



What Is the Role of Ecosystem Engineers in New England Salt Marshes? A Mesocosm Study of the Fiddler Crab and the Purple Marsh Crab

Alexandria Moore¹ 

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Abstract

The services and functions provided by coastal wetlands are numerous and influenced by factors ranging from climate and tidal regime to ecosystem engineers and anthropogenic modifications. In New England salt marshes, fiddler crabs and purple marsh crabs are cooccurring species that are among the most conspicuous burrowing macroinvertebrates in the region. Both are known to influence salt marsh ecosystem functions through their burrowing and feeding behavior, but the ways in which they regulate specific properties, individually and together, is unclear. Using an ex situ mesocosm study, I manipulated the presence of fiddler crabs and purple marsh crabs in order to evaluate their impact on several soil properties and aboveground biomass. Results show that, contrary to previous studies, the fiddler crab had little impact while the purple marsh crab altered soil quality with positive implications for plant growth. This suggests that the purple marsh crab, known to be a voracious consumer of marsh vegetation, may play a much more nuanced role in the maintenance of plant growth than previously thought. Additional ex situ studies should be done to further delineate the impact of these two species.

Keywords Fiddler crab · Purple marsh crab · Mesocosm · Ecosystem functions · Salt marsh

Introduction

Ecosystem engineers are species that, through the modification of their physical environment, influence habitat heterogeneity and maintain high levels of species richness at the landscape level (Jones et al. 1994, 1997). Across much of the northern temperate and boreal regions of North America, dam-building beavers are among the most conspicuous examples of ecosystem engineers (Naiman et al. 1988; Wright et al. 2002). The nutrient-rich sediments trapped by dams, together with the direct and indirect removal of vegetation by beavers, transforms these ecosystems from woody riparian zones to

extensive meadows that can persist for decades (Ives 1942; Terwilliger and Pastor 1999; Wright et al. 2002). This shift in ecosystem type, with associated changes in nutrient availability, promotes a diverse assemblage of plants not observed in adjacent woody riparian patches (Wright et al. 2002).

Coastal wetlands provide numerous ecosystem functions and services that are influenced by myriad factors, including climate (Erwin 2009), tidal regime (Townsend et al. 2011), trophic interactions and ecosystem engineering (Kristensen 2008; Coverdale et al. 2012; Bertness et al. 2014), and anthropogenic modifications (Deegan et al. 2012; Coverdale et al. 2014). Within these dynamic landscapes, burrowing crab species are well-known ecosystem engineers that influence their environment through soil reworking and bioturbation (Kristensen 2008; Smith et al. 2009; Zhang et al. 2013; Peer et al. 2015). Mangrove forests, for instance, are inhabited by a handful of crabs known to strongly influence ecosystem properties and functions (Kristensen 2008; Smith et al. 2009). The combination of burrow excavation activities, such as the burial of plant detritus, and the passive irrigation of soils with water and air enhances soil heterogeneity and the efficiency of microbial decomposition in subsurface sediments (Kristensen 2008; Peer et al. 2015). Further, burrow

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✉ Alexandria Moore
alexandria.moore@yale.edu

¹ School of Forestry and Environmental Studies, Yale University, New Haven, CT, USA

construction may also favor the occupation of new ecological niches as small fauna take advantage of stable environmental conditions, additional food supplies, and protection from predation provided by crab burrows (Kristensen 2008).

In New England coastal salt marshes, fiddler crabs (*Uca pugnax*) are among the most abundant and common macroinvertebrate species (Teal 1958; Crane 1975; Montague 1980; Daiber 1982) and thus may play an important role as ecosystem engineers by generating and maintaining salt marsh ecosystem functioning along the east coast of North America. Their burrowing and deposit-feeding behavior can significantly influence the growth and morphology of smooth cordgrass (*Spartina alterniflora*), a dominant salt marsh plant, with concomitant impacts on total primary production (Bertness 1985; Peer et al. 2015). Experimentation has shown that the reduction in fiddler crab density on the salt marsh flat was associated with reduced penetration of plant roots and rhizomes into the marsh sediment, decreased decomposition of belowground plant debris, and a decrease in soil drainage and sediment redox (Bertness 1985). Lower crab burrow density was strongly associated with a shift in smooth cordgrass morphology, significantly reducing stem heights, flowering, and stem density, with an overall loss of aboveground production by 50% (Bertness 1985).

