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5 Received Date : 27-Dec-2015

6 Revised Date : 13-Nov-2016

7 Accepted Date : 30-Nov-2016

8 Article type : Articles

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11 **Coastal regime shifts: Rapid responses of coastal wetlands to**  
12 **changes in mangrove cover**

13 **Running head:** Responses to coastal regime shifts

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/ecy.1698](https://doi.org/10.1002/ecy.1698)

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30 **Abstract**

31 Global changes are causing broad-scale shifts in vegetation communities worldwide,  
32 including coastal habitats where the borders between mangroves and salt marsh are in flux.  
33 Coastal habitats provide numerous ecosystem services of high economic value, but the  
34 consequences of variation in mangrove cover are poorly known. We experimentally manipulated  
35 mangrove cover in large plots to test a set of linked hypotheses regarding the effects of changes  
36 in mangrove cover. We found that changes in mangrove cover had strong effects on  
37 microclimate, plant community, sediment accretion, soil organic content, and bird abundance  
38 within two years. At higher mangrove cover, wind speed declined and light interception by  
39 vegetation increased. Air and soil temperatures had hump-shaped relationships with mangrove  
40 cover. The cover of salt marsh plants decreased at higher mangrove cover. Wrack cover, the  
41 distance that wrack was distributed from the water's edge, and sediment accretion decreased at  
42 higher mangrove cover. Soil organic content increased with mangrove cover. Wading bird  
43 abundance decreased at higher mangrove cover. Many of these relationships were non-linear,  
44 with the greatest effects when mangrove cover varied from zero to intermediate values, and  
45 lesser effects when mangrove cover varied from intermediate to high values. Temporal and  
46 spatial variation in measured variables often peaked at intermediate mangrove cover, with  
47 ecological consequences that are largely unexplored. Because different processes varied in  
48 different ways with mangrove cover, the "optimum" cover of mangroves from a societal point of  
49 view will depend on which ecosystem services are most desired.

50 **Key words:** coastal ecosystem, ecosystem function, foundation species, mangrove, regime shift,  
51 salt marsh

## 52 **Introduction**

53 Global changes are causing broad-scale shifts in vegetation communities worldwide  
54 (Chen et al. 2011). Given the magnitude and rate of global change, understanding how  
55 consequent ecological regime shifts will affect ecosystem properties and functions is critical for  
56 managing natural systems (Ellison et al. 2005, Laurance et al. 2011, Kominoski et al. 2013). In  
57 particular, shifts among dominant plant species with markedly different traits are likely to alter  
58 ecosystem properties and functions. An example is the encroachment of woody plants into  
59 ecosystems dominated by low-stature graminoids and herbs (Van Auken 2000, Frelich and Reich  
60 2010). In grasslands and savannas, woody encroachment can alter albedo and temperatures  
61 (Lustenhouwer et al. 2012, D'Odorico et al. 2013) and may reduce species diversity (Ratajczak et  
62 al. 2012); woody encroachment in coastal systems is also likely to alter geomorphological  
63 processes and seedling recruitment (Balke et al. 2011, Peterson and Bell 2012, Balke et al. 2013).  
64 Moreover, woody encroachment can alter the quality and the quantity of basal carbon (C)  
65 sources (Jackson et al. 2002, McKinley and Blair 2008), and thus may both drive changes in  
66 herbivore and detritivore species, and alter the flow of C through green and brown food webs  
67 (Holmer and Olsen 2002, Byers et al. 2012, Dijkstra et al. 2012, Schrama et al. 2012).

68 Coastal wetlands provide numerous ecosystem services of high economic value  
69 (Costanza et al. 1997, Costanza et al. 2008, Barbier et al. 2011), but are threatened by global  
70 changes in climate, rising sea levels, increasing nutrient availability, land-use change and  
71 overfishing (Silliman et al. 2009, Kirwan et al. 2010, Deegan et al. 2012). Shifts in coastal  
72 foundation species include the spread of *Phragmites* in the United States (Bertness et al. 2002,  
73 King et al. 2007, Meyerson et al. 2009), worldwide invasions of *Spartina* species into new  
74 geographic regions (Strong and Ayres 2013), and the encroachment of mangroves into salt  
75 marshes worldwide (Cavanaugh et al. 2014, Saintilan et al. 2014). The effects on ecosystem  
76 services of *Phragmites* and *Spartina* encroachment into mudflats or stands of native vegetation  
77 have been extensively studied (e.g. Windham and Ehrenfeld 2003, Gratton and Denno 2005,  
78 Grosholz et al. 2009, Li et al. 2009, Zhang et al. 2010), but few of the effects of mangrove cover  
79 changes have been explicitly quantified.

80 The geographic border between mangroves and salt marsh is dynamic on a decadal scale.  
81 In the United States, black mangroves (*Avicennia germinans*) periodically expand from relict  
82 populations into salt marshes during periods with warm winters, and rapidly die back during  
83 periods with severe freezes (Sherrod and McMillan 1985, McMillan and Sherrod 1986, Stevens  
84 et al. 2006, Cavanaugh et al. 2014). In Texas, for example, mangrove cover increased by 74 %  
85 between 1990 and 2010 (Armitage et al. 2015). With increasing winter temperatures, black  
86 mangroves are predicted to replace salt marshes throughout much of the Gulf Coast of the United  
87 States within this century (Osland et al. 2013). Yet we lack an adequate understanding of how  
88 increases or decreases in mangrove cover will affect coastal ecological processes and ecosystem  
89 functions.

