



# Facilitating your replacement? Ecosystem engineer legacy affects establishment success of an expanding competitor

Rachel S. Smith<sup>1</sup> · Julie A. Blaze<sup>1</sup> · Todd Z. Osborne<sup>2,3</sup> · James E. Byers<sup>1</sup>

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## Abstract

Interactions with resident species can affect the rate that expanding species invade novel areas. These interactions can be antagonistic (biotic resistance), where resident species hinder invasive establishment, or facilitative (biotic assistance), where residents promote invasive establishment. The predominance of resistance or assistance could vary with the abiotic context. We examined how the effects of a resident ecosystem engineer interact with abiotic stress to resist or assist the establishment of an expanding competitor. In Florida salt marshes, native cordgrass, *Spartina alterniflora*, is an influential ecosystem engineer that, when dead, exerts a legacy effect by forming persistent wrack patches. We examined how the legacy effect of *Spartina* wrack varies with spatial context and abiotic conditions to influence establishment of the northward-expanding black mangrove, *Avicennia germinans*. Field surveys documented that *Spartina* wrack and *Avicennia* propagules co-occur in the high intertidal zone, and we conducted two outdoor mesocosm experiments to investigate this association. Wrack positively affected propagule establishment when propagules were beneath wrack, but negatively affected establishment when propagules were above wrack. The abiotic tidal regime influences the magnitude of wrack effects by controlling ambient moisture, and the positive and negative effects of wrack were stronger in low moisture conditions that simulated desiccation stress during harsh neap tides. Thus, the same resident engineer can either resist or assist an expanding competitor and the magnitude of these effects depends on abiotic conditions. We propose that under harsh conditions, there is greater scope for an engineer's mediating influence to affect associated species, both positively and negatively.

**Keywords** Abiotic stress · Context dependent · Foundation species · Mangrove · Salt marsh wrack

## Introduction

Biotic interactions with resident species can affect the rate at which expanding species invade novel areas. These interactions are often characterized as biotic resistance, in which

the resident community reduces establishment success of expanding species through antagonistic interactions (e.g., predation, herbivory, competition and disease) (Elton 1958; Levine et al. 2004; DeRivera et al. 2005). However, biotic interactions can be both positive and negative and often occur simultaneously (Holmgren et al. 1997). It is possible that the opposite process, biotic assistance, in which the resident community facilitates establishment of expanding species, also influences the establishment success of invading species. Despite widespread recognition of the importance and prevalence of positive interactions (Bruno et al. 2003; Callaway 2007), facilitation of species expansion by resident species is rarely considered as a potential mechanism for invader establishment success (Catford et al. 2009). The relative importance of biotic resistance and biotic assistance is unknown and is likely context dependent. In general, the net outcome of biotic interactions can depend on the life stages, sizes, and densities of interacting individuals, on consumer gradients, or on abiotic stress (Bertness and Callaway

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✉ Rachel S. Smith  
Rssmith218@gmail.com

- <sup>1</sup> Odum School of Ecology, University of Georgia, Athens, GA 30602, USA
- <sup>2</sup> The Whitney Laboratory for Marine Bioscience, University of Florida, St. Augustine, FL 32080, USA
- <sup>3</sup> Soil and Water Sciences Department, University of Florida, Gainesville, FL 32611, USA

1994; Callaway and Walker 1997). Thus, an increased understanding of the context-dependency of biotic interactions is essential for predicting expansion dynamics, a task that is especially important considering recent increases in both the spread of invasive species worldwide (Mack et al. 2000) and species range shifts due to climate change (Chen et al. 2011).

Ecosystem engineers are a suite of species that strongly influence the context of biotic interactions by controlling resource availability to other species through changes to the physical environment (Jones et al. 1994, 2010). For example, beaver dam construction slows water flow, creates wetlands, and modifies abiotic processes (e.g., decomposition, nutrient cycling, etc.) that, in turn, change the composition of associated biotic communities (Naiman et al. 1988). Effects of engineers can persist beyond an engineer's lifetime or presence, creating legacy effects that can alter the outcome of biotic interactions by changing the abiotic context (Hastings et al. 2007; Cuddington 2011). Indeed, beaver dams continue to affect associated species for decades after beavers have abandoned these structures (Naiman et al. 1994). Species interactions with legacies of ecosystem engineering do not involve dynamic biotic feedback because the engineer is dead or absent. However, the altered abiotic context created by the engineer legacy persists and continues to affect the net outcome of biotic interactions.

Engineer effects on the abiotic context and the outcome of biotic interactions also depend on background levels of environmental variables relative to species stress tolerances. For example, the stress gradient hypothesis predicts that dominant interactions will shift from negative to positive with increasing stress, as stress-tolerant species ameliorate harsh abiotic conditions for other species (Bertness and Callaway 1994). Facilitative effects of ecosystem engineers are often more apparent in stressful environments, and the magnitude of engineering effects is predicted to increase with abiotic stress (Crain and Bertness 2006). For example, in the Negev desert, the importance of ecosystem engineering by shrub nurse plants increased along a declining precipitation gradient (Wright et al. 2006). If the magnitude and direction of engineering effects vary predictably across abiotic stress gradients, we expect that biotic resistance will be more apparent in benign environments where competitive interactions dominate, and biotic assistance will be more apparent in harsh environments where facilitative interactions are more prevalent.

We examined the relative importance of a resident engineer's legacy on the expansion success of an incoming competitor in different abiotic contexts. Specifically, we studied this interaction for mangrove expansion into salt marshes on the Atlantic coast of Florida, where the effects of wrack produced by native cordgrass, *Spartina alterniflora*, on expanding black mangroves, *Avicennia germinans*, depends on multiple interacting factors. In this area, a decreased frequency

of annual freezes allowed mangroves to double in area from 1984 to 2011 at the expense of salt marsh (Cavanaugh et al. 2014). When temperatures exceed mangrove lower tolerance thresholds, mangroves typically out-compete *Spartina* (Kangas and Lugo 1990; Zhang et al. 2012). With the alleviation of climatic constraints on mangroves in North Florida, *Avicennia* is moving north and interacting with both live *Spartina* and its dead wrack legacy.

