Manipulation Experiment Overstates The Competitive Interactions Occurring Between Mangroves And Salt Marsh Vegetation

by
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A thesis submitted to the Department of Biology and Biochemistry,
College of Natural Sciences and Mathematics
in partial fulfillment of the requirements for the degree of

Master of Science

in Biology

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University of Houston
May 2022

DEDICATION

I dedicate this thesis to my family, both immediate and extended, who have pushed me, motivated me and supported me in everything that I do. Upmost thanks to my dad (Kevin), mom (Tina), brother (KJ), sister (Roo), niece (Rizzo) and grandmother (Mamaw); this could not have been possible without you all.

ACKNOWLEDGMENTS

We are grateful for the efforts by all field and lab assistants that contributed to the setup, maintenance, and data collection of the studies throughout the years; especially Carolyn Weaver and Ashley Whitt. Special thanks to Sayantani Dastidar for conducting the transplant experiment. Our research was supported by the National Science Foundation (DEB-1761414 to A. Armitage, and DEB-1761428 to S. Pennings), and by Institutional Grants (NA10OAR4170099, NA14OAR4170102, and NA18OAR4170088) from the Texas Sea Grant College Program from the National Sea Grant Office, National Oceanic and Atmospheric Administration, and U.S. Department of Commerce.

ABSTRACT

Ecologists use multiple methods for studying community-level interspecific competition, but different approaches may give different answers. We compared four methods to quantify the competitive interactions between *Avicennia germinans* (black mangroves) and salt marsh vegetation in Texas, USA. We compared four methods to quantify the competitive interactions between mangroves and marsh vegetation: two different methods of sampling a large (24 x 42 m) mangrove removal experiment, a transplant experiment conducted within the large experiment, and a natural experiment comparing sites naturally dominated by marsh or mangrove vegetation. We found stronger competition in the mangrove removal experiment than in the natural experiment. This was likely because the site chosen for the mangrove removal experiment had higher densities of mangroves than did the sites chosen for the natural experiment. Outcomes also differed among marsh plant species, and also differed as a function of spatial scale: the strength of competition in the transplant experiment was driven only by the presence or absence of mangroves in the immediate (3x3 m cell) vicinity of the transplanted plants, but natural colonization of 3x3 m cells within the 24 x 42 m plots was also a function of the cover of mangroves at the plot scale. Our findings suggest that manipulation experiments can give results that do not reflect patterns at the landscape scale if study sites are not representative of the landscape. Although global warming is likely to facilitate continued spread of mangroves, marsh plants are likely to persist on the landscape in areas where mangroves do not attain high cover.

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I. Introduction

Climate change is altering environmental conditions and causing shifts in the plant composition of many local communities. Coastal wetlands, situated at the ecotone of aquatic and terrestrial ecosystems, are particularly sensitive to changes in hydrology, climate, and biotic conditions (Cherry et al., 2009; Lomnicky et al., 2019). One major change is in the distribution of mangroves and salt marshes worldwide (Saintilan et al., 2014). For example, the tropical black mangrove, *Avicennia germinans*, has expanded its geographic range northward from the tropics due to warmer winters (Osland et al., 2020a), decreased severe freezing events (Cavanaugh et al., 2014; Osland et al., 2013), changes in precipitation (Osland et al., 2014b), and nutrient enrichment (Weaver et al., 2018). As a result, black mangroves have encroached into what previously were salt marshes of the U.S. Gulf Coast and the Florida Atlantic coast over the past several decades. This species and other mangroves have expanded their ranges during periods of optimal conditions and retreated during periods of suboptimal conditions (Alongi, 2015; Giri et al., 2011; Montagna et al., 2011). As a result, areas near the geographic border between mangroves and marsh habitat often contain both types of species, with stands of each expanding or contracting over time as conditions change.

We used this ecotone to compare different methods for studying competition between mangroves and salt marsh plants. Many studies have looked at how salt marsh plants affect mangrove seedlings (e.g., Guo et al., 2017; Pickens et al., 2019), because mangrove seedlings are easy to manipulate. In contrast, relatively few studies have looked at how adult mangroves, which are difficult to manipulate, affect marsh plants. Based on basic ecological theory (Keddy, 2001), we would expect adult mangroves to be competitively dominant over shorter marsh plants. Ecologists could use a variety of methods to test this hypothesis. One possible approach is to experimentally manipulate mangrove abundance to see the effect it has on marsh plant abundance. To our knowledge, our experiment on Harbor Island, near Port Aransas, Texas, USA is the only study that has taken this approach (Armitage et al., 2020b; Armitage et al., 2021b; Guo et al., 2017). Another approach is to document plant composition in undisturbed areas with and without mangrove cover in a natural setting (a "natural experiment") (Armitage et al., 2021a). Another approach is to document changes to marsh plants and mangroves caused by disturbances from natural disasters (Ferwerda et al., 2007; Osland et al., 2020b) or anthropogenic impacts (Bernardino et al., 2018; Bulmer et al., 2015; Granek et al., 2008). The outcome of these approaches might differ if areas without mangroves—or suffering mangrove loss—had pre-existing differences from areas where mangroves occurred (or persisted), present heterogeneously across a landscape.

The outcome of studies on interactions between mangroves and salt marsh plants is also likely to vary depending on which marsh plant species are examined. Different marsh plant species vary in how well they can tolerate low light, reduced nutrients, and abiotic stressors, differences that underlie patterns of plant zonation (Engels et al., 2010; Pennings et al., 1992), but also should affect vulnerability to competition.

Finally, different types of approaches to understanding interspecific plant interactions are often carried out at different spatial scales. As a result, different outcomes could be a function of spatial scale rather than study approach per se. For example, competition is likely to occur as a local response to resource depletion, but responses to species loss at the landscape scale also are a function of propagule pressure—a species cannot increase locally, even if conditions are favorable, if it is rare on the landscape. Therefore, examining the role of spatial scale is fundamental to understanding why different approaches yield different results.

We worked on the Texas coast, where a number of areas have alternated between marsh and mangrove dominance over the last decades (Montagna et al., 2011). For example, during a recent period of mangrove expansion on the central Texas coast from 1990 to 2010, mangrove cover increased by 74% (Armitage et al., 2015). At the landscape scale at the time of this study, there were some areas dominated by mangroves and other areas where mangroves had not invaded and that were dominated by marsh plants. The areas dominated by mangroves sometimes had marsh plants coexisting in patches or as understory vegetation, whereas the areas dominated by marsh plants often lacked mangrove shrubs (Armitage et al., 2021a).

We used four different methods (a natural experiment, a plot survey in a manipulative experiment, a transect survey in a manipulative experiment, and a transplant experiment in a manipulative experiment) to compare competitive effects of adult mangroves on three species of salt marsh plants. The manipulative experiment also allowed us to examine these interactions at three different spatial scales. We tested three hypotheses. First, we hypothesized that competitive interactions in natural conditions would be weaker than in experimental conditions, because the pre-existing communities among the two landscapes we studied were different. Second, we hypothesized that different marsh plant species would respond differently to mangrove competition, because different marsh species vary in their ability to tolerate abiotic stress, low light, and low nutrients. Third, we hypothesized that the measured effect of competition would be a function of spatial scale, because some methods (e.g., a transplant experiment) bypass the dispersal stage, whereas others (e.g., a mangrove removal) require marsh plants to disperse into areas where mangroves are cleared.

II. Methods

We compared a natural experiment and a manipulative experiment on the central Texas coast of the Gulf of Mexico in Port Aransas, Texas. The manipulative experiment was located within the Mission-Aransas National Estuarine Research Reserve, and most of the natural experiment sites were located within the Mission-Aransas estuary (Appendix: Figure A.1). Water column salinity values at the site of the manipulative experiment were measured every 10 minutes from March to June 2015, average 19.5 PSU ± 0.02 and varied between 12 and 33 PSU (Pennings, unpublished data). Near Port Aransas, coastal wetlands were dominated by either the tropical black mangrove, *Avicennia germinans,* or by a mixture of three common salt marsh plant species, *Spartina alterniflora, Batis maritima,* and *Sarcocornia* spp. (these species will be referred to by genus hereafter). Other plant species present in low abundance at the sites included: *Borrichia frutescens*, *Distichlis spicata*, *Iva frutescens*, *Lycium carolinianum*, *Monanthochloe littoralis*, *Salicornia bigelovii*, *Schoenoplectus robustus*, *Sesuvium portulacastrum*, *Spartina patens*, *Strophostyles helvola,* and *Suaeda linearis*.

We utilized four study approaches to compare the competitive interactions occurring between mangroves and the three common marsh species. The first approach was a natural experiment, consisting of five sites dominated by marsh vegetation (named "marsh" hereafter) and five dominated by mangroves (named "mangrove" hereafter) (Appendix: Figure A.2). The vegetation at these sites established naturally and was not actively planted or managed. Because of the pattern of mangrove colonization of the Texas coast, it was not possible to physically intersperse the sites representing different treatments. At each site (<20 ha), we characterized the plant community in 2015 by estimating percent over of each species in 7-14 quadrats situated along a transect deployed perpendicular to the shoreline. We estimated percent cover for each plant species that was present at the sites independently, regardless of vertical overlap. Therefore, total cover of the plot could exceed 100 percent. In addition to foliar cover of each species, we also estimated percent cover of mangrove pneumatophores (aerial roots). Data are available online (Armitage et al., 2021b).

The manipulative experiment was located on Harbor Island, Port Aransas, Texas, USA (27.86° N 97.08° W). Prior to the initiation of the experiment in 2012, the area was dominated by *Avicennia*, with ~10% cover of salt marsh plants (Guo et al., 2017). Ten plots, each 24 m (parallel to the Lydia Ann Channel) x 42 m (perpendicular to the channel), were demarcated and mangroves were removed within each plot to yield one of ten cover classes of mangroves from 0% to 100% in increments of 11 percent (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%) (Appendix: Figure A.3). This manipulation mimicked mangrove dieback following a hard freeze. We divided each large plot into 3x3 m cells that either had aboveground mangrove biomass removed or left intact. The number of cells that were removed created the appropriate plot-level mangrove cover value (e.g., 0% mangrove cover reflects all cells within the plot removed, 55% mangrove cover reflects about half the cells within the plot removed). This design required salt marsh vegetation to naturally colonize the areas where mangroves were removed. The clearing was completed in a stratified random checkerboard pattern, and manipulated cells were maintained every 3-4 months for the first year and annually thereafter. Within these plots, we estimated the effects of mangroves on marsh plants using three different approaches.

The first approach in the manipulation experiment was a “plot survey” conducted in 2019. We estimated vegetation cover within 3x3 m cells containing mangroves (named “mangrove” hereafter) and cells in which mangroves had been removed (named “marsh” hereafter). Plots were categorized as fringe (the front 12 m of the plot closest to the water) and interior (back 30 m of the plot) zones. There were six replicates of each treatment within each plot (except for the 0 and 100 percent mangrove cover plots, for which only one treatment type was present), for a total of 24 cells (two vegetation treatments x two zones x six replicates) per plot. Data are available online (Pennings, 2021b).

