

Effects of novel, non-native detritus on decomposition and invertebrate community assemblage

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ABSTRACT: When non-native primary producers become successful, the structure and function of native detrital food webs can be fundamentally altered. Salt marsh estuaries of the southeastern USA are in part detritus-based ecosystems and rely on the annual production of detritus from a single native species, the smooth cordgrass *Spartina alterniflora*. Over the last several decades, the success of a novel primary producer, the red macroalga *Agarophyton vermiculophyllum* (formerly *Gracilaria vermiculophylla*), in a system historically devoid of macroalgae provides the opportunity to measure the effect of non-native basal resources on native detrital pathways. We conducted 2 *in situ* experiments to compare (1) decomposition rates of *A. vermiculophyllum* and *S. alterniflora* and (2) invertebrate colonization rates onto dead *A. vermiculophyllum* and *S. alterniflora*. Relative to *S. alterniflora*, we found that *A. vermiculophyllum* decomposes more rapidly, losing 80% or more of its biomass within 3 wk, while *S. alterniflora* lost ~50%. Experimental litterbags with decomposed *A. vermiculophyllum* and *S. alterniflora* harbored similar highly abundant invertebrate communities that differed greatly from denuded areas. Our results demonstrate that *A. vermiculophyllum* provides a complementary source of labile organic matter relative to *S. alterniflora*, boosting the amount of food and available habitat for small invertebrates of intertidal salt marshes and mudflats. Thus, non-native macrophytes may differentially affect community and ecosystem properties just as much when dead as alive, especially when they are biologically distinct from native species.

KEY WORDS: Seaweeds · Non-native species · Salt marsh · Decomposition · Community composition

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1. INTRODUCTION

The identity (e.g. C:N:P content, lability of nutrients, and structural and chemical compounds), quantity, and position of resources within an ecosystem fundamentally shape community structure and ecosystem function (Moore et al. 2004, Shurin et al. 2006, Marcarelli et al. 2011). Thus, alterations to primary producer communities, particularly through the introduction of non-native species, and their entry into trophic pathways can have far-reaching consequences for ecosystems (Vitousek et al. 1997, Crooks

2002). One mechanism by which this occurs is through the alteration of detritus entering the detrital pathway, an important energy and nutrient pathway in many ecosystems (Odum & de la Cruz 1963, Mann 1988). Indeed, the introduction of novel detritus by non-native species, different in kind to that of native species, can shift the composition and distribution of detritivorous guilds (Rodil et al. 2008, Taylor et al. 2010, Vázquez-Luis et al. 2012, Bishop & Kelaher 2013a,b) and alter essential ecosystem processes, such as decomposition and nutrient cycling (Krumhansl & Scheibling 2012).

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In the salt marsh ecosystems of temperate estuaries, a large portion of primary production is stored in vascular plants like *Spartina alterniflora*, which tend to be avoided by higher trophic levels and instead enter the detrital pathway where they are slow to break down and can become buried and stored beneath accruing sediment (Teal 1962, Wainright et al. 2000). In such systems, algae can provide essential carbon and nutrient pools, as they often are composed of less structural, fibrous material and more nutrients than vascular marsh plants, which can make algal biomass easier for grazers and detritivores to assimilate (Polis & Hurd 1996, Adin & Riera 2003). While microalgae and phytoplankton are often the predominant algal resources in estuarine ecosystems (Galván et al. 2011, Chew et al. 2012), macroalgae can also be important. For example, drifting mats of macroalgae can link marine and terrestrial systems, providing important cross-boundary food subsidies (Polis & Hurd 1996, Rodil et al. 2008), with cascading impacts on the abundance and structure of macrofauna (e.g. Dugan et al. 2003, Olabarria et al. 2007, 2010, Piovio-Scott et al. 2013, Haram et al. 2018). Also, macroalgae can contribute quick pulses of labile carbon and nitrogen following burial in marine sediments, on the order of days or weeks (Rossi & Underwood 2002). Yet, increases in macroalgal densities in estuarine systems, especially of non-native species, do not always yield positive impacts on production and other ecosystem processes (Olabarria et al. 2010, Guy-Haim et al. 2018); negative responses by native fauna to introduced macroalgae have been documented because of increases in sediment anoxia or the presence of novel chemical defenses (e.g. Rodil et al. 2008, Taylor et al. 2010, Bishop & Kelaher 2013a,b).

