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Predation restricts black mangrove (*Avicennia germinans*) colonization at its northern range limit along Florida's Gulf Coast

Amy K. Langston · David A. Kaplan · Christine Angelini

Abstract Climate change-driven range expansion of black mangroves (*Avicennia germinans*) is predicted along the northern Gulf of Mexico, where sea level rise is also driving conversion of freshwater forest islands to salt marsh. While climate-driven *A. germinans* range expansion has garnered considerable scientific attention, the role of top-down controls on colonization is largely overlooked. We investigated the effects of abiotic (flooding frequency, soil depth, soil salinity) and biotic (predation, herbivory) controls on *A. germinans* establishment at its northern range limit along Florida's Gulf Coast by comparing fates of caged and non-caged propagules across four landscape positions (from creek edge to forest island interior) and at three sites along a tidal flooding frequency gradient. Within 12 days, grapsid crab, *Sesarma reticulatum*, consumed 99% of non-caged propagules. Among caged propagules, establishment increased with increasing flooding frequency; however, cages did not entirely prevent predation, which remained a primary cause of mortality, except in the rarely flooded island. Propagules that survived to seedlings experienced mild to fatal herbivory across landscape positions and sites. This study revealed that while relict forest islands and surrounding marshes can support *A. germinans*, predation and herbivory strongly suppress colonization, suggesting that mangrove expansion models should incorporate biotic controls.

Keywords Bottom-up · Community reassembly · Herbivory · Predation · Sea level rise · *Sesarma reticulatum* · Top-down

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Introduction

Climate change is driving ecological shifts at population, community, and ecosystem scales globally, altering ecological functions via changes in habitat and species composition (e.g., Walther et al., 2002; Parmesan & Yohe, 2003; Parmesan, 2006; Lancaster et al., 2016). Examples range from phenological shifts in flowering times (Fitter et al., 1995; Dunne et al., 2003; Inouye, 2008), bird migration (Møller et al., 2008; Travers et al., 2015), and butterfly migration (Sparks & Yates, 1997) to geographic shifts in floral and faunal ranges (Grabherr et al., 1994; Perry et al.,

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2005; Kelly & Goulden, 2008). In coastal regions, a notable geographic range shift occurring in response to climate change is the expanded coverage of mangroves into temperate latitudes.

Poleward expansion of mangroves is being observed as warming air temperatures and fewer freeze events promote suitable conditions for mangrove survival (Saintilan et al., 2014; Alongi, 2015; Kilkenny & Galloway, 2016; Osland et al., 2016b; Ward et al., 2016). Sea level rise (SLR) also accommodates landward migration along undeveloped coastlines (Krauss et al., 2011; Nitto et al., 2014). Other effects of climate change, including increasing atmospheric CO_2 and changing precipitation regimes, affect the ability of mangrove species to compete with salt marsh communities, further influencing future distributions of mangroves at temperate latitudes (McKee et al., 2012; Osland et al., 2016a). With the effects of climate change becoming more pronounced at local, regional, and global scales, and mangrove ranges being historically sensitive to major abiotic shifts (Saintilan et al., 2014), considerable research is being conducted to better understand the effects of abiotic factors on future mangrove distributions. However, little work has focused on the coupled effects of bottom-up (abiotic) and top-down (biotic) controls on mangrove expansion at their temperate range limits.

In the southeastern US, the frequency and severity of freeze events dictate periods of mangrove population expansion and contraction and, hence, control mangrove coverage at the northern range limit (Lugo & Patterson-Zucca, 1977; Stevens et al., 2006; Osland et al., 2017). Repeated extreme freezes during 1895–1905 and 1977–1989 seriously reduced mangrove coverage along the Atlantic and Gulf of Mexico Coasts (Stevens et al., 2006). Since the 1980s, recovery and expansion has yielded the greatest mangrove coverage in the northern Gulf of Mexico since at least 1893 (Osland et al., 2017). In Florida (USA), northward mangrove migration is occurring on both Atlantic and Gulf Coasts. Along the Atlantic Coast, Cavanaugh et al. (2014) found that mangrove spatial extent has doubled since 1984, and along the Gulf Coast, Giri & Long (2016) found mangrove area had increased by 25–50% at the northern range limit since 1980.

The northern range of mangroves along the Gulf Coast in Florida occupies a stretch of coastline known as the Big Bend (Fig. 1), a low elevation, low wave energy, and relatively undeveloped region. Three mangrove species grow along the Big Bend: *Avicennia germinans* L. (black mangrove), *Rhizophora mangle* L. (red mangrove), and *Laguncularia racemosa* (L.) C. F. Gaertn. (white mangrove). However, *A. germinans* is the most common due to its higher tolerance to cool temperatures and freeze events (Osland et al., 2015). The transition zone between mangrove- and salt marsh-dominated landscapes along the Big Bend also supports coastal freshwater forests, including islands of remnant forest (hereafter, forest islands) that occur on elevated limestone substrate and are dominated by *Sabal palmetto* (Walt.) Lodd. ex Schult. (cabbage palm) and *Juniperus virginiana* var. *silicicola* Small (southern red cedar). Many of these islands are converting to salt marsh as increased tidal flooding from SLR prevents tree regeneration (Williams et al., 1998, 1999; Castaneda & Putz, 2007; DeSantis et al., 2007). Mangrove encroachment has the potential to modify this freshwater forest-to-salt marsh reassembly trajectory and transform temperate coastal landscapes into regions dominated by saline coastal forests characteristic of tropical and subtropical climates. Mangrove encroachment into salt marsh along the northern Gulf Coast in Texas was found to rapidly alter microclimate, sediment accretion, soil organic carbon, and other ecosystem characteristics (Guo et al., 2017). Similar changes to ecosystem functions are likely from mangrove expansion in salt marsh along the Big Bend, and may be compounded by mangroves replacing freshwater forest as the dominant forest type.

