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Negative outcomes of novel trophic interactions along mangrove range edges

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ABSTRACT

Tropicalization is a phenomenon that is changing the structure of ecosystems around the world. Mangrove encroachment is a particular form of tropicalization that may have cascading consequences for resident fauna in subtropical coastal wetlands. There is a knowledge gap regarding the extent of interactions between basal consumers and mangroves along mangrove range edges, and the consequences of these novel interactions for the consumers. This study focuses on the key coastal wetland consumers, *Littoraria irrorata* (marsh periwinkle) and *Uca rapax* (mudflat fiddler crabs), and their interactions with encroaching *Avicennia germinans* (black mangrove) in the Gulf of Mexico, USA. In food preference assays, *Littoraria* avoided consuming *Avicennia* and selectively ingested leaf tissue from a common marsh grass, *Spartina alterniflora* (smooth cordgrass), a preference which has also been previously documented in *Uca*. The quality of *Avicennia* as a food source was determined by measuring the energy storage of consumers that had interacted with either *Avicennia* or marsh plants in the lab and the field. *Littoraria* and *Uca* both stored approximately 10% less energy when interacting with *Avicennia*, despite their different feeding behaviors and physiologies. The negative consequences of mangrove encroachment for these species at the individual level suggest that there may be negative population-level effects as encroachment continues. Many previous studies have documented shifts in floral and faunal communities following mangrove replacement of salt marsh vegetation, but this study is the first to identify physiological responses that may be contributing to these shifts.

Keywords: Community ecology, salt marsh, trophic interactions, foundation species, tropicalization

Introduction

Climate change encompasses a broad suite of environmental shifts including changing average and extreme temperatures, precipitation patterns, and extreme weather event frequency. These same environmental conditions often control species ranges; thus climate change is increasingly leading to range shifts as species are environmentally excluded from or given access to ecosystems (Chen et al. 2011). In locations where previously temperate ecosystems are warming and communities are shifting to resemble those at more equatorial latitudes, this shift is termed tropicalization. Individual species ranges in tropicalizing environments are expanding at different rates due to the unique array of abiotic and biotic factors that serve as controls for each species (Walther 2010). With these differential expansion rates, novel communities are being created when plants are exposed to novel herbivores and herbivores lose access to their typical food sources, thereby establishing novel trophic interactions (Lurgi et al. 2012).

One form of tropicalization, mangrove encroachment, is re-structuring coastal wetlands across the southeastern United States coastline. Coastal wetlands in the region support commercial and recreational fisheries and benefit ecosystems through flood mitigation, wastewater treatment, and habitat provision (Costanza et al. 2014). However, the structure of these wetlands is fundamentally changing, as the sub-tropical mangrove *Avicennia germinans* (black mangrove, hereafter *Avicennia*) is becoming more common in the region because of climatic drivers including fewer severe freeze events (Osland et al. 2013, Feller et al. 2017). As a result, mangroves are encroaching into coastal marshes, often at the expense of shorter stature marsh plants (Guo et al. 2017, Armitage et al. 2021), and are changing the character and structure of these culturally and environmentally important systems.

Many system-level responses to mangrove encroachment have been identified, such as

increased soil organic content, decomposition rates, accretion rates, and decreased erosion rates and faunal richness (e.g. Saintilan and Rogers 2015; Kelleway et al. 2017; Charles et al. 2020), but changes in organismal behavioral and physiological responses must be considered to fully understand the consequences of mangrove encroachment. Understanding the novel interactions resulting from mangrove encroachment will broadly inform predictions about climate change impacts in many systems beyond coastal wetlands by allowing us to predict consumer responses and general patterns in the many systems undergoing tropicalization (e.g., coral reefs, kelp forests, grasslands) where novel trophic interactions have been identified, but not thoroughly researched (Walther 2010, Vergés et al. 2014, Bartley et al. 2019). The physiological consequences of novel interactions may have wide-reaching effects, including changing carbon cycling and sediment dynamics through effects on ecosystem engineers, impacting tourism and cultural value by changing recreational attractiveness and endangered species presence, and altering the trophic support for economically valuable species (Stunz et al. 2002, Kristensen and Alongi 2006, Rush et al. 2009). Therefore, responses of basal consumers are directly relevant to predicting the system-level consequences of mangrove encroachment in particular and tropicalization in general (Domingos and Lana 2017, Harris et al. 2020).

