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Effects of Changing Vegetation Composition on Community Structure, Ecosystem Functioning, and Predator–Prey Interactions at the Saltmarsh-Mangrove Ecotone

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Abstract: Decreasing frequency of freeze events due to climate change is enabling the poleward range expansion of mangroves. As these tropical trees expand poleward, they are replacing herbaceous saltmarsh vegetation. Mangroves and saltmarsh vegetation are ecosystem engineers that are typically viewed as having similar ecosystem functions. However, few studies have investigated whether predation regimes, community structure, and ecosystem functions are shifting at the saltmarsh-mangrove ecotone. In this study, we manipulated predator access to marsh and mangrove creekside habitats to test their role in mediating vegetation and invertebrate structure and stability in a two-year experiment. We also conducted a survey to evaluate how shifting vegetation is modifying structural complexity, invertebrate communities, and ecosystem functioning at the ecotone. Excluding larger (> 2 cm diameter) predators did not affect vegetation or invertebrate structure or stability in either saltmarsh or mangrove habitats. The survey revealed that the two habitat types consistently differ in structural metrics, including vegetation height, inter-stem distance, and density, yet they support similar invertebrate and algal communities, soil properties, and predation rates. We conclude that although mangrove range expansion immediately modifies habitat structural properties, it is not altering larger predator consumptive effects, community stability, community composition, or some other ecosystem functions and properties at the ecotone.

Keywords: *Spartina alterniflora*; *Avicennia germinans*; habitat complexity; predation; intertidal vegetation; climate change; ecotone

1. Introduction

Coastal ecosystems have long been recognized for their valuable ecosystem services and high productivity [1–5]. With climate change, there is a need to understand how increases in air and water temperatures, mean sea level, and extreme weather events will affect provisioning of these services and the functionality of these ecosystems by affecting the distribution of critical species. One globally relevant dimension of climate change effects in coastal systems is the poleward movement of tropical, habitat-forming foundation species into temperate ranges, such as the range expansion of mangroves

into saltmarshes [6–9]. Mangrove and saltmarsh vegetation encompass multiple species that are adapted to occupy the intertidal zone and their ranges overlap in regions of Australia, Asia, New Zealand, South Africa, and North and South America [10,11]. The intertidal distributions as well as latitudinal interfaces of saltmarsh and mangrove plants are mediated by multiple environmental factors such as species-specific differences in tolerance to winter low temperatures, inundation, salinity, and desiccation. Multiple climatic changes have affected historic distributions of both ecosystems, and warming winters have contributed to mangrove expansion into previously saltmarsh dominated regions [7,10–12]. Mangroves and saltmarshes are both recognized as habitats that generate valuable services, including carbon storage, storm protection, and essential habitat for fish and invertebrates [13–17]. With widespread mangrove encroachment into saltmarshes, it is important to quantify the differences in structure, function, and biodiversity of both systems relative to one another to determine which ecological characteristics are likely to be altered as a result of climate change.

Mangrove trees differ in structure from saltmarsh vegetation: while mangroves consist of woody trees with porous aerial roots, saltmarshes are structured by herbaceous perennial grasses. Southeastern US saltmarshes are primarily dominated by a *Spartina alterniflora* (smooth cordgrass), but also support a growing population of *Avicennia germinans* (black mangrove) at the forefront of the mangrove northern migration. Changes in vegetation structure, canopy shade, total vegetated area, and surface area created by the increase of mangrove vegetation influence intertidal habitat complexity [18]. Habitat complexity can influence native nekton communities by hindering larger predator access, decreasing sightlines to prey, and altering the number of interactions between predator and prey [19]. Changes to predator–prey dynamics may drive variation in community and habitat structure with many coastal systems influenced by top-down predation control. In New England saltmarshes, for instance, predators control *Melampus bidentutus* (common marsh snail) density and size distributions in *S. alterniflora* but not in *Spartina pumilus* (saltmeadow cordgrass), which has shorter inter-stem distances [20]. Factors such as decreased density of mangrove pneumatophores as well as blade thickness in seagrasses have similarly been associated with greater fish detection and higher shrimp predation rates [21,22]. Mangrove vegetation has also been found to be size-selective for feeding fish, with small-medium sized predators preferring to forage in mangroves and larger predators preferring to feed in open mudflats [23]. Since the predation regimes of larger bodied fish are more sensitive to changes in habitat structure they may be disproportionately affected by the expansion of mangroves. One native large predator that may be adversely affected is the highly abundant and popular sport fish, red drum (*Sciaenops ocellatus*), which have been known to heavily utilize *S. alterniflora* lined creeks [24].

Shifts in vegetation type can also mediate belowground habitat availability and suitability for infauna, such as burrowing crabs. Increased sediment stability caused by rooted sub-aquatic vegetation has been associated with increases in infaunal density and diversity, as well as decreasing predation from digging predators [25,26]. Root mat density also affects burrowing behavior of benthic crabs, with increased density relating to decreases in the number of crab burrows and burrow depth [27]. Alterations in soil stability resulting from differences in the root structure of *A. germinans* and *S. alterniflora* may have larger impacts to the ecosystem by affecting abundance of secondary, or dependent, habitat-forming foundation species, such as *Crassostrea virginica* (Eastern oyster), *Geukensia demissa* (ribbed mussel), and burrowing crabs, which increase habitat heterogeneity, and influence both soil drainage and oxidative stress [28–30].

Apart from the influence of vegetation on predation and habitat use, living and dead plant material also serve as a food source for many organisms [31,32]. Replacement of *S. alterniflora*, with the slower decomposing *A. germinans* vegetation may decrease nutrient availability in the system, with previous studies finding that *S. alterniflora* derived litter support ecosystems at higher trophic levels than *A. germinans* derived matter [15,33,34]. However, both *S. alterniflora*-associated (ribbed mussels, marsh mud snails, and mummichogs) and mangrove-associated fauna (sesarmid crabs and some gastropod species) have mixed diets of detrital vegetation and benthic microalgae [35–38]. This suggests that primary productivity of benthic microalgae in both habitats may be important in

determining the abundance and diversity of lower trophic level prey species that can be supported by these systems [35–38].

