

CHANGES IN ARTHROPOD COMMUNITITES AS *AVICENNIA GERMINANS* EXPANDS
INTO GULF OF MEXICO SALT MARSHES

A Thesis

by

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BS, UTAH VALLEY UNIVERSITY, 2014

Submitted in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

in

BIOLOGY

Texas A&M University-Corpus Christi
Corpus Christi, Texas

May 2017

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May 2017

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This thesis meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Climate change is driving poleward shifts in species distributions worldwide. In the Gulf of Mexico (GOM), warming temperatures are allowing cold sensitive black mangroves (*Avicennia germinans*) to move north into coastal wetlands that have previously been dominated by the marsh grass *Spartina alterniflora*. *Avicennia germinans* in the western GOM become established in upper tidal elevations, creating dense monocultures and replacing *S. alterniflora* and other wetland plants (e.g., *Salicornia virginica*, *Batis maritima*). I investigated insect community assemblages in wetlands with and without *A. germinans* to assess potential effects of *A. germinans* expansion on insect fauna. Insect abundance, biomass, richness, diversity, and community and feeding guild composition were measured in both the spring and the fall across varying levels of *A. germinans* abundance and at low and high tidal elevations. Insects were more abundant and had larger biomass contributions in both the spring and the fall in upper tidal elevation wetlands where *A. germinans* have yet to become established. Richness and diversity were not different in any of the wetland types or tidal elevations, however multivariate analysis indicated significant differences in community structure in the wetlands without *A. germinans*. Feeding guild composition was also different; wetlands containing *A. germinans* monocultures had less predator biomass. Thus, shifting vegetation brought on by climate change can alter insect communities in coastal wetlands, illustrating the need for a more comprehensive understanding of climate change effects on fauna in response to shifting foundation species.

ACKNOWLEDGEMENTS

Funding was provided by the US Forest Service Southern Research Station agreements 12-DG-11330101-096 and 13-CA-11330140-116 to D.L. Smee. The NSF-MSP ETEAMS grant #1321319 provided funding for boat time and their interns assisted in the field. Erin Erben from Browne Middle School was especially helpful in sample collection. Members of the Marine Ecology Lab including Joey Reustle, Cole Castleberry, Kelly Kelly, and Meredith Diskin, provided important assistance in the field. I wish to thank my advisor Lee Smee for taking me on and assisting me throughout this process. I wish to thank my family, particularly Jupiter “Squish” Loveless, Brent “Hacksaw” Loveless, and Fred Christensen. I especially wish to thank my wife Tracy Loveless for putting up with all of the baggage that comes with being married to a graduate student. Finally, I wish to thank Vincent Paul Abbott, Darrell Lance Abbott, and Ash Williams for continuing inspiration.

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INTRODUCTION

Climate change is driving a poleward expansion of species across the globe. In the Gulf of Mexico (GOM) milder winters without severe freezing events has allowed *A. germinans* to expand northward into salt marshes previously dominated by *S. alterniflora* (Cavanaugh *et al.* 2014, Osland *et al.* 2013). Salt marshes are among the most abundant and productive habitats on earth, providing numerous ecosystem services including storm surge and coastal erosion protection, carbon sequestration, primary production, and habitat for numerous aquatic and terrestrial species (Pennings and Bertness 2000). Alteration of this vital ecosystem could dramatically disrupt marsh food webs, change ecosystem properties, and create new niches for invasive species (Gedan *et al.* 2009).

Coastal ecosystems are experiencing significant effects of climate change (e.g., rising sea levels; Loarie *et al.* 2009), which is of particular concern because two thirds of the planet's human population and some of its most productive ecosystems and biodiversity hot spots occur within these areas (Agardy *et al.* 2005). The salt marsh-mangrove barrier exists at or near *A. germinans* temperature thresholds (Record *et al.* 2013), suggesting that even a minimal increase in mean annual temperature accompanied by a decrease in severe freeze events (colder than -4° C) could lead to extensive increases in *A. germinans* distribution, altering the structure and function of the entire ecosystem (Cavanaugh *et al.* 2013). Cold temperatures have historically limited the northern range limit for *A. germinans* to around 30° N (Kangas and Lugo 1990). Over the last few decades, however a decrease in the frequency of sustained extreme freezing events has allowed the area of mangrove forests to double at the northern end of this range in the Gulf Coast of the United States (Cavanaugh *et al.* 2013). Yando *et al.* (2016) found the effect of *A. germinans* encroachment on below ground properties (e.g., soil characteristics, biomass, carbon storage, etc.) were more substantial in drier wetlands, suggesting that changes in

evapotranspiration likely accompanied by warmer temperatures could exasperate (or dampen) *A. germinans* effects.

Unlike other marsh-mangrove ecotones where *A. germinans* dominate the lower tidal elevations (Geldenhuys *et al.* 2016), in the western GOM, *A. germinans* tends to occupy the higher tidal elevations replacing *S. alterniflora* in the process (Smee *et al.* 2017). *Spartina alterniflora* protects *A. germinans* seedlings by creating a buffer against cold temperatures (Guo *et al.* 2013), and trapping the *A. germinans* propagules from becoming dispersed outside of optimal retention ranges (Peterson and Bell 2012). As a result, *A. germinans* are outcompeting and replacing the existing flora in the southern GOM. Anticipated warming trends are likely to promote *A. germinans* expansion poleward, displacing *S. alterniflora* and other marsh plants in the process.

Avicennia germinans may reduce some effects of climate change by sequestering carbon (Bianchi *et al.* 2013) and like salt marshes *A. germinans* can also protect coastlines from storm surges and rising sea levels (Comeaux *et al.* 2012). If the current trend of mangrove expansion continues, the increased area occupied by *A. germinans* would increase the overall levels of carbon sequestration in coastal wetlands (Bianchi *et al.* 2013), providing an invaluable carbon sink which could help reduce the levels of CO² gas in the atmosphere. Based on this information, Bianchi *et al.* (2013) suggests implementing *A. germinans* planting programs as a way to help increase the amount of carbon storage available in coastal wetlands.

