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Dune plant species diversity and function in two barrier island biogeomorphic systems

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Abstract

Barrier island dune systems exhibit strong geographic contrasts in the interaction between extrinsic disturbance from storm overwash and intrinsic biogeomorphic recovery processes. To examine how these interactions shape dune plant species diversity, I sampled species cover and topography along frequently storm-overwashed (South Core Banks, North Carolina) and infrequently overwashed (Sapelo Island, Georgia) barrier islands. The observed compositional and diversity patterns were in agreement with a complex systems model in which extrinsic overwash exposure is either reinforced (South Core Banks) or dampened (Sapelo Island) by intrinsic biogeomorphic controls of topography. A large spatial-scale regularity in the distributional pattern of along-shore species diversity was correlated to primary foredune height on South Core. On Sapelo, a fine-spatial scale differentiation of species diversity patterns was less strongly correlated to topographic metrics. There were no significant differences between islands in along-shore alpha diversity (Shannon-Weiner index). However, Sapelo was more diverse given its smaller area and finer-scale habitat heterogeneity. I posit that the relevancy of the Intermediate Disturbance Hypothesis is weak when examining diversity patterns along a shore disturbance gradient. Intrinsic biogeomorphic processes decouple the direct cause-and-effect relationship between disturbance and diversity, a basic assumption of IDH. I posit that the Dynamic Equilibrium Model may be a more generally applicable conceptual framework. DEM incorporates the interaction of intrinsic and extrinsic processes that shape habitat heterogeneity, a prerequisite for understanding how complex systems interactions shape diversity patterns.

Introduction

Patterns of plant species diversity in upland environments have been subject to intense scrutiny, but have been surprisingly neglected on barrier island coasts (Ehrenfeld 1990). The comparative paucity of dune diversity studies is notable given the increasing recognition of complex systems interactions (Perry 1995; Chapin et al. 1997; Malanson 1999), functional species groupings (Peterson et al. 1998; Duckworth et al. 2000), and habitat construction (Jones et al. 1997; Stachowicz 2001) as factors shaping plant species diversity patterns. Barrier island dune landscapes behave as a responsive biogeomorphic system, rather than as a collection of independent components (Odum et al. 1987; Rastetter 1991). These systems are characterized by a small number of species that structure topographically-defined habitats and regulate the spatial pattern of storm-generated overwash disturbance (Godfrey et al. 1979).

Dune plant species vary greatly in the extent to which they mold dune topography (Moreno-Casasola 1986; Hesp 1991). Three dune plant functional types, delineated according to growth form and their topography-modifying responses to sediment mobility, are common along coastal strands (Hosier 1973; Woodhouse 1982; Ehrenfeld 1990): dune-builders, burial-tolerant stabilisers, and burial-intolerant stabilisers. Dune builders have upright growth habits that produce rapid vertical accumulation near the margins of vegetation. Their positive growth responses to burial and slow lateral spread produce steep dune slopes. Burial-tolerant stabilisers also have positive growth responses to burial, but their decumbent growth forms do not promote vertical dune development. Instead, an extensive network of horizontal rhizomes stabilises substrates [“guerilla” growth forms (Harper 1985; Fahrig et al. 1994)]. Burial-intolerant stabilisers are inland-ranging species that colonize protected mesic dunal swales. These species have negative growth responses to burial. Their dense compact growth form facilitates intense resource use by preempting a site (“phalanx” growth forms; Harper (1985)), thus effectively binding substrates. Individual taxa in these three functional groups are referred to as “driver” species (Walker 1992) given that their topography-modifying characteristics influence (and are influenced by) the movement of sediments and patterning of disturbance. The distribution and abundance of these dune plant species functional types, in their capacity to shape dune physiography, is therefore intertwined with the distribution of overwash along a gradient of shore disturbance (Godfrey 1977). A fourth group of coastal dune plants can be categorized as passenger species (Walker 1995), those entrained taxa with no strong or direct functional role in modifying topography (see also structural and interstitial species in Huston (1994)).

In this paper, I investigate how dune plant species abundance and distribution are linked to the emergence of diversity patterns for two barrier island dune biogeomorphic systems spanning a shore disturbance gradient within the Georgia Bight. My first two research objectives explore differences between islands in along-shore alpha diversity and relate these diversity patterns to primary foredune height, a proxy measure of overwash frequency (Hosier and Cleary 1977; Odum et al. 1987). My third research objective explores the association between alpha diversity and species abundances for each island through suppositions embedded in two diversity models, the Intermediate Disturbance Hypothesis (IDH; Connell (1978)) and the Dynamic Equilibrium Model (DEM; Huston (1979, 1994)).

IDH is a widely invoked disturbance model, and posits that high diversity sites develop from a compositional overlap of broadly distributed early and late successional species. DEM proposes that high and low rates of competitive displacement, in concert with disturbance frequency, determine diversity patterns. As such, any intermediate level of disturbance may have very different diversities depending upon local site conditions. Consequently, DEM does not proscribe the direct cause-and-effect relationship between disturbance and diversity implicit in IDH. DEM also makes more detailed assumptions about the scaling of processes which structure diversity patterns. Diversity is most likely to be maximized under conditions when the influence of local processes is relaxed (Figure 1). In its place, variables originating from larger-scale contexts, such as dispersal, habitat heterogeneity, and species pool size determine the maximum number of species that coexist (Huston 1994).

