

Species composition of patches influences mangrove recruitment in a saltmarsh mosaic

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ABSTRACT: Spatial distributions of marine and coastal plant populations are shifting in response to climate change, and interactions among organisms at ecotones may shape patterns of range expansion, such as mangrove encroachment into saltmarshes. Depending upon the environmental context, saltmarsh plants can facilitate or suppress mangrove recruitment. A field study was conducted within a mosaic saltmarsh at the edge of a mangrove forest fringing Tampa Bay, FL, USA, to investigate whether mangrove recruitment is influenced by the species composition of saltmarsh patches within which mangroves develop. Propagules of *Avicennia germinans* were emplaced into experimental plots at the same tidal elevation representing 3 saltmarsh treatments: (1) *Distichlis littoralis* in monoculture, (2) *Sporobolus virginicus* in monoculture, and (3) polycultures containing *D. littoralis*, *S. virginicus*, and at least one other species. Significantly fewer seedlings established in *S. virginicus* monocultures than in *D. littoralis* monocultures. Seedling establishment within the saltmarsh polyculture was intermediate to the grass monoculture treatments. Herbivory was the most commonly observed source of mortality for mangrove propagules, and propagules were more susceptible to herbivory within monocultures of *S. virginicus* relative to *D. littoralis* monocultures. Our results suggest that patch-scale heterogeneity in saltmarsh groundcover may influence spatial patterns of mangrove herbivory and recruitment at landward forest margins. This study builds on prior investigations and demonstrates that interactions between the same mangrove and saltmarsh species may differ between sites. Understanding these context-dependent interactions among saltmarsh plants and mangrove recruits can be useful for forecasting distributional shifts of mangrove populations and for implementing mangrove restoration.

KEY WORDS: *Avicennia germinans* · Boundary · Ecotone · Intertidal · Propagule · Seedling establishment · Herbivory

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INTRODUCTION

Boundaries between ecosystems are dynamic and shifting in response to climatic drivers such as changing rainfall patterns, increasing global temperatures, and sea-level rise (Parmesan & Yohe 2003, Poloczanska et al. 2013, Lenoir & Svenning 2015, Osland et al. 2016). Climate-driven distributional shifts have been primarily investigated in terrestrial ecosystems and have generally focused on animals (Lenoir & Svenning 2015) with fewer studies on climate-driven distributional shifts of marine plants (Short & Neckles

1999, Lenoir & Svenning 2015). However, spatial-temporal shifts driven by changing climatic conditions have been documented in diverse marine ecosystems, ranging from rocky intertidal communities along the coasts of California (Sagarin et al. 1999) and southwest Britain (Southward et al. 1995) to the kelp forests (Wernberg et al. 2016) and seagrass meadows (Hyndes et al. 2016) of western Australia. In subtropical coastal settings, ecotones between mangrove forests and saltmarshes represent dynamic boundaries in this respect at both regional (latitudinal) and local (intertidal) scales (Krauss & Allen

2003, Rogers et al. 2005, Gilman et al. 2008, Saintilan et al. 2014, Armitage et al. 2015, Osland et al. 2016, 2017).

Most studies on climate-driven distributional shifts in marine systems have been conducted at the organismal level, but the effects of certain climatic variables on a study organism may not scale up to higher ecological levels (Harley et al. 2006). Therefore, studies on the responses of populations, communities, and ecosystems to climate change are necessary for effective management (Harley et al. 2006), but such studies are relatively uncommon (Lord et al. 2017). Understanding ecological processes that influence biological boundaries (e.g. spatiotemporal dynamics of ecotonal communities) is of particular importance (Delcourt & Delcourt 1992, Wisz et al. 2013, Jiang et al. 2016). Interactions among foundation species, including interspecific interactions among plants, are recognized as altering community structure and ecosystem functions (Callaway 1995, Padilla & Pugnaire 2006, Angelini et al. 2011, Zhang & Shao 2013) and influencing distributional patterns of plants at ecotones (Risser 1995, Guo et al. 2013). The cumulative effect of plant–plant interactions reflects the outcome of a diverse suite of intraspecific and interspecific interactions that influence the distribution and abundance of each plant species with the community.

Direct interactions between plants such as competition for space, light, and nutrients can reduce the ecological niche space of the weaker competitor (Goldberg & Barton 1992, Bruno et al. 2003). Conversely, positive associations may expand niche space; e.g. one plant mediates abiotic or biotic stresses, improving the success of an associated plant (Bruno et al. 2003, Padilla & Pugnaire 2006). Indirect interactions among neighboring plants and/or sessile benthic organisms in the marine environment may also have important ecological consequences (Callaway & Pennings 2000, Callaway et al. 2005, Barbosa et al. 2009). For example, indirect interactions may decrease or increase the vulnerability of a target plant to herbivory; these types of interactions are referred to as associational resistance (Tahvanainen & Root 1972) and associational susceptibility (Rand 1999), respectively. Associational resistance or susceptibility to herbivory operate in a variety of terrestrial (Callaway et al. 2005, Barbosa et al. 2009), coastal (Stiling et al. 2003, Erickson et al. 2012), and marine habitats (Littler et al. 1986, Levenbach 2008).

Although plant–plant interactions have been widely investigated in temperate saltmarshes (Bertness & Hacker 1994, Levine et al. 1998, Pennings et al. 2003), less is known about the role of interactions

among plants in shaping the composition of other coastal and marine communities. However, ecologically important interactions between mangroves and saltmarsh plants have been documented (McKee & Rooth 2008, Guo et al. 2013, Simpson et al. 2013, Weaver & Armitage 2018), including interactions that affect early life history stages of mangroves. Mangrove recruitment (including propagule dispersal, as well as the initial establishment, growth, and survival of mangrove seedlings) is influenced by neighboring saltmarsh plants (Patterson et al. 1993, 1997, Milbrandt & Tinsley 2006, McKee et al. 2007, Peterson & Bell 2012, Donnelly & Walters 2014, Howard et al. 2015, Coldren & Proffitt 2017, Devaney et al. 2017).

Interactions between saltmarsh plants and mangrove recruits (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m602p103_supp.pdf) are expected to be nuanced based on variation in abiotic and biotic factors among geographic sites leading to constraints on plant populations and potentially fostering different types of interactions between the same (or similar) species (Friess et al. 2012). The challenge, therefore, is to identify which type of interaction has the greatest effect on mangrove recruitment. Edaphic conditions, including propagule susceptibility to desiccation, may inhibit mangrove recruitment at some sites (Clarke & Myerscough 1993, McKee 1995a, Delgado et al. 2001), but saltmarsh plants can facilitate mangrove recruits by ameliorating abiotic stressors, such as temperature and hypoxic soil conditions (McKee et al. 2007).

