

Coastal regime shifts: rapid responses of coastal wetlands to changes in mangrove cover

HONGYU GUO,^{1,2} CAROLYN WEAVER,³ SEAN P. CHARLES,⁴ ASHLEY WHITT,⁵ SAYANTANI DASTIDAR,² PAOLO D'ODORICO,⁶ JOSE D. FUENTES,⁷ JOHN S. KOMINOSKI,⁴ ANNA R. ARMITAGE ⁵ AND STEVEN C. PENNINGS ^{2,8}

¹Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin 300387 China

²Department of Biology and Biochemistry, University of Houston, Houston, Texas 77204 USA

³Department of Ecosystem Science and Management, Texas A&M University, College Station, Texas 77843 USA

⁴Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA

⁵Department of Marine Biology, Texas A&M University at Galveston, P.O. Box 1675, Galveston, Texas 77553 USA

⁶Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904 USA

⁷Department of Meteorology, The Pennsylvania State University, 503 Walker Building, University Park, Pennsylvania 16802 USA

Abstract. Global changes are causing broad-scale shifts in vegetation communities worldwide, including coastal habitats where the borders between mangroves and salt marsh are in flux. Coastal habitats provide numerous ecosystem services of high economic value, but the consequences of variation in mangrove cover are poorly known. We experimentally manipulated mangrove cover in large plots to test a set of linked hypotheses regarding the effects of changes in mangrove cover. We found that changes in mangrove cover had strong effects on microclimate, plant community, sediment accretion, soil organic content, and bird abundance within 2 yr. At higher mangrove cover, wind speed declined and light interception by vegetation increased. Air and soil temperatures had hump-shaped relationships with mangrove cover. The cover of salt marsh plants decreased at higher mangrove cover. Wrack cover, the distance that wrack was distributed from the water's edge, and sediment accretion decreased at higher mangrove cover. Soil organic content increased with mangrove cover. Wading bird abundance decreased at higher mangrove cover. Many of these relationships were non-linear, with the greatest effects when mangrove cover varied from zero to intermediate values, and lesser effects when mangrove cover varied from intermediate to high values. Temporal and spatial variation in measured variables often peaked at intermediate mangrove cover, with ecological consequences that are largely unexplored. Because different processes varied in different ways with mangrove cover, the “optimum” cover of mangroves from a societal point of view will depend on which ecosystem services are most desired.

Key words: coastal ecosystem; ecosystem function; foundation species; mangrove; regime shift; salt marsh.

INTRODUCTION

Global changes are causing broad-scale shifts in vegetation communities worldwide (Chen et al. 2011). Given the magnitude and rate of global change, understanding how consequent ecological regime shifts will affect ecosystem properties and functions is critical for managing natural systems (Ellison et al. 2005, Laurance et al. 2011, Kominoski et al. 2013). In particular, shifts among dominant plant species with markedly different traits are likely to alter ecosystem properties and functions. An example is the encroachment of woody plants into ecosystems dominated by low-stature graminoids and herbs (Van Auken 2000, Frelich and Reich 2010). In grasslands and savannas, woody encroachment can alter albedo and temperatures (Lustenhauer et al. 2012, D'Odorico et al. 2013) and may reduce species diversity (Ratajczak et al.

2012); woody encroachment in coastal systems is also likely to alter geomorphological processes and seedling recruitment (Balke et al. 2011, 2013, Peterson and Bell 2012). Moreover, woody encroachment can alter the quality and the quantity of basal carbon (C) sources (Jackson et al. 2002, McKinley and Blair 2008), and thus may both drive changes in herbivore and detritivore species, and alter the flow of C through green and brown food webs (Holmer and Olsen 2002, Byers et al. 2012, Dijkstra et al. 2012, Schrama et al. 2012).

