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RESEARCH ARTICLE

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Dead litter of resident species first facilitates and then inhibits sequential life stages of range-expanding species

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Abstract

1. Resident species can facilitate invading species (biotic assistance) or inhibit their expansion (biotic resistance). Species interactions are often context-dependent and the relative importance of biotic assistance versus resistance could vary with abiotic conditions or the life stage of the invading species, as invader stress tolerances and resource requirements change with ontogeny. In northeast Florida salt marshes, the abundant dead litter (wrack) of the native marsh cordgrass, *Spartina alterniflora*, could influence the expansion success of the black mangrove, *Avicennia germinans*, a tropical species that is expanding its range northward.
2. We used two field experiments to examine how *S. alterniflora* wrack affects *A. germinans* success during (a) propagule establishment and (b) subsequent seedling survival. We also conducted laboratory feeding assays to identify propagule consumers and assess how wrack presence influences herbivory on mangrove propagules.
3. *Spartina alterniflora* wrack facilitated *A. germinans* establishment by promoting propagule recruitment, retention and rooting; the tidal regime influenced the magnitude of these effects. However, over time *S. alterniflora* wrack inhibited *A. germinans* seedling success by smothering seedlings and attracting herbivore consumers. Feeding assays identified rodents—which seek refuge in wrack—as consumers of *A. germinans* propagules.
4. *Synthesis*. Our results suggest that the deleterious effects of *S. alterniflora* wrack on *A. germinans* seedling survival counterbalance the initial beneficial effects of wrack on *A. germinans* seed establishment. Such seed-seedling conflicts can arise when species stress tolerances and resource requirements change throughout development and vary with abiotic conditions. In concert with the tidal conditions, the relative importance of positive and negative interactions with wrack at each life stage can influence the rate of local and regional mangrove expansion. Because interaction strengths can change in direction and magnitude with ontogeny, it is essential to examine resident–invader interactions at multiple life stages and across environmental gradients to uncover the mechanisms of biotic assistance and resistance during invasion.

KEYWORDS

biotic resistance, herbivory, invasive species, legacy effects, litter, mangroves, ontogenetic shifts, range expansion

1 | INTRODUCTION

The relative importance of positive and negative biotic interactions between species can vary with abiotic conditions, consumer pressure or differences in species' size or density (Bulleri et al., 2014; Callaway & Walker, 1997; Crain, 2008). The magnitude and direction of biotic interactions also varies with life stage, and interactions often change from facilitative to competitive through ontogeny (Yang & Rudolf, 2010). Classic work on species succession and seed-seedling conflict suggests that the same conditions that are favourable for early life stages can become unfavourable during later life stages (Connell & Slatyer, 1977; Rey & Alcántara, 2000; Schupp, 1995; Walker & Chapin, 1986). This pattern is common in interactions with nurse plants whereby nurse plants facilitate the juveniles of other plant species, but then compete with these individuals when they become adults (Flores-Martinez et al., 1994; Miriti, 2006). Variation in species stress tolerances and resource requirements throughout development can explain such shifts in species interactions over spatial and temporal gradients (Leger & Espeland, 2010; Liancourt et al., 2005; Maestre et al., 2009). Facilitative interactions predominate during early life stages that are particularly sensitive to harsh abiotic conditions (Schiffers & Tielbörger, 2006), but with development, plants better tolerate physiological stressors, and competitive interactions become more intense as adult plant resource requirements increase (Sthultz et al., 2007). Understanding how biotic interactions change with both species ontogeny and abiotic conditions is particularly important for species invasions and range expansions, where novel interactions between residents and invaders can cause transformative ecosystem change (Crowl et al., 2008; Mitchell et al., 2006).

During species invasions or range expansions, positive and negative interactions are often framed in terms of whether resident species resist invasion (biotic resistance) via mechanisms such as competition or consumption (Byers, 2002; Levine et al., 2004), or assist invasion (biotic assistance) via mechanisms such as habitat modification or stress amelioration (Badano et al., 2007; Smith et al., 2004). However, it is unclear in what contexts positive or negative interactions between resident and incoming species will predominate. As with seed-seedling conflicts and succession, the degree of biotic resistance varies with ontogeny (Boege & Marquis, 2005), yet few studies have examined the role of biotic assistance in species expansion (Stotz et al., 2016). If the direction and magnitude of interactions between resident and invading species vary with ontogeny, the net effect of the resident community on the invader throughout its development must be positive or the invader will not establish. Thus, because invader success depends on this balance, it is important to examine the contexts—both developmental and environmental—that affect whether biotic resistance or assistance predominates.

Developmentally, we expect that biotic assistance will be more important than biotic resistance during early life stages. Early stages could be particularly vulnerable to stressful abiotic conditions and could benefit from stress amelioration by resident species. We also expect that biotic resistance will become more important during the invader's later life stages, as its resource requirements increase. Environmentally, abiotic factors can influence when ontogenetic shifts occur in development, and shifts from facilitative to competitive interactions can be delayed under harsh abiotic conditions (Roux et al., 2013). Therefore, we expect that the relative importance of biotic resistance and assistance will depend on environmental conditions and that positive interactions will predominate in harsher environments.

Climate change is an environmental stressor that creates novel species interactions by shifting some species ranges to higher latitudes (Parmesan, 2006; Sexton et al., 2009). As in species invasions, climate-driven shifts of dominant plant species can transform the ecological functions of resident ecosystems, and biotic interactions between resident and range-expanding species influence the rate of such regime shifts (Blois et al., 2013; Gilman et al., 2010; Wisz et al., 2013). In particular, woody vegetation has increased in grasslands and savannas world-wide in the past 200 years, changing the microclimate, species composition, productivity, carbon sequestration and hydrology of resident communities (Archer et al., 2017). Climate-driven expansion of mangroves into salt marshes is an example of this woody encroachment phenomenon in coastal wetlands (D'Odorico et al., 2013; Saintilan & Rogers, 2015). Tall, woody mangroves are replacing low-statured herbaceous salt marsh species at the poleward limits of the mangrove distribution on five continents (Adams et al., 2004; Cavanaugh et al., 2014; Eslami-Andargoli et al., 2009; Lee & Yeh, 2009; Saintilan et al., 2014).

Mangrove expansion into salt marshes provides an opportunity to examine the mechanisms of resident biotic assistance and resistance on the success of a range-expanding competitor at different life stages. On Florida's Atlantic coast, declines in the number of annual freezes have caused subtropical mangrove species to expand poleward into salt marshes (Cavanaugh et al., 2014, 2019). The black mangrove, *Avicennia germinans* is the primary species at the leading edge of the mangrove expansion. With expansion, *A. germinans* interacts with resident live salt marsh vegetation, which is dominated by marsh cordgrass *Spartina alterniflora* at the leading edge (Chen et al., 2020; Simpson et al., 2017; Walker et al., 2019). Biotic interactions between mangroves and live *S. alterniflora* vary with mangrove life stage. Specifically, live salt marsh can increase *A. germinans* propagule retention during recruitment (Donnelly & Walters, 2014; McKee et al., 2007; Peterson & Bell, 2012). As seedlings, mangrove interactions with live salt marsh often become increasingly competitive (Guo et al., 2013; McKee & Rooth, 2008; Peng et al., 2018; Simpson et al., 2013; Yando et al., 2019), although salt marsh canopies may facilitate mangrove seedlings via microclimate buffering (Devaney et al., 2017; Guo et al., 2013; Pickens et al., 2019). Once seedlings grow to the sapling and adult stages, *A. germinans* out-competes salt marsh species over extended time periods (Guo et al., 2013; Kangas & Lugo, 1990; Zhang et al., 2012). Although interactions between *A. germinans* and live *S. alterniflora* are well-studied, range-expanding mangroves also interact with *S. alterniflora's* persistent and extensive dead litter legacy (i.e., wrack;

Li & Pennings, 2016; Smith et al., 2020b). However, it is unclear how *S. alterniflora* wrack influences expansion dynamics of different *A. germinans* life stages at the leading edge of their expansion.