Alternatively, hydrological processes influencing propagule dispersal and stranding may limit mangrove recruitment (Ellison 2000). In certain circumstances, entrapment of mangrove propagules by saltmarsh plants may improve stranding and enhance subsequent establishment, thereby facilitating mangrove recruitment (Ellison 2000, McKee et al. 2007, Peterson & Bell 2012, Donnelly & Walters 2014). For example, field tests have indicated that the saltmarsh grass *Sporobolus virginicus* retains mangrove propagules (Peterson & Bell 2012) and reduces the seaward dispersal of mangrove propagules (Peterson & Bell 2015), facilitating recruitment at the landward edge of mangrove forests.

Mangrove recruitment may also be limited by pre- or post-dispersal herbivory on propagules (Smith et al. 1989, Clarke & Myerscough 1993, McKee 1995b, Farnsworth & Ellison 1997, Clarke & Kerrigan 2002, Langston et al. 2017). Herbivory on mangroves is strongly influenced by environmental context (Cannicci et al. 2008, He & Silliman 2016), and mangrove canopy cover affects herbivory on the propagules of

various mangrove species (Sousa & Mitchell 1999, Clarke & Kerrigan 2002, Clarke 2004, Devaney et al. 2017). Herbivory on mangroves also varies along tidal gradients and across zones occupied by different types of coastal vegetation, including saltmarsh plants (Smith 1987, Clarke & Myerscough 1993, Patterson et al. 1993, Langston et al. 2017). However, to date, no studies have examined whether neighboring saltmarsh plants at the same tidal elevation increase or decrease herbivory on mangrove recruits, constituting the types of interactions defined as associational resistance or associational susceptibility to herbivory, respectively (Tahvanainen & Root 1972, Rand 1999).

Our field study examined mangrove recruitment success and identified potential constraints on recruitment, including desiccation and herbivory, in a novel environmental context. Focusing on early life history stages of the black mangrove *Avicennia germinans* in a subtropical coastal ecotone, we followed the fate of mangrove propagules within patches containing different saltmarsh species located at the same tidal elevation. We tested the hypothesis that recruitment success of mangroves (i.e. propagule survival, seedling establishment, and subsequent growth) will vary depending upon the species composition of surrounding saltmarsh plants. Additionally, we hypothesized that the sources of mortality for mangrove propagules will vary among patches containing different saltmarsh species. We used direct observations of mortality to evaluate whether patterns of mangrove seedling establishment reflect abiotic conditions (e.g. death due to desiccation) or ecological interactions (i.e. susceptibility to herbivory).

Given that the morphology of saltmarsh species (i.e. canopy cover) is expected to influence patch-scale patterns of mangrove recruitment, we examined mangrove recruitment within treatments composed of structurally distinct saltmarsh plants. Specifically, mangrove recruitment was investigated within monoculture treatments containing each of 2 saltmarsh grass species with dissimilar morphological features (i.e. *Distichlis littoralis* and *Sporobolus virginicus*). Mangrove recruitment was also evaluated within a saltmarsh polyculture treatment, including both grass species used as monoculture treatments as well as additional saltmarsh species with various growth forms (i.e. forbs, shrubs, and rushes). The polyculture treatment was included as a means of determining the influence of the 2 dominant saltmarsh grass species on mangrove recruitment relative to that of the other constituents of the mosaic saltmarsh community. If mangrove recruitment differs between the 2 grasses (as expected) and

if the dominant grasses exhibit greater influence on mangrove recruitment than the suite of other saltmarsh species present within mixed assemblages, then we predict that the recruitment success of *A. germinans* in polyculture plots would be intermediate to the 2 grass monoculture treatments. Alternatively, if the composite canopy cover of all saltmarsh plants positively (or negatively) influences mangrove recruitment, then we predict that recruitment success would be greatest (or lowest) within the polyculture treatment.

MATERIALS AND METHODS

Background information

This study was conducted at Upper Tampa Bay Park (UTB; 28° 00' 26.7" N, 82° 38' 7.9" W; see Fig. S1 in the Supplement), which has a maximum elevation of approximately 2 m above sea level and supports an extensive salt-tolerant plant community. At UTB, all life history stages of the mangrove *Avicennia germinans* are scattered throughout a mosaic of saltmarsh plant patches that extends from the mangrove fringe (~50 m wide) along the coastline to the edge of the upland forest (~100 m landward of the mangrove fringe). Within this mosaic coastal landscape, small isolated patches of saltmarsh vegetation (typically <3 m in diameter) occur within mudflats and larger continuous patches (varying from 1 to 10s of m wide) border mudflat areas. Some saltmarsh plants form discrete monoculture patches although multispecies assemblages are typically encountered. The species composition of saltmarsh plant assemblages varies across the intertidal gradient. Succulent saltmarsh plants are generally dominant near the mangrove fringe and edges of mudflats; grasses typically dominate higher intertidal areas and the interior portions of saltmarsh patches. Other types of salt-tolerant plants (i.e. forbs, rushes, and shrubs) are scattered throughout the mangrove-marsh mosaic at UTB.

A mixture of saltmarsh patches with different species composition located along the same tidal elevation at UTB provided an optimal setting for investigating the effect of saltmarsh vegetation on mangrove recruitment. The co-occurrence of mangrove propagules and a mosaic of saltmarsh vegetation at the same tidal elevation provides a setting in which the influence of potential confounding effects caused by abiotic and biotic factors that vary across tidal gradients is minimized. Moreover, the study site is historically inundated infrequently (during storm

surges). Inundation of the study site was observed only once during several years of preliminary observations, as evidenced by the wrack line deposited at the upland forest boundary following the passage of Hurricane Isaac in 2012. Following typical high tide events, the wrack line has been located near the landward boundary of the mangrove fringe, approximately 100 m seaward of the study site (Fig. S1). Therefore, tidal dispersal of propagules was predicted to be minimal, considering the low probability of inundation and the capacity for saltmarsh grasses to entrap and retain mangrove propagules (Peterson & Bell 2012).

The fate of mangrove recruits at UTB may include mortality (i.e. lethal damage) or loss (i.e. complete consumption) due to herbivory. Herbivorous crabs are notorious predators of mangrove propagules in Florida and at other sites worldwide (Allen et al. 2003, Bosire et al. 2005, Sousa & Dangremond 2011). *Sesarma* sp. crabs and other known mangrove herbivores, such as grasshoppers and crickets (Orthoptera), are abundant throughout the mangrove–saltmarsh ecotone at UTB (J. Peterson pers. obs.). We visually assessed patterns of damage (i.e. features such as bite marks) made by a few herbivores (i.e. *Sesarma* sp. and Orthoptera) collected at our study site in the laboratory (Fig. S2 in the Supplement), and we used these anecdotal observations to verify herbivory on propagules in this field study.