A recent biological invasion into estuaries of the southeastern USA provides an opportunity to investigate the effects of a novel, non-native primary producer on an ecosystem dominated by vascular *S. alterniflora* detrital inputs (note: we maintain the use of *Spartina* rather than *Sporobolus* following Bortolus et al. 2019). *Agarophyton vermiculophyllum*, a red macroalga from Japan, has colonized much of Europe as well as the North American east and west coasts (Kim et al. 2010, Rueness 2005, Krueger-Hadfield et al. 2017). In the southeastern USA, *A. vermiculophyllum* now dominates the intertidal mudflats, often growing attached to the native tubeworm *Diopatra cuprea* (Kollars et al. 2016). Prior to the introduction of *A. vermiculophyllum* in the late 1990s to early 2000s, the estuarine mudflats of southern South Carolina and Georgia were devoid of macro-

algal beds, making *S. alterniflora* the primary macrophytic detrital input in this system (Teal 1962, Mann 1988). Unlike other regions of its introduced range, in which *A. vermiculophyllum* competes with native macroalgal populations (Freshwater et al. 2006, Thomsen et al. 2006, Nejrup et al. 2013), *A. vermiculophyllum* in South Carolina and Georgia now presents a novel source of detritus that is fundamentally different in identity from *S. alterniflora*.

Contributions of the native vascular plant and non-native macroalga to primary production differ in many ways. Across its range, the salt marsh cordgrass *S. alterniflora* generates aboveground biomass estimated at between 550 and 2000 g dry weight $m^{-2} yr^{-1}$ (Marinucci 1982). Despite this high rate of primary production, less than 5% of the live *S. alterniflora* production in Georgia is consumed and assimilated by grazers (Teal 1962) because of *S. alterniflora*'s high structural lignocellulose content, which requires microbial conditioning prior to consumption (Findlay & Tenore 1982, Anesio et al. 2003). Moreover, complete decomposition following annual senescence in the fall takes over a year (Marinucci 1982, Valiela et al. 1985). In contrast to *S. alterniflora*, in Georgia and South Carolina, *A. vermiculophyllum* is present and alive year-round, averages 42.4 g wet biomass m^{-2} in the summer, rapidly produces biomass (up to 200% net increase in 8 wk), and quickly decomposes (79% loss of biomass upon burial in 10 d) (Byers et al. 2012). *A. vermiculophyllum* is also a leaky source of nitrogen, releasing on average 67% of its gross daily nitrogen uptake in western Atlantic estuaries (Tyler & McGlathery 2006). As a novel source of detritus, *A. vermiculophyllum* has the potential to alter ecosystem processes and community composition in southeastern US estuaries historically dominated by *S. alterniflora*; yet, how *A. vermiculophyllum* contributes to the detrital pathway, both above- and belowground, relative to *S. alterniflora* is understudied.

In the present study, we used 2 *in situ* experiments to (1) quantify differences in decomposition rate between the non-native and native macrophytes, (2) assess how deposition of their wrack in the marsh (on the sediment surface or buried belowground) alters their contributions, and (3) determine how invertebrate communities respond to these wrack resources over time in comparison to bare sediment. Based on previous research and differences in physiology and detrital identity (Marinucci 1982, Valiela et al. 1985, Buchsbaum et al. 1991, Byers et al. 2012), we hypothesized that *A. vermiculophyllum* wrack would decompose much faster than *S. alterniflora*. We also

hypothesized that burial relative to surficial deposition would magnify differences between the macrophytes. Specifically, we predicted that *A. vermiculophyllum* would decay faster when buried because *A. vermiculophyllum* is robust to stranding (UV stress and desiccation; Roleda et al. 2012) and thus would decay slower in aerobic surficial conditions than in burial conditions. We predicted that *S. alterniflora* would decay faster on top of the sediment surface than buried in anaerobic conditions (Hackney 1987). Given its rapid breakdown rates and the presence of anti-grazing defenses (Nylund et al. 2011), we also hypothesized that the non-native *A. vermiculophyllum* wrack would be colonized by fewer invertebrates than the native *S. alterniflora* wrack. Alternatively, *A. vermiculophyllum* is more structurally complex than *S. alterniflora*, which may serve to increase invertebrate densities.

2. MATERIALS AND METHODS

Our experiments and collections of *Agarophyton vermiculophyllum* and *Spartina alterniflora* took place at the same site at the Skidaway Institute of Oceanography on Skidaway Island, Georgia, USA (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m643p049_supp.pdf), within the Wilmington River estuary (31° 57' 44" N, 81° 0' 46" W). At our experimental site, the mid- and high intertidal zones are largely free of both *A. vermiculophyllum* and *S. alterniflora* wrack, thus reducing the potential for migration of extraneous natural wrack into the experimental blocks.

We conducted the experiments in June and July 2015 (midsummer). Both experiments took place in the *S. alterniflora*–mudflat boundary, where the intertidal mudflat habitat abuts the lowest elevation edge of the *S. alterniflora* stand (Fig. S1a). *A. vermiculophyllum*, which is negatively buoyant, is deposited in strandlines within this part of the marsh during high tides and storm events (Fig. S1b). *S. alterniflora* wrack can also be deposited here during the spring and summer months as a result of erosion at the *S. alterniflora* stand edge during storm events (L. E. Haram pers. obs.), though it is often deposited much higher in the intertidal zone given its greater buoyancy following senescence in the fall and winter. This boundary habitat supports a diversity of invertebrate taxa that exhibit cross-boundary distributions, such as the abundant amphipod *Gammarus mucronatus* (Wright et al. 2014). We chose to conduct our experiments in midsummer, before *S. alterniflora*

began to senesce, because we wanted to evaluate breakdown and colonization of wrack when both macrophytes were in optimal condition and invertebrate abundance was at its seasonal peak.