This study was prompted by our observations of *A. germinans* seedlings naturally establishing in salt marsh vegetation positioned along creek edges near transitioning forest islands. These observations motivated three initial hypotheses: (1) *A. germinans* could also establish in forest islands, potentially modifying the forest-to-salt marsh trajectory currently in progress; (2) abiotic factors, particularly tidal flooding frequency, would dictate *A. germinans* colonization success in forest islands; (3) *A. germinans* establishment success would be similar in islands with sufficient flooding and in the surrounding *Juncus roemerianus* Scheele (black needle rush) marsh, and would be higher at creek edges. Creek edges most closely resemble lower elevation, cordgrass-dominated (*Spartina alterniflora* Loisel.) creek bank
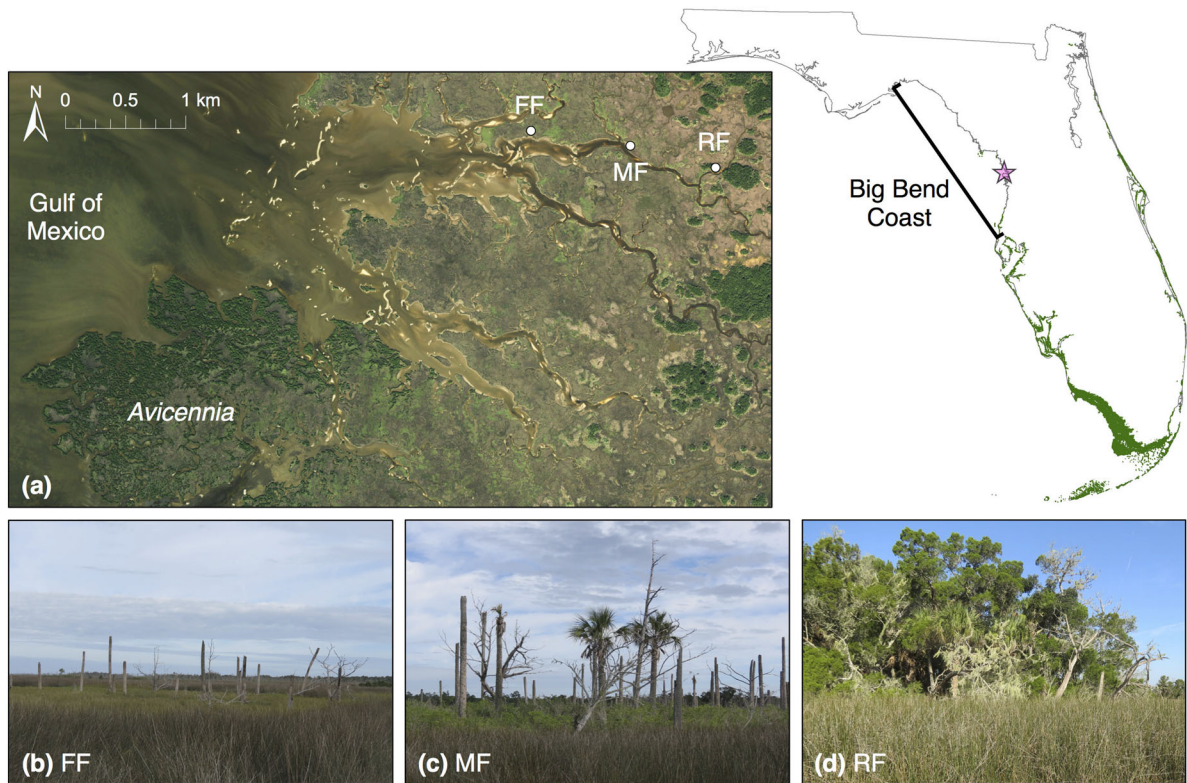
Fig. 1 Location map showing extent of mangrove forest in Florida (FNAI, 2015), locations and images of sites along Turtle Creek, and location of nearest established mangrove forest. *FF* frequently flooded site, *MF* moderately flooded site, *RF* rarely flooded site

habitats where *A. germinans* colonization has been observed in northern Gulf Coast marshes (Patterson et al., 1997; McKee & Rooth, 2008). After discovering high rates of propagule predation by grapsid crab, *Sesarma reticulatum* during our initial experimental deployment, we expanded the study to quantify top-down biotic controls on *A. germinans* colonization through measurements of propagule predation and seedling herbivory.

In tropical regions, propagule predation and herbivory have been investigated extensively to explain regeneration success within mangrove forests, zonation patterns of co-occurring mangal species, and establishment success of mangroves into adjacent habitat (Smith, 1987; Smith et al., 1989; Osborne & Smith III, 1990; McKee, 1995; Farnsworth & Ellison, 1997; Dahdouh-Guebas et al., 1998; Sousa & Mitchell, 1999; Bosire et al., 2005; Cannicci et al., 2008). *Avicennia* are especially susceptible to top-down pressure in the form of propagule predation due

to their soft, fleshy cotyledons that lack a protective coat, relatively high nutrition content, relatively low concentrations of herbivore-deterring compounds, and small size (Smith, 1987; McKee, 1995). These features make them palatable to a variety of fauna including crabs, snails, insects, mammals, and fish (Smith et al., 1989; Steele et al., 1999; Sousa et al., 2003). As seedlings and adults, *Avicennia*, like other mangals, are susceptible to herbivory by insects and crabs that consume leaves, flowers, and woody tissue, which can lead to defoliation, reduced growth rates, and limited propagule production (Cannicci et al., 2008). However, the roles of propagule predation and seedling herbivory in mediating range expansion of *A. germinans* in the northern Gulf of Mexico have not previously been addressed. Here we present our findings on the effects of both bottom-up and top-down controls on *A. germinans* expansion in a region where abiotic conditions are usually considered the primary drivers of mangrove colonization.

Materials and methods

Experimental setting

Manipulative field experiments were conducted along Turtle Creek, a tidal creek in Waccasassa Bay Preserve State Park, located along the Big Bend Coast of Florida (Fig. 1). The study area comprises a mosaic of salt marsh and forest islands in various stages of health, ranging from healthy, regenerating tree stands to relict stands now dominated by salt-tolerant shrubs, forbs, and grasses. Continuous freshwater forest dominated by *S. palmetto* and *J. virginiana* var. *salicicola* and upland pine flatwoods occur landward of the study area (Vince et al., 1989; Williams et al., 2007), and an established population of *A. germinans* is located seaward along the coastal fringe, approximately 3 km to the southwest. Propagules from *A. germinans* float into Turtle Creek and wash up on creek banks, and small scattered stands (<25 m^2) of short (<1 m tall) mangroves are also scattered throughout the marsh.