90 Although some previous studies have examined the effects of different foundation  
91 species (including mangrove and salt marsh vegetation) on ecological processes in coastal  
92 habitats, these studies usually rely on comparisons between areas dominated by different species  
93 (Bloomfield and Gillanders 2005, Perry and Mendelsohn 2009, Comeaux et al. 2012, Bianchi et  
94 al. 2013, Hansen and Nestlerode 2013). This work has been foundational in suggesting possible  
95 effects of mangrove cover changes, but the comparative approach risks confounding effects of  
96 different vegetation types with effects of differing abiotic conditions that promoted the different  
97 vegetation types (Pinsky et al. 2013). Given this concern, manipulative experiments are better  
98 suited to rigorously identifying the effects of mangrove cover changes (Ellison et al. 2010).

99 We experimentally manipulated mangrove cover in 10 plots at a relatively large spatial  
100 scale (24 m × 42 m plots) to test a set of linked hypotheses about how changes in mangrove  
101 cover might affect ecosystem properties and functions of a coastal wetland: higher mangrove  
102 cover and woody stem density (1) affects microclimate by increasing shading and decreasing  
103 wind speed, which affects light availability and temperature, and thereby mediates both plant  
104 community composition and structure; (2) favors higher accretion rates at the water's edge by  
105 enhancing wrack (floating algae and leaf litter) accumulation; (3) increases soil organic content  
106 due to increased litter accumulation and atmospheric deposition; and (4) decreases wading bird  
107 abundance in the wetlands. All these changes induced by changes in mangrove cover directly  
108 affect ecosystem services, including shoreline protection, support of higher trophic levels and  
109 carbon storage, but quantifying these ecosystem services is beyond the scope of this paper.

## 110 **Methods**

### 111 *Study site and experimental plots*

112 In 2012, we demarcated ten large plots, each 42 m (perpendicular to the water's edge) ×  
113 24 m (parallel with the water's edge), on Harbor Island, Port Aransas, TX (27.86°N, 97.08°W;  
114 Appendix S1: Figure S1 and S2). The front edge of each plot faced the Lydia Ann shipping  
115 channel. The plots were initially dominated by black mangrove, *Avicennia germinans*, with  
116 ~10% cover of salt marsh plants, including *Batis maritima*, a perennial succulent *Salicornia*  
117 *depressa* (Sensu USDA 2015), *Salicornia bigelovii* and *Spartina alterniflora*. In July-September  
118 2012, mangrove plants were thinned by clipping aboveground mangrove biomass from  
119 appropriate numbers of 3m × 3m cells (in total there were 8×14=112 cells in each experimental  
120 plot; each cell was either cleared of mangroves or left intact) to create plots ranging from 0 % to  
121 100 % mangrove cover (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88% and 100%).  
122 Aboveground mangrove biomass was removed from the clipped areas to accelerate the transition  
123 from mangrove to marsh, and composted at the study site away from the experimental plots.  
124 Cover treatments were maintained every 3-4 months. Plots were arrayed in three groups, with a  
125 wide range of mangrove densities represented in each group (Appendix S1: Figure S1).

### 126 *Microclimate monitoring*

127 In each plot, we set up a weather station on the center line perpendicular to the water's  
128 edge and ~12 m away from the water's edge. Air temperature was measured at 1 m and 0.5 m  
129 above the ground every 10 minutes, using HOBO U23-002 temperature loggers (Onset  
130 Computer Corporation, Bourne, MA, USA); wind speed and wind direction were measured at  
131 1.5 m aboveground every 5 minutes using Onset S-WSA-M003 wind speed sensors and Onset S-  
132 WDA-M003 wind direction sensors (Onset Computer Corporation, Bourne, MA, USA).  
133 Mangrove height declined from ~2.5 m at the water's edge to 1 m at the back of the plots, such  
134 that, at the location of the weather stations, the upper air temperature sensor was within the upper  
135 part of the mangrove canopy, and the wind speed sensor was at or just above the mangrove  
136 canopy. Wind speed data were filtered to analyze only periods when the wind was blowing into  
137 the plots from the water (defined as a range of 180 degrees). Soil temperature was measured at a  
138 depth of 5 cm every 5 minutes, using Onset S-TMB-M006 temperature sensors (Onset Computer  
139 Corporation, Bourne, MA, USA). For microclimate measurements, we calculated 24 h daily

140 average values and standard deviations (SD) for each experimental plot for the period from  
141 September 10, 2012 to August 20, 2013.

#### 142 *Plot survey*

143 We established two continuous transects through each experimental plot, running from  
144 the front (the water's edge) to the back of the plot. Each transect consisted of 42 contiguous 1 m  
145  $\times$  1 m sub-plots. We surveyed the plant community composition in each sub-plot by visually  
146 estimating the percent cover of each plant species in June 2012 (before the mangrove cover  
147 manipulation), and in August 2014 (after the mangrove cover manipulation). We calculated plot  
148 mean Bray-Curtis dissimilarity for the plant community based on plant percentage cover within  
149 the sampling quadrats in each experiment plot. We collected 8 soil cores (0-10 cm depth) along  
150 the two transects in each plot (4 soil cores along each transect at intervals of 6-10 m) to measure  
151 soil organic matter content in June 2012 (before the mangrove cover manipulation) and in June  
152 2014 (after the mangrove cover manipulation). Soil organic matter content was determined by  
153 the combustion method (USDA 2004). In May 2013, we measured light intensity (SunScan  
154 Canopy Analysis System SS1, Delta-T Devices Ltd, Cambridge, UK) above the canopy and on  
155 the soil surface in each sub-plot along the two transects in each plot, and we calculated light  
156 interception by vegetation for each sub-plot using the formula: light interception by vegetation =  
157  $1 - (\text{light intensity at the soil surface} / \text{light intensity above the canopy}) \times 100\%$ . In August 2014,  
158 we surveyed percentage cover of wrack (deposits of plant leaves and rhizomes, seagrass leaves  
159 and rhizomes, and algae) in each sub-plot along the two transects in each plot, and we recorded  
160 the wrack distribution range (i.e., the location of the wrack deposit farthest from the water's  
161 edge) for each transect.