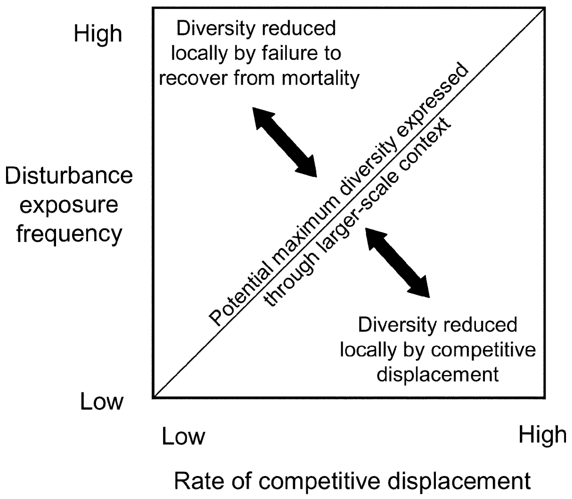

Figure 1. The Dynamic Equilibrium Model of species diversity

Background

Barrier island dune biogeomorphic systems

Central to this study are the two well-documented barrier island morphologic types that emerge along the margin of the Georgia Bight (Hayes 1979; Williams and Leatherman 1993; Trenhaile 1997). Along this sandy coastline, a gradient of increased exposure to winter extratropical cyclones with increased latitude yields a strong geographic continuum of potential overwash exposure (Dolan and Davis 1992; Davis et al. 1993). Onshore deposition of sediment during periodic storm-driven overwash is frequent on low-profile, wave-dominated microtidal barrier island morphologies in the Outer Banks of North Carolina. Return intervals for winter cyclones capable of generating overwash are approximately 10 years for the mid-Atlantic coast (Dolan and Davis 1992). Sediment mobility during overwash clears patches of ground and initiates vegetation recovery (Hayden et al. 1995; Costa et al. 1996). By contrast, incremental sediment mobility predominates on mixed-energy mesotidal barrier island morphologies of Georgia. With infrequent overwash, a greater dune topographic complexity may develop (Oertel and Larsen 1976).

Each barrier island morphology can be characterized by a set of mutually reinforcing interactions between its sediment mobility, landforms, and a set of these topography-modifying species. By modifying topography in the periods between disturbance, these species perpetuate the prevailing patterns of sediment mobility and species abundances in a positive feedback (Wilson and Agnew 1992). Following Peterson et al. (1998) definition of ecological resilience, each morphologic type is a resilient biogeomorphic system that organizes around mutually reinforcing structures and processes by modifying variability in disturbance regime.

After overwash deposition in the Outer Banks, the mobility of sediments is mediated by burial-tolerant taxa, chiefly the rhizomatous perennial *Spartina patens*. *Spartina patens* is not an efficient dune-builder (Woodhouse 1982), but its high tolerance to burial permits it to recover rapidly following overwash and effectively bind deposited sediments (Godfrey and Godfrey 1976). Similar functional attributes have been described for *Hydrocotyle bonariensis* (Hosier 1973) and for mosses in sandy coastal habitats (Martínez and Maun 1999). By stabilising sediments that would otherwise be directly diverted for dune reestablishment, these species contribute to a reduced topography low in resistance to overwash exposure (Godfrey et al. 1979). For this dune system, intrinsic biogeomorphic processes reinforce extrinsic disturbance exposure. Wave energy from passing storms is dissipated across the island surface (Riggs 1976).

With an abundant supply of sediment on mixed-energy mesotidal barriers, an extensive dune ridge-and-swale topography may develop (Hayes 1994; Taylor and Stone 1996). Topographic contrasts along these landforms are maintained by positive relief generated by dune-building taxa, and stabilisation of intervening low swales by burial-intolerant woody shrubs and grass species. This augmented topographic roughness acts as a barrier to the spread of overwash into backshore dune habitats. Instead, wave energy from storms is dissipated through extensive networks of tidal inlets that bound islands (Sexton and Hayes 1991). In this setting, intrinsic biogeomorphic processes dampen extrinsic disturbance exposure.

Methods

Field sampling

To examine diversity patterns in these two biogeomorphic systems, two islands, nested within the larger meteorologic disturbance gradient spanning the Georgia Bight, were selected for study: South Core Banks, North Carolina (34°41′ N, 76°28′ W), and Sapelo Island, Georgia (31°23′ N, 81°15′ W) (Figures 2 and 3). Both islands are largely undeveloped. I confined my sampling on Sapelo to the 5 km of Nannygoat Beach, the southernmost Holocene island, to minimize the confounding influence of multiple tidal inlets. Overwash is infrequent on Sapelo (Deery and Howard 1977). On Nannygoat Beach, only the south end is exposed to this disturbance agent. South Core Banks, part of Cape Lookout National Seashore, is a retreating Holocene barrier with a greater exposure to overwash. Overwash increases in frequency along-island from south to north. Sampling on South Core covered a much larger along-island extent (35 km) in comparison to Sapelo.

Five sites, each containing three randomly-positioned strip transects (at a minimum of 20 m intervening distance), were parsed along the axis of each island. Each transect began at the high water mark, a point along the seaward base of the primary foredunes. The high water mark accurately reflects the position of frequent maximum high-water levels (Morton and Speed 1998). Transects extended inland through dune habitats to the first occurrence of extensive cover of the inland woody shrub *Myrica cerifera*. *Myrica cerifera* invades backshore herbaceous habitats in the absence of overwash (Young et al. 1995).

Vegetation data were collected within contiguous 1 × 2-m quadrats 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 quadrat. Because of the longer distances to stabilised vegetation on South Core Banks, quadrats were systematically sampled in intervals of every other meter. A total of 1082 quadrats was sampled on Sapelo, and 1139 on South Core. Point-frame hits in each quadrat were summed for individual species and expressed as

