

1

2 Effects of mangrove encroachment on tidal wetland plant, nekton, and bird communities in the  
3 Western Gulf of Mexico

4

5

6

7 Anna R. Armitage <sup>\*a</sup>, Carolyn A. Weaver <sup>a,b</sup>, Ashley A. Whitt <sup>a,c</sup>, and Steven C. Pennings <sup>d</sup>

8 *\*Corresponding author:* <sup>a</sup>Department of Marine Biology, Texas A&M University at Galveston,  
9 PO Box 1675, Galveston, TX 77553, USA; ORCID 0000-0003-1563-8026;  
10 armitaga@tamug.edu

11 <sup>b</sup> *Present address:* Department of Life Sciences, Texas A&M University-Corpus Christi, 6300  
12 Ocean Drive, Corpus Christi, TX 78412, USA; ORCID 0000-0002-1447-6371;  
13 Carolyn.Weaver@tamucc.edu

14 <sup>c</sup> *Present address:* School of Life and Environmental Science, Centre for Integrative Ecology,  
15 Deakin University, Burwood Campus; 221 Burwood Hwy, VIC 3125, Australia; ORCID 0000-  
16 0002-4130-8031; awhitt@deakin.edu.au

17 <sup>d</sup>Department of Biology and Biochemistry, University of Houston, Houston, TX 77204-5001,  
18 USA; ORCID 0000-0003-4757-7125

19

20        **Abstract**

21        Woody encroachment is occurring in many marsh-mangrove ecotones across the globe, with  
22 multiple drivers contributing to an increase in mangrove cover. As a result, marsh plant species  
23 are often displaced, resulting in a striking regime shift from grass and forb-dominated habitats to  
24 taller, woody vegetation. Our goal was to quantify the bottom-up effects of mangrove woody  
25 encroachment into coastal wetlands on associated plant, nekton, and bird assemblages. In 2012,  
26 we established several large (> 20 ha) survey areas at tidal wetland sites with or without black  
27 mangroves (*Avicennia germinans*) on the Texas (USA) coast in the Gulf of Mexico, an area  
28 highly susceptible to mangrove encroachment. From 2012-2015, we recorded vascular plant  
29 cover and diversity, sampled nekton at the water-vegetation interface using seine nets, and  
30 compared wintering shorebird and wader use among sites using the citizen science database  
31 eBird. Marsh plant species richness was 50% lower at sites with mangroves, and some species,  
32 such as *Distichlis spicata*, were absent from these sites entirely. The relative abundance and  
33 species richness of nektonic fish and invertebrates was similar between sites, but certain species  
34 (e.g., bay anchovies *Anchoa mitchilli*, grass shrimp *Palaemonetes* spp.) were more common at  
35 sites without mangroves. Citizen science data indicated that shorebird and wader species richness  
36 was 20% lower at sites with mangroves. Shorebird assemblages were markedly different  
37 between site types; six shorebird and three wader species were only detected in marsh sites. Our  
38 results indicate that coastal wetlands dominated by mangroves support different plant and animal  
39 assemblages than marsh-dominated areas. These results were largely consistent with the results  
40 of a previous manipulative experiment in the same area, lending considerable confidence to the  
41 conclusion that mangroves influence the associated plant and animal communities. Therefore, as

42 woody encroachment continues and mangrove cover gradually increases, this change may lead to  
43 complex bottom-up effects on a range of ecosystem processes and services.

44

## 45 **1. Introduction**

46 Foundation species are abundant and ecologically dominant organisms that structure  
47 communities and drive ecosystem processes (Soulé et al. 2003, Ellison et al. 2005). Foundation  
48 species can occupy any trophic level, though this terminology is often applied to a suite of co-  
49 occurring plant species that create a certain habitat (e.g., prairie, marsh; Angelini et al. 2011,  
50 Peters and Yao 2012, Osland et al. 2013) and provide key ecosystem functions for higher trophic  
51 levels (e.g., Reid and Lortie 2012). As global changes cause rapid, broad-scale shifts in plant  
52 communities (Ellis and Ramankutty 2008, Allen et al. 2010, Chen et al. 2011), speciose  
53 assemblages of short plants often transition to a low diversity assemblage of taller canopy-  
54 forming species. A classic example of this shift is the encroachment of woody plants into  
55 terrestrial ecosystems dominated by low-stature graminoids and forbs (Van Auken 2000, Frelich  
56 and Reich 2010). In many cases these shifts decrease productivity (Smith and Knapp 2003), litter  
57 quality (Price and Morgan 2008, Kominoski et al. 2013), and palatability to grazers (Gordijn et  
58 al. 2012). These documented consequences of woody encroachment are primarily derived from  
59 studies in terrestrial grassland and savanna ecosystems, and it is unknown how broadly these  
60 outcomes apply in tidal ecosystems.

61 Woody encroachment in coastal ecosystems is receiving increasing attention in response to  
62 many notable changes in the relative abundance and distribution of mangroves across the globe.

63 In many tropical regions, mangroves are experiencing substantial losses due to a diversity of  
64 anthropogenic and natural drivers (e.g., Richards and Friess 2016, Thomas et al. 2017,  
65 Lagomasino et al. 2019). However, in temperate marsh-mangrove ecotones there have been  
66 increases in mangrove cover, frequently in the genus *Avicennia*, often leading to the  
67 displacement of marsh grasses (e.g., *Spartina alterniflora*) and forbs (e.g., *Sarcocornia* spp.)  
68 (Osland et al. 2013, Saintilan et al. 2014, Armitage et al. 2015, Godoy and de Lacerda 2015, Giri  
69 and Long 2016). In the Gulf of Mexico, increasing black mangrove *Avicennia germinans* cover  
70 is primarily linked to increasing winter temperature minima and sea level rise (Krauss et al.  
71 2011, McKee et al. 2012, Osland et al. 2013, Cavanaugh et al. 2014). This expansion rate may be  
72 accelerated at a local scale by biotic interactions (Guo et al. 2013) and abiotic drivers such as  
73 increasing precipitation (Osland et al. 2014) and anthropogenic nutrient input (Weaver and  
74 Armitage 2018).

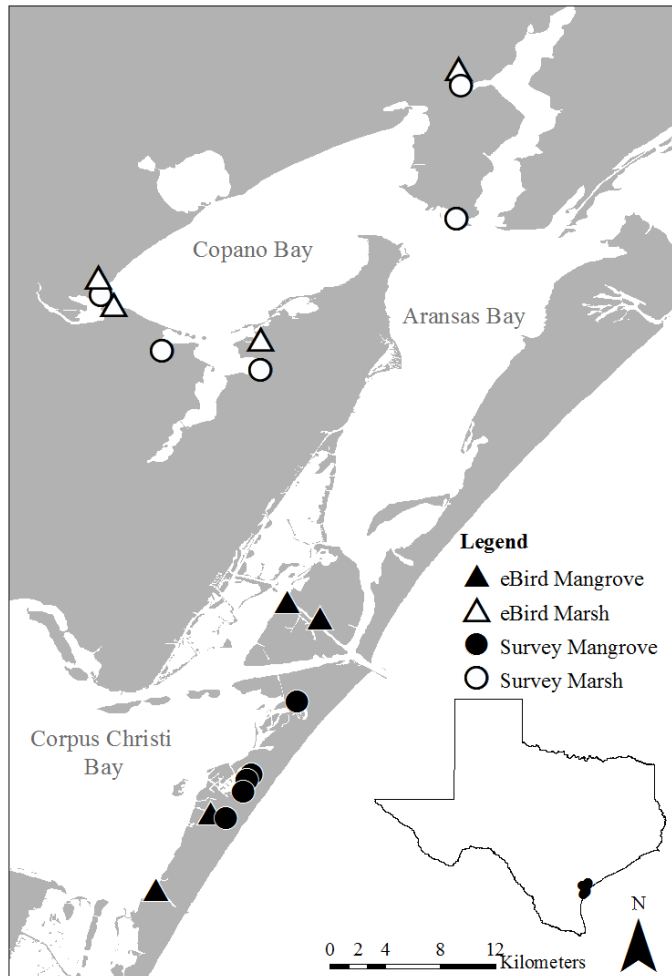
75 A landscape-level shift in the dominant plant community towards mangroves is likely to alter  
76 habitat quality for many wetland and estuarine fauna (Guo et al. 2017). In particular, the growing  
77 body of work on this topic suggests that infauna and nektonic crustaceans may be more abundant  
78 at sites without mangroves (Lunt et al. 2013, Diskin and Smee 2017, Johnston and Caretti 2017,  
79 Smee et al. 2017). Our objective was to broaden the spatial and temporal scope of these  
80 investigations by testing the hypothesis that community assembly across multiple trophic levels  
81 would differ between sites with and without mangroves present.

82        **2. Methods**

83        *2.1 Study areas*

84        We worked within the Coastal Bend region of Texas (Gulf of Mexico, USA) where  
85 mangrove- and marsh-dominated areas are found in relatively close proximity to each other (Fig.  
86 1). A set of seven survey sites containing relatively large (> 20 ha) expanses of emergent tidal  
87 wetlands were identified in 2012. Black mangroves (*Avicennia germinans*) comprised  $77 \pm 3\%$   
88 (mean  $\pm$  SE) of the emergent vegetation cover at four of the sites; mangroves were not present at  
89 the remaining three sites (Table A.1, Figure A.1). One additional site without mangroves was  
90 added in 2013, and two additional sites (one of each site type) were added in 2014, for a total of  
91 five of each site type. In this area, mangroves were primarily located on or near the barrier  
92 islands and sites without mangroves were on the mainland. Therefore, it was not possible to  
93 spatially intersperse different site types. Despite the limitations imposed by the landscape  
94 distributions of mangrove stands, using a “natural experiment” involving large survey areas  
95 enabled us to examine links between mangrove presence and associated community assemblages  
96 at a larger and more representative spatial scale than would be possible using an experimental  
97 approach. This was particularly important for studies of nekton and birds, many of which can  
98 move over large distances in a single day.

99



100

101 Figure 1. Map of study area in the Gulf of Mexico near Port Aransas, Texas, USA.

102

103 To characterize the tidal wetland at each site, we established a linear transect perpendicular  
 104 to the shoreline, extending from the vegetation-water interface to the upper littoral zone. The  
 105 upland transition was clearly delineated by a distinct change from salt marsh vegetation species  
 106 to either salt pan (non-vegetated, high elevation) or upland vegetation species. Since each site  
 107 had a unique shoreline topography, the length of the shoreline-upland transect differed among

108 sites, ranging from 70-180 m. Five stations were established along each transect: one at the low  
109 elevation vegetation (*Spartina alterniflora*) edge, and one at the upland wetland vegetation  
110 boundary, with three additional stations evenly spaced between the upper and lower stations.  
111 Using a Lasermark LM800 GR surveyor, elevation was measured relative to the lowest tidal  
112 extent of *Spartina alterniflora*, which was assumed to occur at a similar elevation across sites in  
113 this region (McKee and Patrick 1988). Edaphic characteristics were measured at each site; soil  
114 analysis methods are summarized in Appendix A.

115

## 116 2.2 Plants

117 We surveyed vegetation each fall (September 2012, October 2013, August 2014, August  
118 2015) by placing a 1-m<sup>2</sup> quadrat every 10 m along each transect. We recorded which marsh and  
119 mangrove plant species were present in each quadrat and tabulated cumulative species richness  
120 at each site in each sampling period. To characterize differences in the relative abundance of  
121 marsh plants at sites with and without mangroves, we calculated the frequency of occurrence (%  
122 of quadrats where a given species was present) of each marsh plant species. Common species  
123 (*Spartina alterniflora*, *Batis maritima*, *Sarcocornia* spp., *Distichlis spicata*) are referred to  
124 generically hereafter. In acknowledgement of current taxonomic debates, we followed Bortolus  
125 et al. (2019) in retaining the genus name *Spartina*, and followed the Flora of North America  
126 (2003) in assigning all perennial species previously identified as *Salicornia* to *Sarcocornia*. A  
127 few individuals of the visually similar annual *Salicornia bigelovii* were also present but difficult

128 to reliably distinguish from perennial *Sarcocornia*, and so they were included in the *Sarcocornia*  
129 group.

130

### 131 *2.3 Nekton*

132 To compare the faunal assemblages at sites with and without mangroves, we sampled  
133 subtidal nekton each fall from 2012-2015. Characterizing nekton communities in microtidal  
134 systems is logistically challenging due to low water levels and little tidal exchange, so the use of  
135 bag seines in the subtidal habitat immediately adjacent to the water-vegetation interface was the  
136 most feasible and consistently applicable sampling technique. Nekton samples were collected at  
137 each site with a 6.1 m (20') bag seine deployed along a 20 m transect parallel to the shoreline.  
138 Nekton were placed in plastic collection bags and euthanized over an ice slurry in accordance  
139 with TAMU Animal Use Protocol 2012-152. In the lab, nekton were identified to the lowest  
140 practical identification level (most often species) and enumerated.