We established three sites along Turtle Creek, each including a forest island. The sites are approximately 0.7 km apart and are referred to by the relative frequency of tidal flooding each island receives: frequently flooded, moderately flooded, and rarely flooded, based on frequencies reported in Williams et al. (1999). Flooding frequencies in the marshes surrounding each island are approximately the same between sites. The frequently flooded island is a relict forest (non-regenerating) with no live trees and has converted to herbaceous salt marsh. The moderately flooded island supports few live trees and has a mixed understory of halophytic shrubs and herbaceous salt marsh plants. The rarely flooded island supports healthy, regenerating forest with an understory of typical coastal freshwater forest vegetation. Islands at all three sites are surrounded by salt marsh dominated by *J. roemerianus*. Along the creek edge, vegetation is dominated by *S. alterniflora* and also includes other plants common in high marsh: *Distichlis spicata* (L.) Greene (salt grass), *Salicornia* sp. (glasswort), and *J. roemerianus*.

Experimental design

At each site, we tested propagule survival and seedling establishment in four landscape positions: island interior, island edge, marsh plain, and creek edge.

We selected island interior positions representative of the overall island habitat and island edge positions that were on the creek side of the islands. Marsh plain positions were located between island edge and creek edge positions. Creek edge positions were within 1 m of the creek bank slope. We calculated tidal flooding frequencies (number of weeks during which flooding occurred over the course of the experiment) in forest island interiors and edges using a model developed by Williams et al. (1999) specifically for these islands. The model requires elevation data, which we obtained for island interiors from Williams et al. (1999) and estimated for island edges using 2007 Light Detection and Ranging (LiDAR) data for Levy County, downloaded from the NOAA Digital Coast website (http://coast.noaa.gov/digitalcoast/). For marsh plain and creek edge positions, tidal flooding was assumed to occur daily during high tide based on observations made during the monitoring visits and previous field work in the area.

In addition to tidal flooding frequency, we quantified soil salinity, soil depth, percent cover of plant species, and crab burrow density for all landscape positions at each site. Soil salinity was measured from five soil samples collected in June 2016 at each landscape position at each site. Samples were air dried for 12 days, then oven dried at 40°C for 3 days, sieved, and analyzed using the saturated paste method (Rhoades, 1996; Reddy et al., 2013) with a 1:5 soil weight per DI water volume ratio. Salinity of the soil slurry was measured using a conductivity meter (Thermo Scientific Orion Star A215). Soil depth was measured at 10 random locations by inserting a pin flag into the soil until it made contact with underlying limestone bedrock, then measuring the length that was inserted with a metric ruler. Percent cover of plant species was measured in four 1-m^2 quadrats. We counted *S. reticulatum* burrow density as a proxy for herbivorous crab density within eight randomly placed 0.25-m^2 quadrats. *Sesarma* burrows were identified by features described in Holdredge et al. (2009).

The initial experimental deployment consisted of placing 10 non-caged *A. germinans* propagules approximately 25 cm apart in four 0.25-m^2 plots in each of the four landscape positions, for a total of 16 plots per site and 48 plots total. Propagules were set out in October 2015 and had hypocotyls extending 0–1 cm. Plots were marked at each corner with a flag and had no physical barriers separating them from the

surrounding area. We planned to count the number of propagules present and record propagule fate approximately every 2 weeks in each landscape position at each site; however, during the first monitoring event on day 12, we observed 99% propagule predation. Based on this finding, the non-caged experiment terminated and the caged experiment (see below) was initiated.

To determine the relative importance of landscape position and flooding frequency on propagule and seedling fates, we attempted to control for *S. reticulatum* predation by placing propagules in cylindrical cages (20 cm height, 10 cm diameter) made of galvanized steel cloth (0.6-cm^2 mesh). Each cage was placed on top of a square of steel cloth buried in the soil and covered by another square of steel cloth secured to the top of the cage with zip ties. Cages were anchored in place with landscape stakes. Ten cages were placed in each landscape position. We placed one propagule each in five cages and five propagules each in the remaining five cages to additionally test for density effects on propagule establishment, survival, and growth. Given observations of equivalent predation and propagule viability across density treatments, data for all caged propagules were later pooled, resulting in $n = 30$ propagules per landscape position per site. Propagules were placed in the cages in December 2015 and typically had hypocotyls extending between 1 and 3 cm but had no budding roots. All propagules used in caged and non-caged experiments were collected from the established mangrove forest southwest of Turtle Creek (Fig. 1) and had already dropped from parent trees. Only propagules with no signs of predation or decay were used.

Fates of caged propagules were recorded on days 2, 7, 15, 32, 54, 78, 100, 140, and 200 of the experiment, a period spanning from December 2015 to June 2016, as the propagules developed into seedlings. On each monitoring date, propagules were assigned one of the following fates (Fig. 2a–d): viable [including viable propagules with predation damage (i.e., hypocotyl and cotyledons intact but with grazing scars or <50% of cotyledons consumed)], total predation (i.e., non-viable propagules, defined as >50% cotyledons consumed and/or the hypocotyl missing or cut through), missing (counted as total predation), desiccated, or rotted. Desiccated and rotted propagules lacked apparent predation damage and were assumed to be

non-viable due to unfavorable abiotic conditions. Viable propagules included all those that became established seedlings over the course of the caged experiment. A propagule was considered an established seedling when it rooted in the ground and supported upright cotyledons. As propagules developed into established seedlings, they remained caged through day 200, during which we continued to record their fates over time. Seedling fates were determined by visually inspecting leaves and stems for signs of damage and consisted of no herbivory, mild herbivory (damage to leaves), moderate herbivory (damage to leaves and stems), and fatal herbivory, defined by the entire aboveground portions of seedlings missing or seedlings uprooted with some portion of leaves and/or stems missing (Fig. 2e–h). Cause of mortality was recorded as "undetermined" for propagules and seedlings with no apparent signs of damage or with damage from multiple sources. We also recorded the height of each seedling at each visit. Metrics for comparing colonization success between landscape positions included percent of live, established seedlings, rate of seedling establishment, and seedling growth. On day 200, all cages were removed, and seedlings in five-propagule cages were thinned so that only the single, healthiest seedling remained; live seedlings in one-propagule cages were left intact. All other seedlings and non-viable propagules were discarded. Remaining propagules were monitored in July 2016 (day 232), and in December 2016 (day 372), during which fate and seedling height were recorded.