Marshes in New England are also characterized by the presence of the burrowing purple marsh crab (*Sesarma reticulatum*). As an herbivore, the purple marsh crab consumes significant amounts of marsh vegetation, directly reducing total plant biomass (Coverdale et al. 2012; Vu and Pennings 2018). Yet, their burrowing behavior may positively influence plant productivity indirectly by improving soil conditions via sediment reworking. How the potentially countervailing effects of purple marsh crabs, along with the additional effects of fiddler crabs, influence soil quality, standing plant biomass, and net ecosystem functionality remains uncertain. Resolving the individual and synergistic effects of these two species may provide key insight into how functions are regulated across salt marsh landscapes. Here I report on an experiment aimed to explore how the presence of fiddler crabs and purple crabs influences several ecosystem properties. Using ex situ mesocosms established to mimic local marsh conditions, I addressed two questions: What affect do fiddler and purple marsh crabs, individually and together, have on (1) soil properties and (2) standing biomass in salt marsh ecosystems?

Materials and Methods

Study System and Hypotheses

This study was conducted at the Yale University coastal field station situated along the Connecticut shoreline of the Long Island Sound in Guilford, CT (41° 15' 32.85" N, 72° 43'

52.75" W). Within this region, tidal salt marsh communities are dominated by salt-tolerant grasses, including smooth cordgrass (*S. alterniflora*), and numerous detritivore, herbivore, and predator species. Of the many species that make up marsh ecological communities, these landscapes are most significantly impacted by a handful of crustaceans, including the fiddler crab (*U. pugnax*) and the purple marsh crab (*S. reticulatum*) (Bertness 1985; Altieri et al. 2012; Coverdale et al. 2012). The fiddler crab is a deposit-feeding burrowing detritivore that alters the marsh landscape by sieving through sediment particulates for organic matter, while the purple marsh crab is a burrowing herbivore that directly consumes marsh vegetation above- and belowground (Miller 1961; Bertness 1985; Holdredge et al. 2009). The natural behavior of these two species may contribute to salt marsh ecosystem functions, such as soil quality and biomass production (Table 1).

The creation and maintenance of burrows by both fiddler and purple marsh crabs increases soil drainage, which oxygenates marsh sediments and improves decomposition of plant-generated debris (Bertness 1985). This burrowing behavior, coupled with the feeding habits of the fiddler crab, can decrease soil organic matter content, increase soil nutrient content, and increase the rate of change in soil nutrient content (a proxy for mineralization rates) as the top layers of soil are constantly turned-over (Table 1) (Wang et al. 2010). Primary production and cover may then be positively impacted by the increased availability of nutrients resulting from this soil bioturbation. However, although purple marsh crabs may indirectly increase primary production via these improved soil conditions, they cause a net loss in biomass through the direct consumption of plant material. This reduction in standing biomass may also mean that less plant matter is left to enter the detrital chain and overall soil organic matter content is reduced (Table 1). The experimental design of this study was therefore set to examine how the fiddler and purple marsh crabs affect these aspects of soil properties, standing biomass and cover.

Table 1 Predicted impact of fiddler crabs and purple marsh crabs on response variables

	Soil organic matter	Nitrogen absorption rate	Cover	Aboveground biomass
Fiddler crab	–	+	+	+
Purple marsh crab	–	+	–	–
Combined effect	–	+	±	±

Predicted impact of fiddler crabs and purple marsh crabs on response variables

The positive symbol indicates a predicted increase in the measured variable relative to control conditions where these species are absent while the negative symbol indicates a predicted decrease in the measured variable relative to the same control conditions. Cells with mixed symbols indicate that the overall impact may be context dependent and variable

