

INSECT COMMUNITIES IN RESTORED
AND REFERENCE TIDAL
SALT MARSHES

by

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ABSTRACT

Recovery of species richness, species composition, and biogeochemistry in restored wetlands often fails to reach levels of reference wetlands. While the effects of restoration on plant and non-insect macroinvertebrate communities are relatively well-studied, much less is known about the impacts of wetland restoration on insect communities. The aim of this research was to determine if observed differences in biological structure between one reference and two restored *J. roemerianus*-dominated marshes extends to insect communities within these ecosystems. Sampling methods included pan trapping, line transect netting, floral observations, floral clippings, and light trapping. All insect taxa and functional groups were identified monthly from April – October 2021 and analyzed for taxa richness, abundance, and H' diversity. Floral density and herbivory scars on *Juncus* shoots were also measured during flowering and peak growing season, respectively. Results indicate that reference marshes supported a more diverse insect community than restored marshes, although insect abundance and taxa richness were similar among sites. Additionally, temporal patterns in the relative abundances of insect taxa and functional feeding groups differed among marshes, and likely reflected differences in habitat surroundings among sites. By researching structural differences in insect communities between reference and restored marshes, we can further understand the community composition of an understudied group of organisms, potentially improve restoration strategies, and support the health of both wetlands and the insects that inhabit them.

LIST OF ABBREVIATIONS AND SYMBOLS

AL	Alabama
ANOVA	Analysis of Variance
cm	Centimeters
CON	Constructed
CON-1	Constructed 1
CON-2	Constructed 2
DC	Direct current
DNRA	Dissimilatory nitrate reduction to ammonium
=	Equals
<i>F</i>	F-statistic
e.g.	For example
H'	Shannon-Wiener Diversity
HSD	Honest significant difference
i.e.	In other words
LULC	Land use/ land cover
<	Less than
L	Liters
m	Meters
m ²	Meters squared
mL	Milliliters

MS	Mississippi
MANOVA	Multivariate analysis of variance
NAT	Natural
NMDS	Non-metric multidimensional scaling
NPP	Net primary production
N	Nitrogen
%	Percent
PERMANOVA	Permutational multivariate analysis of variance
±	Plus or minus
PVC	Polyvinyl chloride
<i>p</i>	Probability of rejecting null hypothesis
SE	Standard Error
SIMPER	Similarity percentage analysis
<i>t</i>	t-statistic
U.S.A.	United States of America
UV	Ultraviolet
V	Volts

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INTRODUCTION

Coastal wetlands provide a multitude of ecosystem services including abating erosion, buffering storm damage, purifying water, transforming and intercepting nutrients, countering the effects of sea level rise, and supporting economically valuable fish and invertebrate species (Moreno-Mateos et al., 2012; Morgan et al., 2009; Nelson & Zavaleta, 2012; Whitfield, 2017). However, human-induced environmental change threatens coastal wetlands and the ecosystem services that they provide (Costanza et al., 2008; Craft et al., 1999; Torio & Chmura, 2013). It is estimated that nearly half of all the wetland ecosystems that existed in the early 20th century have been lost in North America, Europe, China, and Australia (Mitsch & Gosselink, 2007; Moreno-Mateos et al., 2012). Furthermore, with rising sea levels, coastal development, and urbanization, many more coastal wetlands may be lost in the future, leading to further reductions in the delivery of ecosystem services (Craft et al., 1999; Torio & Chmura, 2013). To mitigate these losses, restoration and creation efforts have attempted to recover the structure and function of wetland habitats at levels similar to reference coastal wetlands (Davidson, 2014).

Despite these efforts, restored and created wetlands (hereafter, restored) often fail to reach structural and functional equivalence with reference wetlands. In fact, the majority of restored wetlands fail to achieve similar levels of species richness, species composition, biodiversity, carbon sequestration, or rates of nutrient cycling for decades following restoration (Craft et al., 1999; Langis et al., 1991; Sacco et al., 1994; Tatariw et al., 2021; Zedler & Callaway, 2000). For example, plant communities in restored wetlands may take up to 30 years to recover, while non-insect macroinvertebrate communities may require a decade or more

(Meyer & Whiles, 2008; Moreno-Mateos et al., 2012). Further, biogeochemical functions, including carbon storage, nitrogen removal, and soil organic matter accumulation, are often significantly lower in restored wetlands than reference sites (Craft et al., 1999; Langston et al., 2022; Moreno-Mateos et al., 2012; Zedler & Callaway, 1999). Collectively, these findings suggest that restored marshes functionally lag behind reference marshes in their provision of ecosystem functions and services. While it is established that marsh plant communities and biogeochemical functions often take time to recover, we know considerably less about the potential for insect communities to recover in these restored wetland ecosystems.

Insect communities, particularly within coastal salt marshes, are an important yet understudied component of wetland communities (Sokolov et al., 2018). Prior work on wetland insects has primarily focused on freshwater ecosystems (Dijkstra et al., 2014; Rochlin et al., 2011; Sokolov et al., 2018). Furthermore, while some research has investigated the trophic structure and community composition of salt marsh insects, these studies primarily focused on herbivorous insect assemblages (Cameron, 1972; Denno, 1977; Gratton & Denno, 2006; Noriega et al., 2018; Suter & Cormier, 2015). More research is warranted in this area, as insects are known to shape biological structure and function in salt marsh ecosystems (Merritt et al., 2019; Noriega et al., 2018; Pimentel et al., 1992; Sparks & Cebrian, 2015; Suter & Cormier, 2015). For example, insects belonging to the herbivore and omnivore feeding groups are efficient cyclers of nutrients, such as nitrogen, within various types of wetlands (Low & Sparks, 2017; Merritt et al., 2019; Montemayor et al., 2018). Herbivorous insects are also known to regulate marsh net primary production (NPP) by reducing aboveground biomass, and insects often support higher trophic levels by acting as a major food source for birds and fish (Merritt et al., 2019; Suter & Cormier, 2015). Insect pollinators may play a significant role in wetlands as well, as some are

specialist pollinators of select wetland plant species and there is evidence to suggest that insect pollinators in salt marshes may utilize *Juncus*, a common brackish and salt marsh plant genus, as a floral resource (Center et al., 2002; Huang et al., 2013; Merritt et al., 2019). Therefore, by classifying insects into functional feeding groups, the implications of observed differences in insect community structure on marsh ecosystems can be better interpreted. Additionally, because insects can generally shape community structure and regulate ecosystem functions of wetlands, it is likely that the same is true for constructed tidal salt marshes (Batzer & Wissinger, 1996; Crawley, 1997; Noriega et al., 2018; Pennings et al., 2009).

Through this research, I evaluated the recovery of critical insect communities and functional groups in two restored tidal wetlands and one reference wetland along the northern Gulf of Mexico in Alabama, U.S.A. The objective of this research was to compare the structure of insect communities in these tidal marshes. There are observed differences in the biological structure and ecosystem functions of these sites (Smyth 2020; Ledford et al. 2021; Tatariw et al. 2021), but it is unknown if these differences extend to insect communities. The two main hypotheses for this research were that (1) insect richness, abundance, and diversity are higher in the reference marsh than in either restored marsh, and (2) temporal patterns of change in the relative abundances of taxa and functional groups are similar among marshes while insect community structure varies among marshes.