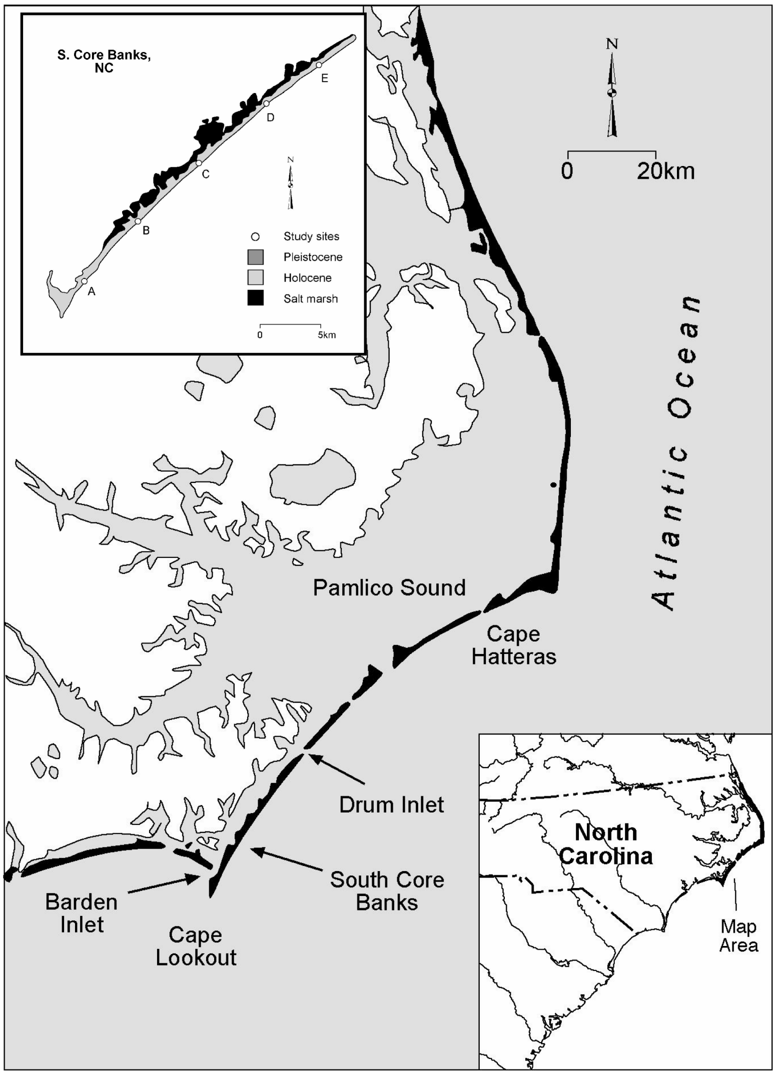

Figure 2. Wave-dominated microtidal barrier islands of the North Carolina coast and study sites (A-E) on South Core Banks

percent absolute cover. 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). Several genera were indistinguishable in the field and were lumped into species complexes.

Regional uniformity in temperature and precipitation regime, especially in the growing season, greatly diminish regional macroclimatic sorting on species composition (Stalter and Odum 1993). As a consequence of climatic uniformity, the dune flora on these barrier islands is potentially similar along the latitudinal breadth of my study region (Duncan and Duncan 1987). General climatic factors may contribute little to inter-island compositional variability when compared to dune microenvironmental factors, such as topography and substrate mobility (Barbour and Johnson 1977).

Data analysis

Are there significant differences between islands in alpha diversity?

To assess species diversity, I calculated the Shannon-Weiner index (H′) of alpha (local) diversity for individual transects (n = 15 per island). The total number of point frame hits for each species per transect was used to calculate H′. To compare islands, I employed

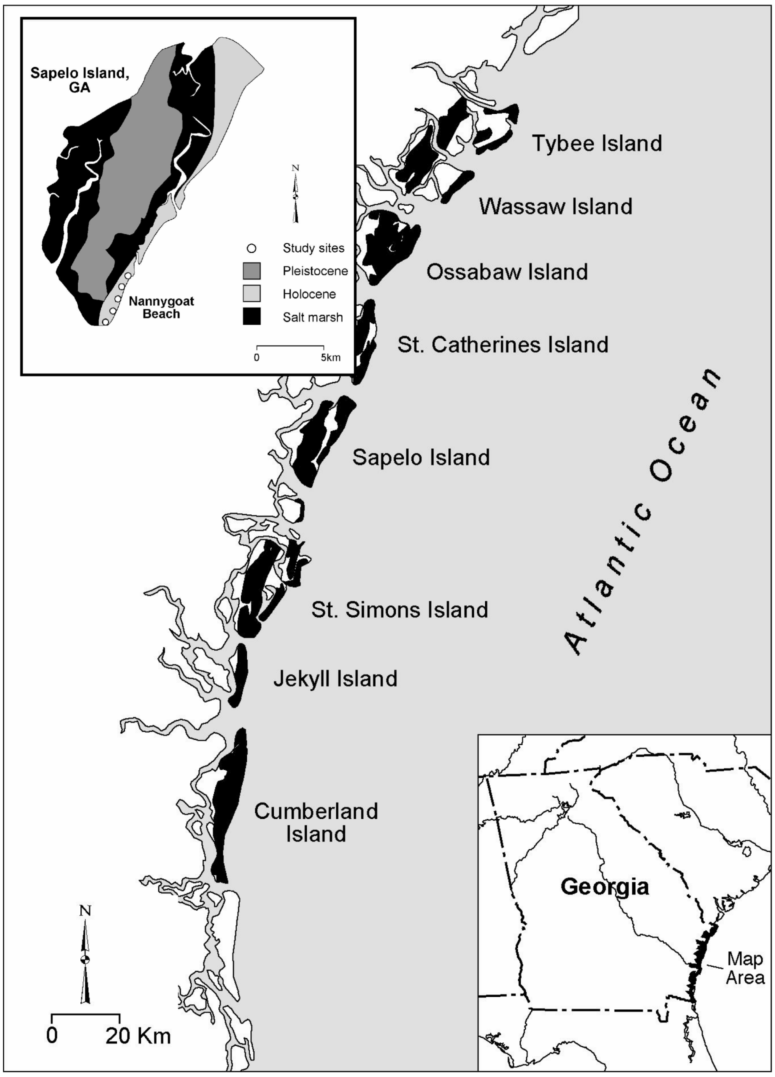

Figure 3. Mixed-energy mesotidal barrier islands of the Georgia coast and study sites (A-E) on Sapelo Island

multi-response permutation procedures (MRPP) as the analytical tool and transect-level Shannon-Weiner indices as my test metric. MRPP tests for group differences by comparing observed and permutated average within-group distances (Biondini et al. 1991). Probability values for MRPP express the likelihood of getting an average group distance as extreme or more extreme than observed, given a distribution of all possible distances. MRRP also calculates a within-group homogeneity statistic (*A*) that can be used to gauge whether observed between-group differences are useful, and not the result of random variation within groups. This statistic ranges from −1 to 1, with values greater than 0 indicating group differences greater than expected by chance. All MRPP significance tests were conducted at the 0.05 significance level in PC-Ord Version 4.04 (McCune and Mefford 1999).