2.1. Decomposition

To examine the differences in decomposition rate between *A. vermiculophyllum* and *S. alterniflora*, we conducted a factorial *in situ* experiment that measured biomass loss over 1 mo, from 20 June 2015 to 20 July 2015. To do so, we collected both species alive from the field, rinsed them with filtered seawater, and defaunated them by hand. We then spun them separately in a salad spinner for 30 s and weighed them for wet weight (g WW). We weighed 25 ± 1 g WW of either species, recorded its initial biomass, placed it in a ~3.8 l Blue Hawk® fine-mesh paint strainer bag (~500 μ m), and closed the bag with a zip tie. The small mesh size helped to retain degrading biomass and exclude macroinvertebrates. Although processing by macroinvertebrates is an important aspect of decomposition, we wanted to gain a better understanding of baseline unaided microbial decomposition in this system. To obtain an estimate of the initial dry weight (g DW) used in each replicate, we separately collected 10 samples of 25 ± 1 g WW of each species from the site, rinsed them, spun them, and weighed them for wet weight (g WW). We then dried them at 60°C until consistent dry weight (g DW) was achieved (after at least 2 d). From this we calculated the average wet:dry weight ratio for each species, enabling estimation of initial dry weight from the wet weight of the focal plant or seaweed material used in each replicate.

To simulate the ways in which wrack can be deposited and decomposed, we crossed the wrack species treatments (*A. vermiculophyllum* vs. *S. alterniflora*) with 2 deposition treatments (burial vs. surface). We boosted the number of replicates of each treatment per block so that we could sample at 3 time intervals throughout the experimental duration. We placed the bags 0.5 m into the *S. alterniflora* stand from its lowest edge on the mudflat, parallel to the water line. The bags were secured to PVC poles and placed on the sediment surface or were buried within the top 10 cm of the mud, depending on deposition treatment. Bags were arranged in 7 blocks, with the blocks spaced at least 1.5 m apart. We placed 3 replicates of each of the 4 treatment combinations within each of the 7 blocks, using a random number generator to determine the order of the repli-

cates, for a total of 12 bags per block and an overall total of 84 bags. One bag of each treatment combination was collected from each block on Days 10, 20, and 30 ($n = 7$ per treatment combination per collection day). After collection, contents in the mesh bags were cleaned of sediment, weighed (g WW), and dried at 60°C until consistent weight (g DW) was achieved. Over the duration of the experiment, 1 bag was lost in both the *A. vermiculophyllum* surface and burial treatments, while 2 bags were lost in both the *S. alterniflora* surface and burial treatments. Because decomposition was assessed per block (detailed below), when a bag was lost in a block, the block could no longer be assessed; this led to a sample size of 6 for *A. vermiculophyllum* and 5 for *S. alterniflora*.

From dry biomass, we calculated the percentage of dry mass remaining (%DMR) for each replicate. Following the methods of Conover et al. (2016), we then used %DMR to calculate the decay constant ($k \text{ d}^{-1}$) by first taking the natural log of %DMR for each collection day and then running a linear regression model across all days per block using the `lm` function in R 3.6.2 (R Core Team 2020). We evaluated residual plots and r^2 values (Table S1 in the Supplement) to assess model fit. $k \text{ (d}^{-1}\text{)}$ is equivalent to the absolute value of the regression slope.

We analyzed our response variable $k \text{ (d}^{-1}\text{)}$ as a function of wrack species treatment (*A. vermiculophyllum*, *S. alterniflora*), deposition treatment (surface, buried), and their interaction. To do so, we ran a generalized linear model (GLM) with a Gamma distribution (Gamma distribution is often used for non-negative continuous variables) using the `stats` package in R. We included block as a fixed effect to further explain variation in our model. To determine if block significantly contributed to model fit, we tested the full model against a reduced model without block using a chi-square test; if the full and reduced models were not significantly different, we removed block from the final model. In the case of $k \text{ (d}^{-1}\text{)}$, block was not significant and was removed.

To further clarify the differences in biomass loss between the 2 species with respect to time, we also analyzed %DMR at each time interval using the above GLM method. To achieve assumptions of normality, we square root transformed %DMR and used a Gaussian distribution for each time interval model. For %DMR, block was not significant and was again removed. It should be noted that we included block as a fixed effect rather than random effect because the experiment was conducted at a single site (thus, between-block variation was likely not substantial) and the number of blocks was relatively small (5–6).