METHODS

Study Site Description

The study sites included one natural (i.e., reference) tidal marsh (NAT, -88.160' N, 30.368' W) and two 34-year-old, restored (i.e., constructed) salt marshes (CON-1, -88.152' N, 30.368' W, and CON-2, -88.151' N, 30.367' W) located near the mouth of the West Fowl River in Mobile County, AL, U.S.A (Figure 1). All three marshes are located within 1 km of each other, with NAT directly connected to West Fowl River and CON-1 and CON-2 hydrologically connected to NAT via a main canal created at the time of marsh construction. All three sites experience diurnal microtides of approximately 0.26 m (Smyth, 2020). The two constructed marshes were created in 1987 as a mitigation site through the harvest and excavation of pine savannah in long, parallel strips that lowered the elevation to near sea level (Vittor et al., 1987). An access road divides CON-1 and CON-2. After the initial excavation of the sites, canals were created through the center of each marsh to connect them to the main canal, which links to a tidal creek originating in the natural marsh (Vittor et al., 1987). The canals and tidal creeks in these marshes are lined with a narrow (< 1 m) band of *S. alterniflora*, but the marsh platforms of all three marshes are dominated by *Juncus roemerianus*. The platform at NAT also contains an assemblage of other salt marsh plant species, such as *Spartina alterniflora*, *S. patens* and *Distichlis spicata* as sub-dominates (Fromenthal, pers. obs.; Smyth, 2020; Tatariw et al., 2021).

Previous studies at these sites demonstrated that NAT and CON marshes differ in their biological structure and ecosystem function. For instance, NAT had greater aboveground and belowground plant biomass, more soil organic matter and carbon content, and higher rates of

denitrification and dissimilatory nitrate reduction to ammonium (DNRA) than CON marshes (Tatariw et al., 2021; Smyth, 2020), although fluxes of carbon dioxide were similar between similarly vegetated plots in NAT and CON marshes (Ledford et al. 2021). These observed differences in biogeochemical pathways may affect nutrient stocks and availability to plants (Batzer & Sharitz, 2014; Belovsky & Slade, 2001; Montemayor et al., 2018). Changes within the soil chemistry can also affect the timing and intensity of flowering in salt marsh plants (Batzer & Sharitz, 2014; Michalski & Durka, 2007). Therefore, given these differences, these sites are appropriate locations in which to examine whether observed differences in plant community structure, soils, and nutrient processing rates between reference and restored marshes also are observed in insect communities.

Insect Sampling

To compare insect communities between reference and restored marshes, I conducted insect surveys in randomly selected *J. roemerianus* stands at each marsh over the full plant growing season (April – September 2021). Four replicate quadrats (approximately 10 m²) were established per marsh within *J. roemerianus* stands to collect insects using a variety of replicated survey methods, including pan trapping, line transect netting, and flower collection, as described below (n = 4 per marsh). Within one randomly selected site per marsh, I also collected insects via light trapping (n = 1 per marsh), which sampled insects from a larger area than the replicated quadrats used for other sampling methods.

Replicated Insect Sampling Methods

To account for pollinators and other flying insect taxa, I established 12 colored pan traps (Figure 2) in each of the four quadrats per marsh. These pan traps (30 mL; 5 cm diameter) were placed on platforms positioned at the average inflorescence height of the surrounding *J.*

roemerianus stand to ensure that they were at an optimal height for attracting pollinators (Figure 2; Montgomery et al., 2021). The platforms were made of PVC pipes with open, 36 x 30 x 8 cm plastic storage containers secured on top, in which the 12 pan traps were placed (Montgomery et al., 2021). Sets of pan traps included four traps of each color that were painted either blue, yellow, or white to attract a variety of insect taxa (Figure 2). They contained a solution of ~2.5 cm of water mixed with several drops of unscented dish soap, which was prepared as described in Montgomery et al. (2021). Once per month, I deployed the pan traps in the field for 20 – 24 hours. Upon collection, insects were preserved in 70% ethanol to later be identified and archived in the lab at the University of Alabama (Boyer et al., 2020).

In addition to pan traps, I conducted line transect netting once per month in each of the four quadrats at each marsh (n = 4 per marsh). Within each quadrat, I established one transect (5 m long) running parallel to the access road and the excavated tidal canal in the constructed and natural marshes, respectively. Around mid-day, I swept each transect for 5 minutes using a 30-cm ringed, fine-meshed net suitable for retaining macroinvertebrates (BIOQUIP Student Insect Net). Upon collection, all insects were preserved temporarily in Ziploc bags containing a paper towel soaked in 70% ethanol before being transferred to scintillation vials filled with 70% ethanol. Upon return to the lab, insects were identified and pinned or otherwise preserved (Boyer et al., 2020).

Light Trap Sampling Method

To attract night-flying insects, I conducted light trapping monthly in one, randomly selected quadrat per marsh using an ultraviolet light (BIOQUIP's Night Collecting Light, DC, 12 Volt, 15 Watt Blacklight). Light traps have been shown to attract flying insects from distances as far as 40 m (Kirkeby et al., 2013), and they capture many more individuals per trap than the

other sampling approaches in this study. To maximize the effectiveness of each trap and for logistical reasons, I deployed only one light trap per marsh ($n = 1$ per marsh), for a total of three light traps overall. Light trapping was conducted in the same quadrat in each marsh from month-to-month. This light trap apparatus consisted of a platform that supported a white plastic container (36 x 30 x 8 cm) holding approximately 2 L of the same soap and water solution used in the pan traps (Montgomery et al., 2021) (Figure 3). A suspended UV light was positioned above each plastic container to attract night-flying insects. Light traps remained in the field overnight, and insects were collected the following morning. Upon collection, they were transferred into 50-mL conical centrifuge tubes (VWR Inc.) containing 70% ethanol for subsequent identification, preservation, and storage in the lab.

Due to the large number of insects captured by the light traps, I used a subsampling method to estimate the composition of insects collected. Similar to that described by Dođramaci et al. (2010), sample compositions were estimated using a grid system. Insect samples were poured into a pan (28 x 20 cm) that was evenly divided into 16 cells. All cells were first scanned by eye and then under a stereo microscope for rare insects (MOTIC SMZ-140 and Meiji Techno EMZ-8TR). Then, four randomly selected cells within each sample were pooled together for identification. Lastly, the total number of insects of each identified taxa were multiplied by four to estimate the overall abundance of insect taxa within the 16-cell pan.

In addition to the insect surveying methods described above, inflorescences were collected once per month during the flowering period of *J. roemerianus* in April, May, and June (Eleuterius, 1975) in each quadrat ($n = 4$) to account for inconspicuous and/or minute taxa. Near mid-day, the inflorescences were clipped and quickly dropped into jars containing 70% ethanol (Montgomery et al., 2021). The inflorescences were later analyzed for insects using stereo

microscopes (MOTIC SMZ-140 and Meiji Techno EMZ-8TR). As with all other insects collected, they were archived in the lab after identification.

Timed floral counts also were conducted monthly in each quadrat per marsh during May, June, and July (Boyer et al., 2020). Timed floral counts consisted of observing and filming *J. roemerianus* inflorescences within a 0.25 m² area for a total of five minutes per quadrat during each of the three months, with observed insect visitations recorded in a field notebook. Insects captured on film were identified to the lowest taxonomic level possible. Identification of insect taxa was largely successful, as subsequent film analysis revealed that several insect taxa were observed visiting *J. roemerianus* inflorescences during floral surveys, including soldier beetles (family *Cantharidae*) during May and June (Figure 4). Thrips belonging to family *Phlaeothripidae* and suborder Terebrantia were also found on inflorescences across the entire sampling period. While most insects visiting inflorescences were identified, minute flying insects could not be visually identified to taxa. Identified taxa were included in abundance counts for the months in which surveys were performed.

Floral Counts and Herbivory

To quantify the density of *J. roemerianus* inflorescences potentially available as a resource to insect pollinators, I counted inflorescences in all four quadrats of each marsh in June. Inflorescence counts were recorded within each quadrat (n = 4 per marsh) by randomly selecting four smaller, sub-quadrats (0.25 m²) per quadrat in each marsh. These smaller samples were averaged to determine inflorescence counts for each quadrat.