Does the relationship between alpha diversity and primary foredune height differ significantly between islands?

Primary foredune height permits inference of the relative frequency at which interior dune habitats have been exposed to overwash disturbance and provides a basis for contrasting IDH and DEM. Increasing dune heights are associated with a reduction in the frequency of overwash. For each island, I calculated a Spearman's non-parametric rank order correlation coefficients for transect-level primary foredune height and Shannon-Weiner indices. Primary foredune height was defined as the maximum surveyed elevation within the first 10 meters of a transect.

Are there distinctive contrasts between islands in how species abundances covary with diversity?
Patterns of diversity along a disturbance gradient may be affected by changes in species abundance through their impact on disturbance variability (Holling 1992; Bendix 1997). To articulate how species abundances and diversity covary, I grouped taxa into the three aforementioned plant functional groups: dune-builders, burial-tolerant stabilisers, and burial-intolerant stabilisers. A fourth group consisted of those species designated as passenger species. Absolute species cover for these four groups were totaled by site and examined in light of the observed levels of alpha diversity and the biogeomorphic interactions ascribed to each island system.

To examine compositional patterns in detail, I employed non-metric multidimensional scaling (NMDS). NMDS is an ordination method used to visualize similarity, expressed as an ecological distance, among sample units in their compositional space (Clarke 1993). Increasing distance between sites in their NMDS ordination space is indicative of greater compositional dissimilarity. NMDS was performed on site-level absolute cover for all species and for passenger species presence-absence data. Monte Carlo significance testing and multiple runs were used to select an optimal NMDS solution. Sorenson's similarity coefficient was employed as the distance metric. All NMDS ordinations were performed in PC-ORD Version 4.04 (McCune and Mefford 1999). I originally hypothesized, as predicated by IDH, that high diversity sites on each island should converge in composition.

Results

Topography

Cross-sections confirmed strong topographic differences between islands (Figure 4). On South Core, a low-profile overwash topography was well developed. Seventy-eight percent of interior quadrats were located below the high water mark, suggesting a greater propensity for overwash to diffuse across the berm slope into backshore habitats. Mean transect primary foredune height declined 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. Cross-sectional topography on Sapelo was more complex. Sapelo profiles suggested a higher degree of topographic resistance to the spread of overwash. Sixty-two percent of the quadrats were located above the high water mark. Topography ranged from protective dune ridges and swales at mid-island sites, to a low-profile terrain on the southern end of the island. Mean transect primary foredune height varied from 1.6 ± 0.1 m relative to mean high water at Site D, to the absence of a primary foredune at Site A. Accretionary conditions at Site A maintained its low hummocky foredunes and a higher exposure to overwash, as evidenced by locally abundant wrack debris. Differences between islands in transect primary foredune heights were non-significant ($A = 0.03$, $p = 0.14$). Continuity of primary foredunes, as reflected in the standard deviation of transect primary foredune heights, was only slight higher on Sapelo (1.1 ± 0.6 m) than on South Core Banks (0.9 ± 0.91 m)

Composition

Total absolute cover on Sapelo was 52% and increased to 71% on South Core. Forty-three species out of a total of 120 were shared by both islands. These shared species comprised 96% of total absolute species cover on Sapelo, and 78% of the total absolute cover on South Core. Of the twelve taxa identified as prominent driver species in coastal dunes, nine were shared by both islands. While island setting did not appear to affect colonization for these shared driver species, it did affect their relative abundance. *Uniola paniculata*, a common dune-building species of the southeastern United States, attained its highest total cover on South Core (Figure 5). South Core also supported a greater cover of two overwash-adapted driver species, *Spartina patens* and *Hydrocotyle bonariensis*. These two burial-tolerant stabilisers increased in cover from south to north in tandem with increasing overwash exposure. An assemblage of burial-tolerant mosses was found only on South Core. Comprised chiefly of the genera *Ditrichum*, these bryophtyes formed a stabilising ground cover at sites B and C. Sapelo was characterized by a higher cover of the dune-building species *Panicum amarum and Sporobolus virginicus.* These two species initiate primary foredune recovery following disturbance