Data analysis

We analyzed the effects of flooding frequency and landscape position on soil salinity, soil depth, percent cover of salt marsh vegetation (i.e., all halophytes), and burrow density using analysis of variance and Tukey's HSD for post hoc multiple comparisons. Fates of caged propagules and seedlings were compared by landscape position at each site using Pearson's χ^2 tests. Because propagule survival was confounded by inconsistent caging effectiveness, we combined viable and predation fates in our statistical analysis of abiotic controls on propagule survival. Additionally, mild and moderate herbivory on seedlings were combined for analysis. We assessed the correlation between caged propagule predation and burrow density using univariate linear regression. To

Fig. 2 Categories of caged propagule fates (**a–d**) and seedling fates (**e–h**). **a** Caged propagules, **b** become non-viable due to predation, or **c** unfavorable environmental conditions that caused desiccation or rot, or **d** developed into established seedlings. Seedling fates were described by degree of herbivory damage: **e** no signs of herbivory, **f** mild herbivory (only on leaves), **g** moderate herbivory [leaves and stem(s) consumed], or **h** suffered mortality from herbivory. Note that seedlings remained caged through day 200. Pictures **e–h** show seedlings after day 200, post-cage removal

correct for an increased chance of Type I error from multiple ANOVA and χ^2 tests, we compared P-values to $\alpha = 0.0167$, instead of a standard $\alpha = 0.05$.

Heights of caged seedlings between monitoring intervals were compared using a repeated measures, mixed model ANOVA, with site and landscape position set as fixed effects. Only live seedlings were included. Because differences in seedling establishment times and mortality created variation in sample sizes between time intervals and overdispersion in the data within landscape positions, the ANOVA model was a poor fit. Therefore, we analyzed the dataset using ANOVA and Tukey's HSD in separate analyses for each site and sampling interval. The effects of environmental variables and burrow density on the survival of pooled post-cage removal seedlings were

evaluated using multiple regression. All statistical analyses were performed in R (R Core Team, 2016).

Results

Characteristics of landscape positions across sites

At the frequently flooded site, model estimates indicated that tidal flooding occurred during every week of the caged experiment (28 weeks) in the island interior and island edge. At the moderately flooded site, tidal flooding occurred during 21 weeks in the island interior and 23 weeks at the island edge. At the rarely flooded site, no flooding occurred in the island interior during the caged portion of the experiment

(though a hurricane flooded the island interior in September 2016), and the island edge flooded during 23 weeks. Marsh plain and creek edge positions at all sites were assumed to have flooding events during every week at all three sites.

Between landscape positions, soil salinity varied least at the frequently flooded site and most at the rarely flooded site (Fig. 3a). At the frequently flooded site, mean conductivity ranged from 6.8 to 11.5 mS/cm. At the moderately flooded site, mean conductivity ranged from 6.0 to 12.7 mS/cm and only differed with regard to the marsh plain, which was more saline than the island interior and edge ($F_{3,12} = 5.39$, P-value $= 0.014$). At the rarely flooded site, conductivity was lowest in the island interior (1.9 mS/cm) and highest along the island edge (9.4 mS/cm), which was similar to conductivity in the marsh plain and creek edge ($F_{3,12} = 14.77$, P-value $= 0.0002$). Soil depths followed a general pattern across sites, with deeper soils occurring at the creek edge and marsh plain and shallower soils occurring in the island interiors and edges (Fig. 3b), as expected based on differences in sediment delivery driven by tidal flooding frequency and distance from creek. Creek edge and marsh plain soil depths ranged from an average of 28.5 to more than 45 cm and were two to three times deeper across all sites than island interior and edge positions, which ranged from an average of 12.4 to 30.4 cm (P-values <0.0001); differences in soil depths between island interior and edge positions were only significant at the moderately flooded site ($F_{3,36} = 106.8$, P-value <0.0001). Both the frequently and moderately flooded sites were characterized by a predominance (>50%) of salt marsh vegetation across all landscape positions (Fig. 3c). At the rarely flooded site, salt marsh cover dominated the creek edge, marsh plain, and island edge positions, but was significantly reduced in the island edge where total vegetation cover was only 10%, of which, 8% was salt marsh vegetation, and was absent in the island interior ($F_{3,12} = 578.7$, P-value <0.0001).

Sesarma reticulatum burrows were present everywhere except the interior of the rarely flooded island, demonstrating the wide distribution of *S. reticulatum* across sites (Fig. 3d). At the frequently flooded site, mean burrow density ranged from 22.5 to 35.5/m² and was not significantly different between landscape positions ($F_{3,28} = 1.46$, P-value $= 0.25$), likely due to similarities in tidal flooding and vegetation cover across the relatively homogeneous, low-elevation site. At the moderately flooded site, mean burrow densities in the marsh plain and creek edge were more than twice as high (32/m²) as in the island edge and interior (9–13.5/m²), given more frequent flooding and deeper soil depths more characteristic of salt marsh closer to the creek ($F_{3,28} = 19.3$, P-value <0.0001). Burrow densities were most variable at the rarely flooded site, where burrow density increased from 0 in the island interior to 41/m² in the creek edge ($F_{3,28} = 26.3$, P-value <0.0001).

