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## **A hurricane alters the relationship between mangrove cover and marine subsidies**

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**Abstract**

As global change alters the composition and productivity of ecosystems, the importance of subsidies from one habitat to another may change. We experimentally manipulated black mangrove (*Avicennia germinans*) cover in ten large plots and over five years (2014-2019) quantifying the effects of mangrove cover on subsidies of floating organic material (wrack) into coastal wetlands. As mangrove cover increased from zero to 100%, wrack cover and thickness decreased by ~60%, the distance that wrack penetrated into the plots decreased by ~70%, and the percentage of the wrack trapped in the first six m of the plot tripled. These patterns observed during four “normal” years disappeared in a fifth year following Hurricane Harvey (2017), when large quantities of wrack were pushed far into the interior of all the plots, regardless of mangrove cover. Prior to the storm, the abundance of animals collected in grab samples increased with wrack biomass. Wrack composition did not affect animal abundance or composition. Experimental outplants of two types of wrack (red algae and seagrass) revealed that animal abundance and species composition varied between the fringe and interior of the plots, and between microhabitats dominated by salt marsh versus mangrove vegetation. The importance of wrack to overall carbon stocks varied as a function of autochthonous productivity: wrack inputs (per m<sup>2</sup>) based on survey data were greater than aboveground plant biomass in the plots (42 × 24 m) dominated by salt marsh vegetation, but decreased to 5% of total aboveground biomass in plots dominated by mangroves. Our results illustrate that increasing mangrove cover decreases the relative importance of marine subsidies into the intertidal at the plot level, but concentrates subsidies at the front edge of the mangrove stand. Storms, however, may temporarily override mangrove attenuation of wrack

inputs. Our results highlight the importance of understanding how changes in plant species composition due to global change will impact marine subsidies and exchanges among ecosystems, and foster a broader understanding of the functional interdependence of adjacent habitats within coastal ecosystems.

Key words: allochthonous inputs; Batis; climate change; food webs; habitat permeability; *Spartina*; woody encroachment; wrack subsidies

### **Introduction**

The flow of energy, material and organisms from one ecosystem to another is ubiquitous in nature (Polis and Hurd 1996, Polis et al. 1997, Loreau et al. 2003). Such flows, termed allochthonous inputs or spatial subsidies, are a major determinant of ecosystem functioning in many systems. By providing an input of organic matter and nutrients, subsidies affect trophic cascades (Leroux and Loreau 2008), primary and secondary productivity (Polis and Hurd 1996, Spiller et al. 2010, Wimp et al. 2010) and nutrient cycling (Leroux and Loreau 2010). Subsidies are important across many habitats, including coastal areas (Rose and Polis 1998), islands (Polis and Hurd 1996), lotic systems (Bastow et al. 2002), lentic systems (Knight et al. 2005) and riparian forests (Willson et al. 2004). Because of the importance of spatial subsidies, it is important to understand how they may be affected by global change.

Global changes, including increased precipitation and temperature, are driving encroachment of woody species into grasslands around the world. In grasslands and savannas, woody encroachment alters albedo and temperatures (D'Odorico et al. 2013), and affects species diversity (Ratajczak et al. 2012), organic-matter cycles and biogeochemistry (D'Odorico et al.

2013). In coastal wetlands, woody encroachment occurs as mangroves expand out of the tropics to higher latitudes (Cavanaugh et al. 2014, Saintilan et al. 2014). For example, in Texas, USA, mangrove cover increased by 74% between 1990 and 2010 over the entire Texas coast, mostly expanding into salt marsh habitats (Armitage et al. 2015). With reductions in winter freeze events, black mangroves (*Avicennia germinans*) are predicted to mostly replace salt marshes along much of the northern Gulf of Mexico within this century (Osland et al. 2013, Gabler et al. 2017).

The shift from salt marsh vegetation, dominated by grasses and forbs, to mangrove vegetation, dominated by woody shrubs and trees, is likely to affect both the amount of allochthonous subsidies from subtidal to intertidal wetlands (by affecting habitat permeability) and their relative importance (by affecting total autochthonous productivity) to the intertidal wetland. In intertidal habitats, allochthonous subsidies consist of a mixture of dead salt-marsh plants, seagrass leaves, algae, benthic invertebrates and dead animals, collectively called “wrack”, that is transported into the intertidal zone at high tide and during storms (Dugan et al. 2003, Spiller et al. 2010). The supply of spatial subsidies transported from subtidal habitats into the intertidal depends not only on supply rates but also on the nature of the boundaries between habitats (Stamps et al. 1987, Cadenasso et al. 2004). In the case of vegetated habitats, the “permeability” of the boundary is largely determined by vegetation structure (Cadenasso and Pickett 2000, Witman et al. 2004). Mangroves and marsh plants differ in morphology: mangroves are taller and stiffer, and so should be more effective at blocking subsidies, but have a lower stem density than salt marsh plants (Chapman 1977), which might make them less effective. In particular, because mangroves are rarely overtopped by the tides except during storms, we expect that mangrove habitats will have

lower permeability to subsidies than marsh habitats. Of course, this is a broad generality because the height and stiffness of both mangroves and marsh plants can vary depending on species and productivity.

In addition, transport processes (e.g., wind, waves, currents) that move materials between donor and recipient sites also affect subsidies (Polis et al. 1997, Liebowitz et al. 2016). Since these transport processes are temporally variable, they may interact with vegetation type to mediate the supply of subsidies over time. In particular, hurricanes and other storms may increase both the supply and the transport of subsidies, and can transport a variety of materials, including sediments, into marsh and mangrove systems (Cahoon 2006, Spiller et al. 2010, Castañeda-Moya et al. 2020).