*Spartina* and *Avicennia* are both well-documented ecosystem engineers. Both create physical structures in coastal systems that affect associated biotic interactions, although they vary in the quality and quantity of habitat created (Gutiérrez 2011; Friess et al. 2012). In addition, *Spartina* has a significant legacy effect (Holdredge and Bertness 2011), as seasonal *Spartina* dieback in the winter creates extensive mats of buoyant, recalcitrant dead wrack that have cascading abiotic and biotic effects in local systems that extend beyond the lifetime of the standing live *Spartina* (Reidenbaugh and Banta 1980). When *Spartina* wrack is stranded in coastal wetlands on high tides, it smothers existing vegetation (Bertness and Ellison 1987), alters local light and moisture regimes, and creates bare patches that can be differentially colonized by fugitive marsh species (Brewer et al. 1998; Tolley and Christian 1999). Although live standing *Spartina* ramets have lifespans of approximately 1 year (Dai and Wiegert 1996), a single *Spartina* wrack pile can persist for more than 2 years in the high marsh (Marinucci 1982; Valiela et al. 1985), creating enduring legacy effects in these systems.

Because *Spartina* wrack alters local abiotic conditions, interactions with wrack could affect *Avicennia* establishment success, which represents a significant bottleneck to mangrove expansion (Friess et al. 2012). *Avicennia* are cryptoviviparous and produce reproductive structures known as propagules that germinate and develop on the parent tree (Hogarth 2015). After mangrove propagules are released from the parent tree, they have an obligate flotation period (Rabinowitz 1978), and, like *Spartina* wrack, propagules are typically stranded in coastal wetlands by high tides. In North Florida, *Avicennia* propagules disperse yearly from mid-October to mid-December, overlapping with *Spartina* wrack deposition, which occurs year-round, with peak accumulations in March (R. Smith, unpublished data). Thus, propagule stranding can coincide with wrack deposition in the high intertidal zone, either because propagules raft in with wrack or respond similarly to common hydrodynamic forces (Minchinton 2006).

After stranding, various abiotic and biotic factors influence propagule establishment, including light, moisture, nutrients, salinity, soil type, inundation, and consumer pressure (Krauss et al. 2008). We predicted that mangrove propagule co-occurrence with wrack could alter these establishment conditions and affect propagule success. Specifically,

we hypothesized that the net outcome of biotic interactions between wrack and propagules would first depend on propagule vertical position relative to wrack, as wrack creates different light and moisture regimes above and below it. If propagules were stranded above wrack, wrack could suppress propagule growth by increasing desiccation, or alternatively, propagules could benefit from greater light. In contrast, if propagules were stranded below wrack, wrack could enhance propagule growth by minimizing evaporation and creating moist conditions (Pennings and Richards 1998), or it could hinder propagules through physical smothering or shading.

We also predicted that the net outcome of biotic interactions between *Spartina* wrack and *Avicennia* propagules would depend on background abiotic conditions, as controlled by the tidal regime. Tidal inundation affects mangrove zonation patterns (Jiménez and Sauter 1991) by altering mangrove establishment and growth (Clarke 1993; Ellison and Farnsworth 1993; McKee 1995b). Mangrove propagules are highly recalcitrant but require a minimum level of inundation to prevent propagule desiccation and begin rooting (Osborne and Berjak 1997; Farnsworth 2000). At the same time, inundation must not be so severe that propagules are subject to excessive physical disturbance by hydrodynamic forces and sediment scouring (Balke et al. 2011). During inundation-free periods, propagules can rapidly allocate energy to root extension so that they can withstand future inundation (Balke et al. 2011). Thus, early mangrove establishment requires a balance between minimizing desiccation and hydrodynamic stress, and tidal regime controls the importance of both stressors. In North Florida, a stranded propagule in the high intertidal zone may be inundated daily during spring tides, yet the same propagule may not be inundated for more than 2 weeks during neap tides, creating distinct abiotic desiccation stress regimes (R. Smith, personal observation). Thus, we hypothesized that propagule spatial relation to wrack would be more influential in the low moisture conditions of harsh neap tides compared to high moisture conditions of more benign spring tides, when desiccation stress is less affected by wrack presence.

To test these hypotheses, we first performed field surveys to document *Avicennia* propagule abundance in *Spartina* wrack compared to adjacent live vegetation without wrack, including the relative spatial positioning of the propagules to the wrack (i.e., above or below wrack). Second, we conducted an outdoor mesocosm experiment in which we varied propagule vertical position relative to wrack (above wrack, below wrack, no wrack) during a simulated neap tide (i.e., low moisture) to quantify the effect of *Spartina* wrack on *Avicennia* establishment. Lastly, we conducted another mesocosm experiment to examine how propagule vertical position relative to wrack interacts with accentuated moisture regimes associated with spring (high moisture) and neap

(low moisture) tidal cycles to affect *Avicennia* establishment. Together, this work explores the relative importance of a prominent resident ecosystem engineer's legacy on the establishment success of an expanding competitor and how the magnitude of these engineering effects changes with abiotic conditions.

## Materials and methods

### Field survey: quantifying wrack legacy and mangrove propagule co-occurrence

To determine how frequently *Spartina* wrack and *Avicennia* propagules co-occur, we surveyed quadrats with and without *Spartina* wrack in November 2015 and November 2017. Within the Matanzas River estuary in St. Augustine, Florida, near the northward edge of *Avicennia*'s present distribution (29.710667° N, 81.243883° W), we selected sites in high intertidal areas of marsh–mangrove transition zone habitat that had distinct wrack deposition lines (five sites in 2015, six sites in 2017). All sites were located within a 20-km stretch of the Matanzas River, and at each site we placed a 30 × 1 m transect line parallel to the water along the existing wrack line, which is often located near mean higher high water (MHHW). Along each transect, we haphazardly sampled 10 wrack patches and 10 horizontally adjacent patches without wrack at the same tidal height that represented a mix of *Spartina* and *Avicennia* vegetation. Although wrack was patchy at most sites, at sites where wrack was present across the entire transect (i.e., unbroken), we alternated choosing non-wrack quadrats that were immediately landward or seaward above and below the wrackline along the transect. Each sample was a 0.25 m<sup>2</sup> quadrat in which we counted *Avicennia* propagules. We defined quadrats as ‘wrack absent’ if they had no wrack and defined quadrats as ‘wrack present’ if they had a minimum of 35 g of wrack dry weight biomass, although most quadrats had substantially more. The average wrack dry weight biomass per wrack plot was 170.41 g ± 123.34 (mean ± SD), and the average maximum wrack depth across all sites was 2.33 cm ± 0.52 (mean ± SD). Additionally, to quantify the relative spatial positioning of *Avicennia* propagules to *Spartina* wrack (above or below wrack), in 2017, we recorded the number of propagules present above wrack and the number of propagules present below wrack within each quadrat. We recorded a propagule as placed “below wrack” if any part of the propagule was covered by wrack, and most of the propagules classified as “below wrack” were 100% covered by wrack (R. Smith, personal observation). To examine propagule abundance in areas with and without wrack, we analyzed propagule counts with a generalized linear mixed model in R 3.1.3 (R Core Team 2017) with the ‘MASS’ package (Venables and Ripley