Avicennia germinans is crypto-viviparous and produces robust, water-dispersed propagules that are deposited in different microhabitats in intertidal salt marshes: in marsh vegetation, on bare sediment or with wrack. Mangrove propagule retention depends on the tidal regime and propagule interactions with live vegetation structure (Peterson & Bell, 2012, 2018; Van der Stocken et al., 2015; Yando et al., 2020). In North Florida, *A. germinans* propagule dispersal spatially overlaps with *S. alterniflora* wrack deposition from late September to early January (Smith et al., 2020b). Tides and currents deposit the buoyant wrack at high marsh elevations, where it smothers vegetation (Bertness & Ellison, 1987), alters moisture, salinity and nutrient conditions (Pennings & Richards, 1998), and provides refuge for intertidal species (Smith et al., 2019). In the high marsh, *A. germinans* propagules are more abundant on and under wrack piles compared to adjacent vegetation (Smith et al., 2018). This pattern suggests that propagules either raft in with wrack (Minchinton, 2006) or are trapped by existing wrack. Thus, wrack could affect mangrove propagule dispersal by influencing initial propagule stranding location and retention.

Once retained, mangrove propagules are sensitive to desiccation stress during establishment and require a certain level of moisture to root (Farnsworth, 2000; Osborne & Berjak, 1997). However, severe inundation can also disrupt propagule establishment if propagules are uprooted by hydrodynamic forces (Balke et al., 2011; Yando et al., 2020). Thus, successful establishment requires a balance between the desiccation and hydrodynamic stressors that are both associated with the tidal regime (Delgado et al., 2001). *Spartina alterniflora* wrack also changes the local moisture regime. In mesocosm experiments, wrack facilitated propagules placed underneath it by increasing moisture, but caused severe desiccation of propagules placed above it (Smith et al., 2018). Wrack could also potentially buffer freezing temperatures and create a more favourable microhabitat for mangrove early life stages that are vulnerable to freezes (Coldren & Proffitt, 2017; Osland et al., 2015).

After *A. germinans* propagules successfully root, they transition into seedlings when they sprout true leaves, which occurs within 2–4 weeks after rooting (Smith et al., 2018). We predicted that wrack could negatively affect seedling survival via two potential mechanisms. First, reduced light can limit seedling survival, growth rates and densities (Feller & McKee, 1999; McKee, 1995a). As a propagule, the plant grows primarily from maternal provisioning provided by its cotyledon, and propagules depend less on light (Hogarth, 2015). However, once a seedling, *A. germinans* competes for light with salt marsh species in marsh-mangrove ecotone habitats (Simpson et al., 2013). Second, herbivory—especially by crabs and insects—drives seedling mortality and the spatial distribution of mangroves (Clarke & Kerrigan, 2002; Smith III, 1987; Sousa & Mitchell, 1999). Consumers can take refuge in wrack piles (Lewis et al., 2007; Reice & Stiven, 1983), but it is not known whether consumers associated with salt marsh wrack eat mangrove propagules or seedlings.

We conducted two field experiments and a series of laboratory mesocosm experiments to examine how resident *S. alterniflora* wrack affects *A. germinans* propagule establishment, seedling survival and seedling biomass. First, we experimentally assessed how different microhabitats (vegetation, bare sediment and wrack) in uninvaded salt marsh influence *A. germinans* propagule recruitment, retention and rooting during the first 2 weeks of propagule establishment during spring and neap tidal sequences. We hypothesized that salt marsh wrack would facilitate mangrove propagule establishment by trapping and retaining propagules. We also expected that the two components of propagule recruitment—delivery and retention—would be negatively correlated and vary with the tidal regime. For example, with more inundation (i.e. spring tides), we expected greater propagule delivery, but reduced propagule retention. We also hypothesized that wrack would facilitate rooting for propagules placed beneath it, but inhibit propagules placed above it. We further expected that the magnitude of these effects would vary with tidal inundation and that wrack would more strongly increase rooting for propagules stranded during dry, neap tidal sequences compared to wet, spring tidal sequences by relieving desiccation conditions.

Second, we experimentally examined how high marsh microhabitats influence *A. germinans* seedling survival and biomass over a multi-month time span. We hypothesized that overlying *S. alterniflora* wrack would inhibit mangrove seedlings' survival by limiting their access to light. Furthermore, we hypothesized that salt marsh wrack would indirectly increase consumer pressure on mangrove seedlings by sheltering herbivores that consume mangroves proximate to their refuge. Lastly, we conducted laboratory feeding assays to identify which common marsh species consume mangrove propagules and to assess whether salt marsh wrack presence influences mangrove consumption. Together, this work explores the context-dependent interactions that influence the rate of local establishment and poleward mangrove expansion into salt marshes. By exploring the relative importance of positive and negative interactions of the dead litter of a resident species on two successive early life stages of its range-expanding competitor, we can better understand overall biotic resistance or assistance and how this balance changes with abiotic conditions.

2 | MATERIALS AND METHODS

2.1 | Field experiments

2.1.1 | Propagule collection

We performed two field experiments to examine the effects of *S. alterniflora* wrack on (a) *A. germinans* propagule establishment (up to 2 weeks) and (b) *A. germinans* seedling survival (1–9 months) in uninvaded salt marsh microhabitats. For both experiments we collected propagules from adult mangrove trees located in the Matanzas River estuary in Crescent Beach, FL (29.761233°N, 81.266917°W; 1200 propagules for propagule establishment experiment, 2100

propagules for seedling survival experiment). We chose propagules from a size range of 26–40 mm, excluding those with herbivory or disease. We floated propagules in seawater in full sunlight for 5–7 days to mimic natural propagule dispersal and approximate optimal flotation time prior to root development (Rabinowitz, 1978; Simpson et al., 2016). For each experiment, we marked the propagules in each treatment with a distinct colour of nail polish. A laboratory study confirmed that nail polish did not affect propagule length, root length or buoyancy relative to unmarked propagules (Appendix 6: Figure S1). Nail polish remained visible on propagules for at least 3 months in the field (R. Smith, pers. obser.).

2.1.2 | Site description

To represent uninvaded salt marsh areas at the leading edge of the mangrove expansion, we selected a salt marsh site in Crescent Beach, FL, located within the Matanzas River estuary (29.76425°N, 81.27485°W). The estuary encompasses some of the most northern mangroves on the Atlantic coast of Florida and exhibits local-scale heterogeneity in the extent of *A. germinans* invasion of salt marshes (Williams et al., 2014). Although mangroves dominate the southern reaches of the estuary, the area from Crescent Beach northward is dominated by salt marsh and our site is representative of uninvaded salt marsh habitat in northeast Florida. The broader region on the northeast coast of Florida has experienced several regime shifts between marsh and mangroves over the past 250 years in response to extreme freeze events that limit mangrove distributions (Cavanaugh et al., 2019), but the history of mangrove expansion at our field site is unknown. Examination of Google Earth imagery dating back to 1994 did not reveal the presence of mangroves at the site during that time frame. Furthermore, we did not observe any dead or stunted trees at the site, so it is likely that salt marsh has dominated the site for at least the last 30 years.

To mimic natural deposition of wrack, we established experimental plots in the high marsh at Crescent Beach at the same elevation as the natural wrack line, maintaining consistent relative elevation (Real-time Kinetic GPS, 0.934 ± 0.109 m above MLLW; mean ± *SD*) so that the plots experienced a common tidal regime. Although no adult mangroves were present at the site, during mangrove propagule recruitment season (September–December), *A. germinans* propagules naturally drift in and strand with *S. alterniflora* wrack in the high marsh. We created 10 blocks in a randomized block design, although plot size and the number of plots per block differed between the two experiments (see below). Prior to the start of both experiments, we removed all naturally deposited wrack and propagules from the plots. *Spartina alterniflora* was the dominant vegetation in all plots, with some *Batis maritima* interspersed. Relative abundance and heights of live and standing dead *S. alterniflora* and *B. maritima* varied seasonally and are described below for each experiment. Dead *S. alterniflora* litter naturally strands at this site year-round (Smith et al., 2020b).

