



Resistance to Hurricane Effects Varies Among Wetland Vegetation Types in the Marsh–Mangrove Ecotone

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Abstract

The capacity of coastal wetlands to stabilize shorelines and reduce erosion is a critical ecosystem service, and it is uncertain how changes in dominant vegetation may affect coastal protection. As part of a long-term study (2012–present) comparing ecosystem functions of marsh and black mangrove vegetation, we have experimentally maintained marsh and black mangrove patches (3 m × 3 m) along a plot-level (24 m × 42 m) gradient of marsh and mangrove cover in coastal wetlands near Port Aransas, TX. In August 2017, this experiment was directly in the path of Hurricane Harvey, a category 4 storm. This extreme disturbance event provided an opportunity to quantify differences in resistance between mangrove and marsh vegetation and to assess which vegetation type provided better shoreline protection against storm-driven erosion. We compared changes in plant cover, shoreline erosion, and accreted soil depth to values measured prior to storm landfall. Relative mangrove cover decreased 25–40% after the storm, regardless of initial cover, largely due to damage on taller mangroves (>2.5 m height) that were not fully inundated by storm surge and were therefore exposed to strong winds. Evidence of regrowth on damaged mangrove branches was apparent within 2 months of landfall. Hurricane-induced decreases in mangrove cover were partially ameliorated by the presence of neighboring mangroves, particularly closer to the shoreline. Marsh plants were generally resistant to hurricane effects. Shoreline erosion exceeded 5 m where mangroves were absent (100% marsh cover) but was relatively modest (<0.5 m) in plots with mangroves present (11–100% mangrove cover). Storm-driven accreted soil depth was variable but more than 2× higher in marsh patches than in mangrove patches. In general, mangroves provided shoreline protection from erosion but were also more damaged by wind and surge, which may reduce their shoreline protection capacity over longer time scales.

Keywords *Avicennia germinans* · *Spartina alterniflora* · *Batis maritima* · Facilitation · Hurricane · Neighbor effects

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Introduction

Coastal wetlands provide many valuable ecosystem services, including the potential to protect and stabilize shorelines, thus reducing erosion and protecting natural and built communities on higher ground (Barbier et al. 2011). The paradigm is that larger areas of wetlands will attenuate more storm surge and thus better stabilize shorelines, reduce erosion, act as a barrier to debris accumulation, and protect wetland functions (Shepard et al. 2011). Even during major storms with large storm surges, wetlands can prevent millions of dollars of damage to buildings, infrastructure, and ecosystems (Barbier et al. 2013; Narayan et al. 2017). The protective benefits of coastal wetlands are widely accepted, but it is also clear that the relationship between wetlands and the mitigation of storm

impacts is more complex than a simple wetland area to surge attenuation ratio (Wamsley et al. 2010). Landfalls by a number of high-profile, destructive storms around the world over the last 20 years (e.g., Odisha super cyclone (1999), Katrina (2005), Cyclone Larry (2006), Ike (2008), Sandy (2012), Matthew (2016), Harvey (2017), Michael (2018)) have reinforced the paradigm that characteristics of the storm, coastline, and the wetland vegetation community also influence the capacity of wetlands to alleviate storm effects (e.g., Marois and Mitsch 2015; Narayan et al. 2017).

In subtropical coastal wetlands around the world, vegetation species composition is shifting, largely in response to climate change and sea level rise. On five continents, coastal wetlands are transitioning from marshes—dominated by low-stature grass and forb species—to mangroves (Saintilan et al. 2014), and it is unclear how a dominance shift from herbaceous to woody plants will influence shoreline protection. Marshes (Wamsley et al. 2010; Shepard et al. 2011; Möller et al. 2014) and mangroves (Krauss et al. 2009; Gedan et al. 2011; Zhang et al. 2012) both provide substantial storm surge attenuation ecosystem services, although hurricanes can severely damage mangroves (Smith et al. 2009; Barr et al. 2012). Most of the evidence for storm attenuation by mangroves is derived from analyses of tall mangrove forests in tropical latitudes. However, in the marsh–mangrove ecotone, mangroves typically have a substantially shorter scrub morphology (Comeaux et al. 2012; Kelleway et al. 2017; Rogers and Krauss 2018), and it is unknown how well these growth forms withstand storm events or attenuate storm damage.

In marsh–mangrove ecotones, vegetation species coexist in a dynamic state of change, and interspecific interactions can be positive or negative. Mangrove and marsh species may compete for nutrients or space; whether mangrove or marsh vegetation is the “winner” in these interactions depends on the life history stage and local abiotic conditions (McKee and Rooth 2008; Guo et al. 2013; Simpson et al. 2013; Pickens et al. 2018). In some circumstances, mangrove and marsh species may facilitate each other by ameliorating abiotic stressors or enhancing seed recruitment (McKee et al. 2007; Peterson and Bell 2012; Guo et al. 2013). Stress or disturbance may enhance positive interactions (Callaway et al. 2002), and the existence of facilitative interactions can improve disturbance recovery (Halpern et al. 2007). However, the nature and magnitude of positive interactions between scrub mangroves and neighboring marsh plants following disturbance events are largely unknown.

