a larger silt-clay content through the more frequent suspension and inland deposition of these finer-grained textures. More variability in energy regime, as expressed in the episodic nature of overwash deposition and the separating intervals of aeolian transport, contributed to a more poorly-sorted distribution of particle sizes on South Core. Higher values of pH observed here may have been derived from increased salt spray inputs of basic cations (van der Valk, 1974), and from carbonates contained in shell fragments. An organic content comparable to Sapelo was initially unexpected for South Core; however, frequent overwash and plant mortality may enhance the cycling and buildup of organic matter in these maritime grassland systems.

The distribution of soil characteristics within islands mirrors these large regional-scale contrasts in soil properties. Overwash varies in its frequency at each of my five study sites per island. On Sapelo, evidence for recent overwash is restricted to the south end of the island. This location, Site A , has peaks in silt-clay content, pH, and carbonate, thus suggesting edaphic characteristics similar to South Core. The only two soil samples containing shell fragments > 2mm were also collected at this disturbed site. For South Core, overwash disturbance increases from south to north. High dunes at Site A on the south end prevent overwash, and foster edaphic characteristics similar to Sapelo. This site had the lowest mean site values for silt-clay content, pH, and carbonate content recorded on the island.

PCA results indicated that pH and organic matter were the predominant factor loadings for the nontrivial principal components on Sapelo and South Core, given their greater captured variance. Of interest however, are the differences between islands in the dimensionality of the principal components that express the loadings for these soil variables. Despite an equivalence in the amount of variance explained by the nontrivial components on each island (Sap = 53%, S. Core = 51%), there were compelling differences in the underlying data structure. In agreement with my initial hypotheses, Sapelo had a lower dimensionality that captured a larger amount of variance, and variable loadings were concentrated on this first principal component. Half of the variance among my samples on Sapelo was summarized by PC1, which had higher loadings for particle size, pH and organic matter. The low dimensionality and large explained variance for this first principal component suggested a high within-island redundancy in particle size, pH and organic matter on Sapelo, and therefore, an increased likelihood of edaphic organization. By contrast, the second and third principal components, rather than the first, were nontrivial on South Core. This is in agreement with my initial hypotheses that South Core soil properties would be summarized on higher-dimensional principal components. These results for South Core suggested a lowered redundancy among the measured soil properties, derived from the edaphic variability introduced by increased overwash. Although PC3 on South Core had strong inverse loadings for particles > 2 mm and the coarse sand fraction, I suggest that this component, while nontrivial, is expressing variance that is not ecologically meaningful, but nonetheless an important to the underlying dimensionality of the data. From this evidence, I infer that there is a decreased likelihood of edaphic organization among the measured soil variables on South Core.

PCA factor loadings also supported my initial hypothesis of increased edaphic organization on Sapelo. pH, organic matter, and sand particle size classes loaded on the same nontrivial principal component on Sapelo. As such, there may be a greater textural association with pH and organic matter. By contrast, sand textural classes on South Core did not load as strongly on the same nontrivial principal component as pH and organic matter. I suggest that the absence of strong loadings for sand textural classes on this second principal component may indicate a reduced association of sand textures with pH and organic matter. On South Core, organic matter and pH may be regulated more by allogenic processes, including the formation of shell lags, or the pulses of organic matter derived from the plant mortality associated with overwash.

Sapelo had a higher significant correlation of the suite of soil variables with species cover when compared to South Core. Differences between islands in the correlation of individual variables with species cover was most evident for pH. pH was more strongly correlated to species cover on Sapelo. Costa *et al.*(1996) found that pH was a significant variable in discriminating among vegetation associations along a shore disturbance gradient on the Brazilian coast. In their study, lower pH was associated with a decreased frequency of disturbance, in agreement with the smaller mean pH observed for Sapelo.

The results of my bivariate correlations of individual species cover with nontrivial principal component scores did not conclusively detail whether or not species are responding differently to the edaphic variability expressed on each island. The trivial second principal component on Sapelo exhibited several significant correlations with species cover. This suggests that ecological meaningful variance may have been partitioned among several axes, and therefore, species correlations on the first principal component alone may not fully detail the soil-vegetation relationship.

In contrast to my initial hypothesis, South Core had a wider range of bivariate correlation coefficients associated with the edaphic variability along its nontrivial component, PC2. However, two species, the dune-builder *Uniola paniculata* (Wagner, 1964) and the sediment stabilizer *Ditrichum pallidium* (Martínez and Maun, 1999), contributed disproportionately to this wide range of correlations. The remaining species had a comparatively more narrow range of correlations, suggesting a weaker response to edaphic variability. Species correlations on Sapelo were more evenly dispersed according to sign, but weaker in magnitude. As on South Core, the higher correlations here were associated with species that play an important role in sediment stability (*Uniola paniculata*, *Muhlenbergia filipes*, and *Myrica cerifera*). To an extent, species on both islands are responding to edaphic variability derived from different mechanisms, in environments that differ in their edaphic organization. These findings suggest that individual species responses to edaphic variability may be more important than the overall responsiveness of vegetation to island-level edaphic variability. In particular, species that act as key regulators of sediment stability exhibited the highest correlations. The responsiveness of these individual species to soil variability reinforces their importance as species that engineer topographically-defined habitats for other species (Jones *et al.,* 1997).

