

**CENTRIFUGAL ORGANIZATION IN A GEORGIA SALT MARSH PLANT
COMMUNITY**

A Thesis
Presented to
the Faculty of the Department of Biology and Biochemistry
University of Houston

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

By
Alana-Rose Astar Lynes
May 2008

**CENTRIFUGAL ORGANIZATION IN A GEORGIA SALT MARSH PLANT
COMMUNITY**

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ABSTRACT

In this study I evaluate whether a centrifugal model helps explain vegetation patterns in a Georgia salt marsh using a combination of sampling data and manipulative experiments.

The centrifugal model predicts that multiple stress gradients radiate out from a shared core habitat and that plants should occupy discrete ranges along these gradients. The results from this study indicated that there were two clear stress gradients, salinity and water-logging, along which species and habitats occupied discrete ranges, supporting the centrifugal model.

The centrifugal model predicts that productivity should be greatest at the benign end of each stress gradient and least at the most stressful end. The results from this study generally supported the centrifugal model. *Juncus* and *Borrichia*, which occupied the most benign habitat, had the highest biomass. The stressful ends of the gradients, occupied by *Salicornia virginica*, short *Spartina alterniflora* and medium *Spartina alterniflora*, all had relatively low biomass.

The centrifugal model predicts that diversity should be highest in intermediate levels of stress. *Salicornia virginica* and *Spartina alterniflora* zones always had the lowest species richness and diversity, supporting the centrifugal model. However, the *Borrichia* zone always had the greatest or second greatest level of species richness and diversity, not supporting the centrifugal model.

The centrifugal model predicts that when species are transplanted outside of the benign habitat they will do poorly, with or without neighbors present, where species at the stressful ends of the gradients will do well when transplanted into the benign habitat

without neighbors, but poorly when neighbors are present. The results of the transplant experiments strongly supported the centrifugal model.

In conclusion, I found strong evidence that the centrifugal model was useful in explaining plant community structure in a Georgia salt marsh. This model also provides a unified theory for vegetation patterns in northeast and southeast USA salt marshes, where zonation due to high salinities caused by increased evapotranspiration in the low-latitude climates can be equated to the disturbance-caused temporary increases in salinity in high-latitude climates.

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INTRODUCTION

Plant communities vary greatly in species composition, species diversity and productivity. Multiple abiotic factors may influence these plant communities to varying degrees, including climate, disturbance, hydrological conditions and other environmental stresses. Biotic factors also influence plant community structure, and include competition, facilitation and herbivory. The existence of structure in biological communities suggests that there may be rules which determine which species can, and cannot, occur together (Diamond 1975). Ecologists have long investigated how abiotic and biotic factors structure communities. As a result two basic mechanisms, with different causes, can be envisioned; those that are environmentally mediated and those due to interactions between species. Their combination can be seen as first having an environmental filter, where the exclusion of species from a local site occurs due to their inability to tolerate the physical stresses, followed by biotic filtering (Wilson 1999). The search for this structure and the underlying processes that generate it are central to community ecology, as stated by MacArthur (1972) '[t]o do science is to search for repeated patterns'.

All plants have common requirements for basic resources and while they all have the potential to grow at the richer end of a resource gradient, they vary in their ability to compete. A general theory proposes a trade-off between the ability of a species to tolerate stressful conditions and the ability to successfully out-compete other species in resource rich environments (Grime 1979, Grace 1989, Keddy 1989b, Wisheu and Keddy 1992). A single resource, disturbance or stress gradient can exist, along which species that are better able to tolerate low resources, high stress and/or disturbed conditions are excluded

from the resource rich, low stress and/or undisturbed environments by the dominant competitors (Fig. 1). Several experimental studies have suggested that an inverse relationship between competitive ability and stress tolerance exists within salt marsh plant communities (Bertness *et al.* 1992b, Pennings and Bertness 2001, Pennings *et al.* 2005).

Realized niches: Competitive hierarchies along a single stress gradient

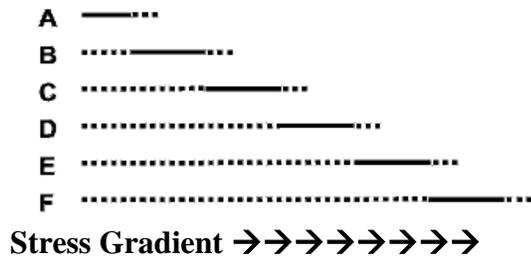


Fig. 1. Realized niches: competitive hierarchies of species, A through F, along a single stress gradient. Solid lines indicate where along the gradient each species occurs. Dashed lines indicate the region from which a species is excluded by one or more competitive species (to the left) or by resource partitioning (to the right). After Wisheu and Keddy (1992).

If multiple environmental gradients exist, this theory could be extended to include multiple peripheral habitats, which would radiate outward from the shared favorable ends of each gradient (Fig. 2) (Keddy 1990, Wisheu and Keddy 1992). As environmental adversity decreases, it is assumed that the relative importance of competitive adversity increases and a central habitat (the core habitat) would occur where the favorable end of all stress gradients would converge (Keddy 1990, Wisheu and Keddy 1992). This core habitat should be an area of low stress, while beyond this core habitat the adverse end of each gradient would create radiating axes supporting species that were adapted to each particular stress, creating a pattern coined as centrifugal organization (Keddy 1990, Wisheu and Keddy 1992). The centrifugal organization model for plant communities assumes that (i) all species perform best at the same end of the same stress gradient, that (ii) there are competitive hierarchies, and that (iii) competition is most extreme in the core habitat (Keddy 1990, Wisheu and Keddy 1992, Keddy 2000)

Predictions regarding diversity and productivity in plant communities can then be made based on the interactions of abiotic and biotic factors. According to the centrifugal model, plant biomass should be the greatest in the core habitat where resources are greatest and least in the peripheral habitats where stress reduces biomass (Keddy 1990, Wisheu and Keddy 1992). Species richness would be highest in intermediate positions where competition is reduced but stressful conditions are not yet extreme (Grime 1979, Wisheu and Keddy 1992).

Salt marshes, which are characterized by stress gradients, such as flooding and salinity, strict zonation and comparatively few plant species, provide an ideal model system in which to study plant community structure (Pennings and Bertness 2001). The

strong stress gradients allow for the study of environmentally mediated patterns of plant species (Chapman 1960, Adams 1963). Further, salt marshes have relatively few plant species, presumably due to the highly stressful environment, thereby proving a comparatively simple system to study (Pennings and Bertness 2001). Salinity can vary within the salt marsh and is moderated by tidal inputs and flushing at low elevations and by freshwater input from rain (Adam 1990). At intermediate elevations, salt water can collect and then evaporate and in some cases hypersaline conditions are created, where salt concentration in the sediment may be several times that of seawater (Adam 1990) and no plant life can exist, producing bare unvegetated areas known as salt pans.

Centrifugal organization has been demonstrated in non-saline wetland communities, where the central habitat has low disturbance and high fertility (Keddy 1990, Wisheu and Keddy 1992). In salt marshes, flooding and salinity gradients may play a similar role (Keddy 2000). Wetlands that have changing or unpredictable inundation may not have a consistent gradient in physical stress across the marsh (Costa *et al.* 2003) and the changing abiotic stresses may prevent competitive hierarchies from establishing.

Multiple stress gradient pattern of centrifugal organization

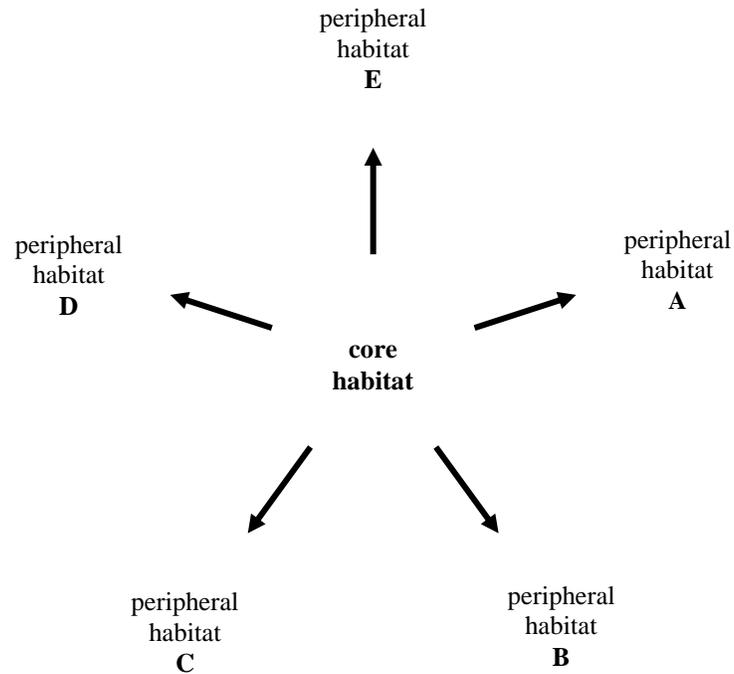


Fig. 2. The centrifugal model postulates that multiple stress gradients radiate from a central core habitat. Stress increases in the direction of the solid arrows towards the peripheral habitats (A-E). Species, of varying stress tolerance, exist along these gradients, ending with the peripheral habitat at the most stressful end of each gradient. The core habitat exists at the benign end of the stress gradients, where competitive dominants are expected to out-compete other species. After Wisheu and Keddy (1992).

I explored whether plant distributions in salt marshes can be usefully explained by a centrifugal model. Salt marshes in Rhode Island display the typical arrangement of salt marsh plants in distinct zones parallel to the shoreline, representing a simple trade-off between competitive ability and stress tolerance to flooding, where competitively superior plants occupy high marsh elevations and poor competitors are displaced to lower marsh elevations (Bertness and Ellison 1987, Bertness 1991a, 1991b, Bertness *et al.* 1992b, Bertness and Hacker 1994). Studies conducted in Georgia suggest that the underlying mechanisms of zonation patterns at lower latitudes could be more complex. The hotter climate at lower latitudes (Bertness and Pennings 2000) increases evapotranspiration, leading to hypersaline conditions at intermediate marsh elevations (Pennings and Bertness 1999). These conditions suggest that flood tolerant plants should occupy the low marsh, salt tolerant plants should occupy the mid-marsh and competitive dominants should occupy the high-marsh (Pennings and Callaway 1992, Pennings *et al.* 2005).

If a centrifugal model is working to structure salt marsh plant communities in Georgia it would be expected that competitive dominant species occupy the least stressful core habitat, whereas poor competitors occupy the flooded and hypersaline peripheral habitats (Fig. 3). Flooding is the most important environmental filter at lower marsh elevations (repeated flushing by tides moderates soil salinity), excluding flood intolerant species from this peripheral habitat. At some intermediate elevation, when water content is moderately low, soil salinity is expected to vary widely, from approximately equal to sea water levels to multiple times that (Adam 1990). At this mid-marsh elevation, salinity is the most important environmental filter, excluding salt intolerant species from the

peripheral habitat. Further, biomass is expected to increase as stressful conditions decrease along each gradient. Variations in flooding and salinity across marsh landscapes are responsible for generating gradients in the sizes of many plants (Richards *et al.* 2005). Biomass production reflects the amount of energy that went into growth after accounting for maintenance costs. Adaptations that counteract stresses have physiological maintenance costs. Therefore, as costs increase due to increased flooding depth and salinity level, growth rates should be lower (Larcher 1995).

Diversity is expected to be highest between the core and peripheral habitats and lowest where stressful conditions (peripheral habitats) and increased competition (core habitat) exist. In general, wetland plant communities have lower species richness compared with plant communities found on drier soils (Sharitz and Pennings 2006). Waterlogged soils are highly stressful, therefore excluding flood intolerant, non-adapted species, resulting in relatively few adapted and unique plant species present within the salt marsh community. Furthermore, species richness of wetland plant communities drops drastically from freshwater to salt marshes (Odum 1988) as fewer species are adapted to the stressful saline conditions (Sharitz and Pennings 2006).

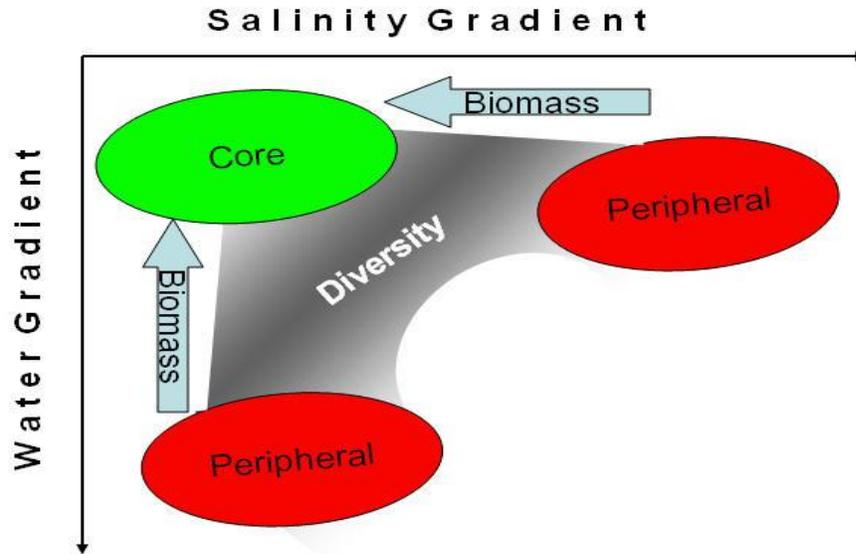


Fig. 3. Proposed model of centrifugal organization for a Georgia salt marsh plant community. Competitive dominant species occupy the core habitat and stress tolerant species occupy the peripheral habitats. Biomass is expected to increase as stressful conditions decrease along each gradient. Diversity is expected to be highest between the core and peripheral habitats.