Relatively little is known about how gradual replacement of *S. alterniflora* with *A. germinans* affects habitat quality, structure, and predation. Hence, here we aimed to quantify some of these ecosystem functions and effects at the ecotone of mangrove expansion front in the Western Atlantic. We conducted a two-year field experiment on the northeastern coast of Florida, USA to determine the role of large predators on multiple ecosystem functions, such as vegetation and invertebrate community structure, algae productivity, and soil properties in both mangrove and saltmarsh vegetation. In this experiment we tested the role of predation both in saltmarsh and mangrove creeks by seasonally monitoring vegetation structure, primary productivity, and invertebrate densities in predation exclusion cages and unmanipulated controls. We also calculated the temporal stability of plant and invertebrate response metrics to evaluate whether one habitat exhibits higher fluctuations in key ecosystem metrics relative to the other. Finally, we surveyed vegetation structure, invertebrate community, and soil composition at an array of sites dominated either by mangroves or saltmarshes across the ecotone to evaluate the consistency with which mangroves are shifting habitat characteristics, soil characteristics, and community structure. The goal of this study is to fill the gap in knowledge concerning what changes in foundation species mean for physical habitat structure, predator–prey dynamics, and community structure, as well as whether these changes can be observed early in the shift in vegetation at the ecotone. Understanding how shifts in the global distribution of mangroves and saltmarsh alters the physical habitat, especially in systems as ecologically valuable as coastal wetlands, will be important when planning policy and strategies for managing the response of coastal ecosystems climate.

2. Materials and Methods

Field data were collected at Guana Tolomato Matanzas National Estuarine Research Reserve (GTMNERR) in St. Augustine, FL. GTMNERR was selected because of its location at the northern range edge of the expansion of mangroves into saltmarsh on the Atlantic Coast of the US. The northern section of GTMNERR is dominated by saltmarsh plant species (*S. alterniflora, Juncus roemerianus, Sarcocornia* spp., and *Batis maritima*) and the southern section is dominated by mangroves (prominently *A. germinans*, with scattered *Rhizophora mangle* and *Laguncularia racemosa*) [39]. With the poleward movement of the freeze-line, GTMNERR has experienced an increase in mangrove stands resulting in an 81% decrease in saltmarsh cover between 2008 and 2013 [7,40]. Current climatic conditions of GTMNEER include an average annual temperature of 22 °C (winter 16 °C, spring 21 °C, summer 27 °C, and fall 24 °C), cumulative average annual precipitation of 432 mm (winter 77 mm, spring 71 mm, summer 158 mm, and fall 126 mm), and an average annual tidal amplitude of 1.3 m.

Within GTMNERR, 10 sampling sites were located on tidal creeks of the Matanzas Inlet and categorized as either mangrove or saltmarsh (five each) depending on its dominant vegetation type (i.e., >75% or coverage of creeks edge). One representative site of each vegetation type was used in the predation exclusion experiment, and all ten sites were included in the ecotone survey. Maximum tidal heights were measured at the creeks edge at all sites using poles painted with water soluble paint, and inundation times were measured using water resistant temperature sensors (Temtop, TemLog 20) to detect a temperature difference between water presence and absence. Tidal measurements were carried out on 1–4 March 2019, all dates with an intermediate tidal range. For the two experimental sites the maximum tidal height of the mangrove site was approximately 69 cm, and the tidal height of the saltmarsh site was 78 cm; average inundation time at both sites was ~6 h/day. For the ten survey sites the average maximum tidal heights of the mangrove sites was 66 cm (max: 75 cm, min: 52, and standard error of the mean—SEM: 1.9), saltmarsh sites had an average maximum tidal height of 59 cm (max: 85 cm, min: 50 cm, and SEM: 2.7). Average inundation time of the five mangrove survey sites were 6 h a day (max: 7, min: 5, and SEM: 0.33), saltmarsh survey sites had an average inundation time of 7 h a day (max: 9, min: 6, and SEM 0.57). We took 30 measurements of % canopy shade (ground

surface photosynthetically active radiation (PAR) / above canopy PAR) using a PAR meter (Solar Light PAM 1000) at the creeks edge in both vegetation types.

2.1. Predation Exclusion Experiment

To evaluate the effect of large nektonic predator on plant, benthic algae, and invertebrates in mangrove and saltmarsh habitats, we established ten 1 m × 1 m × 1 m plots at the creek edge of one mangrove (29°40'33.1" N, 81°13'03.9" W) and one saltmarsh site (29°45'47.3" N, 81°15'45.5" W) about located 10.5 km apart from each other (Figure 1). Plots were haphazardly assigned one of two treatments: predator exclusion or control (*n* = 5, per treatment). Exclusion cages consisted of a wooden frame enclosed by 2-cm-diameter green plastic mesh (Tenax Green HDPE Extruded Mesh Rolled Fencing) and were secured to the surface with lawn staples. Cage tops were covered with a 1-cm diameter mesh netting to prevent birds from accessing the plots. Control plots were marked with wooden posts. Cages of the same size were used in previous studies to evaluate the effects of predatory nekton in saltmarshes [41].
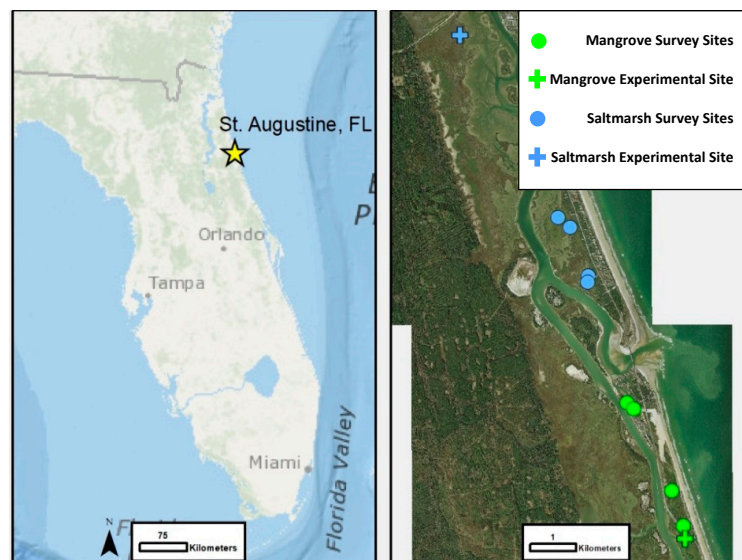