While the increased ability to sequester carbon is desirable, the possible consequences that may arise from loss of salt marsh habitat must be considered. Plants are the primary source of food and habitat for consumers and any shift in the abundances or distributions of existing plant fauna may alter the composition of the organisms that inhabit them (Armitage *et al.* 2015,

Gratton and Denno 2005, Gratton and Denno 2006). In coastal wetland communities, insects are among the common terrestrial organisms with a nearly ubiquitous distribution (Penning and Bertness 2000). Insect families are generally restricted in diet to a small group of related plants due to coevolutionary defense strategies (Borrows 2003, Futuyma and Mitter 1996, Nagelkerken *et al.* 2008). For example, tropical plants generally invest heavily in chemical defenses relative to temperate plants (Coley 1998), and *A. germinans* generally invests more in defense strategies to combat herbivory rather than increasing biomass or the nutritional quality of food that can be used by insect grazers (He and Silliman 2015). Insects play an important role in decomposition and the cycling of nutrients through ecosystems as well as being a major food source for fish, birds, amphibians, reptiles, and other invertebrates making them essential for habitat functional integrity. (Angermeier and Karr 1994).

The effect of *A. germinans* expansion is not limited to the communities that directly utilize salt marsh habitat. For instance, oyster diets are largely derived from salt marshes and intertidal macrophytes (Conway-Cranos *et al* 2015). Consequently, changes in wetland communities could disrupt oyster productivity as well as play an important role in the implementation of oyster management policies and the management of coastal food webs in general (Conway-Cranos 2015). Intertidal productivity does not just affect estuarine benthic organisms; marine-derived resources contribute directly to adjacent food webs in both aquatic and terrestrial systems (Polis and Hurd 1996). For example, in Argentinean salt marshes certain fire ants derived 85% of their diet from marine resources, reducing intertidal polychaete numbers by 50%, and greatly increasing the density of near-shore ant colonies when compared to those without access to marine resources (Garcia *et al.* 2010).

Insects in coastal wetlands provide an important food source to fish and other estuarine species, however changes in insect communities resulting from *A. germinans* encroachment into marshes in the GOM not well understood. The purpose of this study was to determine what changes, if any, are occurring in the GOM estuarine wetland insect communities as *A. germinans* replace salt marsh, and attempt to identify patterns associated with this change.



Figure 1. Map of study area in the western Gulf of Mexico with study sites indicated.

MATERIALS AND METHODS

Samples were collected in estuaries near Port Aransas and Rockport, TX, USA (Figure 1). *Avicennia germinans* have become well established in many areas but are nearly completely absent in others. In some places *A. germinans* has displaced *S. alterniflora* and replaced other marsh vegetation forming dense monocultures while excluding *S. alterniflora* to narrow bands at

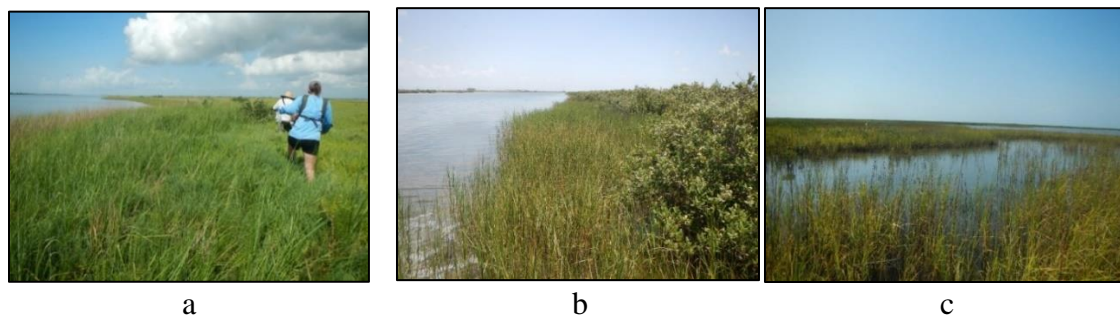


Figure 2. Three wetland types; a) Sa only, *S. alterniflora* abundant, minimal *A. germinans* present (left); b) Sa few, narrow *S. alterniflora* border, abundant *A. germinans* (middle); c) Sa/Ag, both *S. alterniflora* and *A. germinans* abundant (right).

the lowest tidal elevations In other areas *S. alterniflora* remains abundant with *A. germinans* being well established in the upper tidal elevations. In areas where *A. germinans* is rarely present, the lower tidal elevations are dominated by *S. alterniflora* with the upper elevations consisting of other marsh plants including *Salicornia virginica* and *Batis maritima*. In all areas *S. alterniflora* forms monocultures in the lower elevations forming borders around the shoreline. The area occupied by *S. alterniflora* was assessed by measuring the distance from the lowest elevation occupied by *S. alterniflora* to the highest elevations *S. alterniflora* was found. *Avicennia germinans* abundance was estimated similarly by measuring the distance from the lowest to the highest tidal elevations where *A. germinans* were found. In sites with abundant *A.*

germinans, *A. germinans* stretched more than 30 m from lowest to highest elevations. From these measurements, wetlands were categorized into three types based on vegetation width (Diskin 2016): 1) *Spartina alterniflora* abundant with *A. germinans* rare (*S. alterniflora* border >10m; *A. germinans* rare or absent, hereafter Sa only; Figure 2a). 2) *Spartina alterniflora* limited with *A. germinans* abundant (*S. alterniflora* border <5m; *A. germinans* stretching >30 m, hereafter Sa few; Figure 2b). 3) *Spartina alterniflora* and *A. germinans* both abundant (*S. alterniflora* >10m; *A. germinans* > 30 m hereafter Sa/Ag; Figure 2c). In sites with abundant *A. germinans*, the *A. germinans* extended more than 20m from the lowest tidal elevations.

