



Salt Marsh Plant Community Structure Influences Success of *Avicennia germinans* During Poleward Encroachment

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Abstract

Along the Florida coast, decreasing freeze events are promoting the range shift of the mangrove species *Avicennia germinans* northward into temperate salt marsh wetlands. Although plant species' ranges are tightly linked with their climatic tolerances, there is considerable variability in the magnitude by which biotic factors like competition and facilitation may also influence range shifts. Changes in mangrove and marsh plant abundance can alter both the above and belowground environment, which may in turn influence ecosystem services typically associated with these systems such as storm surge abatement and carbon storage. Therefore, it is key to understand (1) how the above and belowground environment of established salt marshes influences establishment of mangroves, and (2) how above and belowground environments shift in response to mangrove encroachment. Using a semi-natural mangrove planting experiment, we investigated the impact of four distinct marsh plant community structures (*Batis maritima*, *Spartina alterniflora*, mixture of *B. maritima* and *S. alterniflora*, mudflat) on mangrove survivorship and decomposition rate. In mixed marsh plots, mangrove survivorship was 42 % higher compared to survivorship in mudflat plots, and decomposition rate was 47 % greater in mixed marsh plots compared to mudflat. However, percent cover of vegetation differed across treatments, and was highest in mixed marsh plots. High survivorship in mixed marsh plots is likely due to increased protection from physical stressors by the dense aboveground cover, and belowground plant root-driven effects such as nutrient availability and oxygen delivery. Our findings suggest that above and below ground differences in salt marsh plant community structure can have an impact on the survival of encroaching mangroves, which may have implications for predicting future mangrove encroachment and improving mangrove restoration techniques.

Keywords *Batis maritima* · Plant community · Facilitation · Mangrove encroachment

Introduction

Stressful conditions drive low species richness in coastal wetland plant communities, which in turn can result in more meaningful competitive and facilitative species interactions (Bertness and Hacker 1994; Emery et al. 2001; Ellison et al. 2005). Competitive interactions between salt marsh plants play an important role in determining species zonation patterns along the coast (Emery et al. 2001), and early colonization of stressful areas such as mud flats may promote

facilitation of different plant species (Milbrandt and Tinsley 2006). As the climate warms, many plant species ranges are shifting in response to sea-level rise and decreases in freezing stress, which impacts the plant community structure of coastal wetlands (Krauss et al. 2011, Saintilan et al. 2014; Cook-Patton et al. 2015). Shifts in foundation species in response to climate change are expected to have cascading effects on ecosystem structure and function (Osland et al. 2013). Though competition and facilitation are key drivers in structuring plant communities, it is largely unknown how these forces may influence the rate at which climate-change induced plant range shifts occur (HilleRisLambers et al. 2013).

Coastal wetland plant community structure is shifting as mangrove ranges are expanding poleward across the globe (Saintilan et al. 2014). In higher-latitude areas, mangroves are increasing in abundance and expanding into salt marshes and tidal flats within their established ranges, though the

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drivers of this “within-range” expansion are varied (Kelleway et al. 2016). In areas of Australia and New Zealand mangrove expansion is caused by increased rates of sedimentation due to changes in land use (Lovelock et al. 2007; Swales et al. 2015), and in some areas of South America landward expansion of mangroves is largely driven by sea-level rise (Godoy and Lacerda 2015). However, mangrove expansion in China is more complex due to extensive mangrove clearing, so the main driver of mangrove expansion remains unknown (Durango et al. 2013; Saintilan et al. 2014). At climate defined poleward limits, mangrove range expansion is predominately attributed to changing temperature thresholds resulting from climate change (Osland et al. 2013; Saintilan et al. 2014). Such is the case along the southeastern coast of the United States, where decreases in freeze events and their severity is driving the poleward shift of mangroves outside of their established range (Cavanaugh et al. 2014). Plant species ranges are tightly linked with their freeze tolerances, and the reduction in freeze events driven by warming temperatures in Louisiana, Texas, and Florida is promoting mangroves encroachment into salt marsh habitat (Perry and Mendelssohn 2009; Cavanaugh et al. 2014).

Though many freeze-sensitive species exhibit greater tolerance for freezing as they age, the black mangrove’s freeze tolerance changes depending on its life stage. Black mangroves have three distinct early life stages; dispersal stage, stranded stage, and established seedling stage (Tomlinson 1986). In the dispersal stage, floating mangrove propagules can withstand fluctuating salinities, temperatures, and degrees of flooding (Rabinowitz 1978; Patterson et al. 1997; Delgado et al. 2001; Sousa et al. 2003). Once established, mangrove seedlings are more susceptible to freeze damage than propagules but become more resistant to freeze damage as they grow (Pickens and Hester 2011). Restoration projects have shown that in addition to size and life stage mangrove success may also be influenced by the presence of foundation species, which are species whose presence imparts a disproportionately large role in structuring ecosystems (Yando et al. 2019). However, it remains unclear how differences in plant community structure influences encroaching mangroves, especially at different life stages.