In the Gulf of Mexico, black mangrove (*Avicennia germinans*) populations fluctuate in response to local and regional climatic conditions (Sherrod and McMillan 1985), but a number of studies have documented regional expansion of mangrove cover since a series of damaging freeze events in the 1980s (Perry and Mendelssohn 2009; Armitage et al. 2015; Rodriguez et al. 2016). As part of a long-term (2012–

present) study of the ecological consequences of mangrove expansion, we experimentally created and maintained marsh (*Batis maritima*, *Salicornia* spp., *Spartina alterniflora*) and black mangrove (*A. germinans*) patches (3 m × 3 m) along a plot-level (24 m × 42 m) gradient of marsh and mangrove cover in coastal wetlands near Port Aransas, TX. Our research site was directly in the path of Hurricane Harvey, which came ashore as a category 4 storm on August 25, 2017. This extreme disturbance event provided an opportunity to quantify three important knowledge gaps within the marsh–mangrove ecotone: (1) Are scrub mangroves or marshes more resistant to hurricane effects, (2) do mangroves ameliorate hurricane disturbance effects on neighboring marsh species, and (3) does mangrove or marsh vegetation provide better shoreline protection?

Methods

Study Design

We utilized an existing experimental gradient of black mangrove (*Avicennia germinans*) and marsh (*Batis maritima*, *Salicornia* spp., *Spartina alterniflora*) cover established on Harbor Island, Port Aransas, TX (27.86° N, 97.08° W) in 2012 (Fig. 1; Guo et al. 2017). We refer to these plant taxa by genus hereafter. Each of the ten plots (24 m × 42 m) was set up with the short axis along the water’s edge and sectioned into three zones relative to the water–vegetation interface: front (12 m), middle (18 m), and back (12 m) (Fig. 1). Average mangrove height was approximately 2.5 m in the front zone and less than 1.5 m in the middle and back zones. At the start of the study, plot elevation (based on publicly available LIDAR and NADV 1983) ranged from 0.2 m above mean lower low water (MLLW) along a small berm at the water’s edge to 0.1 m above MLLW in the remainder of the plots, with a subtly heterogeneous elevation topography in the middle and back zones of the plot. The higher elevation along the shoreline was largely attributable to the accumulation of sediment and wrack trapped by plant stems, trunks, or aerial roots (pneumatophores). Within each plot, mangrove cover (initially close to 100%) was set at a specified level by removing mangroves within 3 m × 3 m patches in a stratified random checkerboard pattern. Marsh vegetation naturally colonized the cleared areas (Guo et al. 2017).

Each patch in every plot was given two “neighbor index” scores (Fig. 1). The Mangrove Neighbor Index (MNI) tallied the number of immediately surrounding patches that had not been cleared and contained intact mangroves; this score ranged from 0 (surrounded by marsh vegetation) to 4 (surrounded by mangrove vegetation on all four sides). All plots were surrounded by mangroves; therefore, patches along the plot edges all had an MNI score of at least 1. There were no