Insects were collected from within these wetland types in both lower and upper tidal elevations during June and October 2016 (late spring and fall). All samples collected in lower elevations were taken from monocultures of *S. alterniflora* because *S. alterniflora* was present in low elevations in all areas. Insect samples in higher elevations were taken from either monocultures of *A. germinans* in sites with abundant *A. germinans* or from a mixture of *S. alterniflora* and other common marsh plants primarily *S. virginica*, and *B. maritima* when *A. germinans* were not abundant. This design was used to test the role of *A. germinans* displacement on insect communities with specific focus on changes in the abundance of *S. alterniflora*, the most abundant marsh plant in the GOM. That is, if insect communities were changing with *A. germinans* encroachment, were the changes observed caused by an increased number of *A. germinans*, a decline the abundance of *S. alterniflora*, or both.

EXPERIMENTAL DESIGN

During both spring and fall, 16 samples were collected from each wetland type, 8 samples in the lowest tidal elevations where *S. alterniflora* was present and another 8 at a higher

elevation dominated by either *A. germinans* or by other marsh plants such as *S. virginica* and *B. maritima* (48 each season, 96 total). Insect specimens were collected using a suction sampler (Figure 3) made from a converted leaf blower-vac. Samples were taken using a sweeping motion from side to side in a near 180° arc with 1 sweep made, then 1 step forward taken, and another sweep made, until 15 sweeps were completed and 15 constituting one sample (Buffington and Redak 1998). *Avicennia germinans* were flowering during spring sampling and not during the fall with no other vegetation flowering in either season while samples were taken. Once collected, insects were stored in 95% ethanol and returned to Texas A&M University Corpus Christi where they were enumerated and identified to the lowest possible taxon. The primary focus of this study was on insect taxa, however spiders were enumerated and simply identified as arachnid for both order and family. Feeding guilds were grouped using the classifications of Papp (2002) and Sinu and Sharma (2013). Herbivores were separated into chewers, sap feeders, and a third miscellaneous category (Pomeroy and Wiegert 1981) encompassing all remaining groups (e.g., gall formers, nectar feeders, *etc.*). Blood sucking insect families (e.g., Culicidae Tabanidae) were considered parasites, and detritivores were characterized as saprophagous. Comparisons of feeding guild compositions were simplified by separating wetland types into two groups, both upper and lower elevation Sa only sites were identified as having few to no *A. germinans* and considered distinct from all other sites which were categorized by *A. germinans* being present. Many of the insects collected were small phorid flies (< 2mm, < 2mg) which contributed substantially to the number of individuals collected, however they contributed very little to total biomass. Because of this, biomass contributions were used when comparing the feeding guilds between the wetland types.



Figure 3. Suction sampler made from converted leaf blower-vac.

Data Analysis

Insect communities were compared among seasons, wetland types, and tidal elevations using a 3-way PERMANOVA. All factors and interactions were significant, and many more insects were collected in spring than fall. Because of this, and the focus of the study being on wetland vegetation and not seasonality, differences in wetland type and tidal elevation were compared separately in spring and fall. Non-metric MDS plots were created for both the spring and the fall to visualize groupings of communities by wetland type and tidal elevation. I also performed a 2-way analysis of similarity (ANOSIM) in PRIMERTM for each season with wetland type and tidal elevation as fixed factors. For univariate analysis, insect abundances, biomass, richness, and diversity (Shannon-Weiner) were compared in the spring and the fall using a 2-way ANOVA in R statistical software version 3.2.2 with tidal elevation and wetland type as fixed factors. In situations where there was a significant interaction between wetland type and elevation, data were analyzed as upper and lower elevation subsets, and separate one-way

ANOVAs were used to compare wetland types (Zuur *et al.* 2009). All post-hoc testing was done using Tukey HSD.

RESULTS

Community Structure

PERMANOVA indicated significant differences for each factor and for all interaction terms at $p=0.001$ (Table 1). Thus, communities were significantly different among wetland type and tidal elevation and also varied by season. MDS plots for the spring (Figure 4) and fall (Figure 5) showed grouping patterns in ordination space based on dominant vegetation type. Areas with *A. germinans* monocultures had distinct insect communities compared to adjacent *S. alterniflora* habitats as well as to Sa only wetlands. Like MDS, ANOSIM confirmed a significant effect of wetland type and tidal elevation in both spring; wetland type across elevation ($R=0.721$; $p=0.001$) and elevation across wetland type ($R=0.808$; $p=0.001$), and fall; wetland type across elevation ($R=0.552$; $p=0.001$) and elevation across wetland type ($R=0.251$; $p=0.001$).

Abundances

In the spring there was a total of 4720 individuals from 38 families and 9 orders with the family Phoridae comprising 37.8% of the total insects collected. There was not a significant difference in total insect abundance in wetland type ($F_{2, 42}=0.255$, $p=0.775$), or tidal elevation ($F_{1, 42}=3.74$, $p=0.054$) and there was a significant interaction between the factors ($F_{2, 42}=4.45$, $p=0.012$). The significant interaction was likely a result of the large number of insects found in upper tidal elevations in the Sa only wetland type where nearly 40% of all insects were collected. Post hoc analysis indicated that Sa only upper elevation sites contained significantly more individuals than the Sa few ($p=0.003$), and Sa/Ag ($p=0.002$; Figure 6) wetland types while Sa

few and Sa/Ag were not different from each other ($p=0.822$). Thus, where *A. germinans* were present, insect abundance was significantly less.