The second approach was a “transect survey” conducted in 2019. We deployed two transects that ran from the back of each plot to the front, with 14 contiguous cells per transect. We recorded percent cover of each species in each cell as described above; data are available online (Armitage et al., 2020a). This method differed from the “plot survey” because it sampled vegetation at the very front of the plots at the water’s edge, in the middle of the plots, and at the very back of the plots, whereas the plot survey stratified sampling within just two zones; fringe and interior.

The third approach was a “transplant experiment”. We transplanted the three most common marsh plants, *Spartina, Batis,* and *Sarcocornia*, as small clones with small (~10 x 10 x 10 cm) root balls, into each plot in March 2013 and harvested them in November 2013. The three species were planted together in individual marsh and mangrove cells, with four replicates of each treatment per plot spread across the fringe and interior (2 replicates in the fringe zone and 2 replicates in the interior zone). The marsh plants were not transplanted into the larger plots with 100% overall mangrove cover or 0% overall mangrove cover, because these plots did not allow a comparison between marsh and mangrove vegetation types. The 3x3 m cells were large enough that the canopies of the three transplanted species did not overlap at the end of the growing season. Thus, it is unlikely that the transplants were interacting with one another. At the end of the growing season in November 2013, the aboveground biomass of the transplants was harvested and dried to a constant mass. Data are available online (Pennings, 2021a).

We used several statistical methods to analyze the competitive interactions of mangroves on the three target marsh species. To test the first hypothesis that competitive interactions in natural conditions would be weaker than in experimental conditions, we first compared species cover (or mass for the transplant experiment) between treatment types (marsh versus mangrove) using two-sample t-tests. To evaluate the effect of the treatments on mangrove cover, we also compared mangrove cover and pneumatophore cover between treatment types. For the t-tests, the unit of replication was the 7-14 quadrats per site in the natural survey (natural experiment), for a total of 64 mangrove quadrats and 52 marsh quadrats. In the plot survey (manipulation experiment) the unit of replication was the 3x3 m cells from each plot, for a total of 102 mangrove cells and 105 marsh cells. The unit of replication in the transect survey (manipulation experiment) was three contiguous 1 m measurements taken within each cell in the 42 m long transects in each plot, totaling 406 mangrove measurements and 397 marsh measurements. The unit of replication in the transplant experiment (manipulation experiment) was the 3x3 m cells from each plot, totaling 32 mangrove cells and 32 marsh cells.

Second, to convert abundance measures into a standard index of competition, we calculated the relative interaction intensity (RII) based on the cover (or mass) of each species of salt marsh plant in areas that represented mangrove and areas that represented marsh. We used the formula RII = $(C_{+M} - C_{-M}) / (C_{+M} + C_{-M})$, where C_{+M} is the cover/mass of salt marsh plants in the mangrove treatments (+), and C_{-M} is the cover/mass of salt marsh plants in the marsh treatments (-). RII values can range from -1 to 1, with negative RII values indicating competition and positive values indicating facilitation. To calculate the RII in the natural experiment, we haphazardly paired marsh versus mangrove sites, to give a sample size of 5 per species. To calculate the RII in the manipulation experiment, we paired the average of the marsh treatment cells with the average of the mangrove treatment cells within each of the eight experimental plots that had both types of cells (thus, excluding 0% overall mangrove cover and 100% overall mangrove cover), to give a sample size of 8 per species.

Third, we performed a nonmetric multidimensional scaling (NMDS) ordination as a representation of dissimilarities among plant communities, using species-specific plant cover as the response metric, based on the Bray-Curtis similarity matrix. Specifically, we compared plant communities in the natural survey, plot survey and transect survey across the marsh treatment and mangrove treatment, and in a separate analysis compared plant communities in the marsh and mangrove treatments across the natural survey, plot survey and transect survey. Because the transplant experiment measured biomass instead of percent species cover, it was omitted from the NMDS analysis.

To test the second hypothesis that different marsh plant species would respond differently to mangrove competition, we evaluated the two-sample t-tests and RII values calculated above. We compared RII values among the three plant species using ANOVA.

To test the third hypothesis that the measured effect of competition would be a function of spatial scale, we first used a two-way analysis of variance (ANOVA) for the plot survey, transect survey, and transplant experiment to compare the effects of treatment type (marsh or mangrove) and zone (fringe or interior) on the species cover or biomass. Second, we used analysis of covariance (ANCOVA) to examine the effect spatial scale, in terms of surrounding competitors, on the competitive interactions. We ran three ANCOVA analyses for each response variable (plant cover or biomass). In each case, the treatment type (marsh or mangrove) in the 3x3 m cell under consideration was the fixed factor, and the covariates were, in turn, 1) the number of mangrove cells in the eight 3x3 m cells immediately surrounding the cell under consideration, 2) the number of mangrove cells in the twenty-four 3x3 m cells directly surrounding the cell under consideration, and 3) the number of mangrove cells in the entire 24x42 m plot (Appendix: Figure A.4). The effects of spatial scale were not analyzed at the natural vegetation sites because the sampling design did not include measures of the vegetation surrounding each sampled plot. All statistical analyses were completed in R 4.0.3.

III. Results

Both the natural experiment and manipulation experiment effectively created distinct treatments with either marsh or mangrove dominance. Mangroves and pneumatophores were absent from plots in the marsh sites in the natural experiment (Figure 1ab), whereas mangroves were present at ~45% cover and pneumatophores at ~48% cover at the mangrove sites.

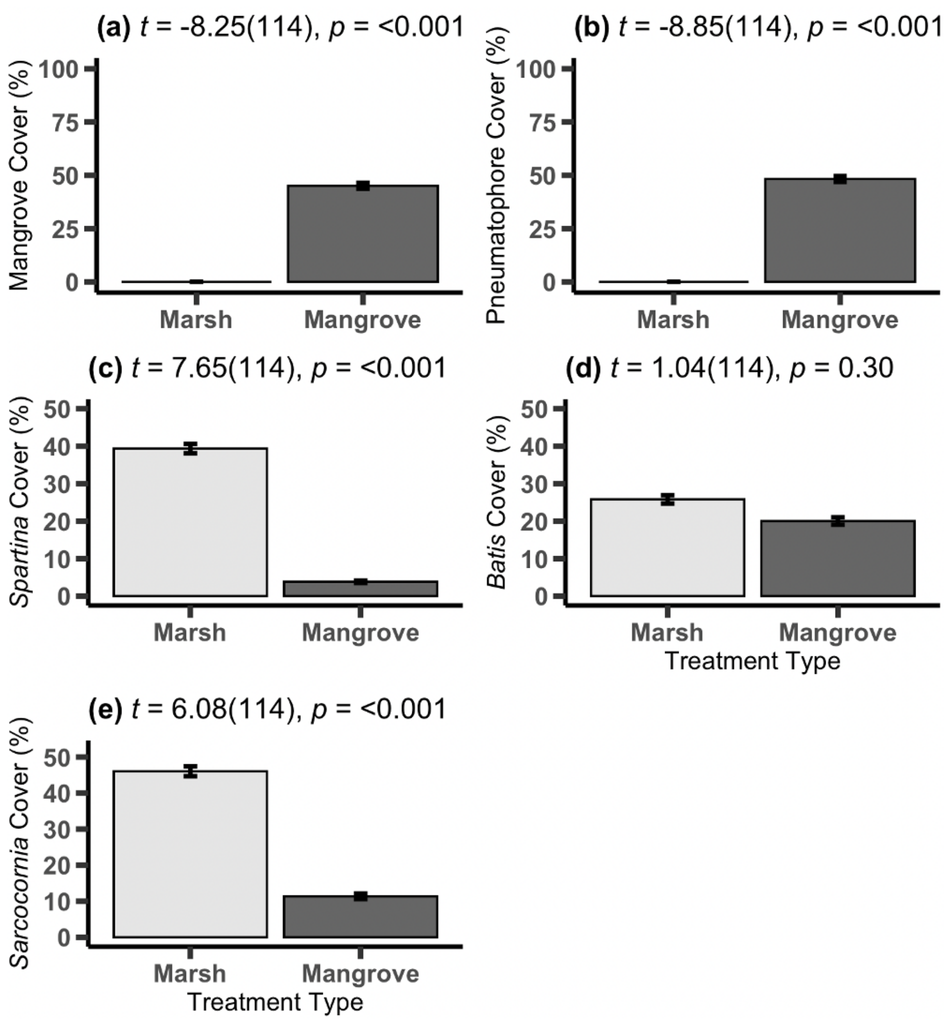


Figure 1. Plant Cover in the Natural Survey.
Effect of treatment type (i.e., marsh = marsh-dominated sites, mangrove = mangrove-dominated sites) on percent species cover of mangroves and the three most common marsh plant species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

In the plot survey within the manipulation experiment, mangrove cover and pneumatophore cover were high (>95%) in mangrove cells (Figure 2ab), but low (~1%) for mangroves and moderate (~45%) for pneumatophores in marsh cells.