Experimental Design

The experiment was conducted during June 2017. This period was chosen due to the smooth cordgrass growing season running from May–August, with peak growth and grass canopy development occurring in June and July before plants begin to senescence in August (Deegan et al. 2012). Twenty-four Rubbermaid 50-gal stock tanks of approximately 1 square-meter area were organized into a grid and assigned to four treatments with six replicates each (Fig. 1) (Gribsholt and Kristensen 2002; Zhang et al. 2013). The four treatments were: 1. Vegetation only (hereafter “Vegetation”), 2. Vegetation with fiddler crabs (hereafter “FC”), 3. Vegetation with purple marsh crabs (hereafter “PMC”), and 4. Vegetation with both fiddler and purple marsh crabs (hereafter “FC + PMC”). Approximately half of the grid layout was continuously shaded by neighboring trees, which was

taken into account for all statistical analyses. Initial conditions were evaluated from June 5–15, experimentation took place from June 15–28, and final conditions were measured from June 28–30.

In June 2016 mesocosm tanks were filled halfway with topsoil from a local landscape supply company (Grillo Services; Guilford, CT). Smooth cordgrass plugs (Environmental Concern Inc.; St Michaels, MD) typical of salt marsh restoration projects were planted every 7.5 cm for a total of thirty-one plugs per mesocosm tank (Fig. 2). Plugs were left to establish until experimentation began in June 2017. In April 2017, additional experimental mesocosms were prepared to supplement tanks in which smooth cordgrass failed to establish. This resulted in 14 tanks planted in 2016 and 10 tanks planted in 2017. Because smooth cordgrass is an annual grass, growth between years is not cumulative; therefore, planting year does not impact total biomass production at the end of a growing season.

Fig. 1 Mesocosm experimental layout. Mesocosm tank set up at the Yale University coastal field station in Guilford, CT. Figure legend is as follows: Unlabeled circles indicate mesocosm tanks where vegetation did not successfully grow and were not used for this experiment; “Vegetation” indicates tanks where crabs were not added; “FC” indicates fiddler crab addition tanks; “PMC” indicates purple marsh crab addition tanks; and “FC + PMC” indicates tanks where both fiddler and purple marsh crabs were added. Grey circles refer to tanks that were planted in 2016, while blue circles refer to tanks that were planted in 2017