Although fewer organisms were collected in the fall, the same trends for tidal elevation and wetland type were seen. These difference were largely driven by the Sa only wetland type in the upper tidal elevation in which over 55% of the insects in the fall were collected. 1794 individuals were collected from 28 families across 8 orders with the family Ephydriidae (20.8%) being the most common. Wetland type was not significant ($F_{2, 42}=0.439$, $p=0.645$), however tidal elevation was ($F_{1, 42}=19.7$, $p<0.001$) and there was a significant interaction between the main factors ($F_{2, 42}=21.5$, $p<0.001$). Post-hoc analysis showed significant differences with the Sa only upper elevation wetland type having more individuals than both Sa few ($p<0.001$), and Sa/Ag ($p<0.001$; Figure 7) with Sa few and Sa/Ag showing no differences from each other ($p=0.896$). No differences were found among any of the wetland types in the lower tidal elevation ($p=0.772$, Figure 7).

Biomass

In the spring, insect biomass was highest in Sa only upper tidal elevations. The family Gryllidae contributed the most biomass comprising 33.11% of the 80.3g of total biomass despite contributing < 2% of the total number of individuals collected. Wetland type was not significant ($F_{2, 42}=0.22$, $p=0.823$), however tidal elevation was ($F_{1, 42}=7.54$, $p=0.006$) and there was a significant interaction between the main factors ($F_{2, 42}=3.22$, $p=0.041$). Post-hoc analysis showed significant differences with Sa only upper elevation wetland type having more biomass than Sa few ($p<0.001$), and Sa/Ag ($p<0.001$; Figure 8). Sa few and Sa/Ag were not different from each other ($p=0.8025$). Lower elevations showed no differences ($p=0.7341$, Figure 8) among any of the wetland types.

In the fall, Arachnids contributed the most biomass making up 24.05% of the 18.67g collected. Wetland type was not significant ($F_{2, 42}=0.201$, $p=0.808$), however tidal elevation was ($F_{1, 42}=16.7$, $p<0.001$) and there was a significant interaction between the main factors ($F_{2, 42}=21.5$, $p<0.001$). Post-hoc analysis showed significant differences in the upper tidal elevations with the Sa only wetland type having more biomass than Sa few ($p=0.0065$), and Sa/Ag ($p=0.0066$; Figure 9). Sa few and Sa/Ag were not different in the upper elevations ($p=0.9762$). Lower elevations showed no differences ($p=0.627$, Figure 9) among any of the wetland types.

Richness and Diversity

Analysis of richness showed no significant differences between wetland type or tidal elevation in either spring or fall sampling. Diversity was also not different in either tidal elevation or wetland type in either season (Table 2).

Feeding Guild

All eight of the defined feeding guilds were represented in each wetland type and tidal elevation. Herbivores (chewers, sap suckers, and miscellaneous) were generally the dominant feeding group in all wetland types and elevations with carnivorous guilds (predators, parasitoids, and parasites, Tables 3-6) making up the bulk what remained. The exception to this pattern was the fall upper elevation where *A. germinans* were present (Table 6). The most common predator sampled were Arachnids. Sites in which *A. germinans* have yet to become established generally contained an herbivore-to-carnivore ratio of 2:1 in both the spring and the fall. In wetlands with *A. germinans* presence this ratio changed to 4:1 in both seasons with the glaring exception of the

fall upper elevation sites with *A. germinans* present which supported a 1:2 herbivore-to-carnivore ratio.

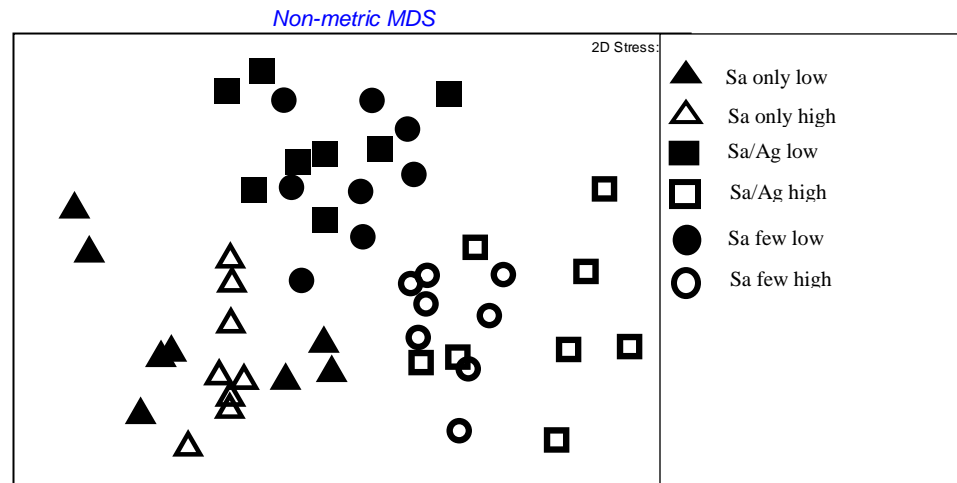
SUMMARY OF RESULTS

- Insects were significantly more abundant in Sa only wetland types (without *A. germinans*) in both the spring and fall in the upper tidal elevations.
- Insects had significantly more biomass in Sa only wetland types (without *A. germinans*) in both the spring and fall in the upper tidal elevations.
- Community structure in the Sa only wetland type was different from the Sa/Ag, and Sa few wetland types.
- Richness and diversity were not different in either wetland type or tidal elevation.
- Feeding guild composition differed with vegetation type

Table 1. PERMANOVA output showing analysis of season, wetland type, tidal elevation, and their interactions.

Source	df	Pseudo-F	P(perm)
Season	1	25.346	0.001
Wetland Type	2	6.8733	0.001
Elevation	1	13.012	0.001
SeasonxWetland Type	2	8.8493	0.001
SeasonxElevation	1	9.4381	0.001
Wetland TypexElevation	2	3.6027	0.001
SeasonxLocationxElevation	2	4.4564	0.001

A.