Here I evaluated whether a centrifugal model helps explain vegetation patterns in a Georgia salt marsh using a combination of sampling data and manipulative experiments. I sampled 500 salt marsh plots on Sapelo Island, Georgia, documenting vegetation composition, richness and biomass and soil salinity, water content and organic content. I used these data to test the hypothesis that different plant species occupy areas with distinctly different soil properties. Because increasing pore water content and salinity are known to be stressful to plants, I also use the data to test the hypothesis that abiotic stress functions to create patterns of high productivity in less stressful habitats and low productivity in high stress habitats. I further use the data to test the hypothesis that species diversity is highest in intermediate habitats. I use published and unpublished data from manipulative experiments to test the basic postulates of the centrifugal model: (1) that core species are excluded from the peripheral habitat by physical stress, and (2) that peripheral species are excluded from the core habitat by competition (Fig. 4).

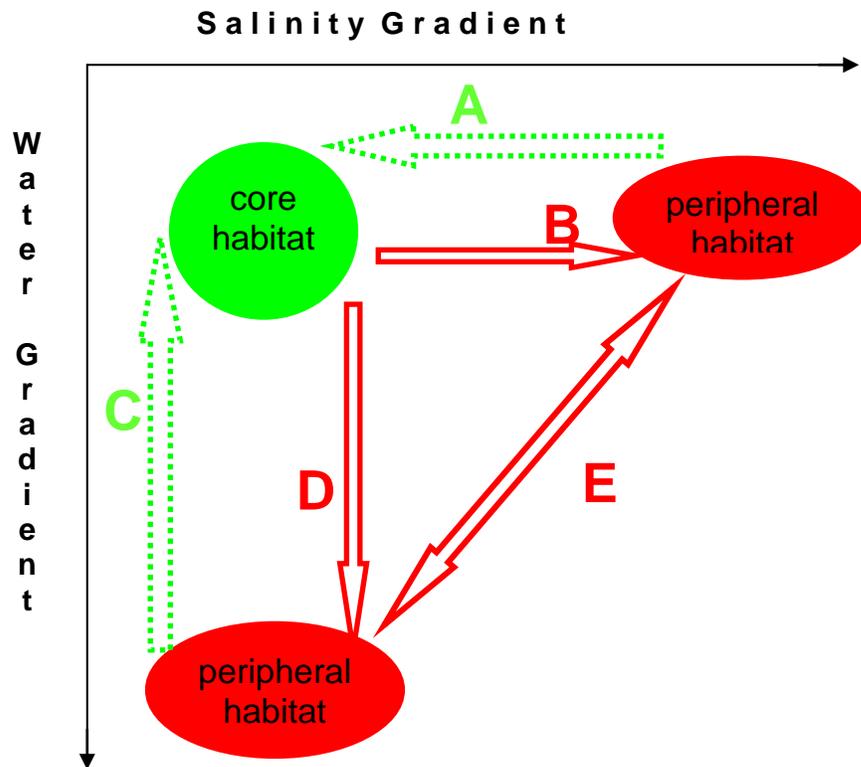


Fig. 4. Transplant experiment predictions: Dashed green arrows (A and C) indicate that stress-tolerant species are predicted to perform best when transplanted anywhere in the opposite direction of the stress gradient (without neighbors present) but poorly with neighbors present, due to competition. Solid red arrows indicate that species are predicted to perform poorly when transplanted in the same direction of the stress gradient (B and D) or into another peripheral habitat (E) with or without neighbors present.

MATERIALS AND METHODS

1. Sampling Data June 2006

a. Study Sites

I sampled 500 salt marsh plots on Sapelo Island, Georgia, 31° 44 N, 81° 27 W (Fig. A1 in Appendix A) from June 20-26, 2006 along 24 transects (Fig. A2 in Appendix A), henceforth referred to as the “June 2006” dataset. Each transect contained approximately twenty 1.0m x 1.0m plots. Transects ran perpendicular to the upland, starting at the high marsh and ending at the low marsh at the banks of a river or creek. For the purposes of this paper I refer to the ‘high marsh’ as marsh elevations dominated by monospecific stands or mixtures of competitive dominant species, *Borrichia frutescens* and *Juncus roemerianus*, the ‘mid-marsh’ as marsh elevations dominated by monospecific stands or mixtures of salt tolerant species, *Salicornia virginica* and *Batis maritima* and the ‘low marsh’ as marsh elevations dominated by monospecific stands or mixtures of the flood tolerant species *Spartina alterniflora*. Plots were stratified to capture various habitats, including monospecific stands and mixtures of *Batis maritima*, *Borrichia frutescens*, *Distichlis spicata*, *Juncus roemerianus*, *Salicornia virginica*, tall *Spartina alterniflora*, medium *Spartina alterniflora*, short *Spartina alterniflora*, as well as unvegetated mud flats and bare salt pans. The classification of *Spartina alterniflora* zones was designated based on height; where tall *Spartina* included plants 100 cm or greater, short *Spartina* included plants less than 40 cm and medium *Spartina* included all heights in between. Throughout the manuscript I refer to plant species generically, except in the case of *Spartina* and *Salicornia* species, where there are more than one species. Table A-1 (Appendix A) has a complete list of the species encountered during the

sampling effort, including the letter codes used for all species and habitat types referred to throughout this manuscript.

b. Plant Richness and Biomass

In order to test the hypotheses that abiotic stress functions to create patterns of high productivity in less stressful habitats and low productivity in high stress habitats and that species diversity is highest in intermediate habitats, I documented vegetation composition, richness and biomass. Plant species within each 1.0 m² plot were noted as present or absent. All standing plant material within a 0.25 m² plot, centered in the 1.0 m² plot, was clipped at ground level. Live plant material was separated from dead plant material and then sorted by species. All plant material was oven dried 65°C to a constant mass and weighed. Total biomass for the plot included all of the plant material. The proportional abundance of each species was used to calculate Shannon's diversity index (Appendix B). Further, I used these proportions to classify each plot as a particular 'habitat type' when more than one species was present in a plot. The habitat type was designated the species with the greatest proportion dried biomass.

c. Soil Organic Content

In order to test the hypotheses that different plant species occupy areas with distinctly different soil properties, I collected a 10 cm-deep soil core from the center of each plot. Cores were placed in plastic bags and stored in a cooler with ice until they were taken to the laboratory. Once in the laboratory, the samples were oven dried at 65°C to a constant mass. The soil core was then homogenized using a mortar and pestle. From each homogenized core a small sample (approximately 4 g), was removed and heated to 450°C for 8 hours. Organic content was estimated as loss of mass on ignition.

d. Water Content

In order to test the hypotheses that different plant species occupy areas with distinctly different soil properties I collected an additional 10 cm-deep soil core from the center of each plot. Cores were placed in plastic cups on ice and taken to the laboratory. Samples were weighed and then oven dried at 65°C to a constant mass. The mass of water in the soil sample was determined to be the loss of mass from the sample upon drying. The proportion of water was determined using the following formula:

$$\text{proportion water} = \frac{m_{\text{water}}}{m_{\text{sample}}}$$

where m_{water} was the mass of water lost from the soil and m_{sample} was the mass of the sample before drying.

e. Soil Salinity

I added a known volume (50 mL) of distilled water to each dried soil sample (from d above). The wet soil sample was then mixed to achieve an even mixture. When the sample settled enough to have a water layer free of debris, a salinity reading using a refractometer was taken. This salinity reading was then used in the following formula to determine the initial salinity of the soil sample:

$$S_{\text{initial}} = \frac{S_{\text{final}} V_{\text{final}}}{V_{\text{initial}}}$$

where S_{final} was the salinity reading from the re-hydrated soil samples, V_{final} was the known volume of water added to the dried sample and V_{initial} was the initial volume of water measured in the sample.

The initial volume of water in the sample was determined using the following formula:

$$V_{\text{water}} = \frac{m_{\text{water}}}{d_{\text{water}}}$$

where m_{water} was the mass lost from the sample upon drying and d_{water} was taken to be 0.998 g/mL, as this is the density of water between the range of 18.6°C -23.1°C (a range that easily encompasses the slight variations in temperature within the laboratory where the samples were processed).

2. Published Sampling Data

In order to determine if the stress gradient patterns obtained from the June 2006 dataset are repeatable, I reanalyzed data from Richards *et al.* (2005). The Richards *et al.* (2005) study was conducted on Sapelo Island, Georgia, and examined twelve common salt marsh plant species (Table A1 in Appendix A). Each of these twelve species was sampled between 75-90 times (with the exception of *Spartina alterniflora*, which was sampled 160 times) and a soil sample was taken adjacent to each sampled plant. The soil samples were used to estimate soil organic content, water content and salinity. For additional details refer to Richards *et al.* (2005). Throughout the manuscript I refer to this dataset as the “Richards” dataset.

3. Unpublished Transplant Data

In order to determine if the mechanisms postulated in the centrifugal model are responsible for creating the patterns observed, I analyzed two unpublished transplant experiments (Pennings unpublished data) conducted in Georgia salt marshes and compiled the results into a data table. See Appendix C for the unpublished methods and materials of these experiments.

4. Published Transplant Data

In order to determine if the mechanisms postulated in the centrifugal model are responsible for creating the patterns observed, I reviewed the results of published transplant experiments conducted in Georgia and South Carolina salt marshes and compiled them into a data table. Only species encountered in both the June 2006 sampling and the Richards dataset were included in the table. Also, only the more common species (encountered ≥ 20 times) from the June 2006 sampling effort were included in the table. Additionally, species and habitats that were ambiguous were excluded from the table. In particular, I excluded *Distichlis*, as its location along environmental gradients was different in the two separate datasets. Further, only transplants that involved species transplanted into or out of habitats clearly defined as either one of the peripheral habitats or the core habitat were included. For the purposes of these tables, I defined *Borrchia* and *Juncus* as belonging to the core habitat, whereas all other species were defined as belonging to either the saline (*Batis and Salicornia virginica*) or flooded (*Spartina alterniflora*) peripheral habitat.

5. Data Structure and Analyses

a. Data structure:

The June 2006 dataset was organized in two ways, by habitat and by species. In the first case I assigned plots to a ‘habitat type’ based on which species had the most total biomass in the plot. Unvegetated plots were visually classified as a mud flat or a salt pan based on soil type.

In the second case I included data points every time a species was present. For example; plot 1 had seven species present, whereas plot 499 had only one species present.

Both of these plots are classified as *Borrichia* habitat, although in plot 1 *Borrichia* accounts for 88% of the biomass compared to 100% in plot 499. When classifying data by species, in contrast, I included data points for each of the seven species present in plot 1, therefore the data points for plot 1 are repeated seven times whereas the data points for plot 499 are represented only once.

There are advantages and disadvantages for each method of data organization. The disadvantage of organization by ‘habitat type’ is that it underestimates the range of each species along the environmental gradients. The advantage of this organizational method, however, is it only uses data from each plot just once. The disadvantage of organization by species, in comparison, is that it uses data from some plots more than once, while other plots are represented only once. The advantages of this organizational method, however, is that the range along each environmental/resource gradient for each species is fully captured.

By using both approaches I ensured that my results were not dependent on the strengths and weakness of any one approach. Each analysis was performed and compared using both data organization methods (by habitat and by species) when appropriate. Additionally, the advantage of using the Richards dataset is the high replicate number per species, the full range of environmental gradients captured for each species and the issue of habitat versus species is eliminated as it is not plot-based. The Richards data set is limited for the purposes of this study however, as it has no richness or biomass data.

b. Regression:

I performed regression analyses of proportion organic versus proportion water using both the June 2006 dataset and the Richards dataset. I also performed regression

analyses of richness or diversity and biomass using the June 2006 dataset. Since tall *Spartina alterniflora* represents a habitat that is both stressful and highly productive (does not fit the conceptual model proposed), I performed the regression analyses of richness or diversity and biomass by first including all of the habitat types and then removing the tall *Spartina alterniflora* zones from the analyses. Regression analyses were performed using Jmp version 7.0.1.

c. ANOVA:

I compared biomass, richness and diversity among habitats from the June 2006 dataset using one-way ANOVA. Species or habitat types that were rare (present less than 3.0 % of the time) were excluded from the analysis to improve power and homogeneity of variance. In order to determine the effect of site, zone and neighbor treatment on the final biomass of *Spartina alterniflora* I analyzed the unpublished *Spartina alterniflora* transplant experiment using a three-way ANOVA. All data were natural log transformed before analysis. Because the unvegetated salt pan zone did not have a with neighbors treatment it was removed from the data analysis. Pairwise comparisons were performed using the Tukey HSD test to control for the error of rejecting a true null hypothesis. All ANOVA were performed using Statistix Version 8.0.

d. Multi-response Permutation Procedures (MRPP):

I performed MRPP analyses based on the three soil characteristics, proportion water, salinity and proportion organic content, for the June 2006 dataset (grouped by habitat and by species) and the Richards dataset (grouped by species). This nonparametric procedure was used to test the hypothesis of no difference between groups (species or habitats). MRPP was chosen because it does not require the distributional

assumptions (multivariate normality and homogeneity of variances) needed for parametric procedures, such as multivariate analysis of variance (MANOVA); therefore it is considered the default choice for community data (McCune and Grace 2002). The dissimilarity measure used was the Sørensen (Bray-Curtis) distance (Appendix E). This distance measure was chosen because it is less prone to exaggerate the influence of outliers (compared to Euclidean distance, for example). Sample sizes for each group (either as species or habitat) are listed in Table E1 (Appendix E). Both the chance-corrected within-group agreement, A, and the set significance value used (all p values were corrected using Bonferroni correction) are indicated in the results section for each MRPP performed. The chance-corrected within group agreement, A, describes the within-group homogeneity, compared to the random expectation (McCune and Grace 2002). MRPP were performed using PCORD Version 5.0 software.

e. MANOVA:

In order to determine the effect of neighbor treatment on the percent cover of *Batis* and *Salicornia virginica*, I analyzed the unpublished *Batis-Salicornia-Borrichia* removal experiment using MANOVA and Pillai's criterion test statistic. MANOVA were performed using the R programming language.