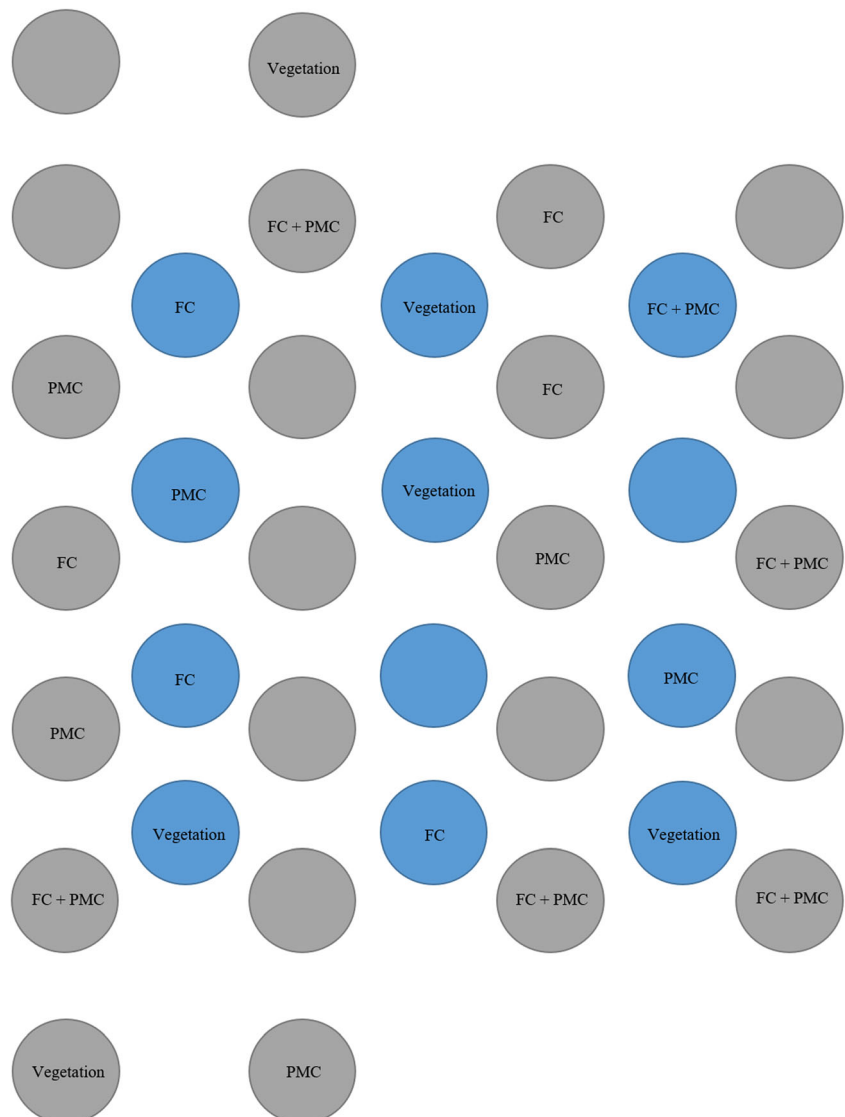


Fig. 2 Mesocosm layout and vegetation planting. **a** Layout of experimental mesocosms. **b** Aerial view of smooth cordgrass planting within each tank



To create conditions consistent with those observed in local salt marshes, mesocosm tanks were immersed with water pumped directly from the Long Island Sound. Moisture levels were monitored and adjusted twice per week to maintain constant soil saturation across all experimental tanks. The tidal regime was not simulated for this experiment in order to focus on evaluating how each species influences functions irrespective of the dynamic physical conditions observed in tidal marshes.

In May 2017, purple marsh crabs were collected from Hammonasset Beach State Park in Madison, CT (41° 16' 11.41" N, 72° 33' 20.36" W) using pitfall traps constructed from 2.4-l plastic buckets and 7.5 cm diameter open-top plastic cylinders (empty tennis ball cans). Drainage holes were drilled into the bottom of each container and traps were sunk until the top edge was flush with the marsh substrate. Eight traps were placed >2 m apart in an area of observed high crab density, left unbaited for 24 h, and checked the following day at low tide. This process was repeated at reasonable low-tide hours each day for 2 weeks and the total number of crabs caught was used to evenly stock mesocosms. During this collection period, purple marsh crabs were transported to the coastal field station where they were placed in a non-experimental tank until the onset of the experiment. Due to the difficulty of collecting at local field density within the sampling timeframe, fiddler crabs were purchased in bulk from an aquarium supply company (Live Brine Shrimp; Oak Hill, FL). On June 15, 2017 experimental mesocosm tanks were stocked by adding two purple marsh crabs to each PMC and FC + PMC mesocosm tank. Fifty fiddler crabs, representing the average burrow density in the region (Coverdale et al. 2013; Moore 2018), were added to each FC and FC + PMC mesocosm tank. Crabs used for stocking were adults that were not individually sexed, with carapace widths ranging from 15 to 20 mm for fiddler crabs and 20–25 mm for purple marsh crabs. The few crabs that died during the course of the experiment were replaced with similar-sized healthy individuals to maintain the disturbance intensity in

crab-present plots. At the end of the 14-day experimentation period, all living crabs were returned to the field.

Measurements and Laboratory Analyses

All measurements, with the exception of aboveground biomass, were taken prior to the onset of the experiment in early June to determine initial conditions and again at the end of June to evaluate treatment effects. Standing biomass was only measured at the end of the study period.