The stress-gradient hypothesis (SGH) predicts that while competition and facilitation co-occur, increased abiotic stressors correlates to increased facilitative interactions in plant communities (Bertness and Callaway 1994), though support for the SGH has depended on numerous factors including individual characteristics of the species involved (Malkinson and Tielbörger 2010; Casalini and Bisigato 2018). The rapid shift of salt marsh to mangrove occurring at the ecotone between these ecosystems provides a unique opportunity to study how competition and facilitation may occur dynamically depending on plant community and mangrove life stage (Risser 1995; Saintilan et al. 2014). Indeed,

many salt marsh plant species have been implicated as both mangrove competitor and facilitator depending on context. In the tropics, the salt marsh succulent *Batis maritima* has been implicated as a potential facilitator of mangrove encroachment due to belowground interactions and dense growth habit (Milbrandt and Tinsley 2006; Whigham et al. 2009; Teutli-Hernández et al. 2019). Similarly, *Spartina alterniflora* may promote mangrove facilitation by providing shade and protection for establishing mangroves (Pickens et al. 2019), though *S. alterniflora* has also been implicated as a mangrove competitor due to allelopathic soil interactions (Chen et al. 2020). Adult mangroves can outcompete many marsh species for space and nutrients due to shading, superior reproduction, and belowground processes (Kangas and Lugo 1990), though restoration projects have indicated that prioritizing foundation marsh species health may promote initial mangrove establishment (Milbrandt and Tinsley 2006; Lewis 2009; Yando et al. 2016).

In addition to aboveground interactions, foundation marsh species can also directly modify aspects of their belowground environment (Rietl et al. 2016; Fujii et al. 2018). Soil environment modification can impact the fitness of plant species, potentially producing a reciprocal interaction commonly referred to as a plant–soil feedback (PSF; Kulmatiski et al. 2008; Allen et al. 2018). Though plant-soil feedback studies in wetlands are rare, plant-soil feedback loops can be particularly strong in areas with lower species richness (Corbin and D’Antonio 2012; Grove et al. 2015) such as coastal salt marshes. Salt marsh plant species can cultivate distinct soil microbial communities (Rietl et al. 2016) and can directly alter numerous abiotic factors in the soil. For example, *B. maritima* can sequester salt in its succulent-like leaves leading to upwards of 55 % decrease in soil salinity compared to mudflats, and *Batis* has also been associated with increases in available soil nitrogen (Teutli-Hernandez et al. 2019). *Spartina alterniflora* has well developed aerenchyma that can leak oxygen into surrounding soils (Maricle and Lee 2002), which can result in soil oxidation, changes in soil redox, and changes in nutrient availability (Howes et al. 1986; Wigand et al. 1997; Perry and Mendelsson 2009). Though *B. maritima* and *S. alterniflora* can directly alter belowground factors, it is not yet clear how these variations in soil environment across a marsh habitat may impact encroaching mangroves.

Mangroves also possess well-developed aerenchyma, and mangrove-associated soils tend to contain more aerobic bacteria than marsh soils (Barretto et al. 2018). This suggests that increases in mangrove abundance may drive the increase of heterotrophic respiration as mangroves encroach into salt marshes (Wolf et al. 2007; Kirwan and Blum 2011). Though biotic and abiotic factors that influence the belowground environment can be numerous, decomposition bags have been

widely used as an integrated measurement of the belowground environment. This method provides a low-cost snapshot of the belowground environment as it relates to decomposition and labile carbon stabilization (Keuskamp et al. 2013; Mueller et al. 2018). Changes in mangrove and marsh plant abundance can both alter the belowground environment and associated ecosystem services, such as carbon storage (Comeaux et al. 2012; Doughty et al. 2016; Coldren et al. 2016; Barreto et al. 2018). Thus, it is key to understand (1) how the belowground environment of established salt marshes influences establishment of mangroves and (2) how belowground environment shifts in response to mangrove encroachment.

Using a site at the ecotone between where mangroves and salt marsh plants dominate in northeastern Florida, we have the unique opportunity to observe how variation in marsh plant community structure influences the success of establishing mangroves. We planted mangrove seedlings in plots with four different marsh plant community compositions, and thus can assess how plant community may impact mangroves' encroachment success at this key life stage. We measured mangrove seedling mortality and growth rates over 9 months and measured percent cover of the marsh plant cover to assess aboveground environment. We measured organic matter decomposition via the Tea Bag Index (TBI), which uses two types of tea to derive a decomposition rate (k) reflecting initial decomposition, and a stabilization factor (S) which reflects the fraction of labile organic matter that becomes stabilized during deployment (Keuskamp et al. 2013; Mueller et al. 2018; Seelen et al. 2019). We hypothesized that (1) mangroves planted in plots with greater percentages of *B. maritima* would exhibit lower mortality rates; (2) mangroves would exhibit low mortality in plots with greater plant percent cover; and (3) plots with planted mangroves would exhibit higher decomposition rates compared to paired plots without mangroves.

Methods

Site Description

This study was conducted at the Guana Tolomato Matanzas National Estuarine Research

Reserve (GTM), located just north of St. Augustine, Florida. GTM is 50 miles south of the northernmost known black mangrove in Florida (30.11 N, 81.37 W) and lies in the ecotone between salt marsh and mangroves (Cavanaugh et al. 2019). Mean elevation is 57 cm, and mean salinity is 38.41 ppt (Table 1). This site is dominated by a mixture of the salt marsh grass *S. alterniflora*, the marsh succulent *B. maritima*, and the mangrove species *A. germinans*.

