

Patterns of Plant Diversity in Georgia and Texas Salt Marshes

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Abstract A fundamental question in ecology is how biological interactions and biogeographic processes interact to determine the biodiversity of local sites. We quantified patterns of plant species diversity on transects across elevation at 59 salt marsh sites in Georgia and 49 sites in Texas. Although these regions have similar climates and floras, we anticipated that diversity might differ because of differences in tidal regime. Diversity was measured at global, regional, site, and plot scales to consider processes occurring at all levels. Species pools were similar between regions. Texas had greater diversity at the site and plot scales, suggesting that processes occurring at the site scale differed. The greater diversity of Texas sites and plots was associated with wider distributions of individual species across the marsh landscape and proportionally more middle marsh (a high diversity zone) and less low marsh (a low diversity zone) than in Georgia marshes. Preliminary data suggested that these differences were not due to differences in salinity regime or standing biomass between regions, leaving differences in tidal regime as the most plausible hypothesis accounting for differences in plant diversity. We speculate that the less-predictable tidal regime in Texas leads to temporal variation in abiotic conditions that limit the ability of any one species to competitively exclude others from particular marsh zones.

Keywords Assembly rules · Biodiversity · Competition · Biogeography · Salt marsh · Species diversity

Introduction

Ecologists have long been interested in understanding the mechanisms that mediate patterns of biodiversity (MacArthur 1972; Huston 1994; Rosenzweig 1995). Despite a great deal of attention, however, the causes of biological diversity remain controversial (Abrams 1995; Oksanen 1996; Stevens and Carson 2002), in part because different processes may be important at different spatial scales.

Studies of diversity conducted at different scales have yielded dramatically different results (Huston 1999; Mittelbach et al. 2001), fostering debate over whether diversity of a target community is determined by the species pool (Ricklefs 1987; Zobel 1992; Gough et al. 1994) or by local processes such as competition (Grime 1973; Tilman 1982). In general, the species pool of an area is determined by biogeographic constraints and abiotic conditions such as climate that determine which species are able to persist in a particular region. Biotic interactions may then reduce, or occasionally expand, the number of species predicted (based on their tolerances to abiotic conditions) to occur in a local area (Gough et al. 1994; Callaway and Walker 1997). Because the species pool sets the upper limit of the number of species that can occur locally, processes at both scales are ineluctably linked, and recent studies have obtained a deeper understanding of diversity patterns by studying them at a range of spatial scales (Pärtel et al. 1996; Harrison et al. 2006; Rajaniemi et al. 2006). In particular, by comparing diversity patterns at multiple scales and the contributions from one scale to the next, we can determine the scale at which differences in diversity are produced and thereby begin to infer the mechanisms responsible for mediating different patterns of diversity under different conditions.

In this study, we compare plant diversity in salt marshes of Georgia and Texas. The Southeast Atlantic and Gulf Coasts of

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the USA have similar climates, and their salt marsh floras overlap considerably in composition. By comparing these two geographic regions, we sought to focus on local diversity patterns while minimizing differences in the size and species composition of the species pool—factors that would confound many geographic comparisons of diversity patterns in other study systems.

There are many general abiotic influences shared between Georgia and Texas. Coastal regions of both states have similar temperature and rainfall patterns (Hargrove et al. 2006), and salt marshes on both coasts are periodically inundated by the tides. These general abiotic conditions create a similar plant species pool in marshes of each geographic region (Duncan and Duncan 1987). But while the patterns of plant diversity and the factors mediating these patterns are relatively well understood for marshes of the northern and southern Atlantic Coast, few studies have examined plant diversity patterns in the Gulf Coast marshes of Texas.

Atlantic Coast salt marshes have been well studied for decades (Ganong 1903; Adams 1963; Chapman 1974). Plant diversity patterns have been well documented in Rhode Island, Georgia, and other Atlantic Coast locations (Bertness and Ellison 1987; Hacker and Bertness 1999; Pennings et al. 2003, 2005). The dominant influence on vegetation pattern in salt marshes is the gradient of waterlogging and salinity created by tidal inundation (Adams 1963; Ewing 1983). Atlantic Coast tides experience a regular, lunar, semi-diurnal flooding schedule, with tidal amplitudes typically 2–3 m from the low to high water mark. Edaphic conditions change gradually with increasing elevation across the intertidal zone (Wiegert and Freeman 1990), with highest elevations flooded only at seasonal spring tides, middle elevations infrequently flooded, and lowest elevations regularly flooded. Atlantic Coast salt marshes have fairly discrete zones of vegetation that form across the edaphic elevational gradient (Pennings and Bertness 2001). Each plant species is limited to a portion of this gradient, depending on its ability to tolerate abiotic stress (Richards et al. 2005). Competitive dominants exclude subordinates from favorable marsh zones, creating abrupt transitions from one vegetation type to another, which defines vegetation zones (Bertness and Ellison 1987; Bertness 1991a, b; Bertness et al. 1992; Pennings and Moore 2001; Pennings et al. 2005). At the same time, dense stands of vegetation may ameliorate harsh abiotic conditions, thereby extending the distribution of species sensitive to abiotic stress and increasing local diversity (Bertness and Shumway 1993; Hacker and Gaines 1997; Hacker and Bertness 1999).