2002), using a negative binomial distribution to account for overdispersion. We used wrack presence as a predictor of propagule abundance in the model and included site as a random intercept, performing separate analyses for 2015 and 2017. In addition, we used a generalized linear mixed model with a negative binomial distribution to examine propagule abundance as a function of propagule location relative to wrack (above or below), again including site as a random intercept for the 2017 survey.

### Experiment 1: Effects of wrack position on propagule establishment

We performed an outdoor mesocosm experiment to assess how *Avicennia* propagule spatial position relative to *Spartina* wrack affected propagule establishment. On October 18, 2016, we collected 1350 mature propagules from adult trees in Crescent Beach, FL, within the Matanzas River estuary (29.761233° N, 81.266917° W) and brought them back to the University of Florida Whitney Laboratory. To maintain propagule uniformity, we selected propagules from a size range of 26–40 mm and excluded those with herbivory or disease (length  $32.1 \pm 2.9$  mm; fresh weight  $2.45 \pm 0.50$  g; mean  $\pm$  SD). To prepare propagules for the experiment, we floated them in seawater in full sunlight for 5 days to mimic natural propagule dispersal and to approximate their optimal flotation time (Rabinowitz 1978; Simpson et al. 2016). Pericarps naturally fell off the propagules within 72 h, and propagules did not develop roots prior to the experiment.

We placed pebbles in the bottoms of 1350 square pots as ballast (9 cm per side) and filled each pot with a 4:1 mixture of commercial, unamended top soil (Timberline©) and sand (Sakrete©) to a depth of 7.4 cm to maintain consistent soil conditions across treatments. We added one propagule to each pot and applied one of three wrack position treatments: propagule below wrack, above wrack, and no wrack as a control ( $n=450$  per treatment). For the wrack treatments, we cut air-dried wrack into 9 cm pieces to fit precisely in each pot and placed an average of 21 pieces of wrack on the soil surface of each filled pot to create wrack depths of 2 cm, approximating mean field measurements in this system. We placed propagules on soil (below wrack and control treatments) and wrack surfaces (above wrack treatment) to mimic natural propagule stranding.

After establishing the three wrack position treatments, we randomly placed seven pots from each treatment into a 27-l plastic bin, and interspersed 65 such bins among each other. To maintain constant moist soil conditions without fully inundating propagules, we filled the bins with seawater to 7 cm (just below the soil surface) to create a low moisture environment characteristic of neap tide conditions, and each pot had four holes in its base that allowed water to wick into the pot. We topped up the bins with

freshwater every 2 days to replace evaporated water and keep salinity constant (35–40 PSU). Each week, we fully changed the seawater in each bin to minimize stagnation and algae growth. We also enclosed the entire experimental array with an electric fence to exclude mammalian herbivores.

To determine wrack position effects on propagule establishment, we measured several aspects of propagule performance. First, we took non-destructive repeated measures on a subset of propagules ( $n=50$  for each wrack position; 150 pots total; repeated measures subset), recording the above-ground height of survivors and noting if each propagule was alive, desiccated, or rooted. We scored a propagule as desiccated if at least one of its cotyledons was fully brown. We measured the same individuals every other day for the first 2 weeks of the experiment and then weekly for an additional 5 weeks.

On a different set of propagules, we took additional non-destructive measurements to determine whether unrooted propagules were more likely to float during an inundation event. We conducted flotation trials for a new randomly chosen subset of propagules every other day for the first 2 weeks of the experiment and then weekly for an additional 2 weeks ( $n=20$  for each wrack position on each date; 600 pots total; flotation subset). We randomly selected pots at each time point from each position treatment without resampling. Then, we placed each pot separately in an inundation chamber that we filled with seawater until it covered the pot ( $>9$  cm), and we scored whether propagules floated. We used each pot only once for a flotation trial, but we allowed all floated propagules to continue growing after flotation so that we could include this subset in endpoint biomass measurements using the destructive procedures described below.

Second, to quantify plant biomass and the force required to dislodge a propagule from the soil, we destructively sampled additional random subsets of propagules every other day for the first 2 weeks of the experiment and then weekly for an additional 2 weeks ( $n=20$  for each wrack position on each date; 600 pots total; destructive measures subset). We used a spring scale to determine the force required to dislodge each propagule from the soil (see Balke et al. 2011); force values were adjusted by subtracting the fresh weight of each propagule. Next, we washed propagules with freshwater to remove soil and salt, cut propagules into components parts (root, hypocotyl, shoots, cotyledons, leaves), and dried them at 60 °C for 3 days. We then measured the dry weight of each part to obtain root:shoot ratios, excluding cotyledons from the shoot biomass measure because we were interested in propagule biomass independent from maternal provisioning (Lin and Sternberg 1995, Farnsworth 2000). On day 51, we used the same methods to measure the biomass of all remaining plants in the experiment (750 total; repeated measures and flotation subsets).



We used the ‘survival’ package in R to perform survival analysis using Cox proportional hazards to evaluate the main effect of wrack position on propagule survival, desiccation, and rooting (Therneau 2015). In cases where there was 100% survival, desiccation, or rooting, we added one dummy record of the unrepresented response to the last time point to allow the hazards model to converge. In the hazards analysis for rooting time, we removed dead propagules. To examine aboveground height, we used a linear mixed model to account for the repeated measures sampling design of this response variable using the ‘lme4’ package (Bates et al. 2015). We examined the interaction of wrack position and time on aboveground height, including variation by day and treatment for each replicate as additional random effects in the model. We then performed a one-way ANOVA on the end point data using wrack position to predict final aboveground height. We also used a binomial generalized linear model to analyze the proportion of floating propagules as a function of wrack position and time.