Fig. 3 Comparisons (mean, sd) of **a** soil salinity, **b** soil depth, **c** % salt marsh vegetation cover, and **d** *S. reticulatum* burrow density between landscape positions at each site. *Letters above bars* denote statistically significant differences between landscape positions
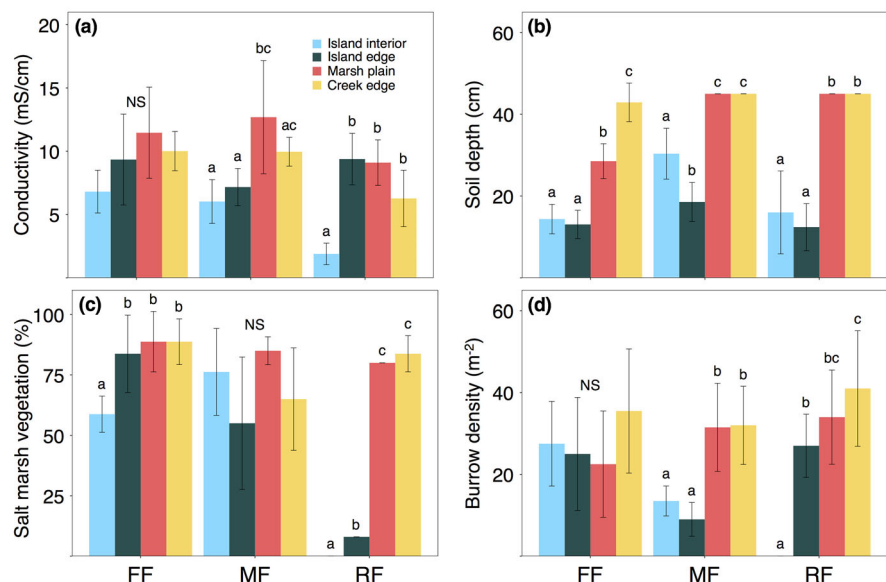
Biotic pressure on non-caged propagules

Non-caged propagules experienced extremely low survival (<1%) regardless of site or landscape position after 12 days, providing a measure of ambient predation pressure. We identified predation by *S. reticulatum* as the primary cause of disappearance based on the moderate to high crab burrow density present across sites and landscape positions (with the exception of the island interior of the rarely flooded site), and video footage of *S. reticulatum* taking a propagule and pulling it into a burrow that we recorded during a separate experiment at the site (Supplemental File). Propagule disappearance in the island interior of the rarely flooded site was likely depredation by other fauna such as small mammals or wild boars, which are present on regenerating forest islands, though we were unable to confirm this assumption.

Caging experiment: propagule establishment success and seedling growth

Over the course of the experiment, we observed crab burrows appearing inside cages, indicating that caging did not completely exclude propagule predation by *S. reticulatum*. Soil disturbance from crab burrowing and tidal flooding likely shifted cages, creating gaps between cage sides and bases through which *S. reticulatum* could burrow. The single caged propagule that was depredated in the island interior of the rarely flooded site was assumed to be consumed by a small predator other than *S. reticulatum*. Despite the susceptibility of caged propagules to predation, more than 50% developed into established seedlings (i.e., were viable; Fig. 4) in island interiors of the frequently and moderately flooded sites, confirming our initial hypothesis that *A. germinans* could successfully establish in forest islands and our second hypothesis that establishment requires sufficient tidal flooding.

When we disregarded predation due to the confounding results of inconsistent caging effectiveness, we found that the fate of caged propagules depended on landscape position at the frequently flooded site ($\chi^2 = 35.7$, *P*-value <0.0001), where rot and undetermined causes of mortality reduced viability in the island interior by 20% and creek edge by 37%. Landscape position was also important at the rarely flooded site ($\chi^2 = 112.5$, *P*-value <0.0001), where desiccation prevented propagule survival in the island
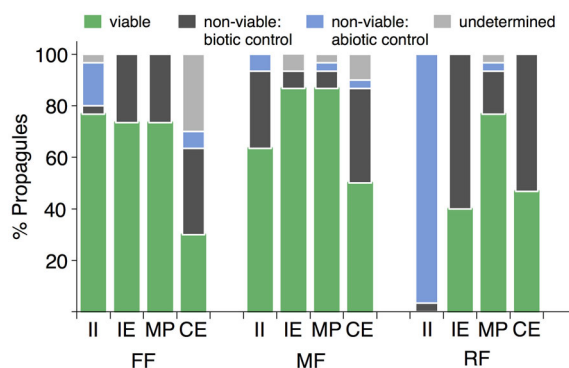

Fig. 4 Percent of caged propagules that met each fate by day 200 in each landscape position at each site. *II* island interior, *IE* island edge, *MP* marsh plain, *CE* creek edge

interior, further demonstrating propagules' reliance on adequate tidal flooding. At the moderately flooded site, non-predation causes of mortality were low and consistent across landscape positions ($\chi^2 = 5.44$, *P*-value = 0.49). Across sites, seedling establishment at creek edge positions was not higher compared to other positions, contrary to our hypothesis. Overall seedling establishment on day 200 was correlated with more frequent tidal flooding and salt marsh vegetation cover and decreased with deeper soils and higher burrow density, but was not affected by soil salinity ($F_{5,90} = 28.3$, *P*-value <0.0001, $r^2 = 0.59$).

Rates of seedling establishment varied over time between landscape positions at all three sites (Fig. 5). Of note, there was a consistently low rate of seedling establishment at the frequently flooded site creek edge (Fig. 5a). At the moderately flooded site, establishment rates were similar among positions over time until days 140–200, when 37% of seedlings in the island interior suffered mortality (Fig. 5b). At the rarely flooded site, a similar mortality event caused 90% seedling mortality in the creek edge position between days 140 and 200 (Fig. 5c), and establishment rates were generally lower than at other sites, with no seedling establishment in the island interior.