B.

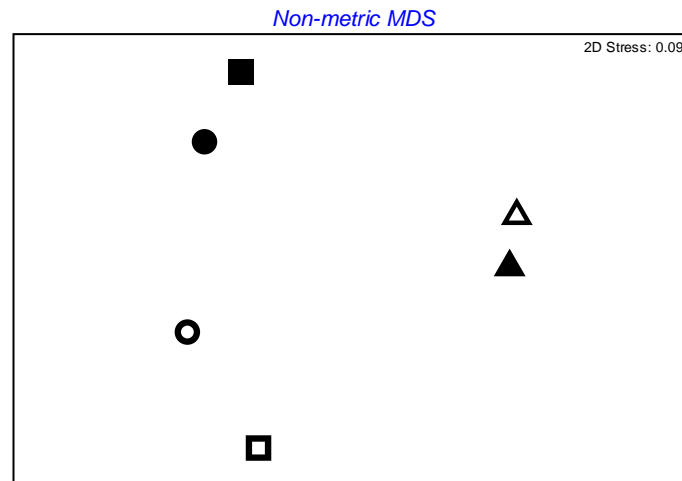
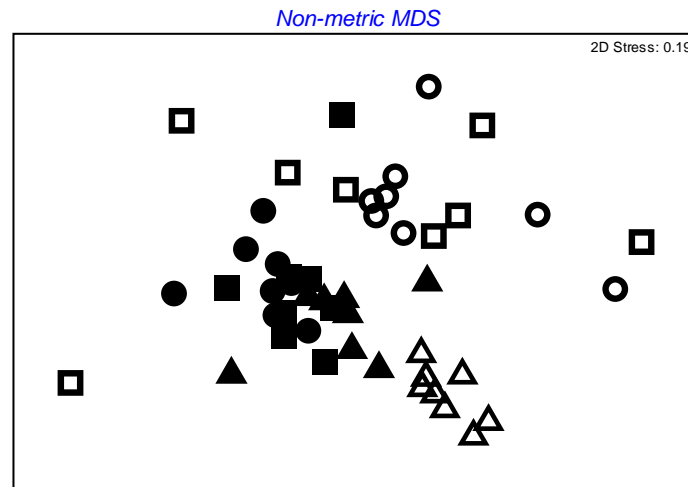


Figure 4. Non-metric MDS plot showing (A) mean and (B) all distances between insect samples from different wetland types in spring 2016. Blackened symbols represent insect communities in low tidal elevations containing only *S. alterniflora*, lighter symbols represent upper tidal elevations containing *Avicennia germinans* or being comprised primarily of *S. depressa* and *B. maritima*. Triangles indicate wetlands without mangroves (Sa only), circles indicate wetlands with little *S. alterniflora* and abundant *A. germinans* (Sa few), and squares indicate wetlands where both *S. alterniflora* and *A. germinans* are abundant (Sa/Ag). Note that the largest differences occur among areas dominated by *A. germinans* vs. those dominated by *S. depressa* and *B. maritima*, and communities are grouped by vegetation type.

A.



B.

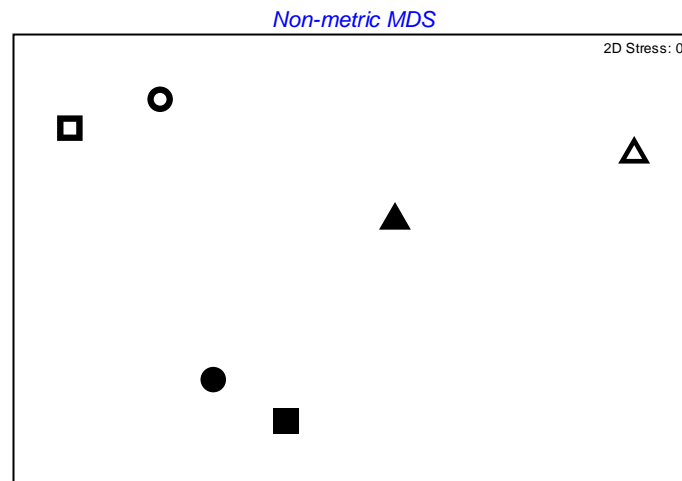


Figure 5. Non-metric MDS plot showing (A) mean and (B) all distances between insect samples from different wetland types in fall 2016. Blackened symbols represent insect communities in low tidal elevations containing only *S. alterniflora*, lighter symbols represent upper tidal elevations containing *A. germinans* or being comprised primarily of *S. depressa* and *B. maritima*. Triangles indicate wetlands without mangroves (*Sa* only), circles indicate wetlands with little *S. alterniflora* and abundant *A. germinans* (*Sa* few), and squares indicate wetlands where both *S. alterniflora* and *A. germinans* are abundant. Note the similar pattern where the largest differences occur among areas dominated by *A. germinans* vs. those dominated by *S. depressa* and *B. maritima*, and communities are grouped by vegetation type.

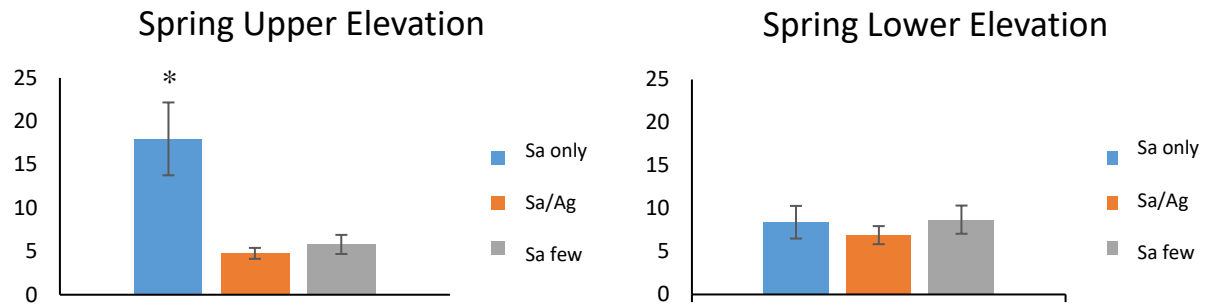


Figure 6. Bar plot showing mean insect abundances and standard error collected in the spring in the upper (left) and lower (right) tidal elevations.