We did in fact conduct a generalized linear mixed model analysis for both the decay constant $k \text{ (d}^{-1}\text{)}$ and %DMR with block as a random factor to see if our categorization of block changed our results. We found only minor differences in our results, none of which caused changes in overall patterns or significance; thus, we retained block as a fixed effect and used GLMs throughout the analyses.

2.2. Invertebrate colonization of wrack

To determine how *A. vermiculophyllum* alters the community structure of macroinvertebrates colonizing wrack, we conducted an *in situ* litter bag experiment from 6 June 2015 to 16 June 2015. We tested the effect of wrack species on invertebrate colonization using non-native *A. vermiculophyllum* and native *S. alterniflora*; we additionally included a control treatment that did not contain either macrophyte (an empty litter bag) to account for any artifacts in colonization that may occur because of the structure of the litter bags. We also assessed the effect of wrack decomposition on invertebrate colonization by quantifying colonization over time.

After rinsing *A. vermiculophyllum* and *S. alterniflora* with filtered seawater and removing invertebrates, we weighed 25 ± 1 g WW of each detritus type, recorded the weight for initial biomass, and placed it in plastic mesh litter bags. The litter bags were 144 cm² with 0.5 cm mesh, sewn closed using monofilament. A larger mesh size was used in this experiment than in the decomposition experiment to allow invertebrates to move freely into the bags to access the macrophyte wrack. Our experimental design consisted of 10 blocks spaced at least 1.5 m apart and 0.5 m into the *S. alterniflora* stand from the mudflat edge; each block contained 2 litter bags of each wrack species treatment (*A. vermiculophyllum*, *S. alterniflora*, and control) for a total of 6 bags per block. Using galvanized steel garden staples, we secured the bags on the sediment surface in a randomized order per block. We collected 1 bag per block for each wrack species treatment on Days 5 and 10 ($n = 10$ treatment⁻¹ d⁻¹). One bag for *S. alterniflora* was lost on both collection days ($n = 9$ d⁻¹). Upon collection, we immediately placed each bag into an individual plastic bin. We then returned the bags to the laboratory and rinsed the contents into a 250 µm sieve. Invertebrates were preserved in 80% ethanol until they were later counted and identified to the lowest taxonomic group possible under a dissecting scope. For crabs, we kept adults, juveniles, and megalopae sep-

arate to increase resolution of age classes. We dried the remaining macrophyte biomass in a drying oven at 60°C until it reached constant weight and weighed it for dry mass (g DW) remaining.

We measured invertebrate diversity within our colonized litter bags using both traditional and more modern model-based biodiversity approaches. For the traditional measures, we calculated the species richness, Shannon-Weaver diversity index (SDI), and Pielou's evenness for each replicate. Species richness was calculated as the number of species present in each replicate. We calculated SDI using the diversity function (vegan package; Oksanen et al. 2019) in R. We then calculated Pielou's evenness using the SDI value for each replicate according to methods detailed in Oksanen (2019).

To analyze our traditional diversity metrics (species richness, SDI, and Pielou's evenness), we constructed GLMs using the stats and MASS (for response variables with negative binomial distribution) packages (Venables & Ripley 2002) in R. We evaluated the presence of an interactive effect between our predictor variables—wrack treatment (*A. vermiculophyllum*, *S. alterniflora*, and control) and collection day (Days 5 and 10)—for all traditional diversity metrics. For total abundance and species richness, which are count data, a negative binomial distribution for the former and Poisson distribution for the latter best fit our data. Gaussian distributions were selected for SDI and Pielou's evenness models. In addition to our main predictor variables listed above, we included block and final biomass (g DW) of wrack species as fixed effects in our models, removing them if they did not significantly contribute to the model outcome. Block was not a significant predictor in all diversity metric models and was removed. Final dry weight (g DW) was a significant predictor for total abundance alone and thus was retained in this instance. We used the glht function (multcomp package; Hothorn et al. 2008) in R to conduct Tukey's post hoc tests on our models, elucidating pairwise differences in the diversity metrics between our wrack treatments—*A. vermiculophyllum*, *S. alterniflora*, and control. Because the interaction between wrack treatments and collection day was not significant across traditional diversity metrics, the interaction was removed from our models before conducting the post hoc tests.