141

### 142 *2.4 Birds*

143 Information on bird use was mined from the citizen science database eBird, a public  
144 repository of sightings reported by birdwatchers (Sullivan et al. 2009). The advancement of  
145 citizen science can aid in understanding changes in coastal bird assemblages, with appropriately  
146 conservative interpretations to account for possible reporting errors or incomplete reports.  
147 Despite their constraints, datasets like eBird make large geographic and temporal scale studies  
148 financially and logistically feasible (Sullivan et al. 2009), and they can complement traditionally



149 designed surveys (Kelling et al. 2009, Dickinson et al. 2010, Reynolds et al. 2017). In our case,  
150 the eBird database included hundreds of relevant observations, providing a taxonomically rich  
151 resource over a much broader spatial and temporal scale than our research team could have  
152 accomplished alone. Therefore, the eBird database made a unique and valuable contribution to  
153 our ecosystem-level analysis of mangrove encroachment effects on coastal ecosystems.

154 We identified eight sites that were designated as eBird “hotspots” within coastal wetland  
155 habitats and were contiguous with our survey sites or with sites that we had previously surveyed  
156 (Guo et al. 2017, Weaver and Armitage 2018). As defined by eBird, hotspots are public birding  
157 locations where observations are aggregated across multiple birders. Therefore, hotspots are not  
158 necessarily areas with high bird abundances, but are areas where birders regularly submit  
159 observations. Within the area of interest, hotspots were identified in coastal wetlands with and  
160 without mangrove vegetation (n = 4 per site type; Fig. 1). Mangrove presence (or absence) at  
161 each hotspot was confirmed by the authors’ visual observations. Detailed characterization of the  
162 extent of available foraging habitat in the vicinity of each eBird hotspot was based on 0.5 m  
163 resolution orthoimagery from 2015 available through the Texas Natural Resources Information  
164 System (TNRIS 2015); detailed methods are described in Appendix A and Table A.3. Sites were  
165 heterogeneous, but there tended to be more suitable aquatic foraging habitat (e.g., tidal flats,  
166 pools) for wetland birds at sites without mangroves (Table A.3). Weather conditions were  
167 variable but relatively mild for most observation dates, suggesting that birdwatchers tended to  
168 report sightings during good weather. This consistency in reporting behavior reduced the  
169 potential for confounding effects of weather conditions on bird sightings. Detailed weather  
170 conditions on observation dates are described in Appendix A.

171 The eBird database was mined to extract all observations from each of the eight hotspots  
172 over the migration and overwintering period, defined as mid-October through mid-May each  
173 year, starting in October 2012 and extending through May 2016 (eBird 2017). Data were filtered  
174 to include only those entries where all species observed were reported and observers followed a  
175 stationary or traveling protocol (Sullivan et al. 2009). Traveling protocols covered an average  
176 maximum distance of 6.2 km at sites with mangroves and 4.7 km at sites without mangroves.  
177 Data were screened to remove duplicate entries (i.e., identical entries from two or more  
178 observers who were birdwatching with a group). Average observation time duration was 64  
179 minutes at sites with mangroves and 44 minutes at sites without mangroves. Observations at  
180 hotspots did not specify bird use of particular vegetation or water features, and most hotspots  
181 likely included observations from upland and developed areas in addition to coastal wetland  
182 habitat. Therefore, for this analysis, we focused on two groups of wetland-dependent birds,  
183 broadly defined as waders (including Families Ardeidae, Threskiornithidae, Gruidae) and  
184 shorebirds (Families Scolopacidae, Charadriidae, Recurvirostridae). The research team and  
185 volunteer bird watchers visited all hotspots and our observations at these sites were consistent  
186 with the data reported by citizen scientists to eBird.

187 The number of observations that met the criteria for inclusion varied between sites with  
188 mangroves (5-26 observations/site) and those without (31-91 observations/site). Therefore, prior  
189 to analyses, data were standardized to control for variation in the number of observations by: (1)  
190 pooling all observations within each calendar year (2012 and 2013 were pooled together because  
191 of the low number of 2012 observations submitted prior to the launch of the eBird mobile app in  
192 2013); and then (2) dividing by the number of observations made that year to give an average

193 number of individual birds spotted per species per site per year. Each individual hotspot was  
194 treated as a replicate, yielding four replicates of each site type (with and without mangroves)  
195 each year.

196

## 197 *2.5 Statistical analyses*

198 Species richness of each taxonomic group (plants, invertebrates, fish, shorebirds, waders)  
199 was analyzed with separate two-way PERMANOVA (PERMANOVA+ v1.0.5) following square  
200 root transformation, where year (2012-2015) and site type (with or without mangroves) were the  
201 independent variables. Total fish and total invertebrate abundance were also analyzed with two-  
202 way PERMANOVA as described above. Differences in plant, fish, invertebrate, and bird  
203 community composition were assessed with two-way analysis of similarity (ANOSIM) with year  
204 and site type as the independent variables, and NMDS plots were used to visualize differences  
205 between sites with and without mangroves and among years (PRIMER v.6.1.15). The species  
206 that contributed the most to community dissimilarity were identified with post hoc SIMPER  
207 (similarity percentages) analyses, and PERMANOVA was used to determine differences in  
208 common species between site types and among years. For birds, we also generated rarefaction  
209 curves to control for the larger observer effort in marshes and to visualize differences in species  
210 richness.

211        **3. Results**

212        *3.1 Site characteristics*

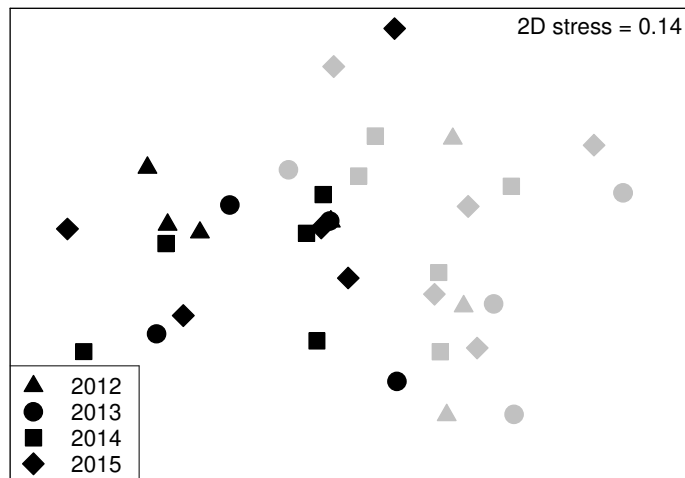
213        The elevation profiles across sites were comparable, with the four lower stations at each site  
214        occupying an intertidal range of ~20 cm above the water-vegetation interface. Patterns of  
215        elevation change did not differ consistently among site types (Figure A.2).

216        Edaphic characteristics differed between sites with and without mangroves, typical of  
217        contrasts between barrier island and mainland sites. Sites with mangroves had significantly  
218        sandier, drier, less salty soils with lower organic content, nitrogen, and phosphorus contents  
219        (Table A.2).

220

221        *3.2 Plants*

222        Marsh plant assemblages differed between sites with and without mangroves but were similar  
223        among years (Fig. 2; ANOSIM site type  $R = 0.424$ ,  $p = 0.001$ ; year  $R = -0.098$ ,  $p = 0.939$ ). Plant  
224        species richness was 50% lower at sites with mangroves (average  $3.4 \pm 0.3$  SE) than at sites  
225        without mangroves ( $5.1 \pm 0.3$ ; Table 1). Based on SIMPER analysis, the two species that  
226        contributed the most to the dissimilarity in marsh plant assemblages were *Distichlis spicata* and  
227        *Sarcocornia* spp., which were relatively rare or absent from sites with mangroves (Tables 1, 2).



228

229 Figure 2. Nonmetric multidimensional scaling plot depicting differences between marsh plant  
 230 assemblages in sites with (black symbols) and without (grey symbols) mangroves over four  
 231 years.  
 232

233 Table 1. Pseudo-F values from 2-way PERMANOVA of site type (sites with and without  
 234 mangroves) and year (2012-2015) on marsh plant species richness and the frequency of  
 235 occurrence of common species.

Factor	Site type	Year	Site type * Year
Species richness	18.63*	0.23	0.90
<i>Distichlis spicata</i>	38.80***	0.76	0.74
<i>Sarcocornia</i> spp.	16.53**	0.26	0.16
<i>Batis maritima</i>	2.23	0.21	0.91
<i>Spartina alterniflora</i>	2.21	0.71	0.89

236 \*p < 0.05; \*\*p < 0.01; \*\*\* p < 0.001

237

238

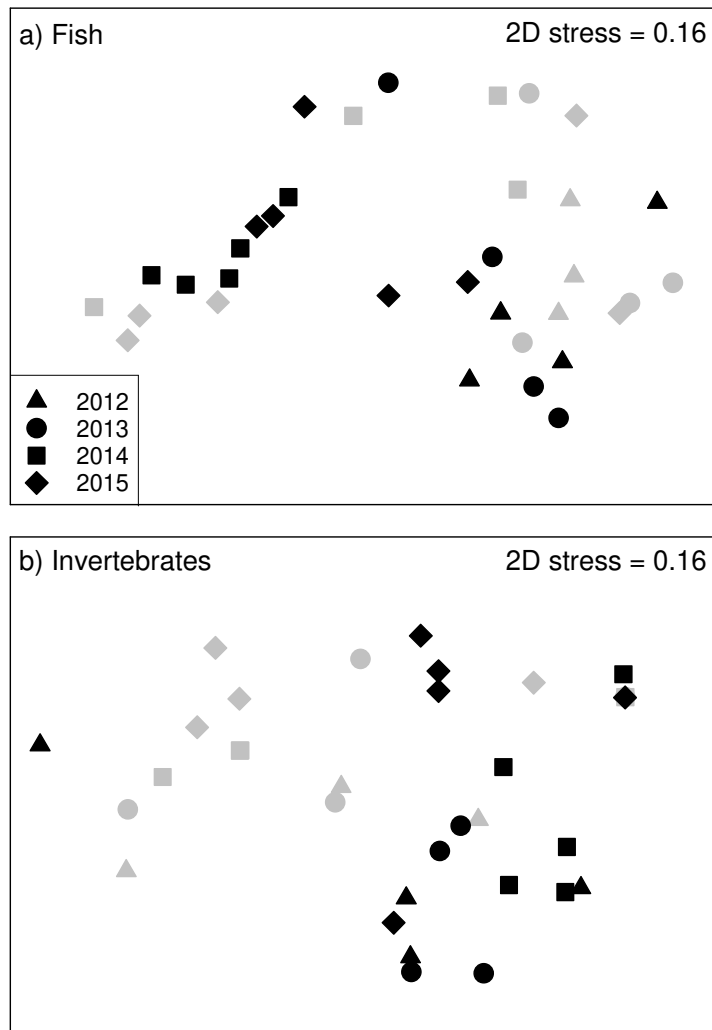
239 Table 2. Average marsh plant frequency of occurrence ( $\pm$  standard error) pooled over all  
 240 observations at sites with and without mangroves, and results of SIMPER analysis to identify the  
 241 species that contributed the most to differences among sites with and without mangroves.