Table 1 Site characteristics of Guana Tolomato Matanzas Research Reserve along the northeastern coast of Florida. Shown with permission from Chapman et al. 2021

Variable	GTM Site Characteristics		
	Mean	Range	SD
Elevation(cm)	57	53–63	3
Longitude	29°50'10.30"N		
Latitude	81°17'42.25"W		
pH	5.94–6.72	4.68	0.53
Redox(mV)	51.13	1–132	33.82
Soil temperature (C)	26.16	24.67–27.71	NA
Air temperature (°C)	16.44	0.47–30.76	1.24
Soil type	Histol/hydrosol		
Bulk density (g/cm ³)	0.69	0.33–0.90	0.11
Salinity(ppt)	38.41	32.00–43.00	3.91

Experimental Design

We established four distinct vegetation treatments that were selected based on the dominant plant community structures present across the low marsh; (1) *S. alterniflora* dominated, (2) *B. maritima* dominated, (3) mixture of *S. alterniflora* and *B. maritima*, and (4) mudflat with no vegetation (Fig. 1). Vegetation in each treatment had established naturally and required no further planting or clipping. Each treatment consisted of ten 1-m² plots, five of which were planted with 10 mangrove seedlings each, and five of which remained unplanted to serve as paired controls for the decomposition study. Survivorship and plant heights were measured in three-month increments beginning in January 2019 at initial planting and concluding in November 2020.

Mangrove Seedling Replanting

Mangrove seedlings were wild collected across a roughly 10 m² area at GTM with proper permissions from GTM managers. Approximately 200 mangroves between 1 and 3 years old and 20–40 cm in height were selected and removed, maintaining as much root biomass as possible. Over the course of two days, mangrove seedlings were selected at random, tagged, measured, photographed, and replanted in one of the 20 planted experimental plots.

Mangrove Mortality

After planting, we assessed mangrove survivorship success in three 3-month intervals. Once every 3 months, all tagged mangrove seedlings were counted as either living or dead. Seedlings were considered “living” if they still had green or yellowing leaves. Seedlings were counted as “dead” if they

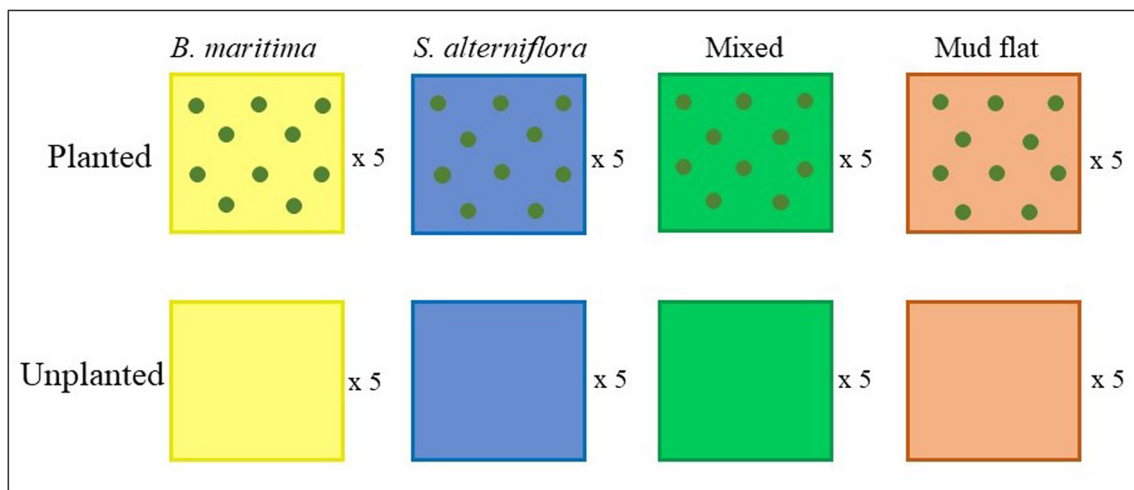


Fig. 1 Experiment design consisted of 40 plots separated into 4 treatments: (1) *S. alterniflora* dominated, (2) *B. maritima* dominated, (3) mixture of *S. alterniflora* and *B. maritima*, and (4) Mudflat with no

vegetation. 5 plots from each treatment were planted with 10 mangrove seedlings each, while the remaining 5 plots in each treatment were unplanted for use as control plots

had no leaves and their stems were fragile and brittle. On two occasions, seedlings that were previously counted as dead resprouted live tissue at the base of their stems. Mortality was calculated by dividing the number of dead mangroves by ten and expressed as a percentage for each plot.

Percent Cover Analysis

During the last mortality measurement in November 2019, we photographed each of the experimental plots that contained vegetation (*B. maritima*, *S. alterniflora*, and Mixed). Photos were taken from approximately 1 m above each plot, aiming directly downward at the vegetation, and included all four edges of the plot. Photos were taken of both planted and unplanted plots during a lower biomass season to establish a baseline of percent cover for each vegetation treatment. Using ImageJ, we minimized the reflectance in each photo and determined the percentage of green pixels in each photograph (Schneider et al. 2012). Percent green served as a means of separating living tissue from dead tissue and sediment, and acts as a proxy for percent cover in each plot.

Salinity

Salinity was measured via porewater sampling in November 2019. Using a sipper constructed with a long piece of ¼ inch tubing with small holes drilled in the end, the tubing was driven into the soil of each plot at least 20 cm deep. Using a syringe, porewater was pulled up through the tubing and collected in scintillation vials. Vials were left undisturbed for an hour to allow sediment to settle, and porewater salinity was measured with a refractometer.