The tidal regime in the Gulf Coast differs from that in the Atlantic Coast. Diurnal tides in Texas are only 0.37–0.52 m in amplitude (Zetler and Hansen 1970). These low-amplitude astronomical tides are routinely overshadowed by tidal forcing from meteorological conditions, such as seasonally changing wind directions and summer tropical

storms (Eleuterius and Eleuterius 1979; Stout 1984; Wang 1997). The unpredictable flooding that results can cause extended periods of waterlogged or exposed conditions. Although Gulf Coast brackish marshes have been extensively studied by Gough and Grace (Gough et al. 1994; Gough and Grace 1997, 1998a,b, 1999), there are relatively few studies of plant diversity patterns and the factors creating these patterns in salt marshes on the Gulf Coast (Dunton et al. 2001; Alexander and Dunton 2002; Forbes and Dunton 2006). Since the physical gradient created by the semi-diurnal tides along the Atlantic Coast results in predictable zones of vegetation, however, it is reasonable to hypothesize that the less regular diurnal tides in the Gulf could result in less ordered and therefore more diverse vegetation patterns.

The purpose of this study was to test the hypothesis that diversity patterns would differ between salt marshes in Georgia and Texas. By documenting any such differences, we can begin to infer how the factors that create diversity patterns may differ geographically. To gain more insight into the processes producing differences in diversity patterns between the two regions, we examined diversity at four spatial scales: global, regional, site, and plot. Although it was outside the scope of this project to experimentally investigate all the potential mechanisms that might mediate diversity patterns, preliminary data suggested that variation in salinity or productivity was unlikely to be causing geographic differences in diversity, leaving geographic differences in flooding as the most plausible hypothesis to explain observed differences.

Methods

Study Sites and Transect Sampling

We sampled 49 salt marsh sites in Texas and 59 in Georgia (Fig. 1) in the late spring (April to May) and early summer (June to July) of 2005, respectively. Because almost all of the plants that occur in these salt marshes are perennials and the few annuals that occur would have germinated early in the year at these low latitudes, all plant species should have been present throughout all four of these months. Sites included a range of landscape positions such as mainland, back-barrier hammock, and barrier island locations. All sites were dominated by salt marsh plant species, and in particular, all sites had abundant *Spartina alterniflora*; sites dominated by freshwater or brackish marsh vegetation were avoided. The salinity of the water column at the sites (a single measurement in the nearest creek or bay on the date the site was sampled) did not differ between the two regions [GA = 20 ± 1 (SE) PSU, TX = 23 ± 1 PSU, $P=0.11$, t test]. Water column salinities are variable over time, and a single measurement is at best a crude indicator of long-term conditions;

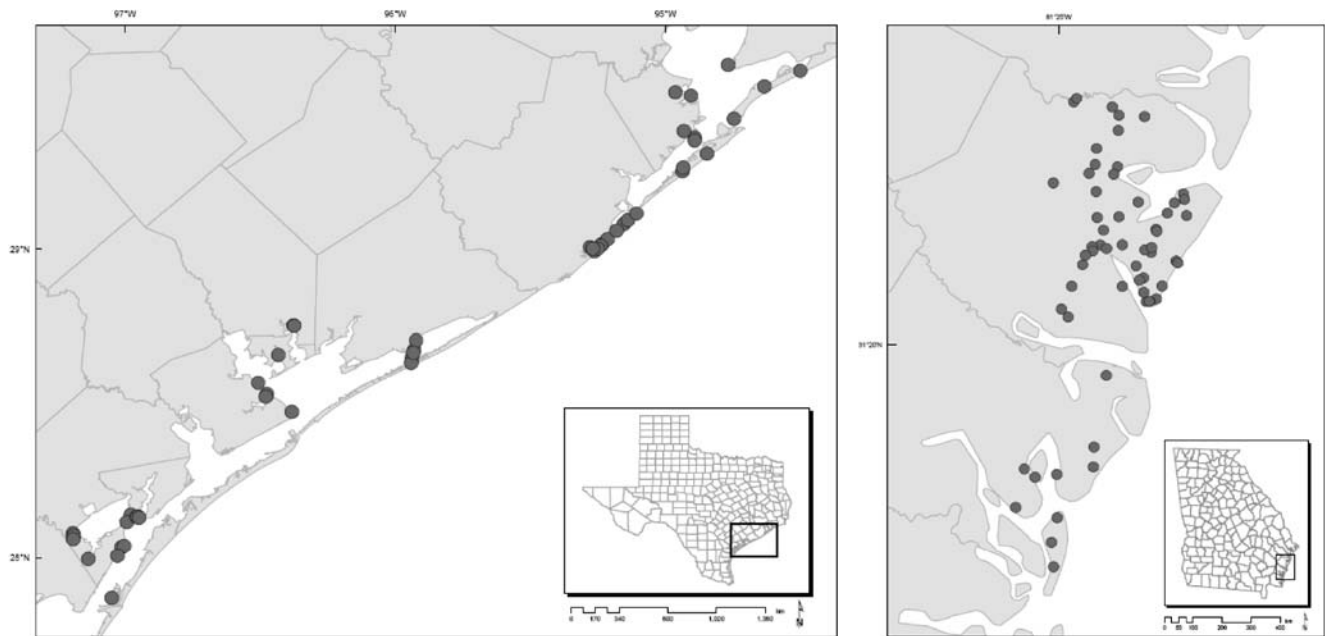


Fig. 1 Maps showing site locations in Texas (*left*) and Georgia (*right*). The Georgia coastline has extensive marsh complexes between the coastal barrier islands and the mainland; both marshes and terrestrial habitats are *shaded* to distinguish them from open water

however, these measurements are consistent with our qualitative impression that we sampled similar types of sites in both geographic regions. Datasets listing site geographic coordinates, landscape positions, dates sampled, and species composition are available from the Georgia Coastal Ecosystems LTER web site (<http://gce-lter.marsci.uga.edu/lter/index.htm>).