Species	Mangroves present	Mangroves absent	Dissimilarity contribution (%)	Cumulative dissimilarity explained
<i>Distichlis spicata</i>	0	0.24 $\pm$ 0.05	21.6	21.6
<i>Sarcocornia</i> spp.	0.28 $\pm$ 0.05	0.68 $\pm$ 0.04	21.2	42.8
<i>Batis maritima</i>	0.44 $\pm$ 0.07	0.51 $\pm$ 0.05	13.2	56.0
<i>Monanthochloe littoralis</i>	0.03 $\pm$ 0.01	0.12 $\pm$ 0.04	13.2	69.2
<i>Spartina alterniflora</i>	0.40 $\pm$ 0.04	0.60 $\pm$ 0.05	12.4	81.6
<i>Borrchia frutescens</i>	0	0.06 $\pm$ 0.02	8.2	89.8
<i>Suaeda linearis</i>	0	0.01 $\pm$ 0.01	2.8	92.6

242

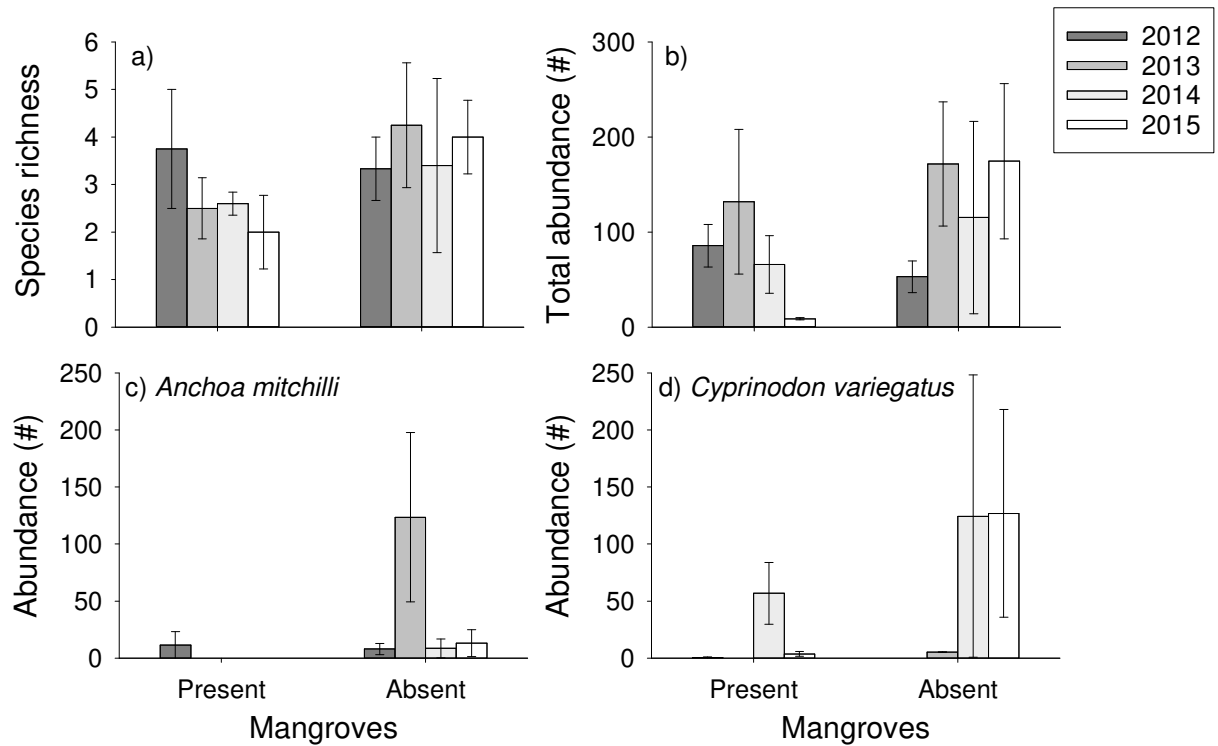
### 243 3.3 Nekton

244 Fish community assemblages differed between sites with and without mangroves and among  
 245 years, though there was some overlap among site types and years as indicated by relatively low  
 246 R values (Fig. 3a; site type R = 0.273, p = 0.007; year R = 0.370, p = 0.001). Fish relative  
 247 abundance and species richness was modestly higher at sites without mangroves, but did not vary  
 248 among years (Fig. 4a-b; Table 3). Based on SIMPER analysis, the two species that contributed  
 249 the most to the dissimilarity in fish assemblages were *Anchoa mitchilli* (bay anchovy) and  
 250 *Cyprinodon variegatus* (sheepshead minnow) (Table 4). *Anchoa* was up to ten times more  
 251 common at sites without mangroves, particularly in 2013 (Fig. 4c, Tables 3, 4). *Cyprinodon*  
 252 abundance was variable but distinctly more abundant in 2014 and 2015, especially in sites  
 253 without mangroves (Fig. 4d; Tables 3, 4).



254

255 Figure 3. Nonmetric multidimensional scaling plot depicting differences between nekton (a) fish  
 256 and (b) invertebrate assemblages in sites with (black symbols) and without (grey symbols)  
 257 mangroves over four years.  
 258



259

260 Figure 4. Fish species richness (a), total relative abundance expressed as average #/sample  $\pm$   
 261 standard error (b), and relative abundance of two common species (c-d) at sites with and without  
 262 mangroves over four years.

263 Table 3. Pseudo-F values from 2-way PERMANOVA of site type (with and without mangroves)  
 264 and year (2012-2015) on nekton fish and invertebrate total abundance, species richness, and the  
 265 frequency of occurrence of common species.

Factor	Site type	Year	Site type * Year
Fish abundance	3.45*	1.05	1.88
Fish species richness	2.92*	0.68	1.01
<i>Anchoa mitchilli</i>	10.85**	1.21	1.09
<i>Cyprinodon variegatus</i>	0.78	4.26**	1.63
Invertebrate abundance	0.95	1.07	0.53
Invertebrate species richness	0.79	1.08	0.20
<i>Palaemonetes</i> spp.	5.73*	0.64	0.40
Cerithiidae	8.13**	2.88*	1.50

266 \*p < 0.05; \*\*p < 0.01

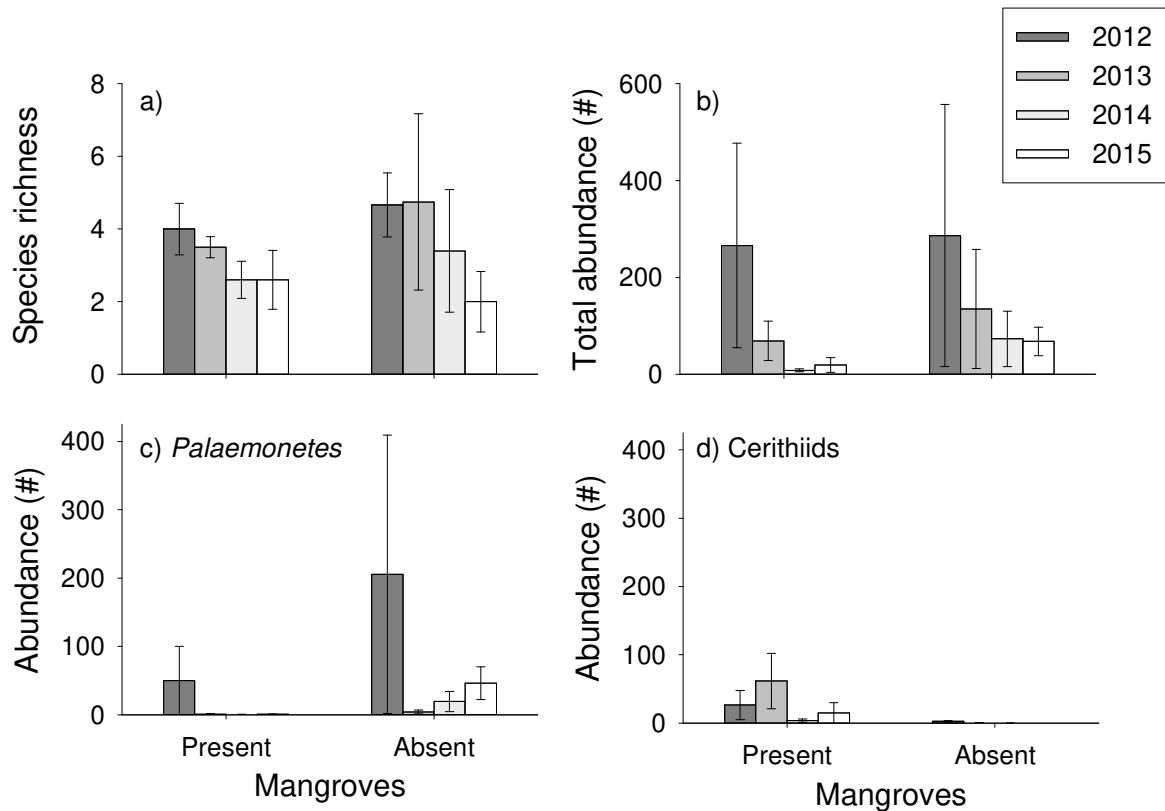


267 Table 4. Average fish abundance ( $\pm$  standard error) pooled over all observations at sites with and  
 268 without mangroves, and results of SIMPER analysis to identify the species that contributed the  
 269 most to differences among sites with and without mangroves.

Species	Mangroves present	Mangroves absent	Dissimilarity contribution (%)	Cumulative dissimilarity explained
<i>Cyprinodon variegatus</i>	16.9 $\pm$ 9.2	70.9 $\pm$ 41.5	26.5	26.5
<i>Anchoa mitchilli</i>	2.6 $\pm$ 2.6	38.6 $\pm$ 21.3	17.2	43.7
<i>Menidia beryllina</i>	40.1 $\pm$ 20.1	16.5 $\pm$ 8.4	13.5	57.2
<i>Fundulus xenicus</i>	1.9 $\pm$ 0.9	5.7 $\pm$ 3.9	9.3	66.5
<i>Cynoscion nebulosus</i>	1.1 $\pm$ 1.0	6.1 $\pm$ 3.6	8.2	74.7
<i>Fundulus grandis</i>	0.1 $\pm$ 0.1	2.5 $\pm$ 1.8	4.1	78.8
<i>Fundulus similis</i>	1.4 $\pm$ 0.8	0	3.2	82.0
<i>Lagodon rhomboides</i>	2.6 $\pm$ 1.8	0.1 $\pm$ 0.1	2.4	84.4
<i>Fundulus pulvereus</i>	0	0.6 $\pm$ 0.3	2.4	86.8
<i>Eucinostomus argenteus</i>	1.2 $\pm$ 0.7	0.2 $\pm$ 0.2	2.3	89.1
<i>Ctenogobius boleosoma</i>	0.1 $\pm$ 0.1	0.4 $\pm$ 0.2	1.7	90.8

270

271 Nekton invertebrate community assemblages were variable over time but differed between  
 272 sites with and without mangroves, though there was a substantial amount of overlap among site  
 273 types, as indicated by relatively low R values (Fig. 3b; site type R = 0.214, p = 0.019; year R =  
 274 0.117, p = 0.08). Invertebrate relative abundance and species richness did not differ between sites  
 275 with and without mangroves or among years (Fig. 5a-b; Table 3). Based on SIMPER analysis,  
 276 the two species that contributed the most to the dissimilarity in invertebrate assemblages among  
 277 site types were *Palaemonetes* spp. (grass shrimp) and snails in Family Cerithiidae (Table 5).  
 278 *Palaemonetes* was three times more common at sites without mangroves, relative to sites with  
 279 mangroves (Fig. 5c; Tables 3, 5). Cerithiid snails were relatively common at sites with  
 280 mangroves but were rare at sites without mangroves (Fig. 5d; Tables 3, 5).



281

282 Figure 5. Invertebrate species richness (a), total relative abundance expressed as average  
 283 #/sample  $\pm$  standard error (b), and relative abundance (c-d) for two common species at sites with  
 284 and without mangroves over four years.  
 285

286 Table 5. Average invertebrate abundance ( $\pm$  standard error) pooled over all observations at sites  
 287 with and without mangroves, and results of SIMPER analysis to identify the species that  
 288 contributed the most to differences among sites with and without mangroves.

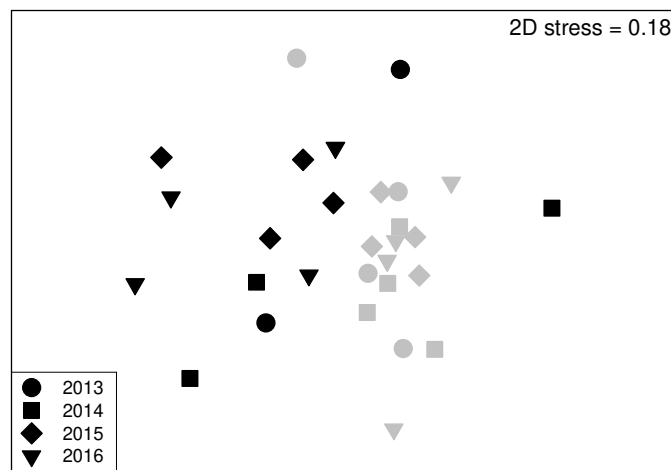
Species	Mangroves present	Mangroves absent	Dissimilarity contribution (%)	Cumulative dissimilarity explained
<i>Palaemonetes</i> spp.	11.7 $\pm$ 11.1	58.9 $\pm$ 38.0	23.3	23.3
Family Cerithiidae	24.8 $\pm$ 11.1	0.7 $\pm$ 0.3	19.1	42.4
<i>Litopenaeus setiferus</i>	0	46.5 $\pm$ 29.3	14.5	56.9
<i>Farfantepenaeus aztecus</i>	10.3 $\pm$ 7.8	4.5 $\pm$ 1.5	10.5	67.4
Class Bivalvia	3.3 $\pm$ 1.2	0.7 $\pm$ 0.6	8.9	76.3
<i>Callinectes sapidus</i>	0.6 $\pm$ 0.3	5.8 $\pm$ 4.2	8.4	84.7
Subclass Branchiura	0.1 $\pm$ 0.1	<0.1 $\pm$ 0.1	3.2	87.9
Order Amphipoda	0	13.2 $\pm$ 11.8	3.1	91.0

289

290 3.4 Birds

291 Shorebird assemblages were distinctly different between sites with and without mangroves  
292 but did not vary among years (ANOSIM site type  $R = 0.477$ ,  $p = 0.001$ ; year  $R = 0.016$ ,  $p =$   
293  $0.387$ ; Fig. 6). Based on SIMPER analysis, the four species that contributed the most to the  
294 dissimilarity between sites with and without mangroves were *Calidris alpina* (dunlin), *Calidris*  
295 *minutilla* (least sandpiper), *Limnodromus scolopaceus* (long-billed dowitcher), and *Tringa*  
296 *semipalmata* (willet) (Table 6). Willets were more common at sites with mangroves, and dunlin,  
297 least sandpipers, and long-billed dowitchers were more common at sites without mangroves  
298 (Table 6).