As *Avicennia* encroaches into wetlands, the density and cover of *Spartina alterniflora* (smooth cordgrass, hereafter *Spartina*) decreases (Harris et al. 2020, Armitage et al. 2021). *Spartina* is the dominant wetland macrophyte throughout the northern Gulf of Mexico and is an important food source for many basal consumers, supporting ubiquitous wetland faunal species including *Littoraria irrorata*, the marsh periwinkle snail (hereafter *Littoraria*), and *Uca* spp., fiddler crabs (Teal 1962, Currin et al. 1995, Goeke and Armitage 2021). *Littoraria* are *Spartina* specialists that primarily feed by creating small wounds on *Spartina* leaves; at high densities,

their feeding activity can decrease *Spartina* density and productivity (Silliman and Ziemann 2001). *Uca* are generalist detritivores, but derive much of their carbon intake from dead *Spartina* as the dominant detritus source in many marshes (Currin et al. 1995). In addition to consuming large amounts of *Spartina* and influencing wetland structure and function, both *Littoraria* and *Uca* serve as prey items for recreationally and commercially important consumers at higher trophic levels including blue crabs, red drum, and coastal wading birds (Peters et al. 1987, Hunt and Slack 1989, Bell and Vose 1998, Dittel et al. 2000).

Given their roles as basal consumers and important trophic links and their important influences on wetland structure and function through feeding and burrowing activities, *Littoraria* and *Uca* are important focal species to examine the trophic consequences of mangrove encroachment. We conducted a series of laboratory feeding studies and field surveys to assess the interactions of *Littoraria* and *Uca* with *Spartina* and *Avicennia* in Texas coastal wetlands and to expand upon our previous work, which demonstrated that multiple species of *Uca* avoid *Avicennia* as a food source and experience negative physiological consequences when exposed to *Avicennia* in the lab (Goeke and Armitage 2021). Here, we report on a complementary set of lab assays that examined *Littoraria* preferences for diets of *Spartina* and *Avicennia*, and their physiological response to those diets. In addition, the physiological condition of both *Littoraria* and *Uca* was examined in individuals collected from field sites with different levels of mangrove encroachment. Given the strength of the well-known *Littoraria-Spartina* interaction and the previously documented responses of *Uca*, we hypothesized that snails would prefer to consume *Spartina* over *Avicennia*, and that increased exposure to *Avicennia* would result in lower physiological condition, as measured by energy stores, for both consumers.

Methods

The preference for and quality of *Avicennia* as a food source for *Uca* has been previously documented (Goeke and Armitage 2021), so here we report the methods and results only for *Littoraria* lab trials. The results of both studies are supplemented with a field study on the physiological condition of *Uca* and *Littoraria* from *Avicennia*- and *Spartina*-dominated sites.

Food Preference

All *Littoraria* and vegetation used in lab studies were collected from marshes surrounding East End Lagoon in Galveston, TX, near the current northern range limit of *Avicennia* (**Figure 1a**). Encroached marshes typically have patchy (< 30%) *Avicennia* cover and >50% *Spartina* cover, and no other mangrove species are present, so the collected *Littoraria* were likely to have had limited prior interactions with mangroves. *Littoraria* food preference was assessed in a mesocosm study performed in October 2020. *Littoraria* were collected directly from *Spartina* stems and were immediately placed in mesocosms and offered four dietary choices: live *Spartina*, dead *Spartina*, live *Avicennia*, and dead *Avicennia*. Live *Spartina* leaves were collected by selecting leaves showing no signs of herbivory from healthy plants, and dead *Spartina* leaves were taken from standing dead *Spartina* stems. Live *Avicennia* leaves without any herbivore damage were picked directly from adult mangroves and fallen dead *Avicennia* leaves were gathered from the ground. Leaves were rinsed with distilled water before being used in experiments, all of which were started within four hours of leaf and snail collection.

Food options were presented as full *Avicennia* leaves and 10 cm sections of *Spartina* leaves placed upright in 250 mL plastic containers (n = 20) with their cut basal end in 10 ml of 20 ppt salinity water. Three *Littoraria* and one leaf of each type (four leaves total) were placed in each container and snails fed freely on the presented leaves for 14 days, uninterrupted except for a container cleaning and water change on day eight. A control treatment where leaves were kept in

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containers without *Littoraria* for the length of the study ($n = 5$) was treated the same. Climate was not strictly controlled during the experiment; due to pandemic safety considerations the study was performed outdoors in a shaded and partially enclosed environment that emulated ambient field conditions.