Coastal wetlands provide numerous ecosystem services of high economic value (Costanza et al. 1997, 2008, Barbier et al. 2011), but are threatened by global changes in climate, rising sea levels, increasing nutrient availability, land-use change and overfishing (Silliman et al. 2009, Kirwan et al. 2010, Deegan et al. 2012). Shifts in coastal foundation species include the spread of *Phragmites* in the United States (Bertness et al. 2002, King et al. 2007, Meyerson et al. 2009), worldwide invasions of *Spartina* species into new geographic regions (Strong and Ayres 2013), and the encroachment of

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⁸Corresponding author. E-mail: spennings@uh.edu

mangroves into salt marshes worldwide (Cavanaugh et al. 2014, Saintilan et al. 2014). The effects on ecosystem services of *Phragmites* and *Spartina* encroachment into mudflats or stands of native vegetation have been extensively studied (e.g., Windham and Ehrenfeld 2003, Gratton and Denno 2005, Grosholz et al. 2009, Li et al. 2009, Zhang et al. 2010), but few of the effects of mangrove cover changes have been explicitly quantified.

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

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

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

METHODS

Study site and experimental plots

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

Microclimate monitoring

In each plot, we set up a weather station on the center line perpendicular to the water's edge and ~12 m away from the water's edge. Air temperature was measured at 1 and 0.5 m above the ground every 10 min, using HOBO U23-002 temperature loggers (Onset Computer Corporation, Bourne, Massachusetts, USA); wind speed and wind direction were measured at 1.5 m aboveground every 5 min using Onset S-WSA-M003 wind speed sensors and Onset S-WDA-M003 wind direction sensors (Onset Computer Corporation). Mangrove height declined from ~2.5 m at the water's edge to 1 m at the back of the plots, such that, at the location of the weather stations, the upper air temperature sensor was within the upper part of the mangrove canopy, and the wind speed sensor was at or just above the mangrove canopy. Wind speed data were filtered to analyze only periods when the wind was blowing into the plots from the water (defined as a range of 180°). Soil temperature was measured at a depth of 5 cm every 5 min, using Onset S-TMB-M006 temperature sensors (Onset Computer Corporation). For microclimate measurements, we calculated 24 h daily average values and standard deviations (SD) for each experimental plot for the period from September 10, 2012 to August 20, 2013.

Plot survey

We established two continuous transects through each experimental plot, running from the front (the water's

edge) to the back of the plot. Each transect consisted of 42 contiguous 1 × 1 m sub-plots. We surveyed the plant community composition in each sub-plot by visually estimating the percent cover of each plant species in June 2012 (before the mangrove cover manipulation), and in August 2014 (after the mangrove cover manipulation). We calculated plot mean Bray–Curtis dissimilarity for the plant community based on plant percentage cover within the sampling quadrats in each experiment plot. We collected 8 soil cores (0–10 cm depth) along the two transects in each plot (4 soil cores along each transect at intervals of 6–10 m) to measure soil organic matter content in June 2012 (before the mangrove cover manipulation) and in June 2014 (after the mangrove cover manipulation). Soil organic matter content was determined by the combustion method (USDA 2004). In May 2013, we measured light intensity (SunScan Canopy Analysis System SS1, Delta-T Devices Ltd, Cambridge, UK) above the canopy and on the soil surface in each sub-plot along the two transects in each plot, and we calculated light interception by vegetation for each sub-plot using the formula: light interception by vegetation = 1 – (light intensity at the soil surface/light intensity above the canopy) × 100%. In August 2014, we surveyed percentage cover of wrack (deposits of plant leaves and rhizomes, seagrass leaves and rhizomes, and algae) in each sub-plot along the two transects in each plot, and we recorded the wrack distribution range (i.e., the location of the wrack deposit farthest from the water's edge) for each transect.

Sediment accretion

We established four feldspar accretion plots (~0.5 × 0.5 m) in each of the 10 experimental plots on March 7 and 8, 2014, to determine surface accretion above a marker horizon (Cahoon and Turner 1989). Accretion plots were divided equally between cells with mangroves present and mangroves removed except in the experimental plots with 0% and 100% mangrove cover, where only one type of cell was present. We cored the accretion plots and measured the accretion above the feldspar marker at 3 points after 372 d (~1 yr). The three measurements within each accretion plot were averaged, and total plot accretion rates were determined as the sum of the average accretion of each vegetation type (mangroves present or removed) multiplied by the proportion of that vegetation type in each plot. Data were normalized to represent mm of accretion per year.