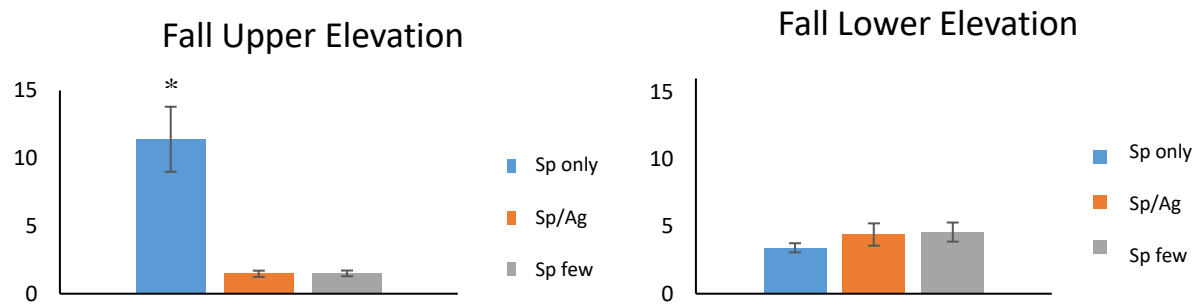


Figure 7. Bar plot showing mean insect abundances and standard error collected in the fall in the upper (left) and lower (right) tidal elevations.



Figure 8. Bar plot showing mean biomass and standard error collected in the spring in the upper (left) and lower (right) tidal elevations.

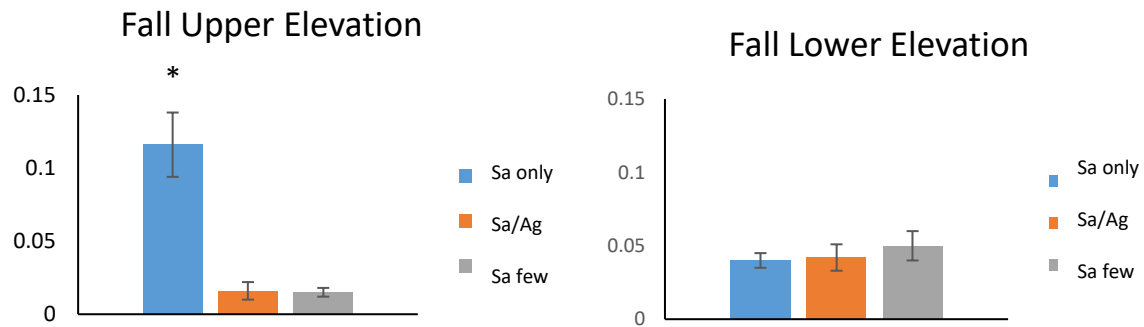


Figure 9. Bar plot showing mean biomass and standard error collected in the fall in the upper (left) and lower (right) tidal elevations.

Table 2. ANOVA output showing analysis of richness and diversity across tidal elevation and wetland type.

Index	Season	Factor	DF	F	P
Richness	Spring	Wetland	2	0.077	0.939
Richness	Spring	Elevation	1	0.29	0.644
Shannon	Spring	Wetland	2	4.26	0.19
Shannon	Spring	Elevation	1	0.364	0.608
Richness	Fall	Wetland	2	7.95	0.111
Richness	Fall	Elevation	1	8.89	0.096
Shannon	Fall	Wetland	2	0.361	0.735
Shannon	Fall	Elevation	1	0.129	0.754

Table 3. Abundance and biomass totals with percent abundance and percent biomass contributions separated by *A. germinans* presence of insects in the spring lower elevation.

Spring Lower Elevation								
S. alterniflora Only					A. germinans Present			
Feeding Group	Abundance	%Abundance	Biomass	%Biomass	Abundance	%Abundance	Biomass	%Biomass
Fungivore	6	0.93	0.01	0.1	17	1.51	0.034	0.2
Herbivore-Chewer	19	2.91	5.4	46.02	19	1.69	2.23	13.41
Herbivore-Misc.	22	3.37	0.172	1.47	339	30.13	1.743	10.48
Herbivore-Sap Sucker	68	10.4	1.135	9.67	399	35.47	10.41	62.6
Parasite	91	13.91	0.44	3.75	15	1.33	0.072	0.43
Parasitoid	16	2.45	0.41	3.49	21	1.87	0.26	1.56
Predator	51	7.8	3.408	29.03	23	2.04	0.964	5.8
Saprophage	381	58.26	0.775	6.6	292	25.96	0.883	5.31
Total	654		11.74		1125		16.63	

Table 4. Abundance and biomass totals with percent abundance and percent biomass contributions separated by *A. germinans* presence of insects in the spring upper elevation.

Spring Upper Elevation								
Feeding Group	S. alterniflora Only				A. germinans Present			
	Abundance	%Abundance	Biomass	%Biomass	Abundance	%Abundance	Biomass	%Biomass
Fungivore	25	1.38	0.05	0.16	15	1.34	0.032	0.16
Herbivore-Chewer	41	2.26	15.46	48.39	33	2.94	8.97	44.94
Herbivore-Misc.	134	7.39	2.083	6.52	592	52.76	5.09	25.5
Herbivore-Sap Sucker	400	22.04	10.46	32.74	135	12.03	2.52	12.63
Parasite	71	3.91	0.33	1.03	123	10.96	0.26	1.3
Parasitoid	6	0.33	0.06	0.19	19	1.7	0.53	2.66
Predator	58	3.2	1.33	4.16	132	11.76	2.1	10.52
Saprophage	1080	59.5	2.19	6.85	73	6.51	0.34	1.7
Total	1815		31.95		1122		19.96	

Table 5. Abundance and biomass totals with percent abundance and percent biomass contributions separated by *A. germinans* presence of insects in the fall lower elevation.