Experimental design

Prior to experimental trials, we collected background information on saltmarsh plants and mangrove recruits to characterize the mosaic landscape at UTB. The community composition of saltmarsh patches was investigated using a series of transects ($n = 6$). Transects extended from the edge of a mudflat, spanned across the supratidal mangrove–saltmarsh mosaic area, and terminated at the upland forest boundary. Transect length ranged from 15 to 60 m. We positioned a quadrat (0.5×0.5 m, subdivided into 16 subsections) at 5 m intervals along each transect and surveyed a total of 48 quadrats. Within each quadrat, we recorded the density of *A. germinans* and quantitatively estimated the ground-cover of each saltmarsh species (i.e. percentage of quadrat subsections within which each saltmarsh species was rooted). Based on this survey, the 2 most abundant saltmarsh species that co-occurred with *A. germinans* were *Distichlis littoralis* and *Sporobolus virginicus* (see 'Results'). These 2 grass species were

therefore selected as focal species for experimental treatments.

To investigate the effect of saltmarsh vegetation on *A. germinans* recruitment, experimental plots (0.5×0.5 m; $n = 30$) were established at UTB within the saltmarsh mosaic positioned between an unvegetated mudflat and upland forest (Figs. S1 & S3 in the Supplement). On 28 September 2012, experimental plots were weeded by hand to establish 10 replicate plots for each of 3 saltmarsh treatments: (1) *D. littoralis* in monoculture, (2) *S. virginicus* in monoculture, and (3) natural polyculture containing both *D. littoralis* and *S. virginicus* and at least one other saltmarsh species. Natural polyculture plots contained mixtures of grasses, forbs, shrubs, and rushes.

Replicate plots of each saltmarsh treatment were interspersed throughout the saltmarsh mosaic; the size of experimental plots and spacing between plots reflected the spatial scale of heterogeneity in saltmarsh plant cover at the study site. Monoculture plots were created where the target grass species was abundant and other saltmarsh plants were sparse to minimize weeding of non-target species, and care was taken to minimize soil disturbance. Polyculture plots were not weeded; instead, the natural assemblage of saltmarsh plants (3 to 6 species) was maintained, and a trowel was used to mimic disturbance that resulted from weeding to create monoculture plots. Neither the biomass nor density of saltmarsh vegetation was quantified or standardized in this field study. The density and biomass of saltmarsh vegetation varied visibly among experimental plots (within and between saltmarsh treatments) due to the natural heterogeneity of saltmarsh plant cover at UTB (Fig. S4 in the Supplement).

Once experimental plots were established, propagules were collected on 28 September 2012 from *A. germinans* trees at UTB. Pericarps were removed from propagules so that propagules could be inspected for pre-dispersal damage by insects, a prevalent problem at our study site (J. Peterson pers. obs.) that can decrease viability of mangrove propagules (Farnsworth & Ellison 1997, Sousa et al. 2003) and subsequent growth of seedlings (Minchinton & Dalby-Ball 2001). Pericarps are typically shed quickly following primary dispersal, and removal of the pericarp does not influence buoyancy (Rabinowitz 1978), unlike propagules of the congeneric mangrove *A. marina* (Clarke & Myerscough 1991).

On 29 September 2012, damage-free propagules were randomly assigned to experimental plots ($n = 9$ plot $^{-1}$; 270 total). This study was conducted relatively late in the fruit-fall season, and the density of

unrooted propagules was low at our site at this time (Table S2 in the Supplement). Any naturally recruited mangroves within and around experimental plots were identified and removed so that only those propagules emplaced into plots were assessed. We placed unmarked propagules flat on the sediment surface approximately 10 cm apart from one another in the center of experimental plots (i.e. the innermost 0.0625 m² section). We determined that tethering of propagules was unnecessary due to the low likelihood of tidal dispersal at our study site. Enclosures were not used to exclude herbivores from plots in this field study because these structures may have altered shading, which could have affected propagule susceptibility to desiccation (see 'Results').

Mangrove monitoring

The fate of propagules was surveyed a total of 7 times, from Day 6 until Day 266 after emplacement into plots. Surveys were conducted 4 times in October 2012, once each in November and December 2012, and once in June 2013. Propagules remaining within experimental plots were counted, and any propagules that were located outside of plots or that were not found (i.e. missing) were recorded as lost. During each monitoring event, all propagules remaining within plots were visually inspected and their condition and viability were noted. Propagules were carefully handled during the assessment so that their condition was not affected. The number of propagules within each plot that had incurred herbivory on cotyledons and the severity of herbivory on cotyledons were recorded. Cotyledon damage was visually assessed for each half of the 2 cotyledons (4 sections), and the number of cotyledon sections damaged was recorded (0 to 4); damage to the hypocotyl was also noted.

Propagule viability was assessed, and the source of mortality (herbivory or desiccation) was recorded. Deaths were attributed to herbivory when the hypocotyl had been fatally damaged or that $\geq 75\%$ (i.e. 3 of the 4 sections) of the propagule cotyledon biomass had been consumed. A threshold of $\geq 50\%$ damage has been used by previous studies to classify propagules as non-viable (Clarke 1992, McKee 1995b), but we utilized a stricter threshold here based upon our earlier observations that propagules that had lost 50% of their cotyledons were able to establish themselves as seedlings. Death was attributed to desiccation if all cotyledons were severely dehydrated, as evidenced by brittle texture and discoloration.

Establishment success was evaluated for all mangroves remaining within plots. Establishment was determined to be successful if a recruit firmly rooted in the sediment and transitioned to an upright seedling. On each sampling date, the number of seedlings that established within plots was counted. The growth of seedlings was determined by measuring height to the nearest 5 mm and counting the number of true leaves.

Statistical analyses

The effect of saltmarsh treatments on the recruitment success of *A. germinans* remaining within experimental plots on the final sampling date, 22 June 2013 (266 d after emplacement) was analyzed with 1-way ANOVA tests for (1) number of established (rooted and upright) seedlings, (2) mean seedling height, and (3) mean number of leaves produced by seedlings. For all ANOVA tests, experimental plot was used as the unit of replication, and propagules remaining within plots were considered subsamples. When a significant effect of saltmarsh treatment was detected ($p < 0.05$), patterns were analyzed using the Tukey post hoc test.