RESULTS

Stress/Resource Gradients

Soil salinity (psu) ranged from 6.3 psu to 306.5 psu (Fig. 5A) in the June 2006 dataset and from 0 psu to 250.1 psu (Fig. 5B) in the Richards dataset. The proportion of water in the soil ranged from 0.080 to 0.65 (Fig. 5A) in the June 2006 dataset and from 0.37 to 0.80 (Fig. 5B) in the Richards dataset. In each case, at lower water contents there was a wide range of variation in salinity, however as water content increased, salinity fell within a lower, narrower range.

Soil organic content ranged from 0.012 to 0.41 (Fig. 6A) in the June 2006 dataset and from 0 to 0.39 (Fig. 6B) in the Richards dataset. At lower salinity values there was a wide range of variation in organic content. As salinity increased, organic content fell within a lower, narrower range. At salinities greater than 100 psu, the proportion organic content was less than 0.05. Plots of organic content versus salinity were essentially mirror images of water content versus salinity. Results from one-way ANOVA using habitats as groups (June 2006 dataset) determined that only soil cores from plots with *Spartina alterniflora* had significantly different soil organic content compared to all other zones (analysis not shown).

Soil organic content was positively correlated with proportion water in both the June 2006 dataset and the Richards dataset (Figs. 7A and 7B). Therefore, I graphed species and habitat types along the flooding and salinity axes only for clarity in Figs. 8, 9A and 9B. In all MRPP analyses (Figs. 8, 9A and 9B), organic content was retained as a separate variable.

Soils from different habitats had significantly different levels of water content and salinity (Fig. 8). Salt pans had very high porewater salinities, *Salicornia virginica* and *Batis* had intermediate values, and all other habitats had relatively low salinity values. Additionally, unvegetated mud had higher salinity values than the *Spartina alterniflora* zones, and the short *Spartina alterniflora* zone was significantly saltier than tall and medium *Spartina alterniflora* zones. Since both the *Salicornia virginica* and *Batis* zones had significantly saltier soils than the other vegetated zones, I classified these zones as sharing the peripheral habitat at the stressful end of the salinity gradient. The *Spartina alterniflora* zones (tall, medium and short) and unvegetated mud zone had relatively wet soils, while the salt pan zone had relatively dry soils. All other habitats had intermediate levels of water content. Additionally, the unvegetated mud zone and short *Spartina alterniflora* zone had lower water content than the tall and medium *Spartina alterniflora* zones. Since all of the *Spartina alterniflora* zones had significantly wetter soils than the other vegetated zones, I classified these zones as sharing the peripheral habitat at the stressful end of the flooding gradient. The *Borrchia* and *Juncus* zones had relatively lower salinity and water content compared to the other vegetated zones; therefore, I classified these zones as sharing the core habitat.

Soils occupied by different species had significantly different levels of water content and salinity using the June 2006 dataset (Fig. 9A). Plots with *Salicornia virginica* had the saltiest soils, plots with *Batis* had intermediate values and plots with all other species had relatively low salinity values. Plots with *Spartina alterniflora* had relatively wet soils while plots with all other species occur had intermediate-low levels of water content.

Soils occupied by different species had significantly different levels of water content and salinity using the Richards dataset (Fig. 9B). Comparing only common species between Figs. 9A and 9B, in each case plots with *Salicornia virginica* had the saltiest soils. Plots with *Spartina alterniflora* had the highest water content. Further, in both cases, plots with *Juncus* and *Borrchia* were in the same relative position to one another, both having relatively low levels of salinity and water content.

For the purposes of the transplant experiments, only the species *Borrchia*, *Juncus*, *Batis*, *Salicornia virginica* and *Spartina alterniflora* will be included in the summary.

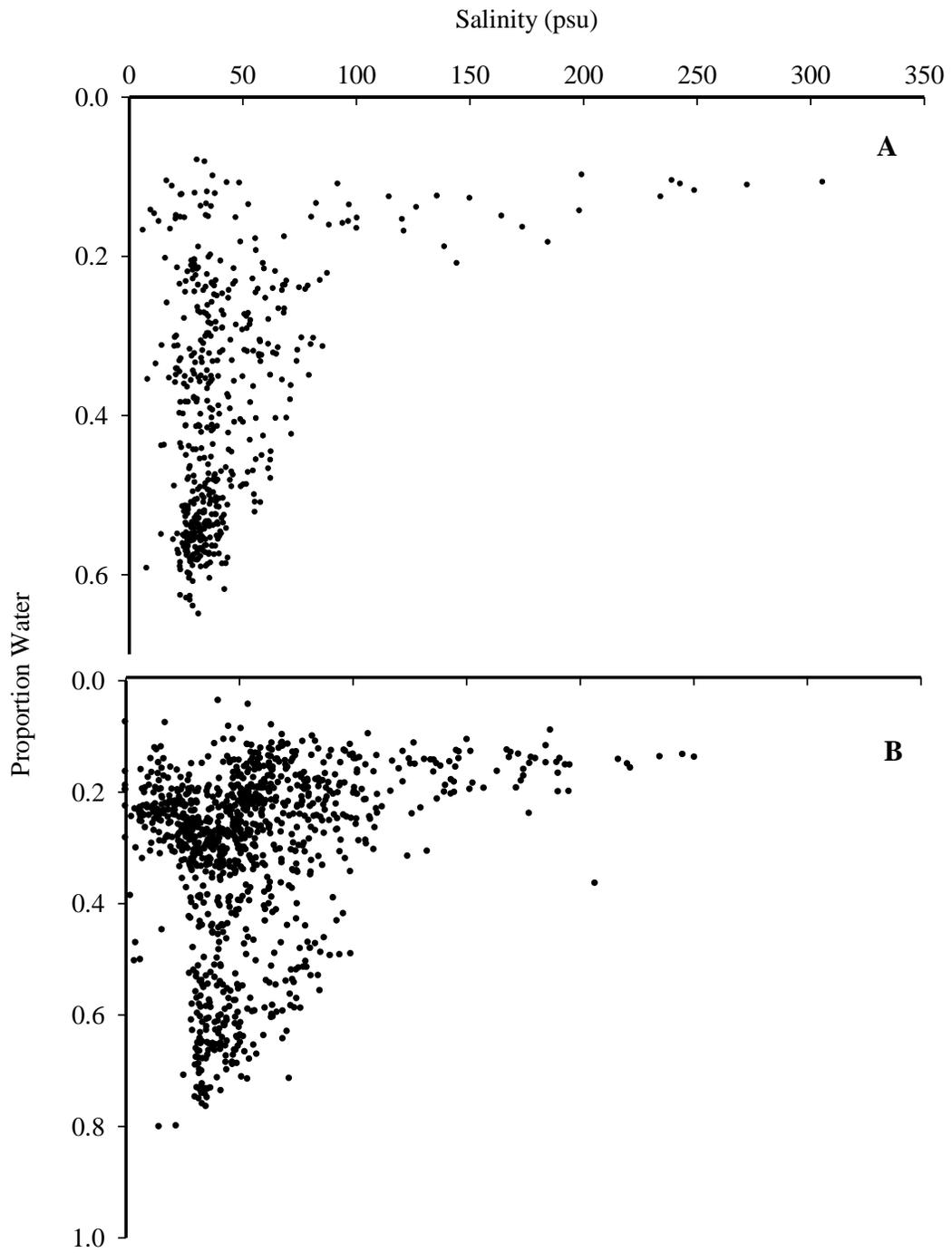


Fig. 5. Scatter-plots of proportion water versus salinity (psu) using the June 2006 dataset (A) and the Richards dataset (B).

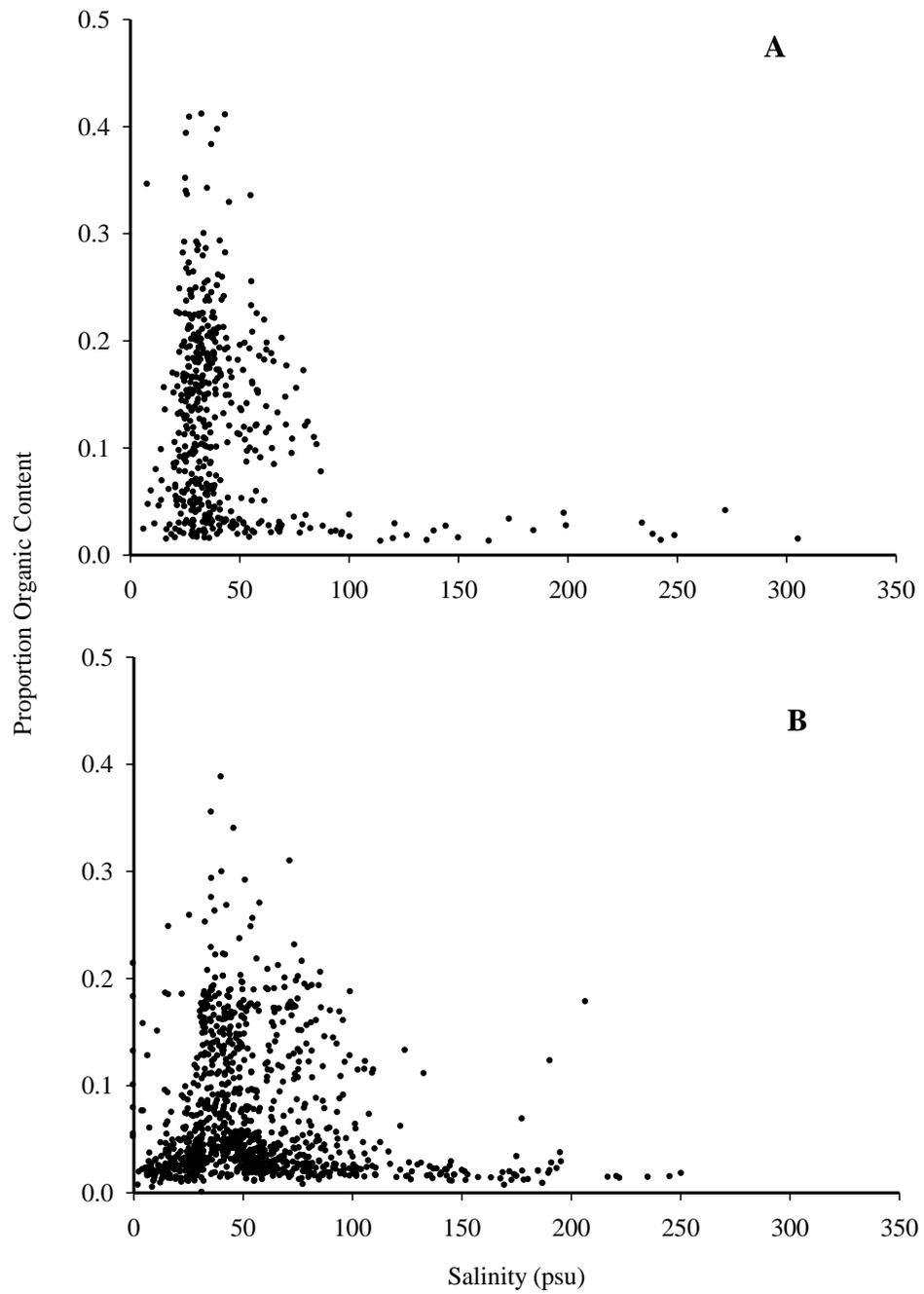


Fig. 6. Scatter-plots of proportion organic content versus salinity (psu) using the June 2006 dataset (A) and Richards dataset (B).

