

ARTICLE

Coastal and Marine Ecology

The influence of salinity and vegetation texture on the ecological roles of insects in tidal marshes in Louisiana

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Email: akergb@gmail.com**Funding information**

Gulf of Mexico Research Initiative, Grant/Award Numbers: 231613-00, R5, x277.000:0007

Handling Editor: Jenifer Dugan**Abstract**

Tidal marsh insect communities are influenced by both salinity and aspects of vegetation texture (vegetation diversity, plant density, and architectural structure). These factors affect the abundances and intra- and interguild interactions of these insects and should result in broad-scale variation in the distribution and ecological functioning of tidal marsh insect communities along these gradients. However, this assumption has not been tested within Gulf Coast marshes, and the insect communities and their ecological roles are not well known. This study identifies how family-level insect biodiversity varies by salinity and which factors are most important in affecting the distribution of insect functional feeding groups within Louisiana's coastal marshes. Insect family diversity was found to decrease as salinity increased for several indices. Vegetation texture and the underlying salinity gradient were found to be important factors affecting the distribution of free-living sucking, stem-boring, parasitic, and filtering functional feeding groups.

KEYWORDSbiodiversity, functional feeding groups, salt marsh, *Spartina*, vegetation texture**INTRODUCTION**

Tidal marsh insect communities, those found in brackish and salt marshes, have complex interactions which are influenced by both salinity and aspects of vegetation texture such as plant composition, density, and structural architecture (Kareiva, 1983; Moon & Stiling, 2002a, 2002b, 2002c, 2004). These factors influence the abundances of certain feeding guilds (Moon & Stiling, 2000, 2002a, 2002b, 2004) and mediate both intra- and interguild interactions (Finke & Denno, 2002, 2004, 2006). Salinity is a primary factor in the distribution and local zonation of host plants in coastal marshes (Bokhorst et al., 2007; Chapin et al., 1993; Elsey-Quirk et al., 2019; Flowers et al., 1977) and additionally affects

host plant nutritional quality (Bowdish & Stiling, 1998), both of which have bottom-up effects on the abundance of herbivorous insects in these marshes (Denno et al., 2016; Moon & Stiling, 2000, 2002b). Additionally, while salinity apparently has a relatively weak effect on the top-down control of herbivorous insects by predators and parasitoids (Moon & Stiling, 2002a, 2002b, 2004), aspects of vegetation texture more strongly influence these downward pressures (Finke & Denno, 2004, 2005). Structurally complex vegetation mediates interactions between predators by creating refuges from intraguild predation (Finke & Denno, 2002, 2006), resulting in higher predator abundances which in turn facilitates stronger suppression of common herbivorous prey (Finke & Denno, 2005, 2006).

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Due to these interactions, it should be expected that tidal marsh insect communities vary by salinity and vegetation texture on a broad scale within coastal marsh habitat. However, the breadth of studies conducted along the Gulf Coast, which accounts for 58% of the nation's salt marshes and has a relatively high proportion of brackish marsh (>40%) when compared to Atlantic and Pacific coast tidal marshes where brackish marsh makes up less than 10% of the total area (Field et al., 1991; Greenberg & Maldonado, 2006), are not sufficient for broadly understanding insect community distribution and ecological functioning. The majority of studies focusing on insects within Gulf Coast marshes primarily explore the effects of large-scale disasters such as the 2010 *Deepwater Horizon* oil spill or hurricanes (Bam et al., 2018; Husseneder et al., 2016, 2018; McCall & Pennings, 2012). Others either had limited sampling periods (Adams et al., 2017; Bam et al., 2018; McCall & Pennings, 2012), many taxa that were not identified below the ordinal level (Bam et al., 2018; McCall & Pennings, 2012), focused on populations of a single species (Husseneder et al., 2016, 2018), or inventoried species within a single order (Sokolov et al., 2018). Although Sokolov et al. (2018) made note of known host plants for selected taxa, no study of Gulf Coast tidal marsh insects has directly explored how the plant texture and underlying salinity gradient affect both the distribution of insects and the ecological roles that they fulfill.

Understanding the effects of salinity and vegetation texture on the ecological functioning and structure of tidal marsh insect communities within Gulf Coast tidal marshes is particularly important as these marshes are currently experiencing heavy decline due to anthropogenic activities (Couvillion et al., 2017; Watzin & Gosselink, 1992), and because the proposed restoration efforts have the potential to induce eutrophication (Coastal Protection and Restoration Authority of Louisiana, 2007, 2012, 2017; Elsey-Quirk et al., 2019) and heavy pressure by herbivorous insects (Bertness et al., 2008; Sala et al., 2008; Tomasula et al., 2023). Therefore, the purpose of this study was to conduct an extensive, year-long inventory of insect families within Louisiana's coastal marshes and to test how insect functional feeding groups vary across multiple salinity zones in two major estuaries with respect to the several aspects of vegetation texture: plant composition, density (ground cover), and between structurally different plant species.