Feeding activity was measured as the change in leaf area. All leaves were photographed before being placed in mesocosms and again at the end of the study. Leaf area in each photograph was measured using the program ImageJ. There was no change in leaf area in the control (no *Littoraria*) treatments, so any leaf area loss in containers with *Littoraria* between the beginning and end of the study was assumed to be due to consumption.

Food Quality

The quality of *Avicennia* and *Spartina* leaves as food sources for *Littoraria* was evaluated by measuring the energy stores of individuals raised on a diet of each plant for 60 days in summer 2020. *Littoraria* and plants for the food quality study were collected from East End Lagoon as described above. The *Avicennia* diet consisted of living *Avicennia* branches containing 5-8 leaves, and dead *Avicennia* leaves from fallen branches and the marsh surface. The *Spartina* diet contained both living and standing dead stems with attached leaves, which were cut 15-30 cm from the marsh surface. Approximately two hundred adult *Littoraria* of similar size were collected in May 2020 and were randomly assigned to one of six 10-gallon (37.8 L) aquarium tanks. All tanks contained 0.5 L of 20 ppt water and two stems/branches of living and dead material of one plant diet ($n = 3$ tanks per diet). Some individuals escaped through gaps in tank covers so final sample sizes were $n=103$ (*Spartina* diet) and $n = 94$ (*Avicennia* diet). At no point during the experiment was all the available leaf tissue consumed. Tanks were covered and housed in a shaded outdoor location exposed to ambient temperature

conditions. Tanks were cleaned and provided with fresh food and water weekly.

After 60 days, *Littoraria* were removed from tanks and frozen. In the lab, shell length was measured (initial shell length measurements were not taken due to restricted lab access during the COVID-19 pandemic), and wet and dry body weights were obtained. To minimize weight differences due to the variability in water storage between organisms, snail bodies were dissected out of shells, rinsed with distilled water, blotted to remove excess water, and weighed to determine shell-less wet body weight. Bodies were dried at 60°C for 48 hours and reweighed to obtain dry weights. The resultant ratio of dry to wet body weight (termed dry-weight density, or DWD) of each snail represents the percent of an individual's total wet body weight that is attributed to tissue as opposed to water. In aquatic gastropods such as *Littoraria*, tissue is replaced with water as energy stores are depleted, resulting in a negligible change in wet weight with a decrease in energy stores, while dry weight is sensitive to decreases in body tissue, so the dry-weight density of individuals is a proxy for estimating energy storage and physiological condition (Zonneveld and Kooijman 1989). As a proxy, DWD decreases in response to starvation, indicating it is sensitive to changes in physiological condition resulting from failure to meet nutritional requirements (Zonneveld and Kooijman 1989, Ter Maat et al. 2007).

Field Body Conditions

Littoraria and *Uca* were collected from Port Aransas, TX in November 2020 and March 2021, respectively (**Figure 1a**). *Avicennia* is abundant in Port Aransas, and *Littoraria* and *Uca* in heavily encroached sites are frequently physically associated with *Avicennia* (Goeke 2021), though their trophic relationships with *Avicennia* are unknown. *Littoraria* and *Uca* were collected from six experimentally maintained 0.1 ha plots across <2 km of coastline that had either low (0, 11, and 22%) or high (77, 88, and 100%) mangrove cover (Guo et al. 2017)

(**Figure 1b**). Each experimental plot was originally mangrove dominated, but mangroves have been selectively removed to create and maintain the target experimental cover levels since 2012. Ten *Littoraria* and between two and five *Uca* (**Appendix S1: Table S3**) were collected from each experimental plot; fewer *Uca* than *Littoraria* were collected due to tides obscuring burrows and limiting collection time. Several species of physiologically and behaviorally similar fiddler crabs occur in Gulf Coast wetlands (Barnwell and Thurman 1984), but we collected only *Uca rapax* (mudflat fiddler crabs), which were the most commonly found species in the plots. Consumers were collected in the vicinity of the dominant vegetation of each plot (i.e., within patches of marsh vegetation in the low mangrove cover plots and underneath or on mangroves in the high mangrove cover plots). *Littoraria* were collected directly on the dominant vegetation while *Uca* were collected from burrow entrances within patches of the dominant vegetation. Due to the site fidelity and limited movement patterns of these species (Knopf 1966, Vaughn and Fisher 1992, Yamaguchi and Tabata 2004), this method of collection ensured individuals had likely been interacting primarily with the dominant vegetation in the preceding weeks. We also collected *Littoraria* from two non-manipulated survey sites; ten *Littoraria* were collected from a fully encroached mangrove site with no nearby marshes and five (the most that could be located during collection) were collected from an un-encroached marsh site (**Figure 1b**). *Uca* have been previously observed in these sites, but none could be located at the time of collection.