#### 162 *Sediment accretion*

163 We established four feldspar accretion plots ( $\sim 0.5 \text{ m} \times 0.5 \text{ m}$ ) in each of the ten  
164 experimental plots on March 7 and 8, 2014, to determine surface accretion above a marker  
165 horizon (Cahoon and Turner 1989). Accretion plots were divided equally between cells with  
166 mangroves present and mangroves removed except in the experimental plots with 0% and 100%  
167 mangrove cover, where only one type of cell was present. We cored the accretion plots and  
168 measured the accretion above the feldspar marker at 3 points after 372 days ( $\sim 1$  year). The three

169 measurements within each accretion plot were averaged, and total plot accretion rates were  
170 determined as the sum of the average accretion of each vegetation type (mangroves present or  
171 removed) multiplied by the proportion of that vegetation type in each plot. Data were normalized  
172 to represent mm of accretion per year.

### 173 *Bird density*

174 Birds were visually counted in each plot in the morning before any other work was done  
175 in the plots (n=33 days during August 20, 2013-August 4, 2015). An observer approached the  
176 plot slowly and walked the perimeter of the plot while recording any birds present.

### 177 *Data analysis*

178 For all the variables, we calculated the average values for each plot, and we regressed  
179 plot averages of each variable on mangrove cover. We also calculated the standard deviation  
180 (SD) of each microclimate variable for each plot, and we regressed the SDs on mangrove cover.  
181 For all the regressions, we examined the fit of linear, quadratic and piecewise models, and  
182 selected regression models based on higher  $R^2$  (or adjusted  $R^2$ ) and significant  $P$ -values. Data  
183 analyses were performed using JMP 9 statistical software (SAS Institute 2010).

## 184 **Results**

185 Before the mangrove cover manipulation, the ten plots did not vary systematically in  
186 wind speed (average and standard deviation), air temperature (average and standard deviation),  
187 soil temperature (average and standard deviation), soil organic matter content, percentage cover  
188 of salt marsh vegetation, or plot mean Bray-Curtis dissimilarity of plant communities (Appendix  
189 S1: Figure S3-S8).

190 Wind speed was highest in plots with low mangrove cover, declining sharply from  $\sim 3.5$   
191  $\text{ms}^{-1}$  at zero mangrove cover to  $\sim 1.5 \text{ms}^{-1}$  at 33 % mangrove cover, and thereafter declining  
192 gradually to  $\sim 1 \text{ms}^{-1}$  at 100 % mangrove cover (Figure 1a). Light interception by vegetation  
193 increased from  $\sim 10\%$  to  $\sim 70\%$  as mangrove cover increased (Figure 1b). Daily average air (1 m  
194 aboveground) and soil temperatures showed hump-shaped relationships with mangrove cover  
195 with maxima at  $\sim 50\text{-}70\%$  mangrove cover (Figure 1c, d).

196 The standard deviation (SD) of wind speed declined sharply as mangrove cover increased  
197 from 0 % to 33 %, and declined more gradually thereafter as mangrove cover increased to 100 %  
198 (Figure 2a). Both the SDs of light interception by vegetation and air temperature (at 1 m  
199 aboveground) showed hump-shaped relationships with mangrove cover (Figure 2b, c). The SD of  
200 soil temperature peaked in the plot with 22% mangrove cover, but there was no statistically  
201 significant relationship between the SD of soil temperature and mangrove cover (Figure 2d). Air  
202 temperature patterns (daily average and SD) at 0.5 m aboveground showed hump-shaped  
203 patterns similar to those at 1 m aboveground (Figure S9).

204 Salt marsh plants (primarily *Batis maritima*, *Salicornia depressa* (Sensu USDA 2015),  
205 *Salicornia bigelovii*, *Spartina alterniflora*, *Sesuvium portulacastrum* and *Lycium carolinianum*)  
206 rapidly expanded in the gaps between mangrove patches in the experimental plots during the two  
207 years after the mangrove cover manipulation. As of August 2014 the response of marsh  
208 vegetation to mangrove cover change was non-linear, with marsh vegetation cover decreasing  
209 sharply from ~80 % at zero mangrove cover to ~20 % at 50 % mangrove cover, and more  
210 gradually if at all at higher mangrove cover (Figure 3a). The plot mean Bray-Curtis dissimilarity  
211 (a measure of community compositional variability or  $\beta$ -diversity) increased with mangrove  
212 cover to a peak in the plot with 22 % mangrove cover, and then gradually declined as mangrove  
213 cover further increased (Figure 3b).

214 Wrack cover in the plots decreased from ~13% to ~ 2% as mangrove cover increased  
215 from zero to 100 % (data not shown). In plots with < 30 % mangrove cover, wrack penetrated 20  
216 m or more into the plots (Figure 3c). In contrast, in plots with > 30% mangrove cover, wrack  
217 never penetrated more than 10 m into the plots. Sediment accretion in plots declined steadily  
218 with mangrove cover, from ~15 mm yr<sup>-1</sup> in plots with < 25% mangrove cover to ~6 mm yr<sup>-1</sup> in  
219 plots with > 75 % mangrove cover (Figure 3d).

220 Soil organic matter content (%) was ~7-10 % in the plots before mangrove cover was  
221 manipulated. In plots where mangroves were removed, soil organic content declined by up to 2.5  
222 % on an absolute scale (i.e., final soil organic content was from ~5 to ~9 %), with the loss of  
223 organic matter proportional to the loss of mangrove cover (Figure 3e).