Figure 1. Map of Florida (left) and the St. Augustine, FL study region (right) with experimental and survey sites. The yellow star marks mangrove-saltmarsh ecotone in St. Augustine, FL. A green cross denotes the mangrove experimental site; green circles denote the mangrove survey sites; a blue cross identifies the saltmarsh experimental site; and blue circles identify the saltmarsh survey sites. Both basemaps provided by State of Florida.

Individuals of a representative subset of the invertebrate community, *Crassostrea virginica* (eastern oyster), *Geukensia demissa* (ribbed mussels), *Littoraria irrorata* (periwinkle snails), and *Aratus pisonii* (mangrove tree crabs) were counted across each plot. Burrowing mud crabs (*Panopeus* spp., and *Eurythium limosum*), marsh crabs (*Sesarma* spp.), and fiddler crabs (*Uca* spp.) were also surveyed by burrow counts within two 25 cm^2 quadrats located inside each plot. The diameter of each burrow within the 25 cm^2 quadrats were also measured.

To then explore whether plant structure and invertebrate communities exhibited similar levels of stability in each ecotype, we calculated the population stability (S_t) of each functional group using the following equation:

$$S_t = \mu_t \frac{\mu_t}{\sigma_t},$$

(1)

where mean count per m^2 (μ_t) of each functional group was calculated in each individual plot across the six sampling dates and their standard deviations (σ_t) of the count were calculated across the six sampling dates [42,43].

We also examined whole community stability using the same equation, however in this iteration, μ_t was calculated as the sum of the mean count of each functional group across the six sampling dates, and σ_t was calculated by the square root of the summed standard deviation of individual functional group counts measures plus the summed covariance of the count of every possible pair functional groups' count over the sampling dates [42,44].

The biomass of the major algal functional groups (cyanobacteria, green algae, and diatoms) at the sediment surface was quantified on each sampling date using a portable handheld field fluorometer (BenthoTorch, BBe Moldaenke, Germany). For each sampling time point, four readings were averaged (one in each quarter of the plot). The height of the vegetation was recorded by measuring 15 randomly selected *S. alterniflora* tillers or 15 *A. germinans* pneumatophores per plot and vegetation density was determined by tallying *S. alterniflora* tiller stems, or *A. germinans* pneumatophores in each plot. The cages were installed by early August 2017, and the plots were surveyed every 3 to 4 months until April 2019.

2.2. Ecotone Survey

To quantify the effect of changing coastal vegetation on habitat structure and ecosystem processes we surveyed vegetation structure, soil properties, invertebrate communities, and predation at five different sites of each vegetation type across the ecotone within GTMNERR.

Vegetation structural attributes such as stem densities, inter-stem distance, height, sightlines, and flexure were surveyed, provided that they affect use of the habitat by nektonic species. To quantify sightlines through both mangrove and saltmarsh vegetation, we used a 5 cm × 7.6 cm orange marking flag held under the height of the vegetation ~5 cm above the sediment, at creeks edge and slowly walked inland until the flag was no longer visible in the creek bed. Sightlines were recorded by the horizontal distance between the flag and the viewer at five different locations at each site, spaced at least 4 m apart. Further, vegetation height may impede nekton movement in vegetated areas if the tidal height is less than the average vegetation height. Therefore, 60 *A. germinans* pneumatophores or *S. alterniflora* tillers were haphazardly chosen to be measured within one meter of the creeks edge at each site. In addition, vegetation density and inter-stem space both influence the size of nekton able to enter vegetated areas [20]. Therefore, pneumatophores and tillers densities were measured in 20, 0.25 m^2 quadrats per site. Inter-stem space was determined by measuring the distance between 120 pneumatophores or *S. alterniflora* tillers and their closest neighbor at each site. Flexure, the resistance of stems to bending, can also create a barrier for nekton entering the vegetated area with more flexibly vegetation allowing for easier maneuverability. The flexure of 10 *A. germinans* pneumatophores and 10 *S. alterniflora* tillers at three different sites was calculated by measuring the force needed to bend stems 45 degrees using a spring scale (Pesola Light Line Spring Scale).

Changes in root structure associated with the shift from saltmarsh to mangrove vegetation can affect soil properties, and in turn, affect habitat use by both benthic and infaunal species. Bulk density, an indicator of soil permeability also important for infaunal communities, was calculated by dividing the weight of the dried soil sample by its known volume. Cylindrical soil cores (10 cm diameter, and 10 cm depth) were collected at each of the survey sites. Soil moisture was calculated as percent water loss from a ~40 g sample after drying at 65 °C for 3 days. Organic content of soil was measured as the percent weight change of ~2 g dried soil samples after burning of in a muffle furnace (500 °C, for 4 h).

The standing biomass of benthic algae (green algae, cyanobacteria, and diatoms) was measured using a BenthoTorch (16 measurements per site). Burrowing mud crab and fiddler crab densities were measured by burrow counts in 20, 0.25 m^2 quadrat at each site. Two hundred burrow diameters were also measured at each site. Abundance of *Geukensia demissa* (ribbed mussels) *Crassostrea virginica* (eastern oyster), *Littorina littorea* (periwinkle snails), and *Aratus pisonii* (mangrove tree crabs) was measured with 10, 1 m^2 quadrats at each site.