For the destructive measures, we used linear models to predict root:shoot ratio, root dry weight, and dislodgement force as a function of the interaction of wrack position and time, excluding dead propagules from these analyses. Because biomass and force measures from the destructive subset were independent over time, we performed separate ANOVAs at each time point for each response variable, using Tukey’s post hoc tests to determine when propagules showed differences between wrack treatments. For the destructive measures, sample size was the same at each time point ( $n=20$  for each wrack position), except for the last time point, day 51, where sample size was much larger ( $n=250$  for each wrack position). For all linear models, we log transformed data where appropriate to meet assumptions of normality and homoscedasticity.

## Experiment 2: Effects of wrack position and moisture on propagule establishment

We conducted a second mesocosm experiment to examine how *Avicennia* propagule spatial position relative to *Spartina* wrack interacted with moisture conditions characteristic of spring and neap tidal regimes to affect propagule establishment. On November 9, 2016, we collected 300 mature propagules from trees in Crescent Beach, FL, and prepared propagules and pots as described for Experiment 1, except that we filled each pot with the top soil–sand mixture to a depth of 5.6 cm to allow greater inundation in each pot. We placed propagules into the same wrack position treatments described in Experiment 1 (above wrack, below wrack, no wrack), with 100 propagules in each wrack position (length  $32.18 \pm 2.74$  mm; fresh weight  $2.75 \pm 0.60$  grams; mean  $\pm$  SD). We also included an additional below wrack depth treatment (4 cm) to isolate smothering effects

(Appendix 2). We randomized replicates of the wrack treatments within 16 bins that we interspersed in the experimental array.

We then randomly assigned half of the bins to one of two moisture treatments that represented sustained neap and spring tidal regimes found in the high intertidal zone where wrack and propagules naturally strand. These treatments applied a constant moisture regime (neap = drier; spring = moister) throughout the experiment, rather than changing over time, as occurs during a natural monthly tidal cycle. By fixing the treatment levels over time, we isolated the role of moisture on *Avicennia* propagule establishment. We created the sustained low moisture neap tide treatment by adding seawater to a depth of 5 cm to keep water levels just below the soil surface, as in Experiment 1. We created the sustained high moisture spring tide treatment by raising water levels to a depth of 7 cm for 2 h, twice a day. Because the pots were 9 cm deep, the inundation did not displace the propagules from their pots. After each 2-h inundation, we drained water out of the bottom of each pot to return each bin to neap tide water levels. Daily timing of the flooded tide conditions followed the natural semidiurnal tidal cycle of the Matanzas River estuary. Every other day during the first 2 weeks, we scored all propagules for survival, desiccation, and rooting responses and measured aboveground height of surviving propagules. We recorded these measures weekly for 2 additional weeks and ended the experiment after 30 days.

We performed survival analysis as described for Experiment 1 to evaluate the interactive effect of moisture level and wrack position on time until propagule survival, desiccation, and rooting. We also used a linear mixed model to analyze aboveground height as a function of the interaction of wrack position, moisture level, and time. In addition to these interactive effects, we included variation in each main effect by plant replicate as random effects in the model. We used two single factor ANOVAs to examine the effect of wrack position on final aboveground propagule height (i.e., on day 30) for low and high moisture treatments separately to compare between wrack position treatments within each moisture treatment. We destructively sampled propagules for biomass measures, and the biomass analysis is included in Appendix 1 (Appendix S1: Fig. S2).

## Results

### Field survey: Quantifying wrack legacy and mangrove propagule co-occurrence

In the November 2015 field survey, *Avicennia* propagules were significantly more abundant in wrack ( $11.09 \pm 2.02$ , mean per  $0.25 \text{ m}^2 \pm \text{SE}$ ) than in the adjacent vegetation with

no wrack ( $2.77 \pm 0.64$ ) at the same tidal height ( $\chi^2 = 39.14$ ,  $df = 1$ ,  $p < 0.0001$ ). Similarly, in the November 2017 field survey, *Avicennia* propagules were also significantly more abundant in wrack ( $29.74 \pm 6.33$ , mean per  $0.25 \text{ m}^2 \pm \text{SE}$ ) than in adjacent vegetation ( $7.50 \pm 1.34$ ) at the same tidal height ( $\chi^2 = 26.74$ ,  $df = 1$ ,  $p < 0.0001$ ). Furthermore, in the 2017 survey, significantly more *Avicennia* propagules were stranded underneath wrack ( $28.70 \pm 6.06$ , mean per  $0.25 \text{ m}^2 \pm \text{SE}$ ) than above wrack ( $1.04 \pm 0.37$ ;  $\chi^2 = 145.39$ ,  $df = 1$ ,  $p < 0.0001$ ).

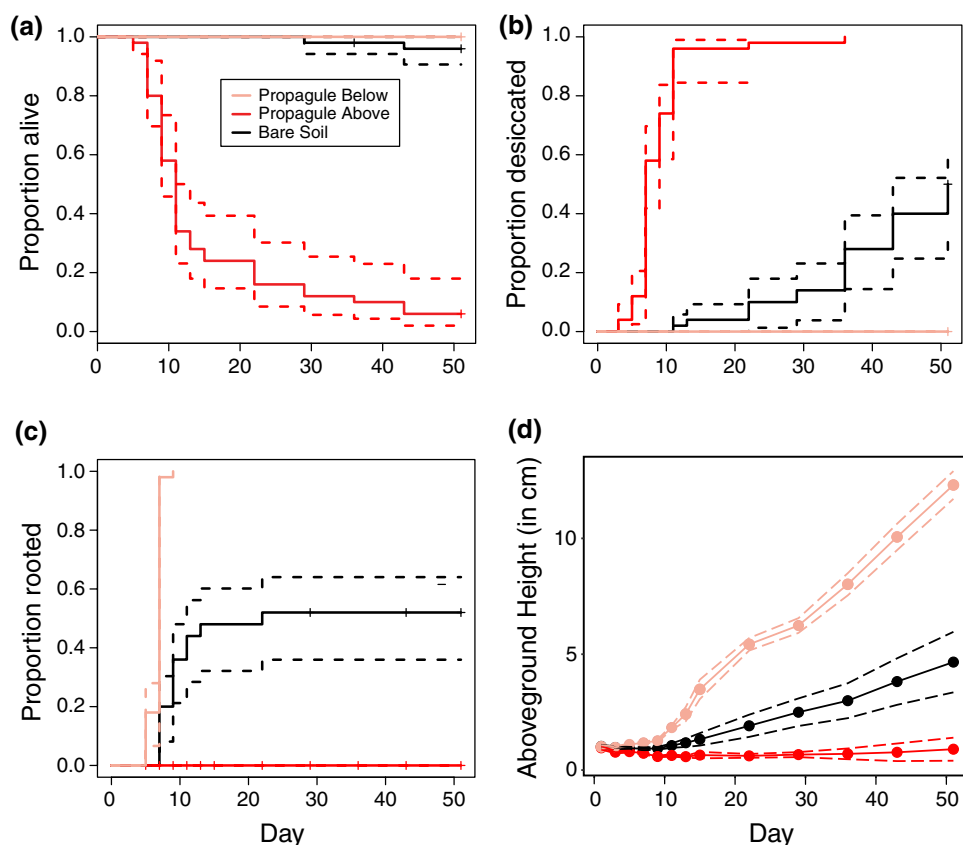
### Experiment 1: Effects of wrack position on propagule establishment