Correlations between soil parameters and vegetation cover, for Mantel tests and bivariate relationships, were weak on both islands. Consistently low correlations between soil variables and species cover were not surprising given that sediment mobility and salt spray as the more direct influences on dune species patterns (Wilson and Sykes, 1999). Salt spray provides the bulk of plant nutrients in maritime dunes, and the storage of these nutrients is short-lived in dune soils (van der Valk, 1974). Although pH, silt-clay, and organic matter had significant but weak correlations with species cover, dune soils may nonetheless be important components of the self-reinforcing feedbacks between topography, species cover, and salt-spray inputs. Plant species create positive feedbacks that reinforce existing patterns of nutrient availability (Hobbie, 1992). For example, on Sapelo, production of litter by *Myrica cerifera* may promote the lower pH and higher organic content of its low swale habitat, thus fostering the low-nutrient edaphic conditions for which this slow-growing evergreen species is competitively superior. This, in turn, may promote the continued stabilization of low elevations by this rhizomatous woody shrub, and the subsequent maintenance of the elevational contrasts that demarcate habitats.

Conclusions

Significant differences in particle size, pH, and carbonate content were expressed between my two barrier island morphologies. Analysis of principal component dimensionality, significance of captured variance, and factor loadings for measured soil variables suggested a greater edaphic differentiation among habitats on Sapelo. This augmented edaphic organization on Sapelo was also associated with relatively higher Mantel correlations between the suite of measured soil variables and their corresponding species covers when compared to South Core. However, individual species correlations with their nontrivial principal component axis score on each island suggested that increased edaphic organization does not necessarily imply stronger island-scale associations between edaphic variability and individual species cover.

Vegetation patterns can be ascribed to the landforms that shape pedogenic properties through their associated physical gradients, and to the geomorphic processes that directly shape landforms. This pedogenic-geomorphic dichotomy is problematic, in that geomorphic processes shape, and are shaped by, landforms and their associated vegetation. Thus, it may be difficult to attribute vegetation patterns to one or the other of these two influences (Parker and Bendix, 1996). In this study, silt-clay content, pH, and organic matter exhibited comparable correlations with total species cover on both morphologies, therefore obscuring any contrasts between islands in their pedogenic and geomorphic setting. Despite these correlative similarities, I posit that soil variables are a landform-mediated, autogenic control of composition on Sapelo, and a process-regulated, allogenic control on South Core. This distinction, as to whether soil variables exert their influence on composition through underlying physical gradients or through geomorphic mobility, is based upon geographical context, and upon the degree of organization exhibited among edaphic variables. From the results in this study, I suggest that the underlying variance structure and dimensionality in edaphic variables can be used to delineate form versus process regulation of vegetation patterns. In conjunction with significant species correlations, a lower dimensionality, derived from a greater multicollinearity among soil variables, may support an interpretation emphasizing edaphic regulation of compositional patterns. A higher dimensional representation of soil data structure may be indicative of process-regulation of compositional patterns.

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CHAPTER 5

CONCLUSIONS

In this field-based study, I described the biogeographic patterns of dune plant species on two barrier island morphologies. I conceptually linked these patterns to each island's contrasts in feedback and threshold processes. My results indicated strong compositional differences between island landforms. Both islands shared many of the same species, but had difference abundances on each, largely due to the expression of differences in species adaptations to the prevailing disturbance regime. Moreover, there was a larger compositional variability and species diversity per unit area on Sapelo, which I ascribed to its greater habitat heterogeneity. I suggested that this habitat heterogeneity arose from the formation of dune ridges and swales, an intrinsic biogeomorphic process operative during the longer periods between overwash events in this island setting. These longer intervals for topographic organization were also associated with an enhanced edaphic organization on Sapelo. Dune soils had a significant correlation with species cover on Sapelo, yet this relationship was weakly expressed.

From this study, several conceptual findings have evolved; each warrant further scrutiny in other biogeomorphic environments. First of all, I suggest that the assumption of a linear relationship between disturbance exposure and effects should be more carefully examined. I postulate a more complex relationship between disturbance and recovery, one in which feedback and threshold processes during recovery may amplify or dampen the effects of a disturbance regime. To a certain extent, these non-linearities are similar to complex responses in riverine environments, as outlined by Schumm (1973). Based on his fluvial examples, I suggest that during the intervals between disturbance events, intrinsic biogeomorphic feedbacks may change the way in which the landscape responds to the next external event.

The diversity patterns observed in this study also indicated that disturbance effects are mediated through intrinsic processes. Habitat stability, envisioned as time since last overwash, affected species diversity differently on each island. On Sapelo, where overwash events are infrequent, species diversity increased with decreasing habitat stability. On the more frequently overwashed landscape of South Core, decreasing habitat stability was instead associated with a lower species diversity. In keeping with Reice (1994), my findings reiterate that disturbance should be viewed as a potential environmental cause of biological change, rather than a direct agent of biotic change. Disturbance was not the sole determinant of the observed diversity on my study islands. Rather, it created opportunities for colonization of vacated spaces, with any subsequent expression of diversity related to spatially and temporally variable recruitment, recovery, and colonization success.