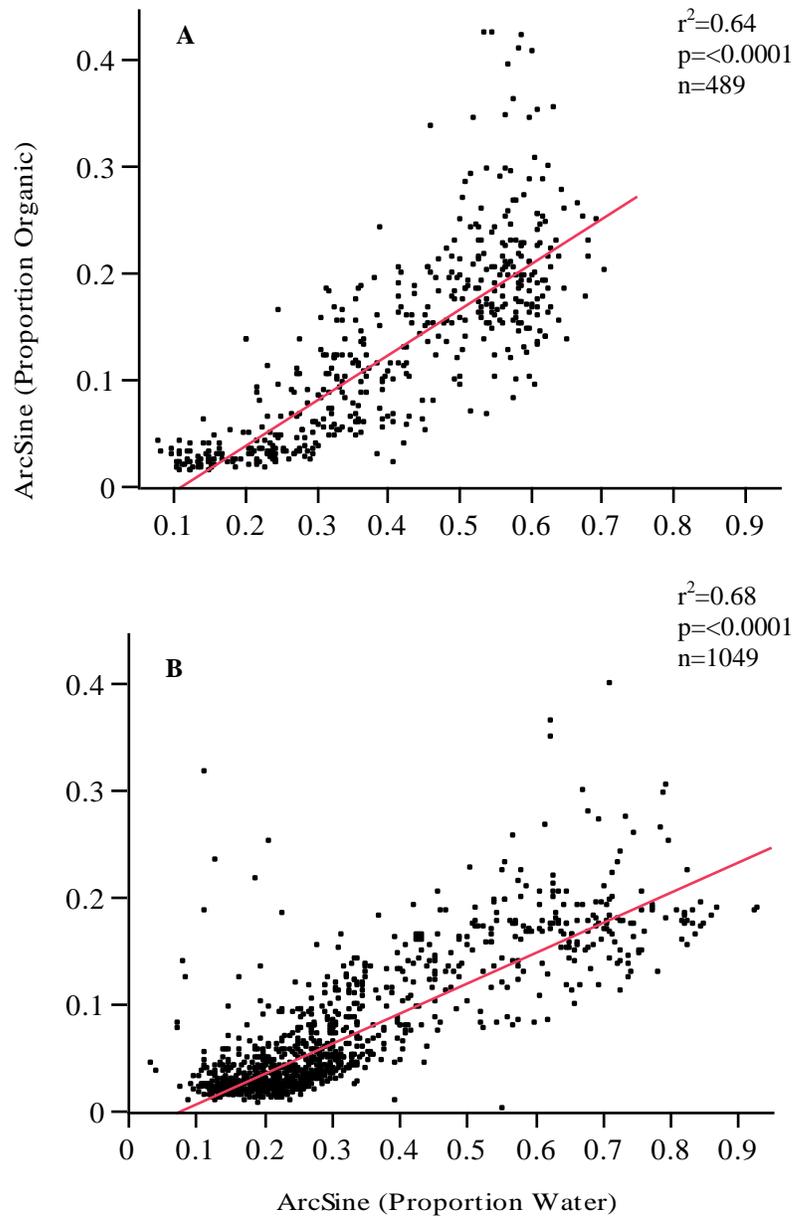


Fig. 7. Linear regression of proportion organic content versus proportion water using the June 2006 dataset (A) and the Richards dataset (B). Data are arcsine transformed.

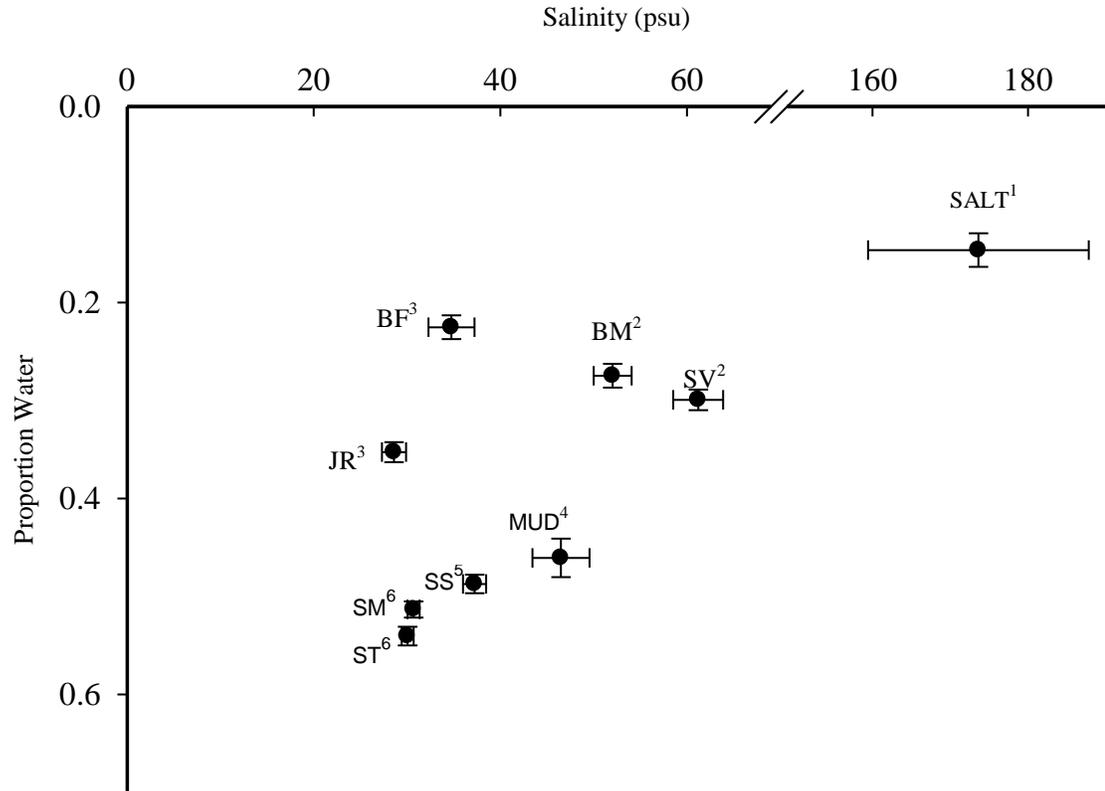


Fig. 8. Habitats plotted along flooding and salinity gradients. Data points are means and error bars are +/- 1 SE. Shared subscript numbers indicate trivariate means that are not significantly different based on MRPP analysis of three soil characteristics: proportion water, salinity (psu) and proportion organic content, where $A = 0.331$ and critical $p = 0.00139$ (corrected using Bonferroni correction).

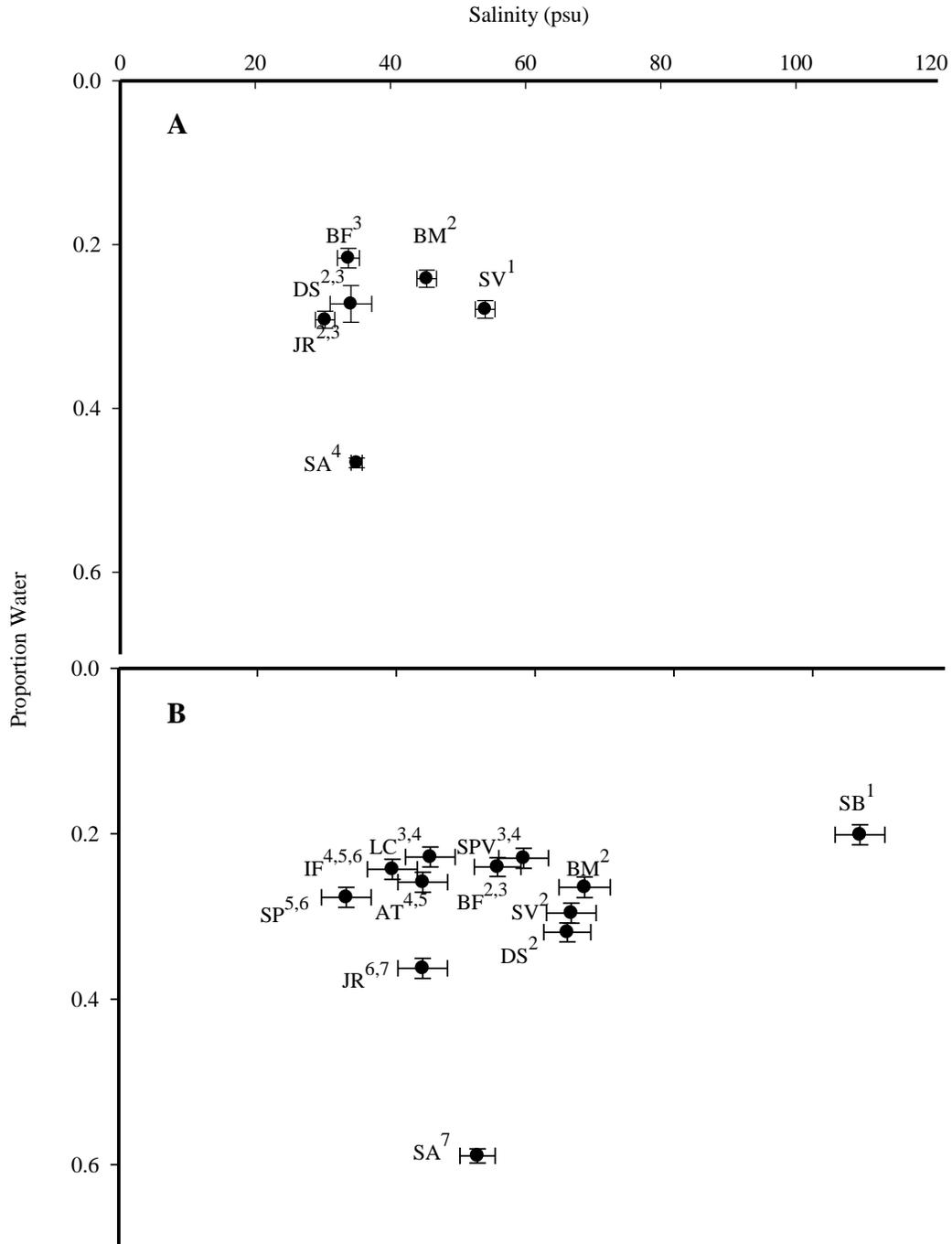


Fig. 9. Species plotted along flooding and salinity gradients using the June 2006 dataset (A) and the Richards dataset (B). Data points are means and error bars are ± 1 SE. Shared subscript numbers indicate trivariate means that are not significantly different based on MRPP analysis of three soil characteristics; proportion water, salinity (psu) and proportion organic content, where $A=0.138$ and critical $p=0.0033$ (A) and $A=0.137$ and critical $p=0.000758$ (B). Both p values corrected using Bonferroni correction.

Productivity and Diversity

Species richness ranged from 1 to 7 species per plot, diversity index (H) ranged from 0 to 3.21 and plant biomass ranged from 11.71g to 461.25g per 0.25m² (Figs. 10A and 10C). There was a weak hump-shaped relationship between species richness or diversity and biomass (Figs. 10A and 10C). Each relationship was re-analyzed with tall *Spartina alterniflora* removed (Figs. 10B and 10D). A weak hump-shaped relationship still occurred between species richness or diversity and biomass (Figs. 10B and 10D).

Mean biomass per 0.25m² ranged from 47.24g to 171.50g by habitat, with mud flats and salt pans omitted (Fig. 11A) and 70.23g to 159.51g by species (Fig. 11B). *Borrichia* and tall *Spartina alterniflora* zones had the greatest biomass while the *Salicornia virginica* and short *Spartina alterniflora* zones had the least biomass (Fig. 11A). Plots with *Borrichia* and *Juncus* present had the greatest biomass whereas the plots with *Batis*, *Spartina alterniflora*, *Distichlis*, and *Salicornia virginica* had the lowest biomass (Fig. 11B).

Mean richness in plots ranged from 1.0 to 3.5 by habitat, with mud flats and salt pans omitted (Fig. 11C) and 1.4 to 5.3 by species (Fig. 11D). The *Borrichia* zone had the highest species richness per plot while all of the *Spartina alterniflora* zones had the lowest species richness per plot (Fig. 11C). Plots with *Distichlis* present had the highest species richness while plots with *Spartina alterniflora* had the lowest species richness (Fig. 11D).

Mean diversity ranged from 0 to 1.56 in plots grouped by habitat (Fig. 11E) and 0.641 to 0.148 in plots grouped by species (Fig. 11F). Both *Batis* and *Borrichia* zones had the highest species diversity per plot while *Spartina alterniflora* zones had the lowest

species richness per plot (Fig. 11E). Plots with *Spartina alterniflora* present had the lowest species diversity compared to plots with all other species (Fig. 11F).