I determined soil organic matter (SOM) content using the standard loss-on-ignition (LOI) method (Nelson and Sommers 1996). Three soil samples were collected from each plot on June 8 using a hand trowel to form a 5 cm diameter core to a depth of 20 cm and immediately transported to laboratory facilities in individual Ziploc bags. Soil samples from each plot were homogenized and oven-dried at 105 °C for 24 h or to constant weight. Dried soil samples were then weighed in porcelain crucibles (pre-weighed) and placed in a muffle furnace at 500 °C for at least 16 h. Crucibles were cooled in a desiccator over calcium chloride and re-weighed. The LOI content of samples was calculated as:

$$LOI, \% = \frac{Weight_{105} - Weight_{500}}{Weight_{105}} \times 100$$

The rate of soil nitrogen absorption was measured in situ pre- and post-experimental period using ion exchange resin strips (Qian and Schoenau 1996). Anion and cation exchange membranes (General Electricals; Watertown, MA) were cut from a bulk sheet down to 2.5 × 10 cm strips and differentiated using a hole punch. On one end of each strip, bright pink zip-ties were affixed through the hole punch to act as a clear visual identifier once placed in the mesocosm tanks. Strips were prepared for use by washing them in hydrochloric acid to remove any existing nutrient ions (Qian and Schoenau 1996). Once regenerated, strips were rinsed with deionized

water and placed into anion and cation-separated, labeled, and clean Ziploc bags until placed in mesocosms.

Two anion and two cation strips were placed into each tank on June 7 for pre-experiment evaluation and June 21 for post-experiment evaluation. The four strips were spread approximately equidistantly within each tank and inserted into slits in the soil to a depth of nearly 10 cm such that 5 mm of the hole-punched end remained above the soil surface. Slits were then firmly closed by hand to create contact between the soil and the strip. Ion exchange resin strips are moisture-sensitive (Szillery et al. 2006) and were therefore left in each tank for 7 days, after which time they were collected, obvious soil residue was removed, and all strips from the same plot were placed into a clean Ziploc bag to be transferred to laboratory facilities (Qian and Schoenau 1996). In the laboratory, anion and cation strips from each mesocosm were placed into 237 ml specimen cups and soil nitrogen was extracted by filling each cup with 2.0 M potassium chloride (KCl) and shaking for 1 hour at 40 rpm (Qian and Schoenau 1996). The extract was then filtered from the cation and anion pairs from each plot, stored in labeled scintillation vials, frozen, and sent to the Morton Arboretum Laboratory (Lisle, IL) analytical facilities. Total nitrogen absorbed ($\mu\text{g}/\text{cm}^2/\text{day}$) was calculated using the following formula:

$$\left[\left(N \text{ Concentration in } \frac{\mu\text{g}}{\text{mL}} \right) \times 70\text{mL of KCl} \right] \\ \div [50.8 \text{ cm}^2 \text{ strip area} \times 7 \text{ days in ground}]$$

Vegetation cover was determined by taking an aerial photograph of each mesocosm using a Canon DSLR camera on June 7 and 28. Photos were viewed on a high definition monitor and cover was determined by visually estimating the proportion of vegetation found in each mesocosm. All cover estimates were evaluated at 5% increments.

Aboveground biomass was evaluated at the end of the experiment on June 30. All standing vegetation within each mesocosm tank was collected by cutting plants at the ground level using garden shears. Vegetation was then placed in labeled paper bags and immediately transported to laboratory facilities. Bags were left out to air dry for several weeks and weighed using a top-loading scale.

Data Availability

All data generated or analyzed during this study are included in this published article and its [supplementary information files](#).

Statistical Analyses

The effect size for each response variable was calculated to quantify the magnitude and direction of manipulation treatment impacts. Here, effect size was defined as $\ln(X_e/X_c)$ where

X_e and X_c are the mean ecosystem response in the crab-addition treatments and vegetation-only treatment, respectively (Osenberg et al. 1997; Hedges et al. 1999; Salo et al. 2010). An effect size $\ln(X_e/X_c) > 0$ means that treatments had a positive impact on the measured ecosystem function relative to the vegetation-only treatment, $\ln(X_e/X_c) \sim 0$ means that manipulations had no significant impact, and $\ln(X_e/X_c) < 0$ means that treatments had a negative impact on the measured ecosystem function. These values were produced to highlight and compare treatment effects in order to understand how these species influence important ecosystem properties.