Lastly, herbivore damage was quantified by clipping *J. roemerianus* stems at the soil surface within four randomly selected 0.25 m² sub-plots in each of the quadrats per marsh in September. Upon collection, clippings were bagged and brought back to the lab for analysis,

where they were then photographed and analyzed for percent surface area of herbivory damage using ImageJ software. To do this, shoots were laid flat and secured. Each side of a shoot was photographed and analyzed using ImageJ software (<https://imagej.nih.gov/ij/>, 1997-2018) to determine its total area and area scarred by herbivore grazing. The percent surface area of herbivory on each side of the shoots was quantified by dividing the area affected by herbivory by the total area of shoots. By measuring damage in September, this approach reflects the cumulative extent of herbivory throughout the growing season (Montemayor et al., 2018).

Habitat Classifications

To explore the possibility of differences in resource availability at the Fowl River sites, I quantified the relative area of habitats at each marsh by creating a land use/land cover (LULC) map using the ESA WorldCover 10m v100 dataset in Google Earth Engine. Around each sampled quadrat ($n = 4$ per marsh), I defined a 250 m radius in which to characterize habitat types. Habitats included open water, herbaceous wetland, grassland (marsh), forests, developed areas, and barren. All quadrats were combined for each marsh and the percent area of each habitat type was determined.

Statistical Analyses

The combination of sampling approaches was designed to target multiple insect taxa across various functional feeding groups (i.e., functional groups) with different phenologies, behaviors, and life history traits. Insect taxa and functional groups were identified to the lowest taxonomic level possible using relevant literature (Center et al., 2002; Eaton & Kaufman, 2007; Holland, 1968; Howard, 1908; Merritt et al., 2019). For some taxa, the lowest taxonomic level was family, so all taxa were subsequently analyzed at the family level to standardize across groups. Once classified, individual taxa were assigned to the following functional groups for

statistical analysis: herbivore, omnivore, pollinator, predator, and mixed feeding group. Classifications were primarily based on those utilized by Gratton and Denno, as well as aquatic macroinvertebrate functional feeding groups (Gratton & Denno, 2005; Merritt et al., 2019). The array of sampling methods utilized allowed for collection and identification of the broader insect communities at these sites, thereby permitting an overall comparison of insect communities between the natural and constructed marshes.

Data were separated by sampling method for statistical analyses because of the lack of replication in light trap samples. Samples collected from all replicated sampling methods (e.g., pan traps, net sweeping, inflorescences, and timed floral surveys) were combined and analyzed using a combination of univariate and multivariate approaches. Taxa richness was quantified by counting the number of taxa identified in each family for all sampling methods. Abundance was determined by counting the number of individuals sampled for each taxa. Lastly, Shannon-Wiener (H') diversity was calculated using the formula $H' = -\sum_{i=1}^R p_i \ln p_i$, where R is the total number of taxa and p_i is the proportion of individuals of the i th species out of the total number of individuals. Differences in taxa richness, abundance, and H' among marshes were tested using one-way analysis of variance (ANOVA) tests with marsh as the fixed effect ($n = 4$ per marsh). Where significant marsh effects were found, I performed Tukey's HSD tests for post-hoc comparisons. Univariate analyses were performed in JMP Pro 15.0.0 (SAS Institute Inc.).

To examine changes in relative abundances of insect taxa and key functional groups over time, I performed separate permutational multivariate analyses of variance (PERMANOVAs) tests with marsh ($n = 4$) and month ($n = 6$) as fixed factors. Repeated observations were nested within marsh as a random effect to account for the repeated sampling of plots throughout the plant growing season. When differences among marshes or months were detected, post-hoc

pairwise t-test comparisons were performed using permutations of residuals. These analyses are a non-parametric approach to analyze the relative abundances of the collected data. Pseudo-F ratios based on a Bray-Curtis similarity matrix of square-root transformed relative abundance data of taxa and functional feeding groups were also generated. Where significant differences were discovered through the PERMANOVA, a similarity percentage analysis (SIMPER) was conducted to identify the taxa or functional groups driving differences. Separate non-metric multidimensional scaling (NMDS) plots for taxa and functional group data were created using a Bray-Curtis similarity matrix of square-root transformed relative abundance data in sampled quadrats. NMDS bubble plots were also created to visualize temporal changes of relative abundances for each functional feeding group. Multivariate tests were performed in Primer 7.0.21 (Primer-e).

The average number of inflorescences was quantified by averaging the number of inflorescences counted in the four 0.25 m² subplots for each marsh to generate one value per quadrat (n = 4 per marsh). Differences in floral counts among marshes were then analyzed using pairwise t-tests. Percent area of herbivory was quantified by taking the average percent area of shoots covered with herbivory scars and dividing it by the total surface area of shoots. Differences among marshes were analyzed using a Wilcoxon rank sum test, as data did not meet assumptions for normality. For all statistical tests, statistical significance was set at $\alpha = 0.05$ level.

RESULTS

An estimated 12,480 individuals were collected during all sampling approaches from April to September 2021, representing 83 unique taxa across the five functional feeding groups (Appendix). Most insects were captured in light traps, which accounted for 11,289 individuals (90.5%) and 49 taxa, 31 of which were found exclusively in light traps. The remaining 1,191 insects (9.5%) were captured through pan traps, floral observations, inflorescence collections, and net sweeps. Functional feeding groups included herbivores, omnivores, predators, pollinators, and a mixed feeding group for taxa whose functional feeding group depends on sex and life history stage. The most abundant taxa identified across all marshes, months, and sampling methods were *Temnothorax* (acorn ants; family *Formicidae*), *Chironomidae* (non-biting midges), and *Ceratopogonidae* (biting midges).

Insect Richness, Abundance, and Diversity Among Marshes

Abundance and taxa richness for insects sampled in replicated pan traps, net sweeps, and floral observations were similar among marshes ($p > 0.05$). However, H' diversity was significantly higher in NAT than in CON-2 ($F_{2,9} = 9.89$, $p = 0.005$). H' diversity was also slightly higher, albeit not significantly, in NAT than CON-1 (Table 1).

Changes in Insect Community Composition Over Time

While the relative abundances of functional groups did not differ significantly among marshes (no marsh effect), they did change significantly over time (month effect: $Pseudo-F_{5,70} = 7.59$, $p = 0.001$). Generally, the relative abundances of the five functional groups were similar early in the growing season but began to diverge after June. Specifically, the relative abundances

of functional groups in June were significantly different from April ($p = 0.015$), May ($p = 0.012$), and August ($p = 0.002$). SIMPER analyses revealed that, between the months of April and May, the average relative abundances of pollinators increased slightly (23.52 to 25.76%), while average relative abundances of both predators and omnivores decreased (25.86 to 13.36% and 20.38 to 15.21%, respectively). June coincided with a large increase in the relative abundance of herbivores, from an average of 14.78% in May to 53.72% in June. August also differed from several other months, including April ($p = 0.013$), May ($p = 0.016$), June ($p = 0.002$) and July ($p = 0.03$). These differences were primarily driven by greater relative abundances of omnivores in August. Lastly, September differed from all other months except August due to greater average relative abundances of omnivores.

More importantly, these patterns of temporal change in insect functional groups were not consistent across marshes (marsh x month interaction: $Pseudo-F_{10,70} = 2.13$, $p = 0.002$) due to differences in their relative abundances early in the growing season. In both April ($p = 0.013$) and May ($p = 0.01$), CON-1 differed significantly from NAT, signifying that the contributions of functional groups to the average relative abundance of each marsh differed. In all other months, however, the three marshes had similar relative abundances of functional groups. In both CON-1 and NAT, omnivores, herbivores, and pollinators were the main contributors to overall relative abundance, while in CON-2, predators were the third largest contributor instead of pollinators. These results demonstrate that marshes behaved differently over time and supported dissimilar relative abundances of functional groups early in the growing season.