The effect of saltmarsh treatments on herbivory observed on propagules during the first survey event on 5 October 2012 (6 d after emplacement) was assessed using 1-way ANOVA tests for (1) frequency of herbivory (percentage of individuals with damage to cotyledons) and (2) severity of herbivory (mean number of cotyledon sections damaged on individuals that had experienced herbivory). The $\sqrt{(x + 1)}$ transformation was applied to data for both metrics of herbivory.

A Cox proportional hazard (CPH) time-to-failure analysis was used to compare the risk of *A. germinans* loss from saltmarsh treatment plots over all sampling dates (Cox 1972, Fox 2001). The hazard ratio output from this analysis describes the relative rate of propagule loss between saltmarsh treatments; if the 95% confidence interval for the hazard ratio includes 1, then no significant effect of the treatment is indicated. The coefficient of the Cox regression indicates whether the treatment was negatively or positively associated with the hazard (i.e. risk of loss). The date on which an individual was no longer recorded as present was designated as the failure time (i.e. number of days after propagule emplacement into plots), and individuals remaining in plots at the end of the experiment were coded as censored (Cox 1972, Fox 2001). Analyses were performed with Statistica 10 and SigmaPlot 12.

Table 1. Characterization of the saltmarsh community at the study site in Upper Tampa Bay on 21–22 September 2012. Transect survey data are reported separately for all quadrats ($n = 48$) and for quadrats containing *Avicennia germinans* ($n = 16$). The frequency of occurrence (% of quadrats containing a particular species) and mean (\pm SE) groundcover (% of subsections in quadrat within which a particular species was rooted) are reported for each saltmarsh plant species. The greatest groundcover value (i.e. maximum % cover) recorded for each saltmarsh species within any of the quadrats containing *A. germinans* is also reported

Saltmarsh species	All quadrats		Quadrats containing <i>A. germinans</i>		
	Quadrats (%)	Cover (%)	Quadrats (%)	Cover (%)	Max. cover (%)
<i>Sporobolus virginicus</i>	72.9	68.9 (6.5)	68.8	59.8 (11.8)	100.0
<i>Distichlis littoralis</i>	47.9	39.3 (6.5)	68.8	56.3 (11.2)	100.0
<i>Batis maritima</i>	70.8	37.2 (4.9)	56.3	42.2 (10.7)	93.8
<i>Borrchia frutescens</i>	56.3	24.2 (4.3)	50.0	23.8 (8.4)	93.8
<i>Sesuvium portulacastrum</i>	41.7	21.7 (4.8)	43.8	27.3 (10.3)	100.0
<i>Limonium carolinianum</i>	29.2	3.9 (1.4)	31.3	2.7 (1.1)	12.5
<i>Blutaparon vermiculare</i>	29.2	11.1 (3.3)	25.0	5.9 (3.1)	43.8
<i>Distichlis spicata</i>	20.8	3.6 (1.2)	18.8	4.3 (2.6)	37.5
<i>Juncus roemarianus</i>	20.8	8.3 (3.2)	6.3	0.8 (0.8)	12.5
<i>Spartina patens</i>	16.7	8.5 (3.5)	6.3	3.1 (3.1)	50.0

RESULTS

Vegetation surveys

Avicennia germinans spanning all life history stages (i.e. propagules, seedlings, and saplings) were present within the saltmarsh mosaic at our study site (see Table S2 in the Supplement), which was proximate to the upland forest boundary (Fig. S1). *A. germinans* co-occurred with a suite of saltmarsh species, including *Batis maritima*, *Sesuvium portulacastrum*, *Borrchia frutescens*, and *Limonium carolinianum* (Table 1). However, these saltmarsh plants generally contributed less to total canopy cover than the 2 dominant saltmarsh grasses, *Sporobolus virginicus* and *Distichlis littoralis*, which frequently co-occurred with *A. germinans* (Table 1). The blade length and shoot height of *S. virginicus* and *D. littoralis* were conspicuously different; blades of *S. virginicus* (typically ≥ 3 cm) were several times as long, and shoots (typically ≥ 20 cm) nearly twice as tall as *D. littoralis* at UTB (J. Peterson pers. obs.). Accordingly, at UTB, the canopy cover provided by *S. virginicus* was markedly greater than that provided by *D. littoralis* (Fig. S4).

The density of early life history stages of *A. germinans* varied across the site. Propagules and seedlings of *A. germinans* were most dense in quadrats proximate to conspecific adults, where the canopy cover of *S. virginicus* was generally high (Table S2). In areas further from adult conspecifics, the density of *A. germinans* propagules and seedlings was typically lower

in quadrats where *S. virginicus* cover was high. Anecdotal observations of *A. germinans* condition during this preliminary survey indicated that cover of *S. virginicus* may influence the fate of mangroves: several propagules in quadrats where *S. virginicus* was absent had signs of desiccation, and a few propagules in quadrats with 100% cover by *S. virginicus* had evidence of herbivory.

Establishment success of mangroves

Black mangrove seedlings successfully established in all 3 saltmarsh treatments (Fig. 1). Propagules began rooting 6 d after emplacement, and the majority

(67%) of propagules remaining within plots had established by 17 October 2012, only 18 d after propagule emplacement into plots. On 14 December 2012, 76 d after propagules were emplaced in experimental plots, 92% of those remaining had successfully established. All *A. germinans* individuals remaining within experimental plots on the final sampling date, 266 d after propagule emplacement into plots, were alive and had successfully established as upright seedlings with true leaves. Overall, 38% of all mangroves examined in this study remained within experimental plots throughout the duration of this experiment and established as seedlings.

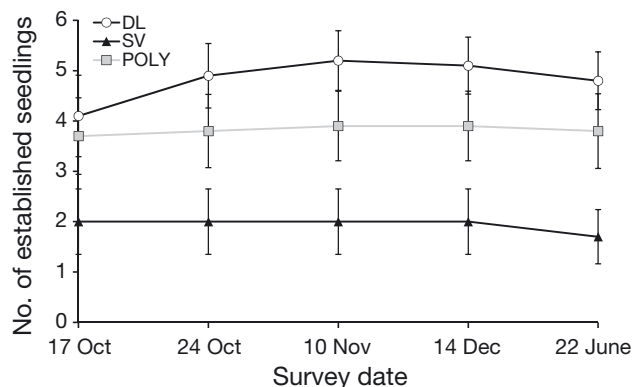


Fig. 1. Mean number of *Avicennia germinans* seedlings established in experimental plots on each survey date. Data for 5 October 2012 are not presented because no seedlings had established at that time. Saltmarsh treatments: DL: *Distichlis littoralis* monoculture; SV: *Sporobolus virginicus* monoculture; POLY: polyculture. Error bars: \pm SE

Establishment success of *A. germinans* (i.e. the number of upright, rooted seedlings within plots) on the final sampling date, 22 June 2013, differed significantly among saltmarsh treatments (ANOVA, $F_{2,27} = 6.419$, $p = 0.005$; Fig. 1). On this date, 38 wk after emplacement, establishment success of *A. germinans* differed significantly between the 2 monoculture treatments (Tukey post hoc test, $p = 0.004$), with higher numbers of seedlings in *D. littoralis* ($n = 48$; 53% of propagules initially emplaced) compared to *S. virginicus* ($n = 17$; 18.9% of propagules) monoculture plots. The number of *A. germinans* that established in polyculture plots ($n = 38$) did not significantly differ from that in *D. littoralis* (Tukey post hoc test, $p = 0.503$) or *S. virginicus* (Tukey post hoc test, $p = 0.062$) monoculture plots.