224 The cumulative number of birds observed in the plots declined from ~90 to ~20 as  
225 mangrove cover increased (Figure 3f). Bird counts declined sharply from zero to low (~33%)  
226 mangrove cover, and plateaued at higher mangrove covers. The majority (84%) of the birds  
227 observed were birds in the families *Ardeidae* (herons), *Rallidae* (rails), *Threskiornithidae* (ibis)  
228 and *Scolopacidae* (sandpipers).

## 229 **Discussion**

### 230 *Effects of mangrove cover change on coastal wetland ecosystems*

231 Our results indicated that changes in mangrove cover, such as those that occur rapidly  
232 with dieback following hard freezes, or more gradually as mangroves expand during warm years,  
233 can affect microclimate conditions, wetland vegetation composition, wrack inputs, soil accretion  
234 and soil organic content after only two years. These effects, however, were often non-linear  
235 functions of mangrove cover, indicating that the consequences of changes in mangrove  
236 abundance may not simply be proportional to mangrove cover.

237 As woody trees with relatively tall canopies compared to salt marsh plants, mangroves  
238 decrease wind speed and attenuate wave energy, and thereby protect coastal areas (Alongi 2008,  
239 Cochard et al. 2008, Das and Vincent 2009, Das and Crépin 2013). Our results, however,  
240 revealed that the effect of mangroves on wind speed was a non-linear function of mangrove  
241 cover. In particular, the majority of wind attenuation was achieved once mangrove cover reached  
242 ~30%, suggesting that a relatively low cover of mangrove trees may be sufficient to provide this  
243 service.

244 Light interception by vegetation increased linearly as mangrove cover increased,  
245 resulting in low understory solar radiation at high mangrove cover, which is consistent with  
246 observations in other ecosystems with a gradient of woody plant cover (Breshears et al. 1997,  
247 Martens et al. 2000, Zou et al. 2010, Royer et al. 2012). Our measurements of light interception  
248 by vegetation were taken during the mid-day and might not represent what happens early and  
249 late in a day when the sunlight strikes the vegetation at a low angle and scattered mangrove  
250 plants may shade adjacent areas without mangroves. Although we modeled this relationship as a  
251 straight line, light interception appeared to stabilize at just above 10 % at the lowest mangrove

252 cover values. This represents the modest levels of light interception by the succulent salt marsh  
253 vegetation (mostly *Batis maritima*) that grew where mangroves were completely removed.

254 Both daily average air temperature in the mangrove canopy and soil temperature showed  
255 hump-shaped relationships with mangrove cover. We hypothesize that this was due to the  
256 combined factors of decreasing wind cooling and increasing canopy shading as mangrove cover  
257 increased. In plots with a lower mangrove cover, the relatively strong wind could carry away  
258 heat from the surface to the overlying atmosphere (Chen et al. 1993), thereby maintaining  
259 relatively low air and soil temperatures. In contrast, in plots with a higher mangrove cover, the  
260 relatively strong shading effect of the mangrove canopy reduces the amount of solar radiation  
261 reaching the ground surface, thereby decreasing air and soil temperatures (Martens et al. 2000,  
262 Villegas et al. 2010, Royer et al. 2012). As a result, plots with intermediate mangrove cover had  
263 the highest temperatures. Air warming may benefit mangroves, which are tropical plants, and  
264 this result suggests that even partial cover of mangroves is sufficient to create a strong warming  
265 effect and possibly facilitate further mangrove expansion. Mangroves may benefit both from  
266 warmer conditions, as shown here, which should increase photosynthesis rates in plants adapted  
267 to high temperatures, and higher minimum temperatures, which should reduce the frequency of  
268 dieback events (Osland et al. 2013), and the relative importance of both in mediating mangrove  
269 expansion remains to be explored.

270 Salt marsh plants expanded into the gaps between mangrove patches relatively quickly  
271 following the mangrove cover manipulation. Two years after mangrove cover was manipulated,  
272 the cover of salt marsh vegetation had increased eight-fold from an initial value of approximately  
273 10 % to approximately 80 % in the zero percent mangrove plot, and was inversely related to  
274 mangrove cover across the range of plots. These results were consistent with previous literature  
275 showing that adult mangroves have strong competitive effects on salt marsh plants (Zhang et al.  
276 2011). Similarly, large woody plants (trees or shrubs) are generally competitively dominant over  
277 grasses in savanna and desert ecosystems, although in both marshes and terrestrial grasslands,  
278 grasses can inhibit growth and survival of woody seedlings (Pieper 1990, Scholes and Archer  
279 1997, Forseth et al. 2001, Zhang et al. 2011, Guo et al. 2013). Marsh plants, however, did not  
280 expand as much as might have been expected at intermediate mangrove cover (the relationship  
281 between marsh plant cover and mangrove cover was concave), suggesting that the competitive

282 effects of mangroves extend outward some distance from their canopies. Because mangroves are  
283 taller than marsh plants, they cast shade some distance away from their canopies at low sun  
284 angles, thereby reducing the availability of direct photosynthetic radiation to adjacent marsh  
285 plants. Similarly, mangrove root systems may extend beyond their canopies to affect adjacent  
286 marsh plants, just as shrubs in other biomes can affect plants outside their canopy (Casper et al.  
287 2003). As a consequence, the growth of marsh plants in a mixed stand of marsh and mangrove  
288 vegetation may be less than would be expected based only on mangrove cover.