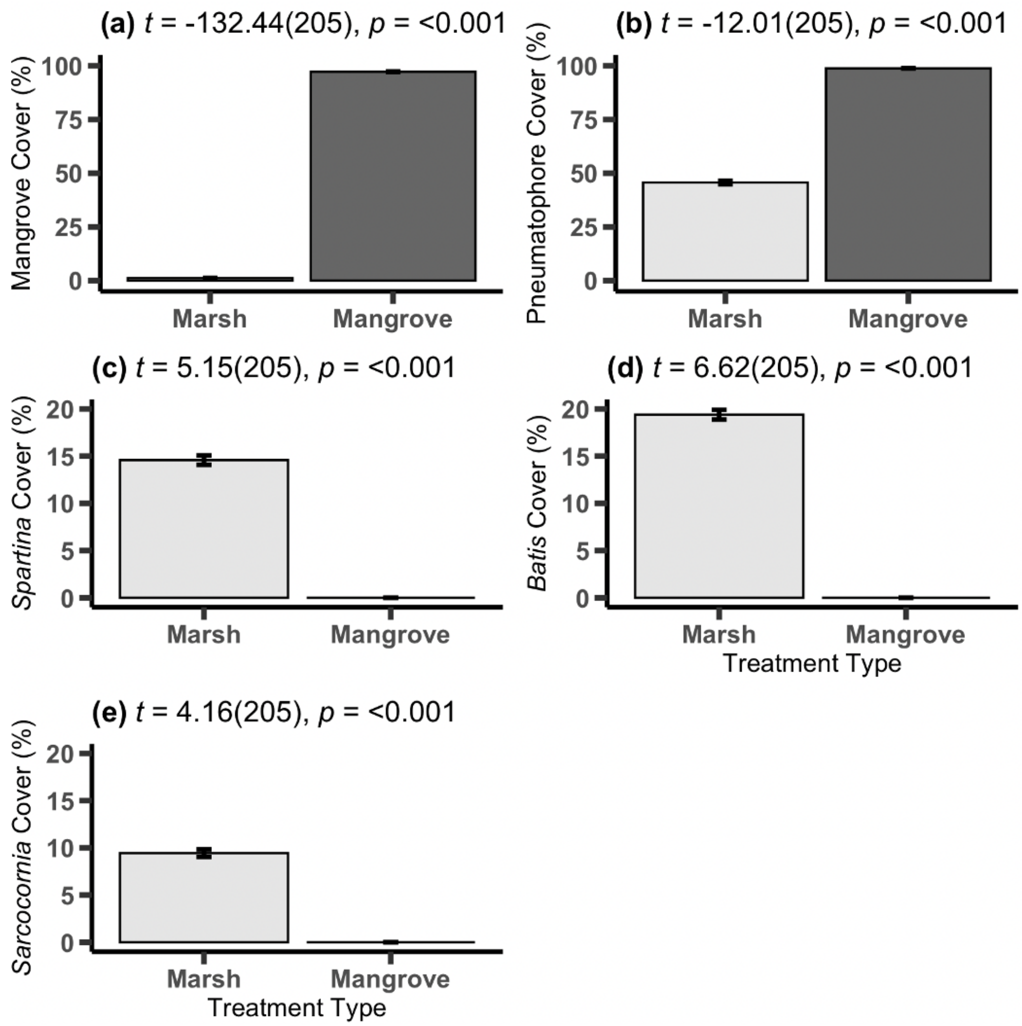


Figure 2. Plant Cover in the Plot Survey.
Effect of treatment type (i.e., marsh = mangrove removed cells, mangrove = mangrove intact cells) on percent species cover of mangroves and the three most common marsh plant species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

In the transect survey within the manipulation experiment, mangrove cover and pneumatophore cover were moderate to high (~30-75%) in mangrove cells but moderate to low (~8-13%) in marsh cells (Figure 3ab).

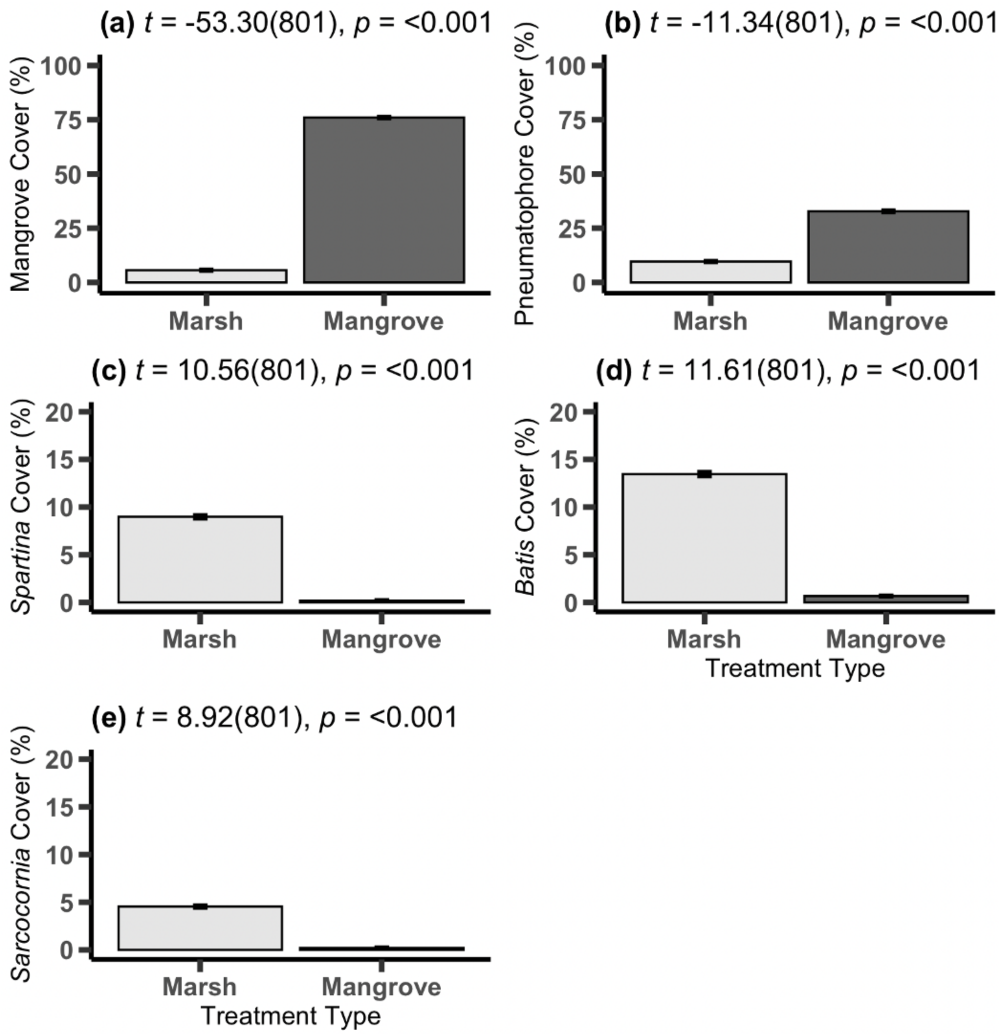


Figure 3. Plant Cover in the Transect Survey.
Effect of treatment type (i.e., marsh = mangrove removed cells, mangrove = mangrove intact cells) on percent species cover of mangroves and the three most common marsh species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

In most cases, marsh plant cover was greater in the marsh treatment than in the mangrove treatment in both experiment types. In the natural experiment, *Spartina* and *Sarcocornia* were abundant (~40-45% cover) in the marsh sites, but rare (~5-10% cover) in the mangrove sites (Figure 1ce). *Batis* did not differ in cover (~20-25%) between the marsh and mangrove sites (Figure 1d). In the plot survey within the manipulation experiment, the three marsh plants were present at moderate cover values (~10-20%) in marsh cells, but absent in mangrove cells (Figure 2c-e). In the transect survey within the manipulation experiment, the three marsh plants were present at moderate cover values (~5-15%) in marsh cells, but almost absent in mangrove cells (Figure 3c-e). Lastly, in the transplant experiment within the manipulation experiment, all three marsh plants grew several times better when planted in marsh cells (by ~3-6 times) than in the mangrove cells (Figure 4).

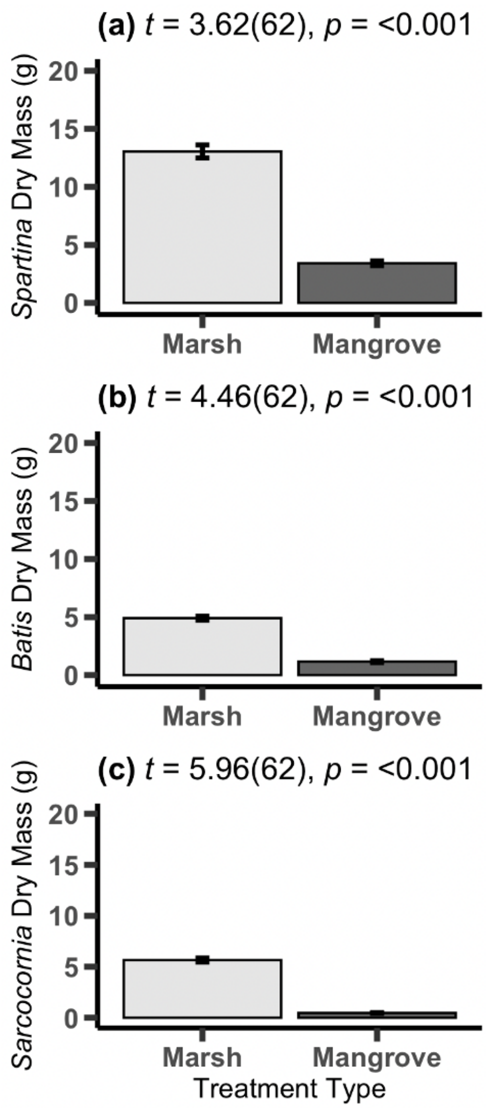


Figure 4. Plant Cover in the Transplant Experiment.
Effect of treatment type (i.e., marsh = mangrove removed cells, mangrove = mangrove intact cells) on harvested aboveground biomass (grams) of the three transplanted marsh species. Error bars indicate standard error of the mean, and *t*-value(df) and *p*-value represent results from a two-sample unpaired t-test.

The NMDS ordination looking at differences between treatment types was consistent with hypothesis one (Figure 5).