Finally, the relative importance of a subsidy decreases with increasing autochthonous productivity of a habitat, because a given amount of subsidy will have a greater effect on a low-productivity recipient habitat than on a highly productive one (Polis and Hurd 1996, Witman et al. 2004, Saintilan et al. 2013). Most past studies have thought of this relationship in terms of how habitat perimeter: area ratios affect the relative magnitude of autochthonous production relative to allochthonous inputs (Polis and Hurd 1996, Polis et al. 1997, Witman et al. 2004), but a shift from a less- to a more-productive vegetation type would have a similar effect on the relative importance of the subsidy.

In the relative low productivity settings where allochthonous subsidies markedly increases total organic matter stocks, subsidies may support a high abundance and diversity of primary and secondary consumers (Dugan et al. 2003, Marczak et al. 2007). Subsidies may provide habitat (Ince et al. 2007) and food for consumers (Pennings et al. 2000, Dugan et al. 2003). By releasing

nutrients and fertilizing plants as they decompose, subsidies may also support the green food web (Spiller et al. 2010). Some of these effects have been studied in salt marshes and salt marsh-mangrove ecotones (Bertness and Yeh 1994, Pennings and Richards 1998, Hanley et al. 2017, McKee and Vervaeke 2017), but little is known about the role of allochthonous subsidies into mangroves (but see Smith et al. 2019, 2020, 2021). This lack of attention is largely because mangroves are considered highly productive ecosystems, with a detrital food web that is dominated by autochthonously sourced material, such that subsidies from adjacent habitats are unimportant (Saintilan et al. 2013). This paradigm, however, may not apply to less productive, short-stature “scrub” mangroves that are common at the range limit of mangroves and elsewhere where abiotic factors limit mangrove productivity (Osland et al. 2013).

Here, we tested how the transition from salt marsh to mangrove forest affects the nature and importance of marine subsidies in coastal wetlands. To do this, we created ten large field plots that varied in cover of mangroves and salt marsh plants (Guo et al. 2017, Charles et al. 2020), and used these plots to test four hypotheses. Increasing plot-level mangrove cover will: 1) decrease the magnitude and distribution of allochthonous wrack in plots with high mangrove cover by decreasing the permeability of the habitat boundary, 2) alter the distribution and reduce the abundance of wetland animals in plots with high mangrove cover by changing the abundance and distribution of the subsidy, 3) decrease the relative importance of coastal subsidies as a proportion of the intertidal carbon budget. Finally, because our plots were affected by Hurricane Harvey (Armitage et al. 2020, Pennings et al. 2021, Kuhn et al. 2021) during the study period, we were also able to test the hypothesis 4) that a severe storm would increase the transport of the wrack

subsidy into the intertidal habitat, regardless of plant composition, both increasing the total magnitude of the subsidy and changing its distribution within the habitat.

## Methods

### *Study site and experimental plots*

Field work was conducted on Harbor Island, Port Aransas, Texas, USA (27.86° N, 97.08° W, Appendix S1: Fig. S1). This area is near the current northern limit of mangroves in the United States, where mangroves have a short “scrub” morphology because of cold winter temperatures and summer salinity stress caused by the arid climate and extended periods of exposure during seasonal low tides (Osland et al. 2014). At the time of the study, Harbor Island tidal wetlands were dominated by black mangroves (*Avicennia germinans*) with ~10% cover of salt marsh vegetation that was predominantly *Batis maritima*, *Sarcocornia* sp. and *Salicornia bigelovii*, with small patches of *Spartina alterniflora* (Guo et al. 2017). *B. maritima* and *Sarcocornia* sp. occur mostly on the intertidal platform, *S. bigelovii* on the levee near the front of the plot, and *S. alterniflora* fringing the wetland along the water's edge. Plots varied from ~0.2 m above mean lower low water (MLLW) along a small levee at the water's edge to ~0.1 m above MLLW in the remainder of the plots (Pennings et al. 2021).

In 2012, we demarcated ten large plots (Appendix S1: Fig. S1a), each 42 m (perpendicular to the water's edge) × 24 m. All plots initially had similar vegetation, elevation and soil characteristics. Each plot was divided into 112 (14 × 8) 3 × 3 m cells, and we defined the first four rows of cells starting at the water's edge as the plot “fringe”, and the remaining 10 rows of cells as the plot “interior”. Fringe patches were characterized by taller mangroves (~2.5 m), whereas

interior patches were characterized by shorter (~1 m tall) mangroves (Appendix S1: Fig. S1c). In the summer of 2012, mangrove plants were thinned by clipping aboveground mangrove biomass from appropriate numbers of  $3 \times 3$  m cells in each plot, mimicking the scale of patchiness in the natural environment (authors' personal observation), to create plots ranging from 0% to 100% nominal mangrove cover (0%, 11%, 22%, 33%, 44%, 55%, 66%, 77%, 88%, and 100%). We maintained these levels of mangrove cover by periodic clipping and weeding.

### ***Wrack distribution***

To document how the distribution of wrack within the experimental plots varied as a function of plot-level mangrove cover, we established two continuous transects through each experimental plot, running from the fringe (the water's edge) to the back of the plot. The two transects were 6 m apart, and each transect consisted of 42 contiguous  $1 \times 1$  m sub-plots. On five dates (August 2014, August 2015, October 2017, September 2018, September 2019) we visually estimated the percent cover of wrack in each sub-plot, and measured the thickness of any wrack found with a ruler. From these data, we also defined the wrack distribution range by noting the greatest distance from the water's edge along each transect at which wrack occurred, and also calculated the percent of wrack that occurred in the first 6 m of the plot.