289 Both wrack cover and wrack distribution range from the water's edge decreased as  
290 mangrove cover increased, indicating that fringe mangroves close to the water's edge played an  
291 important role in trapping wrack deposits. Wrack releases nutrients when it decomposes (Mews  
292 et al. 2006, Rossi et al. 2011, Barreiro et al. 2013, Lavery et al. 2013), and increased nutrient  
293 availability due to wrack trapping by fringe mangroves could favor the growth of fringe  
294 mangroves (Feller et al. 2007, Williams and Feagin 2010, Del Vecchio et al. 2013), resulting in  
295 greater aboveground biomass and more leaf litter, as well as substantial development of root  
296 systems. Both accumulation of leaf litter and the soil binding effect of root systems would  
297 contribute to vertical accretion and thereby an increase of soil elevation (McKee et al. 2007,  
298 McKee 2011). Patterns of sediment accretion were consistent with this scenario. In the presence  
299 of mangroves, sediment accretion rates in plots were low, suggesting that the majority of  
300 sediments delivered from the channel by high tides were being trapped at the water's edge  
301 (unfortunately, none of the accretion measurements were conducted at the very front edge of the  
302 plots where this could have been documented). When mangroves were removed, sediment  
303 accretion rates in the plots were three-fold greater, indicating either that sediments from the  
304 channel were being carried further into the plots, or that sediments eroding from the front edge of  
305 the plots were being translocated farther back into the plots. In either case, we hypothesize that  
306 the outcome of a transition from mangroves to marsh vegetation is that the levee at the front of  
307 the plots will become less pronounced, and overall topographic heterogeneity in the plots  
308 reduced. Because the levee creates a steep barrier between the channel and the wetland that is  
309 overtopped only by the highest tides (authors' personal observations), a reduction in the levee  
310 might create easier and more direct access to the wetland for nekton from the adjacent channel.

311 Soil organic matter decreased when mangroves were removed, suggesting that mangrove  
312 vegetation might increase soil organic matter content. This finding is consistent with previous  
313 reports of relatively high nutrient levels in mangrove versus salt marsh habitats (Duarte and  
314 Cebrián 1996, Chmura et al. 2003, Donato et al. 2011, Osland et al. 2012, Yando et al. 2016). It  
315 also mirrors the similar patterns of higher soil organic matter under tree/shrub canopies versus  
316 herbaceous vegetation in grasslands and savannas (Schlesinger et al. 1996, Klopatek et al. 1998,  
317 Cable et al. 2009). With a much higher standing biomass than salt marsh vegetation, mangroves  
318 should produce more litter accumulation on the soil surface (Bhark and Small 2003, Price and  
319 Morgan 2008, McKee 2011). Moreover, with a relatively large surface area provided by their  
320 foliage, mangrove canopies could also enhance atmospheric deposition of nutrients (Weathers et  
321 al. 2001, DeLonge et al. 2008, Das et al. 2011), further favoring mangrove growth and organic  
322 matter accumulation.

323 The marked difference in canopy structure between relatively short grasses and forbs that  
324 characterize salt marshes and relatively tall woody vegetation of mangroves is likely to affect use  
325 of intertidal wetlands by birds. We observed higher abundances of birds (mostly wading birds) in  
326 plots with lower mangrove cover, suggesting that these species prefer to avoid habitats  
327 dominated by mangroves. Plots with a heterogeneous plant matrix may have provided an ideal  
328 combination of marsh forage habitat and shelter among the mangrove shrubs. Birds use much  
329 larger areas of the landscape than represented by our plots, and so it is possible that these results  
330 would not apply at the landscape scale. Previous observational studies also suggest that wading  
331 birds may decline as mangroves increase, although responses in many cases are species- and  
332 behavior-specific (Wong et al. 1999, Gómez-Montes and Bayly 2010, Santiago-Alarcon et al.  
333 2011).

334 In this study, we examined the relationships between each variable and mangrove cover  
335 separately for clarity; however, some of the variables show correlated responses. Some of these  
336 correlated responses could be due to independent but similar responses of these variables to  
337 mangrove cover changes. For example, cover of marsh vegetation and bird numbers might have  
338 responded independently but in the same manner to mangrove cover. In other cases, there might  
339 be causal relationships among these variables. For example, higher mangrove cover increased  
340 wrack trapping, and higher temperatures in intermediate and high mangrove cover plots would

341 likely increase the decomposition rate of deposited wrack, and together these processes might  
342 increase the organic matter content in soil. Evaluating these potential mechanistic linkages is  
343 beyond the scope of this manuscript, but it is important to note that the variables that we  
344 analyzed may not represent fully independent responses to mangrove cover.

#### 345 *Linear and non-linear effects of mangrove cover*

346 Some of the variables, such as light interception, sediment accretion and changes in soil  
347 organic matter content, showed more or less linear responses to mangrove cover changes. One  
348 simple interpretation of these patterns is that these variables responded mostly to conditions in  
349 each cell. For example, light interception at mid-day was a function of the vegetation canopy in  
350 each cell, and was not affected by conditions in adjacent cells. If so, one would expect the sum of  
351 the cell-level conditions to show linear changes across the experimental plots as the number of  
352 cells with mangroves increased.

353 In contrast, other variables, such as wind speed, temperature, salt marsh plant cover, plant  
354 diversity, wrack distribution and number of birds, showed non-linear relationships with  
355 mangrove cover. In particular, the change in mangrove cover from zero to intermediate values of  
356 30-50 % had much greater effects on these variables than did the change in mangrove cover from  
357 intermediate values to 100 % cover. It is likely that these variables were responding to mangrove  
358 cover at the level of the plot rather than the cell. Wind speed, for example, is affected by any  
359 upwind structure, not just by structure in the immediate 3 m × 3 m vicinity. Similarly, birds can  
360 perceive and respond to the local habitat at a patch scale that is greater than 3 m × 3 m. In many  
361 regards, a mixture of mangrove and salt marsh vegetation creates an ecosystem that functionally  
362 resembles a mangrove stand more than a salt marsh. As a result, many of the changes in  
363 ecological processes and ecosystem services that occur with mangrove expansion are likely to be  
364 largely complete before the mangroves coalesce into a closed stand. This suggests that the  
365 consequences for ecosystem functioning of mangrove expansion into salt marshes might be  
366 realized earlier than one might expect based solely on mangrove cover.