To evaluate potential variation in predation intensity across the ecotone and sites within habitat types, we measured relative predation rates using 'squidpops', which are 60-cm-long light green

fiberglass plant stakes with a 1.3-cm diameter disk of dried squid mantle tethered directly to the top with 4 lb test fishing line [45]. Dried squid was used as bait because of its marine origin, its resistance to degradation (rarely dislodged by processes other than predation), and palatability to a wide range of fishes and invertebrate predators [45]. Ten squidpops were deployed at each site, with pops being placed in the vegetation within 1 m of the creek edge, about 5 m apart from each other, and at a height of ~30 cm to prevent consumption from burrowing crabs. Squidpops were checked after 24 h and were recorded as present or absent (>50% of bait disc missing).

2.3. Data Analysis

All statistical analyses were conducted with Matlab v.2018b. We analyzed the effects of the predation exclusion treatment and time on vegetation structure, benthic algal biomass, and invertebrate densities with repeated measures ANOVA (analysis of variance). Effects of treatment and habitat on population and community stability metrics were analyzed using a one-way ANOVA. We analyzed the effect of habitat type and site on vegetation structure, benthic algal biomass, and invertebrate densities with a mixed effect ANOVA, with site as a random effect and habitat as a fixed effect.

3. Results

3.1. Predation Exclusion Experiment

Overall, we found that the exclusion of large predators had little effect on vegetation height and density ($p < 0.001$, Figure 2A,B). In addition, *S. alterniflora* tiller density and height varied temporally, peaking in summer and fall respectively, whereas *A. germinans* pneumatophore density and height were stable over the two-year-long experiment (Figure 2C,D).
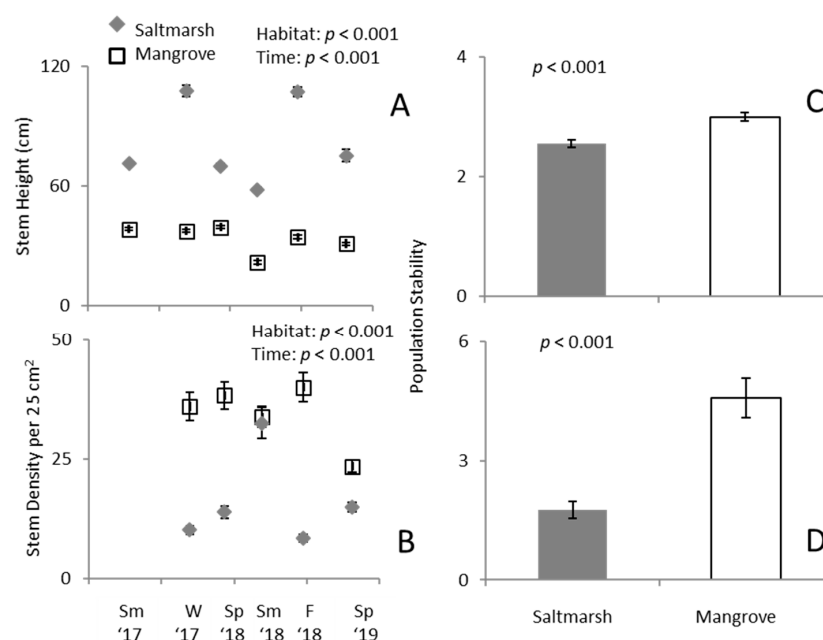

Figure 2. (**A**) Vegetation height, (**B**) density, and stability of (**C**) vegetation height and (**D**) density in saltmarsh (dark grey symbols and bars) and mangrove (white symbols and bars) habitats over the two-year predator exclusion experiment. Significant results are reported in the inset panels. Since experimental treatment was not significant for any metric, data from control and predator exclusion plots were pooled. Data are shown as the mean ± SEM for 10 plots per habitat type.

Benthic microalgal biomass was also not affected by the exclusion of larger predators in either habitat type. Both cyanobacteria and diatom biomass were higher in warmer relative to colder months (Time $p < 0.001$, Figure 3). Green algae were virtually undetectable at most of our sampling dates. All

benthic algae types exhibited similar stability in each habitat type and across experimental treatments ($p > 0.05$).
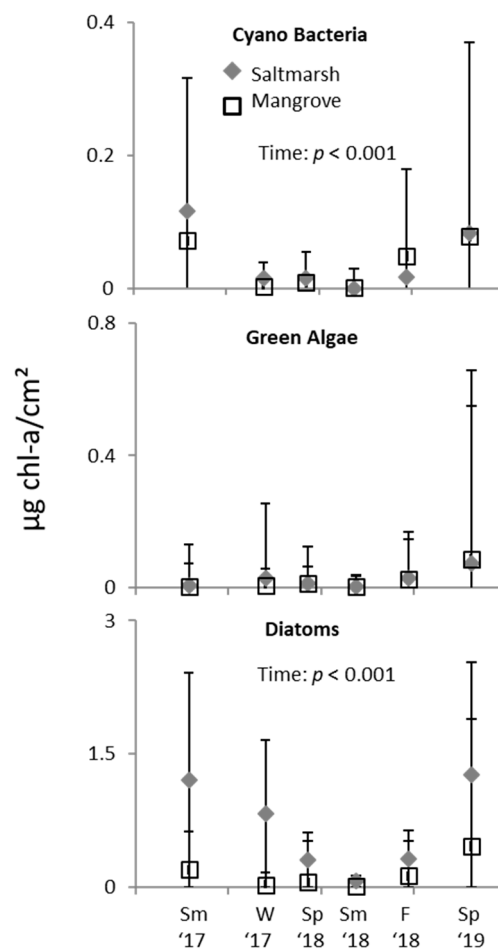

Figure 3. Benthic algae biomass in saltmarsh and mangrove habitat observed over the two-year predator exclusion experiment. Significant results are displayed in the inset panel. Since there was no treatment effect, data from control and predator exclusion plots were combined. Data are shown as the mean ± SEM for 10 replicate plots per habitat type.