To assess the effect of wrack treatment, collection day, and their potential interaction on community composition, we used a quantitative multivariate approach, which simultaneously accounts for both invertebrate identity and abundance. For our multivariate analysis of community structure, we employed

the mvabund package (Wang et al. 2012) in R, which allows for a GLM model-based framework with resampling on community abundance data. This approach is superior to distance-based methods (e.g. MDS, PERMANOVA) because it allows for (1) identification of both community-level and species-level effects through resampling-based hypothesis testing, (2) analysis of differences in treatment blocks, (3) prediction of abundances of each species, (4) proper handling of count data and often associated mean-variance relationships, and (5) resolution of correlations between species (Wang et al. 2012, Warton et al. 2012). Our response variable, invertebrate abundance, was analyzed as a function of wrack species treatment, collection day, and their interaction across the community and for each invertebrate species using the manyglm function (package mvabund; Wang et al. 2012). Our data were best fit with a negative binomial distribution. To focus our analysis on taxa that consistently contribute to the colonizing invertebrate community, we included taxa with at least 5 individuals across the site in our analysis (resulting in the exclusion of 11 individuals total across 5 taxa). As with the diversity metrics, we included block and final wrack biomass (g DW) as fixed effects in our model to help further explain variance in the model. Again, we tested the full model against reduced models using chi-square tests to determine if block and final wrack biomass significantly contributed to model fit; if not, they were removed from the final model. As a result, final wrack biomass (g DW) was retained, while block was removed. We conducted 3 pairwise comparisons between wrack treatments (*A. vermiculophyllum* vs. *S. alterniflora*, *A. vermiculophyllum* vs. control, and *S. alterniflora* vs. control) to assess the relative differences of the treatments from each other and the control. To account for the multiple comparisons and reduce the possibility of type I error, we used a Bonferroni correction and evaluated the results of our pairwise comparisons against an adjusted alpha value ($\alpha = 0.050/3 = 0.017$). To visualize differences in the community composition analyzed with the multivariate analysis, we produced a non-metric multidimensional scaling plot using the vegan package (Oksanen et al. 2019) in R.

3. RESULTS

3.1. Decomposition

On average, the decomposition rate (quantified as k d⁻¹) of *Agarophyton vermiculophyllum* deposited on

the sediment surface ($0.067 \pm 0.010 \text{ k d}^{-1}$) and buried ($0.105 \pm 0.016 \text{ k d}^{-1}$) was approximately 3 to 4 times faster (291–457%) than that of *Spartina alterniflora* in either position ($0.023 \pm 0.002 \text{ k d}^{-1}$ for surface and buried treatments; Table S1). Furthermore, buried *A. vermiculophyllum* decomposed more quickly than did thalli on the sediment surface, while decomposition rates of buried *S. alterniflora* were statistically indistinguishable from those of surface *S. alterniflora* (Table S1). The difference in decomposition rate between *A. vermiculophyllum* and *S. alterniflora* was significant (GLM: $F_1 = 91.440$, $p < 0.001$). Similarly, the difference between deposition treatments was also significant (GLM: $F_1 = 6.127$, $p = 0.024$). However, no interaction was observed between the 2 predictor variables (GLM: $F_1 = 0.594$, $p = 0.451$).

%DMR was also significantly different among wrack species and deposition treatments for all 3 time points. At Day 10, *A. vermiculophyllum* had lost 10 to 30% more biomass than *S. alterniflora* (GLM: $F_{1,20} = 99.967$, $p < 0.001$) and buried macrophytes lost more than surface macrophytes (GLM: $F_{1,19} = 120.060$, $p < 0.001$) (Fig. 1; Table S1), with buried *A. vermiculophyllum* having lost almost 80% of its biomass. A significant interaction between wrack species and deposition was present on Day 10 (GLM: $F_{1,18} = 36.582$, $p < 0.001$). At Day 20, wrack species

(GLM: $F_{1,20} = 74.673$, $p < 0.001$) and deposition (GLM: $F_{1,19} = 11.301$, $p = 0.003$) treatments as well as their interaction (GLM: $F_{1,18} = 5.8587$, $p = 0.026$) were significant. By Day 30, *A. vermiculophyllum* lost most of its biomass in both the surface and burial deposition treatments, with on average only $17.09 \pm 4.33\%$ (mean \pm SE) and $6.46 \pm 2.26\%$ biomass remaining, respectively, while *S. alterniflora* retained 49.92 ± 3.55 and $48.88 \pm 4.20\%$ biomass. There was a significant effect of wrack species (GLM: $F_{1,20} = 76.772$, $p < 0.001$) and burial (GLM: $F_{1,19} = 4.541$, $p = 0.047$) treatment but no interaction (GLM: $F_{1,18} = 3.157$, $p = 0.093$).

3.2. Invertebrate colonization of wrack

Wrack treatment significantly affected total invertebrate abundance, with *S. alterniflora* and *A. vermiculophyllum* wrack significantly increasing total invertebrate abundance by approximately 200% in comparison to the control (empty) litter bag (GLM: $\chi^2_2 = 141.116$, $p < 0.001$; Fig. 2a). However, no difference in total invertebrate abundance was observed between the macrophytes. Collection day (Day 5 vs. Day 10) had no effect on total invertebrate abundance (GLM: $\chi^2_1 = 1.434$, $p = 0.231$); we also detected no in-