In contrast to the strong influence of saltmarsh treatment on establishment success of seedlings, growth of seedlings was not significantly different among saltmarsh treatments. Neither seedling height (ANOVA, $F_{2,22} = 0.628$, $p = 0.543$; Fig. 2a) nor number of leaves (ANOVA, $F_{2,22} = 2.017$, $p = 0.157$; Fig. 2b) differed among saltmarsh treatments. On the final sampling date, the height of seedlings (mean \pm SD) within *S. virginicus* monoculture plots (9.0 ± 2.4 cm) and polyculture plots (8.9 ± 1.4 cm) was only slightly greater than the height of seedlings in *D. littoralis* monoculture plots (8.2 ± 1.2 cm) (Fig. 2a). The overall mean number of leaves per seedling across all experimental plots was 3.9 ± 0.9 at the experiment's conclusion.

Observed sources of mangrove mortality

Direct observations of mortality provided insight into the fate of mangroves that did not successfully establish within experimental plots. Two visually conspicuous sources of mortality (herbivory and desiccation) were identified for mangrove propagules remaining within experimental plots (Table 2). Almost all deaths were attributed to herbivory ($n = 33$); only 6 propagules died from desiccation. Sources of mangrove propagule mortality varied among saltmarsh treatments. Mortality due to desiccation was only recorded in *D. littoralis* monoculture plots,

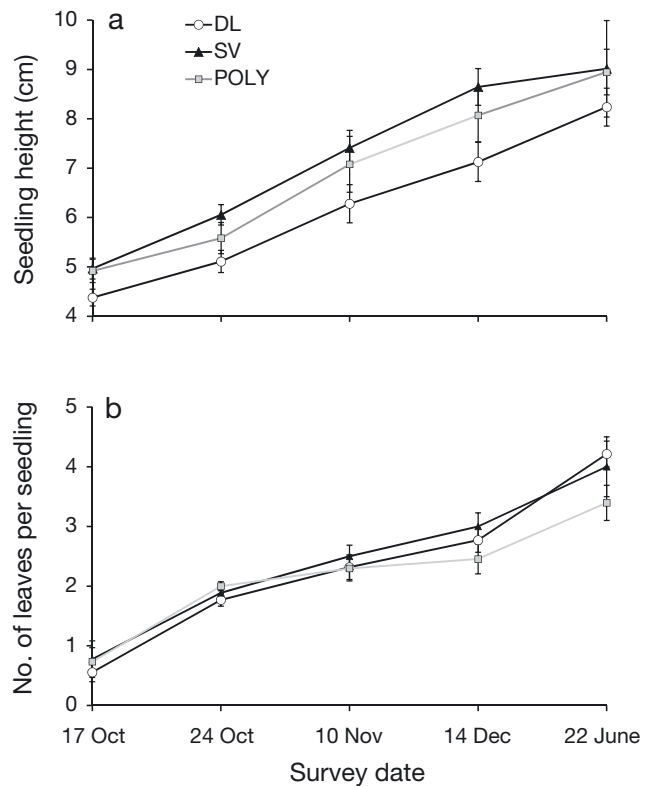


Fig. 2. (a) Mean height (cm) of *Avicennia germinans* seedlings established in each experimental plot on each survey date, and (b) mean number of leaves produced by *A. germinans* seedlings established within experimental plots on each survey date. Data for 5 October 2012 are not presented because no seedlings had established at that time. Saltmarsh treatments: DL: *Distichlis littoralis* monoculture; SV: *Sporobolus virginicus* monoculture; POLY: polyculture. Error bars: \pm SE

Table 2. Fate of propagules (total of 270) originally emplaced into experimental plots ($n = 9$ plot⁻¹, 10 plots treatment⁻¹) by date. The number of *Avicennia germinans* remaining within experimental plots for which the cause of death was directly observed and attributed to desiccation or herbivory is presented. The total number of *A. germinans* lost from experimental plots (i.e. individuals that were not found during visual inspections and the few located outside of experimental plots) for each of the saltmarsh treatments is also presented; loss reported on each survey date represents the cumulative loss from plots. Results are presented for each survey date and for each of the 3 saltmarsh treatments: *Distichlis littoralis* monoculture (DL), *Sporobolus virginicus* monoculture (SV), and polyculture (POLY)

Survey Days	Survey Date	Desiccation			Herbivory			Lost from plots		
		DL	SV	POLY	DL	SV	POLY	DL	SV	POLY
6	5 Oct	0	0	0	1	5	2	14	26	22
11	10 Oct	0	0	0	1	6	9	15	36	29
18	17 Oct	0	0	0	0	1	1	19	65	39
25	24 Oct	0	0	0	1	0	2	25	67	41
42	10 Nov	3	0	0	0	0	2	32	69	45
76	14 Dec	3	0	0	1	0	1	33	70	48
266	22 June	0	0	0	0	0	0	42	73	52

and propagules emplaced into *D. littoralis* monoculture plots had the fewest deaths observed. Deaths attributed to herbivory most frequently occurred within the 2 treatments containing *S. virginicus*: 36 and 52% of the herbivory-related deaths occurred within *S. virginicus* monoculture and polyculture plots, respectively. Over all treatments, propagule mortality due to herbivory was most frequently observed during the first 2 wk of the experiment (Table 2).

A time-to-failure analysis of observed mortality data for *A. germinans* remaining in plots was not possible because of data censorship (Cox 1972, Fox 2001). Data were censored because most *A. germinans* were lost over the duration of the experiment and all *A. germinans* remaining in plots were alive on the final sampling date. All individuals recorded as non-viable were ultimately lost from experimental plots.