Similar to trends in the functional group data, relative abundances of insect taxa did not differ among marshes (no marsh effect) but did vary over time (month effect: $Pseudo-F_{6,71} = 5.78$, $p = 0.001$). Insect communities were most dissimilar early in the growing season before

relative abundances of taxa converged at the peak of the growing season. Also, temporal patterns of relative abundances of taxa differed by marsh (marsh x month interaction: $Pseudo-F_{12, 71} = 1.42, p = 0.002$). Specifically, in both April ($p = 0.039$) and May ($p = 0.037$), CON-1 supported different communities than NAT. Most notably, in April, both *Micropezidae* (stilt-legged flies) and *Lestidae* (spreadwinged damselflies) were found in CON-2 and NAT, but not in CON-1. CON-1 also supported higher average relative abundances of *Syrphidae* (hover flies) in April than the other two marshes. Higher average relative abundances of *Tabanidae* (horseflies) in CON-1 drove significant differences between CON-1 and NAT in May. In June, July, and August, all marshes supported similar relative abundances of taxa. Lastly, September data revealed that relative abundances of insect taxa began to diverge again at the end of the growing season, with CON-2 becoming dissimilar from NAT ($p = 0.043$) due to greater relative abundance of *Drosophila* (common fruit fly) in CON-2.

Herbivory and Inflorescence Counts

During the flowering period in May and June, the average number of *J. roemerianus* inflorescences did not differ between marshes, although it tended to be higher in CON-1 than CON-2 and NAT (Fig 6A). This result suggests that the availability of floral resources for pollinators was similar across sites. However, herbivory damage, which was measured as the percent surface area of *J. roemerianus* shoots affected by insect grazers, was significantly higher in NAT than in CON-1 and CON-2 ($\chi^2_{(2, n=4)} = 7.73, p = 0.02$).

Habitat Classifications

The percent area of habitat types surrounding sampled quadrats varied between sites (Table 2). Specifically, CON-1 and CON-2 had greater percent area of forest habitat (67% and 61%, respectively) than NAT (19%). CON-1 also contained a smaller area of herbaceous, or

regularly-inundated, wetlands than the other two marshes (Figure 7), with CON-1 having 3% of its radii covered in herbaceous wetlands. In contrast, CON-2 and NAT contained 11% and 16%, respectively. The percent area of grasslands (marsh) was similar across all quadrats, but open water habitat made up a much larger percent of the area in NAT (23%) than in CON-1 and CON-2 (0% in both).

Table 1. Mean (± 1 SE) abundance, taxa richness, and diversity of insects in the two constructed marshes (CON-1, CON-2) and the natural marsh (NAT) based on replicated pan trapping, sweep netting, and inflorescence surveys during April – September ($n = 4$ per marsh). Letters denote significant differences among pairwise comparisons tested using Tukey’s HSD. Light trap data were not included due to lack of replication.

Marsh	Abundance	Richness	H' Diversity
CON-1	117 \pm 14.22	19.75 \pm 1.65	1.76 \pm 0.13 ^{ab}
CON-2	190.75 \pm 56.61	19 \pm 2.74	1.04 \pm 0.20 ^b
NAT	83 \pm 33.91	19 \pm 2.83	2.30 \pm 0.25 ^a

Table 2. Percent area (%) of habitat types for each marsh as detected by remote satellite imagery.

Class Code	Habitat	CON-1 % Area	CON-2 % Area	NAT % Area
10	Trees	67%	61%	19%
30	Grassland	27%	25%	33%
50	Developed	0%	0%	3%
60	Barren	3%	3%	6%
80	Open Water	0%	0%	23%
90	Herbaceous Wetland	3%	11%	16%

Figure 1. Map of the study site (indicated by the star) along the Mississippi (MS) – Alabama (AL) state border. The study site included one natural (NAT) and two constructed (CON-1, CON-2) marshes along the West Fowl River in southwestern Mobile County, AL, U.S.A. (inset).

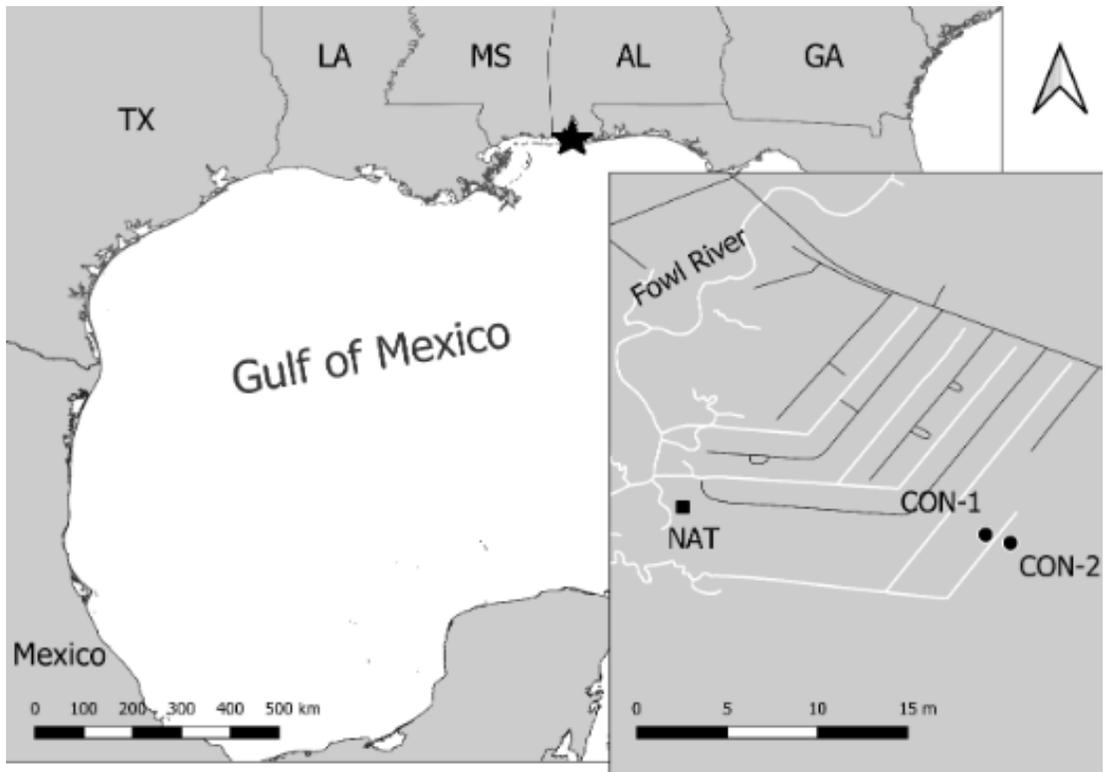


Figure 2. Pan traps of various colors designed to attract a range of pollinator taxa



Figure 3. The light trap apparatus comprised of a platform made of PVC pipes and wood. On the platform sits a 36x30x8 cm plastic storage container filled with dish soap and water. Above this container sits a securely suspended UV light powered by a 12V battery.

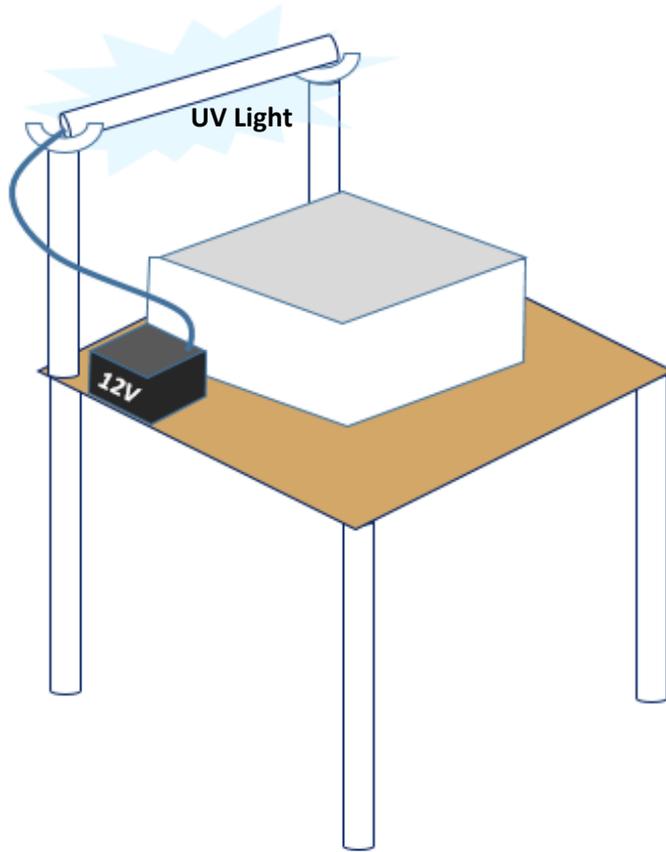


Figure 4. A soldier beetle, circled in white, visits a *J. roemerianus* inflorescence in May.