Plant diversity was documented along a single 5-m wide transect at each site. Each transect began at the lower elevational limit of vegetation (typically at the closest major creek or channel to the upland; sometimes at an open bay if no major creeks or channels were encountered) and continued perpendicular to the water's edge up to the shrub community at the upper marsh border. At each 1-m interval along the transect, we located a 1×5 m plot, with the long axis of the plot parallel to the water's edge and recorded each plant species present in the plot. Each 1×5 m plot contained a single nested 1×1 m subplot, with a single 0.5×0.5 subplot nested within the 1×1 m plot. Subplots were in the same relative location within each 1×5 m plot. The terrestrial edge of these salt marshes was dominated by a zone of shrubs (especially *Borrichia frutescens* and *Iva frutescens*) with a fairly abrupt lower border. Markedly stunted shrubs, however, occur at lower marsh elevations, usually in mixed stands (Bertness et al. 1992; Pennings and Moore 2001). We continued sampling when we encountered stunted shrubs but stopped sampling when we encountered a full-size shrub in the 1×1 m subplot. Transects in GA were somewhat longer than those in TX (122 ± 14 vs. 85 ± 6 m, $P=0.02$, t test).

Because species richness is a crude measure of diversity, we also visually scored the percent cover of each plant species

in each 0.5×0.5 m subplot into one of five cover ranges: less than 5%, between 5% and 12%, between 12% and 25%, between 25% and 50%, and greater than 50%. The midpoint of each percent cover range was used to calculate the Shannon diversity index and evenness.

Data Analysis

Species richness was determined at four spatial scales: (1) the global pool (all species encountered in both regions), (2) the regional pool (all species encountered within each state), (3) the site pool (all species encountered at a site), and (4) the plot (the average number of species in all 1.0×5.0 m plots within a site). In addition to comparing richness values at each scale, we calculated the contributions of each pool to the next scale, e.g., the percent of species from the larger scale present at the next lowest scale (Rajaniemi et al. 2006). Statistical comparisons were made using t tests except for the transition from the global to the regional pools. In this case, significance was assessed assuming a binomial distribution based on a mean (68.5%) probability of a species from the global pool entering the regional pool. We randomly generated 1,000,000 pairs of regional pools and assessed the probability of getting a result as extreme as the one we observed. Diversity indices were compared among regions using two-sample t tests and among zones within regions using analysis of variance (ANOVA). In addition, to better understand patterns of species richness in both regions, we compared the distributions of plot-level species richness values (i.e., the number of plots with 1, 2, ..., n species) between regions using a Kolmogorov–Smirnov test.

To better understand species richness and diversity patterns, we calculated the “amplitude” of each species at each site. This was defined as the number of 1 × 5 m plots in which a species occurred divided by the transect length and is reported as a proportion. We compared species amplitudes between geographic regions for the 13 plant species that occurred in both geographic regions at more than two sites. Data were compared using two-sample *t* tests, with sites as the unit of replication.

To determine whether differences in richness and diversity between Georgia and Texas were due to differences in large-scale marsh zonation patterns, we also calculated the amplitude of three general marsh zones based on the composition of the 1 × 5 m plot: (1) the low marsh, which was defined by more than 50% cover of *S. alterniflora*; (2) the high marsh, which was defined by more than 50% cover of any combination of the rush *Juncus roemerianus* or stunted shrubs *B. frutescens*, *I. frutescens*, and *L. carolinianum*; and (3) the middle marsh, which was defined as whatever was not low or high marsh, and was typically dominated by the succulents *Batis maritima* and *Salicornia virginica*. For species and zone amplitudes, sites from which a species or zone was totally absent were not included in calculations. Amplitude proportions were arcsin (square root) transformed before analysis to improve normality. Data were compared using two-sample *t* tests, with sites as the unit of replication. Comparisons of zones within regions were done using ANOVA, followed by Kruskal–Wallis nonparametric means comparisons.

Results

At the largest scale examined, the global pool, we found 43 species (Table 1). Of these, 16 occurred in both regions. All species are either commonly found in salt marshes (Duncan and Duncan 1987) or are listed by the USDA as obligate or facultative wetland species with some salinity tolerance (<http://plants.usda.gov/index.html>). Rare species (those found only at one site) accounted for over half (64%) of the species exclusive to a single region.

Of the 43 species found in the global pool, similar numbers (27–32) and percentages (63–74%) were found in each regional pool (Fig. 2). Richness at the site and plot level, however, was almost twice as high in Texas as in Georgia. The contribution from the regional scale to the site scale differed between regions, but a similar proportion of species found at the site scale was found at the plot scale. These results suggest that processes at the site scale were the most important in determining differences in diversity patterns between regions.