299 Wader assemblages were not distinctly different between sites with and without mangroves  
300 or among years (ANOSIM site type  $R = 0.046$ ,  $p = 0.328$ ; year  $R = -0.077$ ,  $p = 0.815$ ).



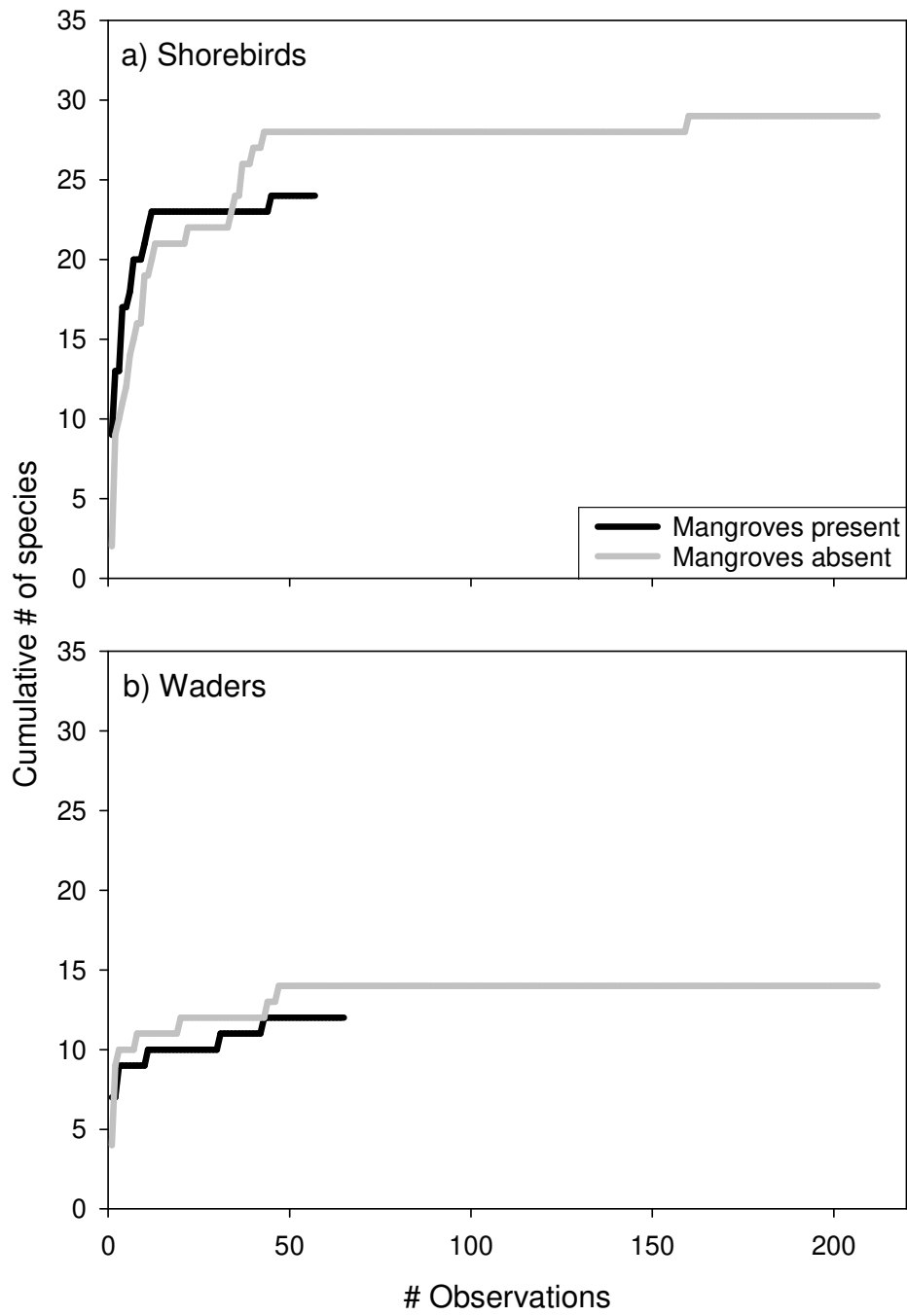
301  
302 Figure 6. Nonmetric multidimensional scaling plot depicting differences between shorebird  
303 assemblages at sites with (black symbols) and without (grey symbols) mangroves over four  
304 years.

305 Table 6. Average number of birds per site each year ( $\pm$  standard error) at sites with and without  
 306 mangroves, and results of SIMPER analysis to identify the species that contributed the most to  
 307 differences among sites with and without mangroves.

Species		Mangroves present	Mangroves absent	Dissimilarity contribution (%)	Cumulative dissimilarity explained
Dunlin	<i>Calidris alpina</i>	9.3 $\pm$ 7.4	12.5 $\pm$ 3.7	11.1	11.1
Least Sandpiper	<i>Calidris minutilla</i>	7.1 $\pm$ 3.9	10.0 $\pm$ 3.0	9.5	20.6
Long-billed Dowitcher	<i>Limnodromus scolopaceus</i>	2.7 $\pm$ 2.3	9.1 $\pm$ 2.9	8.4	29.0
Willet	<i>Tringa semipalmata</i>	11.9 $\pm$ 4.9	2.8 $\pm$ 0.7	7.4	36.4
Short-billed Dowitcher	<i>Limnodromus griseus</i>	0.5 $\pm$ 0.4	4.1 $\pm$ 1.2	6.0	42.4
Western Sandpiper	<i>Calidris mauri</i>	3.2 $\pm$ 3.1	4.3 $\pm$ 2.5	5.4	47.8
Killdeer	<i>Charadrius vociferus</i>	0.2 $\pm$ 0.1	2.8 $\pm$ 0.6	5.4	53.2
Lesser Yellowlegs	<i>Tringa flavipes</i>	0.1 $\pm$ 0.1	3 $\pm$ 0.9	5.0	58.2
Greater Yellowlegs	<i>Tringa melanoleuca</i>	0.7 $\pm$ 0.3	3 $\pm$ 0.6	4.7	62.9
Long-billed Curlew	<i>Numenius americanus</i>	2.3 $\pm$ 0.7	0.7 $\pm$ 0.3	4.2	67.1
Black-bellied Plover	<i>Pluvialis squatarola</i>	1.6 $\pm$ 1	1.6 $\pm$ 0.3	3.9	71.0
Black-necked Stilt	<i>Himantopus mexicanus</i>	0.3 $\pm$ 0.2	1.5 $\pm$ 0.5	3.3	74.3
American Avocet	<i>Recurvirostra americana</i>	0	2.3 $\pm$ 1.4	3.2	77.5
Semipalmated Plover	<i>Charadrius semipalmatus</i>	0	1.1 $\pm$ 0.4	2.9	80.4
Stilt Sandpiper	<i>Calidris himantopus</i>	0	1.1 $\pm$ 0.6	2.9	83.3
Marbled Godwit	<i>Limosa fedoa</i>	0.3 $\pm$ 0.1	0.9 $\pm$ 0.5	2.5	85.8
Ruddy Turnstone	<i>Arenaria interpres</i>	0.6 $\pm$ 0.3	0.3 $\pm$ 0.1	2.1	87.9
Wilson's Plover	<i>Charadrius wilsonia</i>	0.6 $\pm$ 0.4	0.1 $\pm$ 0.1	1.9	89.8
Semipalmated Sandpiper	<i>Charadrius semipalmatus</i>	0	1.1 $\pm$ 0.4	1.7	91.5

308

309 Shorebird species richness was ~20% higher at sites without mangroves (average  $5.6 \pm 0.3$   
310 SE) than at sites with mangroves ( $4.3 \pm 0.4$ ) across all years (PERMANOVA site type pseudo-F  
311 = 7.23,  $p = 0.010$ ; year pseudo-F = 1.3,  $p = 0.281$ ; site type\*year pseudo-F = 1.1,  $p = 0.397$ ).  
312 Wader richness was also higher at sites without ( $5.2 \pm 0.2$ ) than with ( $4.7 \pm 0.3$ ) mangroves (site  
313 type pseudo-F = 11.33,  $p = 0.002$ ; year pseudo-F = 1.9,  $p = 0.132$ ; site type\*year pseudo-F = 0.6,  
314  $p = 0.681$ ). The rarefaction curves (Fig. 7) indicate that this was not solely a result of higher  
315 observer effort at sites without mangroves; all species were detected after a similar number of  
316 observation reports in both site types. For shorebirds, over 95% of the species had been detected  
317 after 43 observations at sites without mangroves and after 45 recorded observations at sites with  
318 mangroves (Fig. 7a). For waders, all species had been detected after 48 observations at sites  
319 without mangroves and 43 recorded observations at sites with mangroves (Fig. 7b). Six shorebird  
320 species and three wader species were detected only in sites without mangroves (Table B.1).  
321 Three shorebird species (whimbrel, sanderling, piping plover) were unique to mangroves, but  
322 these were uncommonly sighted birds reported in fewer than 15% of the observations.  
323



324

325 Figure 7. Rarefaction curves for (a) shorebirds and (b) waders over all observations during  
 326 the four-year study period.

327

328 **4. Discussion**

329 As mangrove encroachment continues on the Gulf of Mexico coastline and beyond (Osland  
330 et al. 2013, Saintilan et al. 2014, Armitage et al. 2015), it is increasingly important for  
331 researchers and managers alike to understand the ecosystem implications of the resultant regime  
332 shift. Our study compared sites with and without mangroves as a proxy for mangrove  
333 encroachment. We demonstrated that mangrove presence is linked to changes in composition and  
334 decreased diversity of coastal wetland plant, nekton, and bird assemblages. These results broadly  
335 agree with previous works documenting differences in plant and animal assemblages between  
336 salt marsh and mangrove site types over relatively short temporal or spatial scales (Bloomfield  
337 and Gillanders 2005, Lunt et al. 2013, Diskin and Smee 2017, Scheffel et al. 2017, Smee et al.  
338 2017, Johnston and Gruner 2018). Our study adds a unique and complementary perspective by  
339 incorporating multiple trophic levels over broader spatial and temporal scales. Our approach  
340 revealed that although producer and consumer assemblages were generally different in wetlands  
341 with mangroves, there was also a substantial amount of heterogeneity over space and time.  
342 Notably, there were dynamic but not necessarily directional changes over time, demonstrating  
343 that the degree or nature of mangrove encroachment effects on coastal wetland faunal  
344 communities is not broadly predictable from short-term studies. A synthetic, ecosystem-level  
345 approach that encompasses a broad spatial and temporal scale is necessary to understand these  
346 dynamic patterns.

347 In studies that use observational approaches to compare marsh- and mangrove-associated  
348 communities (e.g., Bloomfield and Gillanders 2005, Scheffel et al. 2017, Smee et al. 2017), it is  
349 challenging to ascertain whether the observed differences in plant and animal assemblages are a

350 direct result of the presence of mangroves, or a consequence of the patchy spatial distribution of  
351 mangroves across a variable landscape. Rarely, if ever, are the characteristics of wetland plant  
352 and animal assemblages causally linked to the presence of the mangroves themselves, or to  
353 specific associated abiotic features. Our surveys have similar limitations imposed by the  
354 landscape distributions of mangrove stands along barrier islands, which have different soil and  
355 hydrological characteristics than marsh-dominated embayments. However, our “natural  
356 experiment” enabled us to examine links between mangrove presence and a suite of ecosystem  
357 characteristics at a uniquely large spatial scale. Furthermore, results from the natural experiment  
358 reported here and a nearby manipulative experiment (Guo et al. 2017) were usually consistent.  
359 The complementary outcomes from the two different approaches lend considerable confidence to  
360 the broad conclusion that mangroves have at least some driving influence on the associated plant  
361 and animal communities. However, as we discuss below, the mechanisms and relative  
362 importance of mangroves in driving spatial patterns in associated species is likely variable  
363 among taxa.