Bird density

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

Data analysis

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

RESULTS

Before the mangrove cover manipulation, the 10 plots did not vary systematically in wind speed (average and SD), air temperature (average and SD), soil temperature (average and SD), soil organic matter content, percentage cover of salt marsh vegetation, or plot mean Bray–Curtis dissimilarity of plant communities (Appendix S1: Fig. S3–S8).

Wind speed was highest in plots with low mangrove cover, declining sharply from ~3.5 m/s at zero mangrove cover to ~1.5 m/s at 33% mangrove cover, and thereafter declining gradually to ~1 m/s at 100% mangrove cover (Fig. 1a). Light interception by vegetation increased from ~10% to ~70% as mangrove cover increased (Fig. 1b). Daily average air (1 m aboveground) and soil temperatures showed hump-shaped relationships with mangrove cover with maxima at ~50–70% mangrove cover (Fig. 1c, d).

The SD of wind speed declined sharply as mangrove cover increased from 0% to 33%, and declined more gradually thereafter as mangrove cover increased to 100% (Fig. 2a). Both the SDs of light interception by vegetation and air temperature (at 1 m aboveground) showed hump-shaped relationships with mangrove cover (Fig. 2b, c). The SD of soil temperature peaked in the plot with 22% mangrove cover, but there was no statistically significant relationship between the SD of soil temperature and mangrove cover (Fig. 2d). Air temperature patterns (daily average and SD) at 0.5 m aboveground showed hump-shaped patterns similar to those at 1 m aboveground (Appendix S1: Fig. S9).

Salt marsh plants (primarily *Batis maritima*, *Salicornia depressa* (Sensu USDA 2015), *Salicornia bigelovii*, *Spartina alterniflora*, *Sesuvium portulacastrum* and *Lycium carolinianum*) rapidly expanded in the gaps between mangrove patches in the experimental plots during the 2 yr after the mangrove cover manipulation. As of August 2014 the response of marsh vegetation to mangrove cover change was non-linear, with marsh vegetation cover decreasing sharply from ~80% at zero mangrove cover to ~20% at 50% mangrove cover, and more gradually if at all at higher mangrove cover (Fig. 3a). The plot mean Bray–Curtis dissimilarity (a measure of community compositional variability or β -diversity) increased with mangrove cover to a peak in the plot with 22%

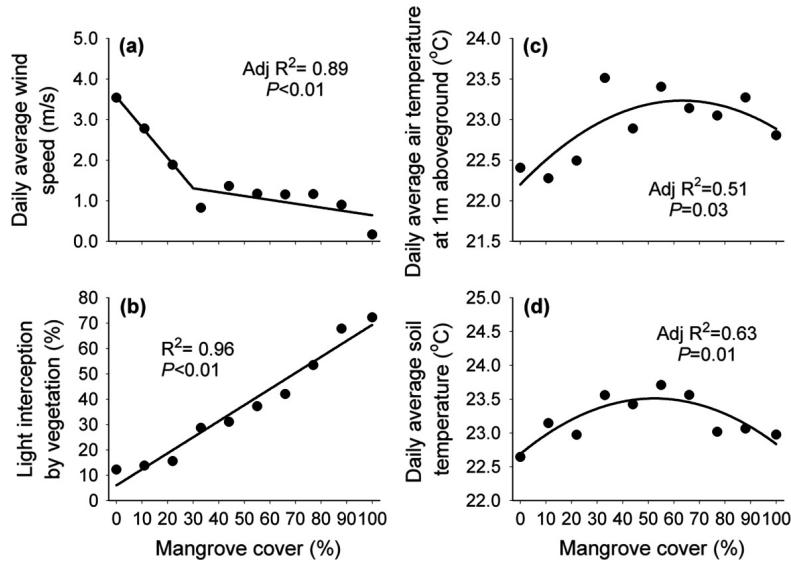


FIG. 1. Microclimate conditions across the mangrove cover gradient. (a) Daily average wind speed (at 1.5 m aboveground, wind direction from shore into plots only); (b) light interception by vegetation; (c) daily average air temperature at 1 m aboveground; (d) daily average soil temperature. Data in panels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

mangrove cover, and then gradually declined as mangrove cover further increased (Fig. 3b).