Tea Bag Index

To measure *in situ* decomposition rates of SOM, we used the tea bag index in each of the 20 plant plots and 20 unplanted plots at GTM as outlined in Keuskamp et al. (2013) to compare how SOM decomposition rates of different community structures changed in response to the presence of mangrove seedlings. This index uses two types of commercially available Lipton tea bags with contrasting decomposability to construct a decomposition curve at one time point (Keuskamp et al. 2013). In each plot, we buried one green tea bag and one rooibos tea bag at a depth of 8 cm roughly 15 cm apart. Tea bags were removed after 3 months, after which they were washed, dried, and weighed to assess changes in mass due to decomposition. The first two sets of tea bags were removed and replaced at 3 months, though due to the COVID-19 pandemic the third set of tea bags were deployed for 6 months.

Statistical Analysis

To determine differences between mean mangrove mortality across treatments, we performed a repeated measures ANOVA with vegetation and time as factors. Differences in percent cover and salinity across vegetation treatments were determined using one-way ANOVAs. We used two separate 2-way ANOVAs to determine differences in both decomposition rate (k) and stabilization factor (S) between planted and unplanted plots and across all vegetation treatments. To find differences in means, we used Tukey's post hoc HSD tests for all analyses. All analyses were conducted in R version 3.1.2 (R Core Team 2019).

Results

Percent Cover

Out of the three treatment types with vegetation, the mixed treatment plots had the greatest average percent cover ($F_{2,27} = 8.356$, $p = 0.0015$, Fig. 2; Table 2). Average percent cover in Mixed plots was 20.9 % greater than percent cover in *B. maritima* plots, and 37.4 % greater than percent cover in *S. alterniflora* plots.

Salinity

Salinity differed across treatments ($F_{3, 34} = 8.111$, $p = 0.00033$, Table 2). Mean salinity in Mudflat plots (29.75 ppt) was significantly lower than all vegetated plots. Mixed plots had the highest average salinity of 34.30 ppt, followed by *B. maritima* dominated plots at 32.80 ppt and *S. alterniflora* dominated plots at 32.30 ppt (Table 2).

Table 2 Average porewater salinity (ppt) in each vegetation treatment. Mud flat salinity was significantly lower than the rest of the treatments

Treatment	Mean salinity (ppt)	SD
<i>B. maritima</i>	32.80	1.686548
<i>S. alterniflora</i>	32.30	1.337494
Mixed	34.30	3.020302
Mudflat	29.75	1.035098

Decomposition

Across the four distinct plant community structures in the decomposition experiment mangrove presence had no effect on decomposition rate (k), though community structure had an effect ($F_{3,26} = 14.735$, $p = 8.36e-06$, Table 3). Mixed treatment plots had the highest average decomposition rate ($k = 0.0116$), which was 47 % greater compared to the lowest decomposition rate in Mudflat plots ($k = 0.007$) (Fig. 3). Mangrove