Fall Lower Elevation								
Feeding Group	S. alterniflora Only				A. germinans Present			
	Abundance	%Abundance	Biomass	%Biomass	Abundance	%Abundance	Biomass	%Biomass
Fungivore	4	1.65	0.01	0.36	16	2.86	0.033	0.57
Herbivore-Chewer	10	4.13	0.16	5.71	11	1.96	0.18	3.21
Herbivore-Misc.	54	22.31	0.56	20	64	11.43	0.51	8.78
Herbivore-Sap Sucker	64	26.45	1.02	36.43	266	47.5	3.81	65.57
Parasite	1	0.04	0.005	0.18	5	0.89	0.12	2.07
Parasitoid	16	6.61	0.19	6.79	30	5.36	0.29	4.99
Predator	41	16.94	0.761	27.18	26	4.64	0.58	9.98
Saprophage	52	21.49	0.104	3.71	142	25.36	0.31	5.34
Total	242		2.8		560		5.81	

Table 6. Abundance and biomass totals with percent abundance and percent biomass contributions separated by *A. germinans* presence of insects in the fall upper elevation.

Fall Upper Elevation								
Feeding Group	S. alterniflora Only				A. germinans Present			
	Abundance	%Abundance	Biomass	%Biomass	Abundance	%Abundance	Biomass	%Biomass
Fungivore	38	4.16	0.108	1.17	6	7.6	0.014	1.76
Herbivore-Chewer	11	1.2	0.18	1.94	1	1.27	0.016	2
Herbivore-Misc.	355	38.89	1.48	15.98	13	16.46	0.089	11.15
Herbivore-Sap Sucker	212	23.22	3.96	42.76	10	12.66	0.114	14.29
Parasite	114	12.49	0.28	3.02	3	3.8	0.006	0.75
Parasitoid	30	3.29	0.59	6.37	6	7.6	0.09	11.28
Predator	105	11.5	2.42	26.13	19	24.05	0.43	53.88
Saprophage	48	5.26	0.25	2.7	21	26.58	0.04	5.01
Total	913		9.26		79		0.798	

DISCUSSION

Abundances

Avicennia germinans encroachment into GOM salt marshes alters marine species (Diskin 2016, Lunt *et al.* 2013, Smee *et al.* 2017), and my results indicate that *A. germinans* also affects insect abundance, biomass, and community structure. The higher abundances found where *A. germinans* have yet to become established is consistent with numerous studies where existing vegetation supports more individuals than areas where vegetation is being outcompeted or replaced (reviewed by Bezemer *et al.* 2013). This pattern is shown in habitats ranging from Polish grasslands (Morón *et al.* 2009), to old-fields in Ontario, Canada (Ernst and Cappuccino 2003); which is important because vegetation shifts can alter the behavior of pollinators and foraging herbivores (Bezemer *et al.* 2013).

Insect communities found in *A. germinans* in this study were different than those reported from tropical mangrove forests. Tropical mangrove forests tend to be dominated by Lepidopteran species influencing pollination (Landry 2012) and herbivory (Menezes and Peixoto 2009), with Dipterans making minimal contributions (Burrows 2003, Murphy 1990, Simberloff and Wilson 1969, and Veenakumari *et al.* 1997). In this study, Lepidopterans only constituted about 5% of the groups collected, while Dipterans were the most abundant (31%). This Dipteran total is lower (40%) than reported in other salt marsh communities (Cameron 1972, Luckett and Gray 1966). Similarly, Burrows (2003), and Murphy (1990) only found herbivorous insects from four orders in mangrove forests. This is lower than the seven orders found in this study, and the 10-12 found in studies looking at salt marshes (Cameron 1972, Wu *et al.* 2009).

There are some similarities between the fauna collected in *A. germinans* in this study, and those collected from tropical climates. For instance, sap sucking insects comprised around 12% of the insects I collected in the *A. germinans* sites compared to around 30% in the *S. alterniflora* sites. These results were similar to studies conducted by Burrows (2003), and Veenakumari *et al.* (1997) which also saw reduced numbers of sap sucking insects in mangrove forests. Similarly, the *A. germinans* in this study, and the tropical mangrove forests sampled by Burrows (2003), and Murphy (1990) found very few Coleopterans, which are abundant in coastal marshes (Cameron 1972). Tropical mangrove forests can show a high degree of insect specialization; for example, several studies have shown that mangrove forests have little to no overlap in herbivorous species when compared to habitat that surrounds them (reviewed by Burrows 2003). This pattern was not seen in this study where every family that was found in the *A. germinans* sites were also found in the *S. alterniflora* sites. This may suggest that *A. germinans* in the GOM are in a transition between the communities found in tropical mangrove forest, and those found in salt marshes.