I suggest that feedbacks and thresholds in biogeomorphic systems play a pivotal role in determining the extent to which disturbance is a direct or indirect agent of biotic change. This was shown to have strong implications for the validity of the two models of species diversity I examined in this study. By reinforcing the coupling between disturbance exposure and effects on South Core, intrinsic feedback and thresholds enhanced a regularity in the along-island patterns of species diversity. The observed species diversity patterns on South Core conformed to a spatial application of the Intermediate Disturbance Hypothesis. On Sapelo, where intrinsic feedbacks and thresholds act to decouple disturbance exposure from its direct effect upon vegetation, IDH weakened as a conceptual tool for framing diversity patterns. IDH, as it is often applied, erroneously assumes a geographically consistent, direct relationship between disturbance exposure and effect. As such, it is a circular argument, one that limits insight into the interplay of extrinsic and intrinsic controls of species diversity patterns (Huston, 1994). Mechanisms controlling species diversity in response to disturbance are not the same as those affecting post-disturbance succession (Collins and Glenn, 1997). In this manner, biogeomorphic feedback and threshold behaviors, recolonization (Glenn and Collins, 1992; Reice, 1994), species adaptations (Bendix, 1999), and recruitment limitation (Hubbell *et al.*, 1999) intercede in shaping disturbance effects following exposure. The Dynamic Equilibrium Model (Huston, 1979, 1994) is a more robust conceptual tool for framing diversity patterns on both of my study islands, given that it defines an ‘intermediate’ frequency of disturbance exposure independently of its effects on species diversity.

Last of all, I suggest that biogeomorphic responses to disturbance regime may act to decouple or maintain hierarchical relationships among landscape components, and thus control the spatial-scale expression of compositional patterns. Feedbacks and threshold behaviors on South Core act to reset and maintain a more hierarchical arrangement of system variables that promotes a large spatial-scale consistency and convergence in compositional patterns. On Sapelo, the absence of disturbance decouples hierarchical geometry, and consequently local-scale topographic and edaphic variables mold a finer spatial mosaic of compositional patterns.

The two biogeomorphic settings in this study, the dune habitats of a wave-dominated microtidal barrier island and a mixed-energy mesotidal barrier island, may represent two stable states along a coastal landscape sensitivity gradient (Figure 5.1). Stability is maintained at each endpoint on this gradient by locale-specific feedback and threshold interactions between species, the prevailing disturbance regime, and subsequent recovery along environmental gradients. Biogeomorphic feedbacks on South Core foster a low morphologic resistance to overwash through a simplified topography (Figure 2.4). Dominant species, such as *Spartina patens,* exhibit high resilience to this disturbance agent. By contrast, biogeomorphic feedbacks on Sapelo confer a high morphologic resistance through increased topographic roughness (Figure 2.5). Species here have a low resilience to overwash burial and flooding, and would be unlikely to recover quickly following an overwash event of a sufficient magnitude to impact back barrier locations. In moving along this gradient, dune habitat organization may become unstable. Species assemblages and topographies intermediate of those at either end of this shore disturbance gradient may not be sufficiently organized to exhibit responsiveness to external forcings. In these transitional configurations, a balance in morphologic resistance and species resilience may not confer stability in landscape structure and function. Table 5.1 summarizes these and other findings that I synthesize into this conceptual model. The intent of this model is to provide a conceptual template for examining biogeomorphic patterns in other environments and on other landforms.

Geomorphic setting, in terms of energy for transport of sediments and the availability of sediments, is distinctively different among my endpoints. Where energy-level is high and sediment availability is low, overwash disturbance is more frequent (Roman and Nordstrom, 1988). Density-independent species adaptations, such as the ability to recover rapidly following disturbance, may be advantageous in these settings. Consequently, feedbacks between vegetation and sediment mobility, and the extrinsic thresholds that result, may have evolved such that there is

Figure. 5.1. Generalized model of a coastal landscape sensitivity gradient.