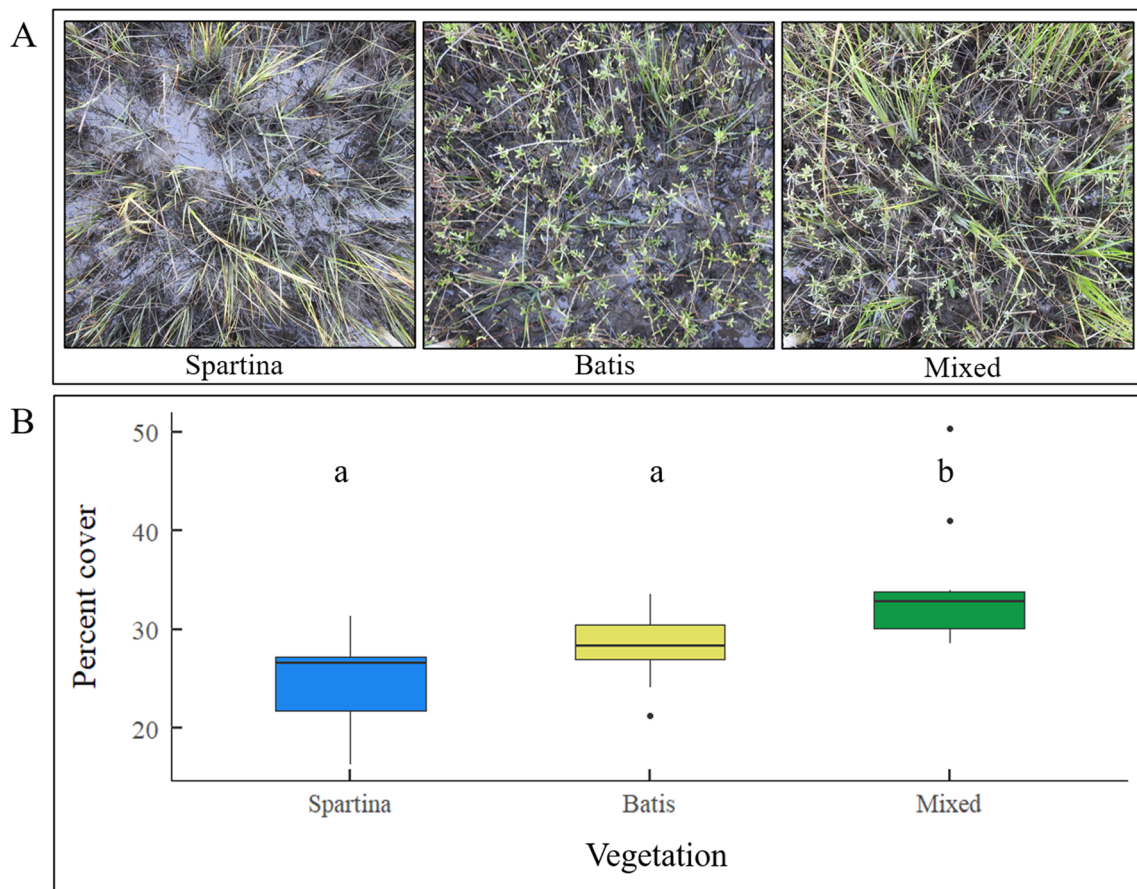


Fig. 2 (A) Representative images from each plant community composition treatment that contained vegetation; *S. alterniflora*, *B. maritima*, and a mixture of the two. Mudflat plots are not pictured, as percent cover was not measured in those plots due to complete lack of vegetation. (B) Percent cover by treatment in each of the plots (planted

and unplanted combined). Mixed plots show a significantly greater percent cover than *S. alterniflora* and *B. maritima* plots ($F_{2,27} = 8.356$, $p = 0.0015$), whereas *S. alterniflora* and *B. maritima* were not statistically different from each other. Error bars indicate standard error, letters indicate significance

Table 3 2-way ANOVA tables for vegetation and mangrove presence by decomposition rate (k) and stabilization factor (S). Bold entries denote statistical significance

	Df	Sum Sq	F Value	P (>F)
Decomposition rate (k)				
Vegetation	3	6.654e-05	14.735	<0.001
Mangrove	1	2.720e-06	1.805	0.191
Vegetation:Mangrove	3	1.2552e-06	0.834	0.488
Stabilization factor (S)				
Vegetation	3	0.01171	2.732	0.0606
Mangrove	1	0.00151	1.060	0.3113
Vegetation:Mangrove	3	0.04430	0.832	0.4864

presence had no effect on stabilization factor (S), though vegetation treatment had a marginal effect ($F_{3,31} = 2.732$, $p = 0.0606$, Table 3). *B. maritima* plots showed the greatest S factor, followed by Mudflat and *S. alterniflora* plots. Mixed plots had the lowest average S factor of 0.0797 (Fig. 3).

Mangrove Survivorship

Mangrove seedling mortality was highest in Mudflat treatment plots, reaching 90 % by the first measurement (May 2019), and 100 % mortality by the second (August 2019) ($p = 3.611e-08$, Fig. 4; Table 4). Similarly, mangrove seedling mortality was also high in the *S. alterniflora* treatment, reaching 68 % by May and maxing out at 96 % by August. Seeding mortality was lower in *B. maritima* plots, reaching 50 % by May and increasing to 70 % by the end of the experiment. Mixed treatment plots showed the lowest mortality overall, reaching 32 % by May and 70 % by the end of the experiment. At the end of the experiment, total

mortality in Mixed treatment plots was 42 % lower than mangrove mortality in mud flat treatment plots (Table 4).

Discussion

We examined how marsh plant community structure and percent cover can affect mangrove survivorship and below-ground decomposition in the mangrove-marsh ecotone of NE Florida. We hypothesized that (1) mangroves planted in plots with greater percentages of *B. maritima* would exhibit lower mortality rates; (2) mangroves would exhibit low mortality in plots with high plant percent cover; and (3) plots with planted mangroves would exhibit higher decomposition rates compared to paired plots without mangroves. We found some support for our first two hypotheses. Mangroves planted in Mixed plots where *B. maritima* was present in mixture with *S. alterniflora* had the highest mangrove survivorship and highest percent cover overall, though the *B. maritima* and *S. alterniflora* monoculture treatments did not differ significantly from each other in any capacity. Decomposition rates were also highest in Mixed plots, and on average decomposition rate in Mixed plots was 47 % greater than average Mudflat decomposition rate, though we did not find any effect of mangrove presence on decomposition. Here we explore possible explanations for the patterns we observed.

One possible explanation for the differential mangrove survivorship across marsh vegetation could be due to variation in percent cover across vegetated treatments. Mangroves do not typically establish in areas devoid of vegetation which corroborates our finding of total mortality of mangrove seedlings in the Mudflat plots. This is unsurprising as mudflats can be harsh environments for establishing plants, including mangrove and other marsh species, due to extreme abiotic conditions such as high salinity, sulfide build-up, and hypoxia