#### 367 *Increased variability at intermediate mangrove cover*

368 Many of the parameters that we measured were more variable at intermediate mangrove  
369 cover than in stands of pure marsh or pure mangrove vegetation. Increased spatial or temporal

370 variability of ecosystem properties can be associated with transitions in ecosystems from one  
371 regime to another (Breshears 2006). Previous studies have suggested that variability of certain  
372 ecosystem properties (e.g., near ground solar radiation, transpiration and biogeochemistry) would  
373 rise when an ecosystem experiences critical changes, such as shifts among vegetation types, and  
374 likely peak at an intermediate point of the transition (Klopatek et al. 1998, Martens et al. 2000,  
375 Huxman et al. 2005). In our study, the standard deviations (SDs) of light interception by  
376 vegetation and air temperature showed hump-shaped relationships with mangrove cover, with the  
377 maximum values near the intermediate range of mangrove cover. Also, the standard deviation  
378 (SD) of soil temperature peaked at ~20% of mangrove cover. These results were consistent with  
379 previous studies on ecosystem variability under regime shifts (Breshears 2006), showing that at  
380 intermediate stages of the regime shift between salt marsh and mangroves there is an increased  
381 variability in some ecosystem properties. In contrast, the standard deviation (SD) of wind speed  
382 decreased as mangrove cover increased, reflecting the greater roughness of mangroves that  
383 reduces wind fluctuations and can thus offer greater protection against storm damages (Das and  
384 Crépin 2013). Plant community dissimilarity (a measure of compositional variability or  $\beta$ -  
385 diversity (Anderson et al. 2011) peaked in the intermediate range of mangrove cover (~30%),  
386 where patches of mangroves alternated with patches of salt marsh vegetation. At high mangrove  
387 cover, community dissimilarity was low because all quadrats were dominated by mangroves, and  
388 salt marsh vegetation was rare. These results, combined with the negative effect of mangroves on  
389 cover of salt marsh plants, suggest that high levels of mangrove encroachment into marshes will  
390 decrease overall plant community diversity in coastal wetlands, even if mangrove encroachment  
391 is not complete. Similarly, in grasslands and savannas, woody encroachment often decreases  
392 plant diversity (Brudvig 2010, Ratajczak et al. 2012, Limb et al. 2014).

393 Taken together, our results indicate that coastal wetlands that are transitioning between  
394 marshes and mangroves are likely to experience high levels of temporal and spatial  
395 heterogeneity. This increased variability likely has important ecological consequences that  
396 deserve further study.

### 397 *Conclusions and management implications*

398 Our experimental results demonstrated that the shift between salt marsh and mangrove  
399 vegetation can cause rapid (2 years or less) alterations in a number of wetland processes and

400 attributes. These results have important implications for coastal ecosystem management. The  
401 shift between marshes and mangroves does not occur as an abrupt transition, but rather includes  
402 areas or times where mixed stands occur. As a result, managers need to consider not just the  
403 extreme states of the regime shift, but also the intermediate states where the two vegetation types  
404 co-occur. Moreover, some of the ecosystem properties and functions responded to mangrove  
405 cover non-linearly, which indicated that there might be optimal points that could achieve  
406 multiple conservation goals in coastal ecosystems experiencing regime shifts (Barbier et al.  
407 2008). For example, our results showed that at ~30 % cover, mangrove trees exert substantial  
408 effects in slowing down the wind speed close to the surface. We also found that plant community  
409 dissimilarity ( $\beta$ -diversity) peaked in the plot with 22 % mangrove cover. Thus, managers of  
410 coastal ecosystems might be able to achieve the goals of wind protection and high biodiversity  
411 by maintaining mangrove cover at around 20-30 %. If the primary goal was to maximize the  
412 organic content of soils, however, the optimum mangrove cover would be 100 %. Thus, the  
413 “best” cover of mangroves will depend on which ecological functions provide the services that  
414 are most valued by human societies. Therefore, a better understanding of how mangrove cover  
415 affects various ecosystem services, coupled with an explicit formulation of management goals,  
416 may enable coastal managers to identify the best conservation strategies for local ecosystems.  
417 Finally, the shift between marsh and mangrove vegetation likely affects the community  
418 composition of organisms at higher trophic levels (such as marine invertebrates, terrestrial  
419 arthropods, nekton, birds and mammals), and the changes in community composition and  
420 microclimate likely alter the rate of wetland carbon cycling. These possibilities need to be  
421 explored by additional research.

## 422 **Acknowledgements**

423 This research was supported in part by an Institutional Grant (NA10OAR4170099) to the  
424 Texas Sea Grant College Program from the National Sea Grant Office, National Oceanic and  
425 Atmospheric Administration, U.S. Department of Commerce. All views, opinions, findings,  
426 conclusions, and recommendations expressed in this material are those of the authors and do not  
427 necessarily reflect the opinions of the Texas Sea Grant College Program or the National Oceanic  
428 and Atmospheric Administration. We thank the University of Houston Division of Research, the  
429 Department of Biology and Biochemistry and the University of Houston Coastal Center for

430 providing matching funds. H. Guo thanks the National Natural Science Foundation of China  
431 (31300357), Tianjin Natural Science Foundation (16JCYBJC44100) and Young Scientist Fund  
432 of Tianjin Normal University (5RL140) for funding. We thank the University of Texas Marine  
433 Science Institute for providing logistical support. We thank Rebekkah Bergren, Katie Bowers,  
434 Zoe Hughes, Courtney Lee, Fan Li, Shanze Li, Wei-Ting Lin, Jessica Lunt, David Moulton,  
435 Kristen Onsgard, Jake Sigren, Kazimierz Więski and Yihui Zhang for help with field work.