METHODS

Sites were selected from low (4.8 ± 2.3 ppt), mid (8.5 ± 4.4 ppt), and high (13.8 ± 5 ppt) salinity zones within

two major Louisiana estuaries: Caillou Bay and Barataria Bay (Figure 1). Monthly salinity data from 2014 until the end of 2017 were obtained from the Coastal Information Management System database (Coastal Protection and Restoration Authority of Louisiana, 2018) from six different Coastal Reference Monitoring Stations which were nearest to each of the six sites with an average distance between the stations and sites of 5.5 ± 5.1 km. In order to ensure that the three salinity zones were distinct and that there was no significant difference in salinity of the zones between the two bays, the salinity data were compared using a two-factor ANOVA with a post hoc Tukey honestly significant difference test. Statistical analyses were performed in R 4.1.2 (R Core Team, 2021). In order to minimize unseen consequences of the 2010 *Deepwater Horizon* oil spill which released over 3,000,000 barrels of oil into the Gulf of Mexico (Malakoff, 2015) on coastal plants and inventoried insects, oil landing data collected from the Environmental Response Management Application (National Oceanic and Atmospheric Administration, 2018) were used to ensure that no oiling had been observed at the collection sites at the time of the oil spill. Within both Barataria and Caillou bays, three 8×16 -m sites were selected from each salinity zone for a total of 18 sites. Sites were selected in areas accessible by boat where the low-growing vegetation of brackish and salt marshes was present as opposed to the taller, shrubby vegetation of mangrove swamps. Additionally, small islands were avoided during site selection to prevent sampling biases.

Insects were collected at each of the 18 sites monthly by sweep net from July 2018 to June 2019 from both Barataria and Caillou bays. Collection permits were obtained from the Louisiana Department of Wildlife and Fisheries (permit number LNHP-18-078). During each monthly collection, five sweep net transects were taken at each site. The transects were parallel to the marsh edge and consisted of 10 sweeps with one step being taken forward at each sweep. The first transect was established adjacent to the marsh edge with sufficient vegetation on each side to conduct sweep netting. Each subsequent transect was 4 m inland from the previous transect. Insects were stored on dry ice for the duration of the trip and placed in a -80°C freezer upon returning to the lab. The collected insects were then sorted and placed in 95% ethanol for long-term storage, except Lepidopterans which were pinned to maintain scale characteristics. Subsequently, the adult insects were identified to the family level using the keys of McAlpine (1981) and Triplehorn and Johnson (2005). The family-level abundances of the insects collected from each sweep net transect from a single site were summed. These summed abundances from each site formed six replicates within

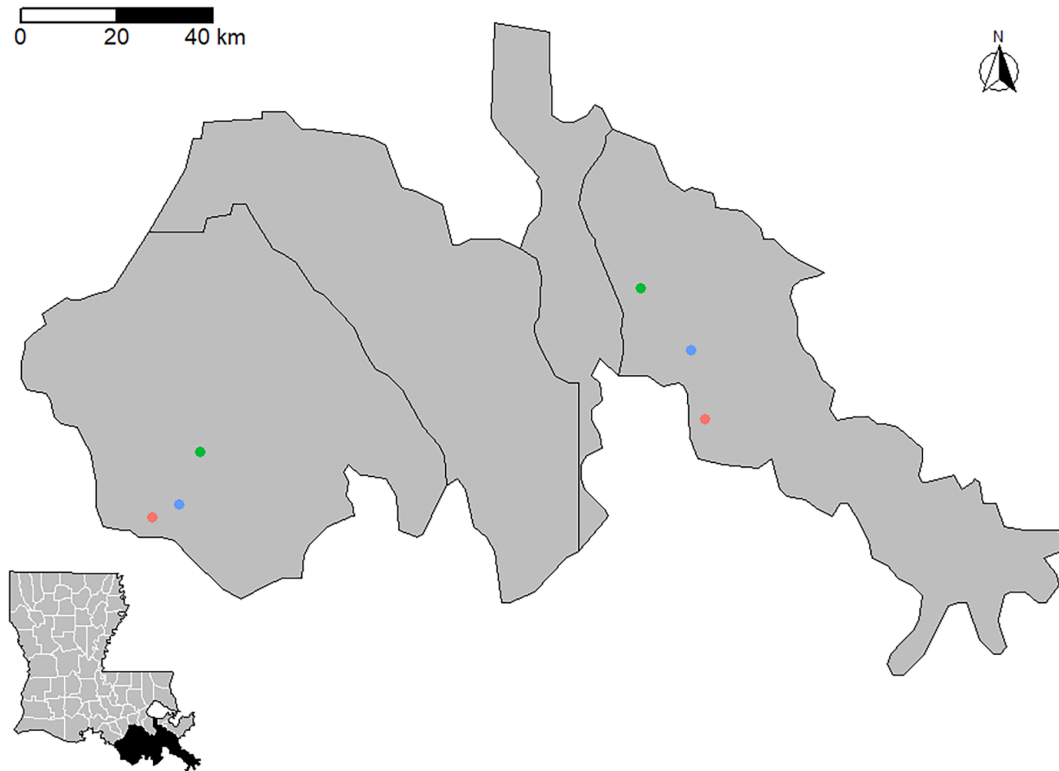


FIGURE 1 The location of insect collection sites in low salinity, mid salinity, and high salinity zones, in Barataria and Caillou bays. Three collection sites are present at each point on the map for a total of six low salinity sites (green), six mid salinity sites (blue), and six high salinity sites (red).

each salinity zone per month for a total of 72 samples per salinity zone (bays combined) over the course of the year-long inventory. The insect family abundance data were submitted to the Gulf of Mexico Research Initiative Information and Data Cooperative (UDI: R5.x277.000:0007).