The DWD of *Littoraria* was determined using the same procedure described above. *Uca* body condition assessment was based on the condition of the hepatopancreas (Goeke and Armitage 2021), which is the main energy storage organ in crustaceans. The hepatopancreas serves as a proxy for physiological condition as its size and contents are sensitive to the effects of starvation and energetically expensive processes (Cockcroft 1997, Sánchez-Paz et al. 2007).

In brief, each collected crab was weighed, sexed, and the hepatopancreas was removed and weighed to calculate the hepatosomatic index (HSI) for each crab, which is the ratio of the hepatopancreas wet weight to the total body wet weight and is a means of standardizing hepatopancreas size to estimate relative energy storage. To confirm if shifts in body condition were related to shifts in diet, muscle tissue was sampled from a subset of the field collected *Littoraria* and *Littoraria* from the lab food quality experiment and was analyzed for stable isotopes alongside potential food sources from the field (**Appendix S1: Section S4**).

Data Analysis

Data were analyzed with a combination of ANOVA tests and generalized linear models (GLM), so all datasets were tested to ensure they conformed to assumptions of normality and homoscedasticity using Shapiro-Wilk tests and Levene's tests respectively. Datasets that did not conform to assumptions were addressed as described below. All statistical analyses were performed in R version 4.2.1 (R Development Core Team 2022).

Littoraria food preference was analyzed with a generalized linear model (GLM, glm function) to determine the effect of treatment (control vs. experimental) and leaf type on leaf area change. Weighted least squares regression was used to compensate for heteroscedasticity in leaf area change. Where a significant effect in the model was identified using a type II ANOVA (Anova function, *car* package), we performed a multiple comparisons of means (MCM) test with Tukey contrasts (glht function, *multcomp* package, Hothorn et al. 2008) to identify what plant type and treatment levels differed.

Shell length, wet body weight, and DWD of *Littoraria* in the food quality experiment were analyzed using linear mixed-effects models (lmer function in the *lme4* package, Bates et al. 2015) with diet as a fixed effect and tank number as a nested random effect. Reported results are

from ANOVA tables computed for fitted models. For *Littoraria* field body condition, the average DWD of *Littoraria* collected from each plot in the field was regressed on plot-level mangrove cover using a linear and quadratic model in a GLM. We examined the fit of the two models and determined the quadratic model had the best fit based on adjusted R^2 value. Only plot-averaged DWD values were used in the regression to avoid pseudoreplication. *Littoraria* from the sampled survey sites were not included in the regression but were used as external points of reference for effects of mangrove cover on DWD in non-manipulated sites. The body condition (HSI) of field-collected fiddler crabs was also averaged by plot and then regressed on mangrove cover in a GLM to determine the effect of mangrove cover, crab sex, and their interaction. Quadratic and linear models were compared, and the linear model was found to have the best fit. The GLM was then analyzed with a type II ANOVA to accurately describe the respective effects of mangrove cover and sex.

Results

Food Preference

Treatment (with or without grazers), plant type, and the interaction of the two all influenced leaf area loss through consumption (GLM; **Appendix S1: Table S1**). Based on comparison of experimental and control treatments, live *Spartina* leaves ($p < 0.001$) and dead *Spartina* leaves ($p < 0.001$) were both heavily consumed by *Littoraria* but there was no evidence of *Littoraria* consumption of *Avicennia* leaves (**Figure 2a, Appendix S1: Table S2**). After 14 days, live *Spartina* leaves had lost 25% of their total area, and dead *Spartina* leaves had lost 37% of their area. There was no difference in consumption between live and dead *Spartina* ($p = 0.156$, **Figure 2a, Appendix S1: Table S2**), and both *Spartina* leaf types were consumed more than either live or dead *Avicennia* leaves ($p < 0.001$ for all comparisons; **Figure 2a, Appendix S1: Table S2**).