Within the experimental plots, invertebrate densities varied significantly between the two habitats but, within habitats, large predator exclusion had little effect. Crab burrow densities and mussel densities were higher at the saltmarsh than the mangrove site, while densities of arboreal mangrove tree crabs and oysters were higher at the mangrove site (Figure 4). Snail densities were generally higher in the saltmarsh site, but only differed significantly between habitat types on a single monitoring date. Moreover, while densities of mobile invertebrate species, including periwinkle snails, mangrove tree crabs, and crabs, were higher in warmer than cooler sampling dates, the densities of sessile organisms, such as mussels and oysters, remained stable year-round (Figure 4). The temporal stability of most invertebrate functional groups, including mangrove tree crabs, burrowing crabs (quantified as burrow densities), oysters, and mussels, did not differ by treatment or with habitat type. Periwinkle snail stability, however, was significantly higher in the *S. alterniflora* predator exclusions, than *S. alterniflora* control and both *A. germinans* treatments. However, the low density of snails (per m^2: mean: 1, max: 9, and min: 0) recorded across all dates and plots resulted in very low stability of the snail population overall. The low density of snails compared to densities shown to mediate primary productivity in higher latitude saltmarshes in the eastern US, indicate that the treatment effect on snail stability is

not likely ecologically significant [46]. Community stability was not significantly different between predator exclusion treatments ($p = 0.7$), or between habitat types ($p = 0.9$).
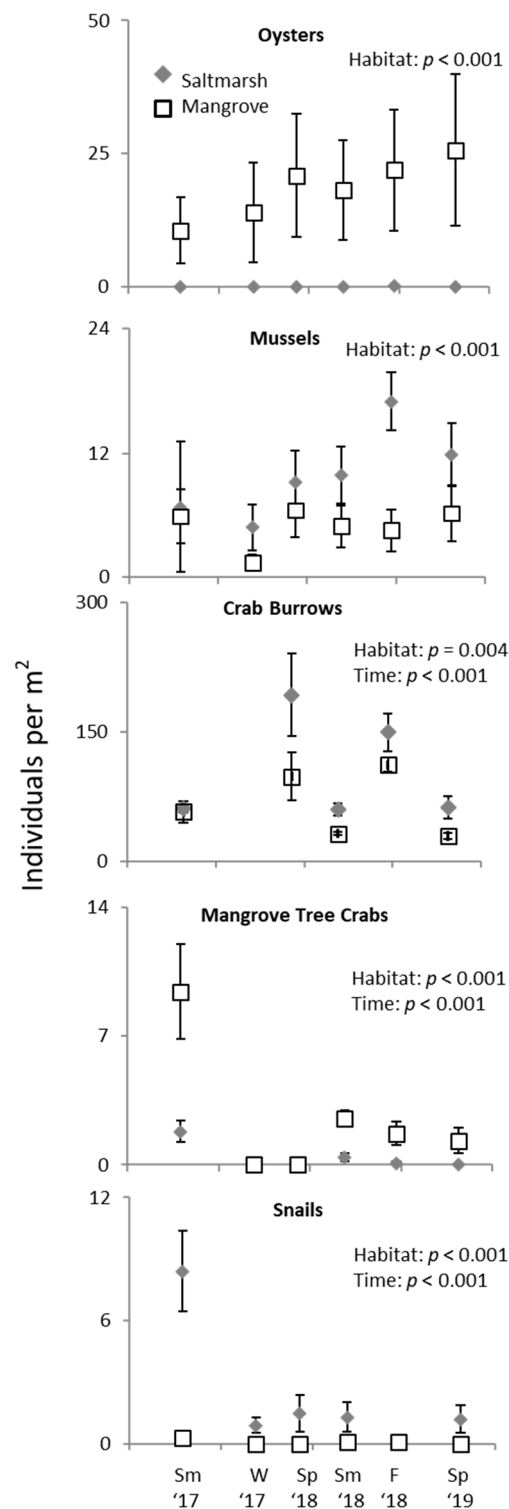

Figure 4. Invertebrate densities over time during the two-year predator exclusion experiment. Significant results are displayed in the inset panels. Since there was no treatment effect, data from control and predator exclusion plots were combined. Data are shown as the mean ± SEM for 10 replicate plots per habitat type.

3.2. Ecotone Survey

Mangrove and saltmarsh vegetation structure was significantly different with respect to height ($p < 0.001$), stem density ($p = 0.001$), inter-stem distance ($p = 0.003$), and sightlines ($p = 0.008$), with *S. alterniflora* tillers being taller and having longer distance of visible sightlines than *A. germinans* pneumatophores (Table 1). Yet, pneumatophores were denser, and exhibited shorter inter-stem distances than *S. alterniflora* tillers (Table 1). Conversely, *S. alterniflora* and *A. germinans* had similar flexure ($p = 0.19$). There was no effect of site on any of the structural attributes in either habitat ($p > 0.05$ for all).

Table 1. Summary of structural attributes of *S. alterniflora* and *A. germinans* sites.

Habitat	S. alterniflora			A. germinans			df	f	p
	Mean	Max	Min	Mean	Max	Min			
Height (cm)	79.00	86.5	73.66	25.96	31.56	73.66	1	412.39	<0.001
Stem Density (per 0.25 m^2)	14.60	17.15	11.30	27.86	34.40	11.30	1	75.68	0.001
Inter-stem Distance (cm)	8.20	9.29	7.54	4.778	5.86	7.54	1	42.97	0.003
Sightlines (cm)	284.69	374.4	223.11	260.36	330.71	223.11	1	23.89	0.008
Flexure (N)	1.65	2.09	1.42	1.10	1.22	0.88	1	3.70	0.19

Data are shown as the mean for five replicate sites.