As propagules matured into seedlings, mild to moderate herbivory was common across sites and occurred in all landscape positions where seedlings established (Fig. 6). Notwithstanding mild and moderate herbivory, >50% of caged seedlings were alive on day 200 in all landscape positions at all sites, except along the creek edge of the rarely flooded site where only one seedling established. Seedling fate depended on landscape position at both the frequently flooded
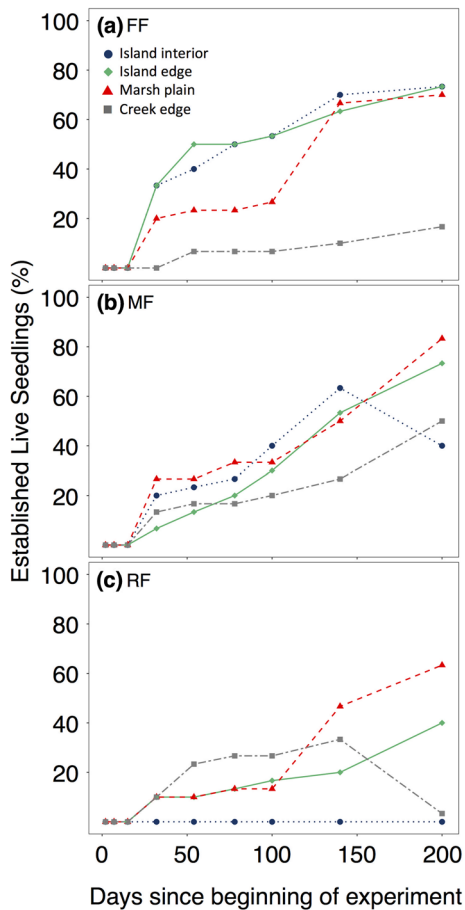
Fig. 5 Percent of established live seedlings from caged propagules over time for each landscape position at **a** frequently flooded, **b** moderately flooded, and **c** rarely flooded sites
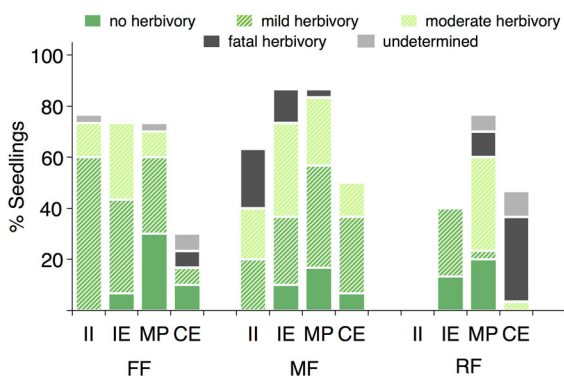

Fig. 6 Caged seedling fate by day 200 in each landscape position at each site. Seedlings include only the subset of propagules that were viable as shown in Fig. 4. *II* island interior, *IE* island edge, *MP* marsh plain, *CE* creek edge

($\chi^2 = 40.2$, *P*-value <0.0001) and rarely flooded ($\chi^2 = 28.8$, *P*-value <0.0001) sites, and varied strongly (nearly significantly) between positions at the moderately flooded site ($\chi^2 = 15.4$, *P*-value = 0.017 vs. $\alpha = 0.0167$). At the frequently flooded site, seedlings with no signs of herbivory were most common in the marsh plain. Non-fatal herbivory exceeded 90% in the island interior and edge, and 22% of seedlings suffered mortality due to herbivory in the creek edge. At the moderately flooded site, herbivory was most intense in the island interior and fatal herbivory decreased from the island interior towards the creek edge. At the rarely flooded site, fatal herbivory was highest in the creek edge (71%) where only one seedling survived. Growth rates of caged seedlings increased in all landscape positions at all sites through March (Fig. 7). When the seedlings began outgrowing their cages in April, moderate and fatal herbivory began to confound growth rates and affect seedling heights. In general, seedlings at the frequently flooded site were significantly taller in the creek edge than in other landscape positions by June ($F_{3,58} = 13.5$, *P*-value <0.0001, Fig. 7a) and were taller in the marsh plain and creek edge than island interior or edge at the moderately flooded site ($F_{3,46} = 14.6$, *P*-value <0.0001, Fig. 7b). At the rarely flooded site, in contrast, seedlings in the island edge consistently grew more than seedlings in other landscape positions ($F_{2,16} = 38.9$, *P*-value <0.0001, Fig. 7c), and by June, had also outgrown seedlings at the other sites.

Seedling survival and growth after cage removal

Post-cage removal, seedling survival declined between June and December 2016 in all landscape positions of all three sites where seedlings had established (Fig. 8a, c, e). Fatal herbivory caused declines in seedling survival through July; causes of mortality were harder to determine in December because missing seedlings in the creek edge and marsh plain positions could have resulted from herbivory or Hurricane Hermine in September 2016. The number of surviving seedlings by December was not correlated with burrow density or any environmental variable ($F_{5,5} = 2.8$, *P*-value = 0.15). Seedling heights were similar between landscape positions at the frequently flooded and moderately flooded sites, except in the island interior of the
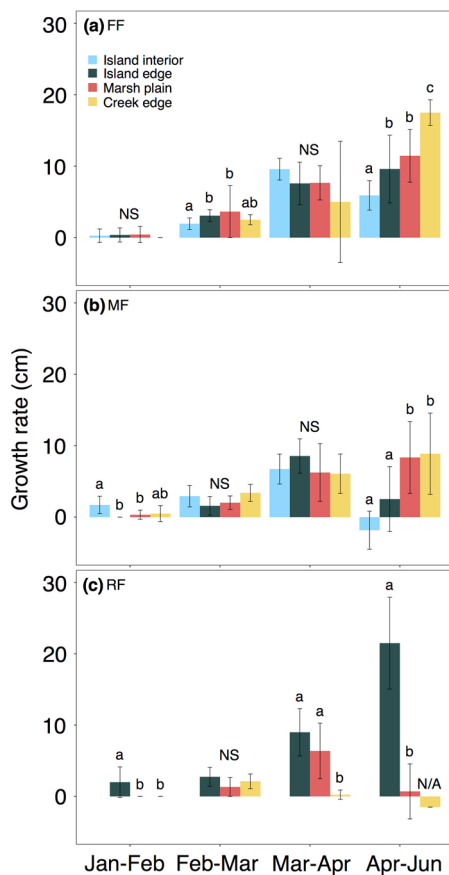
Fig. 7 Mean seedling growth rates (±sd) during caged experiment for each landscape position at **a** frequently flooded, **b** moderately flooded, and **c** rarely flooded sites. Sample sizes between time intervals varied due to seedling mortality over time

moderately flooded site where the short height of the single surviving seedling resulted from moderate herbivory (Fig. 8b, d). At the rarely flooded site, only seedlings in the island edge survived to December, which continued to grow faster than all other seedlings at all other positions and sites (Fig. 8f). The large standard deviation was due to recent herbivory observed in December on one of the seedlings (the top portion of the plant was on the ground) that reduced its height from 100 to 37 cm.