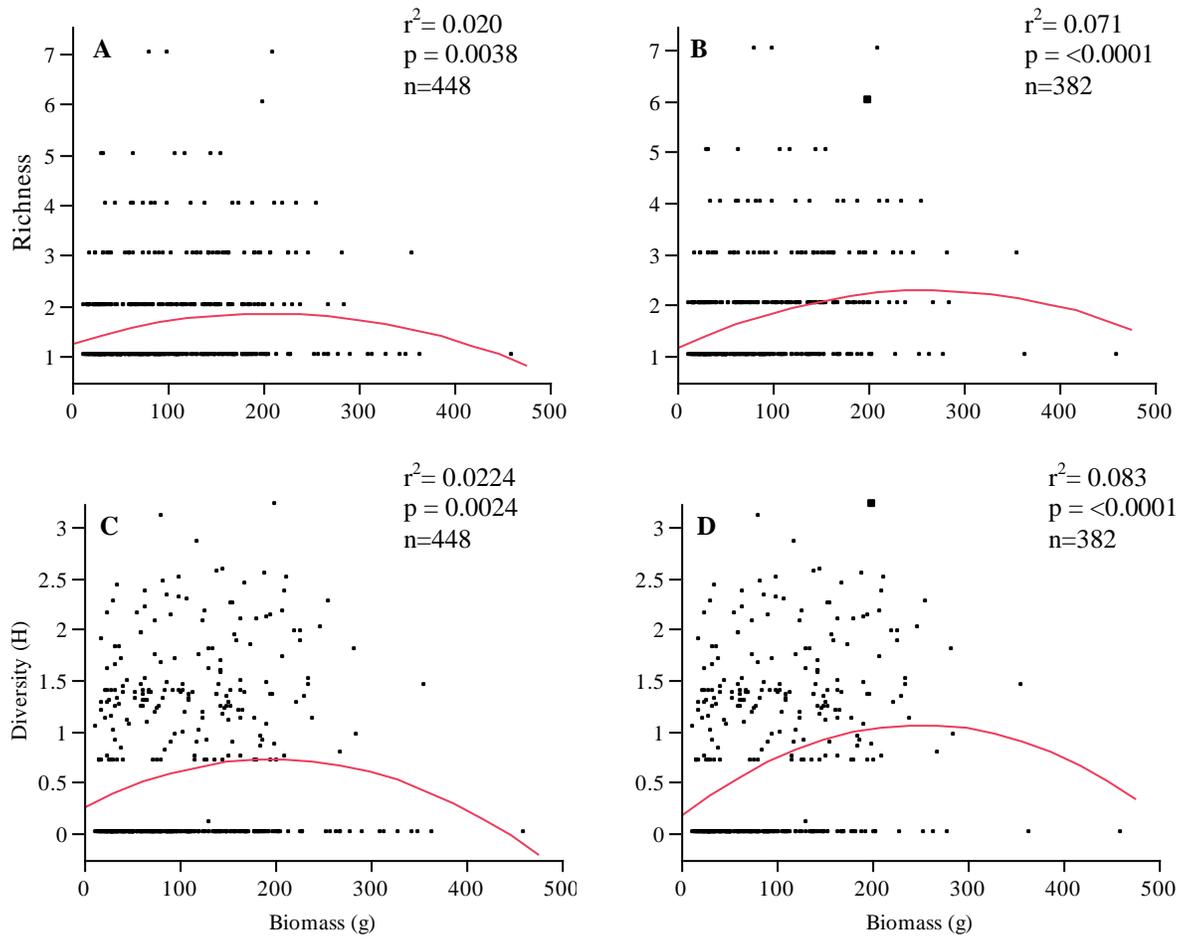


Fig. 10. Relationship between A,B) species richness or C,D) diversity and biomass of marsh vegetation within the 0.25m² plot, with tall *Spartina alterniflora* present (A and C) and with tall *Spartina alterniflora* removed (B and D). The quadratic term was statistically significant ($p < 0.019$) in all cases.

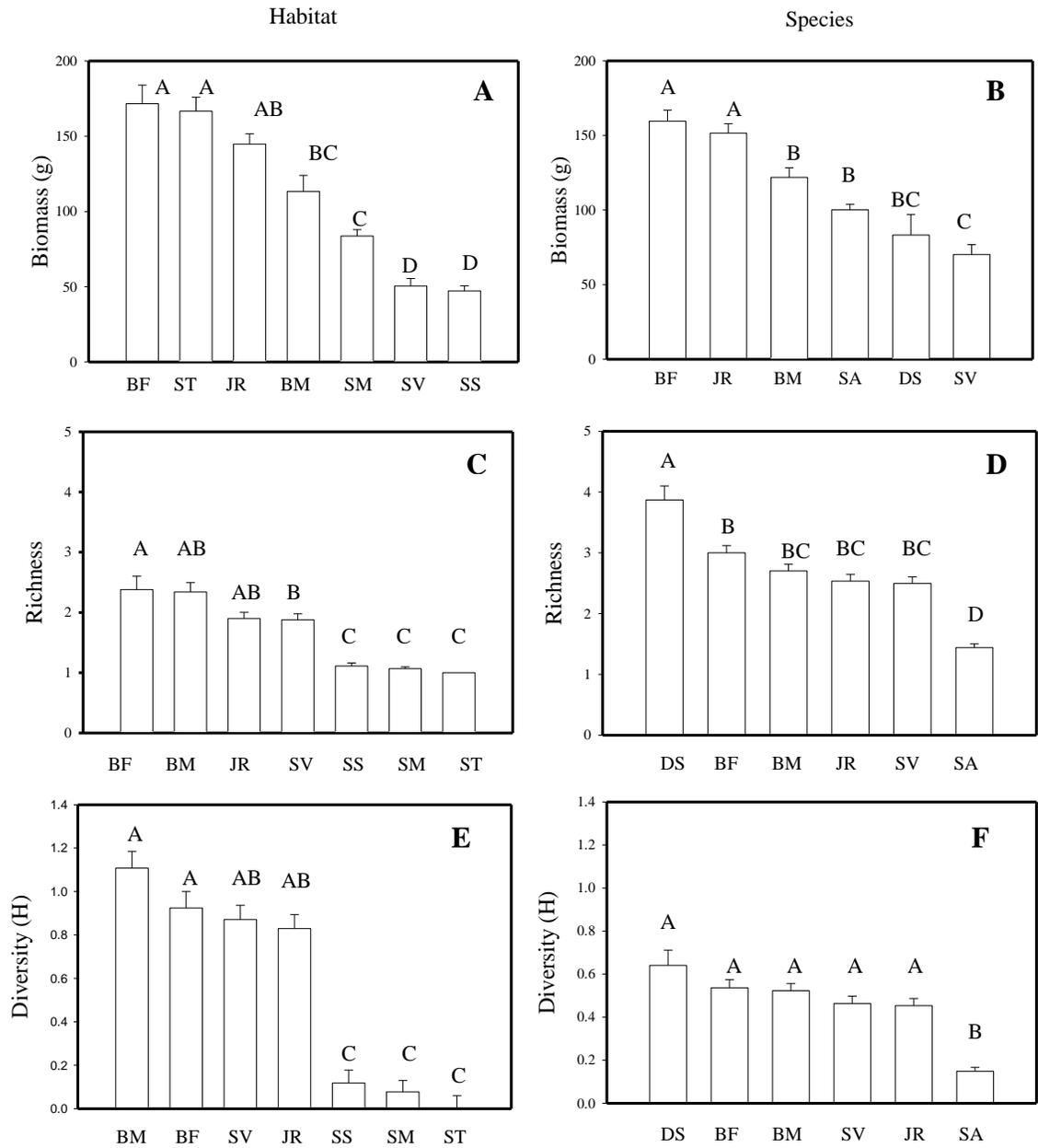


Fig. 11. Plot biomass, richness and diversity. Plots are grouped by habitats (A,C,E) or species (B,D,F). A,B) Biomass; C,D) Richness; E,F) Diversity (Shannon's Index). Data are means + 1 SE. Letters above bars represent groups that are not significantly different (ANOVA followed by Tukey means comparisons).

Centrifugal Organization

The results from the unpublished removal experiment showed that both *Batis* and *Salicornia virginica* performed better (based on percent cover) when *Borrichia* was removed (clipped) compared to when *Borrichia* was not removed (Fig. 12).

The results from the unpublished transplant experiment showed that the performance (based on above ground biomass) of transplanted *Spartina alterniflora* was not significantly different in plots with neighbors removed (Fig. 13), with the exception in the high meadow zone, where *Spartina alterniflora* performed better when neighbors were removed at one of the sites (Light-House) but not the other (Marsh-Landing). Overall, plant growth was significantly different between the two sites and among the zones (Table 1). Additionally there was a strong effect of clipping (removal of neighbors) on plant growth.

Based on the published and unpublished transplant experiments (Tables 2 and 3), all five of the predictions (A through E) were strongly supported, with 29 out of 31 tests reviewed supporting the predictions (Fig. 14). Prediction A, that species transplanted from the saline peripheral habitat into the core habitat will perform well when neighbors are removed and poorly when neighbors are present, was supported in all tests. Prediction B, that species transplanted from the core habitat into the saline peripheral habitat will perform poorly with or without neighbors present, was supported in all tests. Prediction C, that species transplanted from the flooded peripheral habitat into the core habitat will perform well when neighbors are removed and poorly when neighbors are present, was supported in six of the seven tests. Prediction D, that species transplanted from the core habitat into the flooded peripheral habitat will perform poorly with or without neighbors

present, was supported in all tests. Finally, prediction E, that species from the saline peripheral habitat will perform poorly when transplanted into the flooded peripheral habitat, and vice versa, with or without neighbors present, was supported in six of the seven tests.

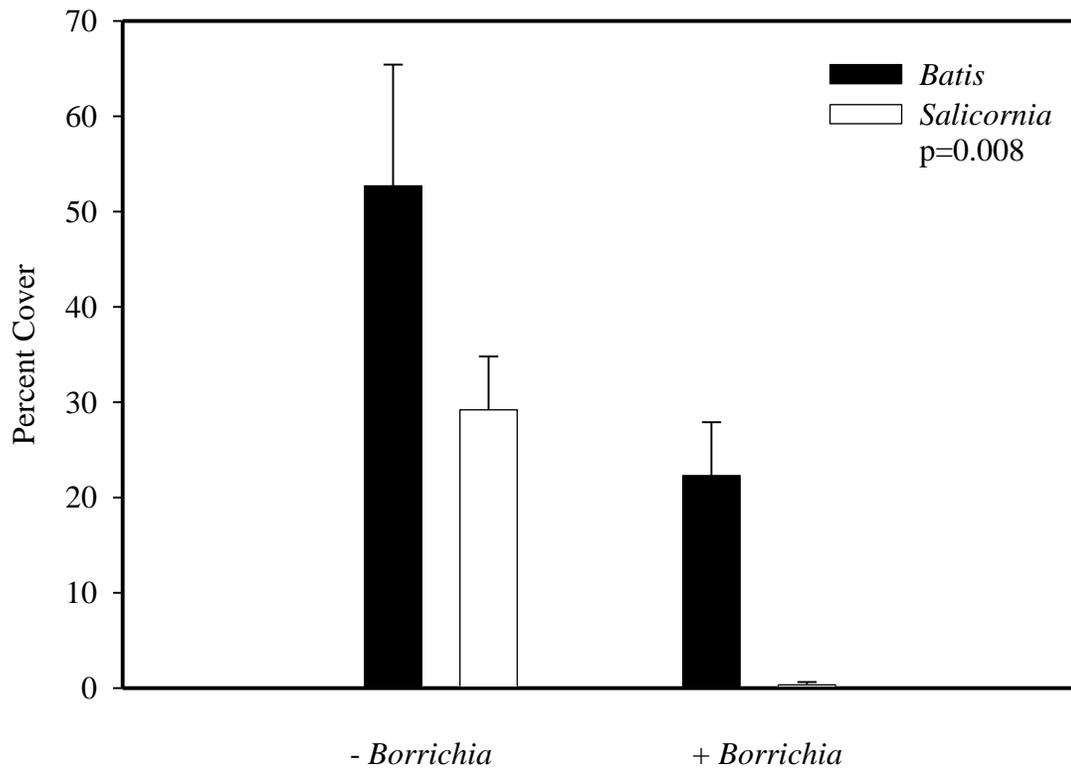


Fig. 12. Percent cover of *Batis* and *Salicornia virginica* in plots with (+) and without (-) *Borrchia* neighbors. Data are means + SE. Data were analyzed with MANOVA, $F(2,9)=8.72$.

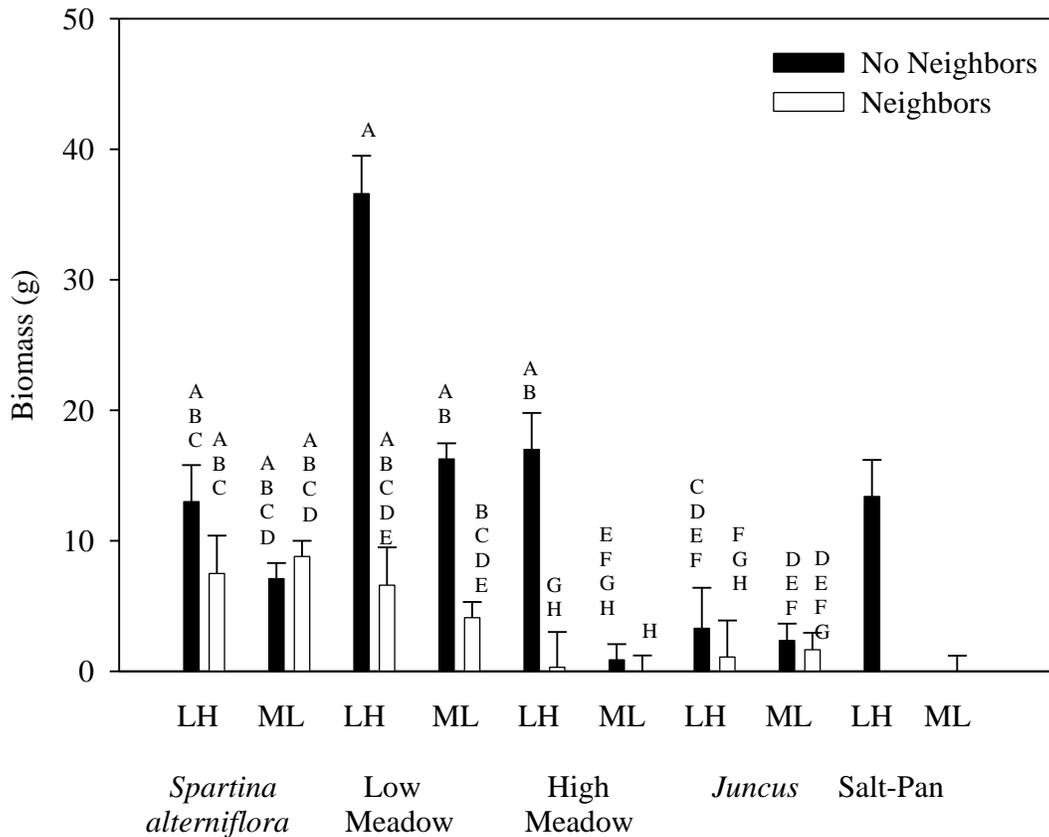


Fig. 13. Final biomass of transplanted *Spartina alterniflora* in plots with and without neighbors. LH and ML indicate Light-House and Marsh-Landing, respectively. Data are means + 1 SE. Data were natural log transformed before analysis and the salt pan zone was removed from the data analyses. Letters above bars indicate groups that are not significantly different (three-way ANOVA, site x zone x neighbor treatment, followed by Tukey means comparisons).