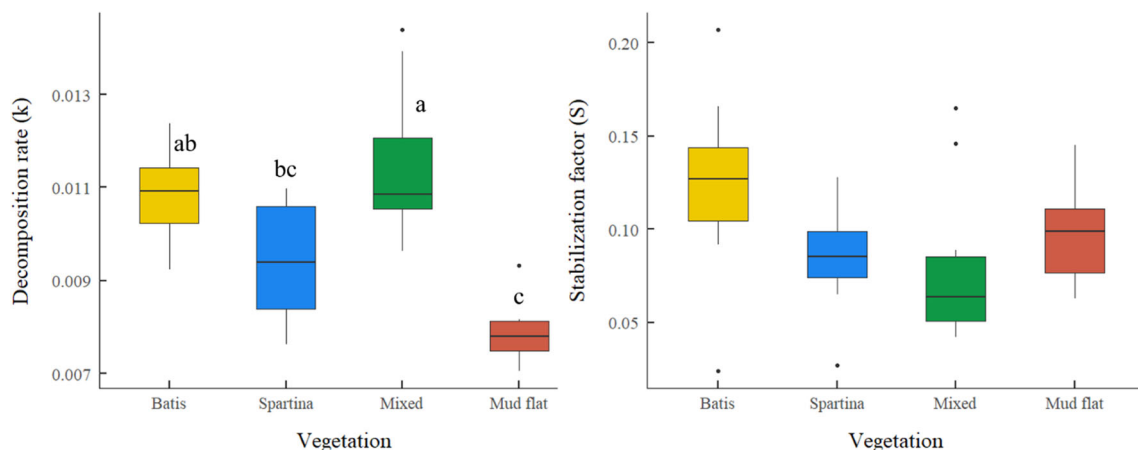
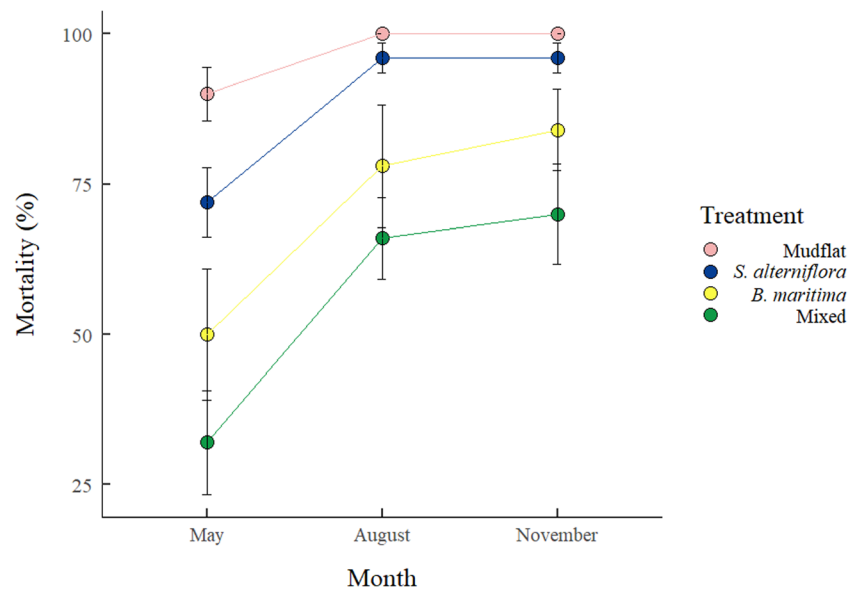


Fig. 3 Two way ANOVA found no effect of Mangrove presence on decomposition rate (k), but Vegetation had a significant effect on k ($p = 8.36e-06$). Mixed plots had the highest k, while Mudflat plots had the lowest k. Two way ANOVA found no effect of Mangrove presence

and no effect of Vegetation on stabilization factor (S). Letters denote significance, figure shows data from planted and unplanted plots as there was no significant difference between those groups

Fig. 4 Repeated measures ANOVA on mortality of mangrove seedlings by vegetation over time. Mangrove mortality increase over time ($p = 1.839e-10$) and by vegetation treatment ($p = 3.611e-08$), but no interactive effects. Mixed and *B. maritima* plots were significantly greater in mangrove survival over time compared to *S. alterniflora* plots and Mudflat plots. Lsmeans used for a posthoc test



(Milbrandt and Tinsley 2006; Lewis 2009; Yando et al. 2016). Among the vegetated treatments, Mixed plots were 37.4 % more dense in cover compared to *S. alterniflora* plots (Fig. 2), and mortality in Mixed plots was 42 % lower compared to Mudflat plots (Fig. 4). The higher rates of mangrove survivorship we found in plots containing some percentage of *B. maritima* correlate positively with a higher total percent cover of vegetation (Fig. 5).

It is possible that the dense cover in Mixed and *B. maritima* plots provided more protection for mangrove seedlings compared to the sparse coverage in *S. alterniflora* plots and complete lack of cover in Mudflat plots. Seedlings at this stage (2–3 years old) are sensitive to temperature fluctuations (Pickens and Hester 2011), and temperature in patches of *B. maritima* have been found to be lower than areas without *B. maritima*, likely due to shading effects (Milbrandt and Tinsley 2006). In addition to shading effects, dense vegetation can slow tidal flow and minimize turbulence, allowing for entrapment of sediment particles and minimizing sediment deposition on leaves (reviewed by Cahoon et al. 2021). In Mudflat plots, the leaves of planted mangroves were covered in sediment at the second timepoint, which may have contributed to total mortality in the Mudflat treatment (Adgie, personal observation). *Batis maritima* also has less fibrous roots compared to

S. alterniflora, which may be able to break up the dense *S. alterniflora* root mat and provide more space belowground for mangroves to establish. We suggest that in mixed plots, the combination of *B. maritima* and *S. alterniflora* provides dense aboveground cover which acts as protection, while also providing more space belowground for mangrove seedlings to establish. Though we did not measure elevation explicitly in this study, small fluctuations in elevation may influence inundation period across treatments and therefore could influence mangrove survival, which we further explore below.