2.1.3 | Propagule establishment experiment

In salt marshes, *A. germinans* propagules establish in different microhabitats, including in vegetation, on bare sediment, and with *S. alterniflora* wrack. Propagules in wrack can be deposited either on top or underneath wrack; this position relative to wrack (above or below) could influence propagule establishment by creating different desiccation conditions (Smith et al., 2018). We quantified three aspects of propagule establishment—recruitment, retention and rooting success—as a function of four experimental microhabitat treatments: (a) vegetation, (b) bare sediment, (c) above-wrack and (d) below-wrack (Appendix 1: Figure S1). For the vegetation treatment, we left natural salt marsh vegetation undisturbed. To create the bare sediment treatment, we cut above-ground salt marsh biomass to the ground. For the two wrack treatments, we collected dead salt marsh wrack from the high marsh and added enough wrack to each plot to cover the salt marsh vegetation present in each plot with a wrack depth of 4 cm, the mean maximum depth of natural wrack deposits (Smith et al., 2020b). In both wrack treatments, wrack floated freely with incoming tides. Each block included each microhabitat treatment, and we created four 0.25-m^2 plots spaced 1.5 m apart within each block (n = 10 blocks). We separated blocks from one another by at least 3 m. At the start of the experiment, live *S. alterniflora* was the dominant vegetation (stem no. per 0.0625 m^2: 10.9 ± 3.7; height: 91.2 ± 11.9 cm; mean ± *SD*), followed by standing dead *S. alterniflora* (stem no. per 0.0625 m^2: 3.5 ± 4.0; height: 28.5 ± 8.9 cm; mean ± *SD*) and *B. maritima* (stem no. per 0.0625 m^2: 0.7 ± 1.2; height: 36.5 ± 7.0 cm; mean ± *SD*).

To examine how timing with the tidal phase affects the relationship between microhabitat and mangrove propagules, we conducted this experiment in two phases: (a) at the start of a spring tide (1.76 m high tide; start date: 16 October 2016; highest high tide per month) and (b) at the start of a neap tide (1.30 m high tide; start date: 1 November 2016; lowest high tide per month). To start each phase, we placed 30 marked propagules into each plot (n = 300 propagules per treatment). In all treatments, we haphazardly placed propagules on either the soil (vegetation, bare sediment, below-wrack) or wrack surface (above-wrack). For the below-wrack treatment, we placed marked propagules on the ground in salt marsh vegetation underneath the wrack. In the above-wrack treatment, we placed marked propagules on top of the wrack; propagules were suspended by the wrack and did not touch the ground. We wanted to mimic natural propagule deposition so we did not bury the propagule hypocotyls in the sediment. Thus, our treatments simulate natural settlement conditions of mangrove propagules in high marsh microhabitats with and without wrack. We sampled the plots every other day for the first 9 days and again on day 15 at the end of the experiment. We ended the experiment after 15 days to capture the phases of propagule establishment—recruitment, retention and rooting. Each time, we counted the number of (a) unmarked propagules recruiting in from outside the plots (recruitment), (b) marked propagules retained in the plot (retention) and (c) marked propagules rooted in each plot (rooting). Because we allowed wrack treatments to float

freely during the experiment, we also recorded the presence or absence of the wrack treatments, and we did not replace missing wrack treatments over time. We did not observe substantial inputs of natural wrack to the plots during the experiment. At each sampling event, we counted and removed all unmarked propagules that recruited in from outside the plots, and summed the cumulative number of unmarked propagule recruits over time.

We used R software (version 3.5.2) to examine how microhabitat treatment affects propagule recruitment, retention and rooting during each tidal phase (R Core Team, 2018). To focus on plots where treatment differences were maintained for the entire experiment, we excluded plots in which the wrack treatment washed away ($n = 6$ [above-wrack], $n = 4$ [below-wrack] washed away in the spring tide; $n = 3$ [above-wrack], $n = 3$ [below-wrack] washed away in the neap tide) from all analyses. For comparison, we include supplemental analyses that did not exclude these replicates (Appendix 2). For each response variable (recruitment, retention and rooting), we used the LME4 package to fit a GLMM with a Poisson distribution and a log link for the final time point (day 15), fitting separate models for each tidal phase (neap and spring) (Bates et al., 2015). We tested for overdispersion and refit models with overdispersed data with negative binomial distributions and log links. We used microhabitat treatment as a fixed effect and block as a random intercept. We used the DHARMA package to examine residual plots and check model assumptions (Hartig, 2020). We used Tukey's post hoc tests to examine differences in propagule response variables among microhabitats.

2.1.4 | Seedling survival experiment

Wrack residence time in the high marsh can last from weeks to years (Bertness & Ellison, 1987; Marinucci, 1982). To examine the effects of microhabitat on mangrove seedling survival and biomass over a 9-month time span, we used the same experimental design as the propagule establishment experiment, with a few modifications to ensure a persistent wrack effect and the integrity of treatments over time. Notably, we increased the size of the plots in each block, and we placed the wrack treatments in mesh bags (see below) to keep them in place over the extended timeline of the seedling survival experiment. We also added an extra plot per block as a procedural control to account for the effects of bagging wrack. Thus, we created five 1-m^2 plots spaced 1 m apart in each of 10 blocks, with blocks separated from one another by at least 2 m. At the start of the experiment, live *S. alterniflora* was the dominant vegetation (stem no. per 0.0625 m^2: 13.9 ± 5.2; height: 69.7 ± 16.2 cm; mean ± *SD*), followed by standing dead *S. alterniflora* (stem no. per 0.0625 m^2: 7.1 ± 4.0; height: 60.2 ± 10.3 cm; mean ± *SD*) and *B. maritima* (stem no. per 0.0625 m^2: 0.7 ± 1.6; height: 33.3 ± 4.5 cm; mean ± *SD*).

On 10 December 2016, we planted 42 marked propagules in a 6 × 7 grid into each of the five treatments ($n = 420$ propagules per treatment). We spaced propagules equally throughout each 1-m^2 plot. We planted propagules into treatments by burying the hypocotyl in the soil (vegetation, bare sediment, below-wrack, procedural control) or into the wrack (above-wrack) to increase initial propagule retention and target the effects of microhabitat on seedling survival (Appendix 1: Figure S2). To create the two wrack treatments, we collected dead *S. alterniflora* wrack from the high marsh and placed it in 1-m^2 mesh bags made from bird netting (4 cm^2 openings). We placed enough wrack in each bag to fill the 1-m^2 experimental plots to a depth of 4 cm. For the procedural control treatment, we used an empty 1-m^2 mesh bag. For the bagged treatment plots (above-wrack, below-wrack, procedural control), we placed a 1.5-m tall PVC pole in each corner and topped each pole with a tee-shaped PVC fitting. We attached the corners of each bag to the PVC poles with loose-fitting zip ties such that the buoyant bags of wrack could float up the pole with incoming tides and return to the same spot as the tide receded. Poles were taller than the highest high tide at the site (Appendix 1: Figure S2). Although some wrack left the bags over time, we did not add wrack to the treatments; wrack bags also did not noticeably accumulate sediment, debris or organic matter over time. At least 2-cm depth of wrack remained in each wrack treatment by the end of the experiment.

At 1, 3, 6 and 9 months, we counted the number of marked *A. germinans* seedlings and the number of those seedlings with signs of herbivory, which we defined as any indication of consumption, regardless of severity. *Avicennia germinans* propagules have two cotyledons, which are nutritional reserves from the parent tree that provide the developing seedling with energy as it grows (Farnsworth, 2000; Hogarth, 2015). Propagules developed true leaves within 1 month of the experiment, and the marked cotyledons remained attached to the seedlings until month 6, when they withered and fell off. We considered propagules to have transitioned to the seedling stage when they developed true leaves. Before the cotyledons dropped, we marked the seedlings with coloured cable ties to keep track of the experimental seedlings. For the below-wrack treatment, we temporarily removed the wrack bag to count marked seedlings beneath the wrack at each sampling point. For the above-wrack treatment, we could not accurately record seedling counts over time without disrupting the treatment and causing propagules to fall through the mesh bag. Thus, for this treatment, we recorded seedling count and herbivory presence only at the final time point. As indirect measures of consumer pressure, we quantified rodent nests (presence/absence; Appendix 3: Figure S2) and crab burrow densities in the plots at each time point. We also measured variables that we expected to covary with microhabitat treatment, including pore water salinity, NO_3, NH_4 and PO_4, and sediment organic content. See Appendix 3 for further description of covariate methods. At the end of the experiment (21 September 2017), we carefully extracted each seedling from the soil by hand and counted its leaves. We then separated the above-ground and below-ground components and dried them in a drying oven for 3 days at 60°C until each sample reached a constant biomass. We weighed the above- and below-ground parts of each seedling and recorded their dry mass.