364 Marsh plants were less abundant and assemblages were less speciose at sites with mangroves  
365 present. Some of these differences may have been due to the landscape position of the sites,  
366 because the marsh sites were located inland of the mangrove sites and were likely exposed to  
367 different abiotic conditions. The largest factor affecting the marsh plants, however, was most  
368 likely the presence of mature mangroves. A variety of mesocosm and field studies have shown  
369 that although marsh vegetation can suppress the growth of mangrove seedlings (e.g., McKee and  
370 Rooth 2008, Howard et al. 2015, Pickens et al. 2019), mangroves are the dominant competitor  
371 once they grow taller than the marsh plants (Clarke and Hannon 1971, Ashton and Macintosh



372 2002, Stevens et al. 2006, Zhang et al. 2012, Guo et al. 2013). Despite the relatively small  
373 mature height of mangroves in our geographic area (Gabler et al. 2017), these mangroves are still  
374 taller than marsh plants and can suppress salt marsh plant cover by more than 75% (Guo et al.  
375 2017). Thus, the differences in marsh plant vegetation we observed were likely caused by the  
376 competitive suppression of marsh plants by mangroves. The most obvious mechanism of  
377 competition is direct shading of shorter herbaceous species by taller woody vegetation (Clarke  
378 and Hannon 1971, Kangas and Lugo 1990, Scholes and Archer 1997, Guo et al. 2017).  
379 Alternative competitive pathways include belowground competition for resources such as  
380 nutrients (McKee and Rooth 2008, Weaver and Armitage 2018, Yando et al. 2018) or water use  
381 efficiency (Krauss et al. 2014).

382       Whatever the mechanism of competition, the suppression of marsh plants by mangroves may  
383 alter a number of ecosystem services supported by coastal wetlands (Barbier et al. 2011,  
384 Kelleway et al. 2017). For example, marsh plants provide both habitat and food for a variety of  
385 other organisms that live in intertidal wetlands. The encroachment of mangroves and subsequent  
386 reduction in marsh plants is a management concern, particularly for endangered *Grus americana*  
387 (whooping crane; Chavez-Ramirez and Wehtje 2012). The change in habitat structure from short,  
388 dense and flexible stems of marsh plants to taller, less dense and stiff woody stems of mangroves  
389 may make mangrove habitat either more or less appealing to a variety of organisms.

390       Although fish and invertebrate nekton assemblages differed between sites with and without  
391 mangroves, there was a substantial amount of overlap and temporal variability at the assemblage  
392 and species levels. The high degree of overlap suggests that nekton assemblages may not have  
393 been directly linked to mangrove presence, at least not as a primary driver. Previous work in the

394 Gulf of Mexico and on the Atlantic coast of Florida has suggested that faunal composition is  
395 different between sites with and without mangroves (Lunt et al. 2013, Diskin and Smee 2017,  
396 Scheffel et al. 2017, Smee et al. 2017, Johnston and Gruner 2018). A notable similarity between  
397 our work and these previous studies is the strong preference of grass shrimp (*Palaemonetes* spp.)  
398 for marsh-dominated habitats. However, in most cases, the temporal and spatial persistence of  
399 relationships between faunal distribution and mangrove cover have not been clearly identified.

400 Multiple potential mechanistic drivers may have contributed to the differences in faunal  
401 assemblages between sites with and without mangroves. The nekton we sampled were captured  
402 in subtidal areas immediately adjacent to the emergent vegetation, and likely moved into  
403 emergent vegetation stands at high tide to forage. Direct mangrove subsidies to estuarine food  
404 webs are often relatively small (Mazumder and Saintilan 2010, Domingos and Lana 2017, Taylor  
405 et al. 2018), but increasing mangrove cover may alter patterns of energy flow at lower trophic  
406 levels (Nelson et al. 2019). Alternatively, the rigid aerial root structures of black mangroves may  
407 increase the refuge value for some nekton species and decrease it for others (Johnston and Caretti  
408 2017, Glazner et al. 2020). Overall, the identity of the emergent vegetation appeared to have a  
409 relatively weak effect on nekton composition. Fish and invertebrate assemblages were more  
410 likely linked to characteristics of the water column (water quality, hydrology) or submerged  
411 vegetation (seagrass), but these characteristics were outside the scope of this particular study.  
412 Further experimental work is needed to identify mangrove-specific drivers that could be directly  
413 influencing nekton and directly or indirectly altering their food sources.

414 Sites without mangroves had more shorebirds and more diverse shorebird and wader  
415 assemblages. These observations are consistent with nearby experimental studies in much

416 smaller (24 x 42 m) plots, where bird abundance was markedly lower in plots with more than  
417 25% mangrove cover (Guo et al. 2017). Tidal flats or ponds are generally the preferred foraging  
418 habitat for these groups of birds (Withers 2002, Darnell and Smith 2004), and sites without  
419 mangroves tended to have more of this ideal habitat (Table A.3). This difference in aquatic  
420 foraging habitat is linked to the location of mangroves on narrow barrier islands, in contrast to  
421 expansive embayments where the marsh-dominated sites were located. Therefore, even if  
422 shorebirds and waders were not using the vegetation per se, differences in assemblages and  
423 species richness were likely influenced by the location and character of the larger wetland  
424 landscape. Similar patterns of lower species richness at sites with mangroves are mirrored in  
425 sites along the entire coast of Texas (Whitt 2016), suggesting that areas where mangroves thrive  
426 are less suitable habitat for wetland birds, relative to salt marshes (Kelleway et al. 2017).

427 Differences in bird assemblages may have been a response to the different morphologies of  
428 mangrove and marsh vegetation. Some shorebird species are attracted to mangrove shrubs for  
429 nesting or roosting habitat (Zwarts 1988). In contrast, mangrove pneumatophore complexes may  
430 physically interfere with bird foraging activities (Meyerriecks 1971) and lead to active avoidance  
431 of mangroves in favor of salt marshes or tidal flats (Chavez-Ramirez and Wehtje 2012, Huang et  
432 al. 2012, Kelleway et al. 2017). Mangroves and other larger wetland plants may provide cover  
433 for ambush predators (Dekker and Ydenberg 2004, Kelleway et al. 2017), subsequently  
434 discouraging shorebirds that forage within wetland vegetation from entering dense mangrove  
435 stands. The eBird database did not provide detailed information on bird behaviors, and it is  
436 possible that birds used mangrove and marsh habitat for different activities (e.g., roosting in  
437 mangroves and foraging in marshes). Therefore, future work on bird activities in these

438 mangrove-marsh ecotones could explore whether a heterogeneous marsh-mangrove mosaic may  
439 facilitate a range of behaviors, including habitat suitable for both foraging and sheltering  
440 activities.

441       Based on the number of eBird reports, birdwatchers clearly preferred visiting marsh sites in  
442 this region and across the coast of Texas (Whitt 2016). There may be a perception that bird  
443 detection probability is lower at sites with mangroves, although this is likely to be a minor  
444 limitation in reality, given the typically short stature of black mangroves in Texas (< 1.5 m)  
445 (Madrid et al. 2014, Gabler et al. 2017). Alternatively, birdwatchers may have selected marsh  
446 sites because of the more diverse assemblages present and the higher incidence of certain rarer  
447 species (e.g., whooping cranes, various sandpipers). The drivers of birdwatcher behavior were  
448 beyond the scope of this study, but this difference in birdwatcher site selection is likely to have  
449 implications for the value of these coastal sites for birdwatchers as mangroves encroach upon  
450 them (Kelleway et al. 2017). This puts at risk the vigorous birdwatching ecotourism industry  
451 (Barbier et al. 2011) that brings millions of dollars to the Gulf Coast economy each year (NMFS  
452 2010, NRDC 2010).

453       Our study is the first to assess mangrove encroachment effects simultaneously across plant,  
454 nekton, and bird assemblages, and revealed that mangroves will likely have complex and  
455 dynamic bottom-up effects on community organization. Our approach compared sites with and  
456 without mangroves in a study design commonly called a “natural experiment.” This design  
457 complemented local field experiments where the variable of interest (in this case, the presence of  
458 mangroves) was directly manipulated by the investigators (Guo et al. 2017). Natural experiments  
459 and field experiments have complementary strengths and weaknesses. Typically, the natural

460 experiment has the advantages of greater spatial and temporal scale. We could not have  
461 manipulated mangrove presence at the scale (hectares) of our study sites, and mangroves have  
462 been present (or absent) at these sites for decades (Sherrod and McMillan 1981), allowing  
463 conditions and associated fauna to colonize and equilibrate. These strengths are particularly  
464 important for evaluating the responses of highly-mobile organisms such as nekton and birds. The  
465 weakness of the natural experiment is that other factors might differ among sites, and affect both  
466 the presence of mangroves and the variables putatively responding to mangrove presence. In this  
467 case, for example, we know that marsh and mangrove sites differ in landscape position and have  
468 somewhat different soil conditions. In the end, because natural experiments and field  
469 experiments have complementary strengths and weaknesses, the most conclusive findings are  
470 those that are supported by both approaches. In this case, results for plants and birds from the  
471 natural experiment reported here are consistent with our previous experimental results in the  
472 same geographic area (Guo et al. 2017). Improved sampling of birds and nekton allowed by the  
473 larger spatial scale of the natural experiment allowed us to refine our understanding of which  
474 species were most affected by mangrove incursion. Our ongoing work continues to explore the  
475 mechanistic links by which mangroves affect associated nekton and benthic organisms.

476 Our study sites are located in an area of the Gulf Coast of the United States that is fairly arid  
477 and can have hypersaline waters (Tolan 2007, Montagna et al. 2011), extremely saline porewater  
478 in the intertidal (Guo et al. 2017), and relatively low-stature and unproductive marsh and  
479 mangrove floras (Gabler et al. 2017). Whether results from this habitat can be extrapolated to  
480 areas such as Louisiana and Florida that are more mesic, with much more productive marshes  
481 and mangroves, is an open question. Although local drivers, dynamics, and implications of

482 mangrove encroachment vary within and across regions, there is widespread evidence of  
483 substantive ecosystem consequences of this regime shift from grass and forb-dominated habitats  
484 to taller, woody vegetation. Given the critical number of ecosystem services supported by coastal  
485 wetlands (Barbier et al. 2011, Kelleway et al. 2017), it is essential to understand the many  
486 complex bottom-up effects on ecosystem processes and services that will result as woody  
487 mangroves encroach and displace grass and forb-dominated habitats.

488

## 489 **5. Acknowledgements**

490 We are indebted to the many field assistants that contributed to data collection efforts for this  
491 study, including Rebekkah Bergren and Scotty Hall. We thank eBird and the Cornell Lab of  
492 Ornithology for the collection and careful management of data used in this study, as well as all of  
493 the local birdwatchers who helped groundtruth our observations and contributed data for the  
494 maintenance and advancement of the eBird citizen science database. We are grateful to the  
495 Aransas National Wildlife Refuge, Goose Island State Park, and Port Bay Hunting & Fishing  
496 Club for granting site access permissions. This research was funded in part by an Institutional  
497 Grant (NA10OAR4170099) from the Texas Sea Grant College Program from the National Sea  
498 Grant Office, National Oceanic and Atmospheric Administration, U.S. Department of  
499 Commerce. All views, opinions, findings, conclusions, and recommendations expressed in this  
500 material are those of the authors and do not necessarily reflect the opinions of the Texas Sea  
501 Grant College Program or the National Oceanic and Atmospheric Administration.