In August 25, 2017, our experimental site was directly in the path of Hurricane Harvey, a category four storm. Hurricane-force winds exceeding 119 kph impacted the site for approximately 6 h, with gusts up to 225 kph (NOAA 2019). As a result, our surveys include four "normal" dates and one date (October 2017) that was two months after a major hurricane. To examine how the distribution of wrack varied as a function of plot-level mangrove cover, we averaged data from the



two transects in each plot in each of the four normal years (2014, 2015, 2018, 2019) and the one hurricane year (2017), and regressed plot averages of each variable on plot-level mangrove cover. We evaluated the strength of the relationships using  $R^2$  values, but also report  $F$  and  $P$  values in the supplementary materials (Appendix S1: Table S1).

### ***Wrack samples in the field***

To characterize the wrack and the animals living in it, we collected wrack samples from the fringe and interior of each plot on three dates (November 2014, March 2015 and July 2015). We selected patches of wrack haphazardly, and sampled them with a circular quadrat (a metal ring with a diameter of 23 cm and a height of 7 cm). We set the quadrat in place, measured the thickness of the wrack with a ruler, and quickly collected all wrack and detritus (but not underlying sediment) into a plastic bag. The vertical sides of the quadrat prevented most animals from escaping. On each date, we attempted to collect one wrack sample from the fringe and one from the interior of each plot, but we often were unable to find wrack in the interior of the plots. We sorted wrack and animals to different taxa (Appendix S1: Fig. S2, Section S1). To characterize the wrack patches and the animals living in them, we calculated the average values of wrack biomass and wrack-dwelling animal abundance for sampled wrack patches across the three sampling dates for each plot, then regressed averages on mangrove cover. For this analysis, we pooled patches from the fringe and interior because we had relatively few samples from the interior zone.

### ***Wrack experiment in the field***

The abundance and composition of the animals present in the samples of wrack that we collected from the field suggested that wrack location affected which animals were present in the wrack;

however, we could not control wrack age, composition or thickness in these samples, and we had a lower sample size for wrack patches in the interior than in the fringe. We therefore conducted an experiment to more rigorously assess the importance of wrack composition, location in the plot and cell vegetation type (mangrove or marsh) in controlling wrack faunal composition.

To assess the importance of wrack composition, we compared seagrass (a mixture of the species present as wrack at the time) with a branching red alga (not identified to species), both of which were common as wrack at the time we did the experiment in November 2014, and both of which were major constituents of wrack on other sampling dates as well (Appendix S1: Fig. S3). We collected both as floating fresh wrack from the water column, spun them in a salad spinner to remove excess water, and put 50 g wet mass of material into a mesh bag ( $18 \times 16$  cm, mesh grid size 3 mm). On November 9, 2015, we tied pairs of mesh bags, one containing red algae and one seagrass (these two taxa were chosen because they were common as wrack at the time we did the experiment), to mangrove trees in cells dominated by mangroves, and to PVC poles in cells dominated by salt marsh plants, in the fringe and interior zone of each plot. The final dataset consisted of 72 mesh bags (two wrack types  $\times$  two vegetation types  $\times$  two locations  $\times$  eight plots, plus four bags in the 100% mangrove plot and four bags in the 0% mangrove plot, because there was only one vegetation type in each of these plots). We retrieved all the bags on March 11, 2016. We separated the animals out of the wrack samples and sorted them to taxa (Appendix S1: Section S1, the composition of the wrack fauna was slightly different in the experiment than in the field sampling, with nine rather than seven common taxa). We used three-way ANCOVA to assess the importance of location (fringe versus interior), vegetation (marsh versus mangrove) and wrack

type (red algae versus seagrass) on animal density (number (No.)/0.0288 m<sup>2</sup>), with plot-level mangrove cover as a covariate. We ran one analysis for all animals pooled, and then followed this with separate analyses for the most common taxa. We used non-metric multidimensional scaling (NMDS) to visualize differences in animal composition between treatments. We used the Adonis function with Bray-Curtis dissimilarity matrix using Hellinger standardization. We used PERMANOVA using distance matrices (R package ‘vegan’) to assess significance of differences. All analyses were performed using R (version 3.5.2; R Core Team 2018).

### ***Effects of mangrove cover on subsidies***

To assess how mangrove cover affected the relative contribution of autochthonous vs. allochthonous sources of organic matter to the wetland, and how this might affect support of wrack-dwelling animals, we calculated plot-level plant biomass, plot level wrack biomass, and plot-level abundance of wrack-dwelling animals for the four normal years and the one hurricane year (Appendix S1: Table S2). Based on previous work in our plots, the aboveground biomass of plants in marsh patches was  $186 \pm 41 \text{ g m}^{-2}$ , and in mangrove patches was  $2717 \pm 253 \text{ g m}^{-2}$  (S. Charles and J. Kominoski, unpublished data). We calculated plot-level aboveground plant biomass as (average aboveground biomass in mangrove cells  $\times$  plot-level mangrove percent cover/100) + (average aboveground biomass in marsh cells  $\times$  plot-level marsh percent cover/100). We calculated plot-level wrack biomass (kg) as plot-level wrack cover  $\times$  wrack biomass ( $\text{g m}^{-2}$ ). We calculated the plot-level abundance of wrack-dwelling animals using numbers from the wrack experiment, as wrack dwelling animals (per 0.0288 m<sup>2</sup>)/(50 g wrack dry mass per 0.0288 m<sup>2</sup>)  $\times$  plot-level wrack biomass.