Plant ground cover was measured 11 times at Caillou Bay and 12 times at Barataria Bay over the course of the study. At each site, plants were identified to the species level using the keys of Tiner (1993) within four randomly placed 20×50 -cm quadrats starting at the marsh edge and moving inland with each sample, and the percentage ground cover for each plant within the quadrat was estimated. The four quadrats were then averaged to determine the overall plant cover for that site (Table 1). Plant voucher specimens were collected, pressed, dried, and deposited in the Shirley C. Tucker Herbarium at Louisiana State University.

Coverage-based rarefaction was performed using the Hill numbers corresponding to the Shannon index ($q = 1$) and inverse Simpson index ($q = 2$) using iNext for each salinity zone to determine whether insect families were adequately sampled (Chao et al., 2014, 2016). Rarefaction curves of the Shannon index-associated Hill numbers versus the numbers of individuals collected

were generated for each salinity zone. Upper and lower CIs for the Hill numbers from each salinity zone were similarly generated using iNext (Chao et al., 2016).

Insects were grouped into three trophic levels (herbivore, consumer, and detritivore) and then further subdivided into feeding guilds based on the literature (Appendix S1: Table S2). If different species within an insect family can belong to separate trophic levels or feeding guilds, family-level ecological studies focusing on coastal insects such as Gratton and Denno (2005) or Bam (2015) were used to make assignments. For any taxa where the trophic level and feeding guild remained unclear, the taxa within the family were identified to either the genus or species level to obtain a correct assignment. If the feeding habits differed between the immature and adult insects, such as in some holometabolous insects, the feeding habits of the immature insects were used to make the assignment. Herbivores were divided into free-living suckers, free-living chewers, and stem borers; consumers into predators and parasites; and detritivores into scavengers/shredders and filterers.

The R package “vegan” (Oksanen et al., 2018) was used to perform a distance-based redundancy analysis (db-RDA) to determine whether selected environmental predictors could explain variation between coastal marsh

TABLE 1 Average estimated monthly ground cover for each plant species identified from low, mid, and high salinity zones within Barataria and Caillou bays.

Species	Low salinity (%)	Mid salinity (%)	High salinity (%)
<i>Spartina alterniflora</i>	8.6	13.3	42.1
<i>Spartina patens</i>	25.5	28.6	0.0
<i>Schoenoplectus americanus</i>	12.5	0.0	0.0
<i>Distichlis spicata</i>	0.7	10.1	1.0
<i>Vigna luteola</i>	5.0	0.0	0.0
<i>Bolboschoenus robustus</i>	0.1	4.0	0.0
<i>Juncus roemerianus</i>	0.0	1.6	1.9
<i>Ipomoea sagittate</i>	2.3	0.3	0.0
<i>Eleocharis</i> species	0.8	0.0	0.0
<i>Spartina cynosuroides</i> (L.) Roth	0.0	0.6	0.0
<i>Iva frutescens</i> (L.)	0.3	0.0	0.0
<i>Symphotrichum tenuifolium</i> (L.) G. L. Nesom	0.2	0.0	0.0
<i>Amaranthus</i> species	0.1	0.0	0.0
<i>Avicennia germinans</i>	0.0	0.0	0.1
<i>Lythrum lineare</i> (L.)	0.1	0.0	0.0

Note: Plant ground cover was measured monthly from July 2018 through June 2019 using four randomly placed 20 × 50 cm quadrats at a total of 18 sites.

insect communities and to visually display how insect functional feeding groups are distributed along important gradients. A db-RDA was selected over other ordination techniques because it is a method of direct gradient analysis which allows for hypothesis testing as opposed to the exploratory nature of indirect gradient analysis. The inputs for the db-RDA were a community data set consisting of the square root transformed counts of each functional feeding group from the monthly collections from each site and an environmental data set consisting of a set of explanatory variables (plant ground cover, salinity zone, and month) with values that correspond to each replicate in the community data set. To avoid introducing too many explanatory variables, only plants that represented above 5% of the total ground cover at an individual marsh vegetation type were used in the analysis. In total, nine predictor variables were used: salinity, seasonality, total percent ground cover (percent GC), and the percent ground covers of *Spartina alterniflora* (Loisel.), *S. patens* (Roth), *Distichlis spicata* (L.) Greene, *Bolboschoenus robustus* (Pursh) Soják, *Vigna luteola* (Jacq.) Benth., and *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller. An ANOVA was used to test whether the db-RDA model predicts the distribution of insect functional feeding groups better than random chance. The exploratory variables and axes of the db-RDA were then tested for being significant predictors of insect distribution using permutation tests with 500 permutations.

A permutational analysis of variance (PERMANOVA) was then performed using Bray–Curtis dissimilarities to determine whether there was a significant effect of salinity on the individual insect functional feeding guilds. Kruskal–Wallis tests followed by Bonferroni corrections for multiple testing were used to test for significance. Post hoc pairwise Wilcoxon rank sum tests were used to identify where significant differences occurred for feeding guilds that were found to have a significant effect of salinity.