Food Quality

Littoraria survival was 100% on both diets. At the experiment end, there was no difference in individual snail size between the two diets as measured by either shell length ($F_{1,4.59} = 0.262$, $p = 0.633$, **Appendix S1: Figure S1**) or wet body weight ($F_{1,4.46} = 0.634$, $p = 0.466$, **Appendix S1: Figure S2**). *Littoraria* raised on the *Spartina* diet had DWDs that were on average 10% higher than those on the *Avicennia* diet ($F_{1,3.96} = 8.202$, $p = 0.046$, **Figure 2b**), representing a 10% loss of body tissue mass in snails that were fed *Avicennia*.

Field Body Condition

DWD of *Littoraria* decreased sharply from zero to 33% mangrove cover, then continued to decrease more gradually at higher levels of mangrove cover (Adj. $R^2 = 0.88$, $p = 0.011$).

Average *Littoraria* DWD values were ~21 when mangroves were absent at the 0% mangrove cover experimental plot, while at the highest mangrove cover sites the average DWD values were ~17, similar to the DWDs of *Littoraria* raised on a mangrove diet in the lab (**Figure 2b, Figure 3a**). Even low levels of cover in the 11% and 22% mangrove cover plots substantially decreased *Littoraria* DWD to ~19 (**Figure 3a**). The DWDs of *Littoraria* from the mangrove survey site were higher than those of individuals from the high mangrove cover experimental plots, but still less than those of snails from the marsh survey site (mangrove survey site mean = 20.2, marsh survey site mean = 21.7). The results are somewhat limited by a low sample size, but the magnitude of the difference between mangrove and marsh survey sites (DWD difference of 1.5) is similar to the magnitude of difference between mangrove and marsh diets in the lab food quality study (mangrove diet mean = 16.2, marsh diet mean = 17.9, DWD difference of 1.7). Stable isotope analysis also revealed a corresponding shift in the $\delta^{13}\text{C}$ values of *Littoraria* exposed to marsh versus mangrove plants in both the lab and the field, indicating a dietary shift

in the absence of *Spartina* (**Appendix S1: Figure S3**) in both cases.

The hepatosomatic index (HSI) of *Uca* decreased linearly with increasing mangrove cover (Adj. $R^2 = 0.77$, $p = 0.042$) although females had higher HSI values than males overall ($F_{1,7} = 24.15$, $p = 0.002$; **Figure 3b**). Male *Uca* have one greatly enlarged cheliped and therefore have higher and more variable body weights at a given carapace size than females, which affects body-weight-based calculations. The decrease in HSI between marsh and mangrove plots was larger in females (~ 3) than in males (~ 1) and we cannot be confident if the decrease in males is meaningful due to the small sample size and high variability of male HSI values. There was no interaction of mangrove cover and sex ($F_{1,7} = 1.39$, $p = 0.277$; **Figure 3b**) since body conditions of both sexes decreased in mangrove plots, suggesting that the HSI decrease in males might prove to be meaningful with a larger sample size.

Discussion

Basal consumers responded differently to *Spartina* and *Avicennia* as food sources; both the extent and the physiological value of trophic interactions were lesser with *Avicennia* than with *Spartina*. Both *Littoraria* and *Uca* preferred to consume *Spartina* over *Avicennia* and had decreased physiological conditions when forced to interact with *Avicennia* (this study, Goeke and Armitage 2021). Although there were taxa and sex-specific differences in the magnitude of this response, and the overall physiological condition of species differed between experimental sites, survey sites, and lab studies, there was a clear universal pattern where all consumers exhibited lower energy storage and thus decreased fitness on diets of *Avicennia* leaves.