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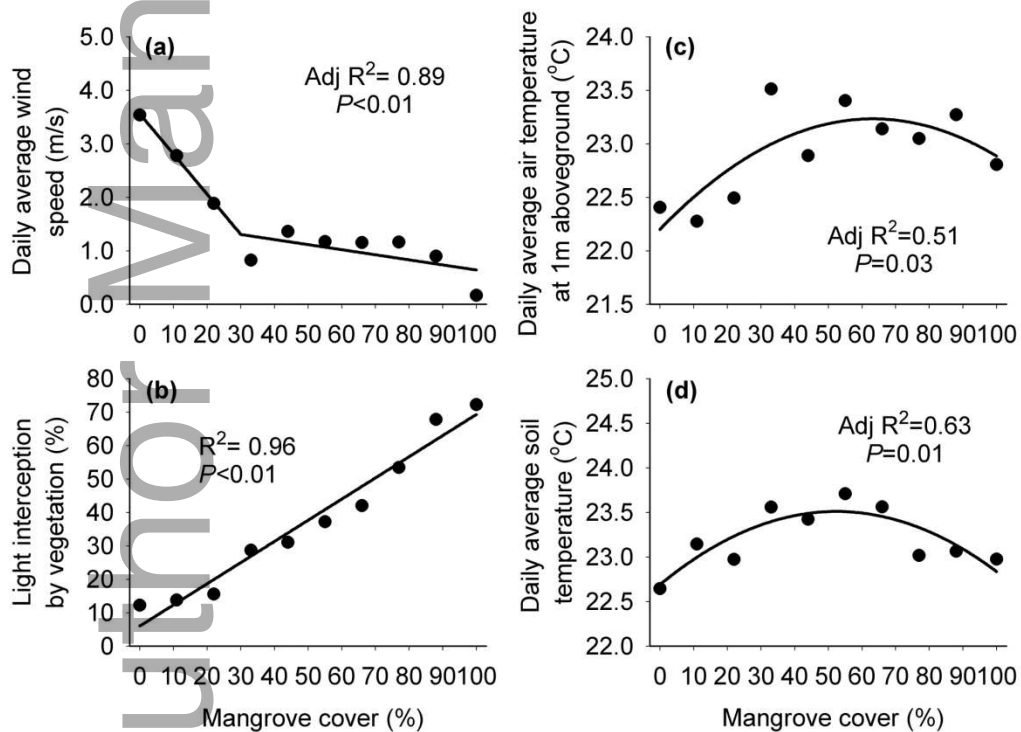
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### 713 **Figure legends**

714 **Figure 1** Microclimate conditions across the mangrove cover gradient. **(a)** Daily average wind  
715 speed (at 1.5 m aboveground, wind direction from shore into plots only); **(b)** light interception by  
716 vegetation; **(c)** daily average air temperature at 1 m aboveground; **(d)** daily average soil  
717 temperature. Data in panels **(a)**, **(c)** and **(d)** were collected during September 10, 2012-August  
718 20, 2013. Data in panel **(b)** were collected in May 2013.  $R^2$  or adjusted  $R^2$ , and  $P$ -values  
719 (piecewise regression in panel **(a)**; linear regression in panel **(b)**; and quadratic regressions in  
720 panel **(b)** and **(c)**) are shown.

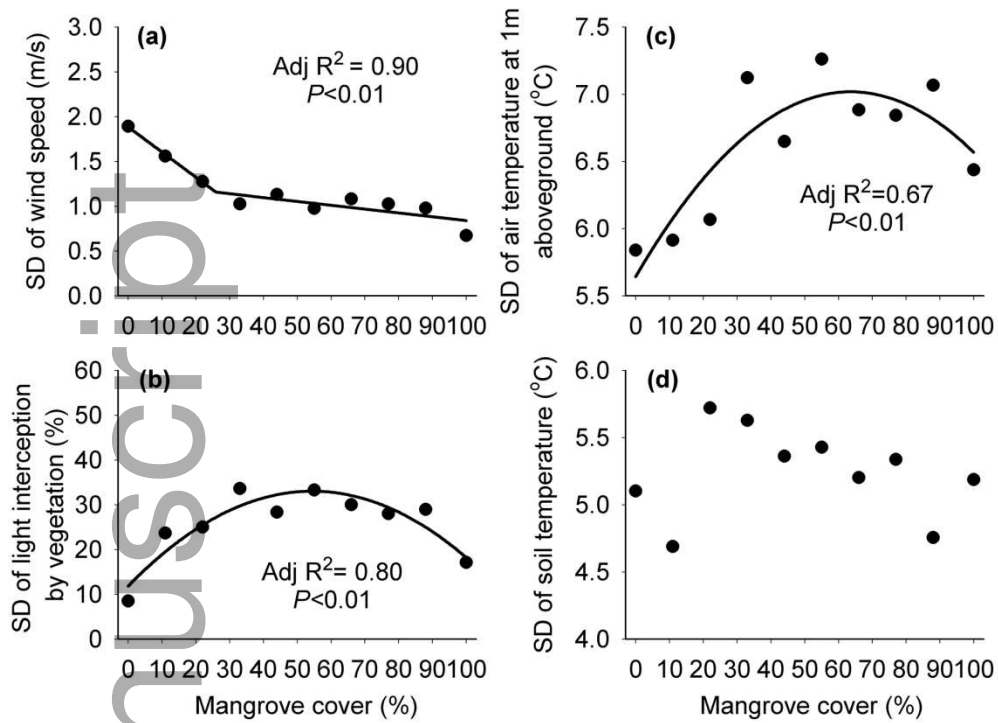
721 **Figure 2** Standard deviation (SD) of **(a)** wind speed (for wind direction from shore into plots  
722 only), **(b)** light interception by vegetation, **(c)** air temperature at 1 m aboveground, and **(d)** soil  
723 temperature, across the mangrove cover gradient. Data were collected during September 10,  
724 2012-August 20, 2013. Adjusted  $R^2$  and  $P$ -values (piecewise regression in panel **(a)**; quadratic  
725 regressions in panels **(b)** and **(c)**) are shown. No statistically significant relationship was found  
726 between SD of soil temperature and mangrove cover in panel **(d)**.