RESULTS

Significant differences in average monthly salinity were found between the low, mid, and high salinity zones ($F_{2,280} = 118.586$, $p < 2.2e^{-16}$); however, no significant differences were found between Barataria Bay and Caillou Bay ($F_{1,280} = 1.903$, $p = 0.169$), and there was no significant interaction between salinity zone and bay ($F_{2,280} = 0.099$, $p = 0.906$). Since there were no differences between the Barataria and Caillou bay sites, they were combined for a total of 18 sites: 6 within the low salinity zone, 6 from the mid salinity zone, and 6 from the high salinity zone (Figure 1).

Over the sampling period, 15 plant species in total were identified (Table 1). There were 12 species present at the low salinity zone, 7 present at the mid salinity zone, and 4 present at the high salinity zone. The plant community present at the low salinity zone consisted

primarily of intermediate marsh vegetation such as *S. patens*, *Sch. americanus*, an *Eleocharis* species, *V. luteola*, and *Ipomoea sagittata* (Poir.), the plant community present at the mid salinity zone consisted of brackish marsh vegetation such as *S. patens*, *D. spicata*, *B. robustus*, and *Juncus roemerianus* (Scheele), and the high salinity zone consisted of primarily of saline marsh vegetation such as *S. alterniflora*, *D. spicata*, *J. roemerianus*, and *Avicennia germinans* (L.) L. (Chabreck, 1970, 1972; Penfound, 1938).

While species composition varied among salinity zones, *Spartina* species had the highest total ground cover at each of the low (48.7%), mid (56.6%), and high salinity (52.3%) zones. Additionally, as salinity increased, *Spartina* species made up an increasing percentage of the total plant community as estimated by ground cover even though their contribution to ground cover remained similar. *Spartina* species made up 60.8% of the plant community at the low salinity zone by ground cover, 72.7% of the plant community at the mid salinity zone, and 93.2% at the high salinity zone.

While *S. alterniflora* and *S. patens* were abundant at both Barataria and Caillou bays, some common plant species differed. *Schoenoplectus americanus* and an *Eleocharis* sp. were present at the low salinity zone in Caillou Bay, but typically absent in Barataria. Additionally, while *V. luteola* was present at both bays, it was more abundant at Caillou Bay. Similarly, *B. robustus* and *J. roemerianus* were present at the mid salinity zone in Caillou Bay and typically absent at Barataria, while *D.*

spicata was present at both bays, but more abundant at Caillou Bay. At the high salinity zone, *D. spicata* was present at Caillou Bay, but not at Barataria Bay.

During the study, 71 insect families were collected with 61 families collected from the low salinity zone, 64 from the mid salinity zone, and 39 from the high salinity zone (Appendix S1: Table S1). Across all salinity levels, individuals from the orders Diptera and Hemiptera were the most abundant although individuals from the orders Hymenoptera, Coleoptera, Thysanoptera, and Odonata were additionally common. In total, 21 families were collected from the order Diptera, 15 from Hymenoptera, 13 from Hemiptera, and 13 from Coleoptera. The remaining orders collected were represented by two or fewer families.

The rarefaction curves using the Shannon index-associated Hill numbers leveled off (Figure 2), and the respective CIs for each of the generated Hill numbers (both $q = 1$ and $q = 2$) were small (Table 2). As such, the family-level insect biodiversity was likely adequately sampled across salinity zones. Of the 71 families collected in this study, individuals of 24 families were assigned to the herbivore trophic level, individuals of 27 families to the consumer trophic level, and individuals of 20 families to the detritivore trophic level (Appendix S1: Table S2). Individuals of the family Miridae were assigned to either the herbivore or consumer trophic levels as the Mirid *Trigonotylus uhleri* (Reuter, 1876) feeds on *S. alterniflora* and the Mirid *Tytthus vagus* (Knight, 1931) is an egg predator of Delphacid

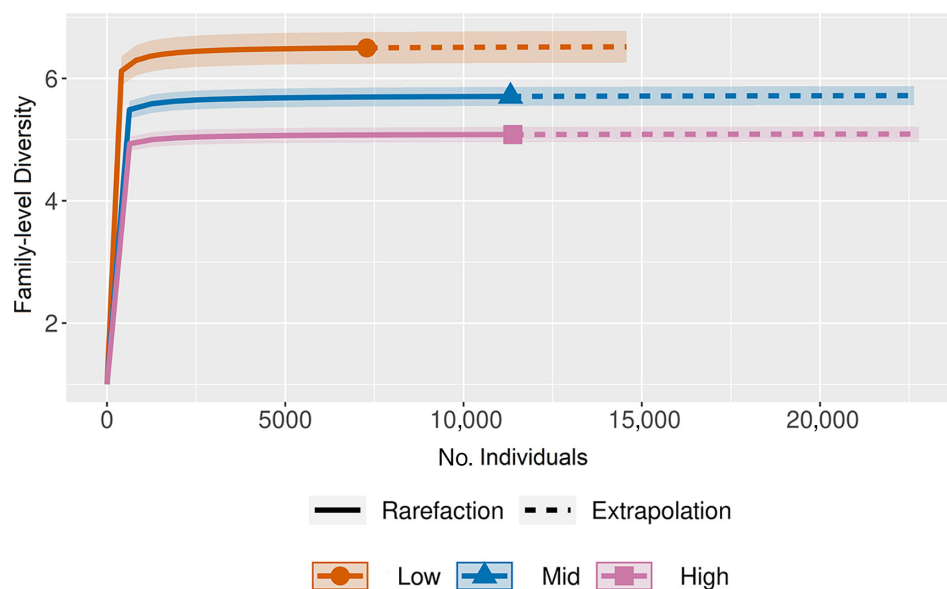


FIGURE 2 Coverage-based rarefaction was performed to view differences in family-level richness between low, mid, and high salinity zones and to determine whether the sampling regimen adequately sampled the families present. The number of individuals collected at each salinity zone (x-axis) is plotted versus the Shannon index-associated Hill number ($q = 1$). Solid lines represent the observed diversity values, while the dashed lines represent the extrapolated diversity values if more individuals were collected.