Wrack cover in the plots decreased from ~13% to ~2% as mangrove cover increased from zero to 100% (data not shown). In plots with <30% mangrove cover, wrack penetrated 20 m or more into the plots (Fig. 3c). In contrast, in plots with >30% mangrove cover, wrack never penetrated more than 10 m into the plots. Sediment accretion

in plots declined steadily with mangrove cover, from ~15 mm/yr in plots with <25% mangrove cover to ~6 mm/yr in plots with >75% mangrove cover (Fig. 3d).

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

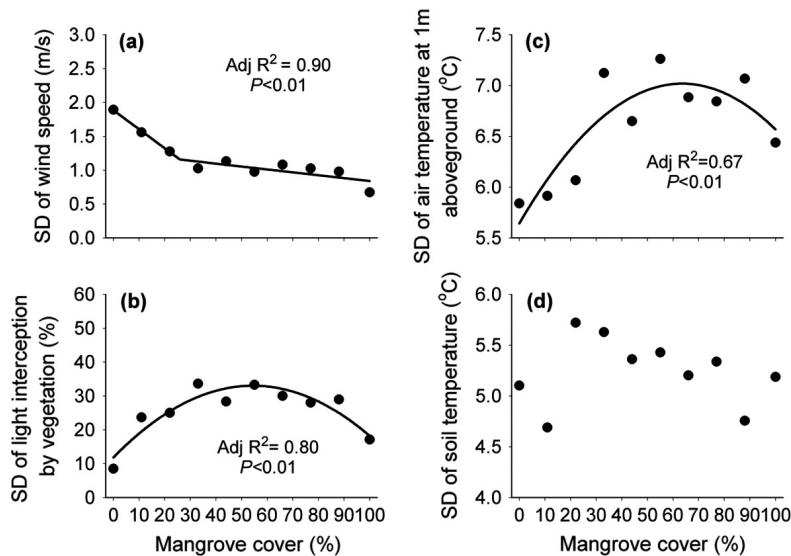


FIG. 2. Standard deviation (SD) of (a) wind speed (for wind direction from shore into plots only), (b) light interception by vegetation, (c) air temperature at 1 m aboveground, and (d) soil temperature, across the mangrove cover gradient. Data were collected during September 10, 2012–August 20, 2013.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