Table 1: Analysis of variance of the final *Spartina alterniflora* above ground biomass (natural log transformed) for the *Spartina alterniflora* transplant experiment.

Source	DF	MS	F	P
zone	3	148.6	42.6	0.0000
neighbor treatment	1	205.3	58.9	0.0000
site	1	17.2	4.9	0.0280
zone*site	3	22.0	6.3	0.0005
neighbor treatment*site	1	30.9	8.9	0.0034
zone*site	3	29.2	8.4	0.0000
zone*neighbor treatment*site	3	7.8	2.3	0.8560
error	139	3.5		
total	154			

Table 2: Summary of predictions and results for unpublished transplant experiments, where +N indicates neighbors were present and –N indicates that neighbors were removed. The prediction tested is indicated in the test column when necessary. The outcome of test is marked by an asterisks (*) when it did not support the hypothesis.

Predictions	Test	Outcome of test
1. <i>Batis</i> will perform well when competitive neighboring dominant plants are removed	1.1 Removal of <i>Borrchia</i> from <i>Batis-Salicornia</i> plots	1.1 <i>Batis</i> performed better in clipped plots compared to unclipped plots (Fig. 12)
2. <i>Salicornia</i> will perform well when competitive neighboring dominant plants are removed	2.1 Removal of <i>Borrchia</i> from <i>Batis-Salicornia</i> plots	2.1 <i>Salicornia</i> performed better in clipped plots compared to unclipped plots (Fig. 12)
3. <i>Spartina</i> will perform	Transplant <i>Spartina</i> into <i>Juncus</i> zone +N (3a)	3.1 <i>Spartina</i> performed poorly (Fig. 13)
a. poorly when transplanted into the core habitat + N	Transplant <i>Spartina</i> into <i>Juncus</i> zone –N (3b)	3.2 <i>Spartina</i> performed poorly* (Fig. 13)
b. well when transplanted into core habitat – N	Transplant <i>Spartina</i> into <i>Salicornia</i> zone +N (3c)	3.3 <i>Spartina</i> performed poorly (Fig. 13)
c. poorly when transplanted into another peripheral habitat, + or – N	Transplant <i>Spartina</i> into <i>Salicornia</i> zone –N (3c)	3.4 <i>Spartina</i> performed well* (Fig. 13)
	Transplant <i>Spartina</i> into <i>Batis</i> zone –N (3c)	3.5 <i>Spartina</i> performed poorly (Fig. 13)
	Transplant <i>Spartina</i> into <i>Batis</i> zone –N (3c)	3.6 <i>Spartina</i> performed poorly (Fig. 13)
	Transplant <i>Spartina</i> into salt pan (3c)	3.7 <i>Spartina</i> performed poorly (Fig. 13)

Table 3: Summary of predictions and results for published transplant experiments, where +N indicates neighbors were present and –N indicates that neighbors were removed. The prediction tested is indicated in the test column when necessary.

Predictions	Test	Outcome of test	Citations
1. <i>Juncus</i> will perform poorly when transplanted outside of the core habitat, + or – N	1.1 Transplant <i>Juncus</i> into <i>Spartina</i> zone +N	1.1 <i>Juncus</i> performed poorly	Pennings <i>et al.</i> 2005 (1.1-1.2) Pennings <i>et al.</i> 2003 (1.3-1.4)
	1.2 Transplant <i>Juncus</i> into <i>Spartina</i> zone –N	1.2 <i>Juncus</i> performed poorly	
	1.3 Transplant <i>Juncus</i> into meadow/ <i>Spartina</i> zone +N	1.3 <i>Juncus</i> performed poorly	
	1.4 Transplant <i>Juncus</i> into meadow/ <i>Spartina</i> zone –N	1.4 <i>Juncus</i> performed poorly	
2. <i>Borrighia</i> will perform poorly when transplanted outside of the core habitat, + or – N	2.1 Transplant <i>Borrighia</i> into <i>Spartina</i> zone +N	2.1 <i>Borrighia</i> performed poorly	Pennings & Moore 2001 (2.1-2.2) Pennings <i>et al.</i> 2003 (2.3-2.4) Stalter & Batson 1969 (2.5-2.6)
	2.2 Transplant <i>Borrighia</i> into <i>Spartina</i> zone –N	2.2 <i>Borrighia</i> performed poorly	
	2.3 Transplant <i>Borrighia</i> into <i>Spartina</i> /meadow zone +N	2.3 <i>Borrighia</i> performed poorly	
	2.4 Transplant <i>Borrighia</i> into <i>Spartina</i> /meadow zone –N	2.4 <i>Borrighia</i> performed poorly	
	2.5 Transplant <i>Borrighia</i> into tall <i>Spartina</i> zone +N	2.5 <i>Borrighia</i> performed poorly	
	2.6 Transplant <i>Borrighia</i> into short <i>Spartina</i> zone +N	2.6 <i>Borrighia</i> performed poorly	
3. <i>Batis</i> will perform a. poorly when transplanted into the peripheral habitat, + or – N b. poorly when transplanted into the core habitat + N c. well when transplanted into the core habitat – N	3.1 Transplant <i>Batis</i> into <i>Spartina</i> /meadow +N (3a)	3.1 <i>Batis</i> performed poorly	Pennings <i>et al.</i> 2003 (3.1-3.4)
	3.2 Transplant <i>Batis</i> into <i>Spartina</i> /meadow –N (3b)	3.2 <i>Batis</i> performed poorly	
	3.3 Transplant <i>Batis</i> into <i>Juncus</i> zone +N (3b)	3.3 <i>Batis</i> performed poorly	
	3.4 Transplant <i>Batis</i> into <i>Juncus</i> zone –N (3c)	3.4 <i>Batis</i> performed well	
4. <i>Spartina</i> will perform a. poorly when transplanted into the core habitat + N b. well when transplanted into the core habitat – N	4.1 Transplant <i>Spartina</i> into <i>Juncus</i> zone +N (4a)	4.1 <i>Spartina</i> performed poorly	Pennings <i>et al.</i> 2003, 2005 (4.1-4.2) Pennings & Moore 2001 (4.3-4.4) Stalter & Batson 1969 (4.5-4.6)
	4.2 Transplant <i>Spartina</i> into <i>Juncus</i> zone –N (4b)	4.2 <i>Spartina</i> performed well	
	4.3 Transplant <i>Spartina</i> into <i>Borrighia</i> zone +N (4a)	4.3 <i>Spartina</i> died	
	4.4 Transplant <i>Spartina</i> into <i>Borrighia</i> zone –N (4b)	4.4 <i>Spartina</i> performed well	
	4.5 Transplant tall <i>Spartina</i> into <i>Borrighia</i> zone +N (4a)	4.5 Tall <i>Spartina</i> died	
	4.6 Transplant short <i>Spartina</i> into <i>Borrighia</i> zone +N (4a)	4.6 Short <i>Spartina</i> died	
5. <i>Salicornia</i> will perform a. poorly when transplanted into the core habitat +N b. well when transplanted into the core habitat –N	5.1 Transplant <i>Salicornia</i> into <i>Juncus</i> zone +N (5a)	5.1 <i>Salicornia</i> performed poorly	Pennings <i>et al.</i> 2003 (5.1-5.2)
	5.2 Transplant <i>Salicornia</i> into <i>Juncus</i> zone –N (5b)	5.2 <i>Salicornia</i> performed well	

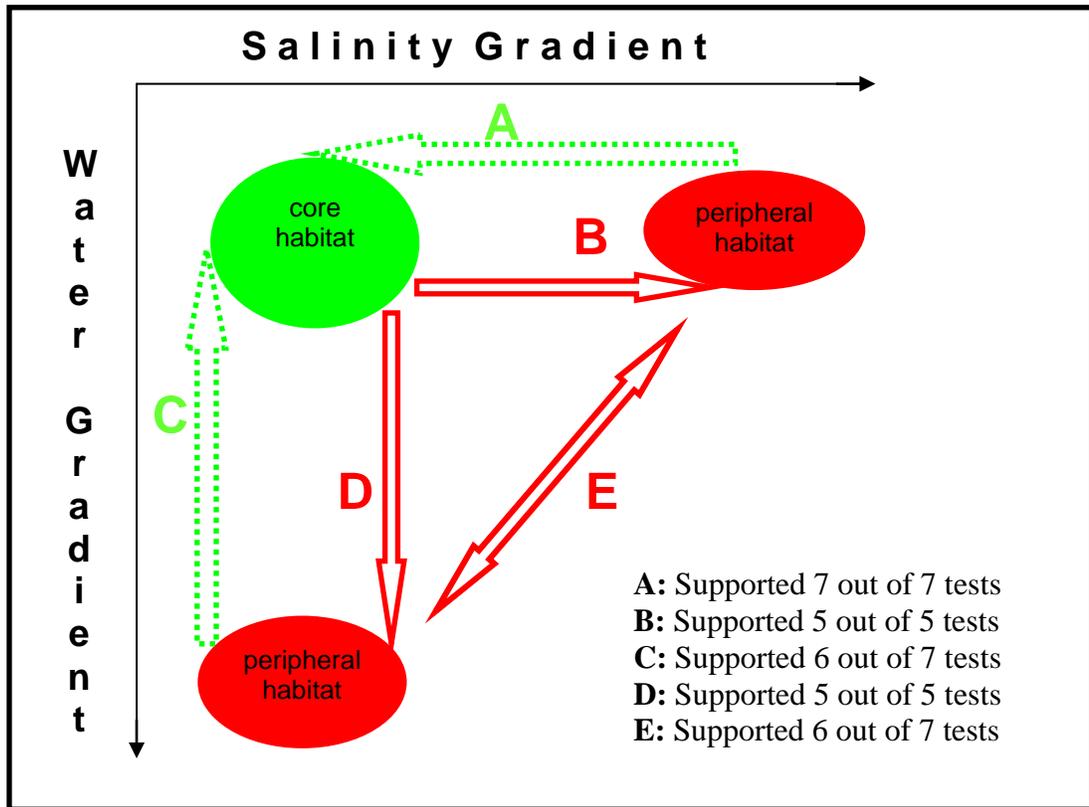


Fig. 14. Summary of support for all transplant experiment results (unpublished and published).

DISCUSSION

My results suggest that a centrifugal model is operating to structure Georgia salt marsh plant communities. Below, I first review the evidence for multiple stress gradients and discuss how plants are sorted along these stress gradients. Next I examine the relationship between species diversity and productivity and summarize the evidence for competitive hierarchies along these gradients. Lastly, I consider how the centrifugal model applies to other salt marshes, wetlands and plant communities in general.

The centrifugal model predicts that multiple stress gradients radiate out from a shared core habitat (Wisheu and Keddy 1992). Both the June 2006 dataset and the Richards dataset documented that there were two clear stress gradients, salinity and water-logging, in Georgia salt marshes, supporting the centrifugal model.

Looking specifically at the June 2006 dataset, the salinity gradient only exceeded 100 psu when soils were less than 20% water by mass. High levels of salt are known to stress plants. Salt can directly affect plants by damaging cellular processes or can indirectly affect plants by lowering the soil water potential, causing water deficiency in the plant even when water is available in the soil (Poljakoff-Mayber 1975, Mendelsson and Batzer 2006). The dominant ions in sea water, sodium and chloride, have direct toxic effects. Sodium can block the uptake of calcium ions, which are required in a variety of enzymatic pathways (Cramer *et al.* 1995) and chloride accumulation in the cytoplasm can disrupt protein synthesis and enzyme activity (Britto *et al.* 2004). Further, the ions in salt water can increasingly inhibit the uptake of nutrients, such as ammonium, as salinities increase (Bradley and Morris 1991).

Soils from the June 2006 dataset ranged from less than 10% to greater than 60% water by mass. All relatively wet cores (greater than 20% water by mass) had a restricted range of salinities (less than 100 psu), undoubtedly due to the fact that these soils are wetter due to the regular tidal flushing that occurs at lower elevations, diluting high salinities. High water content in soil is stressful to plants due to root oxygen deficiency and soil phytotoxin accumulation of manganese, ferrous iron, methane and hydrogen sulfide (Mendelssohn and Batzer 2006). As soil core water content increased from 20-60% water by mass, indicating greater connection to tidal waters, the range of soil salinities decreased progressively to approximately levels of salinity found in sea water. More than two-thirds of the possible parameter space did not occur in nature, in other words there were no soils that were simultaneously wetter than approximately 20% water by mass and saltier than 100 psu.

Soil organic content was positively correlated with soil water content. In wetter soils (greater than 40% water by mass) there was a wider range of variation in soil organic content. Accumulated soil organic matter provides nutrients (Craft *et al.* 1991) and contributes to long-term marsh stability (Craft *et al.* 1993).