planthoppers (Denno, 1977; Denno et al., 2009). Similarly, immatures of *Culicoides mississippiensis* (Hoffman, 1926) have been known to be able to develop solely on nematode prey (Davis et al., 1983) and as such have been assigned to the predator functional feeding group while the remaining Ceratopogonid species were filterers. The ants, Formicidae, were the sole family assigned to the trophobiosis feeding guild as nearly all collected Formicids were individuals of *Crematogaster pilosa* (Emery, 1895), a species which obtains much of its nutrients from honeydew (Murphree, 1947). The herbivores consisted of free-living sucking insects belonging to 12 families, predominately from the order Hemiptera aside from a single Thysanopteran family, free-living chewing insects belonging to three families within Coleoptera and Orthoptera, and stem-boring insects belonging to nine Dipteran, Coleopteran, and Lepidopteran, and Hymenopteran families. The consumer trophic level consisted of predators from 14 Hemipteran, Dipteran, Coleopteran, and Odonatan families and parasites from 13 families within the order Hymenoptera. Of the detritivores, the scavenger/shredding insects belonged to 17 families, which were predominately within the orders Diptera and Coleoptera, although singular families within the orders Thysanoptera, Psocoptera, and Ephemeroptera were present. The remaining detritivores were filter feeders belonging to three families within the order Diptera.

The distance-based redundancy analysis was found to predict the distribution of insect functional feeding groups better than random chance ($F_{9,197} = 6.6799$, $p = 0.001$). Two constrained axes, RDA1 ($F_{1,197} = 29.9470$, $p = 0.001$) and RDA2 ($F_{1,197} = 20.2563$, $p = 0.001$), were found to be significant. Of the nine predictor variables, all but the percent ground cover of *B. robustus* were found to be significant (Table 3). The correlations of the individual insect functional feeding groups with the explanatory factors are displayed graphically along the significant constrained axes (Figure 3). Insects belonging to the sucking and stem-boring feeding groups were positively correlated to sites with elevated salinities where the dominant plant cover is either *S. alterniflora* or *S. patens*. Insects belonging to the parasite, predator, chewing, and scavenger/shredder functional feeding groups were positively correlated to sites with middle to lower salinities and preferred sites where *D. spicata* was abundant. Filtering insects were positively correlated with sites at lower salinities where the rushes *Sch. americanus* and *B. robustus* made up large portions of the plant community. Adult insects from the sucking, stem-boring, and filtering functional feeding groups, and to a much lesser extent the predator, shredder/scavenger, and parasite feeding groups, were correlated to the seasonality explanatory factor and were most abundant

TABLE 2 The Hill numbers ($q = 1$ and $q = 2$) and lower and upper 95% CIs for insect communities found at low, mid, and high salinity zones in Louisiana's tidal marshes.

Salinity zone	Hill no. ($q = 1$)	Lower CI	Upper CI	Hill no. ($q = 2$)	Lower CI	Upper CI
Low salinity zone	6.5	6.24	6.76	3.68	3.6	3.76
Mid salinity zone	5.71	5.55	5.86	3.65	3.58	3.72
High salinity zone	5.08	4.96	5.21	3.36	3.29	3.43

TABLE 3 Explanatory variables from a distance-based redundancy analysis model found to be significant predictors of the variation in the ecological roles of insects in Gulf Coast, tidal marshes ($F_{9,197} = 6.799$, $p = 0.001$).

Terms	df	SS	F	p
<i>Spartina alterniflora</i>	1	1.1371	9.9772	0.001
<i>Spartina patens</i>	1	0.3166	2.7777	0.010
<i>Distichlis spicata</i>	1	1.2368	10.8523	0.001
<i>Bolboschoenus robustus</i>	1	0.2306	2.0236	0.050
<i>Vigna luteola</i>	1	0.3915	3.4255	0.004
<i>Schoenoplectus americanus</i>	1	1.2940	11.3535	0.001
Salinity	1	0.6482	5.6877	0.001
Seasonality	1	1.3470	11.8188	0.001
Percent ground cover	1	0.2500	2.1932	0.029
Residual	197	22.4521		

Note: The p values below 0.05 are significant.

in the winter months (Appendix S1: Figure S1). The abundances of these insects begin to increase in October and November, reach their peaks in February and March, and largely decrease in April and May. Chewing insects were uncommonly collected throughout the year.