Examination of more detailed diversity indices supported the conclusion that diversity at the plot scale was greater in Texas than Georgia, despite greater evenness in Georgia (Table 2). When diversity and evenness were broken down by marsh zone, Texas marshes tended to be more diverse (not significant for the middle marsh zone) but less even. The high evenness of Georgia marshes was in part driven by the high frequency (over 60%) of plots with only one species

Table 1 All plant species encountered

Species found only in Georgia	Shared species	Species found only in Texas
<i>Baccharis halimifolia</i>	<i>Symphyotrichum tenuifolium</i> (= <i>Aster tenuifolius</i>)	<i>Cuscuta indecora</i>
<i>Fibristylis castanaea</i>	<i>Batis maritima</i>	<i>Lycium carolinianum</i>
<i>Spartina cynosuroides</i>	<i>Borrichia frutescens</i>	<i>Rayjacksonia phyllocephala</i> (= <i>Machaeranthera phyllocephala</i>)
Unknown Poaceae	<i>Cynanchum angustifolium</i>	<i>Monanthochloe littoralis</i>
	<i>Distichlis spicata</i>	<i>Sabatia arenicola</i>
	<i>Iva frutescens</i>	
<i>Juncus</i> sp. ^a	<i>Juncus roemerianus</i>	<i>Agalinis maritima</i> ^a
<i>Lilaeopsis chinensis</i> ^a	<i>Limonium carolinianum</i>	<i>Aster</i> sp. ^a
<i>Schoenoplectus americanus</i> (= <i>Scirpus americanus</i> ^a)	<i>Salicornia bigelovii</i>	<i>Avicennia germinans</i> ^a
<i>Solidago sempervirens</i> ^a	<i>Salicornia virginica</i>	<i>Eustoma exaltatum</i> ^a
<i>Spartina bakeri</i> ^a	<i>Schoenoplectus robustus</i> (= <i>Scirpus robustus</i>)	<i>Helianthus annuus</i> . ^a
Unidentified 1 ^a	<i>Spartina alterniflora</i>	<i>Opuntia humifusa</i> ^a
Unidentified 2 ^a	<i>Sporobolus virginicus</i>	<i>Sesuvium portulacastrum</i> ^a
	<i>Spartina patens</i>	Unidentified 1 ^a
	<i>Spartina spartinae</i>	Unidentified 2 ^a
	<i>Suaeda linearis</i>	Unidentified 3 ^a
		Unidentified 4 ^a

Eleven species occurred only in Georgia, 16 only in Texas, and 16 species were shared, for a global pool of 43. Synonyms for some species are given in parentheses.

^aRare species, defined as those species occurring at only one site, are listed at the bottom of the Georgia and Texas columns.

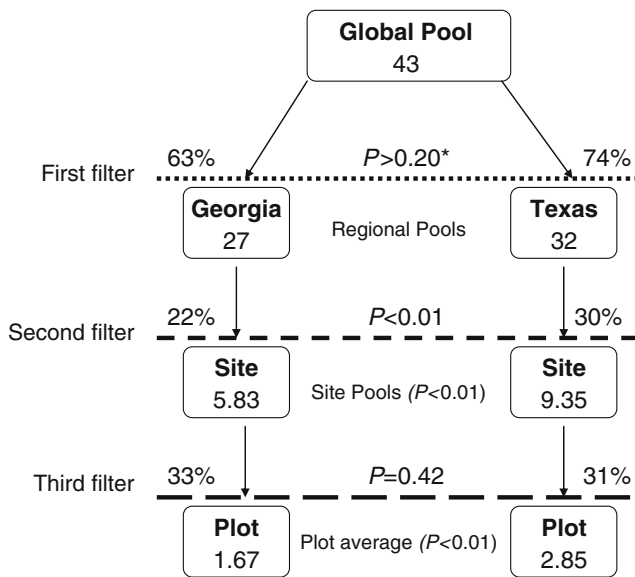


Fig. 2 Filter model comparing richness between the two geographic regions at four spatial scales. Richness values are given within boxes. Contributions of species from larger scales through “filters” to lower scales are given as percentages. Statistical comparisons were made using *t* tests except where indicated by an asterisk. In this case, significance was assessed assuming a binomial distribution based on a mean (68.5%) probability of a species from the global pool entering the regional pool. Generated species pools ($n=1,000,000$) indicate a greater than 20% chance that the regional pool would deviate from the mean (29.5) by less than six species; therefore, the regional pools found in this study are well within the range one would expect by chance

present. In contrast, individual plots in Texas were most likely to have three species present, and plots with one, two, three, or four species all occurred at roughly similar frequencies (the distributions of plot-level species richness values differed between regions, Kolmogorov–Smirnov test, $P < 0.0001$).

S. alterniflora had the greatest species amplitude in both regions, extending over 50% of the horizontal extent of the marsh (Fig. 3). Six species that commonly occur in mixed stands (*Symphytotrichum tenuifolium*, *B. frutescens*, *B. maritima*, *Distichlis spicata*, *I. frutescens*, and *Salicornia bigelovii*) had greater amplitudes in Texas than Georgia. Two species that commonly occur in monospecific stands (*J.*

roemerianus and *S. alterniflora*) had greater amplitudes in Georgia than Texas.

In both regions, the low marsh zone had the greatest amplitude, accounting for more than 50% of the total horizontal extent of the marsh (Fig. 4a). The amplitude of the low marsh was greater in Georgia than Texas, but the amplitude of the middle marsh zone was greater in Texas than Georgia. The low marsh zone had the lowest species richness in both regions (Fig. 4b). Species richness of all zones tended to be greater in Texas, and this difference was significant in the low and high marsh zones.