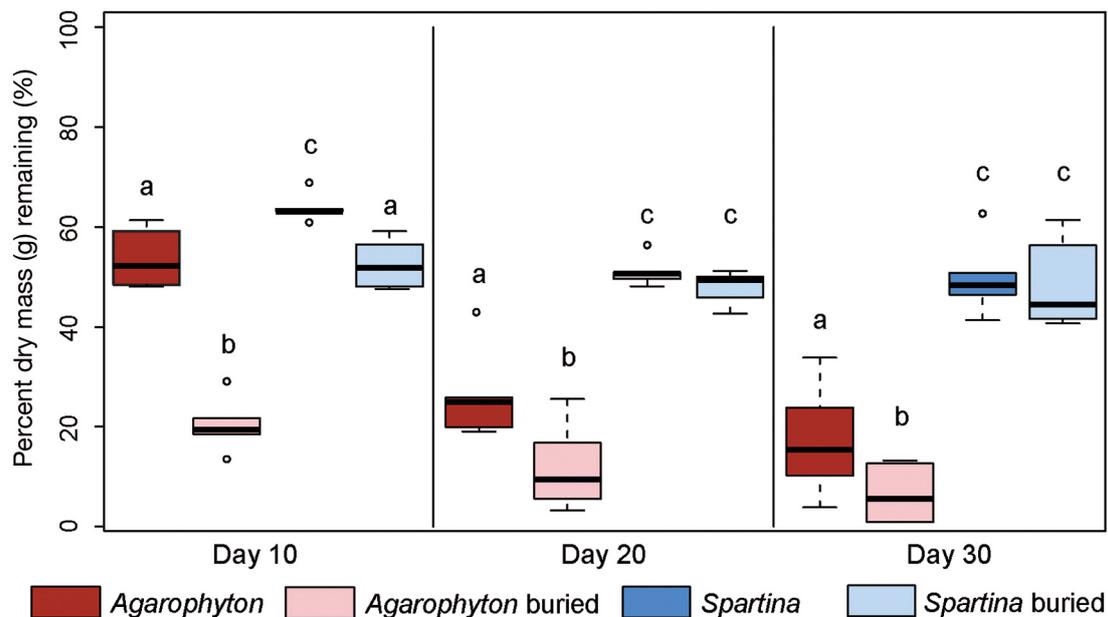


Fig. 1. Median percentage of dry biomass (g dry weight) remaining (%DMR) across wrack species treatment combination—surface *Agarophyton vermiculophyllum* ($n = 6$), buried *A. vermiculophyllum* ($n = 6$), surface *Spartina alterniflora* ($n = 5$), and buried *S. alterniflora* ($n = 5$)—for each collection day (10, 20, and 30). Letters indicate statistical differences between treatment combinations ($p \leq 0.05$), which were evaluated across treatments per collection day using generalized linear models in R. Box and whisker plots represent the median and 25 and 75% quantiles; the lower and upper bars illustrate minimum and maximum values. Open circles represent outliers