Through the use of PERMANOVA, a significant effect of salinity was found on the abundances of free-living

suckers, stem borers, parasites, and filterers, but not for predators, free-living chewers or scavengers/shredders (Table 4). There were significantly more sucking insects from the mid and high salinity zones than at the low salinity zone. Stem borers were significantly more abundant at the high salinity zone than at the mid or low salinity zones. Parasites were more abundant at low- and

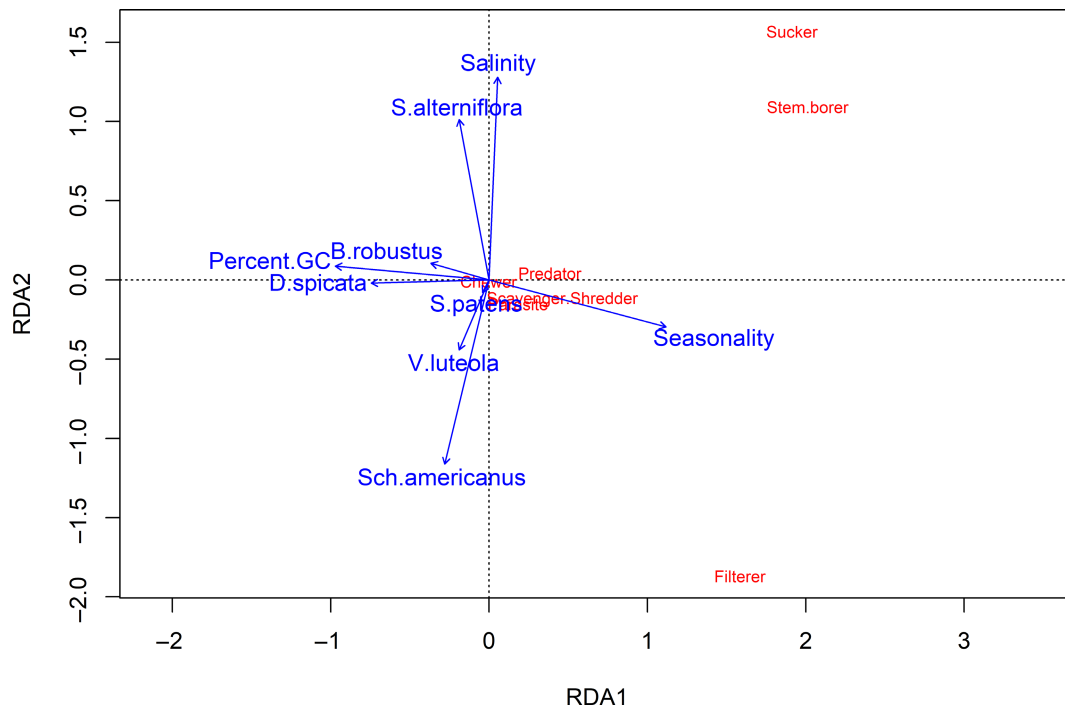


FIGURE 3 Distance-based redundancy analysis (db-RDA) biplot showing the important factors contributing to the variation in insect functional feeding guilds in Louisiana tidal marshes. The insects were collected from sites along the salinity gradient within Barataria and Caillou bays from July 2018 to June 2019. The x and y-axes are the dimensions which explain the most variation in the distribution of coastal Louisiana’s insects. Arrows that point in the same direction are positively correlated, while arrows that point in opposite directions are negatively correlated. The association of functional feeding groups with the explanatory factors is similarly displayed by proximity. For example, insects belonging to the filtering functional feeding group are typically found in low salinity habitat where *Sch. americanus* is present. Functional feeding groups positively correlated with the seasonality explanatory variable are present at similar abundances throughout the year.

TABLE 4 The average number of insects belonging to each feeding guild collected per site per collection trip from low, mid, and high salinity zones in Louisiana’s coastal marshes.

Feeding guild	Low salinity		Mid salinity		High salinity	
	Mean	SD	Mean	SD	Mean	SD
Sucker	15.8 a	18.6	73.2 b	119.2	73.1 b	163.4
Chewer	0.2 a	0.6	0.2 a	0.4	0.1 a	0.3
Stem borer	32.1 a	51.6	33.2 a	36.5	61.9 b	79.5
Predator	2.6 a	2.7	3.5 a	7.8	8.1 a	16.6
Parasite	1.9 a	2.7	2.0 a	2.4	0.9 b	1.1
Shredder/scavenger	4.3 a	3.9	4.2 a	6.3	2.6 a	4.2
Filterer	43.7 a	6.4	39.8 b	115.0	4.5 c	6.8

Note: Average abundances that are followed by the same letter do not differ between salinity zones.

mid salinity zones than at the high salinity zone. Filterers were found to decrease as salinity increased.

DISCUSSION

The composition of the plants present at the study sites (Table 1) was consistent with prior descriptions of typical brackish and salt marshes along the Gulf and Atlantic coasts with sites being dominated by *S. patens* and *S. alterniflora* (Greenberg & Maldonado, 2006; Lin et al., 2016; Lin & Mendelssohn, 1996). Despite differences in the plants present between bays, the plant species in the salinity zones of the two bays coincide with the three brackish and salt marsh vegetation types found in Louisiana and are typically stratified by both salinity and latitude (Penfound, 1938). The plants present at the low salinity zone were exemplary of intermediate marsh plant communities, plants at the mid salinity zone of brackish plant communities, and the high salinity zone of saline plant communities (Chabreck, 1970, 1972; Penfound, 1938).

As the underlying plant community has been shown to be important in affecting the abundance and distribution of native herbivores and because insect biodiversity is positively correlated to vegetation complexity within tidal marshes (Denno et al., 2002, 2009, 2016), it would be expected that as salinity increases, there should be a decrease in the family-level insect biodiversity due to both the decrease in plant species and intolerance to the high salinity environment. This study found that family-level insect biodiversity followed this trend for both the Shannon index- and Simpson inverse-associated Hill numbers (Table 2). Additional sampling is unlikely to change this finding as the rarefaction curves for each salinity zone leveled off (Figure 2).