Herbivory on mangroves

Although fatal herbivory was observed for only 12% of the 270 propagules that were emplaced into experimental plots, non-lethal levels of herbivory were frequently observed on propagules. Herbivory results presented here represent damage to propagules that remained within experimental plots. Herbivory data are not presented for the December 2012 or June 2013 surveys because cotyledons had dropped from seedlings (due to the depletion of nutrients).

Herbivory was greatest during the first 2 wk after propagule emplacement into experimental plots. On 5 and 10 October 2012, 38.8 and 40.8% respectively of propagules had damaged cotyledons. Because a large proportion of propagules were lost from plots after 5 October 2012, herbivory data were analyzed for that survey date only. At this time, propagule damage due to herbivory was observed within all but one of the experimental plots, and the saltmarsh treatment into which propagules were emplaced had a significant effect on the percentage of individuals sustaining herbivory on cotyledons (ANOVA, $F_{2,27} = 3.6583$, $p = 0.039$; Fig. 3a). A significantly greater percentage of *A. germinans* within *S. virginicus* monoculture plots had herbivory on cotyledons compared to those within *D. littoralis* monoculture plots (Tukey post hoc test, $p = 0.031$). Fewer *A. germinans* within polyculture plots had damaged cotyledons (mean \pm SD for plots: $37 \pm 21.7\%$) compared to those within *S. virginicus* monocultures ($55.6 \pm 35.3\%$), although

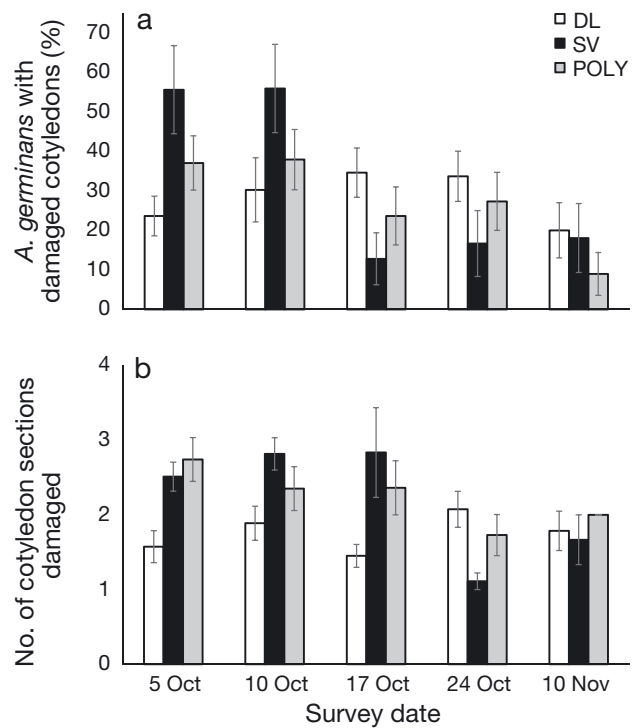


Fig. 3. (a) Frequency of herbivory: mean percentage of *Avicennia germinans* remaining in plots that had damaged cotyledons, and (b) severity of herbivory: mean number of cotyledon sections damaged on *A. germinans* remaining within plots that experienced herbivory. Saltmarsh treatments: DL: *Distichlis littoralis* monoculture; SV: *Sporobolus virginicus* monoculture; POLY: polyculture. Error bars: \pm SE. Herbivory data for December 2012 and June 2013 are not presented because cotyledons had dropped from seedlings prior to these survey dates

this difference was not significant (Tukey post hoc test, $p = 0.340$). Likewise, the percentage of *A. germinans* within polyculture plots with damaged cotyledons was not significantly different from those within *D. littoralis* monoculture plots ($23.6\% \pm 15.9$) (Tukey post hoc test, $p = 0.370$).

On 5 October 2012, the mean number of cotyledon sections damaged per *A. germinans* differed significantly among saltmarsh treatments (ANOVA, $F_{2,26} = 6.8310$, $p = 0.004$; Fig. 3b). Propagules within *D. littoralis* monoculture plots had fewer damaged cotyledon sections compared to propagules within *S. virginicus* monocultures and polyculture plots (Fig. 3b), and both differences were significant (Tukey post hoc test, $p = 0.020$ and 0.005 , respectively). The mean number of cotyledon sections damaged on propagules in polyculture and *S. virginicus* monoculture plots was not significantly different (Tukey post hoc test, $p = 0.830$).

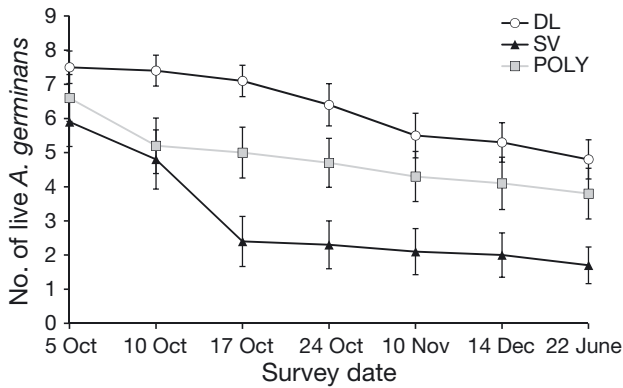


Fig. 4. Mean number of live *Avicennia germinans*, including both propagule and seedling stages, in experimental plots on each survey date. Saltmarsh treatments: DL: *Distichlis littoralis* monoculture; SV: *Sporobolus virginicus* monoculture; POLY: polyculture. Error bars: \pm SE

Loss of mangroves from experimental plots

The number of *A. germinans* remaining alive within experimental plots declined over time (Fig. 4). Loss from plots was the most commonly observed fate of mangroves in this field study. At least one of the emplaced mangroves was lost from each of the experimental plots by the end of this study. Mangrove loss from plots waned over time (Table 2). Mangrove loss from plots was generally greatest between the date of emplacement (29 September 2012) and the first survey (5 October 2012) and was lowest after most individuals had established as upright seedlings (17 October 2012). Only 7 propagules (4.2% of the 167 individuals that were ultimately lost from plots) were located outside of the perimeter of experimental plots during this study; no other individuals recorded as lost from plots were relocated.

The CPH time-to-failure analysis revealed a significant effect of saltmarsh treatment on the risk of mangrove loss from plots over the duration of the experiment (Global chi-squared, $\chi^2 = 25.733$, $df = 2$, $p <$

0.001; Table 3). The risk of loss from plots was significantly greater for the mangroves in *S. virginicus* monoculture plots than in the other 2 saltmarsh treatments ($p < 0.05$; Table 3). On the final sampling date, only 18.9% of the mangroves emplaced into *S. virginicus* monoculture plots remained (Table 2) with 6 of the 10 *S. virginicus* monoculture plots containing mangroves. Conversely, on the final sampling date at least 1 mangrove remained within each of the 10 *D. littoralis* monoculture plots. In fact, 53.3% of *A. germinans* emplaced within *D. littoralis* monocultures and 42.2% emplaced in polyculture plots remained on 22 June 2013 (Table 2). The risk of mangrove loss from polyculture plots was not significantly different from that in *D. littoralis* monoculture plots ($p = 0.071$; Table 3).