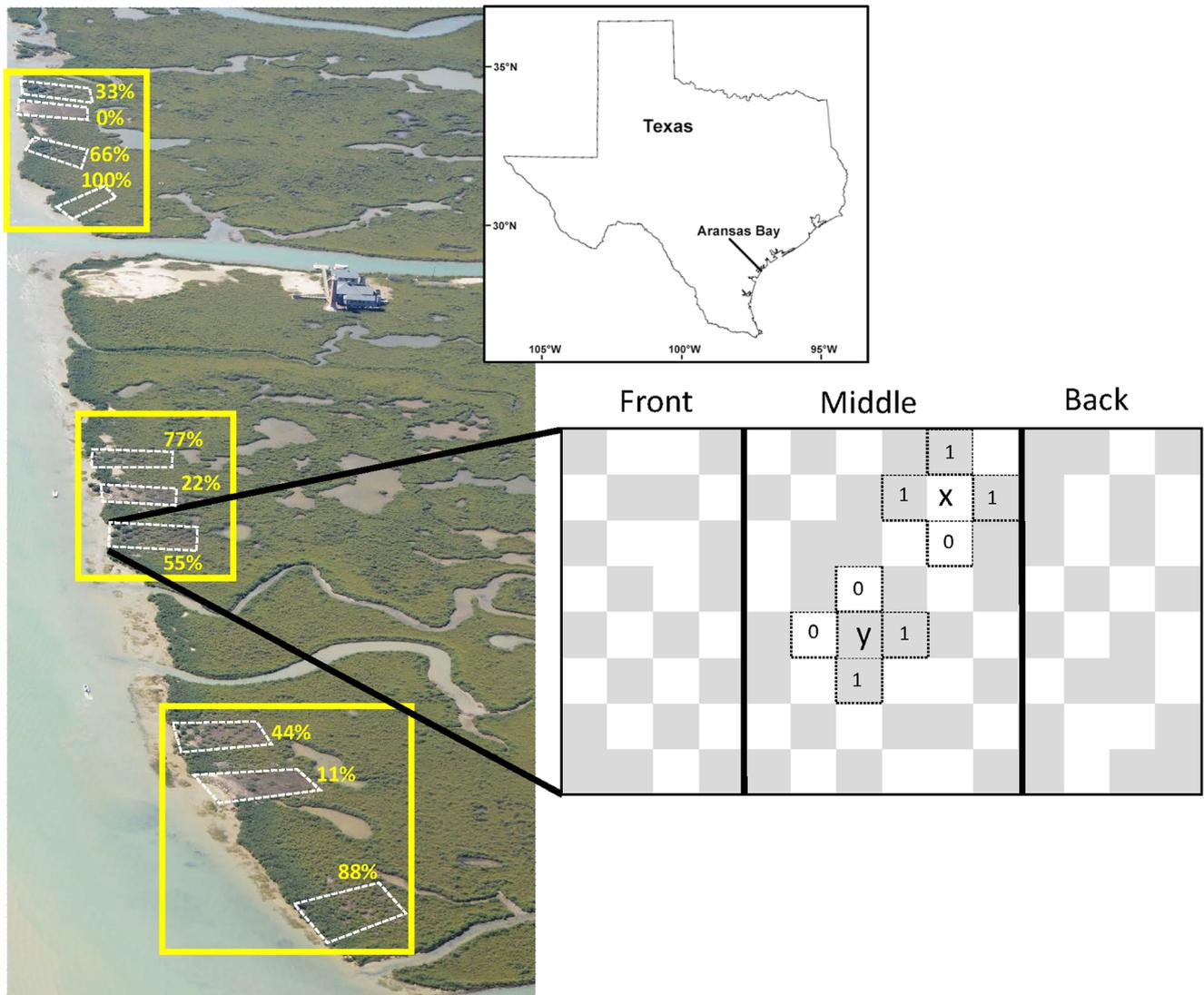


Fig. 1 *Left:* Arrangement of 24 m × 42 m study plots (dashed lines) in three blocks (solid lines) along the coastline; percent values indicate maintained mangrove cover in each plot. Image taken in 2013 shortly after study initiation. *Bottom right:* Schematic of a representative plot depicting mangrove (gray) and marsh (white) patches (3 m × 3 m), zone

delineation, and neighbor indices, where surrounding patches (dashed squares) were scored as “1” for mangroves and “0” for marsh vegetation. For example, in patch x, the front neighbor index (FNI) is 1 and the mangrove neighbor index (MNI) is 3. In patch y, FNI = 0 and MNI = 2

mangroves beyond the front edge of the plots; therefore, patches along the front of the plot had a maximum MNI score of 3. The Front Neighbor Index (FNI) represented the character of the patch immediately shoreward (the direction from which storm-generated wind and waves came) and was scored as either 0 (mangroves removed) or 1 (mangroves present).

Our study site was directly impacted by Hurricane Harvey, which came ashore as a category 4 storm on August 25, 2017. Hurricane-force winds exceeding 119 kph impacted the site for approximately 6 h, with gusts up to 225 kph (NOAA 2019). NOAA National Weather Service tide gauges recorded a storm surge of 1.6 m above MLLW in nearby Port Aransas, TX (NOAA 2019), but U.S. Geological Survey storm surge estimates based on debris deposition and other flood evidence

indicated a storm surge depth of up to 2.4 m (USGS 2019). Major flood stage (0.8 m above MLLW) persisted for approximately 6 h.

Plant Cover

Vegetation surveys were conducted in August 2015 (pre-storm) and October 2017 (post-storm); both of these sampling dates fell within the long growing season of the region. Two permanent transects consisting of contiguous 1 m × 1 m subplots extended from the front (shoreline) to the back of each plot. We visually estimated the cover of each species in each subplot, summed these values to each patch, and calculated absolute change as the difference in cover in each patch

between 2015 and 2017. These calculations were performed for the two most common species in marsh patches (*Spartina* and *Batis*) and for mangroves (*Avicennia*) in the mangrove patches. If a species never occurred in a patch, that patch was not included in the analysis for that species (i.e., a change of “0” was recorded only if a species was present at the same level of cover in both surveys). This change value was the response variable used in the statistical analyses described below.

In 2017, we developed an index to score the extent of storm damage on mangroves (e.g., defoliation, broken branches). Each quadrat was given a score from 1 to 5, where 1 indicated no damage, 2 indicated 1–10% of the mangrove was damaged, 3 indicated 11–50% damaged, 4 indicated 51–75% damaged, and 5 indicated mangroves that were still alive but with evidence of damage on 75% or more of the plant. We did not observe total mortality of any mangroves that remained standing within the plots, but in a few instances, mangroves had been uprooted and displaced out of the study plot, in which case the mangrove cover score was recorded as zero. All cover and damage measurements were performed by the same individual in order to minimize potential observer bias.

Erosion and Accretion

In 2013, we began to monitor shoreline erosion by inserting PVC poles (3 m long \times 2 cm diameter) into the ground to manual refusal (> 1 m deep) in the front third of each plot. Poles were cut to leave 10–20 cm exposed above the sediment surface in order to minimize the possibility that floating debris might disturb the pipe. We deployed these markers in eight locations per plot to minimize the chance that disturbance to any one pole would bias the data. We report vertical erosion or accretion as changes in how much of the pole was exposed from 2016 (pre-storm) to 2017 (post-storm). Horizontal erosion was reported as changes in the distance from the poles to the front of the plot from 2016 to 2017, which was defined in most cases by the vegetation edge or, in a few cases, an eroded edge (less than 5 cm in height) demarking a transition from the relatively flat surface of the intertidal plot to the comparatively flat subtidal zone. We saw no evidence of disturbance to the poles during our sampling other than increased or decreased exposure of the upper part of the pole.

To monitor surface sediment accretion, we established 0.5 m² feldspar marker horizons (Cahoon and Turner 1989) behind the erosion markers in the front zone of all ten plots in June 2013. Four marker horizon locations were placed in each plot: two in marsh patches and two in mangrove patches, except for the 0% and 100% mangrove plots, in which mangrove and marsh patches, respectively, were absent. In October 2017 (post-storm), a 5-cm diameter core to a depth of 30 cm was extracted from each marker horizon location.

Accreted soil depth was recorded as the depth of the core surface to the original (2013) feldspar marker horizon.