Figure 5. Relative abundances of pollinator and herbivore functional feeding groups in marsh plots over time, as shown in a Non-Metric Multi-Dimensional Scaling (NMDS) plot. Bubble size corresponds to the relative abundance of pollinators while colors correspond to months. The closer samples are in ordination space, the more similar the communities are to one another.

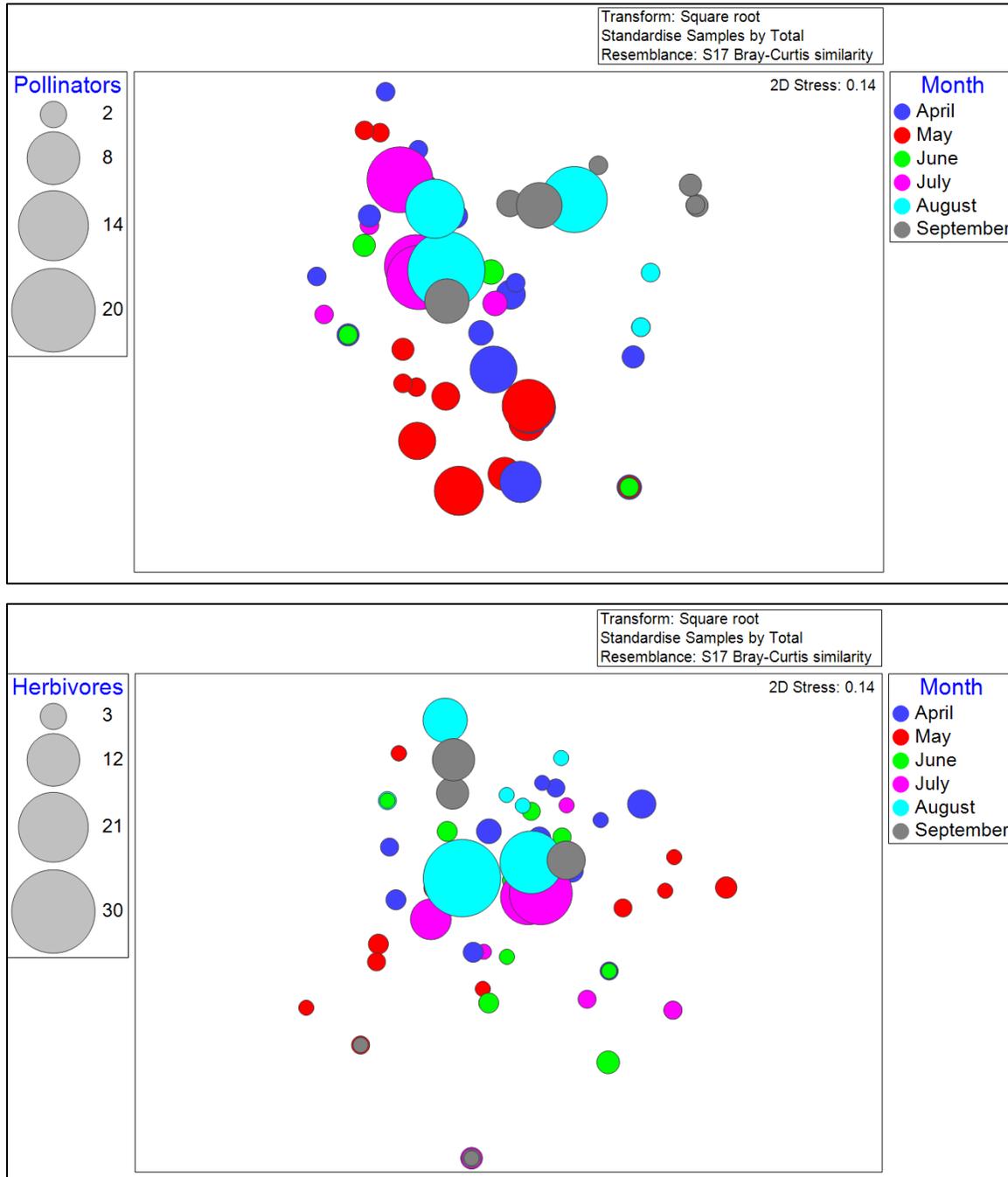


Figure 6. Mean (± 1 SE) (A) *J. roemerianus* inflorescences per 0.25 m² plot (n = 4) and (B) percent surface area of herbivory scars on *J. roemerianus* shoots in each marsh (n = 4). Asterisk denotes significantly greater herbivory in NAT compared to CON-1 and CON-2, based on a Wilcoxon rank sum test.

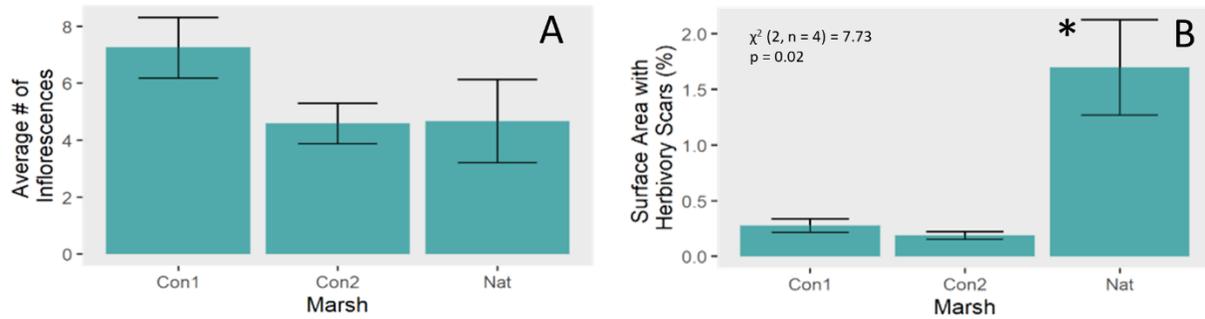


Figure 7. A map of study sites overlaid with land use/land cover (LULC) data. Habitats were classified within a 250 m radius of each sampling quadrat. Habitat classifications: blue = open water; teal = herbaceous wetlands; yellow = grasslands/irregularly inundated wetlands; green = forest habitat; and grey/red = urban/barren areas.



DISCUSSION

Understanding insect communities in tidal salt marshes is valuable, as insects are known to be some of the most abundant yet most understudied macroinvertebrates in these ecosystems (Center et al., 2002; Hatcher et al., 1997). Because insects are highly abundant in wetlands and can regulate ecosystem services (Belovsky & Slade, 2001; Merritt et al., 2019; Montemayor et al., 2018; Suter & Cormier, 2015), differences in trophic structure between restored and reference marshes may have implications for the resilience and functional equivalence of restored sites. This research demonstrated that insect communities in constructed marshes have generally recovered to reference levels of taxa richness and abundance, but they may be less diverse after 34 years. Further, temporal patterns of insect community composition varied among marshes, especially early in the growing season. These differences in insect diversity and temporal patterns of relative abundance may correspond to ecologically relevant differences in trophic interactions among sites, which have yet to be explored, and may reveal the potential role of insects as pollinators of *J. roemerianus*, a dominant salt marsh macrophyte largely believed to be anemophilous. Consequently, these findings also have implications for evaluating restoration outcomes.