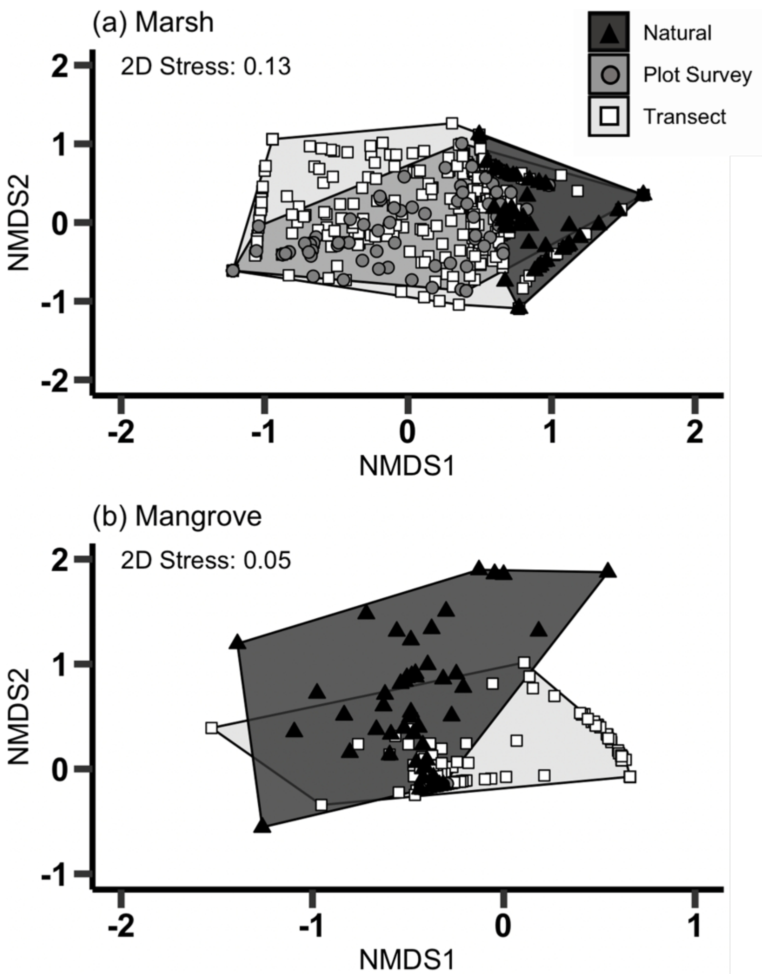
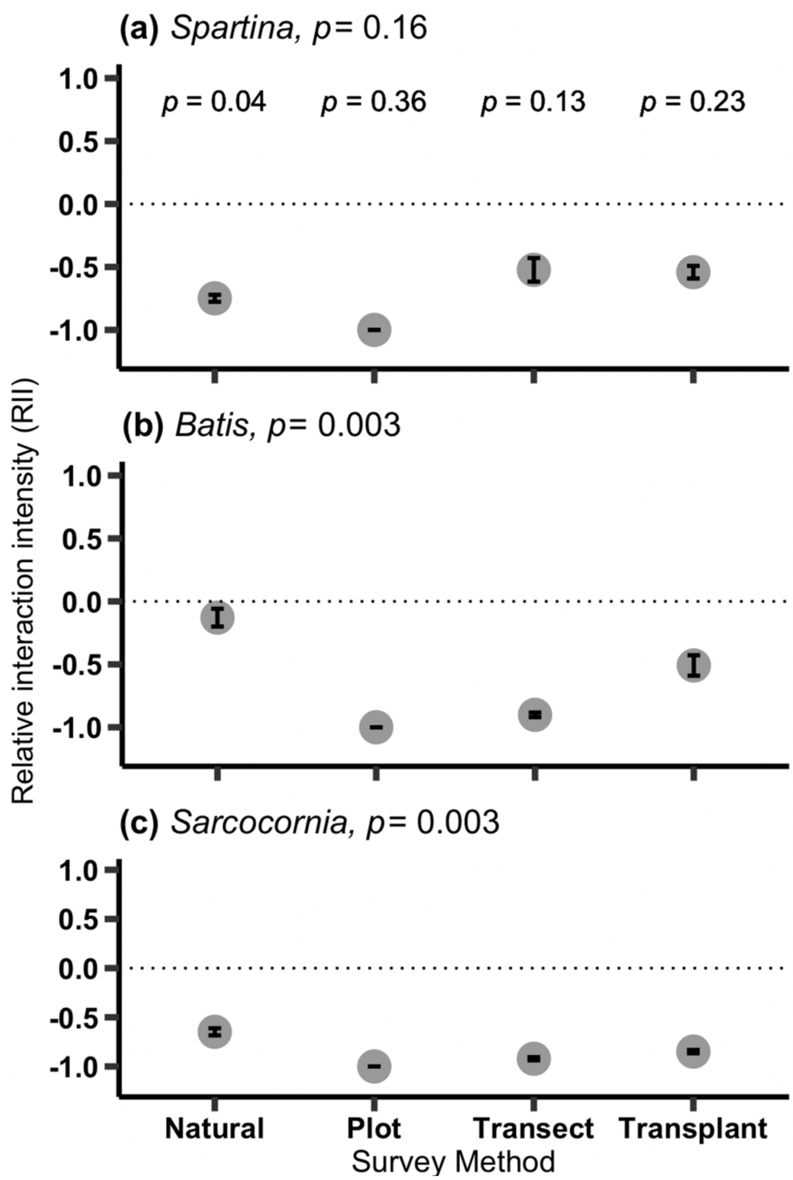


Figure 5. NMDS Compared Between Treatments.
Composition of communities within the natural survey (dark-shaded polygon with black triangles), plot survey (medium-shaded polygon with grey circles), and transect survey (light-shaded polygon with white squares) compared between treatments (marsh and mangrove). The "plot survey" markers are tightly clustered and do not appear well in panel (b). The nonmetric multidimensional scaling (NMDS) ordination is a representation of dissimilarities among treatments based on the Bray-Curtis similarity matrix, square root transformed. 2D stress values are shown.

The composition of the plant communities differed between sampling methods for both the marsh and the mangrove treatments (Appendix: Table A.1, PERMANOVA: marsh, p=0.001; mangrove, p=0.001). Within-treatment variation (dispersion) of the samples also varied for each treatment type (PERMDISP: marsh, p=0.001; mangrove, p=0.001), with more within-group variation in the transect method than the other two methods.

Comparisons of the RII across methods (Figure 6) supported the first hypothesis that the intensity of competition would vary between methods for *Batis* and *Sarcocornia*.

Figure 6. Relative Interaction Intensity Between Species and Methods.
Comparisons of the relative interaction intensity (RII) for each of the three common marsh species across the four study approaches. Negative values represent competition with mangroves whereas positive values represent facilitation by mangroves. Error bars indicate standard error of the mean. The p-values in the title of each panel represent a comparison of methods within each species using ANOVA to test the first hypothesis, that the natural experiment would show less extreme competitive interactions than the methods conducted at the manipulation experiment; the p-values within the first panel in each method's column represent comparisons of species within each method using ANOVA to test the second hypothesis, that the three marsh species would respond differently to mangrove competition. Complete ANOVA tables are provided in the supplementary materials (Appendix: Table A.4).



Batis and *Sarcocornia* performed differently across methods (*Batis*, *p*=0.003; *Sarcocornia*, *p*=0.003), with RII values more negative (indicating stronger competition) in the approaches within the manipulation experiment than in the natural experiment (Appendix: Table A.2). *Spartina* performed similarly across each of the survey methods (*p*=0.16).

NMDS analysis also indicated that the composition of the plant communities differed between marsh and mangrove dominance, regardless of sampling method (Appendix: Figure A.5, Table A.1, PERMANOVA: natural vegetation survey, p=0.001; plot survey, p=0.001; transect survey, p=0.001). Within-treatment variation among samples did not differ for the natural survey (PERMDISP, p=0.60) but did for the plot survey (p=0.001) and transect survey (p=0.001), due to very little variation in species cover within the treatments.

Comparisons of the RII across species (Figure 6) supported the second hypothesis, that the intensity of competition would vary among species in the natural experiment. *Spartina* and *Sarcocornia* both had moderately strong negative RII values (-0.75 and -0.65), indicating strong competitive interactions with mangroves. In contrast, *Batis* had almost neutral (-0.13) RII values, indicating the absence of strong interactions. In the plot survey at the manipulation experiment, all three marsh plants had highly negative RII values indicating very strong competitive interactions with mangroves, with no statistically significant differences between their responses (p=0.36). In the transect survey at the manipulation experiment, *Batis* and *Sarcocornia* had highly negative RII values indicating very strong competitive interactions with mangroves. *Spartina* had less extreme RII values (~-0.50), but this difference was not statistically significant (p=0.13). Similarly, the RII values for the three species were not significantly different in the transplant experiment (p=0.23). Tukey post-hoc comparisons located in Appendix: Table A.2.

The ANOVA and ANCOVA analyses supported hypothesis three, that the measured effect of competition would be a function of spatial scale in the plot survey and transect survey

(Appendix: Table A.3; Table A.4). In the plot survey, the two-way ANOVA analyzing the effects of treatment type (marsh or mangrove) and zone (fringe or interior) were consistent with the t-tests, indicating that treatment type had a significant influence on all species (p<0.0001), and also revealed that mangroves and pneumatophores were affected by zone within the plot (mangrove cover slightly greater in the fringe, and pneumatophore cover higher in the interior) (Pennings, 2021b). Marsh plant cover was not affected by zone. Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found that the covariates were significant in each case except for *Sarcocornia* (Appendix: Table A.3). For *Spartina* and *Batis*, percent cover in the marsh treatment was greater in plots with low overall mangrove cover (Appendix: Figure A.6). In the case of *Sarcocornia*, none of the covariates were significant (Appendix: Table A.3).

Similar results were obtained in the transect survey (Appendix: Table A.4). The ANOVA results were again consistent with the t-tests, indicating that vegetation type had a significant influence on all species (p<0.0001), and also revealed that zone had a significant influence on all species except *Sarcocornia* (p=0.23). Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found that the covariates were significant for each plant variable, with marsh plant cover higher in plots with low overall mangrove cover (Appendix: Figure A.7, Table A.4).

For the transplant experiment, the ANOVA results were again consistent with the t-tests, indicating that treatment type had a significant influence on all transplanted marsh species (Appendix: Table A.5). Plot zone did not affect the outcome for any of the plant species.

Separate ANCOVA analyses with covariates representing mangrove cover at three larger spatial scales found no effects of any covariate in the transplant experiment (Appendix: Figure A.8, Table A.5).

IV. Discussion

As expected, mangroves can strongly suppress the cover and biomass of salt marsh plants. But our understanding of these interactions varied depending on the study method used, the plant species studied, and the spatial scale considered. Our results caution against uncritical acceptance of the results of manipulation experiments that may be affected by site-selection bias, and indicate that a combination of approaches is the best way to extrapolate results from the local scale to the landscape.

Our first hypothesis was that the strength of competition (RII) would be weaker in the natural experiment than in the manipulative experiment because the sites chosen for these experiments had different pre-existing communities. This hypothesis was supported for the two succulent species, *Batis* and *Sarcocornia*. In the natural experiment, mangroves did not achieve high cover in the mangrove sites, and cover of the succulents at the mangrove sites was relatively high. We did not investigate why mangroves did not achieve higher cover at these sites, but it is likely that some patches on the landscape were too saline for mangroves, but acceptable for the succulents which are highly salt-tolerant (Debez et al., 2010; Naidoo et al., 1990). In contrast, the sites chosen for the manipulative experiment had ~90% mangrove cover. Because of this high mangrove cover, there were few open patches that succulents could colonize, and mangroves had a much stronger competitive effect than in the natural experiment. There was no difference in relative interaction intensity across the different methods for *Spartina*, which cannot colonize highly saline soils but instead was often present in a narrow band at lower elevations than the mangroves in both the natural experiment and the manipulation experiment.

We chose our natural experiment study sites for convenient access, and we do not know whether they are representative of sites dominated by mangroves along the entire central Texas coast. When we set up the manipulative experiment, however, we did deliberately avoid areas with patchy mangrove cover in order to obtain a strong contrast between mangrove and marsh vegetation types. Consequently, the results of the manipulative experiment may be most relevant to areas with naturally high mangrove cover. To the extent that these areas are not representative of the Texas coast in general, this would be an example of “site-selection bias”, where scientists choose to study interactions in places where they suspect that those interactions will be strongest (Mentges et al., 2021). Site-selection bias is probably common among manipulative experiments, because it is natural to pick study sites where focal species are common. In contrast, site-selection bias is often less of an issue in natural experiments because of the greater spatial scale typical of natural experiments (Fournier et al., 2019). In our case, where both types of experiments were deployed in the same geographic region, we were able to characterize the range of competition between mangroves and salt marsh plants on the Texas coast. Specifically, when mangroves are common, they strongly suppress salt marsh plants; however, mangroves may be sparse enough at many sites that salt marsh plants are able to coexist with them on a landscape scale.