Data Analyses

Two-way analyses of covariance (ANCOVA) were used to compare hurricane effects on scrub mangrove and marsh vegetation and to assess mangrove amelioration of hurricane disturbance on neighbors. In separate two-way ANCOVA, independent variables were changes in marsh and mangrove cover, and mangrove damage index. Zone within the plot (front, middle, back) and neighbor index (MNI or FNI in separate analyses) were fixed factors, and plot-level mangrove cover (0–100%) was the covariate. For all plant response variables, plot-level mangrove cover had no significant main or interactive effects; therefore, no covariate interaction terms were included in the model. The mangrove damage index was square root transformed to reduce heteroscedasticity of variances.

To determine if mangrove or marsh vegetation provide better shoreline protection, one-way ANOVA was used to analyze erosion and accretion. Vertical erosion and accretion were rank transformed; no transformation was necessary for horizontal erosion. Each of these variables was then analyzed using separate one-way ANCOVA with microhabitat (patch vegetation identity as mangrove or marsh) as a fixed factor and plot-level mangrove cover as the covariate. As above, no covariate interaction terms were included in the model when the covariate had no significant main or interactive effects; the covariate was included only in the model for horizontal erosion. All statistical analyses were performed with SPSS v.24.

Results

Marsh Cover

Cover of the two most common marsh species, *Spartina alterniflora* and *Batis maritima*, did not change overall in response to Hurricane Harvey (Table 1; Fig. 2a, b). There was no *Spartina* in either sampling period in plots with more than 66% mangrove cover. In one analysis (with MNI as a fixed factor), *Spartina* cover increased in plots with low (0–33%) mangrove cover and decreased in plots with moderate (44–66%) mangrove cover (Table 1; Fig. 2a). If FNI was used as a fixed factor, however, the effect of plot-level mangrove cover was not significant (Table 1). Neither zone, neighbor index (MNI or FNI), or their interaction affected the change in cover of *Spartina*. *Batis* cover changed little between 2015 and 2017 in any plot, and there were no significant neighbor or zone effects on the change in *Batis* cover (Fig. 2b).

Table 1 Results from two-way ANCOVA of zone (proximity to water's edge) and plot-level mangrove cover on change in *Spartina alterniflora*, *Batis maritima*, and *Avicennia germinans* cover after Hurricane Harvey. Separate analyses were conducted with Mangrove Neighbor Index (MNI) and Front Neighbor Index (FNI) scores. Covariate interaction terms were not included in the model when the covariate had no significant main or interactive effects

	df	F	p
<i>Spartina alterniflora</i>			
Plot-level mangrove cover	1	9.00	0.005
Zone	2	1.37	0.268
MNI	4	0.53	0.712
Zone × MNI	5	0.525	0.756
Plot-level mangrove cover	1	1.66	0.205
Zone	2	2.26	0.117
FNI	1	1.66	0.204
Zone × FNI	1	1.62	0.210
<i>Batis maritima</i>			
Plot-level mangrove cover	1	2.22	0.140
Zone	2	0.20	0.820
MNI	4	0.99	0.421
Zone × MNI	7	1.09	0.379
Plot-level mangrove cover	1	0.30	0.585
Zone	2	0.13	0.875
FNI	1	0.47	0.497
Zone × FNI	2	0.90	0.411
<i>Avicennia germinans</i>			
Plot-level mangrove cover	1	0.04	0.839
Zone	2	24.15	< 0.001
MNI	4	0.73	0.571
Zone × MNI	8	2.30	0.025
Plot-level mangrove cover	1	1.84	0.177
Zone	2	33.75	< 0.001
FNI	1	1.04	0.309
Zone × FNI	2	5.71	0.004

Mangrove Cover

Cover of *Avicennia germinans* decreased substantially from 2015 to 2017, exceeding 20% loss in many patches (Fig. 2c). Loss of mangrove cover was particularly pronounced in the front zone, where most trees were more than 1.5 m tall. The upper branches of these taller trees in the front of the plots were not inundated by storm surge and were exposed to wind and debris (Figs. 3a, b). Qualitative evidence of some regrowth on broken branches, however, was already apparent within 2 months of landfall (Fig. 3c). In contrast, in the middle and back zone, trees were typically < 1.5 m tall and were largely covered by storm surge and therefore protected from