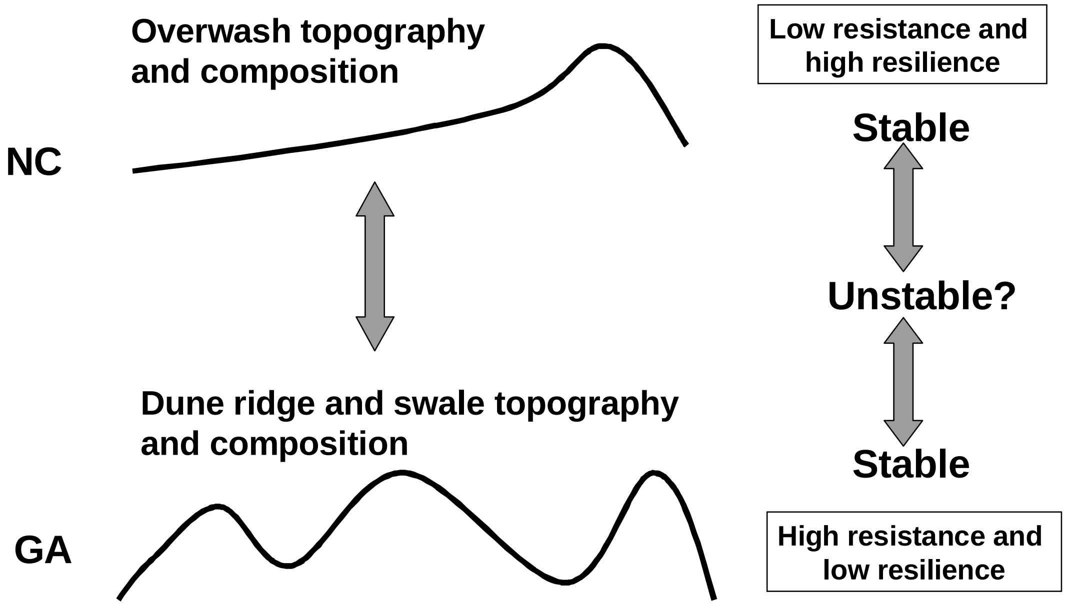
Overwash topography and composition
NC
Dune ridge and swale topography and composition
GA
Low resistance and high resilience
Stable
Unstable?
Stable
High resistance and low resilience

Table. 5.1. Characteristics of coastal landscape sensitivity gradient.

	South Core Banks, NC	Sapelo Island, GA
Energy conditions	High	Low
Prevailing sediment budget	Negative	Positive
Morphologic resistance	Low	High
Species resilience	High	Low
Topography	Simplified	Complex
Coupling of disturbance exposure and effects	Direct, amplified	Indirect, dampened
Compositional patterning	Convergence	Divergence
Extrinsic thresholds	Low	High
Spread of geomorphic disturbance agent	Dispersed	Restricted
Geometry of disturbance and recovery gradients	Overlay	Intersecting
Edaphic dimensionality	High	Low

a reinforcement of disturbance (Laland *et al.*, 1999). In this manner, the environmental conditions for which the disturbance-dependent species is competitively superior, frequent overwash burial and flooding, are perpetuated. At the other end of the gradient, where energy-level is low and sediments are locally abundant, disturbance frequency decreases. Species adaptations may instead reflect density-dependent mechanisms that enhance survivability in the absence of disturbance. For example, species that are able to autogenically engineer distinctive elevationally-defined habitats, either through dune-building or sediment stabilization, will lessen competitive interactions (Wilson and Nisbet, 1997). In consequence, feedbacks between vegetation and sediment mobility, and the extrinsic thresholds that result, may have coevolved to favor the decoupling of disturbance exposure and effects, and thus the perpetuation of the environmental conditions for which these density-dependent adaptations are competitively superior. In this manner, disturbance exposure and effects are more directly coupled in environments where the prevailing disturbance regime favors frequent, predictable disturbance. Where disturbance is infrequent, the absence of disturbance becomes a greater influence on the vegetation than the disturbance itself (Reice, 1994). As such, disturbance exposure and effects are more indirectly coupled.

Extrinsic thresholds on each island confer varying degrees of resistance to disturbance, and thus regulate the degree of this coupling between disturbance exposure and effects. The spread of disturbance is more likely to be dispersed over the landscape where extrinsic thresholds are minimized, as on the low-profile topography of South Core (Figure 2.4). By contrast, where topographic complexity increases the resistance and thresholds to disturbance exposure, disturbance exposure and effects are likely to be restricted to a smaller area of the landscape, as on Sapelo (Figure 2.5). Where topography reinforces the spread of disturbance across a landscape, disturbance exposure and effects are folded into a single overlapping gradient, in effect superimposing disturbance and recovery gradients. This gradient geometry fosters a convergence of compositional patterns over a wide area. Where topography restricts the spread of disturbance across a landscape, disturbance effects are spatially confined, and incorporated as an adjoining zone alongside undisturbed vegetation. This gradient geometry is representative of a divergence in compositional patterns, and a finer scale spatial mosaic. These patterns were identified in the transverse compositional gradients expressed on each island (Figure 2.12).

This research provides insight into the biogeomorphic relationships between feedbacks, thresholds, and the scale of expression of vegetation patterns. On each island, these relationships were circular, and characterized by a complex web of reinforcing behaviors. However, in the two strikingly different geomorphic environments chosen for this study, these feedbacks fostered landscapes with compelling contrasts in their patterns of species composition, diversity, and substrate-vegetation relationships. To strengthen the conceptual linkages drawn from this research, a more exhaustive field study, one in which vegetation is sampled at various time intervals, and on other barrier island systems, is needed to examine other configurations of species and topography. Another approach for strengthening the synthesis presented in this study is through the development of barrier island mathematical models that could simulate the feedbacks and threshold behaviors exhibited among species and landforms. Lastly, the deployment of a similar methodological framework on other biogeomorphic landforms would serve to verify the applicability of my findings. As in this study, disturbance and environmental gradients, acting in concert, engender feedbacks between the flow of sediments and the underlying topography in riparian landscapes (Ward, 1998)

In recent decades, vegetated coastal dunes have received only minor study when compared to upland terrestrial habitats, particularly in North America. Many recent landscape-scale studies of dune vegetation do not fully address the potential theoretical contribution of these systems. The unique characteristics of these responsive systems make them ideal settings to amplify, expand, and generalize biogeomorphic concepts developed in this and other biogeomorphic studies.