Consumer feeding behavior and physiological condition are complex dynamics that are affected not just by exposure to new food sources (such as the appearance of a novel plant in a system undergoing tropicalization), but also by the presence of phytochemicals (i.e. fatty acids,

tannins, phenolics) (Barbehenn and Constabel 2011, Sieg et al. 2013), pollutants, heavy metals, and diseases (Callahan and Weis 1983, De Wolf and Rashid 2008), the fluctuating relationships between diet assimilation efficiency and organism nutritional requirements (Cox and Murray 2006, Morton 2018), and environmental considerations including sediment dynamics, light/shade levels, and the presence of other plant species (e.g. Thurman 1984, Iacarella and Helmuth 2011, Stagg and Mendelssohn 2012). Identifying the drivers of food preference was beyond the scope of this study, but the knowledge that common basal consumers avoid consuming *Avicennia* has important implications for energy flow in encroached wetlands where *Spartina* is disappearing. Based on the controlled nature of the food quality study and the proximity of the field collection sites to each other, the most likely factors contributing to decreases in basal consumer energy storage detected in this study were either decreased consumption of *Spartina*, or a secondary response to increased *Avicennia* exposure. This pattern of food preference and decreased physiological condition in two taxonomically unrelated basal consumers indicates that the responses described by this study are not species-specific, and instead may reflect a more general consequence resulting from mangrove encroachment.

Negative effects of mangrove encroachment on consumers may be exacerbated because *Spartina*, which is being replaced, is a foundational plant species in Gulf of Mexico salt marshes (Yando et al. 2019). *Littoraria* are considered *Spartina* specialists and their growth rates are positively correlated with *Spartina* abundance in the field (Stagg and Mendelssohn 2012), and *Spartina* diets in the lab (Bärlocher and Newell 1994a). *Uca rapax* are generalist detritivores and not *Spartina* specialists, but they are also strongly associated with *Spartina* dominated habitats (Thurman 1984) and regularly consume *Spartina* matter (Currin et al. 1995). With mangrove encroachment and the disappearance of *Spartina*, there is growing evidence that basal consumer

diets are shifting away from *Spartina* (e.g Domingos and Lana 2017, Baker et al. 2021, Goeke 2021) and that benthic and nektonic fauna, such as herbivorous fish fry and filter feeding shrimp, are shifting their distributions to avoid mangrove areas in encroached systems (Smee et al. 2017, Scheffel et al. 2018, Armitage et al. 2021). While some tropical mangrove herbivores (e.g., *Aratus pisonii*) are experiencing range expansions (Riley et al. 2014) and there are species of *Littoraria* and *Uca* that typically occur in tropical mangrove systems, these tropical basal consumers have not been reported across the *Avicennia*-salt marsh ecotone.

In marsh-mangrove ecotones, consumers rarely utilize mangrove plant matter as a food source, and instead are finding alternate food sources as *Spartina* disappears (Nelson et al. 2019, Harris et al. 2020, Baker et al. 2021, Goeke 2021). This aligns with our observation that both *Littoraria* and *Uca* avoided consumption of *Avicennia* matter (this study, Goeke and Armitage 2021). Stable isotope analysis and dietary proportion mixing models from several marsh and mangrove encroached sites along the Texas coast found that both consumers ate minimal amounts of *Avicennia* at mangrove-dominated sites, and instead relied primarily on alternate sources such as particulate organic matter (POM) and benthic macroalgae (BMA) (Goeke 2021). Although we did not include POM or BMA as offered diets in our lab studies, the $\delta^{13}\text{C}$ values of POM and BMA samples collected from the field match the $\delta^{13}\text{C}$ values of mangrove-exposed *Littoraria* from both the lab and the field in this study (**Appendix S1: Figure S3**), suggesting that *Littoraria* raised in the lab may be storing less energy due to the consumption of low quality algae and microorganisms that colonize dead mangrove leaves, as opposed to consumption of mangrove leaf tissue itself.

Exposure to secondary metabolites produced by *Avicennia* may decrease basal consumer body condition, even when *Avicennia* is not being consumed. Secondary metabolites include

phytochemicals such as tannins and phenolics that are generally uncommon or absent in *Spartina*, but abundant in *Avicennia* (Bärlocher and Newell 1994b, Erickson et al. 2004). When *Avicennia* leaves begin to decompose on the marsh surface or in the tanks of the food quality study, these phytochemicals leach out into the environment (Steinke et al. 1993, Kristensen et al. 2008), and the leached compounds may have negative effects on benthic fauna (Alongi 1987). The presence of these phytochemicals may also contribute to the avoidance of *Avicennia* as a food source (Bennett and Wallsgrrove 1994, Barbehenn and Constabel 2011). Consumers in lightly encroached sites where *Spartina* is abundant could still be exposed to secondary metabolites from *Avicennia* leaves even when only small numbers of trees are present.