502

503

## **References cited**

- 505 Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T.  
506 Kitzberger, A. Rigling, D. D. Breshears, and E. T. Hogg. 2010. A global overview of  
507 drought and heat-induced tree mortality reveals emerging climate change risks for forests.  
508 *Forest Ecology and Management* **259**:660-684.
- 509 Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among  
510 foundation species and their consequences for community organization, biodiversity, and  
511 conservation. *BioScience* **61**:782-789.
- 512 Armitage, A. R., W. E. Highfield, S. D. Brody, and P. Louchouart. 2015. The contribution of  
513 mangrove expansion to salt marsh loss on the Texas gulf coast. *Plos One* **10**:e0125404.
- 514 Ashton, E. C., and D. J. Macintosh. 2002. Preliminary assessment of the plant diversity and  
515 community ecology of the Sematan mangrove forest, Sarawak, Malaysia. *Forest Ecology*  
516 *and Management* **166**:111-129.
- 517 Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The  
518 value of estuarine and coastal ecosystem services. *Ecological Monographs* **81**:169-193.
- 519 Bloomfield, A. L., and B. M. Gillanders. 2005. Fish and invertebrate assemblages in seagrass,  
520 mangrove, saltmarsh, and nonvegetated habitats. *Estuaries* **28**:63-77.
- 521 Bortolus, A., P. Adam, J. B. Adams, M. L. Ainouche, D. Ayres, M. D. Bertness, T. J. Bouma, J.  
522 F. Bruno, I. Caçador, J. T. Carlton, J. M. Castillo, C. S. B. Costa, A. J. Davy, L. Deegan,  
523 B. Duarte, E. Figueroa, J. Gerwein, A. J. Gray, E. D. Grosholz, S. D. Hacker, A. R.  
524 Hughes, E. Mateos-Naranjo, I. A. Mendelssohn, J. T. Morris, A. F. Muñoz-Rodríguez, F.  
525 J. J. Nieva, L. A. Levin, B. Li, W. Liu, S. C. Pennings, A. Pickart, S. Redondo-Gómez,  
526 D. M. Richardson, A. Salmon, E. Schwindt, B. R. Silliman, E. E. Sotka, C. Stace, M.  
527 Sytsma, S. Temmerman, R. E. Turner, I. Valiela, M. P. Weinstein, and J. S. Weis. 2019.  
528 Supporting *Spartina*: interdisciplinary perspective shows *Spartina* as a distinct solid  
529 genus. *Ecology* **100**:e02863.
- 530 Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez, and I. C.  
531 Feller. 2014. Poleward expansion of mangroves is a threshold response to decreased  
532 frequency of extreme cold events. *Proceedings of the National Academy of Sciences of*  
533 *the United States of America* **111**:723-727.
- 534 Chavez-Ramirez, F., and W. Wehtje. 2012. Potential impact of climate change scenarios on  
535 whooping crane life history. *Wetlands* **32**:11-20.
- 536 Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of  
537 species associated with high levels of climate warming. *Science* **333**:1024-1026.
- 538 Clarke, L. D., and N. J. Hannon. 1971. The mangrove swamp and salt marsh communities of the  
539 Sydney district: IV. The significance of species interaction. *The Journal of Ecology*  
540 **59**:535-553.
- 541 Committee, F. o. N. A. E. 2003. *Flora of North America North of Mexico, Volume 4,*  
542 *Magnoliophyta: Caryophyllidae, Part 1.* Oxford University Press, New York.
- 543 Darnell, T. M., and E. H. Smith. 2004. Avian use of natural and created salt marsh in Texas,  
544 USA. *Waterbirds* **27**:355-361.
- 545 Dekker, D., and R. Ydenberg. 2004. Raptor predation on wintering Dunlins in relation to the  
546 tidal cycle. *The Condor* **106**:415-419.

- 547 Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological  
548 research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and*  
549 *Systematics* **41**:149-172.
- 550 Diskin, M. S., and D. L. Smee. 2017. Effects of black mangrove *Avicennia germinans* expansion  
551 on salt marsh nekton assemblages before and after a flood. *Hydrobiologia* **803**:283-294.
- 552 Domingos, A. M., and P. C. Lana. 2017. Detecting multiple states of trophic connectivity  
553 between mangroves and salt marshes. *Ecosystems* **20**:1179-1189.
- 554 eBird. 2017. eBird Basic Dataset. Version: EBD\_relMay-2017. Cornell Lab of Ornithology,  
555 Ithaca, New York.
- 556 Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the  
557 world. *Frontiers in Ecology and the Environment* **6**:439-447.
- 558 Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B.  
559 D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W.  
560 V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. V. Holle, and J. R.  
561 Webster. 2005. Loss of foundation species: consequences for the structure and dynamics  
562 of forested ecosystems. *Frontiers in Ecology and the Environment* **3**:479-486.
- 563 Frelich, L. E., and P. B. Reich. 2010. Will environmental changes reinforce the impact of global  
564 warming on the prairie–forest border of central North America? *Frontiers in Ecology and*  
565 *the Environment* **8**:371-378.
- 566 Gabler, C. A., M. J. Osland, J. B. Grace, C. L. Stagg, R. H. Day, S. B. Hartley, N. M. Enwright,  
567 A. S. From, M. L. McCoy, and J. L. McLeod. 2017. Macroclimatic change expected to  
568 transform coastal wetland ecosystems this century. *Nature Climate Change* **7**:142-147.
- 569 Giri, C., and J. Long. 2016. Is the geographic range of mangrove forests in the conterminous  
570 United States really expanding? *Sensors* **16**:2010.
- 571 Glazner, R., J. Blennau, and A. R. Armitage. 2020. Mangroves alter predator-prey interactions  
572 by enhancing prey refuge value in a mangrove-marsh ecotone. *Journal of Experimental*  
573 *Marine Biology and Ecology* **526**:151336.
- 574 Godoy, M. D., and L. D. de Lacerda. 2015. Mangroves response to climate change: a review of  
575 recent findings on mangrove extension and distribution. *Anais da Academia Brasileira de*  
576 *Ciências* **87**:651-667.
- 577 Gordijn, P. J., E. Rice, and D. Ward. 2012. The effects of fire on woody plant encroachment are  
578 exacerbated by succession of trees of decreased palatability. *Perspectives in Plant*  
579 *Ecology, Evolution and Systematics* **14**:411-422.
- 580 Guo, H., C. Weaver, S. Charles, A. Whitt, S. Dastidar, P. D'Odorico, J. D. Fuentes, J. S.  
581 Kominoski, A. R. Armitage, and S. C. Pennings. 2017. Coastal regime shifts: rapid  
582 responses of coastal wetlands to changes in mangrove cover. *Ecology* **98**:762-772.
- 583 Guo, H. Y., Y. H. Zhang, Z. J. Lan, and S. C. Pennings. 2013. Biotic interactions mediate the  
584 expansion of black mangrove (*Avicennia germinans*) into salt marshes under climate  
585 change. *Global Change Biology* **19**:2765-2774.
- 586 Howard, R. J., K. W. Krauss, N. Cormier, R. H. Day, J. Biagas, and L. Allain. 2015. Plant–plant  
587 interactions in a subtropical mangrove-to-marsh transition zone: effects of environmental  
588 drivers. *Journal of Vegetation Science* **26**:1198-1211.



- 589 Huang, S. C., S. S. Shih, Y. S. Ho, C. P. Chen, and H. L. Hsieh. 2012. Restoration of shorebird-  
590 roosting mudflats by partial removal of estuarine mangroves in northern Taiwan.  
591 Restoration Ecology **20**:76-84.
- 592 Johnston, C. A., and O. N. Caretti. 2017. Mangrove expansion into temperate marshes alters  
593 habitat quality for recruiting *Callinectes* spp. Marine Ecology Progress Series **573**:1-14.
- 594 Johnston, C. A., and D. S. Gruner. 2018. Marine fauna sort at fine resolution in an ecotone of  
595 shifting wetland foundation species. Ecology **99**:2546-2557.
- 596 Kangas, P. C., and A. E. Lugo. 1990. The distribution of mangroves and saltmarsh in Florida.  
597 Tropical Ecology **31**:32-39.
- 598 Kelleway, J. J., K. Cavanaugh, K. Rogers, I. C. Feller, E. Ens, C. Doughty, and N. Saintilan.  
599 2017. Review of the ecosystem service implications of mangrove encroachment into salt  
600 marshes. Global Change Biology **23**:3967-3983.
- 601 Kelling, S., W. M. Hochachka, D. Fink, M. Riedewald, R. Caruana, G. Ballard, and G. Hooker.  
602 2009. Data-intensive science: a new paradigm for biodiversity studies. BioScience  
603 **59**:613-620.
- 604 Kominoski, J. S., J. J. Follstad Shah, C. Canhoto, D. G. Fischer, D. P. Giling, E. González, N. A.  
605 Griffiths, A. Larrañaga, C. J. LeRoy, M. M. Mineau, Y. R. McElarney, S. M. Shirley, C.  
606 M. Swan, and S. D. Tiegs. 2013. Forecasting functional implications of global changes in  
607 riparian plant communities. Frontiers in Ecology and the Environment **11**:423-432.
- 608 Krauss, K. W., A. S. From, T. W. Doyle, T. J. Doyle, and M. J. Barry. 2011. Sea-level rise and  
609 landscape change influence mangrove encroachment onto marsh in the Ten Thousand  
610 Islands region of Florida, USA. Journal of Coastal Conservation **15**:629-638.
- 611 Krauss, K. W., K. L. McKee, and M. W. Hester. 2014. Water use characteristics of black  
612 mangrove (*Avicennia germinans*) communities along an ecotone with marsh at a northern  
613 geographical limit. Ecohydrology **7**:354-365.
- 614 Lagomasino, D., T. Fatoyinbo, S. Lee, E. Feliciano, C. Trettin, A. Shapiro, and M. M. Mangora.  
615 2019. Measuring mangrove carbon loss and gain in deltas. Environmental Research  
616 Letters **14**:025002.
- 617 Lunt, J., K. McGlaun, and E. M. Robinson. 2013. Effects of black mangrove (*Avicennia*  
618 *germinans*) expansion on saltmarsh (*Spartina alterniflora*) benthic communities of the  
619 south Texas coast. Gulf and Caribbean Research **25**:125-129.
- 620 Madrid, E. N., A. R. Armitage, and J. López-Portillo. 2014. *Avicennia germinans* (black  
621 mangrove) vessel architecture is linked to chilling and salinity tolerance in the Gulf of  
622 Mexico. Frontiers in Plant Science **5**:503. doi: 510.3389/fpls.2014.00503.
- 623 Mazumder, D., and N. Saintilan. 2010. Mangrove leaves are not an important source of dietary  
624 carbon and nitrogen for crabs in temperate Australian mangroves. Wetlands **30**:375-380.
- 625 McKee, K., K. Rogers, and N. Saintilan. 2012. Response of salt marsh and mangrove wetlands to  
626 changes in atmospheric CO<sub>2</sub>, climate, and sea level. Pages 63-96 in B. A. Middleton,  
627 editor. Global Change and the Function and Distribution of Wetlands.
- 628 McKee, K. L., and W. Patrick. 1988. The relationship of smooth cordgrass (*Spartina*  
629 *alterniflora*) to tidal datums: a review. Estuaries **11**:143-151.
- 630 McKee, K. L., and J. E. Rooth. 2008. Where temperate meets tropical: multi-factorial effects of  
631 elevated CO<sub>2</sub>, nitrogen enrichment, and competition on a mangrove-salt marsh  
632 community. Global Change Biology **14**:971-984.

- 633 Meyerriecks, A. J. 1971. Further observations on use of the feet by foraging herons. *The Wilson*  
634 *Bulletin* **83**:435-438.
- 635 Montagna, P. A., J. Brenner, J. C. Gibeaut, and S. Morehead. 2011. Coastal impacts. Pages 1-26  
636 *in* J. Schmandt, G. R. North, and J. Clarkson, editors. *The Impact of Global Warming on*  
637 *Texas*. University of Texas Press, Austin, TX.
- 638 Nelson, J. A., J. Lesser, W. R. James, D. P. Behringer, V. Furka, and J. C. Doerr. 2019. Food  
639 web response to foundation species change in a coastal ecosystem. *Food Webs*  
640 **21**:e00125.
- 641 NMFS. 2010. Fisheries Economics of the United States, 2009. Tech. Memo. NMFS-F/SPO-118,  
642 172p., U.S. Dept. Commerce, NOAA, National Marine Fisheries Service.
- 643 NRDC. 2010. What's at Stake: The Economic Value of the Gulf of Mexico's Ocean Resources.  
644 Natural Resources Defense Council.
- 645 Osland, M. J., N. Enwright, R. H. Day, and T. W. Doyle. 2013. Winter climate change and  
646 coastal wetland foundation species: salt marshes versus mangrove forests in the  
647 southeastern U.S. *Global Change Biology* **19**:1482-1494.
- 648 Osland, M. J., N. Enwright, and C. L. Stag. 2014. Freshwater availability and coastal wetland  
649 foundation species: ecological transitions along a rainfall gradient. *Ecology* **95**:2789-  
650 2802.
- 651 Peters, D. P., and J. Yao. 2012. Long-term experimental loss of foundation species:  
652 consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere* **3**:1-  
653 23.
- 654 Pickens, C. N., T. M. Sloey, and M. W. Hester. 2019. Influence of salt marsh canopy on black  
655 mangrove (*Avicennia germinans*) survival and establishment at its northern latitudinal  
656 limit. *Hydrobiologia* **826**:195-208.
- 657 Price, J. N., and J. W. Morgan. 2008. Woody plant encroachment reduces species richness of  
658 herb-rich woodlands in southern Australia. *Austral Ecology* **33**:278-289.
- 659 Reid, A. M., and C. J. Lortie. 2012. Cushion plants are foundation species with positive effects  
660 extending to higher trophic levels. *Ecosphere* **3**:art96.
- 661 Reynolds, M. D., B. L. Sullivan, E. Hallstein, S. Matsumoto, S. Kelling, M. Merrifield, D. Fink,  
662 A. Johnston, W. M. Hochachka, and N. E. Bruns. 2017. Dynamic conservation for  
663 migratory species. *Science Advances* **3**:e1700707.
- 664 Richards, D. R., and D. A. Friess. 2016. Rates and drivers of mangrove deforestation in  
665 Southeast Asia, 2000-2012. *Proc Natl Acad Sci U S A* **113**:344-349.
- 666 Saintilan, N., N. C. Wilson, K. Rogers, A. Rajkaran, and K. W. Krauss. 2014. Mangrove  
667 expansion and salt marsh decline at mangrove poleward limits. *Global Change Biology*  
668 **20**:147-157.
- 669 Scheffel, W. A., K. L. Heck, and M. W. Johnson. 2017. Tropicalization of the northern Gulf of  
670 Mexico: impacts of salt marsh transition to black mangrove dominance on faunal  
671 communities. *Estuaries and Coasts*.
- 672 Scholes, R., and S. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology*  
673 *and Systematics* **28**:517-544.
- 674 Sherrod, C. L., and C. McMillan. 1981. Black mangrove, *Avicennia germinans*, in Texas: past  
675 and present distribution. *Contributions in Marine Science* **24**:115-131.