To examine how microhabitat treatment affected seedling survival after 9 months, we used a GLMM fit with a negative binomial distribution and a log link to assess seedling count at the final time

point as a function of microhabitat treatment (vegetation, bare sediment, above-wrack, below-wrack, procedural control), including block as a random intercept. To assess how microhabitat treatment influenced herbivory on seedlings, we defined two stages (early/late) of herbivory based on qualitative differences in herbivory severity and consumer type. During months 1 and 3 (early stage), severe herbivory occurred primarily on cotyledons attached to seedlings (crabs and rodents), but during months 6 and 9 (late stage), cotyledons had dropped from seedlings and mild, sublethal herbivory occurred on seedling leaves (insects; Appendix 3: Figure S1). Thus, we performed separate analyses for early and late-stage herbivory. Excluding plots with no seedlings, we fit separate GLMMs for the presence or absence of herbivory on each seedling at the last time point in each stage (early = month 3; late = month 9), using a binomial distribution and a log link. For each model, we examined the main effect of microhabitat treatment as a function of proportion herbivory and included block as a random intercept. We used the BLME package to refit the model for late-stage herbivory with a Bayesian linear mixed effects model with a binomial distribution to account for partial data separation (Chung et al., 2013). We included the above-wrack treatment only in the model for late-stage herbivory because we only recorded herbivory in that treatment at the final time point (month 9). We used Tukey's post hoc tests to examine differences in proportion herbivory among microhabitat treatments at the final time point in each stage. For total dry mass and the below-ground:above-ground dry mass ratio of the seedlings at the experimental endpoint, we used a linear mixed model (LMM) that included microhabitat treatment as a fixed effect and block as a random intercept. We log-transformed both biomass response variables to meet the assumptions of normality and homogeneity. For leaf number per seedling, we used a GLMM fit with a negative binomial distribution and a log link, using microhabitat treatment as a fixed effect and block as a random intercept. We used Tukey's post hoc tests to examine differences in mass and leaf number responses among microhabitat treatments. As in the propagule establishment experiment, for all models, we examined residual plots to check model assumptions.

2.2 | Herbivore feeding assays

2.2.1 | General experiment design

We performed feeding assays for mangrove consumers to (a) determine which potential consumers eat propagules and (b) assess how wrack presence influences herbivory. We used propagules in the feeding trials because the severe herbivory we observed in the field focused primarily on cotyledons. We targeted a suite of common invertebrate and rodent species observed in our field experimental plots. For each species, we established 'no choice' and 'choice' assays that offered propagules in the presence or absence of wrack. In the 'no choice' assays, we placed consumers in individual mesocosms with pre-weighed propagules placed on bare sand either with or without wrack. In the 'choice' assays, we put consumers in individual mesocosms with pre-weighed, marked propagules placed on bare sand on one side and underneath wrack on the other side of the mesocosm. For both assays, we included additional replicate mesocosms as autogenic controls in which we placed propagules in the same microhabitat combinations, so that we could determine any incidental herbivory in the absence of consumers. We added wrack to a depth of 4 cm for wrack treatments. We kept all animals on a daily light–dark cycle (12 light hours–12 dark hours) in a temperature-controlled room (25°C). At the end of each feeding assay, we recorded whether there was evidence of herbivory on propagules (presence/absence), regardless of severity. In the rodent assays, we also recorded the number of propagules entirely consumed. We returned all animals to the field at the end of the assays. Additional details of experimental set-up for the herbivore feeding assays are described in Appendix 4.

2.2.2 | Invertebrates

For invertebrates, we performed 'no choice' assays for four focal species (the squareback marsh crab *Armases cinereum*, the broadback mud crab *Eurytium limosum*, the marsh fiddler crab *Uca pugnax* and the marsh periwinkle *Littoraria irrorata*; $n = 10$ replicates per species per microhabitat). For the 'choice' assay, we targeted the two consumers that ate the most in the 'no choice' assay (*A. cinereum* and *E. limosum*; $n = 20$ replicates per species per microhabitat). Invertebrates acclimated to mesocosms (36 cm × 21 cm × 30 cm) for 24 hr prior to the start of each assay. We added two propagules per mesocosm in the 'no choice' assay, and four propagules per mesocosm in the 'choice' assay ($n = 2$ in wrack; $n = 2$ in bare sand). Based on invertebrate consumption, we ran each assay for 8 days.

For the 'no choice' assay, we used a logistic regression to examine the probability of herbivory on either of the two propagules based on consumer identity, microhabitat treatment and their interaction for the 'no choice' assay. For the 'choice' assay, we fit a Bayesian linear mixed effects model with a binomial distribution to support model convergence; this model included the same main effects as the 'no choice' assay and also included mesocosm as a random intercept (Chung et al., 2013). We did not include the autogenic controls in either analysis because no herbivory was visible in those treatments.

2.2.3 | Rodents

For the rodent assays, we captured three rodent species (the hispid cotton rat *Sigmodon hispidus*, the marsh rice rat *Oryzomys palustris* and the black rat *Rattus rattus*) from a mixed salt marsh-mangrove site in Crescent Beach, FL (29.761233°N, 81.266917°W). Although background abundances of these consumers are unknown at this site, these species have previously been captured in the Matanzas estuary (Pournelle & Barrington, 1953) and are widely distributed in coastal habitats of the Gulf and Atlantic United States (Esher

et al., 1978; Smith & Vrieze, 1979; Wolfe, 1985). Because we had a limited number of each species, we considered them irrespective of species to examine the general effect of rodents on propagule consumption ($n = 7$ rodents total). In the 'no choice' assay, we had three replicates of each microhabitat treatment (wrack, bare sand). We ran two temporal blocks of the 'no choice' assay to increase sample size, including an extra replicate of the wrack treatment in the first time block and an extra replicate of the bare sand treatment in the second time block. Rodents were randomly re-assigned to microhabitat treatments between temporal blocks. The 'choice' assay had seven replicates. Rodents acclimated in mesocosms (65 cm × 47 cm × 34 cm) for 6 hr prior to the start of each feeding assay. Based on fast rodent consumption rates, we ran the rodent feeding assays for 6 hr each. We added 10 propagules per mesocosm in the 'no choice' assay and 20 propagules per mesocosm in the 'choice' assay ($n = 10$ in wrack; $n = 10$ in bare sand).

We used GLMMs fit with binomial distributions to examine the proportion of propagules fully eaten as a function of microhabitat treatment (bare sand, wrack) for both assays and included mesocosm as a random intercept. For all models, we examined residual plots to check model assumptions. For the 'no choice' assay, we initially included temporal block in the model as a fixed effect, but we reran and report the model without the temporal block because it did not have a significant effect on the proportion of propagules fully eaten.