The influence of vegetation texture (patch size, plant density, vegetation diversity, and host plant architecture) on free-living sucking insects is well understood, especially in coastal marshes (Denno & Roderick, 1991; Kareiva, 1983). Insects belonging to the sucking feeding guild tend to be monophagous or only feed on a small number of host plants, and they tend to be found in higher densities in pure stands of their host plants (Denno & Roderick, 1991; Kareiva, 1983; Risch et al., 1983; Sōgawa, 1982; van Emden, 1978; Wilson & O'Brien, 1987). Additionally, host plants that are more structurally complex support higher abundances of sucking insects (Denno & Roderick, 1991). This study finds that these plant-herbivore interactions differentially lead to elevated abundances of free-living sucking insects at the mid and high salinity zones when compared with the low salinity zone (Table 4). Increased abundances at sites within the high salinity zone are driven by nearly pure

stands of *S. alterniflora*, which is structurally simple (Denno, 1977; Tallamy & Denno, 1979). However, the elevated abundances of sucking insects at sites within the mid salinity zone where mixed host plant stands are common are driven by *S. patens* and *D. spicata*, which are structurally complex and provide increased microhabitats and alter the interactions between herbivorous insects and consumers (Blum, 1968; Denno, 1977; Denno & Roderick, 1991; Döbel, 1987; Tallamy & Denno, 1979). Additionally, while both *S. patens* and *D. spicata* are structurally complex, sucking insects within the mid salinity zone preferred sites where *D. spicata* made up a smaller proportion of the plant community (Figure 3). This is due to the tendency of *D. spicata* to grow intermixed with *S. patens*; sites where *D. spicata* was absent had elevated abundances of sucking insects due to the approach of near monocultures of *S. patens*.

Stem-boring insects similarly were most abundant at elevated salinities (Table 4), preferring sites within the high salinity zone where *S. alterniflora* was dominant (Figure 3). While the effects of vegetation diversity and density on the stem-boring functional feeding guild are not as well studied, it has been shown that stem-boring insects prefer and are more abundant on host plant species with larger stem sizes (Rathcke, 1976). The increased abundances of stem-boring insects at the high salinity zone mirror the shift in *S. alterniflora*, which has the thickest culms of the common host plants present (Blum, 1968; Denno, 1977; Tallamy & Denno, 1979), from existing only in bands at the lowest elevations to making up nearly the entire plant community as salinity increases. Additionally, the smaller patches of *S. alterniflora* at the low and mid salinity zones likely have lower abundances of stem borers due to decreased host seeking and colonization ability of herbivores in more diverse plant communities (Randlkofer, Obermaier, Casas, et al., 2010; Randlkofer, Obermaier, Hilker, et al., 2010; Stanton, 1983). *S. alterniflora* is also typically a low marsh plant (Adams, 1963; Pennings et al., 2005), and plants growing at the lowest elevations within salt marshes have been shown to be preferentially targeted by stem borers (Canepuccia et al., 2010). It should be noted that due to the collection methods employed in this study, stem-boring Lepidopterans appear to be heavily underrepresented when compared with other marsh inventories (Rickert et al., 2012). However, as the most abundant species of Lepidopterans in Louisiana's coastal marshes tend to be Crambid and Pyralid stem borers of *S. alterniflora* (Li & Pennings, 2017; White et al., 2005), it is likely that collections of these individuals would further exemplify the trends observed in this study.

The insects that typify the chewing functional feeding guild in coastal marshes tend to be Orthopteran

grasshoppers, katydids, and crickets found in stands of their preferred host, *J. roemerianus* (Davis & Gray, 1966). The most common chewing herbivore collected and observed in the field in this study were individuals of *Conocephalus spartinae* (Fox, 1912), which are particularly mobile and capable of avoiding sweep net sampling (Vince et al., 1981). While the absence of large stands of *J. roemerianus* (Table 1) and the mobility of individuals of *C. spartinae* partially explain the low abundances of chewing herbivores collected (Table 4), coastal marshes are atypical of grasslands in that they are frequently dominated by sucking as opposed to chewing herbivores (Evans & Murdock, 1968; Vince et al., 1981). Future studies inventorying Gulf Coast marsh insects will likely observe relatively higher abundances of chewing herbivores if conducted in sites with pure stands of *J. roemerianus* or if a different collection method is used, but sucking herbivores are likely to remain far more abundant regardless of plant community composition or collection method.