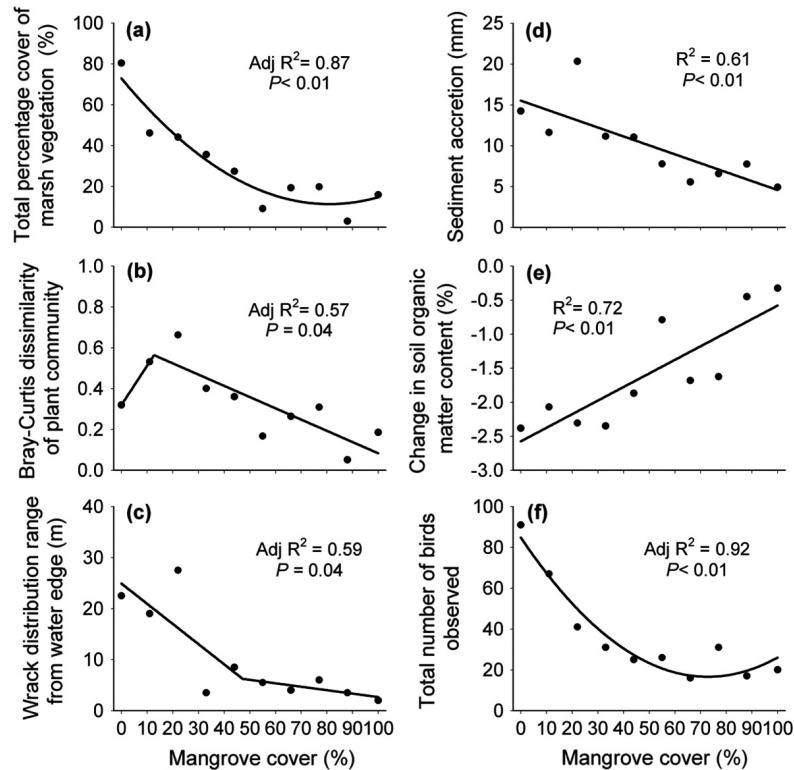


FIG. 3. Ecosystem responses of coastal wetlands to changes in mangrove cover in the study. (a) Total percentage cover of salt marsh vegetation (multiple species); (b) Plot mean Bray–Curtis dissimilarity of plant community; (c) Wrack deposit distribution range from the water's edge; (d) Sediment accretion;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

organic matter proportional to the loss of mangrove cover (Fig. 3e).

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

DISCUSSION

Effects of mangrove cover change on coastal wetland ecosystems

Our results indicated that changes in mangrove cover, such as those that occur rapidly with dieback following hard freezes, or more gradually as mangroves expand during warm years, can affect microclimate conditions, wetland vegetation composition, wrack inputs, soil accretion and soil organic content after only 2 yr. These effects, however, were often non-linear functions of mangrove cover, indicating that the consequences of changes

in mangrove abundance may not simply be proportional to mangrove cover.

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

Light interception by vegetation increased linearly as mangrove cover increased, resulting in low understory solar radiation at high mangrove cover, which is consistent with observations in other ecosystems with a gradient of woody plant cover (Breshears et al. 1997, Martens et al. 2000, Zou et al. 2010, Royer et al. 2012). Our measurements of light interception by vegetation were taken during the mid-day and might not represent what happens early and late in a day when the sunlight strikes the vegetation at a low angle and scattered mangrove plants may

shade adjacent areas without mangroves. Although we modeled this relationship as a straight line, light interception appeared to stabilize at just above 10% at the lowest mangrove cover values. This represents the modest levels of light interception by the succulent salt marsh vegetation (mostly *Batis maritima*) that grew where mangroves were completely removed.

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

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

at low sun angles, thereby reducing the availability of direct photosynthetic radiation to adjacent marsh plants. Similarly, mangrove root systems may extend beyond their canopies to affect adjacent marsh plants, just as shrubs in other biomes can affect plants outside their canopy (Casper et al. 2003). As a consequence, the growth of marsh plants in a mixed stand of marsh and mangrove vegetation may be less than would be expected based only on mangrove cover.

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

Soil organic matter decreased when mangroves were removed, suggesting that mangrove vegetation might increase soil organic matter content. This finding is consistent with previous reports of relatively high nutrient levels in mangrove vs. salt marsh habitats (Duarte and Cebrián 1996, Chmura et al. 2003, Donato et al. 2011, Osland et al. 2012, Yando et al. 2016). It also mirrors the similar patterns of higher soil organic matter under tree/shrub canopies vs. herbaceous vegetation in grasslands and savannas (Schlesinger et al. 1996, Klopatek et al. 1998, Cable et al. 2009). With a much higher standing

biomass than salt marsh vegetation, mangroves should produce more litter accumulation on the soil surface (Bhark and Small 2003, Price and Morgan 2008, McKee 2011). Moreover, with a relatively large surface area provided by their foliage, mangrove canopies could also enhance atmospheric deposition of nutrients (Weathers et al. 2001, DeLonge et al. 2008, Das et al. 2011), further favoring mangrove growth and organic matter accumulation.

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

In this study, we examined the relationships between each variable and mangrove cover separately for clarity; however, some of the variables show correlated responses. Some of these correlated responses could be due to independent but similar responses of these variables to mangrove cover changes. For example, cover of marsh vegetation and bird numbers might have responded independently but in the same manner to mangrove cover. In other cases, there might be causal relationships among these variables. For example, higher mangrove cover increased wrack trapping, and higher temperatures in intermediate and high mangrove cover plots would likely increase the decomposition rate of deposited wrack, and together these processes might increase the organic matter content in soil. Evaluating these potential mechanistic linkages is beyond the scope of this manuscript, but it is important to note that the variables that we analyzed may not represent fully independent responses to mangrove cover.