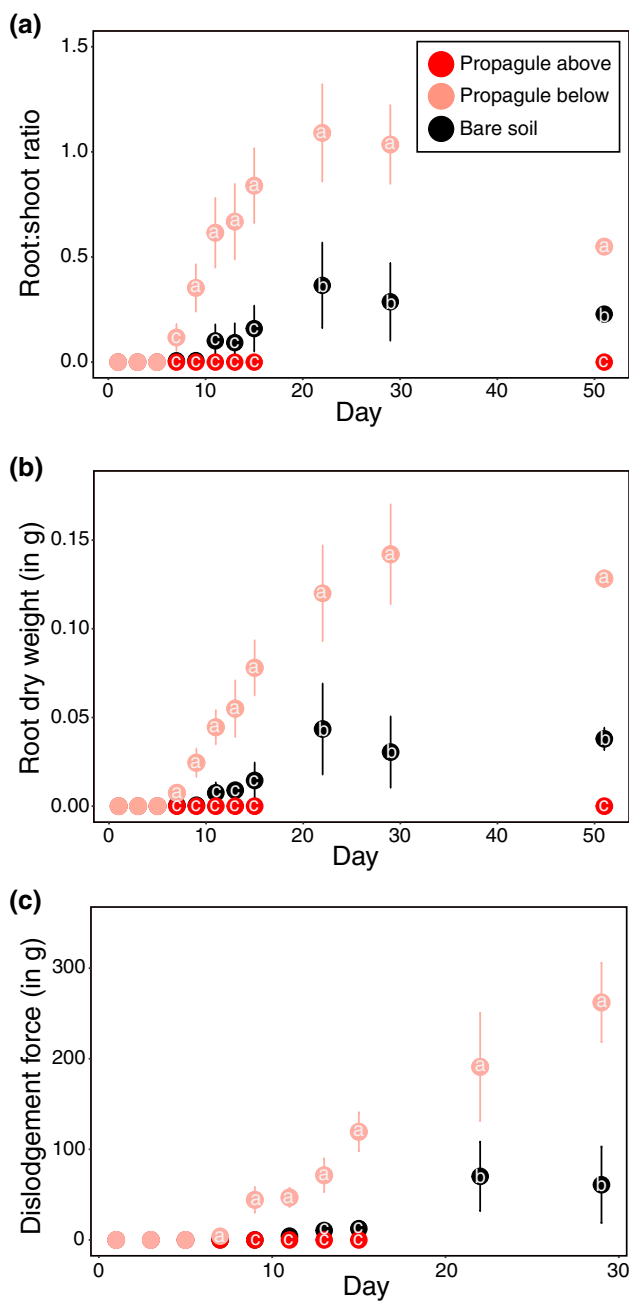
Wrack position significantly affected propagule survival, desiccation, and rooting (Fig. 1; Appendix 1: Table S1). Survival was significantly different among the three wrack positions ( $\chi^2 = 146.65$ ,  $df = 2$ ,  $p < 0.0001$ , Fig. 1a). Although there was 96 and 100% survival in bare soil and for propagules below wrack, survival of propagules above wrack dropped to 6% by the end of the experiment (Fig. 1a; Appendix 1: Table S1a). Desiccation also differed significantly among wrack positions ( $\chi^2 = 194.17$ ,  $df = 2$ ,  $p < 0.0001$ , Fig. 1b). All propagules placed above wrack desiccated by day 36, while no propagules placed below wrack desiccated (Fig. 1b; Appendix 1: Table S1b). In the bare soil control,

56% of propagules desiccated by the end of the experiment (Fig. 1b; Appendix 1: Table S1b). Rooting time also differed significantly among wrack positions ( $\chi^2 = 151.63$ ,  $df = 2$ ,  $p < 0.0001$ , Fig. 1c). All propagules placed below wrack rooted by day 9, but no propagules above wrack rooted by the end of the experiment. In bare soil, 49% of propagules rooted by the end of the experiment (Fig. 1c; Appendix 1: Table S1c). Aboveground height showed a significant interaction between wrack position and time ( $\chi^2 = 294.95$ ,  $df = 2$ ,  $p < 0.0001$ ,  $R^2 = 0.81$ , Fig. 1d). At the end of the experiment, propagules placed below wrack were 2.64 times (+7.65 cm) taller than propagules in bare soil, which, in turn, were 5.16 times (+3.76 cm) taller than the propagules placed above wrack (Fig. 1d). We saw no change in height for propagules placed above wrack.