Our second hypothesis was that the three marsh species would respond differently to competition from mangroves. This hypothesis was supported, but only for the natural experiment, in which *Spartina* was strongly suppressed by mangroves, *Sarcocornia* moderately suppressed, and *Batis* not suppressed at all (Figure 6). As argued above, it is likely that *Batis* and to some extent *Sarcocornia* are able to coexist with mangroves across the landscape by occupying patches that are too saline for mangrove colonization. It is also likely that *Spartina* can coexist with mangroves by occupying areas lower in the intertidal that are too flooded for mangroves to colonize (Naidoo et al., 1992; Xiao et al., 2010; Zhang et al., 2012); however, this strip of lower intertidal is a small fraction of the total intertidal landscape, and was present in both the natural and manipulation experiment. If we are correct, as argued above, that the experimental approaches over-estimated the strength of competition for the succulents, our results suggest that mangroves compete more strongly with *Spartina*, by excluding it from most of the landscape, than with the succulents, which are able to persist throughout the landscape as understory and gap species. A general, although perhaps obvious, lesson from this comparison is that studies of a single species may not be representative of the community as a whole if the landscape consists of varying degrees of species dominance. To the extent possible, studies of mangrove encroachment—or the spread of any new species in any community—should examine effects on as many species in the community as possible in order to understand the range of competitive interactions.

Our third hypothesis was that spatial scale would influence our measures of competition between mangroves and marsh vegetation. We explored this in the manipulation experiment by testing three covariates in three separate analyses: number of mangrove cells surrounding the 3x3 m cell in question in the 24x42 m large plots, the number of mangrove cells in the twenty-four immediate surrounding cells, and the number of mangrove cells in the eight immediate surrounding cells. We did not run a single analysis with all three covariates because they were highly correlated with each other, given that each scale included the smaller one. For the plot survey and transect survey, the analysis revealed that each of the covariates was important for predicting cover of *Spartina* and *Batis*. In other words, for these two species, competition was not solely local at the 3x3 m cell, but rather it was a function of mangrove cover at larger spatial scales as well. Results for *Sarcocornia* cover were ambiguous, perhaps because it was the rarest of these three marsh plants at the site: the covariates were important in the transect survey but not in the plot survey. In contrast, biomass of the transplanted plants was unaffected by any of the covariates, indicating that competition in this case was solely local.

The most likely explanation for these different results is that the results of the plot survey and transect survey were affected both by colonization in the early dispersal life stage and competition for various resources in multiple life stages. Whereas results of the transplant experiment were affected only by competition for various resources in the later life stages, since the transplant methodology by definition ensured that local cells were colonized. Viewed this way, the difference between the methods is consistent with ecological theory. Interspecific plant interactions should be primarily local, because plants deplete resources and experience abiotic conditions at local scales (Kneitel et al., 2004). In contrast, plot-level spatial scales influence community composition primarily by affecting the initial compositional variation among communities and dispersal (Cadotte, 2006). In the case of our manipulation experiment, marsh plants needed to naturally colonize the mangrove removal cells in order to be counted in the plot and transect surveys. They were more successful in doing so in low mangrove cover plots (Appendix: Figure A.6; Figure A.7), likely because they spread clonally by ramets growing from adjacent marsh cells, or from propagules produced by plants in nearby marsh cells. Marsh cover was higher in plots with low mangrove cover, leading to a greater supply of potential colonists to other marsh cells. In contrast, once marsh plants were successfully established, as was ensured in the transplant experiment, competition was solely at the local scale. More generally, studies of competition that rely on removing one species and observing how another responds may commonly underestimate the strength of competition if the focal species is dispersal limited.

Mangroves are expanding in many areas as climate changes, with the result that intertidal vegetation changes dramatically from low-stature, marsh plants to taller, woody mangroves. This shift is ongoing in many areas along the northern US Gulf Coast (Gabler et al., 2017), specifically in areas across Texas (Comeaux et al., 2012), Louisiana (Osland et al., 2014a), western Florida (Osland et al., 2012), and also on the Atlantic coast in eastern Florida (Cavanaugh et al., 2014). Mangrove expansion is also occurring on the coast of China (Peng et al., 2018; Zhang et al., 2012), Peru, the Pacific Coast of Mexico, South Africa (Saintilan et al., 2014), and southeast Australia (Coleman et al., 2021). We show that our manipulative experiments can overstate the consequences of this resulting vegetation shift. The natural experiment showed that marsh plants that previously dominated the wetland may not be totally eradicated from sites colonized by mangroves, but instead may persist on the landscape at low densities. Although manipulative experiments are arguably the gold standard of community ecology, they can be misleading if they do not fully represent the range of variation in the habitat. Instead, the combination of natural and manipulative experiments offers a powerful way to examine the outcomes of competition, and extrapolate these to the landscape scale. Our results, however, were obtained from an area with relatively low-stature mangroves. In other geographic areas where mangroves attain greater heights, competitive suppression of salt marsh plants may be more complete. We recommend that future studies of interactions between mangroves and salt marsh plants in other locations use both natural and manipulative experimental approaches in order to gain a more nuanced understanding of the strength of these interactions.

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APPENDICES

A. Appendix Tables

Table A.1. NMDS statistical results

Method		*F*	R^2	*p*
PERMANOVA	Natural	69.04	0.39	**0.001**
	Plot	104.70	0.34	**0.001**
	Transect	389.86	0.34	**0.001**
PERMDISP	Natural	0.25		0.60
	Plot	379.20		**0.001**
	Transect	1602.00		**0.001**

Treatment		*F*	R^2	*p*
PERMANOVA	Marsh	29.10	0.10	**0.001**
	Mangrove	97.89	0.26	**0.001**
PERMDISP	Marsh	42.41		**0.001**
	Mangrove	234.75		**0.001**

Results from two resemblance-based permutation methods, PERMANOVA and PERMDISP, for both NMDS ordinations; comparing plant abundance across methods (natural survey, plot survey, and transect survey) in Figure 5, and comparing plant abundance across treatment types (marsh versus mangrove) in Appendix Figure A.5. The PERMANOVA detects the differences between groups (method or treatment) while the PERMDISP detects whether some groups (method or treatment) are more variable than others. Significant p-values <0.05 are shown in bold font.

Table A.2. Relative Interaction Intensity (RII) statistical results

ANOVA (1-way)		**df**	**Sum Sq**	**Mean Sq**	***F***	***p***
Spartina	Method	3	1.09	0.36	1.89	0.16
	Residuals	24	4.60	0.19		
Batis	Method	3	2.96	0.99	6.20	**0.003**
	Residuals	25	3.98	0.16		
Sarcocornia	Method	3	0.39	0.13	6.21	**0.003**
	Residuals	24	0.50	0.02		
Natural	Species	2	1.11	0.55	4.10	**0.04**
	Residuals	12	1.62	0.13		
Plot Survey	Species	2	<0.0001	<0.0001	1.08	0.36
	Residuals	19	<0.0001	<0.0001		
Transect	Species	2	0.81	0.40	2.30	0.13
	Residuals	21	3.68	0.18		
Transplant	Species	2	0.56	0.28	1.56	0.23
	Residuals	21	3.79	0.18		

ANOVA (2-way)		**df**	**Sum Sq**	**Mean Sq**	***F***	***p***
RII	Method	3	2.60	0.87	6.96	**0.0003**
	Species	2	0.67	0.33	2.69	0.07
	Method × Species	6	1.81	0.30	2.42	**0.03**
	Residuals	73	9.09	0.12		

Tukey HSD Post-hoc		**Groups**
Spartina	Natural	a
	Plot Survey	a
	Transect	a
	Transplant	a
Batis	Natural	a
	Plot Survey	b
	Transect	b
	Transplant	ab
Sarcocornia	Natural	a
	Plot Survey	b
	Transect	b
	Transplant	ab
Natural	*Spartina*	B
	Batis	A
	Sarcocornia	AB
Plot Survey	*Spartina*	A
	Batis	A
	Sarcocornia	A
Transect	*Spartina*	A
	Batis	A
	Sarcocornia	A
Transplant	*Spartina*	A
	Batis	A
	Sarcocornia	A

1) Results from one-way ANOVA analyzing the effects of survey method on the RII for each of the prominent marsh plants to test hypothesis one. Additionally, results from one-way ANOVA analyzing the effects of each of the three marsh species on the RII for each survey method to test hypothesis three. 2) Results from two-way ANOVA analyzing the effects of method, marsh species, and the interaction between method and marsh species on the RII. All significant p-values <0.05 are shown in bold font. 3) Results from a Tukey HSD post-hoc test to compare species across methods (hypothesis one) and methods across species (hypothesis three) are shown. The different lowercase letters indicate survey methods that are not different from one another for each species. The different uppercase letters represent species that are not different from one another within each study method.

Table A.3. ANOVA and ANCOVA results from the plot survey

ANOVA		**df**	**Sum Sq**	***F***	***p***
Mangroves	Treatment Type	1	476792	17932.75	**<0.0001**
	Zone	1	129	4.86	**0.03**
	Treatment Type × Zone	1	46	1.72	0.19
	Residuals	203	5397		
Pneumatophores	Treatment Type	1	145980	170.84	**<0.0001**
	Zone	1	18564	21.73	**<0.0001**
	Treatment Type × Zone	1	15471	18.11	**<0.0001**
	Residuals	203	173464		
Spartina	Treatment Type	1	11000	26.26	**<0.0001**
	Zone	1	16	0.04	0.84
	Treatment Type × Zone	1	17	0.04	0.84
	Residuals	203	85028		
Batis	Treatment Type	1	19453	43.42	**<0.0001**
	Zone	1	43	0.10	0.76
	Treatment Type × Zone	1	46	0.10	0.75
	Residuals	203	90947		
Sarcocornia	Treatment Type	1	4609	17.57	**<0.0001**
	Zone	1	640	2.44	0.12
	Treatment Type × Zone	1	678	2.59	0.11
	Residuals	203	53256		