3 | RESULTS

3.1 | Propagule establishment experiment

There was a significant effect of microhabitat treatment on the cumulative number of unmarked *A. germinans* propagules that recruited in from outside plots for spring ($\chi^2 = 135.92$, $df = 3$, $p = 2.20 \times 10^{-16}$) and neap tidal phases ($\chi^2 = 42.70$, $df = 3$, $p = 2.86 \times 10^{-9}$). By the end of the experiment, between five and 20 times more unmarked propagules recruited to wrack plots (spring tide: 73.7 ± 17.8 propagules; neap tide: 15.4 ± 2.4; mean ± *SE*) compared to either vegetation (spring tide: 6.6 ± 2.3; neap tide: 2.5 ± 0.9) or bare sediment plots (spring tide: 4.5 ± 2.0; neap tide: 0.9 ± 0.3) during both tidal phases (Figure 1A). Depending on the treatment, 2.5 to 6 times more unmarked propagules recruited during the spring tidal phase compared to the neap tidal phase (Figure 1A). The number of marked propagules retained in the plots declined over time during both tidal phases (Figure 1B). By the end of the experiment (day 15), there was a significant effect of microhabitat on propagules retained for both spring ($\chi^2 = 41.24$, $df = 3$, $p = 5.82 \times 10^{-9}$) and neap tidal phases ($\chi^2 = 76.18$, $df = 3$, $p < 2.2 \times 10^{-16}$). By the end of the experiment, the above-wrack (spring tide: 21.0 ± 1.8 propagules; neap tide: 14.3 ± 3.7; mean ± *SE*) and below-wrack (spring tide: 16.1 ± 1.7; neap tide: 15.7 ± 3.7) treatments retained 2.5 to 4 times more propagules relative to the vegetation (spring tide: 5.2 ± 1.5; neap tide: 4.3 ± 1.5) or bare sediment (spring tide: 6.4 ± 2.01; neap tide: 4.4 ± 1.2) treatments during both tidal phases (Figure 1B). The number of propagules rooted increased over time for both tidal phases. By the end of the experiment, there was a significant effect of microhabitat treatment on propagules rooted for both spring ($\chi^2 = 21.44$, $df = 3$, $p = 8.54 \times 10^{-5}$) and neap ($\chi^2 = 14.91$, $df = 3$, $p = 0.019$) tidal phases (Figure 1C). At the end of the experiment, three to four times more propagules rooted in the below-wrack treatment (spring tide: 11.5 ± 2.1 propagules; neap tide: 9.6 ± 2.7; mean ± *SE*) compared to vegetation (spring tide: 3.5 ± 1.1; neap tide: 2.5 ± 1.5) and bare sediment (spring tide: 3.8 ± 1.3; neap tide: 2.2 ± 0.7) treatments in both tidal phases (Figure 1C). In the spring tide, the number of propagules rooted in the below-wrack treatment did not differ from the above-wrack treatment (8.8 ± 2.7 propagules; mean ± *SE*), but in the neap tide, nearly three times more propagules rooted in the below-wrack treatment relative to the above-wrack treatment (3.6 ± 1.2; Figure 1C).

3.2 | Seedling survival experiment

The number of *A. germinans* seedlings present declined across all microhabitats over time, and by the end of the experiment (month 9), there were at least three times fewer seedlings present in the above-wrack (0.5 ± 0.5 seedlings; mean ± *SE*) and below-wrack treatments (2.3 ± 1.2) compared to the other three treatments (vegetation: 12.2 ± 2.9; control: 6.9 ± 1.8; bare: 10.1 ± 3.4; $\chi^2 = 43.88$, $df = 4$, $p = 6.81 \times 10^{-9}$; Figure 2A). Across all treatments, only one propagule in the bare treatment showed evidence of decay (month 3). The type of herbivory (on cotyledons vs. leaves) and the proportion of seedlings with herbivory changed over the course of the experiment. During the early stages of the experiment (months 0–3), most herbivory occurred on seedling cotyledons. After 3 months there were at least 1.65 times more seedlings with herbivory in the below-wrack treatments (62.8%) relative to the other treatments (vegetation: 27.8%; control: 34.2%; bare: 9.8%; $\chi^2 = 52.55$, $df = 3$, $p = 2.29 \times 10^{-11}$; Figure 2B). We observed rodents fleeing the wrack treatments when we approached the experimental plots to take measurements. For the below-wrack treatments, we found rodent nests in 40% of plots ($n = 4$) after 1 month and in 70% of plots after 3 months ($n = 7$). We did not observe rodent nests in any of the other non-wrack treatments (Appendix 3: Figure S2). However, by months 6 and 9, herbivory switched to target the seedlings' leaves, and there was no difference between treatments ($\chi^2 = 1.48$, $df = 3$, $p = 0.69$; Figure 2C). In all microhabitats, nearly all seedlings had some evidence of leaf herbivory, although the severity of herbivory was qualitatively minor. At months 6 and 9, the presence of rodent nests in below-wrack plots dropped to 10% and 0% respectively.

At the end of the experiment, there were significant differences among microhabitat treatments for seedling total dry mass ($\chi^2 = 101.95$, $df = 3$, $p < 2.2 \times 10^{-16}$), seedling below-ground:above-ground mass ratios ($\chi^2 = 149.88$, $df = 3$, $p < 2.2 \times 10^{-16}$), and seedling leaf number ($\chi^2 = 172.59$, $df = 3$, $p < 2.2 \times 10^{-16}$). All three measures were at least 1.5 times greater for seedlings in the bare sediment treatment compared to the other microhabitat treatments (Figure 3).

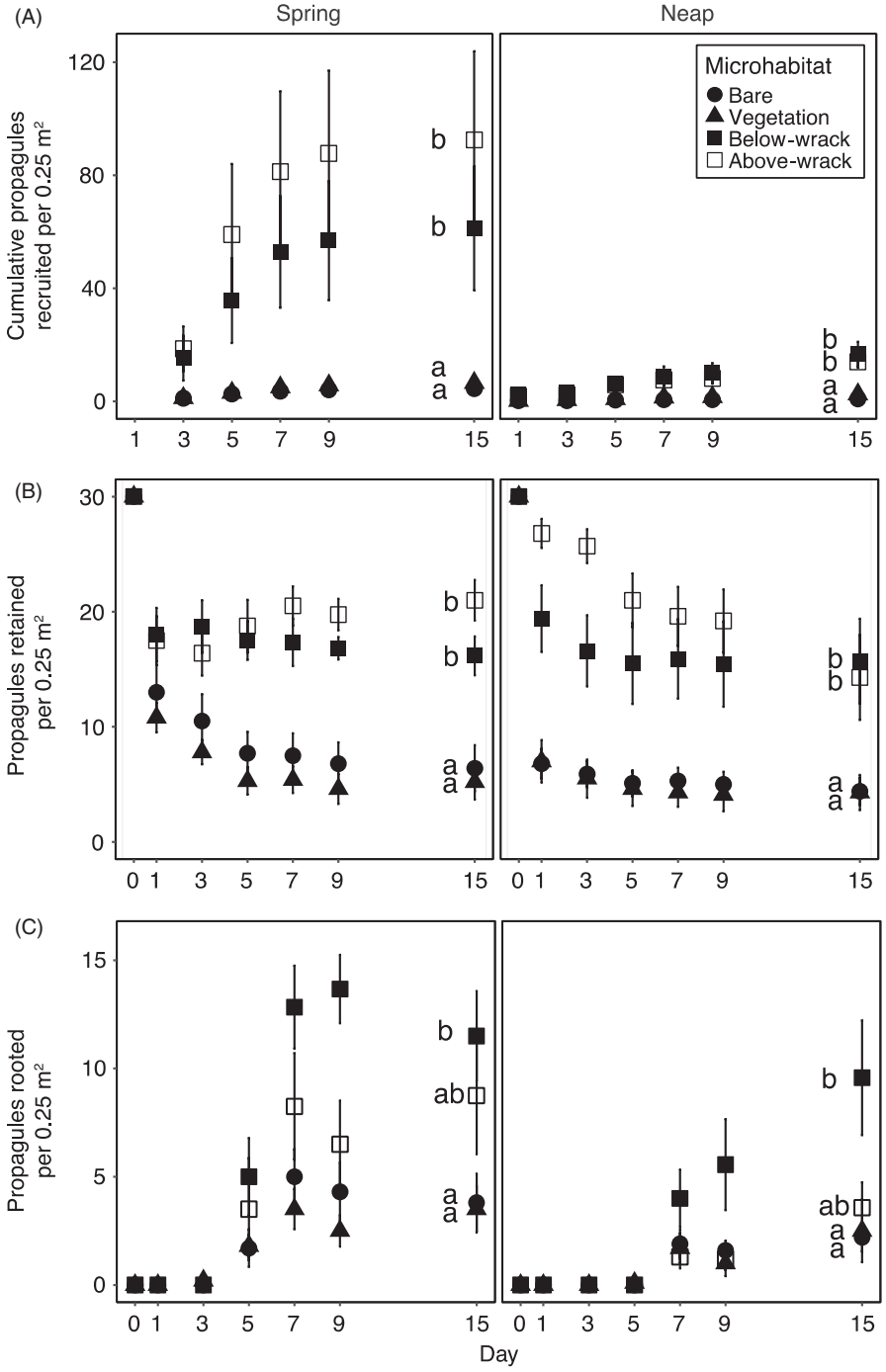

FIGURE 1 For the propagule establishment experiment, mean ± *SE* no. per 0.25 m^2 of (A) unmarked propagules cumulatively recruited from outside plots, (B) marked propagules retained and (C) marked propagules rooted across microhabitat treatments (vegetation, bare sediment, above-wrack, below-wrack) during spring and neap tidal sequences within the first 15 days of propagule establishment. Letters reflect significant results of post hoc tests for the final sampling day (day 15)

Pore water salinity, NO_3, NH_4 and PO_4, crab burrow density and sediment organic content did not vary with microhabitat treatment (Appendix 3: Figures S4 and S5).