Diatoms were the only group of microalgae that differed between the two vegetation types, showing higher biomass in saltmarsh than mangrove sites ($p = 0.04$). However, their low biomass in both habitats suggests that these differences were not ecologically significant. Indeed, the biomass observed in the saltmarsh habitat (2.5 μg chl-a/cm^2), was far below the average biomass observed in temperate marshes (6–16 μg chl-a/cm^2) [47] (Figure 5).
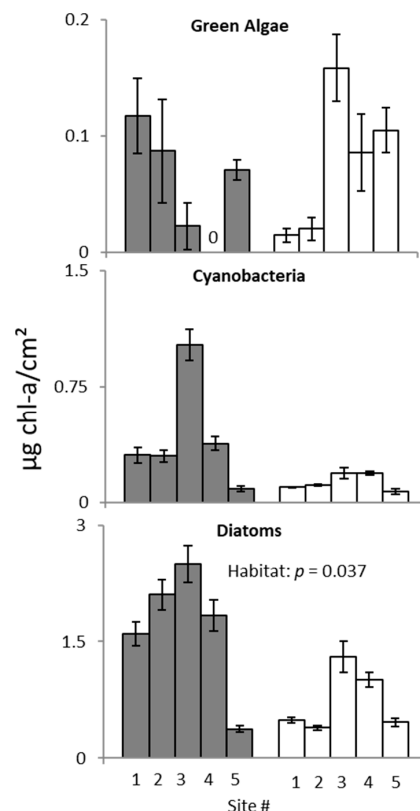

Figure 5. Benthic algal biomass across saltmarsh (dark grey) and mangrove (white) sites along the ecotone. Significant results are displayed in the inset panel. Data are shown as the mean ± SEM for five replicate sites.

In our survey of multiple sites across the saltmarsh-mangrove ecotone, snails were the only invertebrate to differ in density between vegetation types ($p = 0.02$; Figure 6). As in the predator exclusion experiment snail densities at all sites were very low and likely ecologically insignificant (per m^2: mean: < 1, max: 8, and min: 0) [46,48].
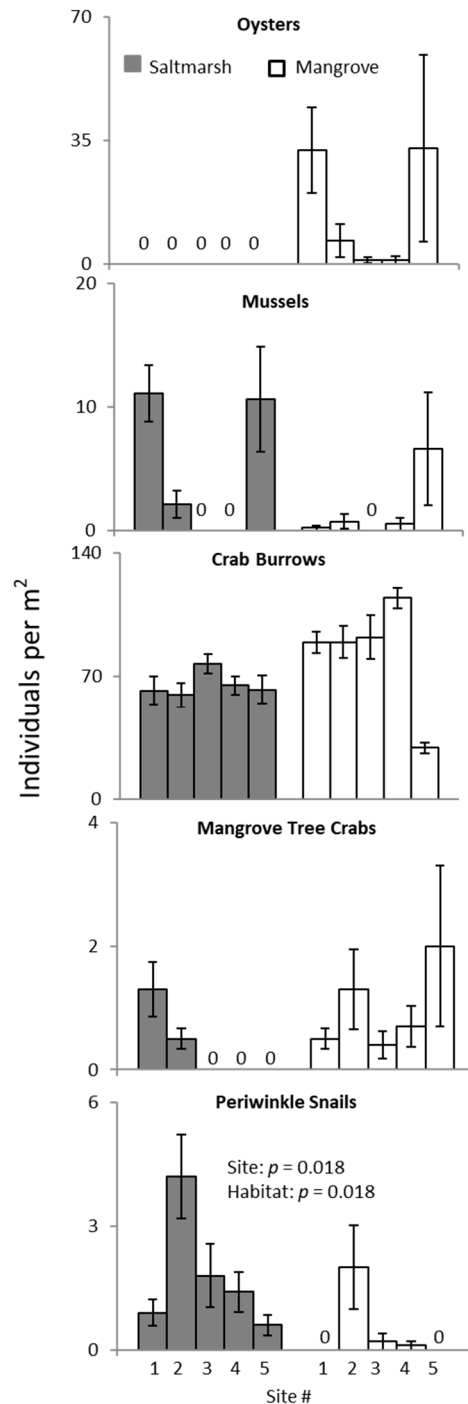

Figure 6. Invertebrate densities across saltmarsh (dark grey) and mangrove (white) sites along the ecotone. Significant results are displayed in the inset panel. Data are shown as the mean ± SEM for five replicate survey plots per site.

Soil organic matter was higher at saltmarsh, than mangrove sites (p = 0.048; Figure 7). However, there was no significant difference in moisture (p = 0.1) or bulk density (p = 0.19) between habitat types at the ecotone (Figure 7).
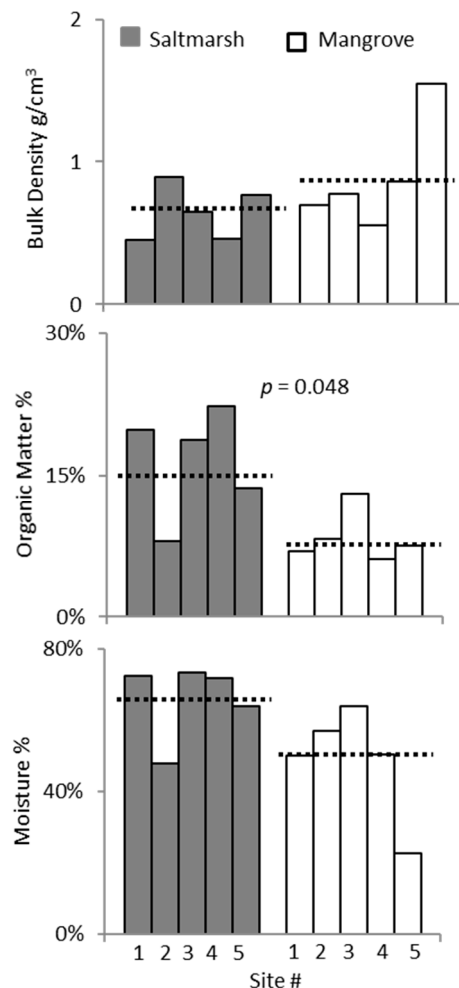

Figure 7. Survey of soil properties across saltmarsh (dark grey) and mangrove (white) sites along the ecotone. Each bar represents an individual site in each habitat, with site 5 representing the experimental site. Dashed lines represent average of all sites. Significant results are displayed in the inset panel. Data are shown as the mean ± SEM for five replicate sites.