ANCOVA		**df**	**Sum Sq**	***F***	***p***
Mangroves	*24×42 m*	9	1341	6.90	**<0.0001**
	Treatment Type	1	428005	19828.61	**<0.0001**
	Residuals	196	4231		
	Surrounding 24	24	1760	3.48	**<0.0001**
	Treatment Type	1	390098	18521.57	**<0.0001**
	Residuals	181	3812		
	Surrounding 8	8	1172	6.56	**<0.0001**
	Treatment Type	1	466248	20873.84	**<0.0001**
	Residuals	197	4400		
Pneumatophores	*24×42 m*	9	58560	8.56	**<0.0001**
	Treatment Type	1	94804	124.76	**<0.0001**
	Residuals	196	148939		
	Surrounding 24	24	57425	2.89	**<0.0001**
	Treatment Type	1	90051	108.61	**<0.0001**
	Residuals	181	150075		
	Surrounding 8	8	35948	5.16	**<0.0001**
	Treatment Type	1	136499	156.75	**<0.0001**
	Residuals	197	171552		
Spartina	*24×42 m*	9	24030	8.57	**<0.0001**
	Treatment Type	1	5384	17.29	**<0.0001**
	Residuals	196	61032		
	Surrounding 24	24	26118	3.34	**<0.0001**
	Treatment Type	1	4774	14.66	**<0.0001**
	Residuals	181	58943		

Table A.3. continued

	Surrounding 8	8	12840	4.38	**<0.0001**
	Treatment Type	1	10520	28.69	**<0.0001**
	Residuals	197	72222		
Batis	*24×42 m*	9	33019	12.39	**<0.0001**
	Treatment Type	1	7820	26.42	**<0.0001**
	Residuals	196	58018		
	Surrounding 24	24	28453	3.43	**<0.0001**
	Treatment Type	1	9634	27.86	**<0.0001**
	Residuals	181	62584		
	Surrounding 8	8	17992	6.07	**<0.0001**
	Treatment Type	1	16812	45.34	**<0.0001**
	Residuals	197	73045		
Sarcocornia	*24×42 m*	9	2588	1.08	0.38
	Treatment Type	1	4461	16.82	**<0.0001**
	Residuals	196	51986		
	Surrounding 24	24	8586	1.41	0.11
	Treatment Type	1	3507	13.81	**0.0003**
	Residuals	181	45988		
	Surrounding 8	8	2650	1.26	0.27
	Treatment Type	1	5132	19.47	**<0.0001**
	Residuals	197	51924		

Results from two-way ANOVA of treatment type (marsh or mangrove) and zone (fringe or interior) and their interaction on mangrove, pneumatophore, *Spartina*, *Batis*, and *Sarcocornia* cover. Additionally, results from separate ANCOVA analyses examine species cover in the 3x3 m marsh or mangrove cells (treatment type) as the fixed factor, with one of three covariates: 1) number of mangrove cells in the eight 3x3 m cells immediately surrounding the cell under consideration, 2) number of mangrove cells in the twenty-four 3x3 m cells immediately surrounding the cell under consideration, and 3) the number of mangrove cells in the entire 24x42 m plot. Significant p-values <0.05 are shown in bold font.

Table A.4. ANOVA and ANCOVA results from the transect survey

ANOVA		**df**	**Sum Sq**	***F***	***p***
Mangroves	Treatment Type	1	995171	2887.53	**<0.0001**
	Zone	1	2294	6.66	**0.01**
	Treatment Type × Zone	1	2913	8.45	**0.004**
	Residuals	799	275371		
Pneumatophores	Treatment Type	1	108210	130.88	**<0.0001**
	Zone	1	10996	13.3	**0.0003**
	Treatment Type × Zone	1	2117	2.56	0.11
	Residuals	799	660613		
Spartina	Treatment Type	1	15509	116.55	**<0.0001**
	Zone	1	2445	18.37	**<0.0001**
	Treatment Type × Zone	1	2589	19.45	**<0.0001**
	Residuals	799	106327		
Batis	Treatment Type	1	32865	141.98	**<0.0001**
	Zone	1	5444	23.52	**<0.0001**
	Treatment Type × Zone	1	4795	20.71	**<0.0001**
	Residuals	799	184953		
Sarcocornia	Treatment Type	1	3780	79.67	**<0.0001**
	Zone	1	69	1.45	0.23
	Treatment Type × Zone	1	69	1.46	0.23
	Residuals	799	37912		

ANCOVA		**df**	**Sum Sq**	***F***	***p***
Mangroves	*24×42 m*	9	25793	8.91	**<0.0001**
	Treatment Type	1	647177	2011.76	**<0.0001**
	Residuals	792	254784		
	Surrounding 24	24	33359	4.37	**<0.0001**
	Treatment Type	1	651078	2046.32	**<0.0001**
	Residuals	777	247218		
	Surrounding 8	8	17545	6.61	**<0.0001**
	Treatment Type	1	740948	2233.83	**<0.0001**
	Residuals	793	263033		
Pneumatophores	*24×42 m*	9	23080	3.12	**0.001**
	Treatment Type	1	47545	57.87	**<0.0001**
	Residuals	792	650646		
	Surrounding 24	24	67938	3.63	**<0.0001**
	Treatment Type	1	58181	74.62	**<0.0001**
	Residuals	777	605789		
	Surrounding 8	8	31311	4.83	**<0.0001**
	Treatment Type	1	72702	89.74	**<0.0001**
	Residuals	793	642416		
Spartina	*24×42 m*	9	33672	38.14	**<0.0001**
	Treatment Type	1	2067	21.07	**<0.0001**
	Residuals	792	77689		
	Surrounding 24	24	36212	15.60	**<0.0001**
	Treatment Type	1	2602	26.91	**<0.0001**
	Residuals	777	75149		

Table A.4. continued

	Surrounding 8	8	14829	15.23	**<0.0001**
	Treatment Type	1	2770	22.75	**<0.0001**
	Residuals	793	96532		
Batis	*24×42 m*	9	83242	65.43	**<0.0001**
	Treatment Type	1	3879	27.44	**<0.0001**
	Residuals	792	111950		
	Surrounding 24	24	79358	22.18	**<0.0001**
	Treatment Type	1	3890	26.09	**<0.0001**
	Residuals	777	115833		
	Surrounding 8	8	48964	33.19	**<0.0001**
	Treatment Type	1	6985	37.88	**<0.0001**
	Residuals	793	146227		
Sarcocornia	*24×42 m*	9	2408	5.94	**<0.0001**
	Treatment Type	1	1134	25.20	**<0.0001**
	Residuals	792	35642		
	Surrounding 24	24	7111.6	7.44	**<0.0001**
	Treatment Type	1	1241.5	31.18	**<0.0001**
	Residuals	777	30938.4		
	Surrounding 8	8	1706	4.65	**<0.0001**
	Treatment Type	1	1438	31.37	**<0.0001**
	Residuals	793	36344		

Results from two-way ANOVA of treatment type (marsh or mangrove) and zone (fringe or interior) and their interaction on mangrove, pneumatophore, *Spartina*, *Batis*, and *Sarcocornia* cover. Additionally, results from separate ANCOVA analyses examine species cover in the 3x3 m marsh or mangrove cells (treatment type) as the fixed factor, with one of three covariates: 1) number of mangrove cells in the eight 3x3 m cells immediately surrounding the cell under consideration, 2) number of mangrove cells in the twenty-four 3x3 m cells immediately surrounding the cell under consideration, and 3) the number of mangrove cells in the entire 24x42 m plot. Significant p-values <0.05 are shown in bold font.

Table A.5. ANOVA and ANCOVA results from the transplant experiment

ANOVA		**df**	**Sum Sq**	***F***	***p***
Spartina	Treatment Type	1	1483.6	12.75	**0.0007**
	Zone	1	10	0.09	0.77
	Treatment Type × Zone	1	7.2	0.06	0.80
	Residuals	60	6983.7		
Batis	Treatment Type	1	224.12	19.50	**<0.0001**
	Zone	1	3.94	0.34	0.56
	Treatment Type × Zone	1	5.98	0.52	0.47
	Residuals	60	689.58		
Sarcocornia	Treatment Type	1	429.99	34.42	**<0.0001**
	Zone	1	0.17	0.01	0.91
	Treatment Type × Zone	1	0.32	0.03	0.87
	Residuals	60	749.47		

ANCOVA		**df**	**Sum Sq**	***F***	***p***
Spartina	*24×42 m*	7	871.2	1.12	0.37
	Treatment Type	1	1483.6	13.31	**0.0006**
	Residuals	55	6129.6		
	Surrounding 24	22	3154.1	1.49	0.13
	Treatment Type	1	918.5	9.55	**0.004**
	Residuals	40	3846.7		
	Surrounding 8	8	896.8	0.99	0.45
	Treatment Type	1	1205.8	10.67	**0.002**
	Residuals	54	6140		
Batis	*24×42 m*	7	102.32	1.35	0.25
	Treatment Type	1	224.12	20.64	**<0.0001**
	Residuals	55	597.18		
	Surrounding 24	22	178.93	0.63	0.88
	Treatment Type	1	129.13	9.92	**0.003**
	Residuals	40	520.57		
	Surrounding 8	8	82.15	0.90	0.52
	Treatment Type	1	206.67	18.08	**<0.0001**
	Residuals	54	617.35		
Sarcocornia	*24×42 m*	7	108.23	1.33	0.26
	Treatment Type	1	429.99	36.85	**<0.0001**
	Residuals	55	641.72		
	Surrounding 24	22	201.29	0.67	0.84
	Treatment Type	1	211.8	15.44	**0.0003**
	Residuals	40	548.66		
	Surrounding 8	8	47.98	0.46	0.88
	Treatment Type	1	282.21	21.71	**<0.0001**
	Residuals	54	701.97		

Results from two-way ANOVA of treatment type (marsh or mangrove) and zone (fringe or interior) and their interaction on *Spartina*, *Batis*, and *Sarcocornia* dry aboveground biomass (g) at the end of the growing season. Additionally, results from separate ANCOVA analyses examine aboveground biomass in the 3x3 m marsh or mangrove cells (treatment type) as the fixed factor, with one of three covariates: 1) number of mangrove cells in the eight 3x3 m cells immediately surrounding the cell under consideration, 2) number of mangrove cells in the twenty-four 3x3 m cells immediately surrounding the cell under consideration, and 3) the number of mangrove cells in the entire 24x42 m plot. Significant p-values <0.05 are shown in bold font.