3.3 | Herbivore feeding assays

3.3.1 | Invertebrates

After 8 days, some invertebrates showed evidence of grazing propagules (Figure 4A,B,E), but the severity of invertebrate herbivory was qualitatively minor compared to rodent herbivory. In the 'no choice' invertebrate assay, there was no significant interactive effect of consumer identity and microhabitat ($\chi^2 = 2.65$, $df = 3$, $p = 0.45$) or microhabitat alone ($\chi^2 = 1.60$, $df = 1$, $p = 0.21$) on the proportion of propagules with herbivory, although there was a significant effect of consumer identity ($\chi^2 = 20.50$, $df = 3$, $p = 1.34 \times 10^{-4}$). A greater percentage of propagules in mesocosms with *A. cinereum* (60% in bare sand; 30% in wrack) and *E. limosum* (40% in bare sand; 20% in wrack) showed signs of herbivory compared to *U. pugnax* (10% in bare sand; 0% in wrack) and *L. irrorata* (0% in bare sand and wrack; Figure 4A).

In the invertebrate 'choice' assay, there was no significant interactive effect of consumer identity and microhabitat ($\chi^2 = 0.032$, $df = 1$, $p = 0.86$), microhabitat ($\chi^2 = 0.95$, $df = 1$, $p = 0.33$) or consumer

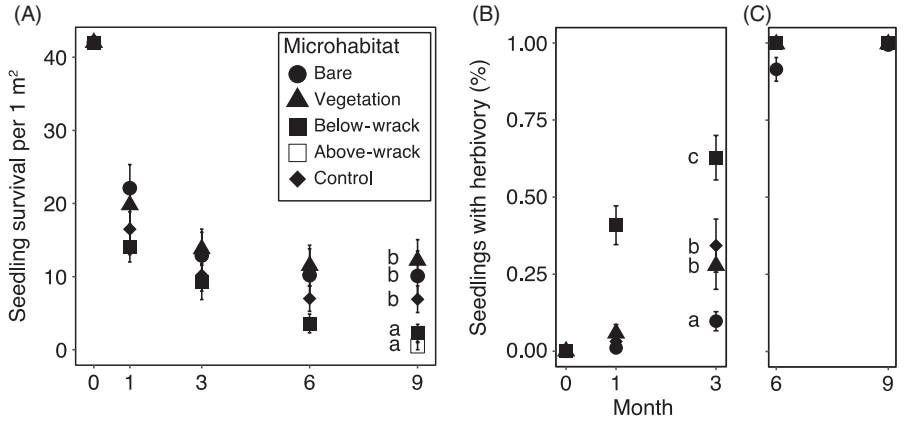

FIGURE 2 For the seedling survival experiment, mean ± *SE* (A) seedling no. per 1 m^2, (B) proportion of propagules (%) with early-stage herbivory (severe, damage to cotyledon) and (C) proportion of propagules (%) with late-stage herbivory (minor, damage to leaves) across microhabitat treatments (vegetation, bare sediment, below-wrack, procedural control) over 9 months of seedling development in the field. Above-wrack treatment is included only for the 9-month time point, due to sampling constraints. Letters reflect significant results of post hoc tests. There was no difference in proportion herbivory after 9 months among microhabitats and all treatments are overlapping

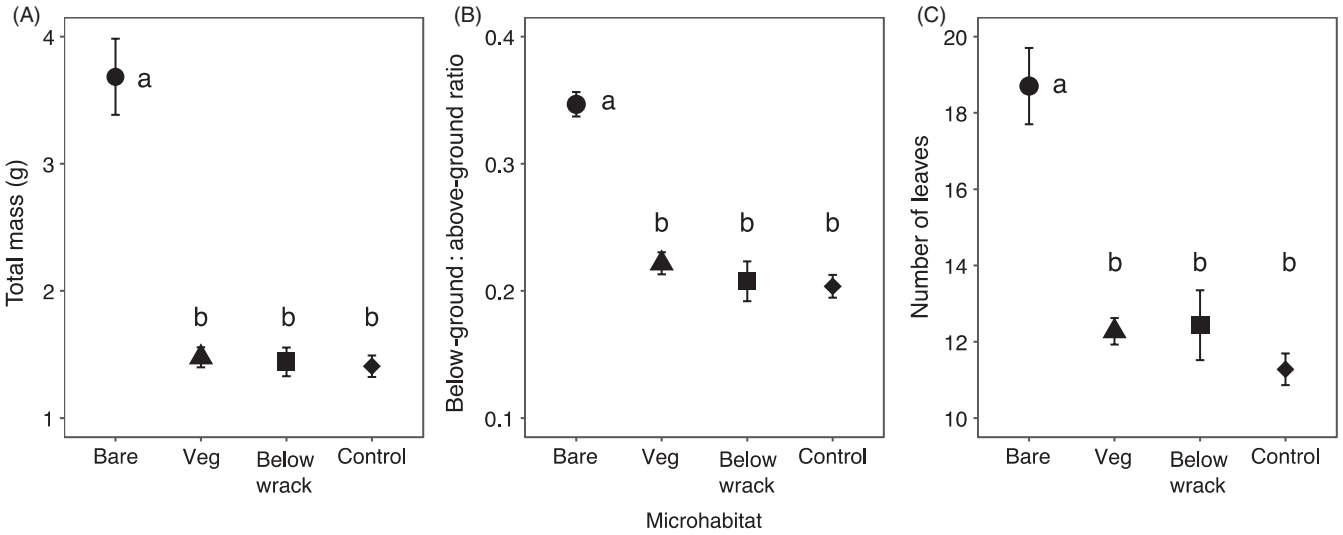

FIGURE 3 For the seedling survival experiment, mean ± *SE* seedling (A) total dry weight biomass (grams), (B) below-ground:above-ground mass ratio and (C) number of leaves per seedling across microhabitat treatments (vegetation, bare sediment, below-wrack, procedural control) after 9 months of seedling development in the field. An insufficient number of seedlings were present in the above-wrack treatment after 9 months for robust analysis of biomass and leaves. Letters reflect significant results of post hoc tests

identity ($\chi^2 = 0.53$, $df = 1$, $p = 0.47$) on the proportion of propagules with herbivory. There was minimal herbivory by both *E. limosum* (11% in bare sand; 16% in wrack) and *A. cinereum* (15% in bare sand; 25% in wrack; Figure 4B).

3.3.2 | Rodent feeding assays

In both rodent feeding assays, rodents consumed multiple mangrove propagules within 6 hr (Figure 4C,D,F). In the 'no choice' assay, 86% of propagules in both wrack and bare sand treatments showed signs of herbivory. Microhabitat did not affect the proportion of propagules that were fully eaten ($\chi^2 = 0.077$, $df = 1$, $p = 0.78$), and on average, rodents ate the same number of propagules in mesocosms with wrack (5.14 ± 1.44; mean ± *SE*) as those without wrack (5.42 ± 1.39; mean ± *SE*; Figure 4C).

In the rodent 'choice' assay, within the same mesocosm, 86% of propagules in bare sand and 100% of propagules with wrack had herbivory. For the proportion of propagules that were fully eaten, there was a significant effect of microhabitat placement ($\chi^2 = 5.06$, $df = 1$, $p = 0.024$). Rodents ate 1.75 times more full propagules present underneath wrack (4.00 ± 0.9; mean ± *SE*) compared to propagules present without wrack (2.29 ± 0.61; mean ± *SE*; Figure 4D). Qualitatively, rodent bite marks on propagules in the mesocosm study visually matched the bite marks observed on cotyledons and propagules in the field.