- 676 Smee, D. L., J. A. Sanchez, M. Diskin, and C. Trettin. 2017. Mangrove expansion into salt  
677 marshes alters associated faunal communities. *Estuarine, Coastal and Shelf Science*  
678 **187**:306-313.
- 679 Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-  
680 random species loss. *Ecology Letters* **6**:509-517.
- 681 Soulé, M. E., J. A. Estes, J. Berger, and C. Martínez Del Rio. 2003. Ecological effectiveness:  
682 conservation goals for interactive species. *Conservation Biology* **17**:1238-1250.
- 683 Stevens, P. W., S. L. Fox, and C. L. Montague. 2006. The interplay between mangroves and  
684 saltmarshes at the transition between temperate and subtropical climate in Florida.  
685 *Wetlands Ecology and Management* **14**:435-444.
- 686 Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: A  
687 citizen-based bird observation network in the biological sciences. *Biological*  
688 *Conservation* **142**:2282-2292.
- 689 Taylor, M. D., A. Becker, N. A. Moltschanivskyj, and T. F. Gaston. 2018. Direct and indirect  
690 interactions between lower estuarine mangrove and saltmarsh habitats and a  
691 commercially important penaeid shrimp. *Estuaries and Coasts* **41**:815-826.
- 692 Thomas, N., R. Lucas, P. Bunting, A. Hardy, A. Rosenqvist, and M. Simard. 2017. Distribution  
693 and drivers of global mangrove forest change, 1996–2010. *Plos One* **12**:e0179302.
- 694 TNRIS. 2015. Texas Natural Resources Information System (TNRIS); Texas TOP Imagery,  
695 2015-12-31. Web.
- 696 Tolan, J. M. 2007. El Niño-Southern Oscillation impacts translated to the watershed scale:  
697 estuarine salinity patterns along the Texas Gulf Coast, 1982 to 2004. *Estuarine, Coastal*  
698 *and Shelf Science* **72**:247-260.
- 699 Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual*  
700 *Review of Ecology and Systematics* **31**:197-215.
- 701 Weaver, C. A., and A. R. Armitage. 2018. Nutrient enrichment shifts mangrove height  
702 distribution: Implications for coastal woody encroachment. *Plos One* **13**:e0193617.
- 703 Whitt, A. A. 2016. Utilizing citizen science to assess bird community composition within a  
704 changing marsh-mangrove ecotone in Texas. Texas A&M University, College Station,  
705 TX.
- 706 Withers, K. 2002. Shorebird use of coastal wetland and barrier island habitat in the Gulf of  
707 Mexico. *The Scientific World Journal* **2**:514-536.
- 708 Yando, E. S., M. J. Osland, and M. W. Hester. 2018. Microspatial ecotone dynamics at a shifting  
709 range limit: plant–soil variation across salt marsh–mangrove interfaces. *Oecologia*  
710 **187**:319–331.
- 711 Zhang, Y. H., G. M. Huang, W. Q. Wang, L. Z. Chen, and G. H. Lin. 2012. Interactions between  
712 mangroves and exotic *Spartina* in an anthropogenically disturbed estuary in southern  
713 China. *Ecology* **93**:588-597.
- 714 Zwarts, L. 1988. Numbers and distribution of coastal waders in Guinea-Bissau. *Ardea* **76**:42-55.
- 715
- 716

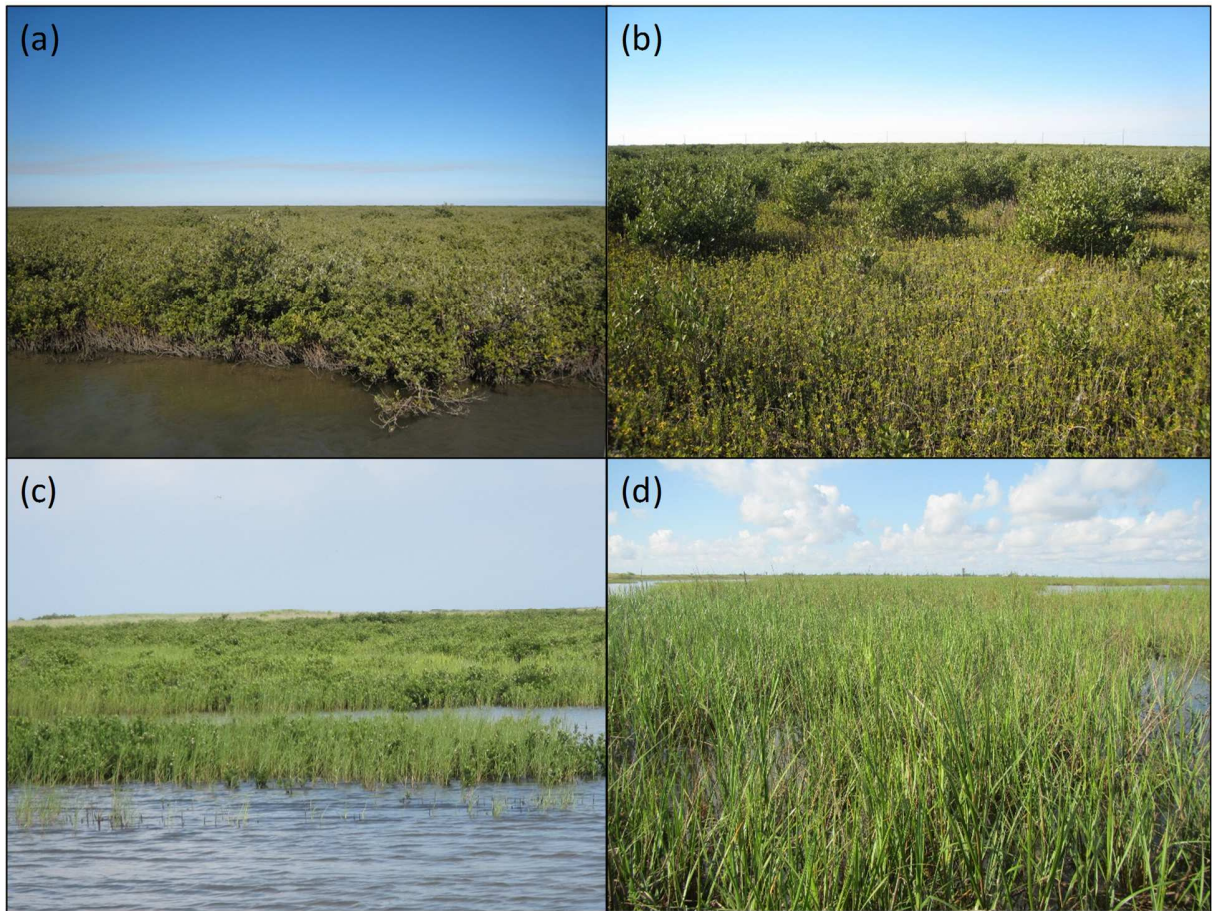
717 **Appendix A**

718 Table A.1. Site coordinates and black mangrove (*Avicennia germinans*) cover, as represented by  
 719 the average frequency of occurrence at five survey sites.

Site name	Latitude	Longitude	Mangrove cover (%)
Mustang Island A	27.767	-97.123	71.4
Mustang Island B	27.762	-97.127	75.0
Mustang Island C	27.755	-97.128	75.0
Mustang Island D	27.813	-97.093	72.7
Wilson's Cut	27.740	-97.139	89.5
Egery Flats	28.079	-97.221	0
Cape Velero Road	28.043	-97.119	0
Port Bay Hunting Club	28.031	-97.117	0
Goose Island State Park	28.129	-96.990	0
Cavasso Creek	28.217	-96.988	0

720

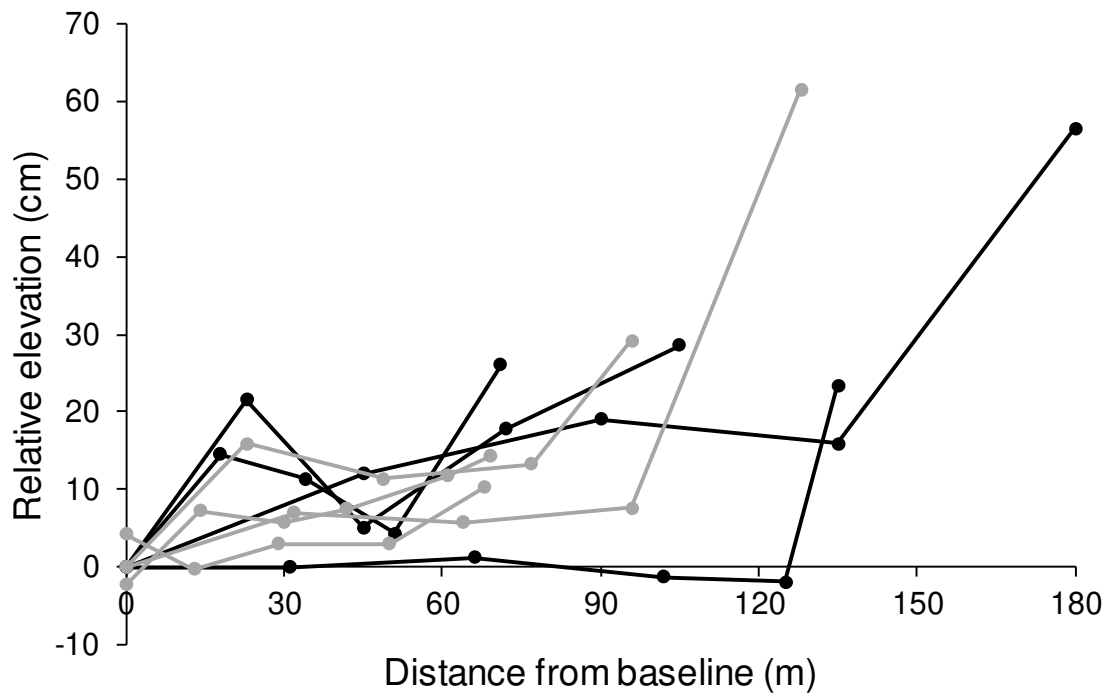
721



722

723 Figure A.1. Representative images depicting the contrast between coastal wetland sites in Texas  
724 with and without black mangroves. (a) *Avicennia germinans* monoculture; (b) mixture of  
725 *Avicennia germinans* and *Batis maritima*; (c) mixture of *Avicennia germinans* and *Spartina*  
726 *alterniflora*; (d) *Spartina alterniflora* monoculture.

727



728

729 Figure A.2. Elevation profiles at eight study sites. Elevations are reported relative to a baseline at  
 730 the water-vegetation interface. Black lines represent sites with mangroves; grey lines are sites  
 731 without mangroves.

732

733 *Soil characterization methods and summary of results*

734 To characterize the edaphic conditions at sites with and without mangroves, we collected two  
 735 soil cores (4 cm diameter, 10 cm depth) in 2014 from each site at the four lower elevation  
 736 stations, for a total of 8 cores per site. The upland station was excluded because only the four  
 737 lower stations were representative of the tidal elevation zone of interest where mangrove  
 738 encroachment occurs. The first core from each station was weighed before and after drying at  
 739 60°C to determine percent water content. A homogenized subsample was rehydrated with 80 ml  
 740 of distilled water and the supernatant salinity was measured after 12 hours. The original  
 741 porewater salinity was then backcalculated (Pennings and Richards 1988).

742 The second core from each station was dried at 60°C, homogenized, and several subsamples  
 743 were extracted for a series of analyses. Organic content was determined before and after loss on  
 744 ignition at 500°C. Nitrogen content was measured with a Costech ECS 4010 Elemental Analyzer  
 745 relative to standard reference material (SRM 1941-b). Phosphorus content was measured by dry-  
 746 oxidation acid hydrolysis extraction followed by colorimetric analysis of the extract (Fourqurean  
 747 et al. 1992). Grain size distribution was measured with the hydrometer method of Bouyoucos  
 748 (1962).

749 Soil data were analyzed with analyses of covariance (ANCOVA), with site type as the fixed  
 750 factor and station number (as a proxy for distance from shore) as the continuous variable. Data  
 751 were log transformed if necessary to improve heterogeneity of variances.