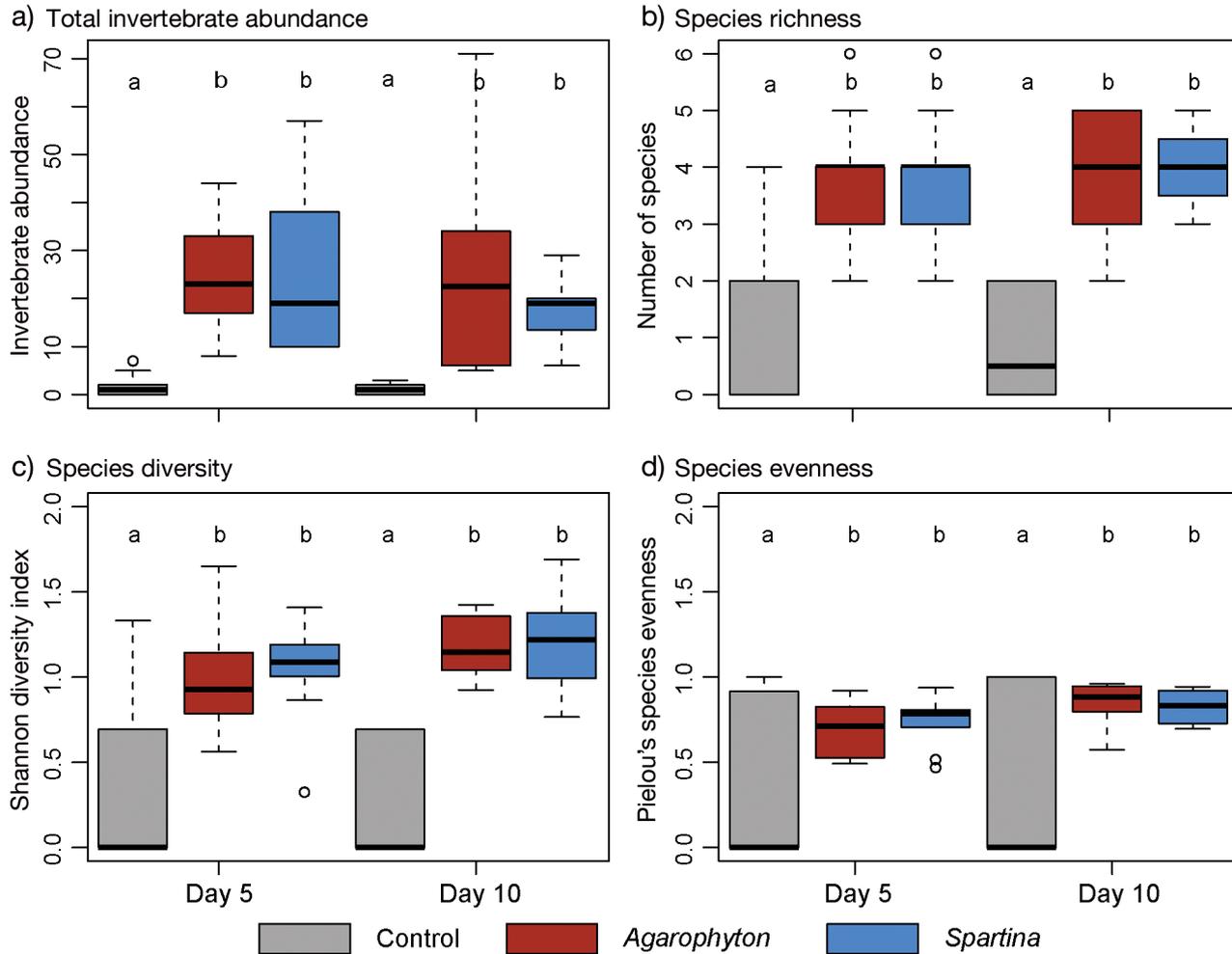


Fig. 2. Median total invertebrate abundance and diversity indices per litter bag across wrack treatments (control [empty litter bag, $n = 10$], *Agarophyton vermiculophyllum* [$n = 10$], and *Spartina alterniflora* [$n = 9$]) and day collected. Diversity indices include (a) total invertebrate abundance, (b) species richness, (c) Shannon-Weaver diversity index, and (d) Pielou's species evenness. All were analyzed using generalized linear models in R. Final wrack dry biomass (g dry weight) was included as a covariate in the model for abundance. Letters indicate statistical differences across treatments within each sampling day ($p \leq 0.05$). See Fig. 1 for definition of boxplots

teraction between day and wrack treatment (GLM: $\chi^2 = 1.732$, $p = 0.421$). Additionally, total abundance trended greater in *A. vermiculophyllum* than *S. alterniflora* wrack but was not significantly different ($p = 0.085$). Final wrack biomass (g DW) significantly influenced total abundance, with invertebrate abundance positively correlating with remaining macrophyte biomass (GLM: $\chi^2 = 4.161$, $p = 0.041$).

With few exceptions, invertebrate diversity (measured as species richness, SDI, and Pielou's evenness) also increased with wrack presence. Invertebrate species richness was greater in the presence of *S. alterniflora* and *A. vermiculophyllum* versus the control (GLM: $\chi^2 = 30.743$, $p < 0.001$), with collection day and the interaction of collection day and wrack treatment being non-significant (GLM:

$\chi^2 = 0.006$, $p = 0.937$ and $\chi^2 = 0.492$, $p = 0.782$, respectively). There was no difference in species richness between *A. vermiculophyllum* and *S. alterniflora* wrack ($p = 0.994$; Fig. 2b). SDI also increased with wrack presence (GLM: $F_{2,54} = 39.137$, $p < 0.001$); we found no difference in SDI between collection days (GLM: $F_{1,53} = 0.668$, $p = 0.418$), and there was no interaction between main effects (GLM: $F_{2,51} = 0.871$, $p = 0.4247$). SDI values for *A. vermiculophyllum* and *S. alterniflora* were not significantly different ($p = 0.987$; Fig. 2c). The invertebrate community on *A. vermiculophyllum* and *S. alterniflora* had greater Pielou's evenness values than did controls (GLM: $F_{2,49} = 9.092$, $p < 0.001$), and there was no difference between collection days (GLM: $F_{1,48} = 0.927$, $p = 0.341$) nor an

interaction (GLM: $F_{2,46} = 0.411$, $p = 0.666$). There was no significant difference between *A. vermiculophyllum* and *S. alterniflora* ($p = 0.993$; Fig. 2d).

For the multivariate analysis of invertebrate colonization, overall invertebrate community composition significantly varied across wrack treatments (GLM: $\chi_2^2 = 157.91$, $p = 0.001$; Fig. 3a; Table 1). Differences in community composition between the wrack treatments and control drove this effect, as there was no significant difference in community composition between *A. vermiculophyllum* and *S. alterniflora* in the pairwise comparison ($p = 0.712$; Table 1). Collection day also significantly influenced community composition (GLM: $\chi_1^2 = 46.63$, $p = 0.001$; Fig. 3b; Table 1). The interaction between treatment and collection day was not significant (GLM: $\chi_1^2 = 25.93$, $p = 0.072$), and final wrack biomass (g DW) was not a significant predictor of overall community composition (GLM: $\chi_1^2 = 11.90$, $p = 0.311$).