Constructed Wetlands Fail to Reach Reference Diversity

It is well-established that restored wetlands struggle to reach structural and functional equivalence to reference wetlands (Moreno-Mateos et al., 2012; Tatariw et al., 2021). Prior research has revealed that macroinvertebrate communities in restored marshes can take up to a decade to statistically converge with reference communities (Craft et al., 1999; Langis et al.,

1991; Sacco et al., 1994; Zedler & Callaway, 2000). These macroinvertebrate assemblages also often fail to reach absolute reference levels of density, abundance, or species richness (Meyer & Whiles, 2008; Moreno-Mateos et al., 2012). Furthermore, in restored wetlands where macroinvertebrate abundances have statistically converged with reference assemblages, differences in taxa composition among wetlands can still persist (Levin & Talley, 2002; Meyer & Whiles, 2008). Results from the replicated sampling approaches in this study are generally consistent with these trends, as the marshes did not differ in taxa richness or abundance but did differ in diversity and temporal patterns of insect composition. Even after 34 years, CON-1 and CON-2 do not support the same biodiversity and community structure as NAT.

Observed differences in insect diversity may be attributable to variation in habitat heterogeneity and plant species richness among marshes. NAT supports a more diverse assemblage of plant species than either of the restored marshes (Fromenthal, pers. obs.; Smyth 2020), and this habitat heterogeneity could support greater insect biodiversity. In fact, niche theory predicts that biodiversity increases with habitat heterogeneity, as variation within the environment and resources leads to niche partitioning (Cameron, 1972; de Souza Júnior et al., 2014). Furthermore, prior work within wetland ecosystems has found that macroinvertebrate richness is positively correlated with habitat area (Moraes et al., 2014). As the LULC data revealed, NAT contains a larger area of regularly inundated wetlands compared to CON-1 and CON-2, which provided more habitat for aquatic insect larvae. Greater wetland habitat, combined with observed spatial heterogeneity in the plant community, likely supported a more diverse insect community in NAT than in either CON marsh.

Biodiversity is also linked with the productivity of an ecosystem, which in wetlands is closely linked to hydrology (Batzer et al., 1999; Galatowitsch, 2016). Hydropatterns of tidal salt

marshes are a dominant driver of wetland community structure (Batzer & Sharitz, 2014). While this is most often documented for wetland plant communities, it is also true for macroinvertebrate communities (Newman et al., 1998; Pires et al., 2019; Whiles & Goldowitz, 2001). Wetlands with short, rapidly-changing hydroperiods tend to support lower insect diversity and richness than wetlands with long, but transient, hydroperiods (Moraes et al., 2014; Newman et al., 1998; Whiles & Goldowitz, 2001). Long hydroperiods provide more stable and nutrient-rich habitat for larval aquatic insects without the stress of desiccation associated with shorter hydroperiods (Batzer & Sharitz, 2014; Merritt et al., 2019; Moraes et al., 2014; Whiles & Goldowitz, 2001). Of the three marshes, NAT is the most hydrologically connected to the West Fowl River and experiences the greatest extent of flushing during diurnal tides. Thus, differences in hydroperiods among sites may explain the greater diversity in NAT.

When more biodiverse, reference sites are likely to exhibit greater trophic redundancy than their restored counterparts, and thus, may be more resilient to environmental change. The greater biodiversity of NAT likely means that there are a greater number of linkages within the trophic web, and therefore, greater habitat stability (Crawley, 1997; Petren, 2001). This stability may help ecosystems resist some of the negative effects of anthropogenic environmental impacts, climate change, and habitat loss. In contrast, marshes like CON-1 and CON-2, where biodiversity is lower and trophic webs may be less complex, may be less resilient to these impacts. Of course, tidal salt marshes are exceptionally valuable and productive ecosystems and provide services such as shoreline stabilization, carbon sequestration, water purification, and flood protection (Moreno-Mateos et al., 2012; Noll et al., 2019). Therefore, reaching reference-level biodiversity to promote ecosystem resilience should be a priority of wetland restoration.

Light Traps Reveal Abundant Insect Communities

Contrary to the results from replicated sampling methods, insect communities from light trap sampling displayed opposite abundance and diversity patterns across marshes. Abundance was highest for insects captured by light traps in NAT compared to CON-1 and CON-2, while taxa richness and diversity were lowest in NAT. This result may be caused by biases of light trap sampling combined with the dominant habitat types surrounding each marsh. Light trap sampling can attract flying insects from distances as far as 40 m (Kirkeby et al., 2013), and therefore, may reflect communities beyond the reference and constructed marshes targeted in this study. The absolute distances are difficult to quantify, as environmental conditions such as weather and moon phases can influence the behavior of night-flying insects (Jonason et al., 2014; Kirkeby et al., 2013; Pan et al., 2021). Insect responses to light traps also vary widely depending on the insect taxa, the wattage of the light used, the height of the light, and the frequency of the light (Kirkeby et al., 2013; Pan et al., 2021). Thus, it is difficult to establish the range in which a particular light trap apparatus has attracted insects. However, it is safe to assume that light trap sampling generally attracted insects from a larger area than the other methods used in this study, such as net sweeps, pan traps, and floral observations.

Because of the larger sampling area captured by light trapping, these samples may reflect differences in surrounding habitats among marshes. For instance, insects captured through light traps likely included specimens that were attracted from surrounding pine savannah habitat, which was greater in CON-1 and CON-2 than in NAT, and therefore, may have contributed to higher diversity in CON-1 and CON-2 than NAT. The forest habitat that surrounds CON-1 and CON-2 may also contribute to edge effects, where biodiversity around wetland edges is greater than within the center of the marsh (Yahner, 1988). Therefore, edge effects of forest habitat,

habitat heterogeneity, and sampling biases likely led to more diverse and rich insect communities at larger spatial scales.

Temporal Patterns of Insect Taxa Community Composition

Larval insects, both those having terrestrial and aquatic imagos, utilize tidal wetlands as habitat (Merritt et al., 2019; Whiles & Goldowitz, 2001). Spring is an especially productive time for larval insects, as this is when aquatic insect taxa in the families *Ceratopogonidae* (biting midges), *Simuliidae* (black flies), and *Lestidae* (spreadwing damselflies) begin to emerge from inundated and/or damp substrate (Blanton & Wirth, 1979; Merritt et al., 2019). In April, CON-2 and NAT supported similarly higher relative abundances of taxa such as damselflies (family *Lestidae*) and stilt-legged flies (family *Micropezidae*), while no individuals of *Micropezidae* or *Lestidae* were captured through any sampling method in CON-1. Little is known about the life history of *Micropezidae*, but larval damselflies are strictly aquatic, with adults emerging in late spring and early summer (Cothran & Thorp, 1982; Merritt et al., 2019; Merritt & Peterson, 1976), and *Lestidae* also have aquatic or semi-aquatic larval life stages that require regular inundation (Eaton & Kaufman, 2007; Moraes et al., 2014; Pires et al., 2019). As detected through habitat classifications of these sites, CON-1 contained the least regularly inundated herbaceous wetlands of the three marshes, which likely limited the availability of suitable larval habitat, driving observed site-specific differences in the relative abundances of *Lestidae* and *Micropezidae* early in the growing season.

These same differences in surrounding habitat likely explain observed differences in insect communities in May. In CON-1, there were greater relative abundances of deer flies and horse flies (family *Tabanidae*) and long-legged flies (family *Dolichopodidae*) than in the other marshes. Both of these taxa have semi-aquatic larval stages and adults that primarily inhabit

grasslands and forest environments (Eaton & Kaufman, 2007; Merritt et al., 2019). CON-1 could be supporting greater abundances of *Tabanidae* and *Dolichopodidae* because it is surrounded by a greater area of forest habitat and is further away from regularly inundated herbaceous wetlands than NAT and CON-2 (Table 2). Edge effects may also be driving relative abundances of *Tabanidae* and *Dolichopodidae*, as the ecotone from wetland to forest habitat can support greater insect abundance (Potts et al., 2016; Yahner, 1988). Furthermore, CON-2 is spatially closer to inundated pine savannah habitat, which could support greater abundances of insects with aquatic life history stages, leading to greater similarity in relative abundances with NAT. After these aquatic and semi-aquatic taxa emerged early in the growing season, relative abundances among insect taxa were similar among marshes.