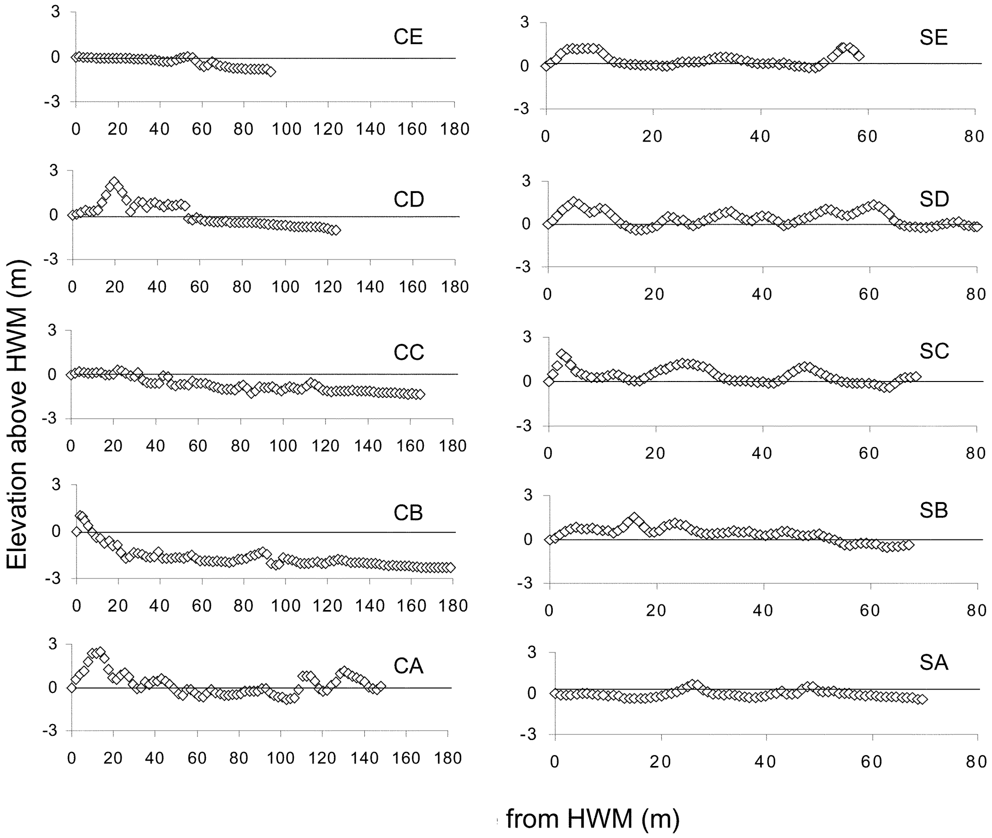

Figure 4. Topographic cross-sections for representative transects from each site on S. Core Banks, North Carolina (left) and Sapelo Island, Georgia (right). Zero represents high water mark datum. Diamonds indicate individual quadrats. Sites arranged from A (south) to E (north) (Sapelo = S; South Core Banks = C).

(Woodhouse 1982). *Panicum amarum* and *Sporobolus virginicus* were abundant at Site A, the only overwashed location on Sapelo. Well-protected swale habitats at sites C, D, and E on Sapelo augmented the cover of the burial-intolerant stabilisers *Muhlenbergia filipes, Phyla nodiflora, Andropogon* spp., and *Myrica cerifera*.

The more abundant taxa on each island were driver species that reinforced each island's characteristic topography and geomorphic processes (Figure 6). Passenger species, while individually low in cover on both islands, were more numerous. A sharp discontinuity developed between islands in the distribution of driver species. Sapelo had a higher cover of burial-intolerant stabilisers, while South Core had a higher cover of burial-resistant stabilisers.

Alpha diversity

In general, peaks in alpha diversity corresponded to the distribution of passenger species cover and number. Site A on Sapelo had the highest mean transect alpha diversity (H′ = 2.70 ± 0.07) of any sampled location. The number and cover of swale passenger species (*Sabatia stellaris*, *Rumex hastalus*, *Juncus marginatus*) may have increased at this site because of a lower cover of the competitively dominant woody shrub *Myrica cerifera*. Furthermore, the frequently disturbed dunal strandline at Site A promoted establishment of passenger species that were rare at other island sites. This local increase in sediment mobility associated with overwash, in proximity to older, stabilised habitats at Site A, also contributed to a high alpha diversity by fostering more evenness in driver species. Another peak in alpha diversity on Sapelo developed at Site E (H′ = 2.31 ± 0.13). At this site, erosion and landward retreat of the shoreline has de-

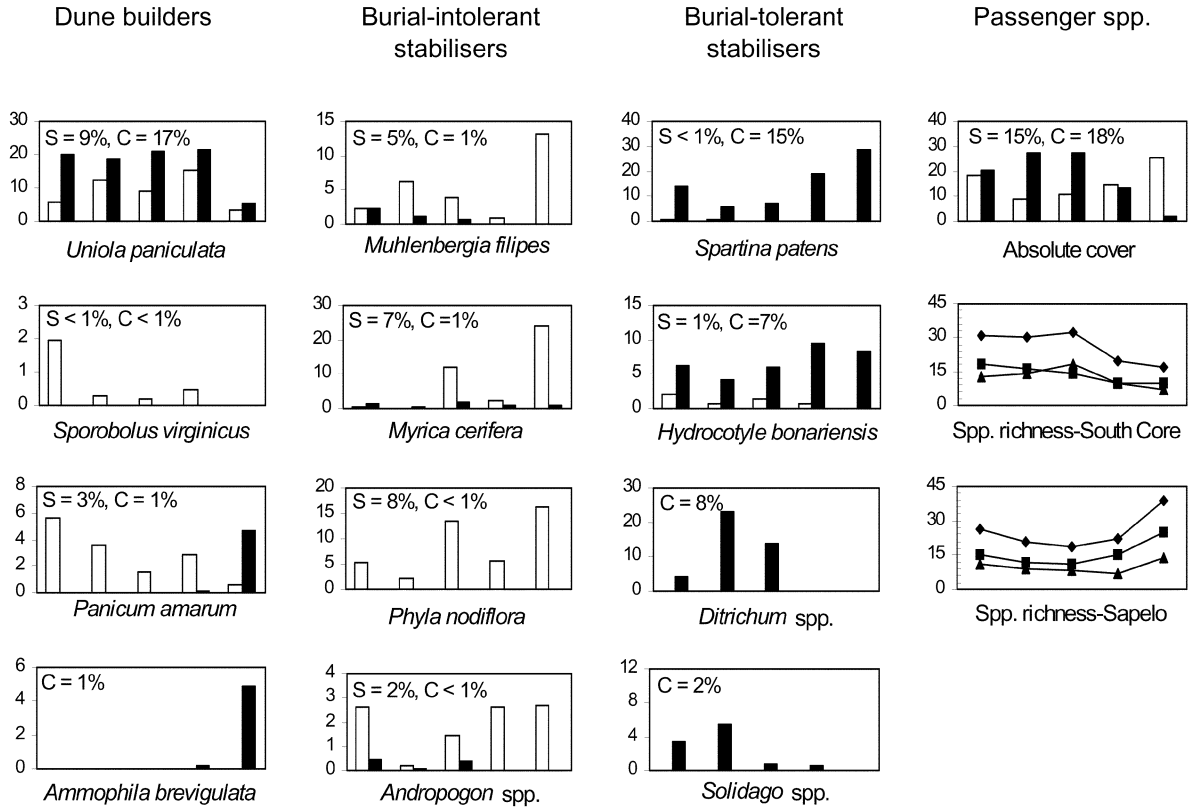

Figure 5. Percent absolute species cover by site and function for each island (Sapelo = white bars; South Core Banks = black bars). Sites arranged from A (south) to E (north) left to right across x axis. Total island absolute species cover noted by letters above bar graphs (Sapelo = S; South Core Banks = C). Passenger species plots: ● = total number of species; ▲ = total number of annuals; ■ = total number of perennials.