According to the centrifugal model, plants should occupy discrete ranges along the multiple stress gradients due to environmental filtering (Grime 1979, Wisheu and Keddy 1992). Species and habitats did occupy discrete ranges along the salinity and water gradients. Species and habitats, however, were not found to occupy distinct ranges along the organic content gradient. Only soils classified as the *Spartina alterniflora* habitat had significantly greater soil organic content compared to all other species and habitats.

The habitat- and species-level approaches to the June 2006 dataset yielded slightly different community arrangements along the stress gradients. Resolution between short, medium and tall *Spartina alterniflora* zones along the water gradient was possible when data were grouped by habitat. Short *Spartina alterniflora* occupied significantly drier and more saline soils. Studies have shown that significant variation exists in the growth responses of different *Spartina alterniflora* populations to hypersalinity (Richards *et al.* 2005). Plots with unvegetated mud had drier and more saline soil. This result is likely due to the lack of shading from plants that have died, rather than an indication that these conditions were unsuitable for *Spartina alterniflora*. The causes of vegetative dieback are varied and remain unclear in most cases (Ogburn and Alber 2006) but may include disturbance, such as accumulation of *Spartina alterniflora* wrack (Bertness and Ellison 1987). Bare salt pans exist at the driest and most saline ends of the gradients, indicating that the conditions are too stressful for any plants to occur. High soil salinities in low-latitude marshes lead to the development of permanent bare areas lacking plant cover which are typically fringed by extremely salt-tolerant flora (Callaway *et al.* 1990, Pennings and Richards 1998).

The June 2006 dataset and the Richards dataset yielded slightly different arrangements of species along the stress gradients. Two factors contributed to these differences. First, the datasets are temporally different from one another. Each dataset was collected over a short time period (3-6 days), but the datasets themselves were collected seven years apart from one another (1999 vs. 2006), and environmental conditions are expected to be variable over time. There was a general shift toward the stressful end of the salinity gradient for all species in the Richards dataset compared to

the June 2006 dataset. Second, the methodology of choosing plants and/or habitats was vastly different in both cases. In the June 2006 sampling effort, plots were chosen based on a stratified design focused on homogenous habitat types. Richards *et al.* (2005) focused on individual species and attempted to capture the greatest range possible along the two stress gradients in order to study plasticity and intraspecific variation. What is surprising is how similar the results were to one another, considering how different the two methods were, further supporting that the common salt marsh species included in these studies do occupy distinct ranges along the environmental gradients.

The centrifugal model predicts that productivity should be greatest at the benign ends of stress gradients and least at the most stressful ends, as stress reduces biomass (Wisheu and Keddy 1992). My data generally support the centrifugal model. When grouped by habitat type, the *Juncus* and *Borrichia* zones, classified as core habitats, had the highest biomass, whereas the *Salicornia virginica*, short *Spartina alterniflora* and medium *Spartina alterniflora*, all classified as peripheral habitats, had relatively low biomass. The one exception to this general agreement with the centrifugal model is the very high biomass in the tall *Spartina alterniflora* zone, as it is at the furthest end of a stress gradient and would therefore be expected to have relatively low biomass. I believe that this occurred because the water gradient is an oversimplification. Measuring water content in soils is a convenient way of estimating stresses such as oxygen deficiency and phytotoxin accumulation that are caused by and correlate with water content. However, this correlation between water content and stress breaks down in the creek-bank habitat. Plant productivity is maximized close to creeks because the influence of tidal action delivers nutrients and flushes toxins from these soils (Pennings and Bertness 2001).

Productivity of *Spartina alterniflora* is thought primarily to be nitrogen limited (Smart and Barko 1980) and sulfide concentrations, which affect the ability of plants to uptake nutrients, are lowest near creek banks (King *et al.* 1982). Further, creek banks have relatively greater pore-water drainage, increasing sediment oxidation (Mendelsson and Seneca 1980) and plant growth (Howes *et al.* 1986). However, creek banks were not benign enough that any other plant species occurred there.

The centrifugal model predicts that diversity should be highest at intermediate levels of stress and lowest in both the core and peripheral habitats (Grime 1979, Wisheu and Keddy 1992). The diversity results only partially support the centrifugal model. The peripheral habitat species, *Salicornia virginica* and *Spartina alterniflora*, always had the lowest species richness and diversity, supporting predictions of the centrifugal model. The core habitat species *Borrchia*, on the other hand, always had either the greatest or second greatest level of species richness and diversity, not supporting predictions of the centrifugal model. However, the classification of habitats as only core or peripheral, with no identified intermediate habitats limits the interpretations that can be gained from these data. A sample design that allows for classification of habitats as intermediate would be necessary to appropriately evaluate the predictions of the centrifugal model in regards to species richness and diversity.

A hump-shaped relationship between plant species richness and productivity has been commonly documented in ecology (Grime 1979, Tilman 1982), although there are many exceptions (Garcia *et al.* 1993, Gough *et al.* 1994). Grime (1979) proposed that species richness should be low at low productivity due to high levels of stress and low at high productivity due to the dominance of a few string competitors. I analyzed the June

2006 dataset by graphing individual plots by richness or diversity and biomass. These analyses produced a weak hump-shaped relationship in all cases, but there was a large amount of unexplained variability and the relationship was statistically weak. Further, the weak hump-shaped relationship could be an artifact due to sampling design, where the use of small quadrats of fixed size will show maximum species richness at intermediate biomass (Oksanen 1996).

The centrifugal model predicts that when core species are transplanted outside of the core habitat they will do poorly with or without neighbors, but peripheral species will do well when transplanted into the core habitat without neighbors and poorly when neighbors are present (Wisheu and Keddy 1992). The results of the transplant experiments strongly supported the centrifugal model, although the unpublished *Spartina alterniflora* transplant experiment had unexpected results. There was no significant difference in the performance of *Spartina alterniflora* in plots in which neighbors were removed, with the exception of the high meadow zone at the Light-House site. These results do not support the predictions of the centrifugal model in two ways. First, although *Spartina alterniflora* is predicted to perform best in the *Juncus* zone without neighbors and poorly with neighbors, there was no significant difference in final aboveground biomass between the with and without neighbors treatment. Second, *Spartina alterniflora* is expected to perform poorly in the saline peripheral habitat, with or without neighbors. However, the final aboveground biomass was highest in the high meadow zone without neighbors, suggesting that it is out-competed by the salt tolerant species in this habitat, but is adapted to tolerate higher levels of salinity than it naturally occurs in. The methodology of the *Spartina alterniflora* transplant experiment was

dubious, however, as the removal of neighbors was not on a large enough scale (only 0.25m² plots) to assure that below-ground root competition and above-ground shading was eliminated.

The results from this study suggest that a centrifugal model is operating to structure Georgia salt marsh plant communities. How does this compare to studies conducted in other salt marshes? Transplant experiments conducted in southern California salt marshes indicate that flooding, soil salinity and competition all interact to determine plant zonation patterns, but the relative importance of these factors varied at different marsh elevations (Pennings and Callaway 1992). Mediterranean-climate marshes, such as the Capintertia Salt Marsh in which Pennings and Callaway (1992) performed their study, experience interactions between flooding and salinity, which creates a band of superior habitat mid-marsh, where both factors are moderate. The results from Pennings and Callaway (1992) generally support that competition is more intense and important at the benign end of each species' range, but the severity of the physical environment is not simply a function of marsh elevation, rather it is dependant upon the tolerance of each species both to flooding and salinity, consistent with the results found in this study. That is, both this study and the Pennings and Callaway (1992) study suggest that multiple permanent stress gradients occur in low latitude salt marshes.

The mechanisms operating to structure high latitude salt marshes may be different than those at low latitudes. New England salt marshes have been heavily studied and results from these high-latitude studies indicate that in undisturbed vegetation there is a simple trade-off between competitive ability and tolerance to flooding, where competitively superior plants occupy high marsh elevations and poor competitors are

displaced to lower marsh elevations (Bertness and Ellison 1987, Bertness *et al.* 1992b, Bertness and Hacker 1994).

Local disturbances are also more common in high latitude marshes, compared to low latitude marshes, where ice can cause severe erosion (Redfield 1972) and floating mats of dead plant material (wrack) can bury sections of the marsh (Bertness and Ellison 1987, Pennings and Richards 1998). Disturbances that remove large sections of vegetation at intermediate marsh elevations may lead to hypersaline soils (Bertness *et al.* 1992a). Following this disturbance, secondary succession occurs through a combination of facultative and competitive interactions; first invasion of salt tolerant plant species into the bare patches shades the soil, which alleviates the salinity stress and facilitates the colonization of other less salt tolerant species that ultimately out-compete the salt-tolerant species (Bertness and Ellison 1987, Bertness *et al.* 1992a). Therefore, a salinity gradient does occur at high latitudes, but it is transient. Comparatively, at lower latitudes, hypersaline soils occur at intermediate marsh elevations due to increased evapotranspiration in the hotter climate (Pennings and Bertness 1999) and the establishment of salt tolerant species does not have the same facultative effect on soil salinities. Therefore, the two stress gradients, salinity and water, are constant in Georgia salt marshes, while only the water gradient is constant in New England salt marshes.

The relative importance of competition and facilitation may also vary at different latitudes. Positive interactions between species involving the amelioration of desiccation, high salinities or any other abiotic stress are typically believed to be more important under conditions of increasing abiotic stress (Bertness and Callaway 1994, Bertness and Leonard 1997, Bruno and Bertness 2001). Pennings and Bertness (1999) predicted that

the positive interactions among plants should be stronger and more common in low latitudes compared to high latitudes, due to the increased salinity stress in the hotter climates (Pennings and Bertness 1999). At a regional scale positive interactions were more common in Rhode Island salt marshes (south of Cape Cod) compared to Maine salt marshes (north of Cape Cod) (Bertness and Ewanchuck 2002). At a larger scale, however, Pennings *et al.* (2003) found that interactions between plants in Georgia and Alabama salt marshes were almost always strongly competitive. Likely explanations for these contrasting results are the differences between the floras of northern and southern salt marshes, where northern marsh plant communities are dominated by salt-sensitive species that are likely to be facilitated by neighbors and southern marsh plant communities are dominated by salt-tolerant species unlikely to benefit significantly from neighbor amelioration of soil salinities (Pennings *et al.* 2003).

These studies suggest that while facilitation and competition both play an important role in salt marsh plant communities, competitive interactions are stronger and more common in low latitude salt marshes. The published and unpublished manipulative experiments reviewed in this study support that competitive interactions are more important than positive interactions in structuring Georgia salt marsh plant communities. If positive interactions were more important in structuring the Georgia salt marsh plant community, plants would be expected to perform better when transplanted into plots with neighbors, rather than without neighbors. Transplanted species generally performed better when neighbors were removed, indicating competition is more important than facilitation in structuring Georgia salt marsh plant communities.

A centrifugal model of organization has been well documented in non-saline wetland plant communities, where the central habitat has low disturbance and high fertility (Keddy 1990, Wisheu and Keddy 1992, Keddy 2000). Further, the centrifugal model appears to be useful for explaining plant community structure in salt marshes at high latitudes, where disturbance creates a temporary salinity gradient and low latitudes, where consistently high levels of salinity create a permanent salinity gradient. Relatively few studies, however, have attempted to apply a centrifugal model to terrestrial plant communities. Although preliminary work has shown that terrestrial plant communities can be arranged into centrifugal patterns, more objective tests are still needed (Keddy 1989a, Wisheu and Keddy 1992, Malanson and Butler 1994, Vujnovic *et al.* 2000). Keddy (2005) suggests that while the centrifugal model can summarize patterns in landscapes containing multiple gradients, such landscapes are complicated in structure and composition, and therefore tend to be ignored in more theoretical models that assume homogeneous habitats. Most studies on terrestrial plant communities have found that other models are better suited to explain community structure than the centrifugal model of organization (Donovan and Richards 2000, Hubbell 2001, Stubbs and Wilson 2004, Malanson *et al.* 2007). I am unaware of other attempts to apply the centrifugal model to the organization of terrestrial plant communities. It may be that severe stress gradients are rare in terrestrial plant systems at moderate spatial scales, such that scientists look to competition or neutral theories to explain community organization and discount the role of abiotic stress.

CONCLUSIONS

In conclusion, I found strong evidence that the centrifugal model was useful in explaining plant community structure in a Georgia salt marsh. Additionally this model provides a unified theory for vegetation pattern in northeast and southeast USA salt marshes. Plant zonation due to high salinities caused by increased evapotranspiration in hotter climates at lower latitude marshes can be equated to the disturbance-caused temporary increases in salinity at high-latitude marshes.

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Appendix A: Sampling data June 2006



Fig. A1. Sapelo Island is a barrier island located off the coast of Georgia. The Duplin River is to the immediate west of Sapelo Island.

GPS Transects



- ▲ BM ▲ SA
- ▲ JR ▲ SV
- ▲ MUD



Data Source: AISA Eagle
Projection: UTM, Zone 17N
Datum: World Geodetic System 1984

0 50 100 200 300 400 500 Meters

Fig A2. Six transects along the Duplin River, Sapelo Island, GA. Triangles represent individual plots. Sapelo Island is to the east of the Duplin River.

Table A1. Species and habitat types used in this manuscript, with their respective codes.