Spatiotemporal patterns of mangrove propagule loss from plots were similar to direct observations of herbivory on *A. germinans* remaining within plots. Specifically, propagule loss from plots and the frequency of lethal and non-lethal herbivory on propagules remaining within plots were the greatest during the first several weeks of the experiment. Moreover, *S. virginicus* monoculture plots had the greatest number of propagules lost, and the treatments containing *S. virginicus* had the greatest number of observed deaths due to herbivory, as well as the greatest frequency and severity of herbivory on propagules remaining within plots. Based on these results, we postulate that the loss of propagules from plots at UTB for which a source of mortality could not be directly observed nor definitively assigned may reflect their complete consumption.

DISCUSSION

As mangrove boundaries shift toward higher tidal elevations and higher latitudes (Gilman et al. 2008, Krauss et al. 2014, Osland et al. 2016), mangrove recruits at the leading edge of expansion interact with

diverse assemblages of saltmarsh species including grasses, shrubs, rushes, and forbs. Understanding the suite of potential ecological interactions by which saltmarsh species may inhibit or facilitate recruitment of mangroves is therefore of critical importance to predict and manage retreat of these coastal plant commu-

Table 3. Cox proportional hazard results, including 95% confidence intervals (CI) and standard error values (SE), are presented for the risk of propagules lost from experimental plots over the study duration, 29 September to 22 June 2013. See Table 2 for number of *Avicennia germinans* lost from experimental plots. Results are presented for each of the 3 saltmarsh treatments: *Distichlis littoralis* (ML) monoculture, *Sporobolus virginicus* (SV) monoculture, and polyculture (POLY). Significant p-values are in **bold**

	Hazard Ratio (CI)	Coefficient (CI)	SE	Wald χ^2	p-value
SV (vs. DL)	2.557 (1.740–3.757)	0.939 (0.554–1.324)	0.196	22.844	<0.001
SV (vs. POLY)	1.757 (1.228–2.515)	0.564 (0.205–0.922)	0.183	9.479	0.002
DL (vs. POLY)	0.687 (0.457–1.033)	-0.375 (-0.782–0.032)	0.208	3.260	0.071

nities. By following the fate of early life history stages of mangroves within a saltmarsh mosaic, we revealed evidence of ecologically significant interactions between saltmarsh species and *Avicennia germinans*. Our results demonstrate a 2-fold difference in mangrove establishment success at the scale of meters, related to the spatial heterogeneity in saltmarsh plant assemblages. While previous reports have documented that saltmarsh plants displaying contrasting growth forms (i.e. succulents vs. grasses) differentially affect mangrove dispersal, stranding, and seedling establishment (Peterson & Bell 2012, 2015), findings from the current study emphasize that, post-stranding, the fate of recruiting mangroves is affected by the structural features of saltmarsh grass canopies.

Notably, the results of this field study suggest that interactions between mangrove recruits and saltmarsh grass canopies are dependent upon the environmental setting. We demonstrated that mangrove recruits within patches containing *Sporobolus virginicus* experienced associational susceptibility to herbivory at UTB. Yet at another field site in Naples, FL (where herbivory was minimal), the same grass species facilitated recruitment at landward forest margins by entrapping propagules and reducing seaward dispersal (Peterson & Bell 2012, 2015). Mangrove–saltmarsh interactions are also known to be variable along intertidal and latitudinal gradients (Guo et al. 2013) and with respect to the concentration of nitrogen and carbon dioxide (McKee & Rooth 2008). Thus, interactions between the same mangrove and saltmarsh plants may differentially influence patterns of mangrove encroachment at disparate sites in Florida and other parts of the world where these species co-occur.

Our results emphasize a key suite of interactions between saltmarsh plants and mangroves during their earliest life history stages. The results of our field study reaffirm evidence from prior studies showing that herbivory on mangrove propagules is most intense prior to seedling establishment, during the stranding phase, when propagules are in a prone position on the sediment (Bosire et al. 2005). However, seedling growth (i.e. height and leaf number) at UTB was not affected by the composition of saltmarsh plant patches, indicating that the only long-term consequence of saltmarsh–mangrove interactions during the course of our experiment was the number of individuals that established. Previous studies on larger mangrove seedlings and saplings have documented that the growth rate and leaf characteristics of mangroves can be altered by competi-

tion with saltmarsh plants (Patterson et al. 1993, McKee & Rooth 2008, Simpson et al. 2013). Given that plant–plant interactions between the same species can differ between life history stages (Guo et al. 2013, Wright et al. 2014), the species composition of saltmarsh plant assemblages within which mangroves recruit may have different ecological consequences during later life history stages than those examined in our study. Therefore, an examination of all possible interactions across every life history stage is necessary to determine the net effect of saltmarsh associates on mangroves (see Table S1).

Identifying principal interactions between mangrove and saltmarsh plants that have the greatest effect on propagule mortality and/or recruitment failure is essential for managing sustainable mangrove populations. In this study, herbivory was the most frequently observed source of mortality for propagules within experimental plots. Although previous work has shown that mangrove herbivory varies depending on landscape context, such as intertidal location (Patterson et al. 1997) and type of mangrove canopy (Smith et al. 1989, McKee 1995b, Erickson et al. 2012), our findings provide novel evidence that the identity of saltmarsh grasses influences the relative susceptibility of mangrove propagules to herbivory within a subtropical mangrove–saltmarsh ecotone.

The specific ecological processes operating at our study site that resulted in significant differences in herbivory on mangrove propagules within 2 distinct saltmarsh grass monocultures occupying the same intertidal position and separated by only a few meters remain to be determined. However, Barbosa et al. (2009) and Hambäck et al. (2014) noted that the nature of associations between neighboring plants is determined by traits of those plants and their herbivore(s) that affect the foraging behaviors of herbivores. Differences in the susceptibility of mangroves to herbivory within the saltmarsh treatments examined in our study could be due to plant traits that affect their relative palatability to local herbivores, such as nutritional value or defense mechanisms. If so, then the reduced susceptibility of propagules to herbivory within the *Distichlis littoralis* treatment at UTB may be analogous to reports of reduced consumption of several taxonomically and morphologically distinct species of marine algae by herbivorous fish in the presence of the chemically defended brown alga, *Styopodium zonale* (Littler et al. 1986).