stabilised dunes. Formation of disturbance gaps in *Myrica cerifera* thickets as a result of increased sediment mobility augmented the number of colonizing passenger species, particularly ruderals (*Cnidoscolus stimulosus*, *Eupatorium* spp., *Vulpina octoflora*). While passenger species number was high at this site, their total cover was low. Several vine species (*Mikania scandens*, *Smilax* spp., *Ampelopsis arborea*) that invade senescing *Myrica cerifera* thickets (Crawford and Young 1998) also contributed to the higher mean transect diversities at Site E and at Site D (H′ = 2.32 ± 0.12). Slight declines in alpha diversity at sites B (H′ = 2.06 ± 0.13) and C (H′ = 2.10 ± 0.24) were associated with a reduction in the number and cover of passenger species. Based on MRPP of transect-level alpha diversity, Site A on Sapelo was significantly different from a group defined by Sites B through E (*A* = 0.28, p < 0.001).

A wide range of topographically-defined habitats contributed to a high mean transect alpha diversity at Site A on South Core (H′ = 2.39 ± 0.03). High phenotypic plasticity in *Hydrocotyle bonariensis* (Costa et al. 1996) and the local abundance of a variety of *Spartina patens* adapted to less exposed, brackish swales (Godfrey et al. 1979; Silander 1979) may explain the abundance of these two species at this infrequently overwashed site. Similar alpha diversities at Sites B (H′ = 2.39 ± 0.07) and C (H′ = 2.40 ± 0.27) were associated with an increased number of passenger species (*Ambrosia artemisiifolia*, *Arenaria serpyllifolia*, *Gaillardia pulchella*). Declines in diversity metrics were observed for Site D (H′ = 1.83 ± 0.01) and Site E (H′ = 1.49 ± 0.08) in response to increasing overwash. These sites were characterized by low relief, numerous overwash fans, a dense cover of *Spartina patens*, and a decrease in the number and cover of passenger species. Based on MRPP of transect-level alpha diversity, Site A, B, and C on South Core were significantly different from a group defined by Sites D and E (*A* = 0.40, p < 0.001).

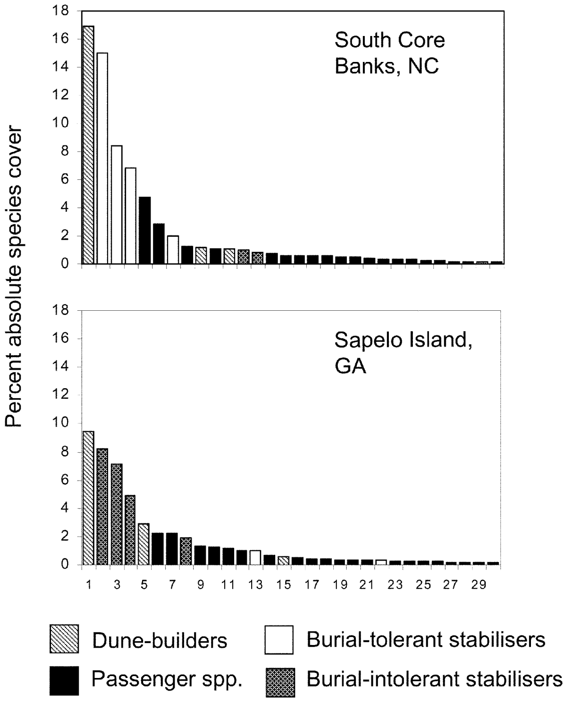

Figure 6. Ranked individual species percent absolute cover by functional group. Total richness of species and species complexes: Sapelo = 88; South Core = 74.

MRPP indicated no significant inter-island difference between islands in transect-level alpha diversity (*A* = 0.02, p = 0.15). Spearman's rank correlation coefficient for transect-level alpha diversity and primary foredune height was weakly non-significant and negative ($r_s = -0.49$, p = 0.07) on Sapelo, and significant and positive on South Core Banks ($r_s = 0.65$, p = 0.01). Differences between islands in transect-level species richness were also non-significant (*A* = 0.01, p = 0.28). In reference to IDH, alpha diversity had a linear to weakly unimodal relationship with overwash exposure on South Core (Figure 7). On Sapelo, the along-shore covariation of alpha diversity and dune height is not as well defined. In this setting, a weakly linear relationship developed between disturbance and site alpha diversity.

A two-dimensional final solution was selected for the site-level NMDS of absolute species cover (Figure 8). Monte Carlo randomizations (n = 999) indicated a significant reduction in stress (p = 0.02) for this dimensionality. A strong separation of island sites in my NMDS plot confirmed that distinctive island abundances were expressed, despite the strong overlap in species distributions. No trend toward similar compositions was apparent among the high diversity sites of each island. Sites A and E on Sapelo show strong compositional dissimilarities from their high diversity counterparts, Sites B and C on South Core. A two-dimensional NMDS (n = 999; p = 0.05) of presence/absence data for passenger species indicated a similar compositional divergence. Dissimilar suites of passenger species were expressed among these high alpha diversity sites.