Based on our results here and prior evidence of both trophic and physical avoidance of mangroves in encroached systems, food webs of encroached marshes are likely to experience trophic shifts, at least at the basal consumer level, as *Spartina* becomes less common. These trophic shifts, and the resulting decreased body condition of basal consumers indicated by this study, may have long term effects on basal consumer populations. For example, gastropod body condition is correlated with respiration and metabolism (Ter Maat et al. 2007) and is linked to the number of eggs produced during reproduction (Hughes and Roberts 1980, Zonneveld and Kooijman 1989). Crustacean hepatopancreas energy storage is related to increased molting frequency and growth (Cockcroft 1997) and increased reproductive activity (Pillay and Nair 1973). Decreases in body condition may affect populations of basal consumers over time, and when combined with the changing abundance and avoidance of *Avicennia* in other consumers, indicate the potential for mangrove encroachment to decrease prey availability and destabilize energy flow to higher trophic levels.

Conclusions

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In addition to having important implications for systems undergoing mangrove encroachment, our findings highlight some of the ecological consequences of tropicalization. While responses to tropicalization in a system are highly dependent on species' identities and interactions, two general conclusions can be drawn from the literature and the results reported here: **(1)** shifts in herbivore-plant interactions as a result of tropicalization are highly context dependent and differ depending on if the tropical migrant is a consumer or a producer and on the individual species' characteristics. The expansion of tropical herbivores into temperate ecosystems often leads to increased herbivory as the local plant community has few defenses against the novel herbivore (e.g. Walther 2010, Vergés et al. 2014, Zarco-Perello et al. 2020), while the expansion of tropical plants can lead to increased herbivory if local herbivores find the novel plants palatable (e.g., Walther 2010), or decreased herbivory if local herbivores avoid consuming the novel plants (e.g., this study, Cummings and Williamson 2008). **(2)** Generalist species can adapt to and persist in tropicalized systems more easily than specialists (Le Roux and McGeoch 2008, Lurgi et al. 2012), as demonstrated in this study when even low levels of mangrove cover had negative physiological consequences for the specialist *Littoraria*, whereas the generalist *Uca rapax* was only affected by high mangrove cover and was affected in a sex-specific manner.

Although the above patterns have been recognized in multiple systems, this work is one of the first to investigate the mechanisms explaining these responses. While previous studies have demonstrated shifting faunal assemblages and trophic pathways that are linked to mangrove encroachment, this work goes further, demonstrating an active avoidance and physiological consequences of *Avicennia* interaction for two key basal consumers. Our findings reinforce the importance of studying novel trophic interactions and other effects of ecosystem-level changes

(such as tropicalization) across multiple scales, from individual physiology to community shifts. Our work provides novel quantitative evidence that *Avicennia* is not equivalent to *Spartina* in terms of basal consumer trophic support and highlights the value of experimentally evaluating the novel trophic interactions that are resulting from tropicalization. Thus, this work contributes to growing literature on both mangrove encroachment and tropicalization and reinforces an evolving understanding of the mechanisms and extent of community shifts that might be expected from both phenomena.

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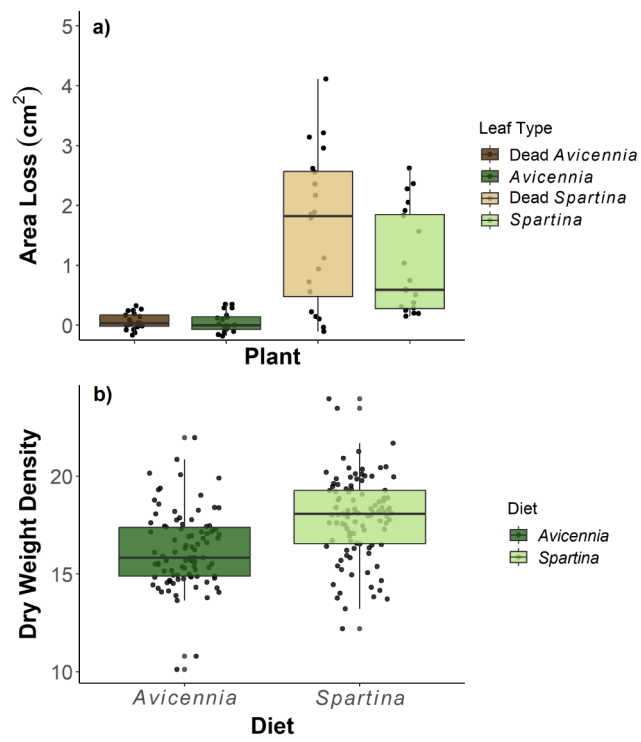
to *Lymnaea stagnalis* (L.). Functional Ecology 3:269.