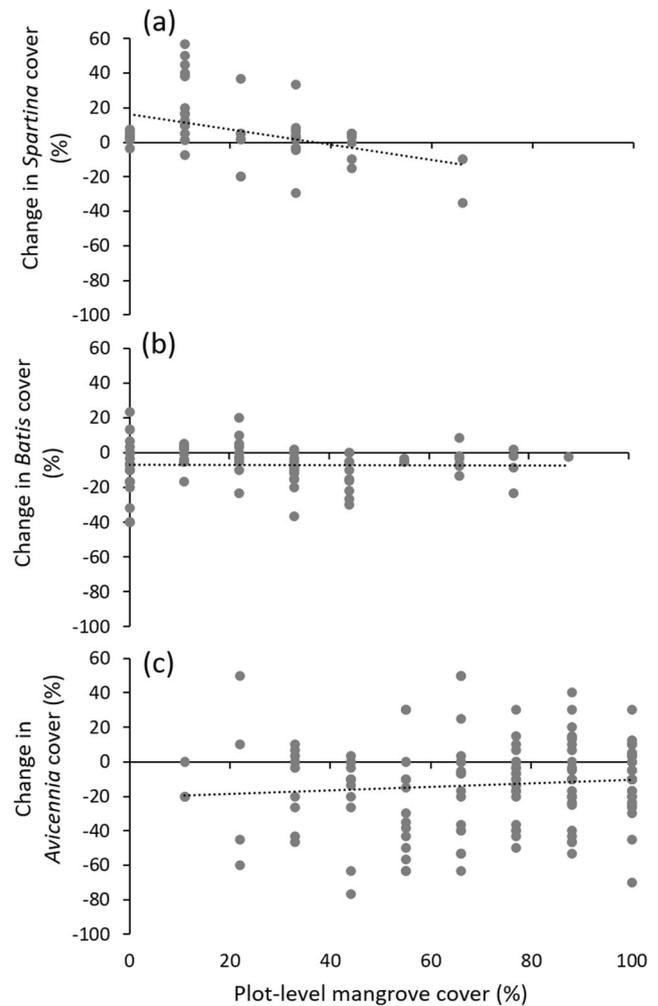


Fig. 2 Change in cover of two common marsh plant species **a** *Spartina alterniflora*, **b** *Batis maritima*, and **c** black mangroves *Avicennia germinans* from 2015 to 2017, across a range of mangrove cover in experimental plots

wind damage. There were significant zone × neighbor effects on change in *Avicennia* cover (Table 1). The MNI (mangrove neighbor index) effect was largest in the front zone, where patches with no mangrove neighbors (i.e., isolated patches of mangroves) and patches surrounded on all sides by mangrove neighbors (i.e., closed canopy) lost the least cover (loss −20–30%), relative to heterogeneous canopies (MNI 1–3; loss −35–40%) (Fig. 4a). The presence of a mangrove patch as a front neighbor (FNI) was beneficial in the middle zone and detrimental in the front and back zones (Fig. 5a). There was no significant effect of plot-level mangrove cover on changes in mangrove cover within patches.

Mangrove Damage Index

There was a significant zone effect on *Avicennia* damage index, with substantially higher damage in the front zone relative to the other zones (Table 2; Figs. 4b and 5b). Mangroves

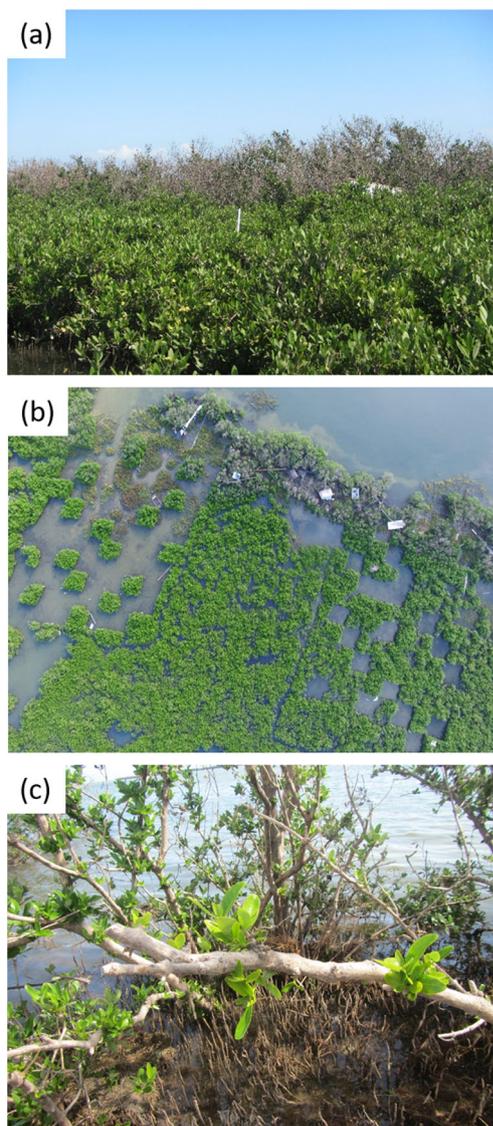


Fig. 3 Patterns of *Avicennia germinans* damage and recovery following Hurricane Harvey. **a** Damage was evident on taller trees; shorter plants were relatively undamaged. **b** Damage was most extensive along the shoreward edge of the study plots. **c** Regrowth on damaged branches was evident within 2 months of storm landfall

in the front zone had an average index score of 4.1 (i.e., 51–75% of the mangrove was damaged). In contrast, mangroves in the middle and back zones had scores of 2.2 and 1.8, respectively (i.e., only 1–10% of the mangroves were damaged). Mangrove damage index was neither affected by either neighbor index (MNI or FNI) nor did it vary with plot-level mangrove cover.

Erosion and Accretion

Horizontal erosion between 2016 (pre-storm) and 2017 (post-storm) varied significantly with plot-level mangrove cover and microhabitat (ANCOVA interaction $p = 0.040$; Table 3).