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APPENDIX 2.1. TRANSECT TOPOGRAPHIC DESCRIPTORS AND MRPP STATISTICS

Location	Transect length (m)	Primary foredune height above HWM (m)
Sapelo		
AT1	69.54	0.00
AT2	70.36	0.07
AT3	69.34	0.22
BT1	73.52	1.33
BT2	67.03	1.09
BT3	67.08	0.84
CT1	69.11	1.04
CT2	67.33	1.12
CT3	68.65	1.86
DT1	80.03	1.60
DT2	84.46	1.62
DT3	84.03	1.61
ET1	58.15	1.21
ET2	56.40	1.40
ET3	58.51	1.17
Mean	69.57 ± 8.46	1.08 ± .57
Median	69.11	1.17
South Core		
AT1	148.07	2.39
AT2	145.07	2.59
AT3	135.33	2.31
BT1	193.80	1.45
BT2	193.77	1.31
BT3	192.97	1.00
CT1	166.57	0.88
CT2	164.80	0.18
CT3	137.04	0.75
DT1	124.09	0.32
DT2	120.40	0.26
DT3	125.00	0.23
ET1	79.00	0.02
ET2	79.53	0.00
ET3	92.86	0.02
Mean	139.89 ± 38.26	.914 ± .91
Median	137.04	0.75
MRPP		
T	-13.60	-0.97
p	0.00*	0.14
Distance Sapelo	9.53	0.65
Distance Core	44.81	1.03

Note:* = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance

APPENDIX 2.2. QUADRAT SAMPLING INTENSITY AND MRPP STATISTICS

Location	Number of quadrats
Sapelo	
AT1	71
AT2	72
AT3	71
BT1	76
BT2	69
BT3	69
CT1	71
CT2	71
CT3	71
DT1	83
DT2	87
DT3	87
ET1	61
ET2	62
ET3	61
Total quadrats	1082
Mean	72 ± 8
Median	71
South Core	
AT1	76
AT2	75
AT3	71
BT1	66
BT2	66
BT3	99
CT1	85
CT2	84
CT3	70
DT1	64
DT2	62
DT3	64
ET1	81
ET2	81
ET3	95
Total quadrats	1139
Mean	75 ± 11
Median	75
MRPP	
T	-0.08
p	0.33
Distance Sapelo	9.14
Distance Core	13.22

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.

APPENDIX 2.3. TRANSECT PERCENT BARE GROUND AND MRPP STATISTICS

Location	Percent bare ground
Sapelo	
AT1	58.87
AT2	51.60
AT3	53.31
BT1	67.17
BT2	61.30
BT3	66.59
CT1	61.62
CT2	38.94
CT3	39.44
DT1	55.54
DT2	52.01
DT3	56.15
ET1	18.61
ET2	20.16
ET3	6.89
Mean	47.21 ± 18.6
Median	53.31
South Core	
AT1	39.61
AT2	23.00
AT3	21.06
BT1	20.00
BT2	6.44
BT3	14.55
CT1	11.65
CT2	18.21
CT3	35.29
DT1	38.83
DT2	27.18
DT3	39.30
ET1	43.21
ET2	51.23
ET3	41.00
Mean	28.70 ± 13.40
Median	27.18
MRPP	
T	-13.60
p	0.00*
Distance Sapelo	9.53
Distance Core	44.81

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.