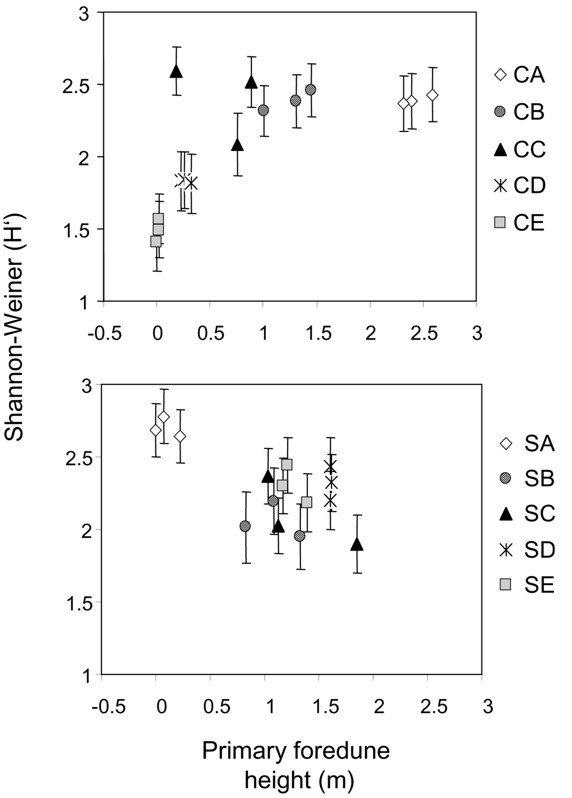

Figure 7. Transect alpha diversities and primary foredune height by island. First letter denotes island (Sapelo = S; South Core Banks = C) and second letter (A-E) denotes sites Error bars indicate standard deviation.

Discussion

Peaks in alpha diversity on each island were associated with differing overwash exposure frequencies. On Sapelo, increasing sediment mobility associated with overwash (Site A) enhanced alpha diversity, perhaps by reducing the competitive dominance of the woody shrub *Myrica cerifera*. On South Core, higher alpha diversities (Sites A, B, and C) were associated with decreased exposure to mortality-inducing over-

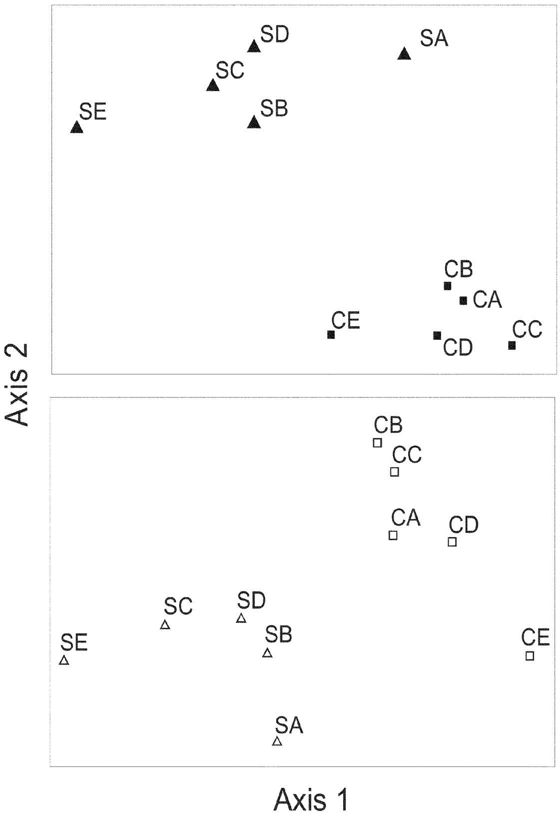

Figure 8. NMDS plots of site compositional similarity for absolute species cover of all species (top), and presence-absence of individual passenger species (bottom).

wash. These trends corroborate studies that document the role of overwash in augmenting species diversity (Schroeder et al. 1979) or decreasing it (Hayden et al. 1995). Thus the effect of overwash disturbance on diversity is dependent upon the historically prevalent disturbance regime of each island (Denslow 1980)

The equivalence between islands in species diversity may reflect the compensatory effects of the locally abundant driver species that mold topography (see Bruno (2000) and Hacker and Gaines (1997)). Through their influence on topography, these driver species facilitated species coexistence on each island through their modification of habitat heterogeneity. On South Core, burial-tolerant driver species stabilise overwash sediments, and thus may facilitate the colonization of passenger species, particularly annuals, that are unable to germinate in unstable substrates (Hosier 1973; Fahrig et al. 1993). On Sapelo, dune-builders and burial-intolerant stabilisers maintain elevational habitats along ridge-and-swale topography for a suite of passenger species. Similar driver species facilitation of local diversity has been described in salt marshes for *Juncus roemarianus* (Hacker and Bertness 1999) and *Spartina alterniflora* (Bruno and Kennedy 2000).

A significant positive correlation between primary foredune height and species diversity was expressed on South Core. Frequent disturbance on South Core may constrain patch recovery to early successional stages relative to Sapelo, and thus may inhibit compositional sorting derived from competitive displacement by woody shrubs such as *Myrica cerifera*. On the simplified topography of South Core, this fostered the strong correlative relationship between recovering dune height and alpha diversity, one that varied geographically in tandem with time since last disturbance. On Sapelo, the longer intervals between disturbance increases topographic complexity. In consequence, there is potentially more directional sorting of vegetation through time along these topographic gradients. This, in effect, decouples the co-developmental linkage among disturbance, fronting dune height, and vegetation recovery. Consequently, alpha diversity and the fronting dune height show less along-island association.

The explanatory effectiveness of IDH was weak within each island. The relationship between diversity and disturbance frequency on Sapelo Island and South Core Banks was predominantly linear rather than unimodal. IDH was most clearly an ineffective concept for explaining the alongshore distribution of diversity on Sapelo. Along-island alpha diversity bore no systematic unimodal association with primary foredune height, a proxy measure of relative overwash disturbance frequency. On South Core, a systematic, along-island variation in disturbance exposure roughly approximated a geographic expression of IDH. Alpha diversity had a weak unimodal peak at mid-island site C, where dune heights suggested an intermediate level of overwash exposure. IDH may be more often ascribed to environments such as South Core, where IDH's assumption of a strongly coupled cause-and-effect relationship between disturbance and diversity has more validity. On Sapelo, by contrast, formation of a complex topography during the longer intervals between overwash exposure may decouple the control of diversity from disturbance to biotic processes operating on more variable spatial and temporal scales. Thus any between-patch examination of IDH fails on Sapelo, in part because an intermediate level of disturbance cannot be geographically defined at the scale applied in this study.