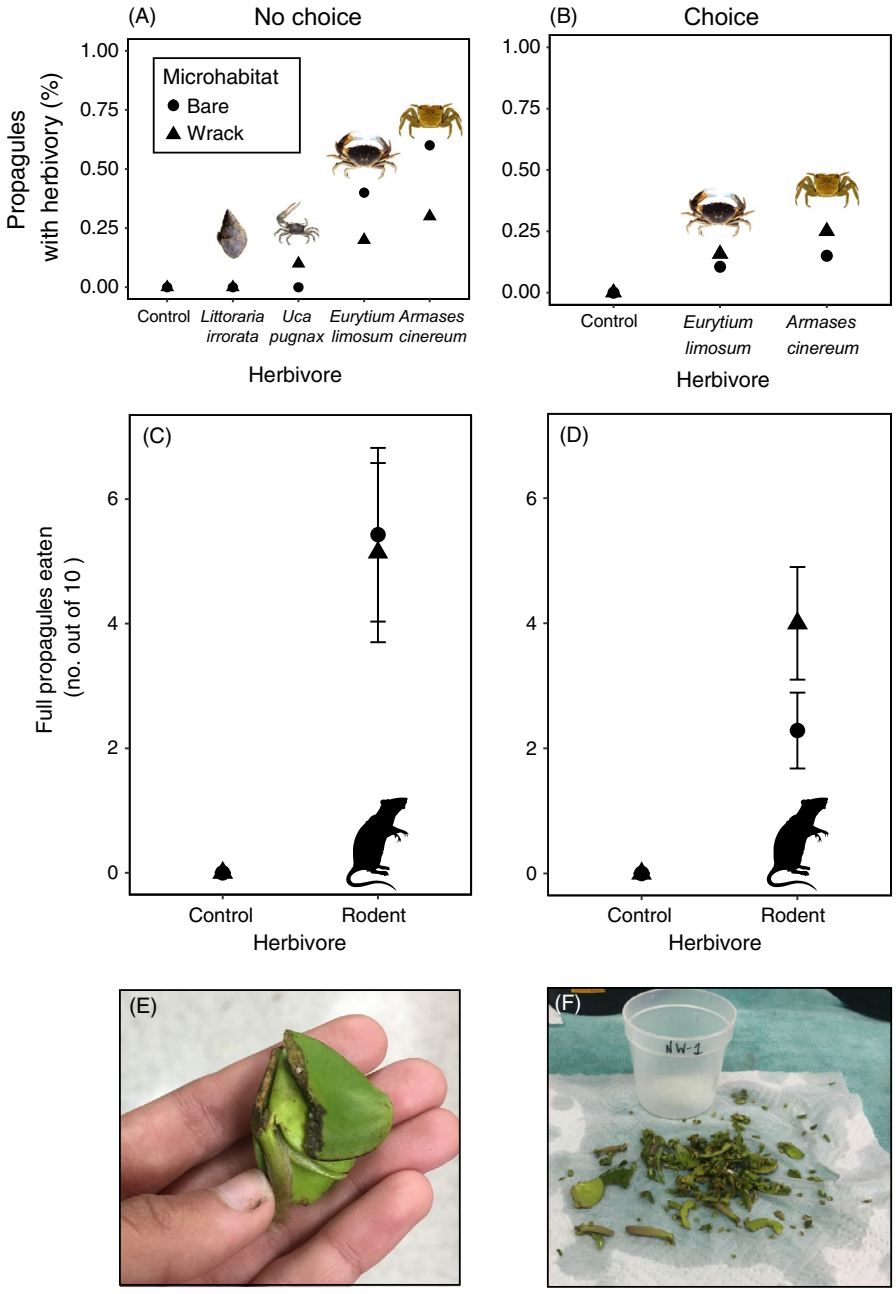

FIGURE 4 Proportion of propagules (%) with any sign of herbivory per mesocosm for invertebrates given (A) no choice of propagules' microhabitat and (B) a choice of propagules' microhabitat (bare sand, wrack) after 8 days. Mean ± *SE* number of propagules fully eaten (out of 10 propagules per microhabitat) after 6 hr for rodents given (C) no choice of propagules' microhabitat association and (D) a choice of propagules' microhabitat association. Temporal blocks of the 'no choice' rodent assay are averaged together. Photographs of (E) invertebrate herbivory on propagules after 8 days and (F) rodent herbivory on propagules after 6 hr. Illustration credits are in Appendix 7

4 | DISCUSSION

Wrack of the dominant resident salt marsh species, *S. alterniflora*, can either facilitate or inhibit its range-expanding mangrove competitor, *A. germinans*, depending on the mangrove's life stage. During mangrove establishment, salt marsh wrack significantly increased mangrove propagule recruitment, retention and rooting (Figure 1; Appendix 5: Figure S1). Wrack's buoyant structure trapped floating propagules, held them in the place and created a moist environment that encouraged propagule rooting. However, after mangrove propagules rooted, salt marsh wrack inhibited mangrove seedling survival (Figure 2A; Appendix 5: Figure S1). Seedling mortality was greater under wrack, likely because wrack blocked light and attracted herbivores. Our feeding assays of common marsh consumers revealed that rodents have a strong appetite for *Avicennia* propagules in the laboratory, especially when given propagules with wrack (Figure 4D; Appendix 5: Figure S1). Our results indicate that as mangroves expand poleward into salt marshes, resident salt marsh species provide biotic resistance to mangrove seedlings that counterbalances the initial biotic assistance that occurs during propagule establishment.

4.1 | Wrack effects on mangrove propagule establishment

Habitat modification and stress amelioration by resident species can facilitate sensitive early life stages. Our work supported the hypothesis that facilitative interactions would be more important during

early life stages, when species are particularly sensitive to harsh abiotic conditions. The physical structure created by salt marsh wrack facilitated initial mangrove propagule recruitment and establishment; by trapping and retaining propagules, wrack helped propagules withstand the hydrodynamic forces that can uproot propagules or prevent propagule settlement (Ellison & Farnsworth, 1993; Patterson et al., 1997; Sousa et al., 2007). In fact, few propagules recruited to salt marsh microhabitats in wrack's absence (Figure 1A). Wrack also improved rooting success, likely by retaining moisture and minimizing desiccation stress (Smith et al., 2018). Mangrove propagules are particularly vulnerable to desiccation stress during establishment (Clarke & Myerscough, 1993; McKee, 1995b; Patterson et al., 1997). Surprisingly, propagules placed above- or below-wrack had similar propagule establishment responses, despite hypothesized differences in associated desiccation stress. The short experimental duration and the frequent shading of the plots by the adjacent upland forest likely minimized propagule desiccation in the field. Some propagules in the above-wrack treatment also naturally fell through the wrack over time, which reduced differences between the wrack treatments. Regardless of propagules' initial placement, wrack facilitated their establishment by increasing propagule delivery, retention and rooting. These results support the hypothesis that biotic assistance may predominate during early life stages.

The magnitude and direction of salt marsh wrack effects on mangrove establishment varied with the tidal regime. Although hydrodynamic forces can disrupt propagule establishment, propagules also depend on tidal inundation to deliver them to suitable habitats and prevent desiccation after arrival (Balke et al., 2011; Van der Stocken et al., 2019). All trials occurred during the peak mangrove dispersal season, and wrack trapped more recruiting propagules during the higher spring tides, likely because more propagules were delivered to the high marsh with higher water levels. However, spring tides also decreased propagule retention rate, because the same high water levels and tidal energy increased hydrodynamic forces that uprooted propagules or floated them away prior to rooting (Delgado et al., 2001). This effect is muted in Figure 1B because we only included plots where wrack treatments did not wash away. When all replicate plots are included, more propagules are still present in the wrack treatments relative to the other microhabitats, but fewer propagules on average are retained in the wrack treatments during the spring tide trial than the neap tide trial (Appendix 2: Figure S1b). Indeed, propagule retention in live salt marsh is also more likely to be sustained in areas that are not regularly inundated following deposition by storms or spring tides (Peterson & Bell, 2012, 2015; Yando et al., 2020). Wrack is more buoyant than propagules and when wrack floats away with the tide, it can relocate mangrove propagules that are on top of wrack or trapped within wrack. It is unclear where missing propagules and wrack are subsequently deposited, which limits our capacity to predict establishment outcomes for these relocated propagules. Indeed, patches of high mangrove propagule retention can be spatially mismatched with the areas of high mangrove seedling density within the same marsh-mangrove ecotone (Yando et al., 2020). Nonetheless, the tidal regime ultimately affects the degree to which wrack facilitates mangrove propagule recruitment by controlling the relative strength of propagule delivery and retention both within the marsh-mangrove ecotone and as mangrove propagules disperse poleward into salt marsh habitats.