## Results

### *Wrack distribution*

Wrack cover, wrack thickness, wrack distribution range and the percent of wrack in the first 6 m of the plot were all strongly related to plot-level mangrove cover in the four normal years (Fig. 1,  $R^2 = 0.31-0.78$ , Appendix S1: Table S1). The relationships between these variables and plot-level mangrove cover were considerably weaker in the hurricane year (Fig. 1,  $R^2 = 0.00-0.27$ , Appendix S1: Table S1). Wrack cover decreased with increasing plot-level mangrove cover in three of four normal years. Wrack thickness, averaged across all wrack patches, decreased from ~2.4 cm to ~0.25 cm with increasing plot-level mangrove cover in normal years. In plots with < 30% mangrove cover, wrack penetrated 30 m or more into the plots, whereas in plots with > 30% mangrove cover, wrack never penetrated more than 20 m into the plots. The percentage of the wrack that was trapped in the first 6 m of the plot increased from ~10 at low mangrove cover to ~100% at high mangrove cover in normal years.

In August 2017, our experiment was directly in the path of Hurricane Harvey. In this year, wrack cover was higher than in the normal years (~5% to ~38%, Fig. 1c), wrack was thicker (~0.4 to 2.7 cm, Fig. 1h), wrack penetrated further into the plots (up to 42 m, Fig. 1m), and the percentage of the wrack that was trapped in the first half of the fringe zone was lower (up to 45%, Fig. 1r). None of the variables (wrack cover, wrack thickness, wrack distribution range, percent of wrack in the first 6 m) was a function of plot-level mangrove cover in the hurricane year (Fig. 1, Appendix S1: Table S1).

### *Wrack samples*

The biomass of the wrack patches that we sampled was positively correlated with plot-level mangrove cover, but the effect was only marginally significant (Appendix S1: Fig. S4a,  $P = 0.06$ ). Samples collected from the fringe were  $\sim 3$  times heavier than those from the interior of plots (Fig. 2a, Appendix S1: Table S3). Animal abundance (No.  $g^{-1}$  of wrack) did not vary as a function of plot-level mangrove cover (Appendix S1: Fig. S4b). Animals were  $\sim 40\%$  more abundant in samples from the interior than from the fringe of plots (Fig. 2b, Appendix S1: Table S3), but this trend was not statistically significant due to low replication of interior samples (Fig. 2b,  $P = 0.35$ ). Animal abundance in samples increased with wrack mass, indicating that animals were rare in the absence of wrack (Appendix S1: Fig. S4c). The most abundant taxonomic groups in the wrack samples were Gastropoda, Polychaeta, Amphipoda, Foraminifera and Insecta which together comprised  $> 80\%$  of the individuals in the samples (Appendix S1: Table S4). Polychaeta, Insecta, and other species were more abundant in the interior zone. Amphipoda were more abundant in the fringe zone. Gastropoda and Foraminifera did not differ between the fringe and interior zones. Different wrack-dwelling species differed in whether they were more abundant in wrack samples from the fringe versus the interior (Appendix S1: Tables S4, S5, Section S2).

### ***Wrack experiment***

The number of animals per wrack sample did not differ between seagrass and red algal wrack (Appendix S1: Table S6). Animals were most abundant (3.5–5 times) in wrack placed into salt marsh vegetation in the interior of the plots (Fig. 3a, Appendix S1: Table S6). The overall community composition of wrack-dwelling animals in the experiment differed between replicates from the fringe and interior (Fig. 3b, stress = 0.17, location: PERMANOVA  $P < 0.001$ ). Vegetation

type (marsh or mangrove) had no effect on community composition (Appendix S1: Table S7).

Different wrack-dwelling species varied by whether they were more abundant in the fringe versus interior and in mangrove versus marsh vegetation (Appendix S1: Figs. S5, S6, Section S2). Copepoda, eggs and Polychaeta were more abundant (2~20 times) in wrack placed into salt marsh vegetation in the interior of the plots. Amphipoda were more abundant (2~5 times) in salt marsh vegetation in the interior of the plots but more abundant in wrack placed into mangrove vegetation in the fringe. Other species, such as Insecta, did not respond to either vegetation type or location (Appendix S1: Fig. S6, Table S8).

#### ***Effects of mangrove cover on subsidies***

Mangrove cover affected the relative importance of autochthonous versus allochthonous sources of organic matter. In normal years, plot-level plant biomass increased as mangrove cover increased (Charles et al. 2020). At the same time, plot-level wrack biomass decreased (Figs. 4a, b, d, e, Appendix S1: Table S2). As a result, the ratio of wrack biomass to plant biomass decreased sharply from plots with no mangroves to plots with mangroves present (Figs. 4f, g, i, j). In the plot with 0% mangrove cover, wrack biomass was as the same as or greater than plant biomass in normal years. In plots with 11% and 22% mangrove cover, the ratio of wrack biomass to plant biomass was ~0.3, indicating that one sixth of the labile plant material in the plots had come from marine subsidies. In plots with higher mangrove cover, the ratio of wrack biomass to plant biomass was ~0.05, indicating modest wrack subsidies. The plot-level density of wrack-dwelling animals decreased as plot-level mangrove cover increased in normal years (Figs. 4k, l, n, o). In the hurricane year, none of these variables were related to plot-level mangrove cover (Figs. 4c, h, m,

Appendix S1: Table S2). The total amount of wrack biomass and the ratio of wrack biomass to plant biomass in the plots, however, increased ~10-fold compared to normal years.