APPENDIX 2.4. NUMBER AND PERCENT ABSOLUTE COVER FOR SHARED SPECIES BY ISLAND SITE

Species	Percent absolute cover by site									
	Sapelo					South Core				
	SA	SB	SC	SD	SE	CA	CB	CC	CD	CE
Ampelopsis arborea (L.) Koehne		0.05		0.27	0.43			OT		
Andropogon spp.	2.59	0.19	1.43	2.65	2.69	0.45	0.09	0.42		
Baccharis halimifolia L.	0.05					OT	0.06		0.03	
Cenchrus spp.	0.54	0.09	2.96	2.80	4.92	0.38				
Chloris petrea Swartz.	OT					0.18	1.17	1.38	0.11	
Croton punctatus Jacquin	0.91	3.57	1.22	4.03	0.76	0.05				OT
Dicanthelium aciculare (Desv. ex Poir) Gould & Clark					0.84	0.95	1.49			
Eragrostis spp.	5.00	OT	0.09		0.03	0.79	0.67	0.67	0.08	
Fimbristylis spp.	1.29	0.02	0.89	1.60	2.42	0.32	0.22	0.02		
Galactia volubilis (L.) Britton					OT					OT
Hydrocotyle bonariensis Lam.	1.96	0.70	1.43	0.70	0.03	6.15	4.16	6.09	9.55	8.37
Ilex vomitoria Aiton					OT		OT			
Iva imbricata Walter	0.86	0.51		0.19		1.15	0.13	0.25		
Juncus marginatus Rostk.	1.10			0.02	0.33	0.02	0.04			
Juncus megacephalus M. A. Curtis	0.16					OT				
Juniperus virginiana L.				OT	0.05		OT			
Milkania scandens (L.) Willd.			OT	OT						OT
Muhlenbergia filipes M.A. Curtis	2.29	6.33	3.90	0.89	13.0	2.27	1.17	0.75	0.11	
Myrica cerifera L.	0.63	0.21	11.9	2.45	23.9	1.26	0.48	1.69	0.82	0.89
Oenothera humifusa Nuttall	0.02	0.35	0.35	0.08	0.35	1.46	5.84	5.50	1.00	0.08
Opuntia pusilla (Haw.) Haw.	OT	0.21	0.07	0.23	0.43		OT	0.04		
Panicum amarum Ell.	5.56	3.55	1.53	2.82	0.57			OT	0.08	4.65
Phyla nodiflora (L.) Greene	5.37	2.17	13.4	5.60	16.1	0.05				
Physalis viscosa L. ssp maritima (Curtis) Waterfall		0.02		0.02	0.19	0.02	0.11	0.59	0.18	0.39
Smilax spp.		0.02	0.02		2.17			0.59	0.13	OT
Spartina patens (Aiton) Muhl.	0.77	0.51		0.18	0.03	14.1	5.76	7.01	18.7	28.7
Sporobolus virginicus (L.) Kunth	1.96	0.30	0.19	0.49					OT	
Uniola paniculata L.	5.89	12.1	8.97	15.1	3.18	20.1	18.6	20.7	21.6	5.43
Vitis aestivalis Michaux					OT					0.16
Total cover shared perennials	36.9	31.0	48.3	40.1	72.5	49.7	40.0	45.7	52.4	48.6
Cakile edentula (Bigelow) Hooker				OT		0.11	0.06		OT	0.08
Chamaesyce spp.	0.02		0.14	0.49	0.05	0.32	0.37	0.25	0.05	0.04
Cirsium spp.	OT		0.09	OT	0.03		OT	0.02	0.03	0.04
Conyza canadensis L. Cronq.	0.98	0.21	0.02	0.74	0.16	1.55	1.77	1.86	1.21	0.14
Gnaphalium purpureum L.	2.24	0.14	0.05	0.19	0.73		0.04			
Heterotheca subaxillaris (Lam.) Britton & Rusby	2.20	0.75	1.67	1.11	0.08	5.54	8.29	6.21	4.11	
Lepidium virginicum L.					OT	0.23	0.13	0.17	0.05	

Parietaria floridana Nuthall		OT	0.66	OT	0.03	0.02				
Plantago virginica L.	OT	0.02				0.11	0.17			
Rubus spp.		0.23		0.02	0.54			0.25	0.26	0.04
Sabatia stellaris Pursh	0.82	0.02				1.40	0.15			
Strophostyles helvola (L.) Ell. (OS)	OT					0.07	1.15	0.82	1.79	
Triplasis purpurea (Walter) Chapman	1.00	1.54	1.71	1.26	1.33	3.02	1.26	0.90	0.37	
Vulpina octoflora (Walt) Rydb.		OT			1.96		0.17	0.77		
Total cover shared annuals	7.27	2.92	4.34	3.81	4.92	12.3	13.5	11.2	7.87	0.33
Total cover shared species	44.2	33.9	52.7	43.9	77.5	62.1	53.6	57.0	60.3	48.9
Total number of shared species	29	28	23	29	33	29	30	25	22	17
Total number of unique species	17	11	12	15	29	15	14	19	11	11
Total number of species	46	39	35	44	62	44	44	44	33	28

Note: ‘OT’ designates off-transect species. All species numbers include off-transect and on-transect species.

APPENDIX 2.5. NUMBER AND PERCENT ABSOLUTE COVER FOR SPECIES UNIQUE TO SOUTH CORE

Species	Percent absolute cover				
	CA	CB	CC	CD	CE
Ammophila brevigulata Fernald				0.2	4.9
Baccharis angustifolia (Michaux)					0.4
Borrichia frutescens L. DC					0.0
Centella asiatica L. Urban	0.3				
Cladonia spp.	0.1	OT			
Commelina erecta L.	0.0	0.8	1.4	0.2	0.3
Cynanchum angustifolium Pers	0.2	0.5	2.0	0.1	0.0
Ditrichum pallidum	4.1	22.9	14.0	0.1	
Galium triflorum Michaux			0.1		
Ipomoea sagittata Cav.			0.2	0.1	0.0
Juncus roemerianus Scheele	0.6	0.8	0.4		
Linum medium (Planch.) Britt	0.0	0.1			
Oxalis stricta L.			OT		
Parthenocissus quinquefolia L.		0.5			
Rhus radicans L.	OT	0.2		0.1	0.3
Schizachyrium scoparium (Michx.)	OT				
Scirpus americanus Pers.		0.0	0.0		
Scleria spp.	0.5				
Setaria geniculata (Lam.) Beauv.	0.0				0.1
Solidago spp.	3.4	5.4	0.8	0.5	OT
Total cover unique perennials	9.3	31.2	19.0	1.3	6.1
Ambrosia artemisiifolia L			0.5		
Arenaria serpyllifolia L.		1.1	1.5		
Cuscuta gronovii Willd. ex R. & S.	0.1		0.0		
Diodia teres Walter	0.3	0.1	0.3	0.8	0.0
Gaillardia pulchella Foug.	0.1		0.5	2.4	
Gaura angustifolia Michaux			0.1		
Lactuca canadensis L.				OT	0.0
Polygonella gracilis (Nuttall) Meissner		OT			
Setaria magna Griseb.			OT		
Spermolepsis divaricata (Walter) Raf.		0.2	0.1		
Sphenopholis obtusata (Michaux.)			0.1		
Trichostema dichotomum L.			0.0	OT	
Total cover unique annuals	0.5	1.4	3.1	3.2	0.0
Total cover unique species	9.8	32.6	22.1	4.5	6.1
Total cover shared species	62.1	53.6	57.1	60.3	49.0