The relative changes in SOM, rate of nitrogen absorption, and cover were calculated for each mesocosm. Relative change was defined as the difference between initial and final conditions divided by the initial conditions. I analyzed treatment effects on the final conditions for each variable and the relative change in SOM, rate of nitrogen absorption, and cover using one-way analysis of variance (ANOVA) and linear mixed effects models. ANOVA analyses were used to evaluate the sole effect of experimental treatment on measured response variables while linear mixed effects models were used to evaluate treatment effects in the presence of potentially confounding variables. Eta-squared, an effect size measure that represents the proportion of variation in the response variable associated with treatment group membership, was calculated for each ANOVA. For linear mixed effect models, treatment was set as a fixed effect with initial conditions as a covariate, while planting year and shading were set as random effects. Akaike information criterion (AIC) scores and the fit of the data were used to select the best model for each response variable. I analyzed the models using the “lme4” library (Bates et al. 2015) along with the “lmerTest” (Kuznetsova et al. 2016) and “multcomp” libraries (Hothorn et al. 2008) to get significance estimates. All statistical analyses were carried out using RStudio (v. 1.0.136).

Results

Effect Sizes

Crab-addition treatment impacts were small relative to the vegetation-only treatment, with the exception of SOM, but varied in magnitude when crab-addition treatments were compared to one another (Table 2). The effect size of each treatment was similar for SOM content and nitrogen absorption rate but varied considerably for cover and biomass (Table 2). Specifically, the effect of the FC + PMC treatment on cover was notably smaller than the PMC treatment and opposite in direction relative to the FC treatment. For biomass, the positive effect of the FC + PMC treatment was an order of magnitude greater than the individual FC and PMC treatments.

Table 2 Mean effect size for the final condition of each response variable by experimental treatment

Treatment	SOM	Nitrogen absorption rate	Cover	Aboveground biomass
Vegetation	0	0	0	0
FC	-0.15886	-0.01993	-0.03015	0.038185
PMC	-0.19266	-0.02173	0.08536	0.017498
FC + PMC	-0.18979	-0.09622	0.009852	0.181291

Effect size was defined as $\ln(X_e/X_c)$ where X_e and X_c are the mean crab-addition and vegetation-only treatments ecosystem function response, respectively

Soil Organic Matter

Treatment was not a significant predictor for final SOM content ($F_{3,19} = .985$, $p > 0.4$), but was a significant predictor for the relative change in SOM ($F_{3,19} = 4.323$, $p = 0.0175$). Treatment group explained 13% of the variation in final SOM content and 41% of the variation in the relative change in SOM content (Table 3). Soil organic matter content was marginally less in the PMC treatment relative to the Vegetation treatment ($p = 0.0768$) and the relative change in SOM content was significantly less in the PMC treatment relative to the Vegetation treatment ($p = 0.002$, Fig. 3a). There were no differences between any other treatment combinations.

Rate of Soil Nitrogen Absorption

There was no treatment effect on the final rate of soil nitrogen absorption ($F_{3,17} = .216$, $p > 0.8$) or the relative change in absorption ($F_{3,17} = .687$, $p > 0.5$). Treatment group explained only 4% of the variation in the final rate of soil nitrogen absorption and 11% of the variation in the relative change from the onset of the experiment (Table 3). Additionally, none of the treatment combinations differed significantly for soil nitrogen absorption or the relative change ($p > 0.7$ for both, Fig. 3b).

Table 3 ANOVA effect size (eta-squared) calculations for treatment effects on final conditions and relative change of response variables

	SOM	Nitrogen absorption rate	Cover	Aboveground biomass
Final conditions	0.1346	0.03667	0.0752	0.08044
Relative change	0.4056	0.10816	0.0713	NA

Eta-squared calculations for the final conditions and relative change in response variables by treatment. Values represent the proportion of variation in each response variable that is associated with treatment group

Cover

Treatment was not a significant predictor for the final vegetation cover ($F_{3,20} = .542$, $p > 0.6$) or the relative change in cover ($F_{3,20} = .512$, $p > 0.6$). Only 8% of the variation in final cover and 7% of the variation in the relative change in cover was explained by treatment grouping (Table 3). There was marginally more cover in the PMC treatment relative to the FC treatment ($p = 0.0919$, Fig. 3c), but there were no treatment combination differences in the relative change in vegetation cover ($p > 0.5$).