Squidpops further indicated that predation rates do not differ between habitat type (p = 0.2), or between survey sites (p = 0.7). Predation across the ecotone was moderate to relatively low with all sites having less than 50% of the squidpops eaten. However low predation rates could be a result of squidpop position 30 cm above the sediment surface and 24-h deployment resulting in limited inundation time and nekton access.

4. Discussion

Our experimental results suggest that large nektonic predators did not play a significant role in influencing primary productivity, invertebrate densities, and their stability at the mangrove-saltmarsh ecotone in northeast Florida. Our survey of both habitats at the ecotone revealed that there were significant differences in habitat structure between the two vegetation types, but emergent ecosystem attributes of these habitats including soil properties, predation rates, and invertebrate and algal structure remain largely the same after expansion of mangroves into previously marsh-dominated

habitat. These findings were contrary to prior studies, which have shown predation to be important in structuring plant and invertebrate communities further north in temperate saltmarshes, such as the top-down control of *S. alterniflora* productivity through predator mediation of periwinkle snails and *Sesarma* crabs in southeastern and northeastern Atlantic saltmarshes, respectively [41,49,50]. Similarly, our survey of invertebrate abundance and algal biomass also produced contradictory results to previous studies with markedly lower abundances in some functional groups at our ecotone sites compared to homogeneous saltmarshes [46,47]. This may indicate that although ecosystem attributes were similar among habitat types at the ecotone, this system may have already experienced shifts in ecosystem functions at a landscape scale since mangrove intrusion.

One possible explanation for the difference in the role of larger predators in mediating plant and invertebrate assemblages at the ecotone compared to saltmarshes at higher latitudes is a difference in the abundance or diversity of fish. A 2008–2018 census of inshore marine recreational fishing in Georgia and the east coast of Florida suggests that the lack of top-down predation control at the ecotone is not due to decreased density of larger fish, as Eastern Florida produces an average of 41 fish per 100 surveyed angler trips (per unit effort; PUE), compared to an average of 12 fish PUE in Georgia [51]. The same survey also showed that many of the most abundant fish species were similar both in Georgia and the east coast of Florida, including drum (*Sciaenidae*; GA: 24 PUE; and FL: 51 PUE), Mullet (*Mugilidae*; GA: 6 PUE; and FL: 35 PUE), and Porgy (*Sparidae*; GA: 7 PUE, and FL: 22 PUE) all of which are opportunistic benthic feeders [51]. However, the larger trends observed at the statewide level may differ from the ecotone where there is high habitat connectivity between saltmarsh and mangroves. With increased habitat connectivity being correlated with higher fish abundances, biomass, and decreased species evenness, it is possible that, at the smaller scale of the ecotone, different fish compositions and densities are observed relative to that which is reported in the state level database [52]. This may result in differences in the use of intertidal habitats, yet, to our knowledge, fish landings have not been recorded at the local levels needed to test the hypothesis that the heterogeneity of the ecotone results in lower fish abundance.

It is also logical to assume that differences in the density of grazing invertebrates between temperate saltmarshes and the ecotone may also affect utilization of the intertidal zone by large predators. For example, densities of the *S. alterniflora*-grazing periwinkle snails range from 200–800 individuals per m^2 in their more northern range (VA, NC, SC, GA, and LA), which largely exceeds the low densities observed in saltmarsh habitats both in our survey and experimental plots (0–9 individuals per m^2; Figures 4 and 6) [46]. Similarly, the densities of fiddler crabs, an algal grazer, were also far lower at our sites than in higher latitude saltmarshes. Indeed, McCraith et al. (2003) estimated densities of 308 fiddler crab burrows per m^2 in creek banks of a South Carolina *S. alterniflora* marsh, while our survey found an average fiddler crab burrow density (burrows with diameters < 15 mm) density of 108 burrows per m^2 in our *S. alterniflora* sites, and 55 burrows per m^2 in our *A. germinans* sites [53]. Our experimental findings also suggest that numbers of periwinkle snails and fiddler crabs at the ecotone are found at low densities even when released from predation pressure, suggesting that they may not be a major food source for large nektonic predators. It is possible that cage size may have dampened the observable effect of predation on mobile prey such as benthic crabs and periwinkle snails. However, our design was consistent with cage sizes used in a previous study [41].

Another potential explanatory factor for the lack of evidence for top-down predation control in our experiment is that smaller predators, such as benthic crabs or small fish not excluded by our caging treatment, are more important than the larger predators in structuring both ecosystems at the ecotone. Several nektonic species have been observed to occupy coastal vegetation as soon as water level is high enough for them to swim through and leave the vegetation once water reaches that same level during ebb tides [54]. This allows for smaller nekton to occupy the inundated vegetation longer than larger bodied predators. Therefore, they may have a larger influence on coastal structure than larger predators, which may explain the similarly low levels of snail invertebrates and algal biomass in our caging experiments. Vince et al. (1976) found that predation by *Fundulus heteroclitus* (mummichogs), a

small fish 35–95 mm in length, controlled size distributions of *Melampus bidentatus* (common marsh snail), and *Orchestia grillus* (saltmarsh flea) in a Massachusetts tidal saltmarsh [20]. Relatively small benthic crabs such as mud crabs (*Xanthidae*) have also been shown to prey on young oysters [55,56]. Johnson and Smee (2014) found that mortality of juvenile oysters significantly increased when the mesh diameter of predator exclusion cages was increased from 1 cm^2 to 5 cm^2, exposing the oysters to intermediate-sized predators such as Xanthid mud crabs [57]. Smaller predators native to the ecotone such juvenile blue crabs, killifish, and mud crabs are also less likely to be affected by the structural differences observed in our vegetation survey (see Table 1), which were observed to influence predation by larger predators in previous studies [19,20].