Temporal Patterns of Insect Functional Groups

Temporal patterns of functional feeding groups also differed among marshes, with pollinators in April driving dissimilarities between CON-1 and other marshes. Dissimilarities in relative abundances of pollinators in April may be explained by differences in floral resources in the surrounding habitats. CON-1 has greater forest habitat in its surroundings than CON-2 and NAT, which could impact pollinator communities that rely on wildflower, shrub, and tree resources. Also, although not significant, CON-1 tended to have more *J. roemerianus* inflorescences per area than the other two marshes, which may contribute to differences among pollinator communities over time.

Although there were some differences in the abundance of pollinators among marshes over time, pollinators were key components of their respective insect communities in all three marshes. It is unclear, however, to what extent, if any, these pollinators relied on wetland floral resources or facilitated the reproduction of wetland plants. The majority of wetland plants

reproduce clonally through rhizomes or sexually via wind pollination, but recent data suggests that wetland plant-pollinator interactions may be a vital part of improving coastal restoration strategies (Culley et al., 2002; Huang et al., 2013; Michalski & Durka, 2015; Yando et al., 2019). Insect pollinators may support wetland plant reproduction by aiding in pollination efficiency, thereby promoting genetic diversity in the plant community and in seedbanks (Bossuyt & Honnay, 2008; Culley et al., 2002). Plant-pollinator interactions may be particularly valuable in tidal wetlands dominated by *J. roemerianus*, a foundation species in many Gulf of Mexico and Atlantic Coast marshes (Woerner and Hackney 1997; Battaglia et al., 2012). While *J. roemerianus* primarily reproduces asexually through rhizomes, its genetic diversity and pollen-to-ovule ratio are not what is expected of a clonal plant (Michalski & Durka, 2015; Tumas et al., 2018; Yando et al., 2019). Its unusually low pollen-ovule ratio correlates with a higher degree of outcrossing typical of wind or animal pollination (Huang et al., 2013). Furthermore, its genotypic diversity and observed heterozygosity are unusually high for a primarily clonal genus (Tumas et al., 2019; Michalski & Durka, 2015; Yando et al., 2019), which suggests that sexual reproduction may be more important for this species than previously thought.

While wind pollination could explain some of this genetic diversity, *J. roemerianus* displays traits synonymous with insect-pollinated plants, such as pollen produced in tetrads, low accumulated daily concentrations of pollen, and pulsed flowering (Huang et al., 2013). Tetramerous pollen is thought to have evolved to increase the efficiency of pollen transfer during insect pollination (Kress, 1981). The low daily accumulations of pollen also suggests that *J. roemerianus* does not rely on wind pollination because anemophilous plants tend to produce large volumes of pollen (Huang et al., 2013; Michalski & Durka, 2007). Pulsed flowering, a rare flowering strategy in angiosperms in which flowers bloom in alternating periods of synchronous

flowering (Michalski & Durka 2007), may also suggest utilization of insect pollination by *J. roemerianus*. Pulsed flowering has been hypothesized as a method for increasing the efficiency of pollination in animal-pollinated species, but the origins and implications of pulsed flowering are poorly understood (Munguía-Rosas & Sosa, 2010). Collectively, these plant traits, along with the results of this study, suggest that insect pollinators may utilize *J. roemerianus* as a resource, thereby promoting its sexual reproduction. Further research is needed to document insect pollination in *J. roemerianus* and aid our understanding of the biology and reproduction of this widespread wetland plant species (Eleuterius, 1976; Tumas et al., 2018).

In addition to pollinators, higher relative abundances of the mixed functional feeding group in CON-1 accounted for differences among marshes early in the growing season. Insect taxa in the families *Tabanidae* (horseflies) and *Ceratopogonidae* (biting midges) comprised this functional feeding group and have been found through numerous studies to be some of the most abundant insects within tidal salt marshes (Kirkeby et al., 2013; MacKenzie, 2005; Merritt et al., 2019). *Ceratopogonidae* is especially abundant in tidal salt marshes, and consistent with this study, adults were most abundant from mid-March through May (Kline, 1986). *Tabanidae* also followed a similar pattern where insect emergence peaks around May (Hansens & Robinson, 1973). Across all marshes, these emergence patterns coincided with observed peaks in May of relative abundances of the mixed functional feeding group.

As with observed differences in light trap samples, temporal differences in insect taxa and functional feeding groups may be due to proximity to surrounding habitat and the influence habitat has on early insect emergence patterns. Habitat classification revealed that the combined radii of CON-1 quadrats contained less regularly inundated herbaceous wetlands than the other two marshes. Furthermore, CON-1 is surrounded by a greater proportion of forest habitat, which

may lead to edge effects that shape insect community structure. Insect community structure is dependent on the dispersal and establishment capabilities of those macroinvertebrates (MacKenzie, 2005; Merritt et al., 2019; Whiles & Goldowitz, 2001). This is especially true for insect taxa that inhabit tidal salt marshes, as many of them have aquatic larval stages and require reliable inundation or soil saturation for pupation and emergence (MacKenzie, 2005; Merritt et al., 2019; Whiles & Goldowitz, 2001). The spatial isolation of CON-1 away from other regularly inundated wetlands could be a driver of observed differences between CON-1 and NAT (Morris et al., 2012). Additionally, habitat composition and heterogeneity could regulate the community structure of insect functional groups. In studies on microhabitat preferences of aquatic insect macroinvertebrates, it was found that freshwater benthic macroinvertebrate functional feeding group assemblages are dictated by microhabitat conditions, such as substrate type, water velocity, and depth (Vilenica et al., 2018). The same could be true in tidal salt marshes, where aquatic larval insects inhabit several microhabitats within and around the quadrats sampled, and this is reflected in observed differences in spring when many mixed functional feeding group insects are emerging. Therefore, influences from the surrounding forest habitat in CON-1 and its relatively greater distance from regularly inundated sediments in surrounding wetland habitats could account for early season differences in taxa and functional groups among sites.

Lastly, in July and August, the relative abundances of herbivores peaked across all marshes. This functional group was the second most abundant across all three marshes, but they exhibited greater grazing activity in NAT compared to CON-1 and CON-2. Shoots of *J. roemerianus* collected in September displayed a significantly greater surface area of insect herbivory scars than shoots from the CON marshes. Across ecosystems, the nutritional quality of plants strongly regulates insect herbivore populations, with more fertile areas supporting more

grazing (Bowdish & Stiling, 1998; Gratton & Denno, 2006; Sparks & Cebrian, 2015). Plant nitrogen content is especially influential on insect herbivory in wetlands and has been found to regulate the abundance of herbivorous insects (Bowdish & Stiling, 1998; Rode et al., 2017; Salgado & Pennings, 2005; Vince et al., 1981). Hydrology drives plant nitrogen content, as tidal regimes regulate nitrogen cycling and aboveground biomass production (Batzer & Sharitz, 2014; Bowdish & Stiling, 1998; Nelson & Zavaleta, 2012). Furthermore, greater aboveground biomass and nutrient stocks, as has been documented in NAT (Ledford et al., 2021; Smyth, 2020), suggests that regular tidal pulsing has stimulated production by flushing toxins and importing nutrients, making plant tissue more nutrient-rich and palatable for herbivorous insects (Belovsky & Slade, 2001; Bowdish & Stiling, 1998; Merritt et al., 2019). Thus, I hypothesize that the greater hydrologic connectivity in NAT likely increased plant nutrient content and palatability, which encouraged greater herbivore grazing activity. Additional studies are needed to test this hypothesis.