Aboveground Biomass

Treatment was not a significant predictor of final aboveground biomass ($F_{3,20} = .583$, $p > 0.6$) and there were no differences in treatment combinations ($p > 0.5$, Fig. 3d). Treatment group explained only 8% of the variation in aboveground biomass (Table 3).

Discussion

Burrowing crabs are known to have significant impacts on soil properties and aboveground biomass within coastal salt marsh ecosystems (Kristensen 2008; Coverdale et al. 2012; He and Silliman 2016). In this study, the relative change in soil organic matter differed significantly between groups, but SOM was only marginally impacted by crab-addition treatments. Specifically, the purple marsh crab treatment had slightly less SOM relative to the vegetation only treatment and SOM declined significantly with purple marsh crabs present in comparison to its increase under the vegetation only treatment (Table 3, Fig. 3a). Further, though not statistically significant, the purple marsh crab treatment exhibited a greater increase in the rate of soil nitrogen absorption, a proxy for nitrogen mineralization, relative to the vegetation only treatment (Table 3, Fig. 3b). Together, these findings suggest that the burrowing and feeding behavior of the purple marsh crabs may play an important ecosystem engineering role beyond what has been traditionally ascribed within New England coastal salt marshes. Further, as a sesarimid, the purple marsh crab consumes roughly half of handled litter, with an assimilation efficiency ranging from 40 to 70% (Lee 1997; Thongtham and Kristensen 2005). The solid faecal material that remains supports faster microbial decay than solid leaf material (Kristensen 2008). Here, the significant decrease in SOM and a trend towards an increase in nutrient mineralization supports the ecosystem engineering effects of the purple marsh crab in New England coastal marshes.

Although treatment effects were not present for any of the other, an evaluation of the magnitude and direction of treatment impacts indicates that fiddler crabs and purple marsh