4.2 | Wrack effects on mangrove seedling survival

As individuals develop, changes in their resource requirements and stress tolerance can lead to corresponding shifts in biotic interactions. The seedling survival experiment supported our hypothesis that interaction outcomes would shift from positive to negative with seedling development, as invader resource requirements changed with ontogeny. Although salt marsh wrack facilitated mangrove propagule establishment, at the end of seedling survival experiment, seedlings in the wrack treatments had the fewest survivors, with near complete mortality (Figure 2A) and low biomass and few leaves (Figure 3). Indeed, if wrack stays in place throughout mangrove seedling development, the magnitude of this negative effect on seedling survival strongly counterbalances initial positive effects of wrack on propagule establishment. Wrack residence time in the high marsh varies based on where it is deposited relative to the tides; timing can range from weeks to years (Bertness & Ellison, 1987; Marinucci, 1982). Sustained negative effects of salt marsh wrack on mangrove seedlings are more likely in high marsh areas with persistent wrack piles that are less regularly disrupted by tidal inundation. In the above-wrack treatment, wrack inhibited mangrove survival via desiccation and smothering; we observed several blackened, desiccated propagules in these treatments, especially during months 1 and 3. In the below-wrack treatment, wrack smothering—which includes the effects of low light, anoxia and physical crushing—likely caused mangrove seedling mortality. Indeed, seedlings planted in bare sediment plots that were released from light limitation had nearly double the biomass of seedlings in the other treatments (Figure 3). Declines in resident salt marsh species in the wrack plots also suggest that smothering was an important source of mortality (Appendix 3; Figure S3). Maternal provisioning in the cotyledon initially allows propagules to root, stand up, respire and grow without photosynthesis (Hogarth, 2015). As propagules develop true leaves and become seedlings, they increasingly depend on photosynthesis and divert resources towards above-ground biomass. Thus, light becomes more necessary during seedling development (Lopez-Hoffman et al., 2007).

Wrack also potentially inhibited mangrove seedling survival indirectly by attracting herbivore consumers. In the early stage of the seedling survival experiment (1–3 months), the prevalence and intensity of herbivory was greatest on seedlings planted below-wrack (Figure 2B). Herbivory manifested as large bites taken from seedling cotyledons (>5 mm) and, in some cases, from significant portions of the seedling stems and leaves (>50% consumed; Appendix 3: Figure S1a); similar levels of herbivore damage caused seedling mortality and stunted growth in other studies (Minchinton & Dalby-Ball, 2001; Sousa et al., 2003). In contrast, in the late

stages of the experiment (6–9 months), nearly all seedlings had some evidence of insect leaf herbivory, but this herbivory was mild and likely sublethal (Appendix 3: Figure S1b). Crabs and insects are the most commonly cited consumers of mangrove propagules, and crabs presumably limit *A. germinans* expansion in marsh-mangrove habitats on Florida's Gulf Coast (Langston et al., 2017). Yet, the large bite marks observed during the early stage of the experiment suggested that small rodents could also consume mangrove propagules and rodents nested in wrack treatment plots during the early stage of the seedling survival experiment (Appendix 3: Figure S2). Feeding assays confirmed that both rodents and crabs consume propagules, and rodent herbivory was dramatically more severe. Our work offers preliminary evidence that salt marsh wrack could provide refuge for rodents to hide and feed out of the sight of predators—rodents even built nests in our mesocosms when wrack was present. Indeed, when given a microhabitat choice, rodents ate 1.75 times more full propagules in wrack compared to bare sand. Although rodents enthusiastically consumed propagules in the laboratory, more work is needed to confirm the role of rodents as natural propagule consumers in high intertidal microhabitats in the field and to remove any sampling artefacts associated with mesocosm size or single food offering. Several studies document rodents as important consumers in other marsh and mangrove systems (Crain, 2008; Greenberg et al., 2006; Zhang et al., 2018). We suggest that rodents could be important marsh consumers that can provide additional biotic resistance to mangrove expansion, especially when aided by salt marsh wrack.

4.3 | Predicting net effects of early life stages

Mangrove propagules and seedlings are two important life stages in mangrove systems where bottlenecks can occur (Friess et al., 2012). Indeed, early establishment and seedling stages are typically the most vulnerable in woody plant life cycles and are the life stages that most constrain woody encroachment world-wide (Archer et al., 2017). In mangroves, the outcome of propagule-seedling demographic transitions can affect long-term success as seedlings progress to juvenile and adult life stages (Lopez-Hoffman et al., 2007). We found that the persistent presence of salt marsh wrack on top of mangrove seedlings counterbalances the positive effects of wrack on mangrove propagules during establishment. To examine the net quantitative effect of salt marsh wrack on these two life stages, we combined the results of our two experiments to roughly calculate the expected late-stage seedling survival (9 months+), given differential propagule recruitment and rooting in spring and neap tides (Appendix 5: Table S1). Net expected late-stage seedling survival is greater for seedlings below salt marsh wrack, although the magnitude of this effect varies with initial tidal conditions. Overall, this result suggests that wrack's facilitative effect on mangrove propagules might slightly outweigh its negative effects on seedlings (Appendix 5: Table S1). However, these calculations only estimate the net numerical effect and do not consider differences in seedling quality; for example, compared to bare treatments, the quality of surviving seedlings below-wrack was lower, and seedlings had less mass and fewer leaves (Figure 3). Although the net effect of persistent *S. alterniflora* wrack on *A. germinans* may be slightly positive, these calculations also reveal that the effect of salt marsh wrack reverses between the mangrove propagule and seedling life stages. Wrack initially facilitates propagule recruitment, retention and rooting, but ultimately reduces seedling survivorship and stature.

In the broader context of mangrove expansion into salt marshes, temperature is considered the primary constraint that limits mangrove distributions in transitional habitats (Cavanaugh et al., 2014; Osland et al., 2019). Early mangrove life stages may be more resistant to freezing temperatures relative to adult trees (Osland et al., 2015), which highlights the need to understand the relative importance of other biotic and abiotic factors that determine range expansion success during early life stages of leading edge mangrove populations. Assuming that temperatures exceed minimum temperature thresholds for mangroves, we find that expansion success conditionally depends on the interaction of wrack presence, tidal regime and mangrove propagule delivery. When these specific conditions are known, we can predict whether salt marsh wrack will assist or resist mangrove expansion. At a population or landscape scale, documenting the frequency distributions and timing of wrack, propagule delivery and the tidal regime to determine their co-occurrence would enhance the predictions of poleward mangrove expansion into salt marshes.

5 | CONCLUSIONS

In summary, our work with climate-driven mangrove expansion into salt marshes highlights that the effect of resident species on invading or range-expanding competitors can shift across different life stages of the expanding species. This finding has implications for understanding similar expansion and invasion processes in other systems, such as during woody encroachment. Specifically, our work illustrates that different mechanisms for biotic resistance or assistance can predominate at different life stages (Becerra & Bustamante, 2011; Deng et al., 2009; Rius et al., 2014). For example, we found that biotic assistance predominated during early life stages by ameliorating abiotic conditions, but that biotic resistance became more important during later life stages as species became more limited by available resources. Our results show that net interaction outcomes between species can be composed of several opposing interactions that occur at successive life stages. Stages of species expansion are sequential, and interaction outcomes at each phase of expansion either accentuate or dampen outcomes from previous stages (Battaglia et al., 2009). Additionally, our work suggests that the magnitude of interaction outcomes at each life stage is context-dependent and varies with abiotic conditions. Understanding how the relative biotic resistance and assistance of native biota changes with invader life stage and environmental conditions can improve the predictions of invasion and range expansion success in coastal and terrestrial systems.

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AUTHORS' CONTRIBUTIONS

R.S.S., J.A.B. and J.E.B. conceived the ideas and designed the methodology; R.S.S. and J.A.B. collected the data; R.S.S. analysed the data and led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13586.

DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the data provided by Smith et al., 2020b, https://doi.org/10.5061/dryad.w3r2280pm (Smith et al., 2020a).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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