Considerations for Restoration

Historically, insects in aquatic ecosystems have been understudied compared to other taxonomic groups despite their established importance for regulating wetland health and structure (Batzer & Sharitz, 2014; Crawley, 1997; Harms & Grodowitz, 2009; Noriega et al., 2018; Suter & Cormier, 2015). This research shows that insect communities in restored wetlands fail to recover even decades after creation. Biodiversity in wetlands is an important factor to consider when determining restoration success. Because constructed marshes were found to not reach reference-level biodiversity for most sampling methods, they may not exhibit the same resilience or trophic web structures as reference marshes despite having otherwise similarly abundant and rich insect communities. Therefore, conditions that influence insect community

structure, such as plant species, plant nutrition, surrounding habitat, and hydrological connectivity, should be considered when constructing or restoring tidal wetlands. Consideration of factors that influence some of the most abundant macroinvertebrates in tidal salt marshes may improve restoration outcomes relative to reference marshes.

In Summary

Originally, we hypothesized that (1) insect richness, abundance, and diversity were higher in reference marshes than in either restored marsh and (2) temporal patterns in relative abundances of functional feeding groups and taxa would change similarly over time. Results indicated that neither of these proposed hypotheses was fully supported. While restored marshes generally recovered to reference levels of taxa richness and abundance, insect diversity had not recovered after 34 years post creation when examined using replicated pan traps, sweep netting, and floral surveys. Furthermore, the temporal patterns of insect communities varied between marshes, likely as a result of differences in surrounding habitat, hydrology, and plant nutrition among sites, suggesting that these factors should be considered more broadly when designing and monitoring restoration projects.

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APPENDIX

Abundance of insect taxa identified from all sampling methods used in this study. Taxa are listed by family, with their respective common names and functional group assignments indicated.

Abundance data are provided for all three marshes (total), as well as for the natural (NAT) and constructed marshes (CON-1 and CON-2).

Taxa	Common Name	Functional Feeding Group	Total	CON-1	CON-2	NAT
Acrididae	Grasshoppers	Herbivore	37	25	10	2
Anthicidae	Ant-like flower beetles	Omnivore	8	4	4	0
Anthomyiidae	Root maggot flies	Omnivore	2	0	2	0
Apidae	Bees	Pollinator	2	0	1	1
Belostomatidae	Giant waterbugs	Predator	8	4	4	0
Braconidae	Braconid wasps	Pollinator	2	0	0	2
Calliphoridae	Blow flies	Omnivore	14	5	3	6
Cantharidae	Soldier beetles	Pollinator	27	21	1	5
Carabidae	Ground beetles	Predator	44	20	8	16
Ceratopogonidae	Biting midges	Mixed	1676	76	90	1510
Cercopidae	Spittlebugs	Herbivore	35	15	12	8
Chalcidae	Chalcid wasps	Pollinator	4	0	0	4
Chironomidae	Non-biting midges	Mixed	1957	299	366	1292
Chloropidae	Frit flies	Herbivore	12	9	2	1
Chrysomelidae	Leaf beetles	Herbivore	4	0	4	0
Cicadellidae	Leafhoppers	Herbivore	84	20	13	51
Cixidae	Planthoppers	Herbivore	6	2	2	2
Clusidae	Druid flies	Omnivore	1	0	0	1
Coccinellidae	Lady beetles	Omnivore	8	4	0	4
Coenagrionidae	Narrow-winged damselflies	Predator	2	0	1	1
Corixidae	Water boatmen	Predator	464	32	0	432
Crambidae	Grass moths	Pollinator	999	368	241	390
Culicidae	Mosquitoes	Mixed	28	12	0	16
Curculionidae	Weevils	Herbivore	244	124	96	24
Delphacidae	Planthoppers	Herbivore	150	86	31	33

Depressariidae	Depressariid moths	Pollinator	4	0	0	4
Derbidae	Planthoppers	Herbivore	28	24	0	4
Dictyopharidae	Planthoppers	Herbivore	8	8	0	0
Dolichopodidae	Long-legged flies	Predator	50	26	15	9
Drosophilidae	Common fruit flies	Omnivore	1721	289	714	718
Dysticidae	Predaceous diving beetle	Predator	68	36	4	28
Elateridae	Click beetles	Omnivore	12	8	4	0
Empididae	Dagger flies	Omnivore	102	41	37	24
Ephydriidae	Shore flies	Omnivore	39	20	2	17
Erebidae	Tussock moths	Pollinator	16	8	8	0
Erotylidae	Pleasing fungus beetles	Omnivore	1	0	0	1
Formicidae	Ants	Omnivore	50	7	6	37
Gelechiidae	Twirler moths	Pollinator	20	16	4	0
Geometridae	Geometrid moths	Pollinator	8	4	4	0
Gryllidae	Crickets	Herbivore	4	1	1	2
Halictidae	Halictid bees	Pollinator	1	0	0	1
Hydrophilidae	Water scavenger beetles	Herbivore	996	180	780	36
Ichneumonidae	Ichneuomid wasps	Pollinator	41	20	8	13
Issidae	Planthoppers	Herbivore	21	0	13	8
Lauxaniidae	Lauxaniid flies	Omnivore	12	4	4	4
Lestidae	Spreadwing damselflies	Predator	28	4	3	21
Libellulidae	Skimmers	Predator	40	8	20	12
Limacodidae	Slug moths	Pollinator	8	0	8	0
Lonchaeidae	Lance flies	Omnivore	1	1	0	0
Micropezidae	Stilt-legged flies	Omnivore	8	1	3	4
Muscidae	House flies	Omnivore	10	7	0	3
Mycetophilidae	Fungus gnats	Omnivore	4	0	2	2
Nitidulidae	Sap beetles	Herbivore	40	16	12	12
Noctuidae	Owlet moths	Pollinator	70	36	22	12
Pentatomidae	Shield bugs	Herbivore	36	20	12	4
Perlidae	Stoneflies	Herbivore	4	4	0	0
Phengodidae	Glowworm beetles	Predator	1	0	0	1
Phlaeothripidae	Thrips	Omnivore	5	1	4	0
Phoridae	Phorid flies	Omnivore	1	1	0	0
Psocodae	Bark lice	Herbivore	16	3	4	9
Psychodidae	Drain flies	Omnivore	120	6	78	36
Pyralidae	Snout moths	Pollinator	60	36	12	12
Sarcophagidae	Flesh flies	Omnivore	27	3	4	20
Saturniidae	Saturniid moths	Pollinator	24	12	12	0
Scarabaeidae	Scarab beetles	Herbivore	36	16	20	0

Sciaridae	Dark-winged fungus gnats	Omnivore	3	2	0	1
Sciomyzidae	Marsh flies	Omnivore	3	1	1	1
Simuliidae	Black flies	Mixed	2	0	2	0
Sphaeroceridae	Small dung flies	Omnivore	3	3	0	0
Sphecidae	Sphecid wasps	Pollinator	1	1	0	0
Sphynigidae	Sphinx moths	Pollinator	16	8	8	0
Staphylinidae	Rove beetles	Predator	152	28	28	96
Syrphidae	Hover flies	Pollinator	58	33	14	11
Tabanidae	Horseflies	Mixed	63	21	4	38
Temnothorax	Acorn ants	Omnivore	2516	104	172	2240
Tephritidae	Fruit flies	Herbivore	4	0	3	1
Terebrantia	Thrips	Pollinator	38	0	6	32
Tettigoniidae	Katydid	Herbivore	25	17	8	0
Tineidae	Fungus moths	Herbivore	1	0	1	0
Tipulidae	Crane flies	Omnivore	8	4	0	4
Trichoptera	Caddisflies	Pollinator	8	0	8	0
Ulidiidae	Picture-winged flies	Herbivore	20	4	4	12