The hypothesis that smaller predators are playing a dominant role at the ecotone is supported by our squidpop predation survey, which showed that differences in structural attributes had no effect on squidpop predation between habitats. Supporting this claim, our experimental results also indicate that larger predators were not influential at the ecotone. Densities of potential invertebrate prey—oysters, mussels, and crabs (censused as burrow counts)—for larger predators were not affected by predator exclusion in either experimental site, or habitat type in the invertebrate survey (Figure 4). However, it should be noted that although inundation times were not drastically different between the two vegetation types, ~6 h of inundation at the mangrove survey sites, and ~7 h in the saltmarsh survey sites, previous studies from the Australian ecotone have shown inundation time to be an important factor influencing population densities of some gastropod species [58].

Conversely, temporal trends in invertebrate densities did differ between the two habitat sites over the two-year experiment, which may be related to differences in vegetation stability. Community and population stability metrics are typically used to quantify how community and species populations vary temporally, and are indicators of susceptibility to species extinctions, reliability of ecosystem processes, and ability to predict change in a system [59]. Population stability metrics of vegetation height and density revealed lower stability of both parameters in saltmarsh plots over the two-year-long experiment in response to the higher seasonality of *S. alterniflora*. Higher variability in habitat structure may result in associated fluctuations in invertebrates such as correlated increases in primary productivity and population densities. This could potentially explain the trends of higher seasonality of crab burrowing and periwinkle densities in the saltmarsh habitat observed in our experiment. However, it is worth noting that densities of all mobile invertebrates (crab burrows, mangrove tree crabs, and periwinkle snails) varied over time in both vegetation types.

Stability of all invertebrate groups was similar across both habitats in the ecotone survey. Likewise, stability of invertebrate groups was similar in both treatments in the predator exclusion experiment. This suggests that none of the invertebrates measured would be at greater risk of extinction in either vegetation at the ecotone, nor by the absence of large predators. Community stability of all invertebrate groups was also not influenced by habitat type. Theory suggests that greater species richness creates communities that are more stable due to increased species interactions [60,61]. Although we did not measure species richness in this study, species migration in conjunction with mangrove vegetation may increase the overall species richness at the ecotone. One such example of species migration that we observed was the presence of mangrove tree crabs, which have historically been associated with mangrove trees, but were regularly observed within saltmarsh habitat at the ecotone (Figure 6) [62]. The patchy distribution of mangrove and saltmarsh vegetation are certainly increasing habitat heterogeneity which may in turn enhance species richness and invertebrate population stabilities at landscape-scales [42,63,64].

Benthic algal biomass, a potential food source for many of invertebrates, was very low across the ecotone (Figures 3 and 5). This diverges from previous hypotheses that shading from mangrove canopy cover negatively affects photosynthetic benthic algae production [65]. However, in a survey of 30 different plots of each habitat in the ecotone, we found that the shading effect of mangroves was only 10%, compared to 24% in the saltmarsh. Since our plots were on the creek's edge many mangrove

plots only contained pneumatophores with most tree trunks and canopies being set back further inland and hence the relative influence of canopy shade was likely limited.

We also found similar soil moisture as well as bulk density across the ecotone (Figure 7). Soil moisture and density affect oxygen availability for benthic algae. Such similar soil properties also support our findings of similar algae biomass across the ecotone. Henry and Twilley (2013) found similar results in their longitudinal study (1959 to 2009) of soil properties within a Louisiana saltmarsh transitioning to mangrove, with vegetation shifts having no effect on bulk density [66]. However, unlike Henry and Twilley (2013) we found a significant difference in soil organic matter with higher organic matter occurring at the *S. alterniflora* sites (Figure 7) [66]. While their study measured organic matter in soil in 2009 and cited mangrove invasion as occurring in 1995, we collected our samples in 2019 with mangroves increasing in abundance since their dieback in 1989 [67]. The sixteen-year difference in invasion histories between studies may indicate that soil organic matter changes more slowly over time with the legacy effect of *S. alterniflora* remaining in earlier in invasions. This would be consistent with findings of higher root density of *S. alterniflora* than mangroves at their ecotone in China [27].

5. Conclusions

Overall, this study indicated that the northern expansion of mangrove trees was changing the stability and physical structure of intertidal coastal vegetation but was not immediately changing the predation pressure exerted by large predators, as well as microalgal biomass, invertebrate densities, and community and population stability at the ecotone. The close proximity between mangrove and saltmarsh habitats that were the focus of this work suggest that they were highly connected, and thus likely to exhibit similar biotic diversity and abundance, dynamics that might differ from saltmarsh and mangrove habitats occurring within their established ranges. Previous studies have found overlapping foundation species increase species richness at the patch scale [28]. With the heterogeneous landscape created by the overlapping mangrove and saltmarsh vegetation and their associated secondary foundation species, oysters and mussels, it is likely that the ecotone supports a different assemblage of species than homogeneous mangrove or saltmarsh habitats. This may result in ecosystem level changes occurring at first introduction of mangroves and the creation of a heterogeneous habitat, and then changing again with the transition to a homogenous mangrove environment. The creation of a habitat with high connectivity of multiple ecologically valuable foundation species at the ecotone might also result in a more stable habitat. Yet, its transitional nature means that these systems may undergo multiple ecosystem changes, potentially in a short timespan with increasing climate change allowing for quicker mangrove migration. Continuing to examine the effects of mangrove encroachment on ecosystem process, as well as ecological differences over time ahead and behind the mangrove migration front, is vital for developing a holistic understanding of how ecotones differ in ecological functioning as climatic changes are forcing species migrations on a global scale.

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