The zonation of vegetation in coastal salt marshes is largely dictated by physical stressors, namely tidal flooding, and this zonation can also contribute to seedling mortality (Pennings and Callaway (Pennings and Callaway 1992; Bertness and Hacker 1994). *Spartina alterniflora* has a higher flooding tolerance than the black mangrove, resulting in mangroves growing at higher elevations in comparison to *S. alterniflora* in many coastal ecosystems (Patterson and Mendelsohn 1991). *Batis maritima* tends to grow in the transitional area from the high marsh to the low marsh but cannot tolerate the same level of flooding as *S. alterniflora*. Though this study took place solely in the low marsh, subtle fluctuations in elevation may ultimately be the driver of plant zonation in this area. It is possible that the optimal elevation ranges for *S. alterniflora* and *B. maritima* overlap in an elevational range that may be most suitable for mangrove success. Subtle differences in elevation across vegetation types may therefore be a driver for mangrove survival (Rogers et al. 2014). Elevation differences also drive differences in timing and extent of flooding, which could impact soil oxygenation. The higher decomposition rates in Mixed plots we found may reflect less intense tidal flooding due to higher elevation, improving oxygen availability and subsequently promoting mangrove survival. Plants also contribute to increases in soil surface

Table 4 Repeated measures ANOVA table of mangrove mortality by vegetation over time. Bold entries denote statistical significance

Source	Df	Chi Sq	P (>Chi Sq)
Vegetation	3	37.4976	<0.001
Time	1	40.6305	<0.001
Vegetation:Time	3	6.7549	0.08014

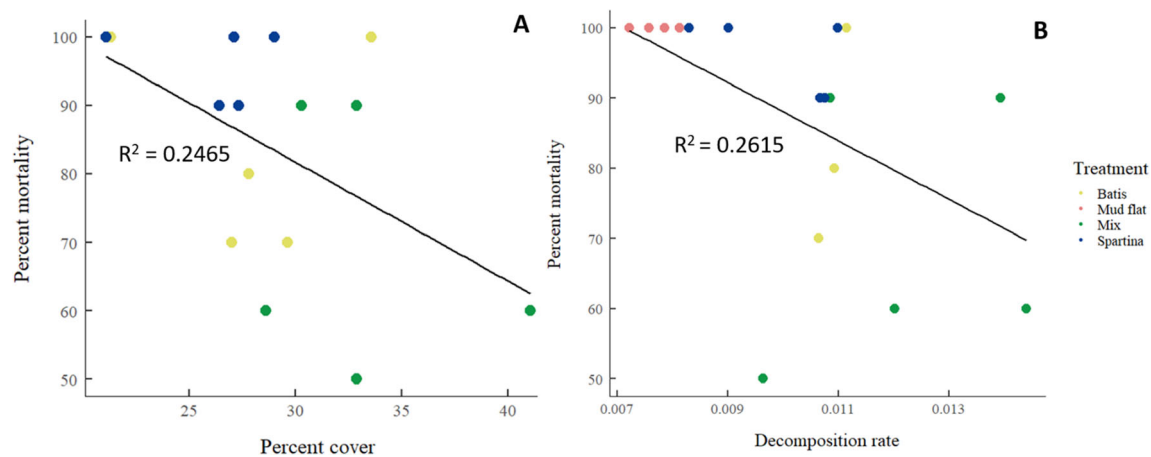


Fig. 5 **A**) Percent mortality of mangrove seedlings tends to decrease with increasing percent cover of treatment plots ($r^2 = 0.2465$, $p = 0.0598$). **B**) Percent mortality of mangrove seedlings tends to decrease as decomposition rate increases ($r^2 = 0.2615$, $p = 0.0359$)

elevation by trapping sediment particles and contributing to soil volume via root and rhizome production (Reviewed by Cahoon et al. 2021), but the exact contributions of individual marsh plant species to overall marsh elevation gain is not well understood. It is therefore possible that subtle differences in elevations across the low marsh could in part be an artifact of plant community structure and zonation and should be further studied.

Belowground parameters such as plant-soil feedbacks, nutrient availability, and oxygen delivery may also be a driver of differences in mangrove survivorship across treatments. As *S. alterniflora* can have allelopathic effects on surrounding vegetation (Wu et al. 2006; Chen et al. 2020) and *B. maritima* has been implicated as a facilitator of mangrove encroachment (Milbrandt and Tinsley 2006; Teutli-Hernandez et al. 2019) we were surprised to find that the Mixed treatment where *B. maritima* and *S. alterniflora* were present in equal proportion exhibited the highest mangrove survivorship. Recent studies on the effects of fertilization show that *A. germinans* takes advantage of increased N availability to accelerate growth, whereas *S. alterniflora* shows no comparable growth response in similar conditions (Simpson et al. 2013; Weaver and Armitage 2018; Macy et al. 2020). At a site close to ours, Dangremond and others (Dangremond et al. 2020) showed that *A. germinans* growth is N limited. *B. maritima* can increase concentrations of available soil N (Teutli-Hernandez et al. 2019), and thus higher survivorship of mangroves in plots with some percentage of *B. maritima* may be due to higher concentrations of available soil N. Further, differences in root architecture between *B. maritima* and *S. alterniflora* may result in differences in root exudates and oxygen delivery across plant community types. We propose that synergistic effects of variation in aboveground cover with differences in belowground root-driven nutrient availability and oxygen delivery may explain differences in mangrove mortality across plant community types.