FIGURE LEGENDS

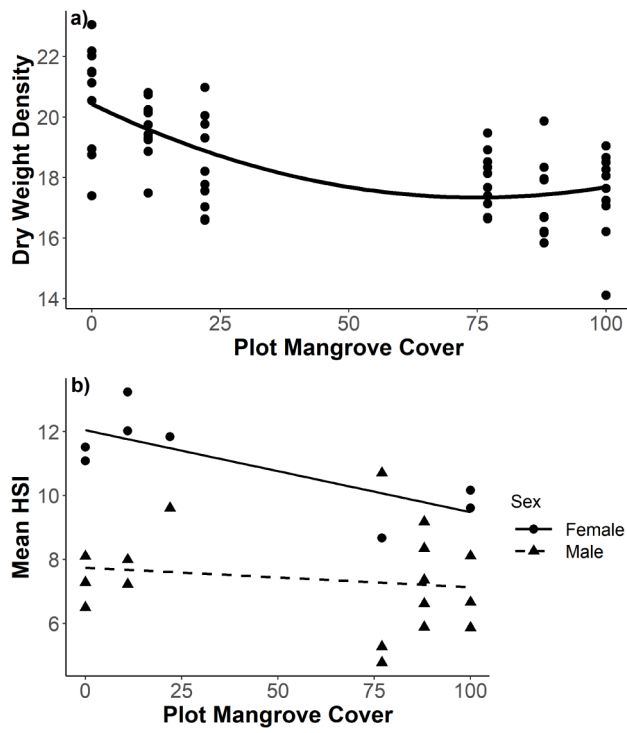
Figure 1: Maps of basal consumer collection sites. Map **a)** shows the locations of Port Aransas, where both *Littoraria* and *Uca* were collected for analyses of field body condition, and Galveston, where *Littoraria* were collected for lab feeding experiments, along the Texas coast in the Gulf of Mexico, USA. The inset map **b)** shows the locations of survey sites and the experimental plots in Port Aransas where basal consumers were collected.

Figure 2: *Littoraria* responses to *Avicennia* and *Spartina* in the lab showing **a)** area lost by leaf type in leaves exposed to *Littoraria* herbivory in the feeding preference study (only experimental replicates are shown; n = 20), **b)** body condition (dry-weight density) of *Littoraria* raised on *Spartina* or *Avicennia* diets after 60 days

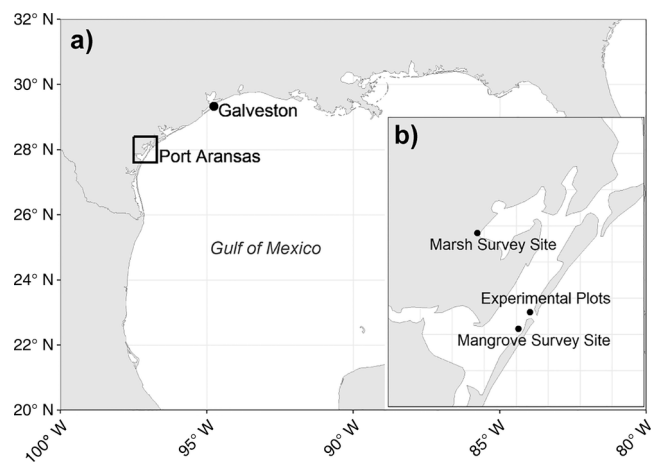
Figure 3: Body condition of herbivores collected from *Avicennia* or *Spartina* dominated field sites; **a)** body condition (dry-weight density) of *Littoraria* collected from sites with varying levels of mangrove cover and the quadratic regression calculated using the plot average dry-weight density values and **b)** body condition (hepatosomatic index) of male (triangles) and female (circles) *Uca rapax* collected from experimentally manipulated plots dominated by marsh or mangrove vegetation and the linear regression of mangrove cover on plot average hepatosomatic index for males (dashed line) and females (solid line).



ECY_4051_Goeke_Ecology_Figure 2.tif



ECY_4051_Goeke_Ecology_Figure 3.tif



ECY_4051_Goeke_Ecology_Figure_1.tif