Discussion

Our general understanding of diversity patterns in salt marshes is heavily influenced by studies of plant zonation conducted in regularly flooded salt marshes of the Atlantic Coast of the USA (Bertness and Ellison 1987; Bertness 1991a,b; Hacker and Gaines 1997; Pennings and Moore 2001; Pennings et al. 2005). On the Atlantic Coast, the combination of predictable physical conditions created by semi-diurnal tidal inundation and interactions among plant species forms distinct zones of vegetation (Brewer et al. 1997; Hacker and Bertness 1999; Pennings and Bertness 2001). Because salt marsh plant communities of the Gulf Coast have been much less studied, it is not known to what extent similar processes are operating. A useful way to study diversity patterns is to consider how diversity changes within a set of nested scales (Pärtel et al. 1996). A variety of processes reduce diversity from larger to smaller scales (Rajaniemi et al. 2006), and by examining these changes, we can gain insight into which processes are “filtering” species at each spatial scale. Below, we compare diversity patterns between Georgia and Texas salt marshes at four spatial scales and discuss possible mechanisms responsible for observed differences.

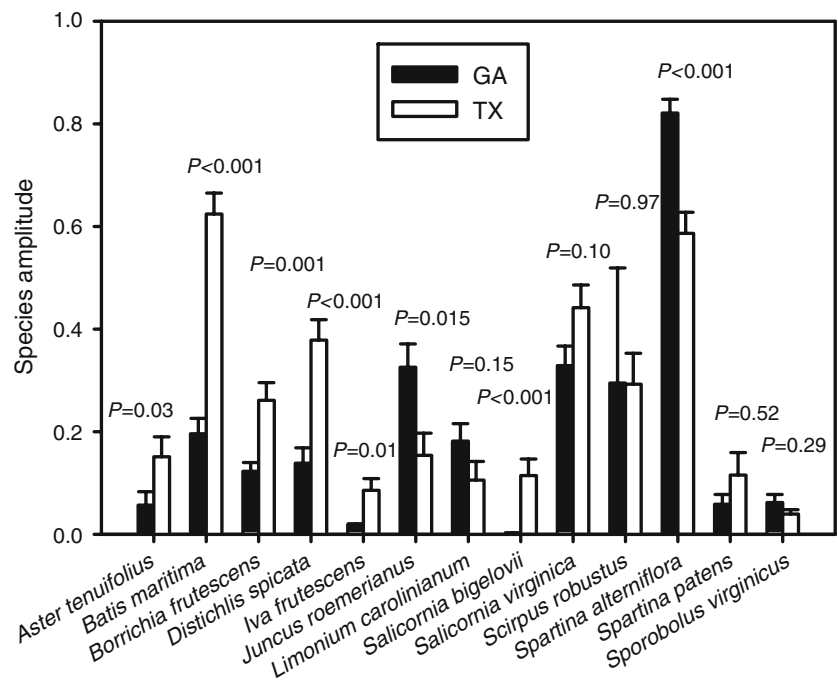
The largest scale examined in this study, the global pool, included all species capable of existing in either region (Pärtel et al. 1996). Because we sampled only in salt marshes, the global pool was limited by wetland conditions, such as flooding and salinity, that are stressful to most plant species.

Table 2 Diversity (Shannon index) and evenness for Georgia and Texas sites

	Site		Low marsh		Middle marsh		High marsh	
	Diversity	Evenness	Diversity	Evenness	Diversity	Evenness	Diversity	Evenness
Georgia	0.17	0.90	0.15	0.92	0.40	0.80	0.41	0.82
Texas	0.47	0.76	0.37	0.79	0.51	0.74	0.83	0.73
<i>P</i> value	<0.001	<0.001	<0.001	<0.001	0.10	0.04	<0.001	0.002

Calculations were made at the level of the whole site and broken down by zones. Data were compared between geographic regions with two-sample *t*-tests.

Fig. 3 Species amplitudes of 13 plant species in Georgia and Texas. Data are means+1 SE. Amplitude proportions were arcsin (square root) transformed before t-tests to improve normality



As a result, the global pool was exclusively composed of halophytic plants and, despite representing a large geographic area, was small compared to that of other ecosystems such as forests or grasslands.

Regional climate patterns and dispersal barriers act as a biogeographic filter that prevents some species found in the global pool from occurring at the regional scale (Rajaniemi et al. 2006). In this study, effects of the regional filter were modest (removing about one third of the global pool) and similar between regions, leading to regional pools of similar sizes. Although coastal Texas and coastal Georgia have similar climates (Hargrove et al. 2006), USDA databases (<http://plants.usda.gov/index.html>) confirm that some of the species encountered have geographic ranges that do not include both regions. For example, of the 16 species we found only in Texas, at least eight have not been recorded near the Georgia sites. Similarly, of the 11 species we found only in Georgia, two (*Spartina bakeri* and *Schoenoplectus americanus*) have not been recorded near the Texas sites. In other cases, a lack of overlap between regional pools was more likely due to incomplete sampling of less common species. For example, one of the rare species encountered only in Texas, *Opuntia humifusa*, does occur in Georgia but was simply not encountered during our sampling. Similarly, of the species encountered only in Georgia, at least three (*Baccharis halimifolia*, *Solidago sempervirens*, and *Spartina cynosuroides*) occur in Texas but were not encountered during our sampling. In sum, when comparing Georgia and Texas marshes, we see some effects of a biogeographic climate/dispersal filter, but in general, the floras were quite

similar in richness and composition, especially when the rare species were not considered.