The factors influencing the abundances of insects in the consumer trophic guild are more complex than those affecting the distribution of herbivorous insects. While insects belonging to the consumer trophic level have been shown to be positively correlated with plant diversity and plant architectural structure, the factors behind this are debated; increased prey densities, access to alternative prey, decreased intraguild predation, and alternative resources have been argued as possible mechanisms (Langellotto & Denno, 2004). Notably, pollen has been shown to be an important alternative resource for predatory coccinellid beetles in coastal marshes, increasing populations by up to 400% when present (Long & Rinehart, 2019; Rinehart & Long, 2018). It is likely that both the dampening of intraguild predation due to increased plant architectural structure (Finke & Denno, 2005; Langellotto & Denno, 2004) and the access to alternative resources available in the more diverse plant communities at the low and mid salinity zones play an important role in explaining the distribution of insects at the consumer trophic level. In this study, insects belonging to the predatory feeding guild did not exhibit differences in abundances between salinity zones even though both the mid and high salinity zones had far more potential herbivorous prey than the low salinity zone (Table 4). Similarly, insects belonging to the parasitic feeding guilds collected in this study were most abundant at the more vegetatively diverse low and mid salinity zones where structurally complex grasses made up most of the ground cover despite the decrease in potential target hosts and with increased difficulty in locating target hosts on structurally complex plants and within habitats with increasingly diverse plant

communities (Kruidhof et al., 2015; Obermaier et al., 2008; Randlkofer, Obermaier, Casas, et al., 2010; Randlkofer, Obermaier, Hilker, et al., 2010). Taken together, these findings indicate that within coastal marshes the refuge from intraguild predation and access to the alternative resources present at the low and mid salinity zones offset the higher abundances and easier location of prey and host insects at the high salinity zone for predatory and parasitic insects.

The distribution of detritivorous insects within the filtering functional feeding group is predominantly explained by salinity (Figure 3). As the larval life stages of these insects develop either aquatically or in frequently inundated soils and because the adults may have poor dispersal ability, the distribution of the detritivores insects is limited primarily by their salinity tolerance with far lower abundances of filtering insects being collected as salinity increases. Insects belonging to the shredders/scavenger trophic guild were collected far less often than filtering insects and were not highly influenced by salinity (Table 4). Similarly, they do not appear to be highly influenced by the plant community (Figure 3). It is likely that many noninsect invertebrates such as salt marsh snails and crustaceans are more important in fulfilling the role of shredder/scavenger in these coastal environments (Rietsma et al., 1982; Zimmer et al., 2004).

Throughout the year-long inventory, all insect functional feeding guilds, except for the uncommonly collected chewing guild, displayed similar patterns of seasonal abundances (Appendix S1: Figure S1) with the total number of insects peaking in February and March. Due to the unexpected winter occurrence of feeding guild population peaks in this study and the high explanatory value of seasonality for certain feeding guilds (Figure 3), future studies on Gulf Coast insect functional feeding groups should make sure to take these seasonal fluctuations into account. Seasonality has also been shown to be an important factor in structuring the family-level distribution of insects in Louisiana's coastal marshes (Aker, 2020), furthering the need for more temporally broad studies when focusing on insect taxa.

The salinity gradient and the shift in the diversity and structural complexity of the coastal plant community which it underlies are major sources of variation in the most abundant herbivore, consumer, and detritivore feeding guilds. Structurally complex plant species support elevated abundances of sucking and parasitic feeding guilds and appear to mediate the distribution of predatory insects while increasingly vegetatively diverse plant communities appear to be primarily beneficial only for functional feeding groups within the consumer trophic level. The high salinity zone has the largest abundances

of herbivorous insects despite being dominated by a structurally simple plant as it consists of nearly pure stands of the large-stemmed *S. alterniflora* which benefits both sucking and stem-boring insects. Filtering insects within the detritovore trophic level are most directly influenced by salinity of any of the functional feeding groups, being in direct contact with brackish and saline water during their immature life stages. The chewer and scavenger/shredder functional feeding groups are relatively rare compared with other groups within their trophic levels (Appendix S1: Tables S1 and S2) and neither respond heavily to changes in the salinity gradient or plant community. The free-living sucking, stem-boring, and filtering functional feeding groups are the most abundant and, along with the parasitic functional feeding group, the most sensitive to changes within Louisiana's coastal marshes. As such, these functional feeding groups are the most important to monitor to provide the best insights into how changes in the salinity regime through freshwater diversions or saltwater intrusion are affecting coastal habitats. For example, monitoring of insect communities following a freshwater diversion should detect an increase in overall biodiversity as well as an increase in individual insects from the parasite and filterer functional feeding groups and a decrease in herbivorous insects, whereas the opposite could be predicted to occur in an area heavily impacted by saltwater. Overall, these data illuminate how insect functional feeding groups are distributed within a Gulf Coast marsh in relation to the plant community and underlying salinity gradient and provide much-needed baselines for possible long-term ecological monitoring programs for the Gulf of Mexico.

ACKNOWLEDGMENTS

We thank M. Becker, D. Davis, and J. Lucero for their assistance in data collection; I. Sokolov for providing reference material for coastal Hemiptera and Diptera; and N. Lord for his advice on manuscript preparation. This work was supported by a grant to Lane D. Foil and Claudia Husseneder by the Gulf of Mexico Research Initiative Research Board (grant agreement no. 231613-00). Insect family abundance data collected in this experiment were submitted to the Gulf of Mexico Research Initiative Information and Data Cooperative (UDI: R5.x277.000:0007).


CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Aker et al., 2021) are available from the Gulf of Mexico Research Initiative Information and Data Cooperative: <https://doi.org/10.7266/W11BZDDR>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Aker, Benjamin G., Claudia Husseneder, and Lane D. Foil. 2023. "The Influence of Salinity and Vegetation Texture on the Ecological Roles of Insects in Tidal Marshes in Louisiana." *Ecosphere* 14(12): e4692. <https://doi.org/10.1002/ecs2.4692>