Linear and non-linear effects of mangrove cover

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

conditions to show linear changes across the experimental plots as the number of cells with mangroves increased.

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

Increased variability at intermediate mangrove cover

Many of the parameters that we measured were more variable at intermediate mangrove cover than in stands of pure marsh or pure mangrove vegetation. Increased spatial or temporal variability of ecosystem properties can be associated with transitions in ecosystems from one regime to another (Breshears 2006). Previous studies have suggested that variability of certain ecosystem properties (e.g., near ground solar radiation, transpiration and biogeochemistry) would rise when an ecosystem experiences critical changes, such as shifts among vegetation types, and likely peak at an intermediate point of the transition (Klopatek et al. 1998, Martens et al. 2000, Huxman et al. 2005). In our study, the SDs of light interception by vegetation and air temperature showed hump-shaped relationships with mangrove cover, with the maximum values near the intermediate range of mangrove cover. Also, the SD of soil temperature peaked at ~20% of mangrove cover. These results were consistent with previous studies on ecosystem variability under regime shifts (Breshears 2006), showing that at intermediate stages of the regime shift between salt marsh and mangroves there is an increased variability in some ecosystem properties. In contrast, the SD of wind speed decreased as mangrove cover increased, reflecting the greater roughness of mangroves that reduces wind fluctuations and can thus offer greater protection against storm damages (Das and Crépin 2013). Plant community dissimilarity (a measure of compositional variability or

β -diversity (Anderson et al. 2011) peaked in the intermediate range of mangrove cover (~30%), where patches of mangroves alternated with patches of salt marsh vegetation. At high mangrove cover, community dissimilarity was low because all quadrats were dominated by mangroves, and salt marsh vegetation was rare. These results, combined with the negative effect of mangroves on cover of salt marsh plants, suggest that high levels of mangrove encroachment into marshes will decrease overall plant community diversity in coastal wetlands, even if mangrove encroachment is not complete. Similarly, in grasslands and savannas, woody encroachment often decreases plant diversity (Brudvig 2010, Ratajczak et al. 2012, Limb et al. 2014).

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

Conclusions and management implications

Our experimental results demonstrated that the shift between salt marsh and mangrove vegetation can cause rapid (2 yr or less) alterations in a number of wetland processes and attributes. These results have important implications for coastal ecosystem management. The shift between marshes and mangroves does not occur as an abrupt transition, but rather includes areas or times where mixed stands occur. As a result, managers need to consider not just the extreme states of the regime shift, but also the intermediate states where the two vegetation types co-occur. Moreover, some of the ecosystem properties and functions responded to mangrove cover nonlinearly, which indicated that there might be optimal points that could achieve multiple conservation goals in coastal ecosystems experiencing regime shifts (Barbier et al. 2008). For example, our results showed that at ~30% cover, mangrove trees exert substantial effects in slowing down the wind speed close to the surface. We also found that plant community dissimilarity (β -diversity) peaked in the plot with 22% mangrove cover. Thus, managers of coastal ecosystems might be able to achieve the goals of wind protection and high biodiversity by maintaining mangrove cover at around 20–30%. If the primary goal was to maximize the organic content of soils, however, the optimum mangrove cover would be 100%. Thus, the “best” cover of mangroves will depend on which ecological functions provide the services that are most valued by human societies. Therefore, a better understanding of how mangrove cover affects various ecosystem services, coupled with an explicit formulation of management goals, may enable coastal managers to identify the best conservation strategies for local ecosystems. Finally, the shift between marsh and mangrove vegetation likely affects the community composition of organisms at higher trophic levels (such as marine

invertebrates, terrestrial arthropods, nekton, birds and mammals), and the changes in community composition and microclimate likely alter the rate of wetland carbon cycling. These possibilities need to be explored by additional research.

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