The local abiotic environment acts as a filter that prevents some of the species found in the regional pool from occurring at particular sites (Rajaniemi et al. 2006). This filter was strong in both regions, but especially in Georgia, where only 22% of species from the regional pool were found at any particular site. The flora of any particular salt marsh site can be quite variable (Jacobson and Jacobson 1989). Steep gradients in salinity and waterlogging that are characteristic of salt marshes vary in intensity from site to site and can mediate which species are present. Because we deliberately sampled a range of sites that might be expected to vary environmentally, it is not surprising that only a modest proportion of the regional pool was present at any one site. The fact that a smaller proportion of the regional pool was found at Georgia than Texas sites could indicate that we sampled sites representing a wider range of abiotic conditions in Georgia than in Texas. Because we limited our study to sites dominated by salt marsh vegetation, because average water column salinity levels were similar between regions, and because regional species pools were similar between regions, we consider this possibility unlikely. It is theoretically possible, however, that sites in Georgia varied more than sites in Texas in ways (e.g., soil composition and nutrient levels) that we were not aware of. An alternative hypothesis that we discuss in detail below is that temporally variable conditions at Texas sites limited competitive exclusion, thereby increasing site-scale species richness.

Although we did not formally evaluate an “elevational filter” because we determined zone borders based on

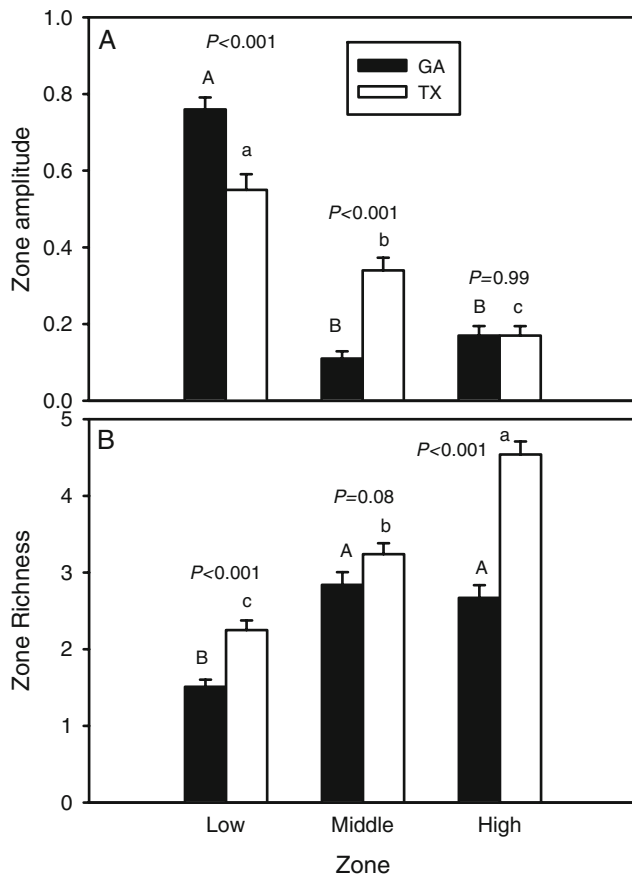


Fig. 4 Graphs of **a** zone amplitude and **b** richness values for the three marsh zones. Data are means+1 SE. *P* values indicate differences among regions (*t* tests). Letters indicate significantly different means within regions (ANOVA, followed by Kruskal–Wallis one-way nonparametric comparison for amplitude and Tukey comparison for richness)

vegetation rather than independent abiotic variables, the general patterns of diversity across elevation were consistent with past research (Brewer et al. 1997; Hacker and Bertness 1999). In particular, we found low species richness in the low marsh, where flooding creates stressful physical conditions associated with waterlogging (Ponnamperuma 1972), and high diversity in the high marsh zone, which experiences relatively infrequent flooding. The low marsh had greater amplitude in Georgia than in Texas, suggesting either that the hypsometry of marshes in the two regions varied or that low elevations in Texas marshes are not as consistently stressful as in Georgia (see below).

Ecologists have long argued that plant biomass, which drives competitive exclusion, can limit diversity at local scales (Grime 1973; Tilman 1982; Rajaniemi et al. 2006). Thus, one possible explanation for greater diversity in Texas at the plot scale would be that biomass of Texas marshes, and hence the intensity of competition, was less than in Georgia marshes. Preliminary sampling, however (Kunza, unpublished data), suggested that standing biomass in Texas marshes was

greater than or equal to that in Georgia marshes when standardized by marsh zone (Turner 1976); therefore, we consider this possibility unlikely. Moreover, although plot-scale diversity was greater in Texas than Georgia, contributions of species from the site to the plot scale were similar between regions (removing about two thirds of the site pool), suggesting that diversity differences between regions are not primarily determined at the plot scale.

An alternate possibility is that the mechanisms producing plant zonation patterns, and hence also patterns of zone amplitude (which are defined here by vegetation) and zonal diversity, differed between regions. Where a plant species occurs in a salt marsh is determined by an interaction between physical stress and biological interactions (Snow and Vince 1984; Bertness and Ellison 1987; Pennings and Callaway 1992). Each species has a range of physical conditions that it can tolerate, and biological interactions commonly exclude it from part of this range or, in some cases, facilitate its presence outside this range. How much of the marsh is included within the realized range of a species (the species amplitude) is therefore determined in large part by the hydrological regime of the marsh because the primary physical stressors (waterlogging, salinity, sulfides, etc.) are driven primarily by tidal flooding. Given that tidal flooding is more variable in Texas than in Georgia, we speculate below that the more variable flooding regime reduces species loss due to physical stress or competition, leading to higher site and plot richness.