Alternatively, morphological differences between the saltmarsh grasses could explain patch-scale differences in the susceptibility of mangrove propagules to herbivory. The comparatively high suscepti-

bility of propagules to herbivory (i.e. associational susceptibility) within patches of *S. virginicus* at UTB may be explained by the superior canopy cover of this grass. Herbivores at UTB may preferentially forage for mangrove propagules under the shaded canopy of *S. virginicus* and forage less frequently within the comparatively more exposed patches of *D. littoralis*, whose smaller blades provide less protection from desiccation (Fig. S4). This aligns with our observations that propagules only died from desiccation within the *D. littoralis* monoculture plots, as well as the propagule desiccation and herbivory we noted during preliminary vegetation surveys.

The intermediate success of mangrove recruitment within the saltmarsh polyculture treatment relative to the 2 grass monoculture treatments indicates that the presence of these 2 dominant grasses may have a stronger influence on early life history stages of *A. germinans* than other species of saltmarsh plants at UTB. Based on our prior work (Peterson & Bell 2012, 2015), we suspect that the structure of *S. virginicus* may have a disproportionately large effect on mangrove recruitment. Additional work is necessary to quantify the biomass, shoot density, and morphometrics of saltmarsh plants in monoculture and mixed assemblages. Gathering information on the structure and abundance of saltmarsh plants combined with direct measurements of abiotic conditions (i.e. irradiance and temperature) and herbivore foraging behaviors should provide insight into the specific mechanisms by which saltmarsh plants alter mangrove susceptibility to herbivory.

We suggest that the effect of saltmarsh plant canopy structure on abiotic conditions may alter herbivore behavior and influence spatial patterns of mangrove recruitment in other ecotonal saltmarshes with heterogeneous patch composition such as those at UTB. This suggestion of amelioration of abiotic conditions altering herbivore foraging behavior aligns with observations in other coastal and marine systems; for example, He & Cui (2015) demonstrated that the foraging range of the herbivorous crab *Helice tientsinensis* at a saltmarsh–upland ecotone was expanded when abiotic stress was ameliorated by a nurse shrub, *Tamarix chinensis*. Similarly, in the rocky-intertidal, the herbivorous chiton *Katharina tunicata* preferentially forages under the canopy-forming alga *Hedophyllum sessile*, which serves as a refuge from sublethal thermal stress (Burnaford 2004). However, amelioration of abiotic conditions is not the only feasible explanation for differences in herbivore foraging behavior among our experimental treatments; herbivores seeking refuge from pre-

dition may also prefer to forage in areas with dense canopy cover. For example, herbivory on *Posidonia australis* seeds differs between seagrass patches because seagrass herbivores in this case preferentially forage within the patches with greater structural complexity to avoid predators (Orth et al. 2006).

Based upon our findings that spatial differences in patterns of mangrove recruitment may be linked to susceptibility to herbivory, we suggest that identifying specific ecological processes that influence herbivory on mangroves at UTB is of paramount importance. The effect of herbivory on mangrove recruitment at UTB becomes more remarkable if one considers that the complete consumption of propagules by herbivores may be the underlying cause of propagule loss from plots reported in this field study. We suspect that propagule loss was the result of complete consumption by herbivores based upon the similar spatiotemporal patterns of herbivory observed on propagules remaining within plots and propagule loss from plots. The complete consumption of *A. germinans* propagules at UTB appears to be a feasible scenario given our observations that herbivores consume all parts of propagules (cotyledon and hypocotyl biomass), and on some occasions only small fragments of propagules remained within plots prior to the complete loss of these individuals. Herbivores (e.g. grasshoppers, crickets, and *Sesarma* sp. crabs) were also observed in and near experimental plots during this study. Moreover, if tidal dispersal of propagules out of plots was responsible for loss, then we would have expected plots containing *S. virginicus* to have had the least loss (Peterson & Bell 2012); the opposite was observed at UTB.

The suggested depletion of propagules by herbivores has been offered previously; many other studies on post-dispersal seed predation have reported the complete removal of seeds by herbivores (Hulme 1998). In fact, *Avicennia* propagules are often consumed by herbivores because of their high nutritional value and low levels of defensive compounds (Smith 1987, McKee 1995b, Sousa & Dangremond 2011). McKee (1995b) reported that all *A. germinans* propagules emplaced within the *Rhizophora mangle* zone inland of a Belizean creek bank were fatally damaged by herbivores within 6 d of emplacement. Similarly, Smith et al. (1989) found 72% of *A. germinans* propagules at a site in south Florida to be damaged fatally after only 4 d. In northern Florida, Langston et al. (2017) found that 99% of uncaged *A. germinans* propagules were consumed by grapsid crabs within 12 d. These findings suggest that herbivory may reduce the recruitment success of *A. ger-*

minans at sites throughout Florida and the Caribbean. Yet to date, no regional studies have been done to investigate the conditions under which associational susceptibility to herbivory influences mangrove recruitment.

Interactions between saltmarsh plants and mangroves, such as the associational susceptibility of *A. germinans* to herbivory that was demonstrated in this field study, may not obstruct mangrove recruitment entirely. At UTB, some mangrove propagules escape herbivory or establish despite herbivory, as evidenced by the fate of recruits in our experiment and by the presence of mangrove seedlings and saplings throughout the saltmarsh mosaic landscape (Figs. 1, S1 & S3, Table S2). However, the effects of herbivory during recruitment should not be considered inconsequential for *A. germinans*. Viewed more broadly, factors that limit recruitment success will likely reduce the rate of landward expansion for this species. Mangrove–saltmarsh interactions that decrease recruitment should therefore be considered when forecasting spatiotemporal patterns of mangrove encroachment with sea-level rise.

Additionally, we suggest that understanding context-dependent mangrove–saltmarsh interactions and their effects on mangrove seedling establishment is pertinent to designs for wetland restoration. For example, interactions that facilitate or impede mangrove recruitment should be considered when selecting saltmarsh species to plant at restoration sites. Science-based management of coastal plant communities, including the application of empirical evidence on plant–plant interactions at ecotones such as reported here, will be critical to ensure the continued provision of coastal ecosystem functions (Granek & Ruttenberg 2007, Barbier et al. 2011, Moody et al. 2013, Friess & Webb 2014, Mukherjee et al. 2014). Ecosystem management will be especially important as mangroves continue to expand their distribution into areas currently occupied by saltmarshes (Armitage et al. 2015, Doughty et al. 2016, Yando et al. 2016, Kelleway et al. 2017, Smee et al. 2017).

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