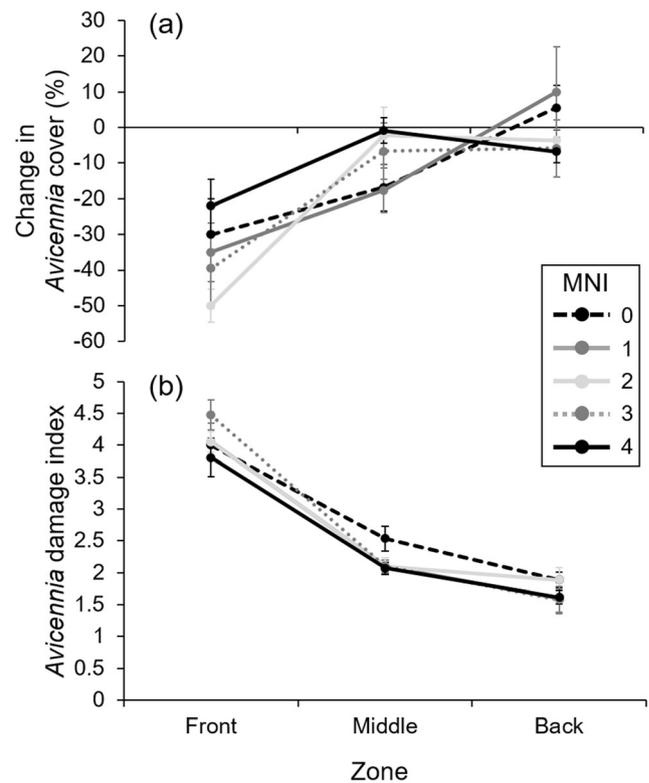


Fig. 4 Effects of mangrove neighbor index (MNI, where 0 = no mangrove neighbors and 4 = fully surrounded by mangrove neighbors) on change in *Avicennia germinans* cover from 2015 to 2017 (**a**) and damage index (**b**) in three zones, relative to the water–vegetation interface. Bars represent SE

Horizontal erosion during that period exceeded 5 m in the plot with no mangroves but was relatively modest (<0.5 m) in plots with mangroves present (plots with 11–100% mangrove cover). The pronounced horizontal erosion in the 0% mangrove plot drove the plot cover \times microhabitat interaction (Fig. 6a). There was no significant effect of plot-level mangrove cover or microhabitat on vertical erosion between 2016 and 2017 (Table 3), though this measure of elevation change was considerably more variable in marsh patches, some of which showed large amounts of erosion and others large amounts of accretion, relative to mangrove patches (Fig. 6b). Accreted soil depth over feldspar markers from 2013 to 2017 was heterogeneous but averaged more than two times higher in marsh patches than in mangrove patches (Table 3; Fig. 6c). There was no effect of plot-level mangrove cover on accreted soil depth.

Discussion

The effects of wind and surge damage from Hurricane Harvey differed markedly between mangrove and marsh vegetation. Marsh plants experienced much less damage than did mangroves, likely because the shorter stature marsh species were

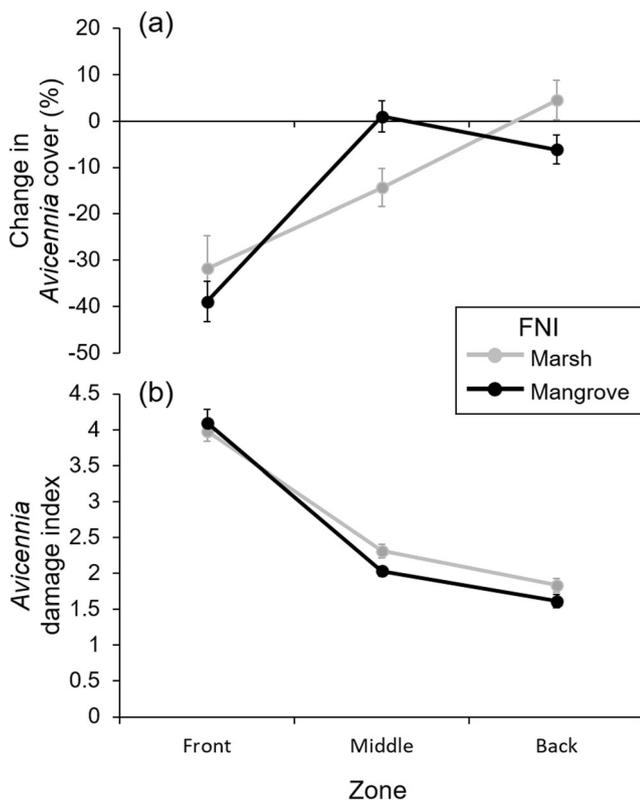


Fig. 5 Effects of front neighbor identity (FNI: marsh vs. mangrove vegetation) on **a** change in *Avicennia germinans* cover from 2015 (pre-hurricane) to 2017 (post hurricane) and **b** damage index in three zones, relative to the water–vegetation interface. Bars represent SE

covered by the storm surge, protecting them from hurricane-force winds (Smith et al. 1994). Mangroves sustained more damage, as the storm surge up to 1.6 m did not completely submerge the taller trees near the water’s edge (front zone), exposing them to wind damage (Feller et al. 2015). As a result, extensive damage occurred, primarily on the taller trees exceeding 2.5 m in height, which were only in the front zone of

Table 2 Results from two-way ANCOVA of zone (proximity to water’s edge) and plot-level mangrove cover on *Avicennia germinans* damage index score after Hurricane Harvey. Separate analyses were conducted with Mangrove Neighbor Index (MNI) and Front Neighbor Index (FNI) scores. Covariate interaction terms were not included in the model when the covariate had no significant main or interactive effects

	df	F	p
Plot-level mangrove cover	1	0.26	0.611
Zone	2	123.40	<0.001
MNI	4	0.95	0.439
Zone × MNI	8	0.70	0.695
Plot-level mangrove cover	1	0.26	0.612
Zone	2	163.98	<0.001
FNI	1	1.12	0.293
Zone × FNI	2	1.04	0.356