Total cover all species	71.9	86.2	79.1	64.8	55.1
Total number of unique perennials	12	10	9	7	9
Total number of unique annuals	3	4	10	4	2
Total number of unique species	15	14	19	11	11

Note: ‘OT’ designates off-transect species. All species numbers include off-transect and on-transect species.

APPENDIX 2.6. NUMBER AND PERCENT ABSOLUTE COVER FOR SPECIES UNIQUE TO SAPELO

Species	Percent absolute cover by site				
	SA	SB	SC	SD	SE
Bumelia tenax (L.) Willd.		OT		0.1	0.7
Callicarpa americana L.					OT
Chrysopsis graminifolia (Michx.) Ell.					OT
Cnidoscolus stimulosus (Michaux) Engelm. & Gray					0.3
Cyperus esculentes L.	0.0				0.3
Cyperus globulosus Aubl.				OT	
Cyperus polystachos (Torr.) Fern.	0.0				0.0
Cyperus retrorsus Chapm.					OT
Dicanthelium acuminatum (Sw.) Gould & Clark					0.3
Dichromena colorata L. Hitchcock		OT			
Distichlis spicata L. Greene	OT				
Galium hispidulum Michaux					0.2
Hedyotis procumbens (Walt. ex J.F. Gmel.) Fosb.		0.2	OT	OT	0.1
Helianthemum corymbosum Michaux					OT
Hypericum hypericoides (L.) Crantz			0.1		
Juncus dichotomous Ell.					0.1
Ludwigia maritima Harper	0.0				
Ludwigia virgata Harper	OT				
Melothria pendula L.		OT	0.0	0.0	0.2
Opuntia humifusa (Raf.) Raf.			OT	0.1	0.2
Paspalum spp.				0.5	0.8
Pinus elliotti Engelm.	OT				
Pinus taeda L.			OT	0.6	1.3
Polyprenum procumbens L.	OT	0.0	0.0	OT	
Quercus geminata Small			0.1		
Quercus myrtifolia Willd.					OT
Serenoa repens (Bartr.) Small					OT
Sesuvium portulacastrum L.	0.0				
Stenotaphrum secundatum (Walter) Kuntze				0.1	0.2
Xanthoxylum clava-herculis L.		OT			OT
Yucca aliofolia L	0.0		OT		OT
Yucca filamentosa L.			OT		
Yucca gloriosa L.	0.0	0.3		OT	
Total cover unique perennials	0.2	0.5	0.2	1.4	4.6
Atriplex arenaria Nutthall	0.1				
Chenopodium ambrosioides L.		OT		OT	0.0
Croton glandulosus L.				0.1	
Eupatorium spp.	OT	OT	0.4	OT	2.4
Hypericum drummondii (Grev. and Hooker) T. & G.					OT

Hypercium gentianoides (L.) BSP	0.1	0.2	OT		0.1
Juncus bufonius L.					OT
Pluchea purpurascens (Swartz) DC	OT				
Rumex hastatulus Baldwin ex Ell.	0.8	0.3	OT	OT	0.1
Salicornia europaea L.	0.0				
Salsola kali L.	0.0			OT	OT
Specularia perfoliata (L.) A. DC.					0.0
Total cover unique annuals	1.0	0.5	0.4	0.1	2.6
Total cover unique species	1.2	1.0	0.6	1.5	7.3
Total cover shared species	44.2	33.9	52.7	44.0	77.5
Total cover all species	45.4	34.9	53.3	45.5	84.8
Total number of unique perennials	10	7	9	10	21
Total number of unique annuals	7	4	3	5	8
Total number of unique species	17	11	12	15	29

Note: ‘OT’ designates off-transect species. All species numbers include off-transect and on-transect species.