The low marsh zone of both regions was dominated by *S. alterniflora*, which is more resistant to extended flooding with sea water than other salt marsh plants (Bertness and Ellison 1987; Bertness 1991b; Crain et al. 2004). On the Atlantic Coast, low marsh zones are composed primarily of monospecific stands of *S. alterniflora* because other plant species cannot tolerate regular flooding. In contrast, the low zone of Texas marshes commonly consisted of a mixture of *S. alterniflora* and one or two other species, perhaps indicating that Texas marshes are flooded less regularly, stressful conditions occur for shorter periods of time, and additional plant species are able to persist in the low zone.

Almost all salt marsh plant species are capable of living in the infrequently flooded high marsh. In Atlantic Coast salt marshes, however, competition from high-marsh dominants commonly excludes other species, resulting in low diversity (Brewer et al. 1997; Hacker and Bertness 1999; Pennings et al. 2003). On the southeast Atlantic Coast, many high-marshes zones are composed of almost monospecific stands of *J. roemerianus* (Wiegert and Freeman 1990). *J. roemerianus* dominates these low-stress habitats because it is a superior competitor that excludes other species (Pennings et al. 2005). *J. roemerianus* had a lower amplitude in Texas than Georgia, likely because the irregular flooding schedule in Texas creates occasional periods when high marshes dry out and become highly hypersaline, creating stressful conditions

that *J. roemerianus*, which is stunted at salinities > 45 PSU (Eleuterius 1989), is unable to tolerate (Pennings et al. 2005). Occasional periods of hypersaline conditions could also explain the greater amplitude of the mid-marsh zone in Texas because this zone is dominated by succulents that are tolerant of a wide range of abiotic conditions (Richards et al. 2005).

Ecologists have long speculated that, in temporally variable environments, temporal variation in abiotic conditions may prevent competition from reducing local diversity (Hutchinson 1959). Fluctuating conditions can favor first one species, then another, allowing no single species to dominate over time and competitively exclude others. We speculate that the more variable tidal regime in Texas, which can cause marshes to cycle among periods of high salt stress due to evaporation during extended low tides, low salinity following heavy rains, and waterlogging during extended high tides, does not consistently favor any single species in any particular zone and thereby leads to greater species amplitudes and higher diversity in Texas than in Georgia. A similar argument has been applied to explain weak zonation patterns in irregularly flooded salt marshes in Brazil (Costa et al. 2003). Rigorously evaluating this argument for Texas versus Georgia marshes would require time series of abiotic conditions coupled with measurements of competition intensity at replicate sites in both geographic regions. Conducting such experiments was outside the scope of this project but is a long-term goal of our laboratory.

Whatever the factors responsible for differences in site and plot-scale diversity between Texas and Georgia sites, the fact that differences exist suggests that plant communities in the two regions are structured differently. Managers of Gulf Coast marshes should not assume that paradigms developed from studies conducted on the Atlantic Coast will automatically apply to Gulf Coast marshes but should critically evaluate these paradigms before applying them to local management issues.

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References

- Abrams, P.A. 1995. Monotonic or unimodal diversity productivity gradients-what does competition theory predict? *Ecology* 76: 2019–2027.
- Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44: 445–456.
- Alexander, H.D., and K.H. Dunton. 2002. Freshwater inundation effects on emergent vegetation of a hypersaline salt marsh. *Estuaries* 25: 1426–1435.
- Bertness, M.D. 1991a. Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72: 125–137.
- Bertness, M.D. 1991b. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* 72: 138–148.
- Bertness, M.D., and A.M. Ellison. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecological Monographs* 57: 129–147.
- Bertness, M.D., and S.W. Shumway. 1993. Competition and facilitation in marsh plants. *American Naturalist* 142: 718–724.
- Bertness, M.D., K. Wikler, and T.O.M. Chatkupt. 1992. Flood tolerance and the distribution of *Iva frutescens* across New England salt marshes. *Oecologia* 91: 171–178.
- Brewer, J.S., J.M. Levine, and M.D. Bertness. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. *Oikos* 80: 333–341.
- Callaway, R.M., and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965.
- Chapman, V.J. 1974. Salt marshes and salt deserts of the world. In *Ecology of halophytes*, eds. R.J. Reimold, and W.H. Queen, 3–19. New York: Academic.
- Costa, C.S.B., J.C. Marangoni, and A.M.G. Azevedo. 2003. Plant zonation in irregularly flooded salt marshes: relative importance of stress tolerance and biological interactions. *Journal of Ecology* 91: 951–965.
- Crain, C.M., B.R. Silliman, S.L. Bertness, and M.D. Bertness. 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85: 2539–2549.
- Duncan, W.H., and M.B. Duncan. 1987. *The Smithsonian guide to seaside plants of the Gulf and Atlantic coasts from Louisiana to Massachusetts, exclusive of lower peninsular Florida*. Washington, DC: Smithsonian Institution Press.
- Dunton, K.H., B. Hardegee, and T.E. Whitley. 2001. Response of estuarine marsh vegetation to interannual variations in precipitation. *Estuaries* 24: 851–861.
- Eleuterius, L.N. 1989. Natural selection and genetic adaptation to hypersalinity in *Juncus roemerianus* Scheele. *Aquatic Botany* 36: 45–53.
- Eleuterius, L.N., and C.K. Eleuterius. 1979. Tide levels and salt marsh zonation. *Bulletin of Marine Science* 29: 2471–2485.
- Ewing, K. 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. *Canadian Journal of Botany* 61: 1105–1116.
- Forbes, M.G., and K.H. Dunton. 2006. Response of a subtropical estuarine marsh to local climatic change in the southwestern Gulf of Mexico. *Estuaries and Coasts* 29: 1242–1254.
- Ganong, W.F. 1903. The vegetation of the Bay of Fundy salt and diked marshes: an ecological study. *Botanical Gazette* 36: 161–186, 280–302, 350–367, 429–455.
- Gough, L., and J.B. Grace. 1997. The influence of vines on an oligohaline marsh community: results of a removal and fertilization study. *Oecologia* 112: 403–411.
- Gough, L., and J.B. Grace. 1998a. Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* 117: 527–535.
- Gough, L., and J.B. Grace. 1998b. Herbivore effects on plant species density at varying productivity levels. *Ecology* 79: 1586–1594.
- Gough, L., and J.B. Grace. 1999. Effects of environmental changes on plant species density: comparing predictions with experiments. *Ecology* 80: 882–890.
- Gough, L., J.B. Grace, and K.L. Taylor. 1994. The relationship between species richness and community biomass: the importance of environmental variables. *Oikos* 70: 271–279.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344–347.