Discussion

We found that top-down biotic pressure exerted significant control over *A. germinans* propagule and seedling survival, establishment, and growth from creek edges to forest island interiors across a range of tidal flooding regimes. In the absence of caging, propagules suffered nearly 100% predation. *Sesarma reticulatum* was the primary predator, but propagules in the island interior of the rarely flooded site, where *S. reticulatum* burrows were absent, also suffered intense predation, likely by small mammals or wild boars. Herbivory also decreased survival of established seedlings. Caging reduced but did not exclude predation on propagules or herbivory on seedlings as they grew to cage capacity. Soil disturbance from tidal flooding and burrowing activity (by *S. reticulatum* and other crab species present in the area, including *Uca* spp., which do not consume propagules) likely shifted the sides of cages off their bases, creating subsurface gaps through which *S. reticulatum* could access propagules. Soil disturbance is likely most intense in creek edge positions due to stronger effects of tidal flooding and generally higher burrow densities (Fig. 3), which may explain high predation rates on caged propagules in that landscape position.

Where caging successfully prevented predation, propagules were able to survive in forest islands and develop into seedlings, provided there was sufficient tidal flooding, as hypothesized. Only in the rarely flooded island interior, where propagules suffered desiccation in the absence of tidal flooding during the experiment, did abiotic conditions exert greater pressure on caged propagules than did top-down biotic controls (Fig. 4). Rot and undetermined cause(s) of mortality reduced propagule survival in other landscape positions at each site, and resulted in significant differences in propagule viability between landscape positions at the frequently flooded site, but no clear pattern emerged across sites that could be explained by differences in landscape position characteristics.

Relatively fast rates of seedling establishment in the island interior and edge of the frequently flooded site suggest that conditions at these landscape positions might be more favorable than in the surrounding marsh, though slower establishment in the marsh plain did not result in lower total establishment compared to other positions at the three sites (Fig. 5). Unfortunately, the inconsistent exclusion of *S. reticulatum* from cages undermines our ability to clarify the relationships between increased seedling establishment and increased flooding, salt marsh vegetation, and decreased soil depth and burrow density across all

Fig. 8 Number of surviving post-cage removal and mean heights (±sd) in June, July, and December 2016
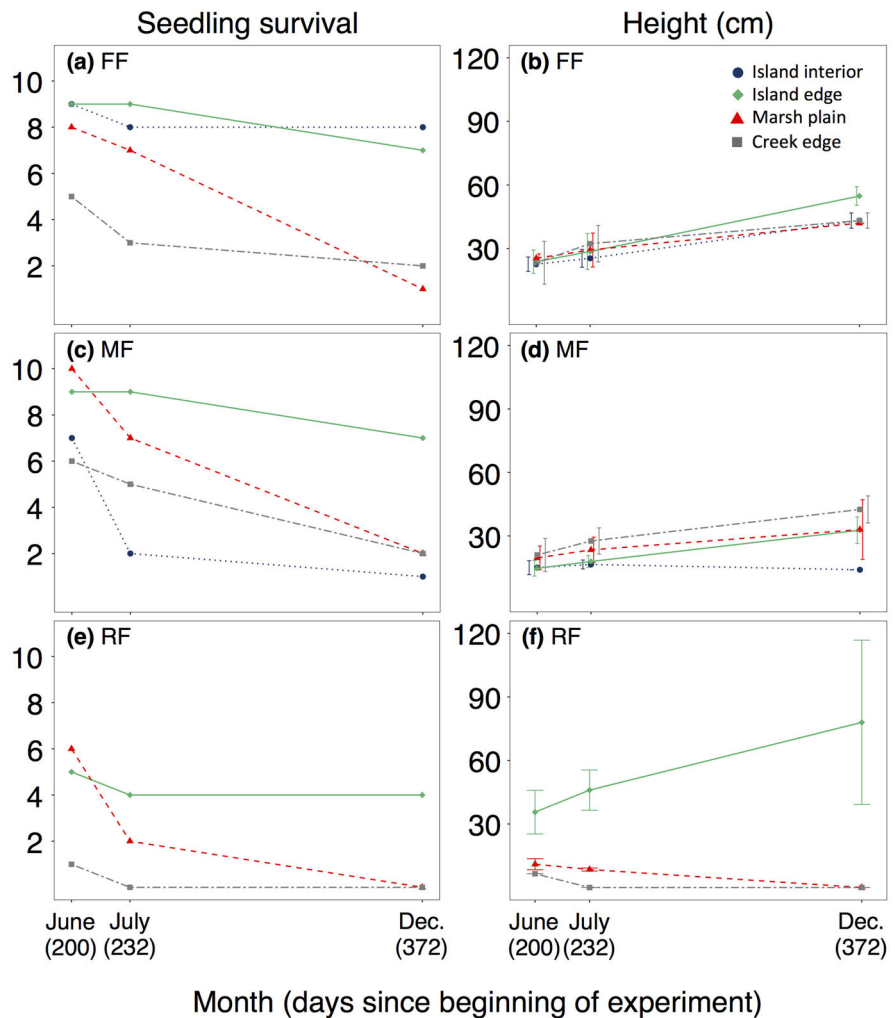
positions and sites. Consequently, it is unclear from these results whether sufficiently flooded forest islands provide bottom-up conditions that support *A. germinans* colonization success at rates similar to the surrounding marsh or whether creek edges, in the absence of predation, provide more (or less) favorable abiotic conditions for seedling establishment compared to other landscape positions. Ambient predation intensity observed at the frequently, moderately, and rarely flooded sites is comparable to *Avicennia* propagule predation reported in tropical and subtropical mangrove forests: 72% of *A. germinans* propagules were non-viable from predation within 4 days in south Florida (Smith et al., 1989); 60% of *A. germinans* propagules were depredated within 9 days in Belize (McKee, 1995); 100% of *A. marina*

propagules in northern Australia were consumed within 20 days (McGuinness, 1997); and 98–100% of *A. schaueriana* propagules were consumed within 18 days in Brazil (Souza & Sampaio, 2011). Among the more extreme cases, 100% of 200 *A. marina* propagules were non-viable from predation within 60 min in Kenya (Van Nedervelde et al., 2015). Whether intense predation pressure and generally high burrow densities of *S. reticulatum* along Turtle Creek are representative of other potential mangrove colonization areas along the Big Bend requires further investigation. Critically, studies investigating *A. germinans* colonization in temperate regions focus largely on abiotic drivers (Stevens et al., 2006; McKee & Rooth, 2008; Comeaux et al., 2012; Osland et al., 2013; Cavanaugh et al., 2014; Saintilan et al., 2014).