APPENDIX 2.6. TRANSVERSE COMPOSITIONAL DESCRIPTORS BY TRANSECT AND MRPP STATISTICS

Location	NMS Axis 1 standard deviation	NMS Axis 2 standard deviation	Wilson and Shmida Bt
Sapelo			
AT1	0.343	0.689	6.49
AT2	0.543	0.578	8.38
AT3	0.478	0.568	5.62
BT1	0.407	0.547	7.09
BT2	0.369	0.661	8.45
BT3	0.418	0.729	9.05
CT1	0.298	0.499	5.18
CT2	0.385	0.580	6.14
CT3	0.333	0.656	6.34
DT1	0.369	0.595	6.96
DT2	0.343	0.614	4.84
DT3	0.433	0.572	7.92
ET1	0.376	0.511	6.12
ET2	0.498	0.418	8.58
ET3	0.419	0.482	8.51
Mean	0.401	0.580	7.05 ± 1.4
Median	0.385	0.578	6.96
South Core			
AT1	0.585	0.462	7.98
AT2	0.653	0.459	5.35
AT3	0.605	0.423	8.60
BT1	0.496	0.363	5.13
BT2	0.528	0.320	5.77
BT3	0.475	0.355	6.52
CT1	0.572	0.402	5.92
CT2	0.570	0.324	4.35
CT3	0.439	0.277	7.19
DT1	0.709	0.299	4.99
DT2	0.605	0.286	4.93
DT3	0.643	0.360	5.80
ET1	0.619	0.418	3.48
ET2	0.499	0.364	3.43
ET3	0.336	0.291	5.12
Mean	0.556	0.360	5.64 ± 1.5
Median	0.572	0.360	5.36
MRPP			
T	-9.69	-14.89	-3.08
P	0.00*	0.00*	0.02*
Distance Sapelo	0.077	0.097	1.60
Distance Core	0.109	0.072	1.69

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.

APPENDIX 3.1. TRANSECT MORPHOMETRICS AND MRPP STATISTICS

Location	Dune habitat width (m)	Primary foredune height above MHW (m)	Topographic roughness
Sapelo			
AT1	69.54	0.00	9.56
AT2	70.36	0.07	9.58
AT3	69.34	0.22	10.23
BT1	73.52	1.33	13.34
BT2	67.03	1.09	11.69
BT3	67.08	0.84	10.61
CT1	69.11	1.04	12.75
CT2	67.33	1.12	13.97
CT3	68.65	1.86	14.42
DT1	80.03	1.60	18.60
DT2	84.46	1.62	18.09
DT3	84.03	1.61	19.10
ET1	58.15	1.21	11.51
ET2	56.40	1.40	13.20
ET3	58.51	1.17	14.31
Mean	69.57 ± 8.46	1.08 ± .57	13.40 ± 3.14
Median	69.11	1.17	13.20
South Core			
AT1	148.07	2.39	20.10
AT2	145.07	2.59	20.38
AT3	135.33	2.31	20.27
BT1	193.80	1.45	14.37
BT2	193.77	1.31	13.46
BT3	192.97	1.00	14.87
CT1	166.57	0.88	13.12
CT2	164.80	0.18	11.84
CT3	137.04	0.75	11.76
DT1	124.09	0.32	12.00
DT2	120.40	0.26	10.45
DT3	125.00	0.23	9.65
ET1	79.00	0.02	9.05
ET2	79.53	0.00	7.20
ET3	92.86	0.02	6.71
Mean	139.89 ± 38.26	.914 ± .91	13.01 ± 4.4
Median	137.04	0.75	11.99
MRPP			
T	-13.60	-0.97	0.58
P	0.00*	0.14	0.66
Distance	9.53	0.65	3.60
Distance	44.81	1.03	5.08

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.

APPENDIX 3.2. TRANSECT SPECIES RICHNESS, ALPHA DIVERSITY, AND MRPP STATISTICS

Location	Number of species and species complexes	Shannon-Weiner index of alpha diversity
Sapelo		
AT1	26	2.68
AT2	32	2.78
AT3	24	2.64
BT1	18	1.95
BT2	23	2.20
BT3	23	2.02
CT1	19	2.37
CT2	20	2.02
CT3	19	1.90
DT1	20	2.20
DT2	23	2.32
DT3	27	2.43
ET1	30	2.44
ET2	32	2.18
ET3	32	2.30
Mean	24	2.30 ± .27
Median	23	2.30
South Core		
AT1	28	2.40
AT2	31	2.43
AT3	33	2.36
BT1	29	2.46
BT2	33	2.38
BT3	33	2.31
CT1	33	2.52
CT2	29	2.59
CT3	28	2.08
DT1	18	1.81
DT2	20	1.84
DT3	22	1.83
ET1	10	1.57
ET2	11	1.41
ET3	18	1.49
Mean	25	2.10 ± .40
Median	28	2.31
MRPP		
T	-0.22	-0.85
P	0.28	0.15
Distance	5.89	0.315
Distance Core	9.07	0.465

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.

APPENDIX 3.3. SITE SPECIES RICHNESS, ALPHA DIVERSITY, AND MRPP STATISTICS

Location	Number of species and species complexes	Shannon-Weiner index of alpha diversity
Sapelo		
A	46	2.85
B	39	2.23
C	35	2.26
D	44	2.46
E	62	2.48
South Core		
A	44	2.56
B	44	2.43
C	44	2.56
D	33	1.91
E	28	1.57
MRPP		
T	0.33	-0.36
P	0.52	0.41
Distance Sapelo	12.2	0.29
Distance Core	8.6	0.53

Note: * = MRPP significantly different at $p < 0.05$. Distance is mean Euclidean inter-transect distance.