- Hacker, S.D., and M.D. Bertness. 1999. Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. *Ecology* 80: 2064–2073.
- Hacker, S.D., and S.D. Gaines. 1997. Some implications of direct positive interactions for community species diversity. *Ecology* 78: 1990–2003.
- Hargrove, W.W., B. Hayden, D. Urban, J. MacMahon, J. Franklin, and F.M. Hoffman. 2006. Development of a domain map for nodes of the National Ecological Observatory Network (NEON). In Proceedings of the 21st Annual Symposium of the International Association for Landscape Ecology, United States Regional Association (US-IALE), San Diego.
- Harrison, S., H.D. Safford, J.B. Grace, J.H. Viers, and K.F. Davies. 2006. Regional and local species richness in an insular environment: serpentine plants in California. *Ecological Monographs* 76: 41–56.
- Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press.
- Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86: 393–401.
- Hutchinson, G.E. 1959. Homage to Santa Rosalina, or why are there so many kinds of animals? *American Naturalist* 93: 145–159.
- Jacobson, H.A., and G.L.J. Jacobson. 1989. Variability of vegetation in tidal marshes of Maine, U.S.A. *Canadian Journal of Botany* 67: 230–238.
- MacArthur, R.H. 1972. *Geographical ecology: patterns in the distribution of species*. New York: Harper and Row.
- Mittelbach, G.G., C.F. Steiner, S.M. Scheiner, K.L. Gross, H.L. Reynolds, R.B. Waide, M.R. Willig, S.I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82: 2381–2396.
- Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology* 84: 293–295.
- Pärtel, M., M. Zobel, K. Zobel, and E. van der Maarel. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* 75: 111–117.
- Pennings, S.C., and M.D. Bertness. 2001. Salt marsh communities. In *Marine Community Ecology*, eds. M.D. Bertness, S.D. Gaines, and M.E. Hay, 289–316. Sunderland: Sinauer.
- Pennings, S.C., and R.M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73: 681–690.
- Pennings, S.C., and D.J. Moore. 2001. Zonation of shrubs in western Atlantic salt marshes. *Oecologia* 126: 587–594.
- Pennings, S.C., M.-B. Grant, and M.D. Bertness. 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. *Journal of Ecology* 93: 159–167.
- Pennings, S.C., E.R. Selig, L.T. Houser, and M.D. Bertness. 2003. Geographic variation in positive and negative interactions among salt marsh plants. *Ecology* 84: 1527–1538.
- Ponnamperuma, F.N. 1972. The chemistry of submerged soils. *Advances in Agronomy* 24: 29–95.
- Rajaniemi, T.K., D.E. Goldberg, R. Turkington, and A.R. Dyer. 2006. Quantitative partitioning of regional and local processes shaping regional diversity patterns. *Ecology Letters* 9: 121–128.
- Richards, C.L., S.C. Pennings, and L.A. Donovan. 2005. Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology* 176: 263–273.
- Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235: 367–371.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Snow, A., and S.W. Vince. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *Journal of Ecology* 72: 669–684.
- Stevens, M.H.H., and W.P. Carson. 2002. Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecology Letters* 5: 420–426.
- Stout, J.P. 1984. *The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile*. Washington, DC: US Department of the Interior, Fish and Wildlife Service.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton: Princeton University Press.
- Turner, R.E. 1976. Geographic variations in salt marsh macrophyte production: a review. *Contributions in Marine Science* 20: 47–68.
- Wang, F.C. 1997. Dynamics of intertidal marshes near shallow estuaries in Louisiana. *Wetlands Ecology and Management* 5: 131–143.
- Wiegert, R.G., and B.J. Freeman. 1990. *Tidal salt marshes of the southeast Atlantic coast: a community profile*. Washington, DC: US Department of the Interior, Fish and Wildlife Service.
- Zetler, B., and D. Hansen. 1970. Tides in the Gulf of Mexico: a review and a proposed program. *Bulletin of Marine Science* 20: 57–69.
- Zobel, M. 1992. Plant species coexistence—the role of historical, evolutionary and ecological factors. *Oikos* 65: 314–320.