B. Appendix Figures

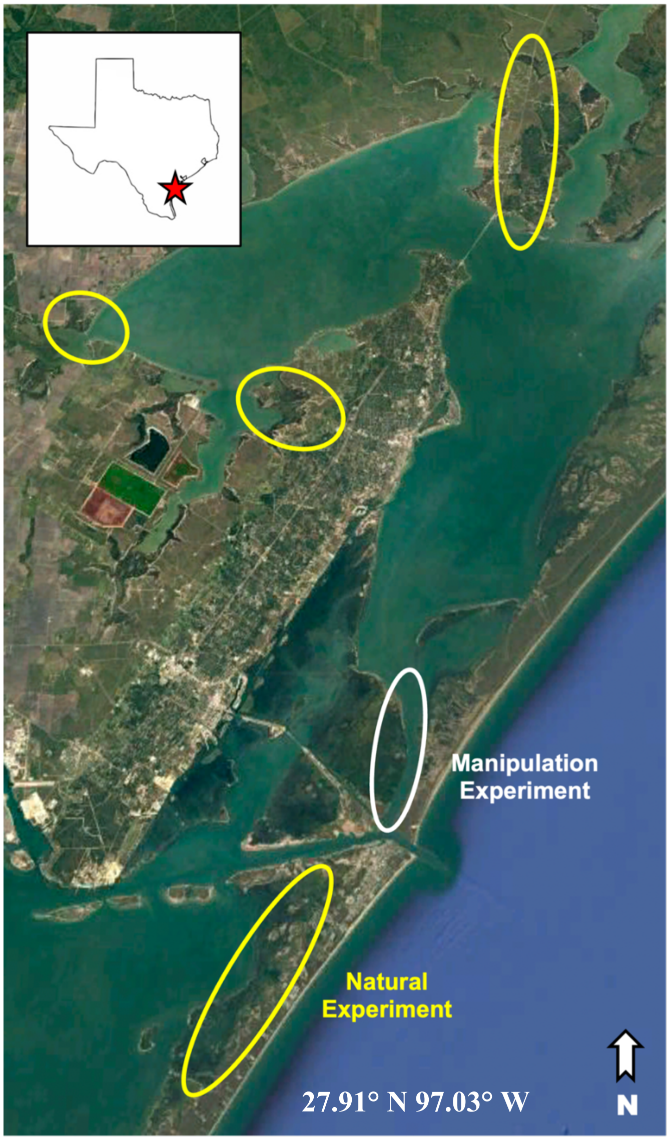

Figure A.1 Location of the natural experiment and manipulation experiment. Pictured are the locations for the ten survey sites in the natural experiment (outlined in yellow), and the ten experimental plots in the manipulation experiment (outlined in white). The manipulative experiment is located within the Mission-Aransas National Estuarine Research Reserve, and most of the natural experiment sites are located within the Mission-Aransas estuary. Both are along the central Texas coast of the Gulf of Mexico. Zoomed in locations of sites/plots are in figures below.

Figure A.2 Layout of the natural experiment.
Pictured are the ten sites; five sites dominated by marsh vegetation (white circles) and five dominated by mangroves (yellow circles).

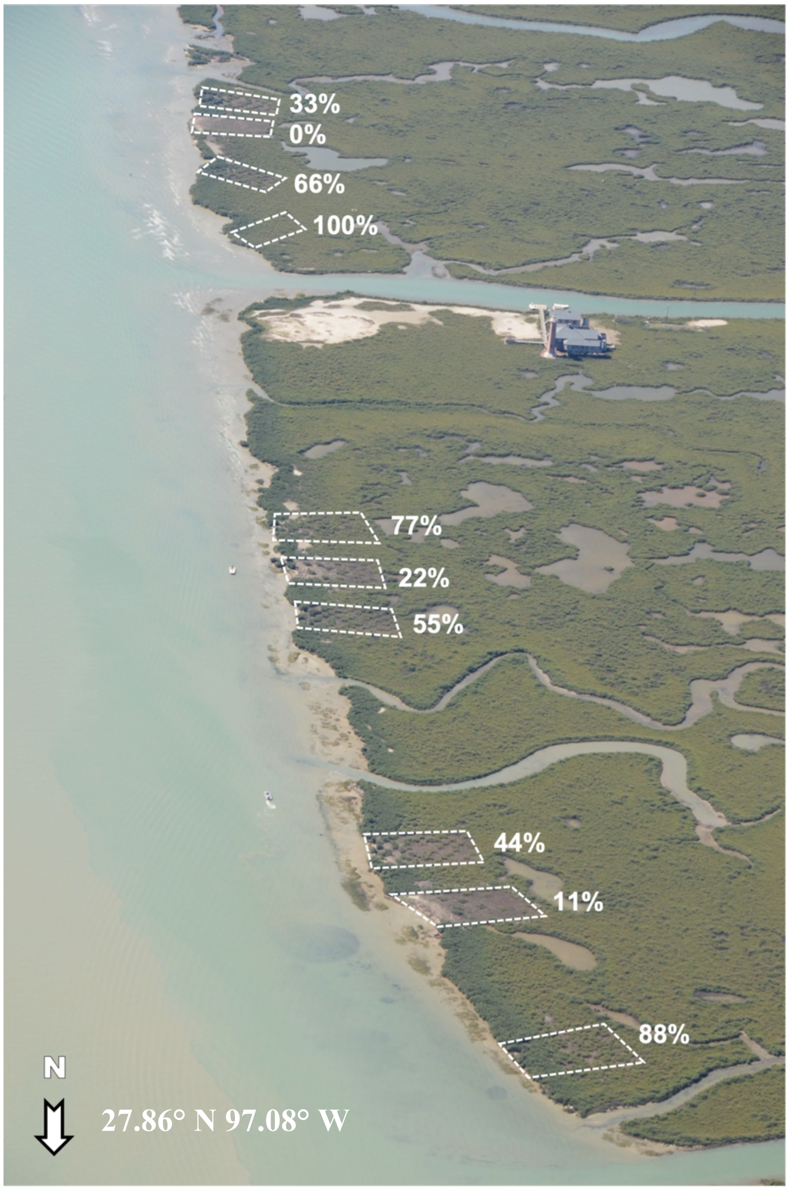

Figure A.3 Layout of the manipulation experiment.
Pictured are the ten plots, each 24 m (parallel to the Lydia Ann shipping channel) x 42 m (perpendicular to the shipping channel), that were demarcated and mangroves removed within each plot to cover classes from 0% to 100% in increments of 11 percent (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%). Plots are outlined in dotted-white, and percent overall coverage is marked next to the plots. Photo by Anna Armitage.

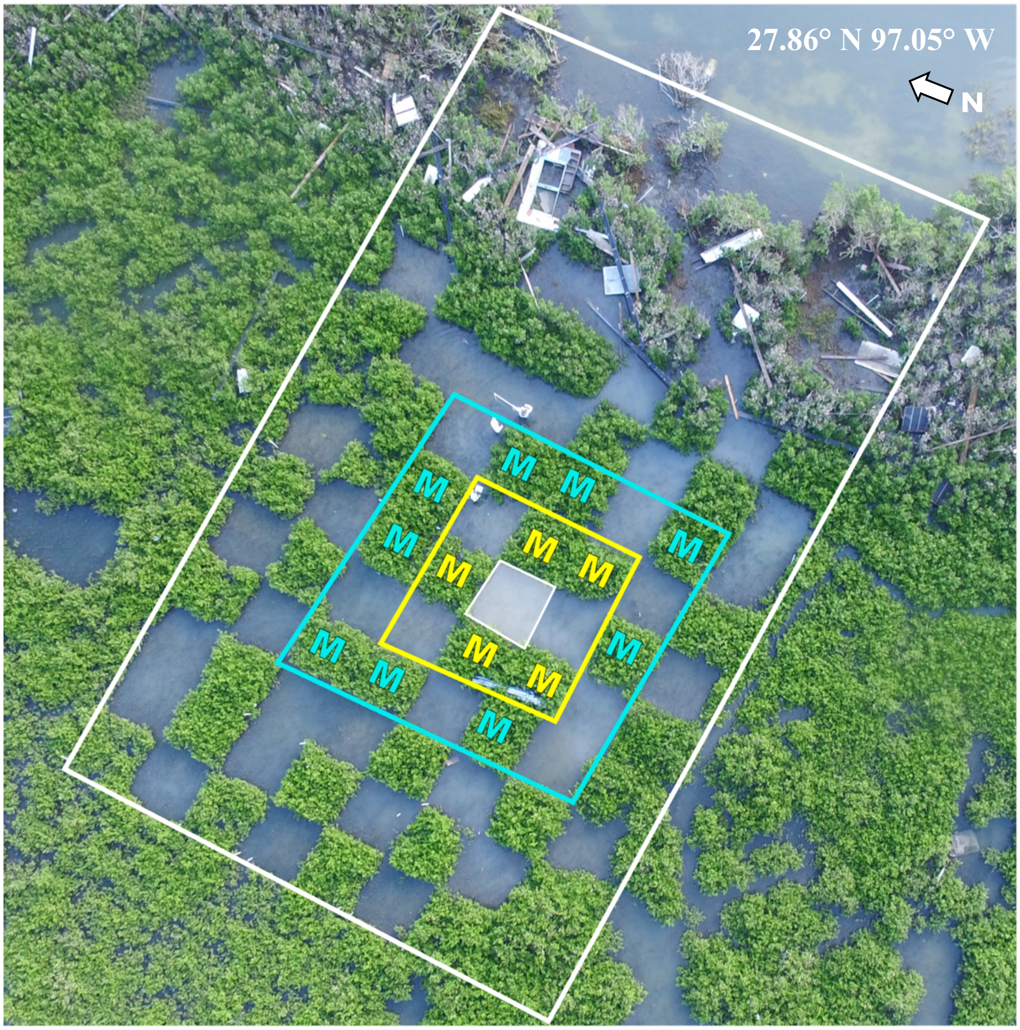

Figure A.4 Design of the ANCOVA analyses.
Pictured is a visual example of the layout of a plot (55%) to represent how the spatial factors were configured. The 3x3 m marsh or mangrove cells, in this case a marsh cell shaded in white, are the focal treatment type treated as a fixed factor. The three covariates were: 1) Number of mangrove cells in the eight 3x3 m cells immediately surrounding the cell under consideration; outlined in yellow (in this case there are 5), 2) Number of mangrove cells in the twenty-four 3x3 m cells immediately surrounding the cell under consideration; those outlined in blue plus those outlined in yellow (in this case there are 14) and 3) the number of mangrove cells in the entire 24x42 m plot; area outlined in white (in this case there are 62; exact locations not shown to avoid clutter). This image depicts one 3x3 m cell as an example, but the analysis was performed for each of the 3x3 m cells that were monitored using each survey method. The debris in and at the front of the plot is from the aftermath of Hurricane Harvey in 2017; photo taken shortly after. Photo by Rachel Glazner, permission granted from Anna Armitage.