## **Discussion**

Subsidies from one habitat to another can strongly mediate primary and secondary production, but their effects are context-dependent, varying as a function of how large the “edge” is between the two habitats, the permeability of the edge, and the relative primary productivity of the two habitats (Polis et al. 1997, Dugan et al. 2003, Witman et al. 2004, McCary et al. 2021). These factors vary spatially and temporally. Global change is driving woody encroachment into salt marshes in subtropical latitudes (Cavanaugh et al. 2014, Saintilan et al. 2014, Armitage et al. 2015). We found that this encroachment is changing the nature of marine subsidies into the intertidal at our study site, affecting the distribution of subsidies, their magnitude, their effect on secondary production, and indirectly changing the species composition of the wrack-dwelling fauna at the plot level by concentrating wrack in the fringe rather than the interior. These long-term consequences of woody encroachment, however, were temporarily overwhelmed in 2017 by the short-term effects of a hurricane disturbance.

### ***Mangrove cover changed wrack distribution, but not during a hurricane***

The ability of a subsidy to cross a habitat boundary is a function of the “permeability” of the boundary (Stamps et al. 1987, Witman et al. 2004). One factor affecting permeability is the density, stiffness and height of vegetation in the ecotone (Cadenasso and Pickett 2000, Witman et al. 2004). Our results showed that as mangroves replaced salt marsh plants, increasing the stiffness and height of the wetland vegetation (authors’ personal observations), both overall wrack cover and

the distribution of the wrack decreased. This pattern that wrack cover decreased as mangrove cover increased occurred because, if mangroves were present, the trapped wrack was deposited close to the water's edge, but if they were absent, wrack moved into the interior of the plot. Although this decreased the subsidy to most of the plot, it concentrated it at the front edge of the mangrove stands where all the wrack was trapped. These results are similar to an earlier study from our sites that found reduced sediment accretion rates in plots with higher mangrove cover (Charles et al. 2020, Smith et al. 2020). A number of studies have shown that vegetation structure plays an important role in mediating subsidies of detritus and animals (Cadenasso and Pickett 2000, Witman et al. 2004, McCary et al. 2021). For example, in salt marshes, tall marsh plants trap wrack subsidies (Bertness and Yeh 1994), and in grasslands, vegetation intercepts and retains insect subsidies (McCary et al. 2021). At our experimental site, marine-derived wrack was restricted to the fringe of plots with high mangrove cover, indicating that mangroves both limited the total amount of the subsidy and changed its distribution, almost completely concentrating wrack subsidies in the fringe habitat.

Permeability of habitat boundaries is affected not only by vegetation but also by physical forces such as currents, waves and wind that move subsidies across boundaries (Polis et al. 1997, Witman et al. 2004). Generally, the input of allochthonous material increases with the strength of these physical drivers (Witman et al. 2004, Guntenspergen et al. 1995, Lovelock et al. 2011). We found that, following Hurricane Harvey, wrack cover was greater than in normal years, wrack deposits were thicker, and the wrack was distributed throughout the entire area of the plots, regardless of mangrove cover. This likely happened because the 1.6 m storm surge and associated



waves flooded the plots (NOAA 2019), making it easier for the strong waves and 119 kph winds to move the wrack into the interior of the plots. These results are consistent with previous findings that hurricane-generated wrack deposits are larger and are transported further inland than are normal, tidally-generated wrack deposits (Bush et al. 1996). Thus, although mangroves may impose a barrier to marine subsidies, this barrier is not absolute, because it can be penetrated during extreme events. However, because extreme events are rare, wrack subsidies to the interior of the wetland are likely to be routine events in salt marshes but unusual events in mangroves.

### ***Effects of wrack subsidies on marsh animals***

Detrital subsidies usually increase secondary productivity by increasing resources available to detritivores and their predators (Polis and Hurd 1996, Polis et al. 1997, Dugan et al. 2003, Liebowitz et al. 2016). Our results indicated that allochthonous wrack subsidies strongly increased the abundance of small animals, with animal density increasing linearly with wrack biomass (Appendix S1: Fig. S4c). Animal community structure differed between the fringe and interior habitats, probably because wrack in these two locations differed in wave exposure, thickness and water content, and different species preferred one or the other set of conditions (Orr et al. 2005, Ince et al. 2007). By altering the distribution of wrack between the fringe and interior, mangroves indirectly affected plot-level composition of the animal community, both by limiting the total amount of the wrack subsidy and by changing its distribution (Fig. 1, Appendix S1: Fig. S5, S6). Finally, for some groups of animals, density differed between mangrove and marsh vegetation patches, perhaps because mangroves affected microclimate (Guo et al. 2017), habitat structure (Wimp et al. 2019), vulnerability to predators (Nomann and Pennings 1998) or availability of other

food sources (Smith et al. 2019). Thus, the cover of mangroves had multiple effects on the abundance and composition of wrack-dwelling animals by changing the quantity of the wrack subsidy, the distribution of the wrack subsidy among habitats that differed in suitability for the animals (plot fringe versus interior), and finally by the local vegetation type having a direct effect on animal abundance even when wrack was experimentally held constant. Given these various effects, the spread of mangroves to higher latitudes is likely to alter the abundance and composition of small animals present in wetlands that mangroves invade.