the study plots (Guo et al. 2017). The decrease in mangrove cover was largely attributable to the loss of twigs and leaves on the upper branches, as well as stem breakage and uprooting of some trees at the water’s edge. Foliage on lower branches was submerged by the storm surge and thereby protected from the most intense winds and as a result remained largely intact. Despite the extensive defoliation on upper branches, initial recovery was evident within weeks of the storm, with leaves resprouting from branches. *Avicennia germinans* is a rapidly growing mangrove species (Tomlinson 2016); however, complete canopy recovery following a disturbance may take multiple growing seasons (Armentano et al. 1995). Similar patterns of damage and rapid recovery in this species of *Avicennia* followed Hurricane Andrew (1992) in Florida (Smith et al. 1994; Baldwin et al. 2001). Likewise, other major storms that caused complete defoliation of *Avicennia* did not necessarily result in tree mortality (Roth 1992; Imbert et al. 2000), demonstrating that this species can be relatively resilient to storm disturbances. Our observations suggest that mangrove mortality linked to Hurricane Harvey was relatively modest; only a few individuals near the shoreline had been uprooted and displaced, likely due to a combination of wind and surge forces and of erosion of soil around the roots. In contrast, other 2017 storms in the Gulf of Mexico (Irma: Radabaugh et al. 2019) and the Caribbean (Maria: Branoff this volume) resulted in more substantial mortality of *Avicennia* and other mangrove species, up to 25% or more, likely due to higher wind speed and duration, and to the susceptibility of taller trees in the tropics to wind damage (Smith et al. 1994).

Although many individual mangroves at our study site experienced substantial damage, similar levels of damage did not occur at other sites impacted by Hurricane Harvey. Substantial mangrove damage was limited to the portions of the coast exposed to the highest (over ~190 kph) wind speeds (Patrick et al. this volume). Sites that were further removed from the eye of the storm experienced little change in mangrove cover following the storm (Patrick et al. this volume). This pattern was similar to that found in other studies: acute wind damage to mangroves is typically constrained to the area near the landfall of the storm’s eye with the highest wind speeds (Armentano et al. 1995; Smith et al. 2009).

Wind damage near hurricane landfall is often accompanied by sediment deposition events, which can alter the character of the site for many years after the storm (Smith et al. 2009). Deposition of sediment by hurricanes may enhance the capacity of mangrove forests to adapt to sea-level rise, especially in areas like the Florida Everglades, where hurricanes are relatively frequent events (Castañeda-Moya et al. 2010), although large deposition events in this area can precipitate the conversion of mangrove forests to mudflats (Osland et al. this volume). Storm deposition events may also change the density and species composition of salt marsh plants (Nyman et al.

Table 3 Results from one-way ANCOVA of microhabitat type (mangrove or marsh) and plot-level mangrove cover on changes linked to Hurricane Harvey: (a) vertical erosion from 2016 to 2017, (b) horizontal erosion from 2016 to 2017, and (c) accretion from 2013 to 2017. Covariate interaction terms were not included in the model when the covariate had no significant main or interactive effects

	df	F	p
(a)			
Plot-level mangrove cover	1	2.96	0.091
Microhabitat	1	0.10	0.759
(b)			
Plot-level mangrove cover	1	13.35	< 0.001
Microhabitat	1	6.87	0.011
Plot-level mangrove cover × microhabitat	1	4.44	0.040
(c)			
Plot-level mangrove cover	1	0.78	0.390
Microhabitat	1	4.56	0.049

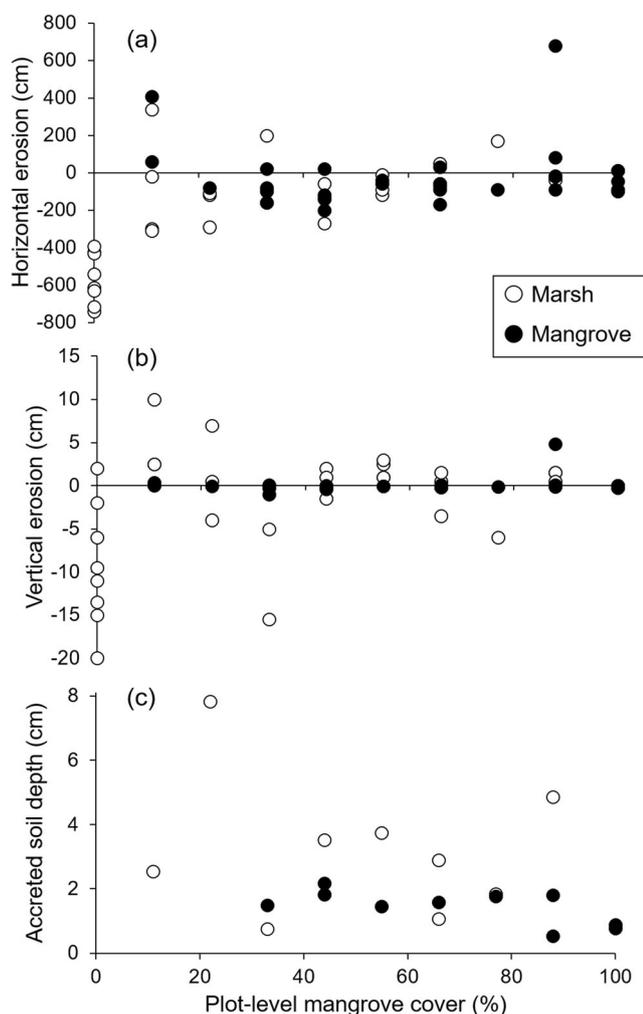


Fig. 6 Hurricane-related erosion and accretion patterns within patches of mangrove or marsh vegetation and across a range of mangrove cover in experimental plots. **a** Horizontal erosion, represented as change from 2016 to 2017; **b** vertical erosion, represented as change from 2016 to 2017; and **c** accreted soil depth over feldspar markers from 2013 to 2017

1995; Courtemanche et al. 1999). Each hurricane is unique in its depositional properties: Hurricane Irma (2017) deposited over 3 cm of carbonate-rich soil in the Florida Everglades (Breithaupt et al. [this volume](#)), but we found relatively little sediment deposition directly linked to Hurricane Harvey at our site. Accretion between 2016 and the post-storm sampling in 2017 was about two centimeters. This value is higher than the baseline accretion rates of 0.5–1 cm year⁻¹ in the region (Callaway et al. 1997; Bianchi et al. 2013) but is relatively modest as a hurricane deposition event, which often exceed several centimeters of deposition in a single storm (Turner et al. 2006; Smith et al. 2009; Breithaupt et al. [this volume](#); Osland et al. [this volume](#)). As such, this site may have experienced a comparatively minor deposition event that is unlikely to either benefit or suppress mangrove and marsh vegetation on a near-term time scale.