Wrack position also significantly affected propagule biomass over time. We observed a significant interaction between wrack position and time for root:shoot ratio ( $F_{5, 974} = 173.10$ ,  $p < 0.0001$ ,  $R^2 = 0.47$ , Fig. 2a), and post hoc analyses revealed different growth timelines based on wrack position (Fig. 2a; Appendix S1: Table S2). Propagules placed below wrack had greater root:shoot ratios than the other treatments by day 7, and this treatment maintained the greatest root:shoot ratio for the rest of the experiment (Fig. 2a). Propagules in bare soil had a greater root:shoot ratio than propagules above wrack by day 22, and this trend

**Fig. 1** Propagule responses over time for *Avicennia* propagule **a** survival, **b** desiccation, **c** rooting, and **d** average aboveground height in each wrack position treatment (above wrack, below wrack, bare soil;  $n = 50$  propagules per treatment,  $n = 150$  total propagules) under the low moisture levels representative of neap tide conditions in Experiment 1. Results are from an outdoor mesocosm experiment (Experiment 1) conducted at the UF Whitney Laboratory in Marineland, Florida. Dashed lines represent upper and lower 95% confidence intervals





**Fig. 2** Average propagule measures of **a** root:shoot ratio, **b** root dry weight (g), and **c** dislodgement force (g), across wrack position treatments (above wrack, below wrack, bare soil) over time under the low moisture levels representative of neap tide conditions in Experiment 1. Sample size is  $n=20$  per wrack position treatment for the first 10 time points for a–c ( $n=600$  total propagules), and  $n=250$  per wrack position treatment for the final time point for a–b (Day 51;  $n=750$  total propagules). No force measurements were taken on day 51. Error bars are upper and lower 95% confidence intervals. Growth measures were statistically independent, so we performed one-way ANOVAs for each time point with wrack position as the main effect. Statistically significant results of Tukey’s post hoc comparisons at  $p < 0.05$  are represented by letters inside the data points for each plot

continued for the rest of the experiment (Fig. 2a). However, root:shoot ratio dropped significantly from day 29 to day 51 when propagules were below wrack (Fig. 2a).

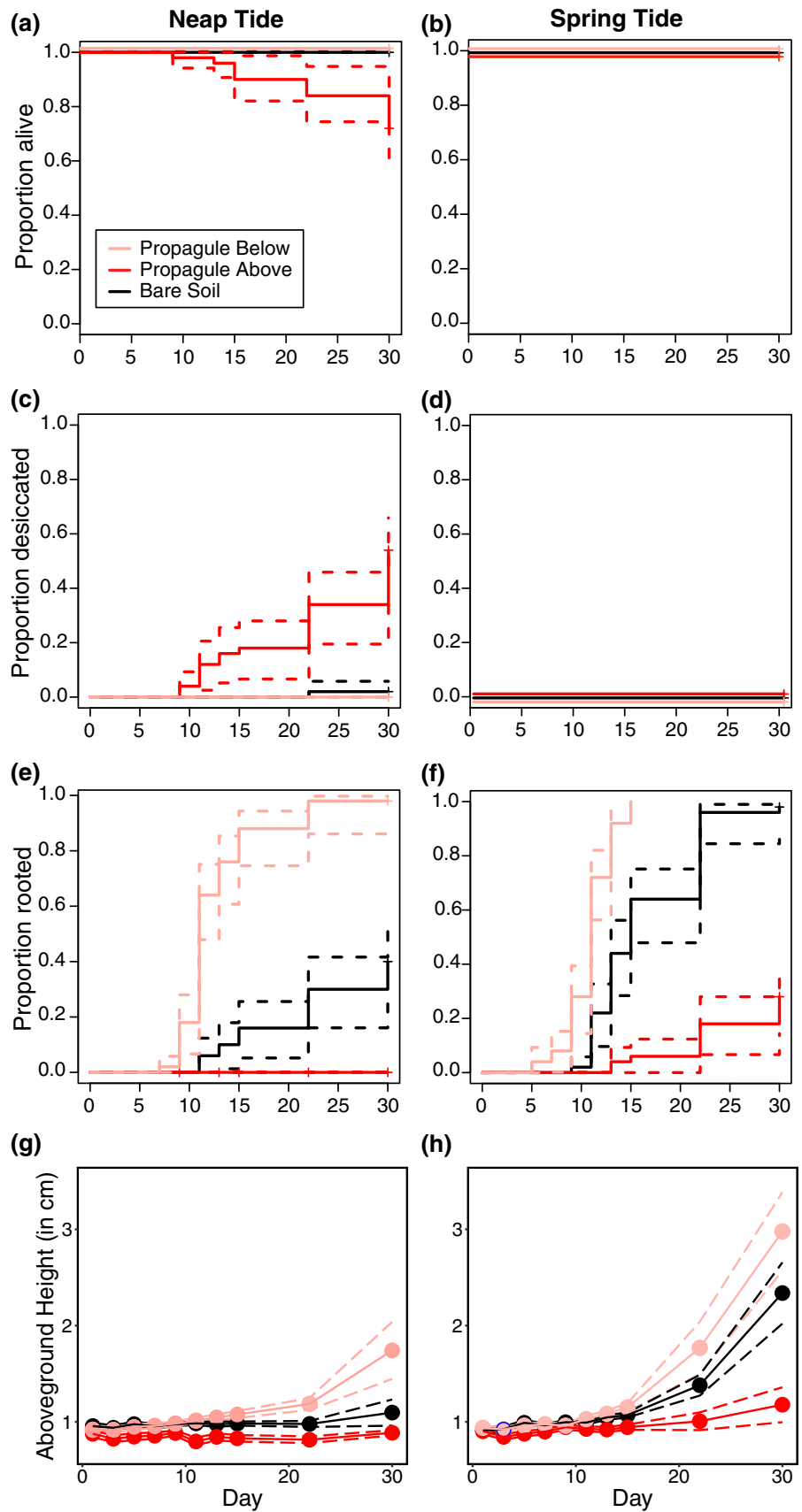
Propagule dislodgement force ( $F_{5,475} = 162.50$ ,  $p < 0.0001$ ,  $R^2 = 0.63$ ) and root dry weight ( $F_{5,475} = 187.40$ ,  $p < 0.0001$ ,  $R^2 = 0.66$ ) both showed a significant interaction between time and wrack position (Fig. 2b, c). Propagules placed below wrack had a significantly greater root dry weight by day 7 and took significantly more force to dislodge than the other treatments by day 9. In each case, responses remained significantly different from the other two treatments for the rest of the experiment (Fig. 2b, c). Force and root dry weight of propagules in bare soil did not diverge from propagules placed above wrack until day 22, and these two responses were highly correlated ( $R^2 = 0.96$ ) regardless of wrack position (Appendix 1: Table S2, Fig. S1).

Lastly, we observed significant differences in propagule ability to resist floating over the course of the experiment based on wrack position ( $\chi^2 = 21.14$ ,  $df = 2$ ,  $p < 0.0001$ ,  $R^2 = 0.62$ ). All propagules above wrack were still floating by the end of the experiment, as these propagules had not rooted. In contrast, only 5–10% of propagules placed below wrack were floating on days 7–11, and all had stopped floating by day 13. In the bare control treatment, 25% of propagules were floating at the end of the experiment (Appendix 1: Table S1d).