In contrast to findings from other systems and mangrove system in other place (Bloomfield and Gillanders 2005, Bishop and Kelaher 2013, Smith et al. 2019), animal density and composition was not affected by wrack type in our study, suggesting either that the two wrack types that we tested provide similar nutritive value, or that animals were using the bags of wrack as physical habitat more than for food. We did not directly test the quality of the two types of wrack as food; however, differences in food quality among live plants tend to decrease during decomposition (Mann 1988), so the first possibility could be correct if wrack-dwelling fauna are feeding mostly on microbes and heavily-decomposed wrack. The second possibility, that the animals were using wrack as habitat, is also plausible, because the wrack would act as a sponge, providing a moist refugium on the soil surface that might reduce desiccation during low tide or provide shelter from predators (Ince et al. 2007, Smith et al. 2019, 2020). Both possibilities deserve future attention. We were not able to test all the major types of wrack, however, because the composition of wrack in the environment changed over time, and these results might have changed if we had included other common wrack types, such as brown algae (*Sargassum* sp.), in the experiment.

### *Effects of wrack subsidies on carbon flow and secondary production*

In plots with little mangrove cover, wrack was an important subsidy of organic matter to the wetland, with the standing stock of wrack approximately equal to the standing stock of plant biomass. As mangrove cover and biomass increased, the relative importance of the wrack subsidy decreased, with wrack making up about a fifth of the aboveground matter in plots with low mangrove cover, but only about five percent in plots with high mangrove cover. For this reason, assuming that standing stocks of wrack and plant biomass are a reasonable estimate of rates of wrack input and primary production, detrital food webs in intact mangrove forests are typically dominated by autochthonously sourced material (Saintilan et al. 2013). In a similar way, the importance of wrack subsidies to ecosystem metabolism of small islands is an increasing function of the island perimeter: area ratio (Polis and Hurd 1996).

Wrack releases nutrients when it decomposes (Pennings and Richards 1998, Spiller et al. 2010, Lovelock et al. 2011, Lavery et al. 2013). Mangroves are typically taller in fringe versus interior habitats, a pattern that is related to increased nutrient availability in the fringe habitat (Feller et al. 2003, Lovelock et al. 2004). Although we did not test this idea, we speculate that the trapping of wrack by mangroves in the fringe may further increase nutrient availability and growth of plants. In addition, trapping of large amounts of organic matter in the fringe may contribute to building soil elevation, helping to create the levees that occur at the fringe in some stands of mangroves (Pennings et al. 2021).

We found that wrack subsidies were important for supporting densities of a variety of wrack-dwelling animals. Because these species are food for the various birds, fish and crabs that

occupy higher trophic levels (Stapp et al. 1999, Dugan et al. 2003), wrack subsidies likely have effects that propagate up throughout the entire food web (Polis and Hurd 1996, Polis et al. 1997). For example, extensive removal of wrack on shoreline habitats has negative effects on shorebirds and other species that feed on wrack fauna (Kirkman and Kendrick 1997, Spiller et al. 2010). Investigating the effects of wrack subsidies in mangrove habitats on similar larger consumers was outside the scope of this project, but deserves future attention since these larger consumers represent the species that are of the most importance to humans, both as food and as wildlife.

One limitation of our study is that it relied on annual sampling of wrack distributions. As a result, we don't know how the distribution of wrack, nor the composition of the animal community, might have changed over the course of a year. Our impression is that wrack patches tend to get entangled with the vegetation once deposited at this site, and so would not likely change enough to alter the patterns that we documented. However, exploring seasonal patterns of wrack distribution and the associated faunal community would be an interesting topic for future work.

### ***Global changes and marine wrack subsidies***

With reductions in winter freeze events, 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). This increase in mangrove cover is likely to change the distribution of wrack subsidies within plots, and the abundance and composition of animals living in the wrack. At the same time, severe storms are likely to become more frequent in a warming world (Tate and Battaglia 2013, Krauss and Osland 2020). Because these storms have the ability to push wrack subsidies into mangrove forests, they may be important drivers of marine subsidies, especially in marshes with increasing mangrove

cover (Smith et al. 2019). More generally, identifying when and where communities and food webs are likely to be subsidized given global changes will foster a broader understanding of the interdependence of adjacent habitats and ecosystems and a better understanding of potential impacts to community ecology at larger spatial and temporal scales.

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## Figure Legends

**Figure 1.** Wrack deposition survey. Wrack cover in normal (a) 2014, (b) 2015, (d) 2018, (e) 2019, and hurricane (c) 2017 years; Wrack thickness in normal (f) 2014, (g) 2015, (i) 2018, (j) 2019, and hurricane (h) 2017 years; Wrack deposit distribution range from the water's edge in normal (k) 2014, (l) 2015, (n) 2018, (o) 2019, and hurricane (m) 2017 years; Percent of wrack deposited in first 6 m in normal (p) 2014, (q) 2015, (s) 2018, (t) 2019, and hurricane (r) 2017 years. # indicates  $0.05 < P < 0.1$  (dashed grey lines); \* indicates  $P < 0.05$ ; \*\* indicates  $P < 0.01$ ; \*\*\* indicates  $P < 0.001$  (all with solid black lines). Triangle symbols indicate hurricane year.

**Figure 2.** Natural wrack patches. (a) Wrack mass (mean + SE), (b) animal abundance (No.  $g^{-1}$ ).

**Figure 3.** (a) Total animal abundance (mean + SE) in the wrack experiment as a function of location (interior versus fringe) and vegetation type (salt marsh versus mangrove). Letters indicate means that were significantly different (Tukey HSD) in two-way ANOVA. (b) Community structure of wrack-dwelling animals in interior and fringe zone. Two-dimensional NMDS ordination of animal assemblages based on Bray-Curtis similarity. The stress value was 0.17. PERMANOVA indicated a significant effect of location but no effect of vegetation type and no interaction between location and vegetation type (Appendix S1: Table S7).