752

753 Table A.2. Soil conditions (average ± standard error) at sites with and without mangroves. F-  
 754 values are site type effects from 1-way ANCOVA.

	Mangroves present	Mangroves absent	Site type effect (F value)
% Moisture	29.9 ± 2.4	42.6 ± 2.7	12.48***
Salinity (ppt)	7.5 ± 1.2	14.5 ± 2.1	6.62*
% Sand	89.9 ± 1.0	61.7 ± 2.9	56.9***
% Nitrogen	0.02 ± 0.01	0.19 ± 0.06	9.02**
% Phosphorus	0.007 ± 0.001	0.021 ± 0.003	23.20***
% Organic content	3.0 ± 0.4	8.9 ± 1.7	17.88***

755 \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001

756

757 **References**

758 Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analyses of soils.  
 759 *Agronomy Journal* 54:464-465.

- 760 Fourqurean, J. W., J. C. Zieman, and G. V. N. Powell. 1992. Phosphorus limitation of primary  
761 production in Florida Bay: evidence from C:N:P ratios of the dominant seagrass *Thalassia*  
762 *testudinum*. *Limnology and Oceanography* 37:162-171.
- 763 Pennings, S. C., and C. L. Richards. 1998. Effects of wrack burial in salt-stressed habitats: *Batis*  
764 *maritima* in a Southwest Atlantic salt marsh. *Ecography* 21:630-638.



765 *Habitat characterizations and weather conditions at eBird observation hotspots.*

766 The habitat in the vicinity of each eBird hotspot were characterized based on 0.5 m resolution  
 767 orthoimagery from 2015 available through the Texas Natural Resources Information System  
 768 (TNRIS 2015). We overlaid a 100-m radius circular plot over aerial images (0.5 m pixel  
 769 resolution) each of the hotspots, using the hotspot GPS coordinates provided by eBird as the  
 770 center point. The 100-m radius represents a reasonable detection distance estimate; bird detection  
 771 distance is variable for species and site type, ranging from 40-100+ m for most species in  
 772 wetlands (Roeder et al. 1987, Marques et al. 2007, Fitzsimmons et al. 2012). Based on  
 773 examination of true color images, we created layers of emergent vegetation (marsh and/or  
 774 mangrove), aquatic foraging habitat (shallow flats), and unsuitable habitat (salt pans, roads, deep  
 775 water channels) within each circular area. In addition, a relative comparison of site size was  
 776 estimated by delineating the total potential viewing area (PVA) of wetland habitat over which an  
 777 observer could have recorded observations without getting back in a vehicle. Site characteristics  
 778 were heterogeneous, with a similar distribution and range of site types at site with and without  
 779 mangroves (Table A.3).

780

781 Table A.3: Hotspot habitat characteristics. Values are reported as percent of total area unless  
 782 otherwise noted.

Site name	Latitude	Longitude	Mangrove presence/ absence	Emergent vegetation	Aquatic foraging habitat	Unsuitable foraging habitat	Potential viewing area (km <sup>2</sup> )
Aransas Pass	27.879	-97.100	+	8.8	2.0	89.2	0.2
Lighthouse Lakes	27.869	-97.078	+	48.6	50.9	0.0	2.8
Mustang Island State Park	27.692	-97.185	+	5.9	16.4	77.7	1.8
Wilson's Cut	27.742	-97.149	+	15.7	19.8	64.5	1.3
Cavasso Creek	28.219	-96.988	-	54.3	6.7	39.0	0.3
Egery Flats	28.064	-97.212	-	7.2	92.8	0.0	0.7
Cape Valero	28.042	-97.117	-	34.1	52.5	13.3	0.2
Black Point	28.082	-97.223	-	32.6	66.5	0.9	0.3

783

784 Weather conditions were variable but relatively mild for most observation dates, suggesting  
785 that birdwatchers tended to report observations during good weather, reducing the potential for  
786 confounding effects of weather conditions on bird sightings. Records of temperature, wind, and  
787 weather conditions at the nearest NOAA weather station (Corpus Christi International Airport,  
788 station ID: KCRP) indicated that 74.2% of the dates where eBird observations were reported had  
789 high temperatures between 7.2-26.7°C, 94.5% of the dates had sustained wind speeds < 32 kph,  
790 and 95.8% of the days had less than 2.5 mm of rainfall.

791

## 792 **References**

793 Fitzsimmons, O. N., B. M. Ballard, M. T. Merendino, G. A. Baldassarre, and K. M. Hartke.  
794 2012. Implications of coastal wetland management to nonbreeding waterbirds in Texas.  
795 *Wetlands* 32:1057-1066.

796 Marques, T. A., L. Thomas, S. G. Fancy, and S. T. Buckland. 2007. Improving estimates of bird  
797 density using multiple-covariate distance sampling. *The Auk* 124:1229-1243.

798 Roeder, K., B. Dennis, and E. O. Garton. 1987. Estimating density from variable circular plot  
799 censuses. *Journal of Wildlife Management* 51:224-230.

800 **Appendix B**

801 Table B.1. Complete list of birds observed in eBird hotspot reports. Values are averages ( $\pm$   
 802 standard error) pooled over all observations at sites with mangroves and sites without  
 803 mangroves. @ denotes species found only at sites with mangroves; \* denotes species found only  
 804 at sites without mangroves. Shorebird species in bold are those that contributed the most to  
 805 dissimilarity between sites with and without mangroves.

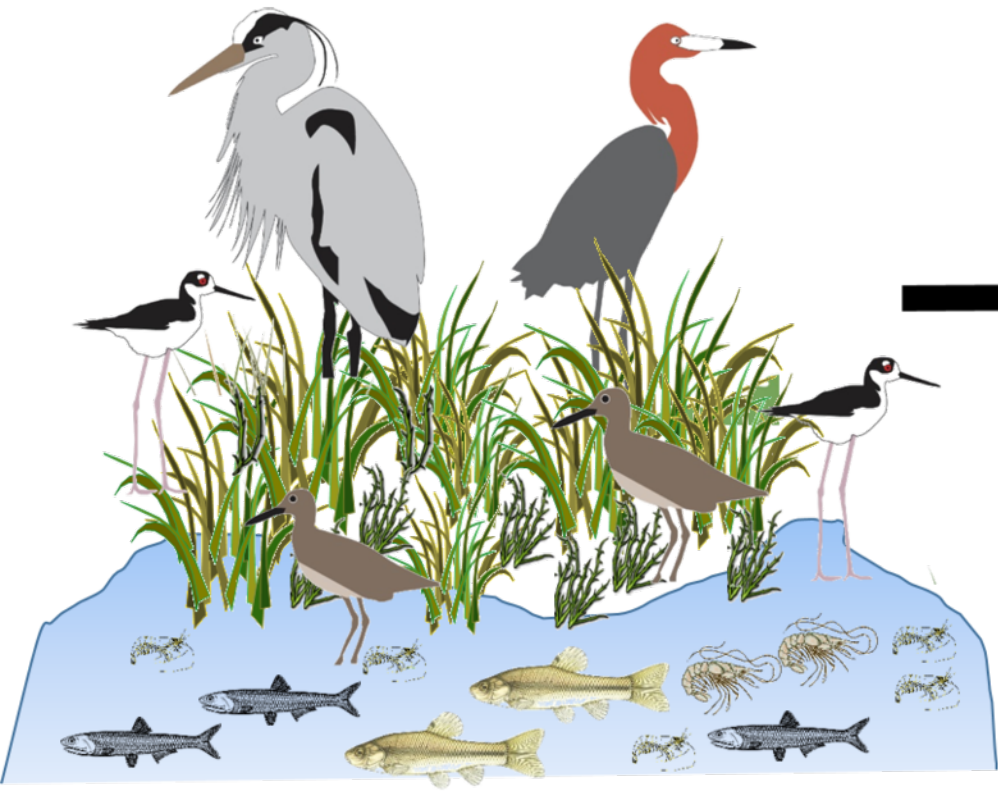
		Mangroves present	Mangroves absent
<b>Shorebirds</b>			
Family Scolopacidae			
<b>Dunlin</b>	<i>Calidris alpina</i>	<b>9.3 <math>\pm</math> 7.4</b>	<b>12.5 <math>\pm</math> 3.7</b>
Greater Yellowlegs	<i>Tringa melanoleuca</i>	0.7 $\pm$ 0.3	3 $\pm$ 0.6
<b>Least Sandpiper</b>	<i>Calidris minutilla</i>	<b>7.1 <math>\pm</math> 3.9</b>	<b>10 <math>\pm</math> 3</b>
Lesser Yellowlegs	<i>Tringa flavipes</i>	0.1 $\pm$ 0.1	3 $\pm$ 0.9
Long-billed Curlew	<i>Numenius americanus</i>	2.3 $\pm$ 0.7	0.7 $\pm$ 0.3
<b>Long-billed Dowitcher</b>	<i>Limnodromus scolopaceus</i>	<b>2.7 <math>\pm</math> 2.3</b>	<b>9.1 <math>\pm</math> 2.9</b>
Marbled Godwit	<i>Limosa fedoa</i>	0.3 $\pm$ 0.1	0.9 $\pm$ 0.5
*Pectoral Sandpiper	<i>Calidris melanotos</i>	0	0.5 $\pm$ 0.4
Ruddy Turnstone	<i>Arenaria interpres</i>	0.6 $\pm$ 0.3	0.3 $\pm$ 0.1
@ Sanderling	<i>Calidris alba</i>	0.3 $\pm$ 0.2	0
Semipalmated Sandpiper	<i>Calidris pusilla</i>	0.6 $\pm$ 0.6	0.2 $\pm$ 0.1
Short-billed Dowitcher	<i>Limnodromus griseus</i>	0.5 $\pm$ 0.4	4.1 $\pm$ 1.2
Spotted Sandpiper	<i>Actitis macularius</i>	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1
*Stilt Sandpiper	<i>Calidris himantopus</i>	0	1.1 $\pm$ 0.6
Western Sandpiper	<i>Calidris mauri</i>	3.2 $\pm$ 3.1	4.3 $\pm$ 2.5
@ Whimbrel	<i>Numenius phaeopus</i>	0.1 $\pm$ 0.1	0
<b>Willet</b>	<i>Tringa semipalmata</i>	<b>11.9 <math>\pm</math> 4.9</b>	<b>2.8 <math>\pm</math> 0.7</b>
*Wilson's Snipe	<i>Gallinago delicata</i>	0	0.3 $\pm$ 0.1
Family Charadriidae			
Black-bellied Plover	<i>Pluvialis squatarola</i>	1.6 $\pm$ 1	1.6 $\pm$ 0.3
Killdeer	<i>Charadrius vociferus</i>	0.2 $\pm$ 0.1	2.8 $\pm$ 0.6
@ Piping Plover	<i>Charadrius melodus</i>	0.3 $\pm$ 0.2	0
*Semipalmated Plover	<i>Charadrius semipalmatus</i>	0	1.1 $\pm$ 0.4
*Snowy Plover	<i>Charadrius nivosus</i>	0	0.2 $\pm$ 0.2
Wilson's Plover	<i>Charadrius wilsonia</i>	0.6 $\pm$ 0.4	0.1 $\pm$ 0.1

806

Family Recurvirostridae			
*American Avocet	<i>Recurvirostra americana</i>	0	2.3 ± 1.4
Black-necked Stilt	<i>Himantopus mexicanus</i>	0.3 ± 0.2	1.5 ± 0.5
Waders			
Family Ardeidae			
*Black-crowned Night-Heron	<i>Nycticorax nycticorax</i>	0	0.1 ± 0
Cattle Egret	<i>Bubulcus ibis</i>	0.4 ± 0.2	0.9 ± 0.3
Great Blue Heron	<i>Ardea herodias</i>	2.1 ± 0.5	2.7 ± 0.4
Great Egret	<i>Ardea alba</i>	2.1 ± 0.3	4 ± 0.6
Little Blue Heron	<i>Egretta caerulea</i>	0.9 ± 0.2	0.4 ± 0.1
Reddish Egret	<i>Egretta rufescens</i>	0.8 ± 0.2	1.1 ± 0.2
Snowy Egret	<i>Egretta thula</i>	1.2 ± 0.4	3.9 ± 1
Tricolored Heron	<i>Egretta tricolor</i>	1.1 ± 0.3	2.4 ± 0.6
Family Threskiornithidae			
Roseate Spoonbill	<i>Platalea ajaja</i>	1.2 ± 0.3	2.9 ± 0.9
White Ibis	<i>Eudocimus albus</i>	6.1 ± 2.9	4 ± 1.2
*White-faced Ibis	<i>Plegadis chihi</i>	0	0.6 ± 0.3
Family Gruidae			
Sandhill Crane	<i>Antigone canadensis</i>	0.1 ± 0.1	1.8 ± 0.7
*Whooping Crane	<i>Grus americana</i>	0	0.2 ± 0.1

807

# Salt marsh



# Mangrove