Stress or disturbance may enhance intra- or interspecific positive interactions within plant communities (Callaway et al. 2002), and positive interactions may enhance disturbance recovery (Halpern et al. 2007). Within mangrove forests, conspecific and interspecific neighbors can act as competitors or facilitators following disturbances; the nature of the interaction depends on the species identity and the nature of the disturbance (Uriarte et al. 2004). Our observations did not fall neatly into either end of the competition–facilitation spectrum. We detected some complex patterns of positive neighbor interactions among mangroves, where mangroves somewhat reduced the hurricane damage index for neighboring mangroves in the shoreward zones of the study plots. This type of neighbor amelioration of wind effects on neighboring mangroves has not been previously documented in tropical or subtropical mangrove stands but is reasonable, given that mangroves partially block the wind (Guo et al. 2017) and so should have reduced wind-generated damage to adjacent plants.

Effects of mangrove neighbors on change in mangrove cover were more ambiguous than the effects on mangrove damage. Studies of facilitation within mangrove stands are rare (Feller et al. 2010); most documented cases are linked to the amelioration of harsh soil conditions following disturbances (Huxham et al. 2010). This type of facilitation is most pronounced at early developmental stages or early successional stages following a disturbance, and often turns to density-dependent competition at later developmental stages (Proffitt and Devlin 2005; Vogt et al. 2014). However, in regions susceptible to sea-level rise, dense mangrove stands have higher accretion rates than marshes, and this benefit can exceed the cost of density-dependent competition (Kumara et al. 2010). Prior to the storm, mangrove density at the study site (outside our experimental plots) was relatively high, creating a nearly continuous mangrove canopy (Guo et al. 2017). However, given the complex nature of intraspecific neighbor facilitation in our study, there was no clear net benefit—or cost—to high

pre-storm density on the *Avicennia* cover response to disturbance at this site. It is possible that the strong winds from Hurricane Harvey may have been sufficient to reduce cover of the mangroves at the shoreline, regardless of any ameliorating effects of neighbors.

A robust body of literature on mangrove–marsh interactions has identified many interspecific facilitative dynamics, largely where early life stages of mangroves benefit from the presence of marsh neighbors. For example, marsh plants can increase mangrove survival, but this benefit primarily manifests at the seedling stage (Guo et al. 2013). There is little evidence that this type of positive interaction is reciprocal—marsh species do not generally benefit from the presence of mangrove neighbors. Another type of positive interaction manifests when herbaceous marsh plants facilitate mangrove propagule establishment after hurricanes by ameliorating soil conditions or trapping propagules (McKee et al. 2007; Peterson and Bell 2012). As mangroves reach maturity, facilitative interactions diminish and mangroves generally end up as the superior competitor for space and light (Kangas and Lugo 1990). We observed no positive interactions between mangroves and salt marsh plants; if anything, *Spartina* cover decreased more with increasing mangrove cover.

Much of the current research on the dynamic changes in marsh–mangrove ecotones centers on comparisons of the ecosystem services that these two types of vegetation provide. Of particular interest in the context of large storm disturbances is the potential for marsh and mangrove vegetation to protect and stabilize shorelines. In particular, there has been broad speculation that the transition from marshes to mangroves that is underway on the U.S. Gulf Coast and elsewhere around the world may improve shoreline protection services of wetlands, but there has been little quantitative evidence to demonstrate if, and under what circumstances, this is true (Kelleway et al. 2017). Our study provided a unique opportunity to quantify the shoreline protection value of the scrub mangroves commonly found in marsh–mangrove ecotones, including those on the U.S. Gulf Coast, while holding factors such as fetch, aspect (wind and wave exposure), and coastal geomorphology constant. Vertical erosion was much more variable in marsh patches and was particularly pronounced when mangroves were absent. This trend suggests that at a larger temporal or spatial scale, mangroves may provide better protection against erosion. However, taller mangroves were more damaged by wind and surge, which may reduce their long-term capacity to protect shorelines from erosive forces from modest but persistent daily wave action. The fact that mangroves are damaged by severe storms also means that mangroves may not be able to provide storm protection services in the rare cases where an area experiences storms in successive years.

Despite the destructive nature of Hurricane Harvey on many coastal ecosystems (Patrick et al. [this volume](#)) and built communities, the amount of coastal erosion at our study site

was surprisingly modest. Beyond the immediate coastline, the broader storm-related benefits of vegetated coastal wetlands are likely to be drawn from their potential to attenuate storm surge (Möller et al. 2014). Although our study did not address surge attenuation, the protective value of both marsh and mangrove vegetation types is often positively related to wetland area (Shepard et al. 2011) and, in the case of mangroves, will be higher in tropical regions where mangroves are taller (Temmerman et al. 2013). To that end, protecting expansive areas of either vegetation type can be an important part of an ecosystem-based coastal defense strategy.

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