The nearest study conducted in a similar habitat that addressed predation took place in Louisiana, where Patterson et al. (1997) found only 11% mortality of *A. germinans* from propagule predation [by *S. cinereum* and *Littoria irrorata* (snail)] in a *Spartina*-dominated marsh, suggesting there may be significant spatial variability in predation pressure across the northern mangrove range limit.

Propagules that survived predation continued to face mild to intense herbivory as seedlings (Fig. 6). Seedling mortality from herbivory was not as prevalent as crab predation of propagules, though most seedlings suffered some degree of herbivory. *Sesarma reticulatum* may have contributed to seedling herbivory by continuing to consume fleshy cotyledons of young seedlings. Then, as seedlings matured and produced true leaves, insects most likely replaced crabs as the main seedling consumers, limiting survival and growth (Fig. 7). Insects are important herbivores in mangrove forests, affecting all stages of tree development (Robertson et al., 1990; Sousa et al., 2003; Minchinton, 2006; Cannicci et al., 2008). We suspect that grasshoppers were responsible for most seedling herbivory at our study site, as they are common grazers of *J. roemerianus* in marshes along the Gulf Coast (Parson & De La Cruz, 1980; Sparks & Cebrian, 2015) and were present in spring 2016 when seedlings were leafing out.

In addition to top-down biotic controls, competition with salt marsh may have also affected seedling growth. Seedlings grew best at the edge of the rarely flooded island, appearing healthier and developing faster than all seedlings at the frequently and moderately flooded sites. This was most apparent at the end of the caging experiment (April–June, Fig. 7) and post-cage removal (Fig. 8). The tallest seedling (115 cm) had developed visible pneumatophores by December 2016 (day 372). Salt marsh vegetation cover was much lower than at all other landscape positions where seedlings established (Fig. 3c), suggesting these seedlings may have faced less pressure from competition with salt marsh plants. Patterson et al. (1993) and McKee & Rooth (2008) found that growth rates of *A. germinans* decreased in the presence of *S. alterniflora*, and Guo et al. (2013) found that biomass of *A. germinans* seedlings was lower when grown adjacent to salt marsh plants, all of which were attributed to resource competition. However, other studies have found that salt marsh plants can benefit

seedling establishment (Lewis & Dunstan, 1975; McKee et al., 2007). Further work is needed to better understand the role of competition as an additional biotic control on mangrove range expansion.

This study demonstrates that as remnant forest islands convert to salt marsh and become more suitable for mangrove colonization, they also become more suitable for fauna that commonly regulate mangrove populations. *Sesarma reticulatum* is common in salt marshes in the eastern and southeastern US (Bertness et al., 2009), and grapsid crabs are among the most pervasive and intensive propagule predators worldwide (McGuinness, 1997; Smith et al., 1989; Van Nedervelde et al., 2015). Though not observed depredating propagules at Turtle Creek, snails and salt marsh insect grazers may also become common fauna in relict islands, creating additional potential predation pressure on propagules and seedlings as islands convert to salt marsh. The flooding regime of the marsh and transitioning islands along Turtle Creek may also contribute to predation intensity. Time between daily tidal inundation is greater than the period of time in which the marsh, including creek edge, is flooded (personal observation) and transitioning forest islands are more often not flooded than flooded. Time between flooding events could allow plenty of opportunity for foraging, a hypothesis posed by Osborne & Smith III (1990) to explain higher predation in high versus low intertidal zones in Australia.

As the effects of climate change drive increased tidal flooding and fewer freeze events in the region, favorable habitat for mangrove colonization will increase in the northern Gulf of Mexico and US Atlantic Coast. However, our findings suggest that natural colonization of persisting and encroaching mangrove populations will require high propagule density to overcome biotic pressure. Currently, natural propagule density along Turtle Creek is relatively low (which we mimicked in our study), and crab densities were sufficiently large to prevent propagule establishment in non-caged experiments. Delivery of high densities of propagules from coastal storms may be required to sustain encroaching mangrove populations, and we are currently working to identify propagule density thresholds (if present) required to overcome predation pressure. Critically, the long-term persistence and expansion of mangrove populations in any location will be driven by the interactive effects of

environmental variables (SLR, stochastic freeze events, coastal storms) and biotic controls (propagule density, predation, competition). Thus, both bottom-up and top-down drivers need to be considered when projecting future mangrove range expansion.

Conclusion

As sea level rises and global warming accelerates, more coastal habitat will become suitable for mangrove colonization. Along the Big Bend coastline in the northern Gulf of Mexico, we showed that forest islands that are currently transitioning to salt marsh and adjacent marsh landscapes can also support *A. germinans* colonization. The current freshwater forest-to-marsh trajectory may be thus modified to include the eventual replacement of a freshwater forest community by a mangrove community, shifting the temperate coastal landscape to one dominated by tropical saline forest. However, as forest islands convert to salt marsh, they also support fauna that regulate mangrove populations via herbivory. Without large influxes of propagules, mangroves may be unable to overcome the resulting strong, top-down predation control present in these transitioning habitats. While bottom-up controls like temperature and tidal flooding are known to dictate large-scale patterns and rates of mangrove expansion, our study supports the recommendation by He & Silliman (2016) that top-down controls need to be evaluated alongside abiotic controls when investigating and modeling mangrove expansion in coastal systems.

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