### Experiment 2: Effects of wrack position and moisture on propagule establishment

There was not an interactive effect of moisture level and wrack position on propagule survival ( $\chi^2 = 4.15$ ,  $df = 2$ ,  $p = 0.13$ ), although moisture level ( $\chi^2 = 11.56$ ,  $df = 1$ ,  $p = 0.0006$ ) and wrack position ( $\chi^2 = 19.15$ ,  $df = 2$ ,  $p < 0.0001$ ) had significant, independent effects on survival. For those exposed to low moisture conditions characteristic of neap tides, only 72% of propagules placed above the wrack were alive by day 30 (Fig. 3a, Appendix 1: Table S3a), whereas under high moisture conditions characteristic of spring tides, all propagules in all treatments were still alive after 30 days (Fig. 3b). Moisture level and wrack position did have a significant interactive effect on propagule desiccation ( $\chi^2 = 6.96$ ,  $df = 2$ ,  $p = 0.031$ ). In the low moisture pots, 52% of propagules placed above wrack and 2% of those in bare soil desiccated, and none of those placed below wrack desiccated (Fig. 3c, Appendix 1: Table S3b). For the high moisture pots, no propagules desiccated, regardless of wrack position (Fig. 3d, Appendix 1: Table S3b). Rooting time also showed a significant interaction between moisture level and wrack position ( $\chi^2 = 17.73$ ,  $df = 2$ ,  $p = 0.0001$ ). For low moisture pots, 98% of propagules below wrack, 40% in bare soil, and none placed above wrack had rooted by the end of the experiment (Fig. 3e, Appendix 1: Table S3c). For

**Fig. 3** Propagule responses over time for *Avicennia* propagule **a, b** survival, **c, d** desiccation, **e, f** rooting, and **g, h** average aboveground height over time in each wrack position (above wrack, below wrack, bare soil) and treatment for low (**a, c, e, g**) and high moisture (**b, d, f, h**) treatments representative of neap and spring tide conditions in Experiment 2 ( $n = 50$  per treatment combination,  $n = 300$  total propagules). Results are from an outdoor mesocosm experiment (Experiment 2) conducted at the UF Whitney Lab in Marineland, Florida. Dashed lines represent upper and lower 95% confidence intervals





high moisture pots, all propagules below wrack had rooted by day 15. By the end of the experiment on day 30, 98% of those in bare soil and 28% of those above wrack had rooted (Fig. 3f, Appendix 1: Table S3c).

For aboveground height, we observed a three-way interaction among moisture level, wrack position, and time ( $\chi^2 = 75.37$ ,  $df = 2$ ,  $p < 0.0001$ ,  $R^2 = 0.58$ ). Overall, we saw greater growth in high moisture versus low moisture conditions, and by the end of the experiment there were significant differences among wrack position in both high moisture ( $F_{2,147} = 55.09$ ,  $p < 0.0001$ ,  $R^2 = 0.43$ ) and low moisture ( $F_{2,133} = 36.75$ ,  $p < 0.0001$ ,  $R^2 = 0.36$ ) treatments (Fig. 3g, h). By day 30, relative to the low moisture conditions, propagules in the high moisture conditions were 2.13 times taller (+ 1.24 cm) in the bare soil treatment, 1.71 times taller (+ 1.24 cm) when placed below wrack, and 1.32 times taller (+ 0.292 cm) when placed above wrack. These patterns were also consistent for root:shoot ratio (Appendix S1: Fig. S2). The additional below wrack depth treatment (4 cm) did not differ significantly from the below wrack (2 cm) treatment for any measure (Appendix 2).

## Discussion

*Spartina* wrack and *Avicennia* propagules commonly co-occurred in the field, and mesocosm experiments showed that the direction and magnitude of wrack engineering effects on propagule establishment depended on both relative spatial position and moisture level. Wrack had positive effects on propagule survival, rooting, and growth when propagules were placed under wrack and negative effects on these same measures when propagules were placed above wrack (Fig. 1). The magnitude of these engineering effects further depended on background abiotic stress, whereby effects were accentuated in simulated neap tide (low moisture) conditions compared to spring tide (high moisture) conditions (Fig. 3). Engineering effects on invader establishment, whether positive or negative, can intensify with abiotic stress. As mangroves expand into salt marshes, tide-dependent interactions between resident *Spartina* wrack and incoming *Avicennia* propagules will create spatial and temporal variation in propagule success: greater establishment will occur during spring tides and in the presence of wrack if propagules are beneath the wrack. In the field, a high proportion of propagules were stranded underneath wrack, suggesting that, in this system, conditions can often align where a resident engineer facilitates the establishment of an invading replacement species.

Mechanistically, *Spartina* wrack affects the establishment of *Avicennia* propagules by controlling desiccation stress. When propagules are below wrack, wrack minimizes desiccation stress and retains moisture for rapid root development.

Wrack accelerates rooting time for propagules beneath it (Fig. 1c), minimizing the time period where propagules are vulnerable to flotation (Appendix 1: Table S1d). Indeed, dislodgement force and root biomass are positively correlated ( $R = 0.96$ , Appendix 1: Fig. S1), suggesting that wrack can facilitate propagules by shortening the time necessary for them to develop roots and withstand the hydrodynamic forces that are known to limit propagule establishment at lower tidal heights and in high-energy locations (Ellison and Farnsworth 1993; Patterson et al. 1997; Sousa et al. 2007).

Although propagules placed below wrack showed immediate, greater energy allocation to root growth relative to bare soil, the root:shoot ratio declined after day 29 for this treatment, suggesting a shift in energy allocation from below- to aboveground biomass with time (Fig. 2a). Propagule morphology is highly plastic (Simpson et al. 2013), and propagules have known trade-offs in below- and aboveground biomass allocation based on limiting resources (McKee 1995a; Farnsworth and Ellison 1996; Krauss et al. 2008; Simpson et al. 2016). Propagules placed below wrack did shift to greater aboveground biomass allocation before the other treatments, but this shift occurred after most propagules broke through the wrack layer (after day 22). Also, there was no difference in propagule success with the addition of more wrack (Appendix 2: Fig. S1). In this case, wrack's role in reducing propagule desiccation and accelerating rooting outweighed costs of light limitation or smothering. However, these costs could be accentuated in the field, where wrack depths can exceed 4 cm or persist over longer time periods.