**Figure 4.** Effect of plot-level mangrove cover on estimated biomass of wrack biomass in normal (a) 2014, (b) 2015, (d) 2018, (e) 2019, and hurricane (c) 2017 years; wrack biomass input/plant biomass ratio in normal (f) 2014, (g) 2015, (i) 2018, (j) 2019, and hurricane (h) 2017 years; total animals in normal (k) 2014, (l) 2015, (n) 2018, (o) 2019, and hurricane (m) 2017 years. # indicates  $0.05 < P < 0.1$  (dashed grey lines); \* indicates  $P < 0.05$ ; \*\* indicates  $P < 0.01$ ; \*\*\* indicates  $P <$

0.001 (all with solid black lines). Triangle symbols indicate hurricane year.

Figure 1

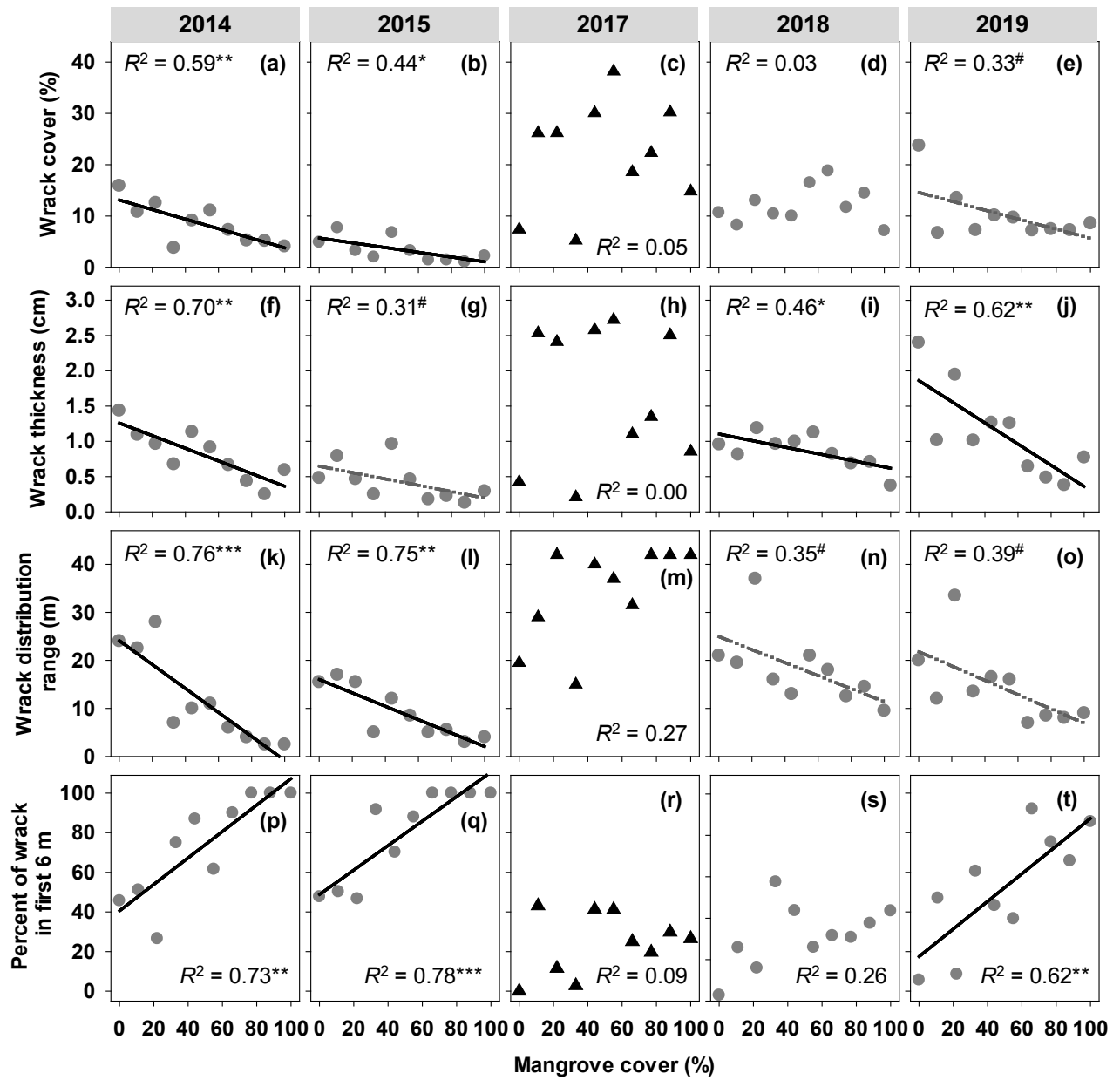




Figure 2

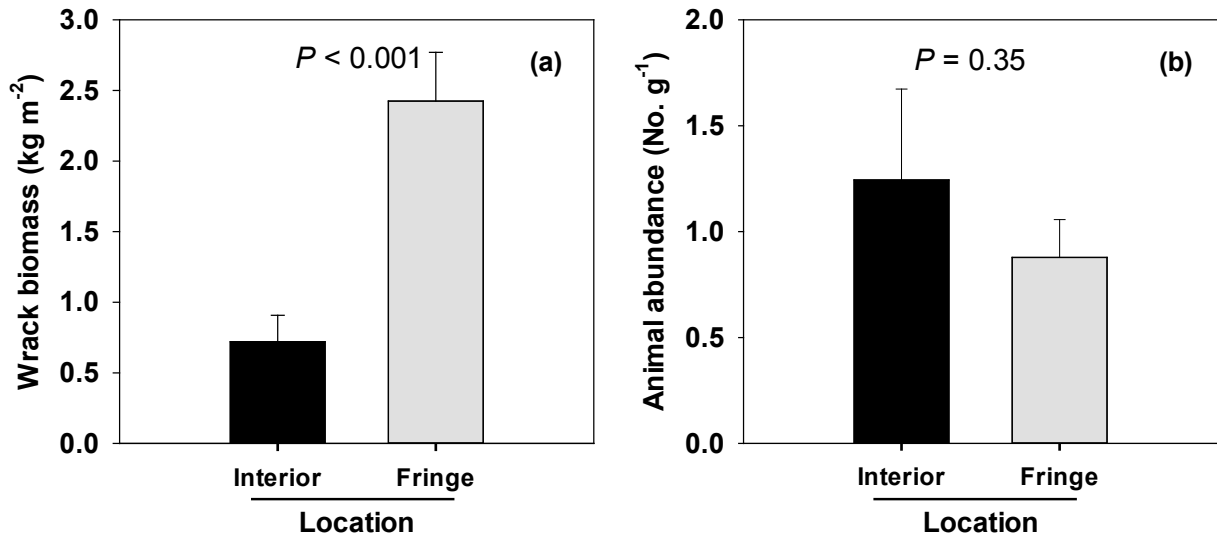


Figure 3

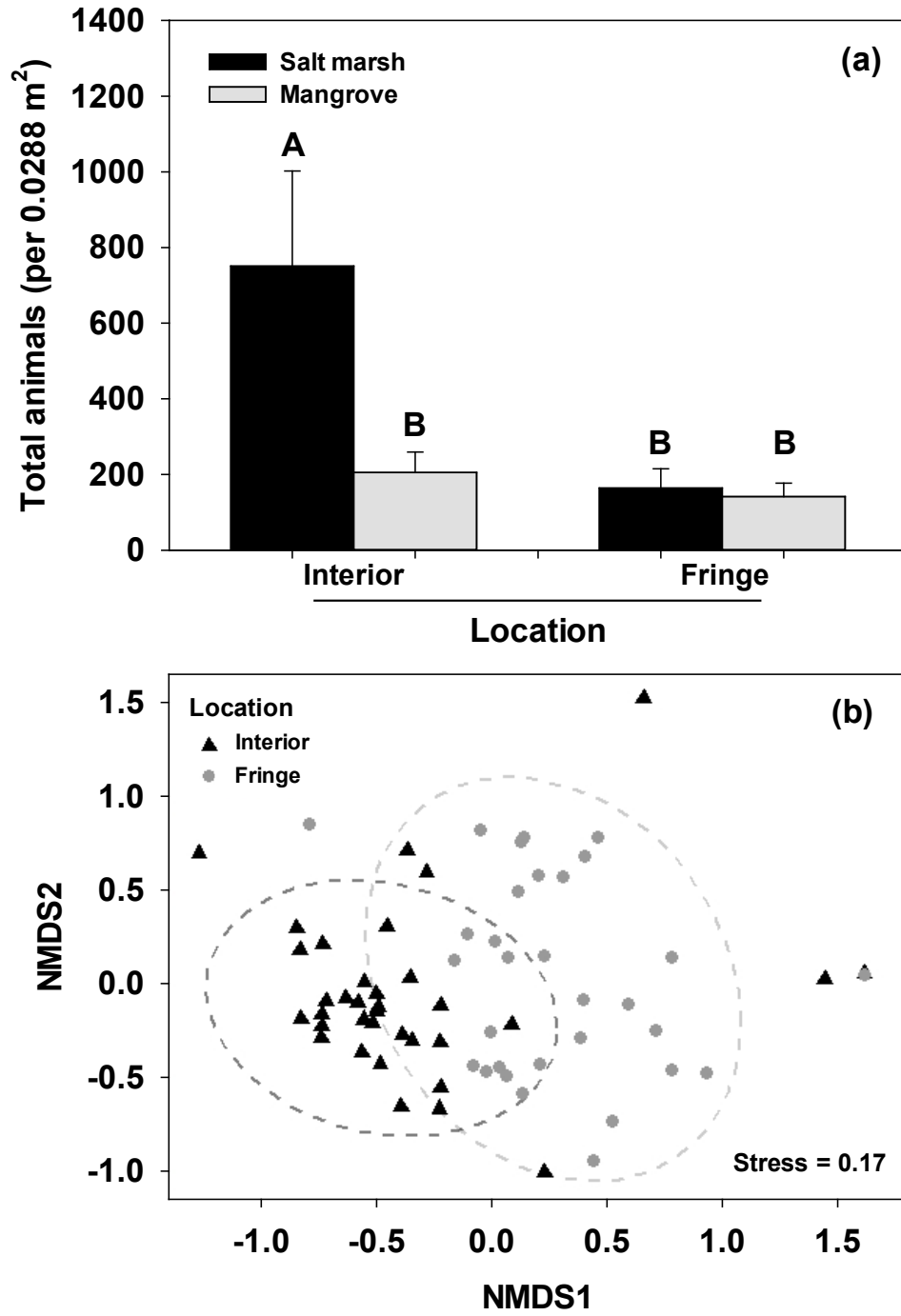


Figure 4