We found that marsh plant community composition impacted decomposition rates and marginally changed stabilization factor (Table 4). In addition to the highest survivorship of mangroves and highest percent cover, Mixed plots also showed the highest decomposition rates (Fig. 3; Table 4). Conversely, the Mudflat treatment had the lowest decomposition rate in addition to total mangrove mortality and no vegetation coverage. We suggest that differential decomposition rates are driven by plant root dynamics. SOM decomposition is a process regulated by soil microbial communities (Allison et al. 2013), and influenced by temperature, litter input, and soil oxygen levels (Couteaux et al. 1995; Zhou et al. 2017). Wetlands are particularly oxygen limited which allows for inordinate amounts of C stabilization, but climate-driven shifts in vegetation may result in changes in oxygen delivery to wetland soils (reviewed by Chapman et al. 2019). Root-mediated changes to the soil environment can provide soil microorganisms with oxygen or other substrates that alter microbial community structure (Noll et al. 2005; Lipson et al. 2015), implying that increased decomposition rates in Mixed plots may indicate the presence of more aerobic bacteria compared to the other vegetation treatments. Though only marginally significant, low stabilization factor in Mixed plots indicates that only a small amount of material was sequestered rather than decomposed (Seelen et al. 2019), indicating a more active and efficient microbial community in mixed soils. As mangrove soils typically contain more putatively aerobic bacteria as compared to marsh-dominated soils (Barreto et al. 2018), increased oxygen availability in Mixed plots which would benefit early life-stage mangroves that lack well-developed aerenchyma (Pezeshki et al. 1991). It is also possible that increased decomposition rates in Mixed plots is the result of increased biomass associated with high percent cover in Mixed plots. Increased root mass can increase oxygenation of the soil, thereby increasing decomposition rate. It is therefore difficult to determine whether high decomposition

rates in Mixed plots was driven by increased diversity, species-specific effects, or simply an increase in root biomass. Though differences in vegetation can impact decomposition rates via leaf litter quality and plant morphology (McKee and Seneca 1982; Melillo et al. 1984), we cannot exactly tease apart the relationship between vegetation and decomposition in this study. However, we believe that the linkage between decomposition, salt marsh vegetation, and mangrove mortality is clear and it would be useful to further explore the drivers of this relationship in future studies.

Counter to our hypothesis that planting mangroves would increase decomposition, we found that mangrove planting had no influence on decomposition or stabilization factor (Fig. 4; Table 2). Adult mangroves have well-developed aerenchyma, which aids in oxygenation of their roots and may drive increased SOM decomposition in mangrove soils (Howes et al. 1986; Wigand et al. 1997; Perry and Mendhelsson 2009). However, this study used mangroves at the seedling stage which may not have well-developed enough oxygen-transporting systems to effect root oxygenation (Pezeshki et al. 1991). Furthermore, previous findings have shown that total soil respiration is highest in established mangroves compared to marsh-dominated or transitional areas (Simpson et al. 2019). Though mangrove encroachment can rapidly alter an abundance of ecosystem services, it may take anywhere from 3 years to a few decades of mangrove presence to influence SOM decomposition, if at all (Perry and Mendelsohn 2009; Osland et al. 2012; Henry and Twilley 2013; Doughty et al. 2016; Kelleway et al. 2016; Guo et al. 2017; Simpson et al. 2019). Out of 200 mangroves we planted, 120 (60 %) died within the first 3 months of our experiment, increasing to 84 % by the end of the study. It is likely that the high mangrove mortality and short duration of this study combined with the age of planted mangroves and overall dominance of marsh plant species mitigated any mangrove-driven effects on decomposition due to lack of sufficient mangrove root biomass. Though relative mangrove loss has slowed in certain parts of the world over the past few years (Friess 2016; Feller et al. 2017; Friess et al. 2020), nearly 2 % of the world's mangrove coverage has been lost between 2000 and 2012 (Hailton and Casey 2016) largely due to deforestation and habitat conversion in the tropics (Valiela et al. 2001; Spalding et al. 2010). Continued conservation efforts have contributed to the slow of mangrove decline (Freiss 2016, Freiss et al. 2020), though many attempts to restore large areas of mangrove wetlands via planting tend to fail due to a combination of inappropriate planning and lack of post-planting care (Lewis 2009; Kodikara et al. 2017). Though establishing appropriate hydrology is key for mangrove restoration (Lewis 2009), restoration efforts have shown some success in also promoting mangrove establishment

via promotion of foundational marsh species (Yando et al. 2019). Our study further supports the importance of established marsh species for mangrove success and suggests that areas of increased marsh species diversity may aid in successful mangrove restoration efforts.

Despite continued efforts to understand the global poleward encroachment of mangroves, little is understood about how existing salt marsh plant community structures may influence both continued encroachment and future mangrove restoration projects and management. Our results show that marsh plant community composition can influence the survival of mangrove seedlings, indicating that community level dynamics and plant root-driven effects may play an integral role in the continued encroachment of mangroves into salt marsh. Our study also shows that high percent cover and high decomposition rates in mixed marsh plots corresponded to increased mangrove survivorship, though the exact drivers of this relationship remains unclear. Percent cover and decomposition therefore may be developed as low-cost, simple metrics for understanding continued mangrove encroachment and for determining site suitability for mangrove restoration projects. Studies examining how salt marsh plant community composition and species zonation may relate to marsh elevation would be a valuable next step in understanding how encroaching mangroves are impacted by marsh plant community structure. Ultimately, it is important to consider the established salt marsh community structure and potential plant-root driven belowground effects as factors in understanding mangrove encroachment in a future warmer world with higher sea levels.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code Availability The code generated to analyze datasets during this current study are available from the corresponding author on reasonable request.

Declarations

Ethics Approval N/A.

Consent to Participate N/A.

Consent for Publication N/A.

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