Island sites diverged in compositional similarity as mean site alpha diversity increased. In both NMDS plots, high diversity sites for Sapelo (A and E) and South Core Banks (A, B and C) were well separated in compositional space. IDH makes no explicit assumptions about compositional variability, but suggests that peak diversities converge toward a compositional overlap of broadly distributed early and late successional species. DEM, however, affords an explanation for the relatively larger compositional distances among high diversity sites. Insofar as DEM predicts that variables originating from larger-scale contexts (dispersal, habitat heterogeneity, and species pool size) maximize diversity when local-scale processes are relaxed, there exists a potential divergence in compositions at peak diversities along a disturbance gradient. As observed in this study, high diversity sites expressed a varied range of habitats and species compositions. High diversities were derived from the dispersal and germination of dissimilar suites of passenger species into active overwash patches (Site A on Sapelo), within disturbance gaps in late successional shrubs (Site E on Sapelo) and within inactive overwash patches (Sites B and C on South Core).

The abundance of plant functional types were markedly different on each the two study islands. I posit that these functional group abundances may have imposed the observed linearities between diversity and disturbance on each island. By either dampening (Sapelo) or reinforcing (South Core Banks) disturbance along a gradient, the local driver species modify disturbance variability and constrain the local abundance of patch sizes uncharacteristic of the prevailing disturbance regime. For each island, bifurcation in gap sizes and in the species adapted to colonize them may restrict the development of any broad unimodal overlap of species coexistence postulated by IDH.

A simulation of forest development by Savage et al. (2000) provides support for the compositional and diversity patterns observed in this study. Compositional responses that emerged along a simulated forest fire disturbance gradient over multiple successional simulations followed two dominant trajectories. At low disturbance levels, composition was characterized by the dominance of late successional species that functionally excluded disturbance. High levels of disturbance shifted composition toward a state characterized by an oscillation between early successional species and large disturbance events. I posit that the dune habitats of South Core Banks and Sapelo represent two such similar trajectories, or attractors. For each island, the abundance of plant functional types modifies overwash so at to reinforce its presence in a positive feedback. In addition, the simulation by Savage et al. (2000) revealed that intermediate levels of disturbance manifested a greater range of compositions and diversity configurations. Similarly, in this study, high diversity sites along the disturbance gradient spanning the study islands exhibited a divergence in their composition.

Conclusions

Observed along-island species composition and function supported the systems interactions described for each barrier island morphologic type. On South Core, extrinsic disturbance and intrinsic biogeomorphic processes maintained a regularity in the distributional pattern of along-shore species diversity that was strongly correlated to primary foredune height. Sapelo represents a landscape in which the interaction of extrinsic and intrinsic structuring agents fostered a fine-spatial scale differentiation of landscape patterns of species diversity that was less strongly correlated to topographic metrics. No significant overall differences in dune plant species diversity developed between these two islands. However, in terms of species richness per unit area, Sapelo was by far the more diverse dune habitat, given its smaller dimensions. Based on plant species lists for Core Banks (US National Park Service 1977) and Sapelo Island (Duncan 1982), the delineation of species complexes from genera into their potentially-occurring constituent species would likewise favor a greater species richness in the dunal strands of Sapelo Island.

While it is well-recognized that diversity is associated with habitat heterogeneity, usually only an external source of the heterogeneity is assumed (Bascompte and Rodriguez 1999). In this study, the habitat heterogeneity structuring diversity patterns was generated by intrinsic biogeomorphic responses, as well as extrinsic disturbance from overwash. Bascompte and Rodriguez (1999) and Therriault and Kolasa (2000) emphasize the importance of intrinsic, self-generated heterogeneity, and its interaction with extrinsic disturbance, as controls of diversity patterns. Potentially higher species diversities may be expressed on Sapelo because any extrinsically-generated overwash would be superimposed upon the topographically complex landscape that develops in the intervals between infrequent disturbance, as observed at Site A. The fine-scale spatial variation in topography at this site may have reinforced species coexistence by diversifying the patterning of disturbance exposure, a conclusion also suggested by Pollock et al. (1998) for wetland habitats.

Applications of IDH have yielded inconsistent results as well as questions of its intent (Collins and Glenn 1997; Roberts and Gilliam 1995). Along a shore disturbance gradient, the utility of the Intermediate Disturbance Hypothesis may weaken because of complex system interactions. IDH does not incorporate intrinsic processes (Shiel 1999) such as topographic modification, or their subsequent modification of disturbance exposure. Morever, these complex systems interactions may linearize diversity responses to disturbance. This study and others (Baker 1990; Bendix 1997) have found departures from the unimodal relationship between diversity and disturbance, often uncovering linear decreases or increases in plant species diversity along disturbance gradients. While temporal and spatial scales chosen to delimit tests of IDH may constrain its expression to linear trends (Bendix 1997), I posit that linear trends may also emerge through the influence of driver species that may dampen or augment disturbance exposure. IDH may best apply where a disturbance gradient spans an abrupt transition in plant functional types, where disturbance regimes are changing, or where the intensity of an individual disturbance greatly exceed that which has been historically prevalent.

I suggest that the Dynamic Equilibrium Model may be a more generally applicable framework for examining plant diversity patterns along shore disturbance gradients. DEM acknowledges that disturbance does not determine diversity, but only sets the stage for its expression through post-disturbance succession (Reice 1994; Collins et al. 1995; Hubbell et al. 1999; Petraitis et al. 1989). By incorporating an interaction of intrinsic and extrinsic structuring agents, DEM is better suited to address the complex formation of habitat heterogeneity. The general applicability of DEM also arises through its independence from any geographically-invariable scaling of intermediacy in disturbance frequency. Intrinsic biogeomorphic processes along a disturbance gradient may change the scale-expression of the agents structuring diversity, and complicate the consistent scale identification of intermediate disturbance frequencies. Although we only examined two islands in this study, future plant diversity studies may find it productive to quantify linkages between the complex formation of habitat heterogeneity and the distributional abundance of plant functional types.

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