727 **Figure 3** Ecosystem responses of coastal wetlands to changes in mangrove cover in the study.  
 728 (a) Total percentage cover of salt marsh vegetation (multiple species); (b) Plot mean Bray-Curtis  
 729 dissimilarity of plant community; (c) Wrack deposit distribution range from the water's edge; (d)  
 730 Sediment accretion; (e) Change in soil organic matter content (%); (f) Total number of birds  
 731 observed in plots. Data in panel (a), (b), (c) were collected in August 2014; data in panel (d)  
 732 were collected in March 2015 (after 372 days of the deployment of the feldspar markers); data in  
 733 panel (e) are the difference between values in May 2012 before the mangrove removal and in  
 734 June 2014 after the mangrove removal; data in panel (f) were collected during each visit to the  
 735 study site from August 20, 2013 to August 4, 2015.  $R^2$  (linear regression in panel (d) and (e)) or  
 736 Adjusted  $R^2$  (quadratic regression in panel (a) and (f); piecewise regression in panel (b) and  
 737 (c)), and  $P$ -values are shown.



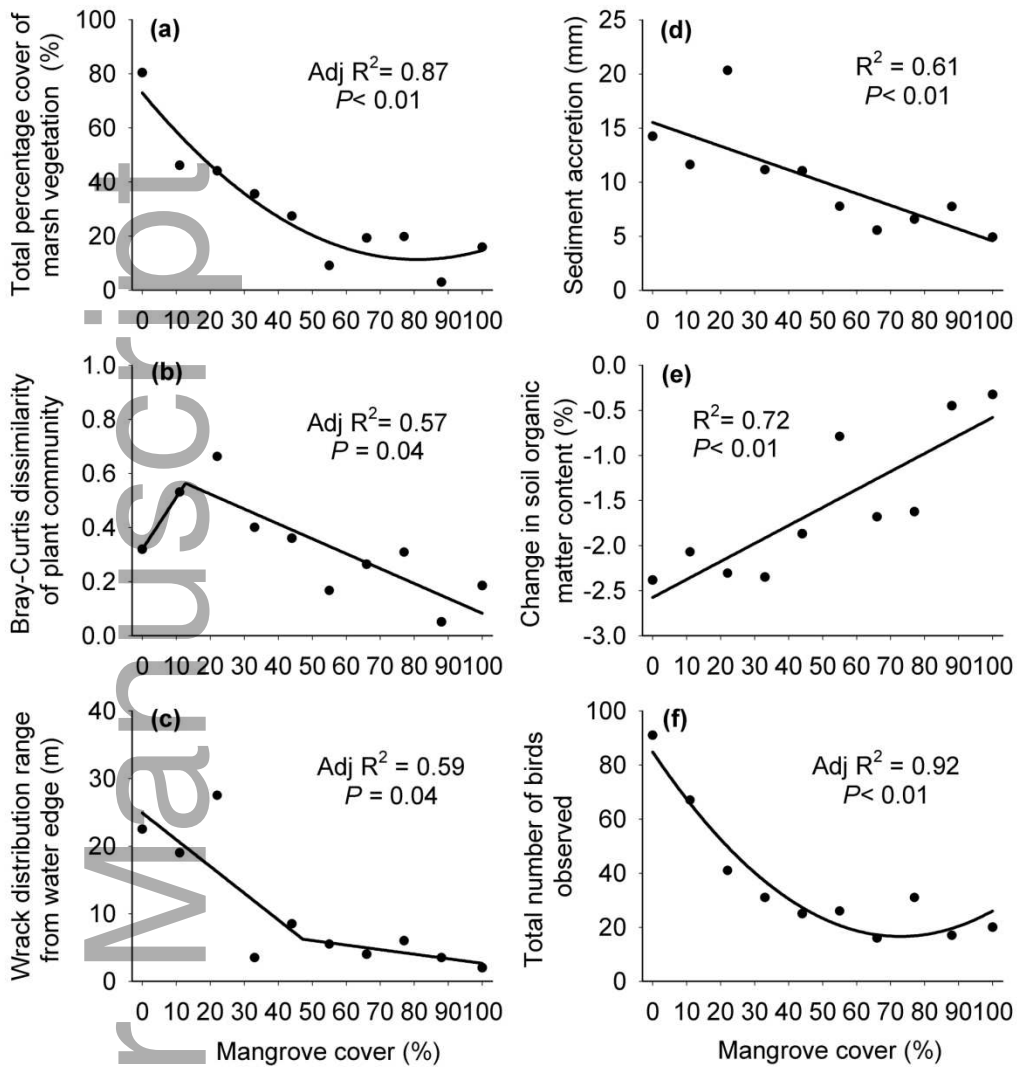
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739 **Figure 1**



740

741 **Figure 2**



742

743 **Figure 3**