Differences in abundances, like the ones found in this study, are clear indications of individual organisms showing a preference to habitat type and tidal elevation (LaSalle and Bishop 1987). The Sa only upper elevation wetland type supported a larger diversity of plant species (e.g., *S. virginica*, *B. maritima*, *S. alterniflora*) than both the lower elevations which are dominated by *S. alterniflora* monocultures, or the Sa few and Sa/Ag upper elevation sites which are dominated by *A. germinans* monocultures. It is not uncommon for encroaching plants to eliminate existing vegetation by competitive exclusion leading to extensive loss in plant diversity (Harvey *et al.* 2010, Quan *et al.* 2016, Wu *et al.* 2009). For example, in China the area occupied by *S. alterniflora* increased from 260 ha (Chung 1989) to 112,000 ha (An *et al.* 2007) in only 15

years with this expansion coming at the expense of the existing vegetation (Wu *et al.* 2009). Numerous studies have shown the diversity of lower trophic levels exert significant controls on abundances of the upper trophic level that utilize them (Knops *et al.* 1999, Murdoch *et al.* 2011, Siemann *et al.* 2013). Encroaching plants can alter habitat structure as they are establishing, influencing the existing arthropod communities (Gratton and Denno 2005). Upper elevation sites should be exposed to similar abiotic factors (salinity, temperature, precipitation, etc.), and thus, the higher plant diversity, accompanied by the more labile plant materials associated with *S. virginica*, *B. maritima*, and the changes in the habitat structure are likely primary contributors to the higher insect abundances and biomass found in Sa only upper elevations.

The lower tidal elevations were not different from each other in either insect abundance or biomass regardless of season. These areas were dominated by *S. alterniflora* and experience small tidal fluctuations (Yando *et al.* 2016). The stability of water level is a key factor in determining insect community composition and influencing production in wetlands (Larsen and House 1990, Nolte 1989). With tides in the GOM that can range from as low as 15-45cm (Noble *et al.* 1996), the *S. alterniflora* in the lower tidal elevations tend to spend a significant amount of time completely inundated (Bertness *et al.* 1992). Being frequently inundated is not necessarily detrimental for estuarine insects. For example, it is generally beneficial to aquatic larvae (Batzer & Wissinger 1996), however emergent vegetation in frequently inundated wetlands rarely support high insect densities (Batzer & Wissinger 1996, Wrubleski and Rosenberg 1990). Low tidal fluctuation may also help explain the nearly complete lack of ants (2) found in this study. Ants are generally one of the most important and numerous insect species found in mangrove forests (Cannicci *et al.* 2008, Nagelkerken *et al.* 2008, and Simberloff and Wilson 1969),

however most ants are ground dwellers making it difficult for them to become established in areas that are frequently inundated (Cannicci *et al.* 2008).

Richness and Diversity

Richness and diversity were not different among the different tidal elevations or wetland types in either the spring or the fall. In similar studies, patterns in richness and diversity have shown mixed results. For example, in the Yangtze River estuary no overall differences in insect richness or diversity were seen within the monocultures of existing and encroaching vegetation types, however plots that contained mixtures of plant species supported higher richness, diversity, and densities. In a separate study, Gratton and Denno (2005) found no differences in insect diversity, richness, or abundance in wetlands that contained the original plant species, however all three metrics were lower in wetlands where monocultures of encroaching vegetation had become established. One common thread between these studies and this one is that multivariate analysis revealed that encroaching vegetation altered insect community structure. Coastal wetland communities often experience harsh gradients of abiotic stresses and shifting salinities (Pennings and Bertness 2000). These extremes limit the taxa that can tolerate the physical stresses and incorporate marsh materials into secondary production, probably accounting for the similarities in richness and diversity values identified in this study

Feeding Guilds

Changing community compositions can alter food web structures (Gratton and Denno 2005, Gratton and Denno 2006, Harvey *et al.* 2010, Levin *et al.* 2006), however patterns of community change have varied widely. For example, in coastal marshes in southeastern Australia, differences in feeding guilds are driven by predators and herbivores; with habitat that has not experienced encroachment containing more numerous and diverse predator assemblages

than the marshes where encroachment has taken place (Harvey *et al.* 2010). In the northeastern United States, Gratton and Denno (2005) found feeding guilds in encroached marshes to shift from a roughly 2:1:1 predator-to-herbivore-to-detritivore ratio, to one composed primarily of detritivores (46%), and predators (45%), with changes being driven by altered plant composition and physical structure. In my study, herbivores were the dominant guild in both the *S. alterniflora* and *A. germinans* habitat with the *A. germinans* dominated wetlands generally having fewer predators. The one exception to this pattern was fall upper elevation sites where *A. germinans* were present. While it is possible that some environmental factor exists to explain this, it is more likely that the dearth of fauna collected in these wetland types has skewed the data. For example, only 18 arachnids were collected within these wetland types, however this small number accounted for nearly 23% of individuals, and just under 52% of the total biomass.

Insect herbivory in salt marshes does not generally exert considerable control of vegetation patterns of the dominant plant species (Pennings and Bertness 2000), however in mangrove forests, herbivores have been shown have similar impacts to that of forest ecosystems (Burrows 2003) where insect herbivores influence growth, reproduction, and survivability (Crawley 1989, Schowalter, 1986). This is indicative of mangrove forests being similar to terrestrial forest ecosystems, especially for insects that occupy the mangrove canopy (Cannicci *et al.* 2008) or are host specific (Burrows 2003).

Harsh abiotic conditions limit the diversity of organisms that utilize the lower tidal elevations for habitat, however in the upper tidal elevations, *A. germinans* monocultures are replacing more diverse vegetation assemblages. This, in turn, is driving a shift in community structure which may prove to be detrimental to coastal wetlands and the nearby ecosystems that rely on them. For instance, terrestrial arthropod species comprise a significant proportion of the

diet of commercially important fish species in estuaries (Gray *et al.* 2002, Romanuk and Levings 2005) which further enforces the importance of wetland vegetation in estuarine food webs (Morely *et al.* 2012). This habitat loss is even more alarming when considered with other studies showing *A. germinans* presence to adversely affect marsh nekton and benthic communities as well (Diskin 2016, Lunt *et al.* 2013, Smee *et al.* 2017). While the idea of using mangroves to help mitigate the effects of climate change is intriguing, future studies are needed to elucidate the affect this would have on coastal wetland communities. Information gained would allow better action in the construction and implementation of future conservation policies.

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