Species	Species code
<i>Aster tenuifolius</i>	AT
<i>Batis maritima</i>	BM
<i>Borrichia frutescens</i>	BF
<i>Distichlis spicata</i>	DS
<i>Iva frutescens</i>	IF
<i>Juncus roemerianus</i>	JR
<i>Limonium carolinianum</i>	LC
<i>Salicornia bigelovii</i>	SB
<i>Salicornia virginica</i>	SV
<i>Spartina alterniflora</i>	SA
<i>Spartina patens</i>	SP
<i>Sporobolus virginicus</i>	SPV
Habitat	Habitat code
<i>Batis maritima</i>	BM
<i>Borrichia frutescens</i>	BF
<i>Distichlis spicata</i>	DS
<i>Juncus roemerianus</i>	JR
<i>Salicornia virginica</i>	SV
tall <i>Spartina alterniflora</i>	ST
medium <i>Spartina alterniflora</i>	SM
short <i>Spartina alterniflora</i>	SS
unvegetated mud flats	MUD
salt pans	SALT

Appendix B: Diversity indices

While species richness is an easy measure of diversity, it assumes an equal abundance of species. There are a variety of diversity measures that differentially weight the proportion of species richness and species abundance, including Shannon's diversity index (Margurran 1988).

- 1. Shannon's diversity index (H)** includes richness and relative abundance of each species.

Formula used:

$$H = - \sum_{i=1}^S p_i \ln p_i$$

where S is the total number of species in the community (richness) and p_i is the proportion of S made up of i th species.

Of the indices, Shannon's diversity index is most sensitive to species of intermediate importance

Literature cited

Magurran, A. E. 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.

Appendix C: Methods and materials for unpublished transplant experiments

***Batis-Salicornia-Borrichia* removal experiment**

To examine interactions between *Borrichia* and the two succulents, *Batis* and *Salicornia virginica*, Pennings completely clipped all vegetation from six 0.5 x 0.5 m quadrats in a mixed stand of *Borrichia*, *Batis* and *Salicornia virginica* at Dean Creek, Sapelo Island, Georgia in June 1997. Six interspersed plots were left unmanipulated as controls. *Borrichia* was weeded from the manipulated plots every 6 months but other plant species were allowed to re-invade. Percent cover of *Borrichia*, *Batis* and *Salicornia virginica* (no other species were present) in the plots was monitored on August 16, 2001 using a 0.5 x 0.5 m quadrat divided into 100 cells. Each species was scored as present or absent in each cell of the quadrat. Data were analyzed using MANOVA and Pillai's criterion test statistic.

***Spartina alterniflora* transplant experiment**

To determine the importance of abiotic stress and competition on the zonation of *Spartina alterniflora*, Pennings conducted a transplant experiment at two sites, Marsh-Landing and Light-House, on Sapelo Island GA. Culms of *Spartina alterniflora* (15x15x20-cm blocks of soil with 2-3 live shoots) were transplanted into the short *Spartina* zone, the low meadow zone (dominated by *Salicornia virginica*), the salt pan, the high meadow zone (dominated by *Batis*, *Distichlis* and *Sporobulus*) and the *Juncus* zone (N= 20/zone). Neighboring vegetation was removed from an area of 0.5 x 0.5 m surrounding every other replicate by clipping every month. Plants were transplanted on March 11-12, 1998 and all aboveground biomass of the transplants was harvested on October 5-6, 1998 and dried at 60°C to constant mass. Data were analyzed with three-

way (site x zone x neighbor treatment) ANOVA followed by Tukey means comparisons.

Because the unvegetated salt pan zone did not have a with neighbors treatment it was removed from the data analyses

Appendix D: Sørensen (Bray-Curtis) distance

Sørensen distance, also known as Bray-Curtis distance, is a proportion coefficient measured in city-block space, where the distance (or dissimilarity) between items i and h is:

$$D_{i,h} = \frac{\sum_{j=1}^p |a_{ij} - a_{hj}|}{\sum_{j=1}^p a_{ij} + \sum_{j=1}^p a_{hj}}$$

where there are p attributes of the objects (McCune and Grace 2002).

The Sørensen coefficient is considered more useful for ecological community data, compared to Euclidean distance, as it gives less weight to outliers and retains sensitivity in heterogeneous data sets (McCune and Grace 2002).

Literature cited

McCune, B. and J.B. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design, Glenden Beach, OR.

Appendix E: Samples sizes of groups used in MRPP analyses

Table E1: Sample sizes of groups (species or habitat) used in MRPP analyses

June 2006 dataset grouped by habitat	
Group	N
BF	42
BM	42
JR	59
MUD	16
SALT	21
SM	89
SS	68
ST	68
SV	55
June 2006 dataset grouped by species	
Group	N
BF	78
BM	100
DS	22
JR	103
SA	312
SV	96
Richards dataset grouped by species	
Group	N
AT	79
BF	89
BM	75
DS	89
IF	78
JR	80
LC	80
SA	160
SB	79
SP	80
SPV	80
SV	80

Appendix F: Results of MRPP analyses by species for 3 soil properties; salinity (psu), proportion water and proportion organic content

Table F-1: Multiple Pairwise Comparisons (June 2006 dataset using habitats as groups)

			T	A	p
BF	vs.	BM	-17.54065309	0.12948022	0.00000001
BF	vs.	JR	-4.44516892	0.02352854	0.00333941
BF	vs.	MUD	-12.34321059	0.13074040	0.00000159
BF	vs.	SALT	-35.65905751	0.42686266	0.00000000
BF	vs.	SM	-30.92663496	0.12757469	0.00000000
BF	vs.	SS	-26.73941396	0.13544292	0.00000000
BF	vs.	ST	-40.52826645	0.19363692	0.00000000
BF	vs.	SV	-26.10510974	0.17896731	0.00000000
BM	vs.	JR	-34.22580127	0.20035954	0.00000000
BM	vs.	MUD	-8.24820655	0.08677093	0.00004151
BM	vs.	SALT	-34.61542665	0.42439482	0.00000000
BM	vs.	SM	-58.19073063	0.27190516	0.00000000
BM	vs.	SS	-36.33793244	0.20057824	0.00000000
BM	vs.	ST	-57.86711565	0.34984122	0.00000000
BM	vs.	SV	-5.29661626	0.03508770	0.00188300
JR	vs.	MUD	-15.86322401	0.12307557	0.00000001
JR	vs.	SALT	-48.46962208	0.43015600	0.00000000
JR	vs.	SM	-21.09048786	0.08053190	0.00000000
JR	vs.	SS	-25.49650578	0.11468448	0.00000000
JR	vs.	ST	-31.27012414	0.13411121	0.00000000
JR	vs.	SV	-43.44430759	0.24086341	0.00000000
MUD	vs.	SALT	-21.09689133	0.48296007	0.00000000
MUD	vs.	SM	-16.41719100	0.08572903	0.00000000
MUD	vs.	SS	-5.57317031	0.03749737	0.00086574
MUD	vs.	ST	-20.59231466	0.12968978	0.00000000
MUD	vs.	SV	-8.27261636	0.07363418	0.00007123
SALT	vs.	SM	-69.25185783	0.46705140	0.00000000
SALT	vs.	SS	-53.62673034	0.45248788	0.00000000
SALT	vs.	ST	-58.00178806	0.54706536	0.00000000
SALT	vs.	SV	-34.45374224	0.31181961	0.00000000
SM	vs.	SS	-8.67637404	0.03014879	0.00003151
SM	vs.	ST	-1.23513263	0.00421762	0.11025116
SM	vs.	SV	-64.97228592	0.29415241	0.00000000
SS	vs.	ST	-11.64500394	0.04454070	0.00000063
SS	vs.	SV	-40.94013474	0.21473669	0.00000000
ST	vs.	SV	-60.63331611	0.34770214	0.00000000

Table F-2: Multiple Pairwise Comparisons (June 2006 dataset using species as groups)

			T	A	p
BF	vs.	BM	-10.05184476	0.03464494	0.00001846
BF	vs.	DS	0.26623024	-0.00150545	0.49345842
BF	vs.	JR	-2.92317724	0.00873815	0.01793072
BF	vs.	SA	-53.67714699	0.07469417	0.00000000
BF	vs.	SV	-33.46756205	0.12346216	0.00000000
BM	vs.	DS	-3.92989090	0.02046223	0.00751651
BM	vs.	JR	-23.69610264	0.06607264	0.00000000
BM	vs.	SA	-63.52939125	0.08666227	0.00000000
BM	vs.	SV	-7.98532251	0.02687940	0.00019467
BM	vs.	JR	-0.76822935	0.00329862	0.18014082
DS	vs.	SA	-12.28935728	0.02037685	0.00000028
DS	vs.	SV	-13.63383479	0.07710528	0.00000076
JR	vs.	SA	-47.50681974	0.06142308	0.00000000
JR	vs.	SV	-50.87175910	0.15355241	0.00000000
SA	vs.	SV	-80.79163038	0.11563799	0.00000000

Table F-3: Multiple Pairwise Comparisons (Richards dataset using species as groups)

			T	A	p
AT	vs.	BF	-4.07369713	0.01643170	0.00691667
AT	vs.	BM	-13.36298999	0.06028254	0.00000116
AT	vs.	DS	-10.04248590	0.04108154	0.00002285
AT	vs.	IF	-2.32034694	0.01091359	0.03736740
AT	vs.	JR	-3.29629524	0.01481525	0.01473434
AT	vs.	LC	0.59438191	-0.00277393	0.66637212
AT	vs.	SA	-8.40827410	0.02501234	0.00013359
AT	vs.	SB	-33.57477989	0.15536111	0.00000000
AT	vs.	SP	-4.36928520	0.01716377	0.00405806
AT	vs.	SPV	-3.69675445	0.01615577	0.00936137
AT	vs.	SV	-7.14921787	0.03171441	0.00039201
BF	vs.	BM	-1.93055222	0.00773544	0.05361414
BF	vs.	DS	-1.12593584	0.00422707	0.11700721
BF	vs.	IF	-13.27588044	0.05357455	0.00000115
BF	vs.	JR	-9.93231829	0.04008826	0.00003417
BF	vs.	LC	-5.05976625	0.02087017	0.00281057
BF	vs.	SA	-7.62719668	0.02176106	0.00032195
BF	vs.	SB	-29.20851166	0.12169038	0.00000000
BF	vs.	SP	-17.12990014	0.06173893	0.00000000
BF	vs.	SPV	-7.37980977	0.02926926	0.00022881
BF	vs.	SV	-1.30946181	0.00524826	0.09781629
BM	vs.	DS	-0.36822167	0.00168621	0.24104891
BM	vs.	IF	-26.58500298	0.12093864	0.00000000
BM	vs.	JR	-20.01143720	0.09731982	0.00000001
BM	vs.	LC	-13.69534480	0.06305303	0.00000083
BM	vs.	SA	-14.31766262	0.04809547	0.00000117
BM	vs.	SB	-22.86964607	0.11027942	0.00000000
BM	vs.	SP	-30.09736195	0.11775547	0.00000000
BM	vs.	SPV	-12.88603901	0.05737088	0.00000089
BM	vs.	SV	-1.30475533	0.00617276	0.09741430
DS	vs.	IF	-20.79777484	0.08578342	0.00000000
DS	vs.	JR	-14.57160818	0.06385151	0.00000054
DS	vs.	LC	-11.25088525	0.04667644	0.00000674
DS	vs.	SA	-8.70643289	0.02734671	0.00013771
DS	vs.	SB	-23.62488402	0.10747308	0.00000000
DS	vs.	SP	-25.20951153	0.09002283	0.00000000
DS	vs.	SPV	-10.71790157	0.04380238	0.00000802
DS	vs.	SV	-0.49893212	0.00220148	0.21052442
IF	vs.	JR	-2.36772240	0.01143425	0.03580795
IF	vs.	LC	-3.75878218	0.01817376	0.01009825
IF	vs.	SA	-14.25645783	0.04221875	0.00000048
IF	vs.	SB	-47.05933902	0.22813967	0.00000000
IF	vs.	SP	-5.38806797	0.02212217	0.00157945
IF	vs.	SPV	-11.55683000	0.05093365	0.00000339
IF	vs.	SV	-18.98887937	0.08376973	0.00000000
JR	vs.	LC	-7.01357042	0.03182682	0.00045732
JR	vs.	SA	-4.29946126	0.01391765	0.00640472
JR	vs.	SB	-46.36073047	0.22894207	0.00000000
JR	vs.	SP	-10.26603603	0.03915317	0.00000486
JR	vs.	SPV	-14.91867035	0.06290800	0.00000008
JR	vs.	SV	-14.36961517	0.06626651	0.00000074
LC	vs.	SA	-14.21903330	0.04177271	0.00000049

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LC	vs.	SB	-30.09230908	0.14023048	0.00000000
LC	vs.	SP	-4.51783106	0.01800302	0.00372809
LC	vs.	SPV	-1.70628626	0.00768605	0.06668432
LC	vs.	SV	-7.33983280	0.03302490	0.00032836
SA	vs.	SB	-58.17327511	0.18792474	0.00000000
SA	vs.	SP	-24.37914969	0.06228568	0.00000000
SA	vs.	SPV	-21.89796597	0.06188899	0.00000000
SA	vs.	SV	-11.10101667	0.03550737	0.00001769
SB	vs.	SP	-41.70977970	0.17408568	0.00000000
SB	vs.	SPV	-15.81752596	0.07520914	0.00000015
SB	vs.	SV	-15.96795096	0.07646904	0.00000016
SP	vs.	SPV	-7.24335805	0.02800923	0.00016978
SP	vs.	SV	-19.37782484	0.07443415	0.00000000
SPV	vs.	SV	-5.17293728	0.02299531	0.00224086