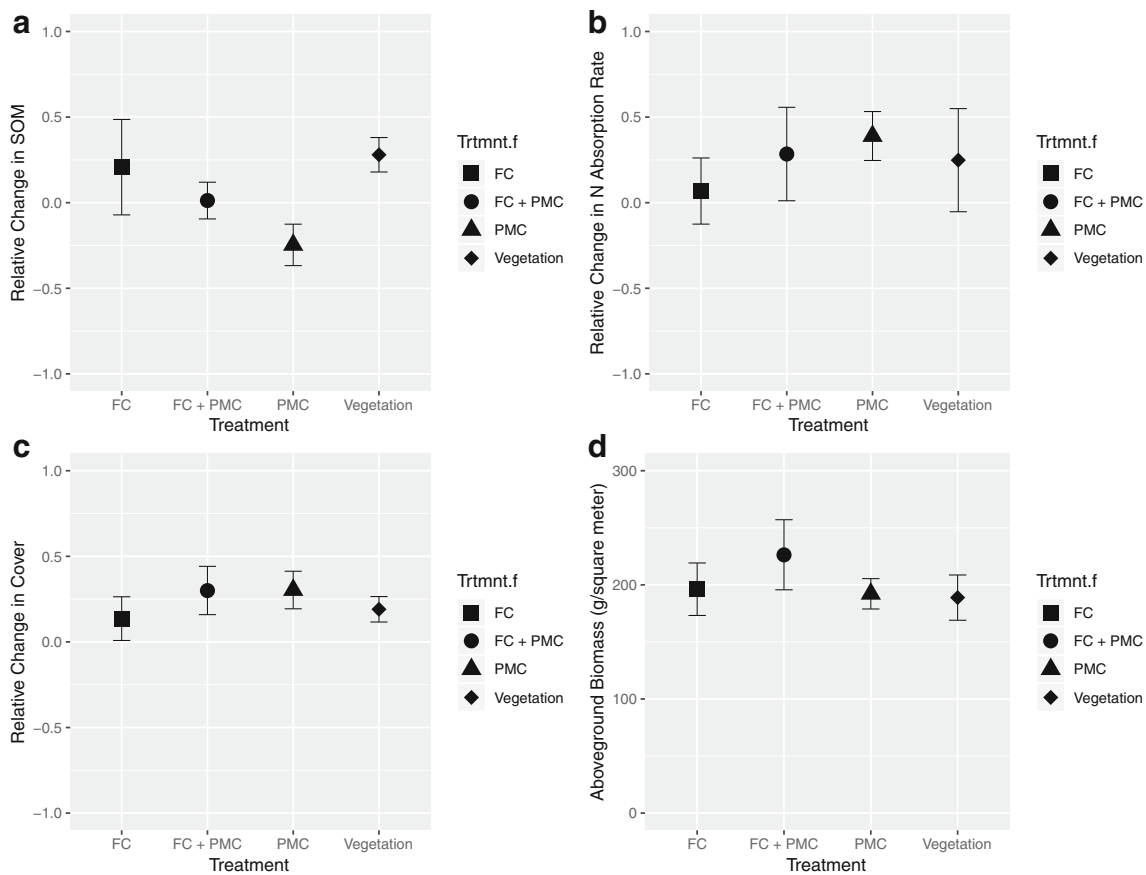


Fig. 3 Relative change in and final conditions of response variables by experimental treatment. **a** SOM content, **b** Rate of nitrogen absorption, **c** Vegetation cover, and **d** Final aboveground biomass

crabs differentially influence ecosystem properties (Table 2). Most notably, the impacts of fiddler crabs and purple marsh crabs individually were an order of magnitude greater than their combined effect on vegetation cover but were an order of magnitude less than their combined effect on aboveground biomass. Cover increased across all treatments, but the greatest increases were exhibited in the purple marsh crab treatment and the combined crab treatment (Table 3, Fig. 3c). The combined crab treatment also contained the largest quantity of aboveground biomass at the end of the experiment (Table 3, Fig. 3d). The positive effect on biomass growth in the combined crab treatment suggests that the influence on soil quality may outweigh the direct consumption of marsh vegetation by the purple marsh crab. Crab burrows have been shown to aerate otherwise oxygen-limited wetland soil, improving drainage and increasing the decomposition of belowground debris (Bertness 1992). Improved aeration and drainage, in association with a reduction in SOM and an increase in soil nutrient mineralization, may create conditions that support additional biomass production. These findings, however, contradict studies in which purple marsh crabs significantly reduce aboveground biomass production in the absence of top-down consumer control (Holdredge et al. 2009; Coverdale

et al. 2013; Bertness et al. 2014; Vu and Pennings 2018). This may be due to the design and duration of this study. Given enough time, it is possible that the positive effect of improved soil conditions on biomass production would be exceeded by the negative impact of sustained herbivory. Such diverse results indicate that the role that the purple marsh crab plays in salt marsh productivity may be multifaceted and highly variable.

Conclusions

In this study, the presence of burrowing crabs significantly altered soil quality and influenced biomass production. The burrowing behavior of the purple marsh crab, along with the burrowing and feeding behavior of the fiddler crab, positively influenced soil quality with implications for biomass production. The results presented here suggest that the purple marsh crab, known to be a voracious consumer of marsh vegetation, may play a much more nuanced role in the maintenance of plant growth than previously thought. Recognizing the ways in which these species and their interactions influence ecosystem functions provides additional understanding of how salt

marsh ecosystems are regulated and maintained. As an ex situ mesocosm study, the conditions created here, though similar, are not identical to those found in natural coastal wetlands. Tidal regime, community composition, consumer control and prey behavior, and anthropogenic influence all shape the impact that species have on ecosystem properties. To clearly delineate these effects, additional ex situ studies that incorporate these factors should be conducted to identify the generalizability of these results.

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