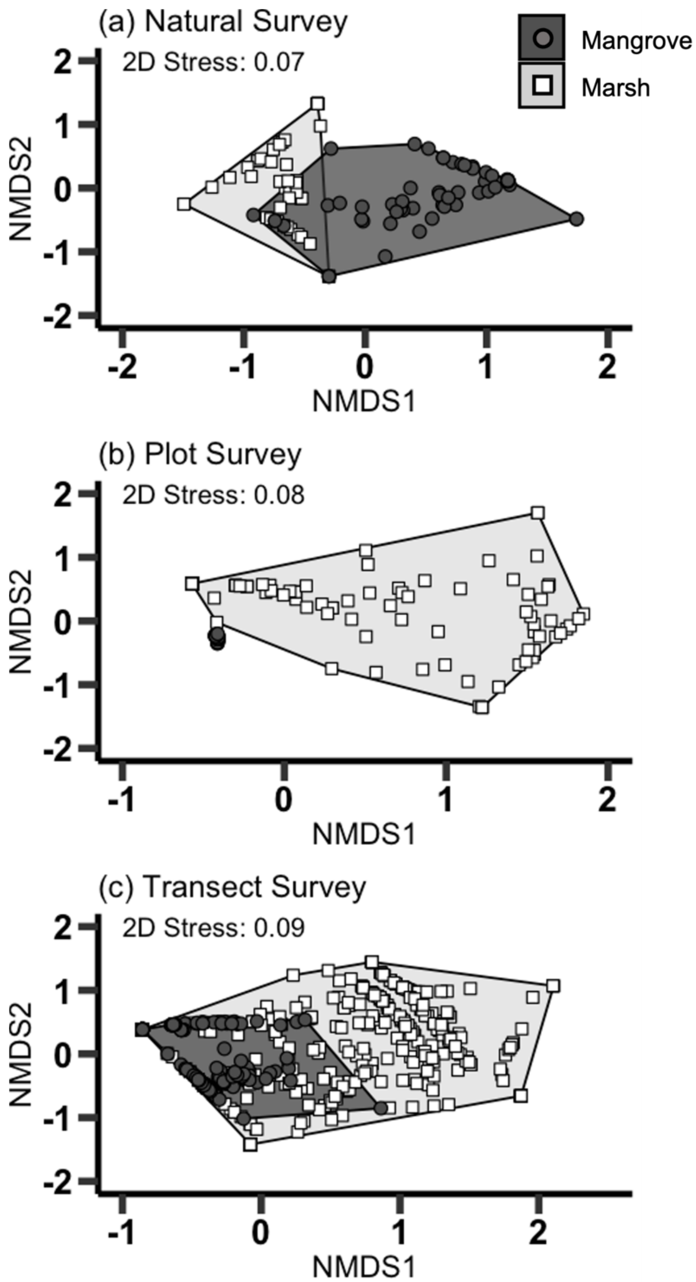

Figure A.5 NMDS comparing between treatment types for each sampling method. Multivariate composition of communities within marsh (light-shaded polygon with white squares) or mangrove (dark-shaded polygon with grey circles) treatments in a) the natural survey (natural experiment), b) plot survey (manipulative experiment), and c) transect survey (manipulative experiment). The nonmetric multidimensional scaling (NMDS) ordination is a representation of dissimilarities among treatments based on plant abundance using the Bray-Curtis similarity matrix, square root transformed. 2D stress values are shown.

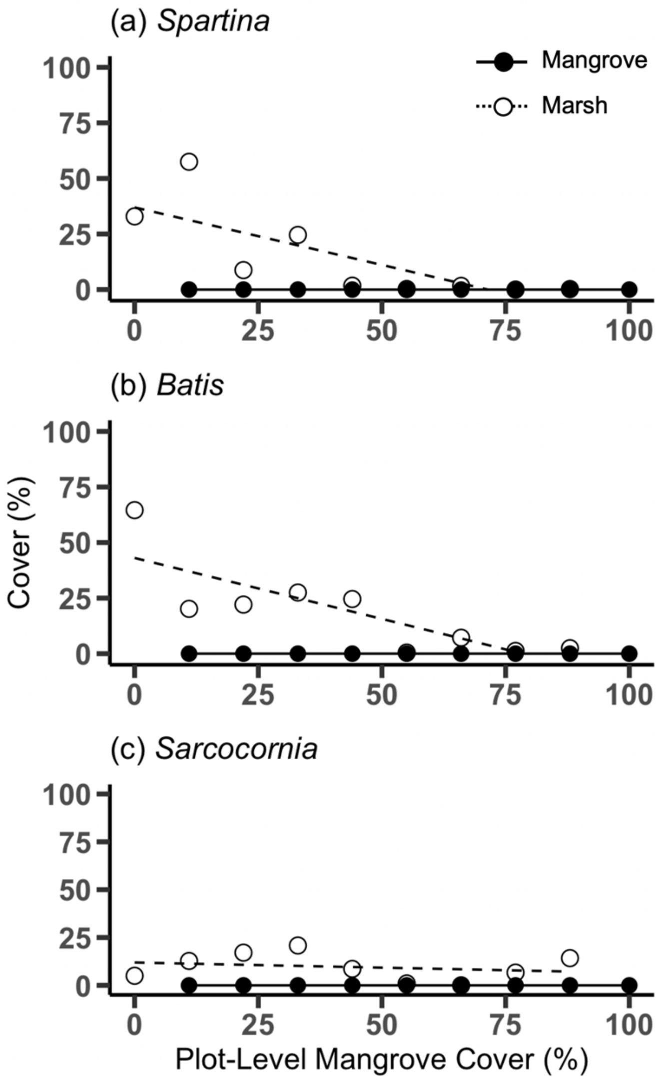

Figure A.6 Effect of plot-level mangrove cover on marsh plant cover in the plot survey. Effect of plot-level mangrove cover (0-100%) on percent species cover of *Spartina*, *Batis,* and *Sarcocornia*. Filled circles with solid lines represent average abundance at each plot-level mangrove cover within mangrove cells. Open circles with dotted lines represent average abundance at each plot-level mangrove cover within marsh cells.

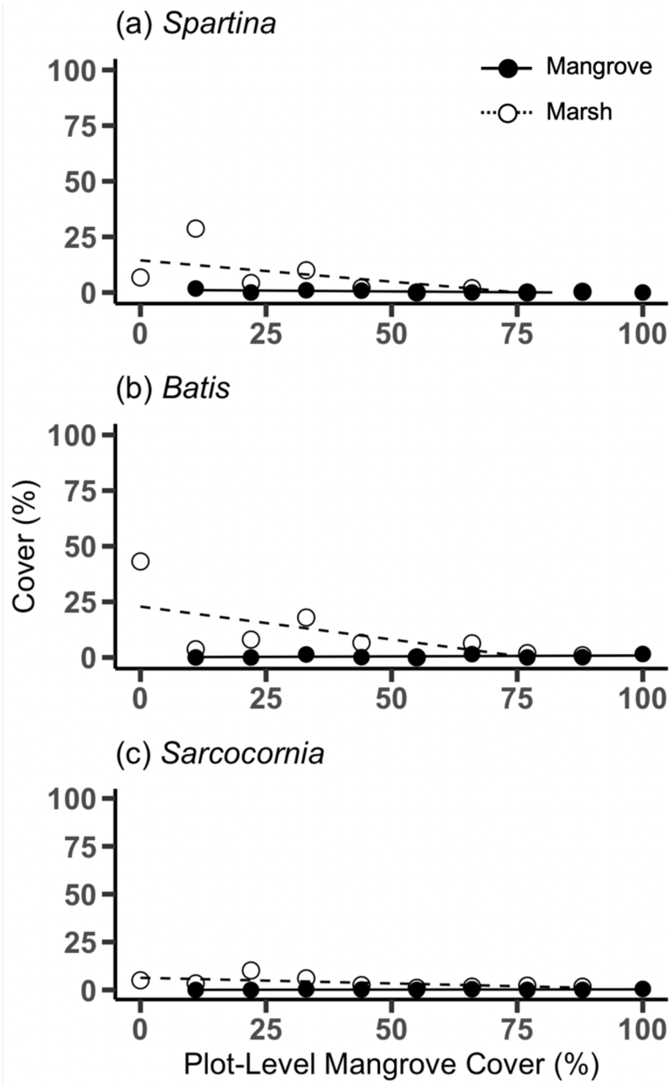

Figure A.7 Effect of plot-level mangrove cover on marsh plant cover in the transect survey. Effect of plot-level mangrove cover (0-100%) on percent species cover of *Spartina*, *Batis,* and *Sarcocornia*. Filled circles with solid lines represent average abundance at each plot-level mangrove cover within mangrove cells. Open circles with dotted lines represent average abundance at each plot-level mangrove cover within marsh cells.

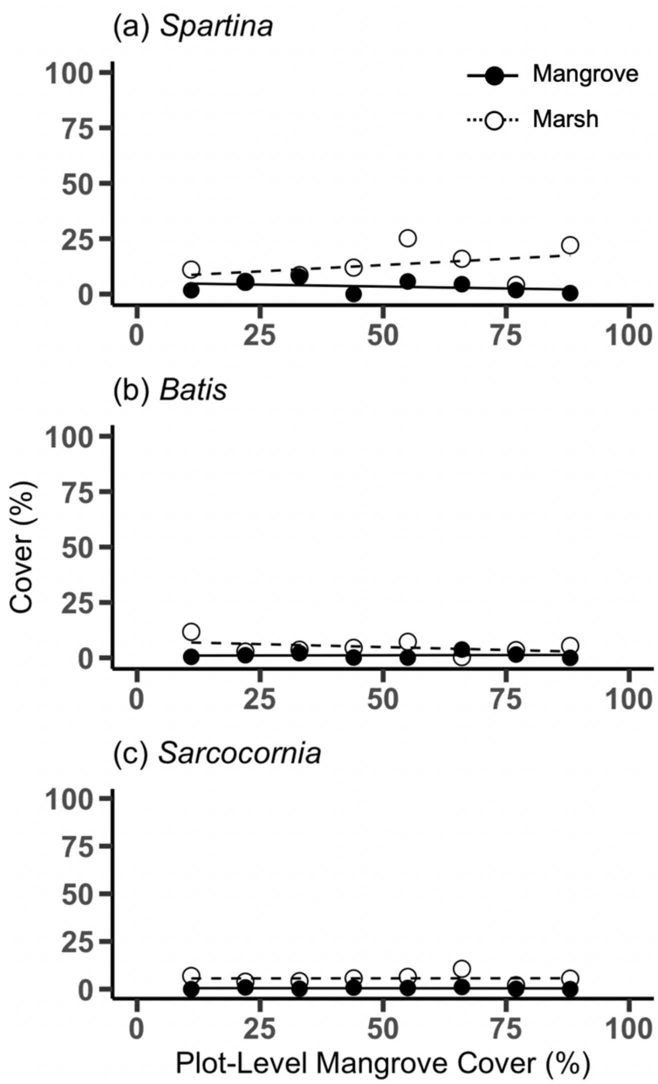

Figure A.8 Effect of plot-level mangrove cover on marsh plant cover in the transplant experiment.

Effect of plot-level mangrove cover (0-100%) on percent species cover of *Spartina*, *Batis,* and *Sarcocornia*. Filled circles with solid lines represent average abundance at each plot-level mangrove cover for marsh plants planted within mangrove cells. Open circles with dotted lines represent average abundance at each plot-level mangrove cover for marsh plants planted within marsh cells. Transplants were not performed for 0% or 100% plot-level mangrove cover because those plots did not allow comparisons between treatment types.