In contrast, when propagules were above wrack, wrack had strong negative effects on propagule establishment by increasing desiccation. In our studies, placement above wrack accelerated evaporation, suggesting that wrack has a strong depth evaporation gradient. This phenomenon also occurs naturally, as we have observed black, desiccated propagules lying on top of wrack in the field, and desiccation is a known cause of mortality for *Avicennia* propagules at high tidal heights (Clarke and Myerscough 1993; McKee 1995b; Patterson et al. 1997). Desiccated propagules are unable to root and recover (Appendix 3: Table S1, Fig. S1), leading to eventual mortality. Thus, our results likely underestimate some effects. For example, we observed 96% survival in bare soil by the end of Experiment 1, but 56% of these live propagules were desiccated. With more time, these propagules would likely have died, accentuating survival differences between bare soil and propagules below wrack.

Overall, the mesocosm experiments suggest that the spatial positioning of propagules relative to wrack determines whether the resident engineer legacy facilitates or hinders its competitors. Given that we observed higher densities of propagules underneath wrack in the field, wrack likely has a primarily facilitative effect on *Avicennia* propagule

establishment in this system. Thus, in this case, the resident engineer, *Spartina* wrack, likely provides biotic assistance to expanding *Avicennia* propagules during establishment, even though *Avicennia* adults competitively exclude live *Spartina* in the climax community (Kangas and Lugo 1990; Zhang et al. 2012). However, in addition to the effects of spatial positioning on the outcome of the wrack–propagule association, it is also important to consider that the timing of wrack–propagule stranding with the tidal cycle also influences the outcome of this interaction by controlling the magnitude of these positive and negative effects.

Our work supports the prediction that engineering effects are more important in physically stressful environments (Crain and Bertness 2006), and we observed stronger effects of wrack positioning in the heightened desiccation stress of the simulated neap tide (low moisture) relative to the simulated spring tide (high moisture). Although facilitative effects are predicted to be particularly important in harsh environments, we observed that both positive and negative effects were accentuated in the harsher environment. Because ecosystem engineers control the degree to which interacting species are exposed to or sheltered from background environmental conditions, we propose that in harsher environments, engineer control of exposure should be more influential in both directions. In contrast, in more benign environments, there is less scope for the engineer's mediating influence to affect associated species.

In addition to spatial positioning and tidal timing, other external factors could also affect the context-dependent relationship between *Spartina* wrack and *Avicennia* propagules, potentially accounting for observed differences in propagule establishment success between Experiments 1 and 2. For example, we observed 98% desiccation in propagules above wrack on day 29 in Experiment 1, but propagules in the same moisture treatment in Experiment 2 showed only 52% desiccation by the same time point. We started Experiment 2 two weeks after Experiment 1, which could have led to differences in initial propagule maturity or ambient environmental conditions. Mean air temperatures were 5.7 °C higher during the first 2 weeks of Experiment 1 relative to Experiment 2 (Appendix 4: Table S1), perhaps increasing desiccation. Precipitation was negligible during both experiments (Appendix 4: Table S1), but precipitation likely controls desiccation stress in other field conditions (Gilman et al. 2008). Thus, external factors could affect the role of both wrack position and tidal regime on propagule establishment.

The experimental duration of simulated tidal regimes could also influence *Spartina* wrack effects on *Avicennia* establishment. We designed the moisture treatments to sustain moisture differences characteristic of neap and spring tides and not to mimic natural tidal cycles in this system, in which propagules can be inundated daily during spring tides for 7–14 days and not inundated at all for 7–14 days

during neap tides, depending on the month. However, to examine effects under more natural conditions with shorter durations of each moisture extreme, we analyzed the data for both mesocosm experiments over a truncated time period of 15 days (Appendix 5). In both experiments, we observed the same effects of wrack position treatment and tidal regime after 15 days that we did for the full experimental time frames (51 days for Experiment 1, 30 days for Experiment 2), although effect sizes were weaker overall (Appendix 5: Tables S1, 2; Figs. S1, 2). This analysis suggests that wrack position and moisture level interact to determine propagule establishment success under shorter time frames that may more accurately represent natural field conditions. As in the full analysis, the truncated results indicate that at a landscape scale, mangrove propagules are more likely to establish in moist conditions, including underneath wrack and during spring tidal cycles.

It is also important to examine the effect of *Spartina* wrack on *Avicennia* over longer temporal durations, because the effects quantified here could change over time. Our results only reflect the effects of *Spartina* wrack on *Avicennia* during propagule establishment. Optimal growth conditions could change over the course of mangrove development, and wrack smothering, fertilization, or herbivory effects could be more pronounced in later mangrove life stages, when plants are not as vulnerable to desiccation. For example, previous work suggests that the effects of optimal inundation regimes during initial propagule establishment are less important in later mangrove life stages (Ellison and Farnsworth 1997; Krauss et al. 2006).

In summary, our work reveals that *Spartina* wrack can both positively and negatively affect *Avicennia* propagule establishment, depending on spatial positioning relative to propagules. Furthermore, the magnitude of these engineering effects depends on the tidal moisture regime, and both positive and negative effects are accentuated under the harsher, drier conditions of simulated neap tides. This result suggests that, in general, in harsh abiotic conditions, there is greater scope for ecosystem engineers to have strong positive and negative effects on associated species, as compared to benign conditions. Thus, both spatial (e.g., wrack–propagule position) and temporal factors (e.g., tidal regime timing) interact to determine whether resident species provide biotic resistance or assistance to invading species. Conditions can align in which the resident *Spartina* wrack can provide biotic assistance to its expanding mangrove competitor during establishment, notably during spring tide conditions or when propagules are located underneath wrack. In the field, propagules are stranded underneath wrack in high densities, suggesting that facilitative effects of wrack predominate under natural conditions in this system. Despite this potential initial biotic assistance from *Spartina* wrack during establishment, in the climax community, *Avicennia*

ultimately competitively excludes its facilitator. Understanding the context-dependency of interactions between native and expanding species is essential to better predicting expansion dynamics and to determining the relative importance of biotic resistance and assistance in different scenarios.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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