The amphipod *Ampithoe valida* was the most abundant species, accounting for 41.33% of the 888 invertebrates evaluated. Significantly more *A. valida* colonized *A. vermiculophyllum* and *S. alterniflora* than the empty control bags, though no difference was observed between

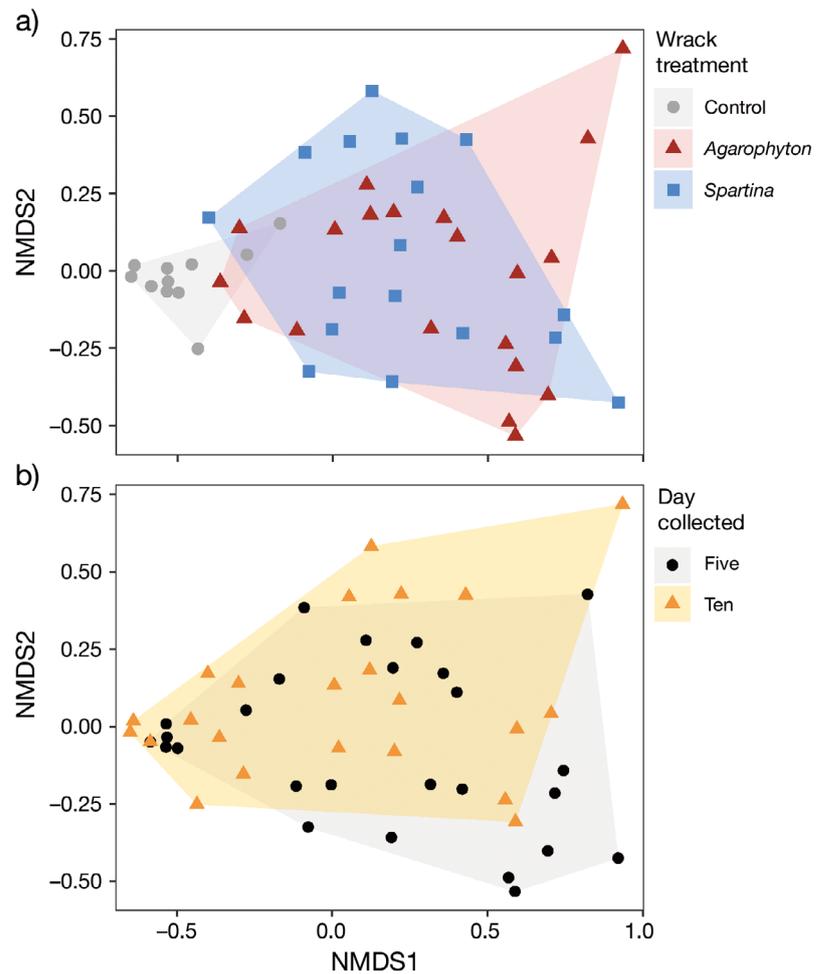


Fig. 3. Non-metric multi-dimensional scaling (NMDS) ordination of community assemblage by (a) wrack treatments (control [empty litter bag, $n = 10$], *Agarophyton vermiculophyllum* [$n = 10$], and *Spartina alterniflora* [$n = 9$]) and (b) collection day (5 or 10). Stress value = 0.098

Table 1. Analysis of deviance results for the multivariate generalized linear regression analysis (manyglm) of community-level invertebrate composition across wrack treatments (*Agarophyton vermiculophyllum*, *Spartina alterniflora*, or control) and collection days (5 and 10). Results are presented for analyses of treatments with and without the control. The control treatment consisted of an empty litter bag. These data were analyzed using the mvabund package in R, which allows for model-based multivariate and univariate analysis of community composition. For the overall model, significance was evaluated with $\alpha = 0.05$, with **bold** indicating a significant difference ($p \leq 0.05$) and *italics* indicating a trend ($0.05 < p < 0.10$). For post hoc pairwise comparisons, we used a Bonferroni correction, leading to an alpha value of 0.017 ($\alpha = 0.05/3$); for these, **bold** indicates significant differences ($p \leq 0.017$). DW: dry weight

Treatment comparisons	Wrack species			Day			Wrack treatment \times Day			Final wrack biomass (g DW)		
	Residual df	Deviance	p	Residual df	Deviance	p	Residual df	Deviance	p	Residual df	Deviance	p
Overall effect												
<i>Agarophyton</i> vs. <i>Spartina</i> vs. Control	54	157.91	0.001	53	46.63	0.001	50	25.25	<i>0.072</i>	44	11.90	<i>0.311</i>
Post hoc pairwise comparisons												
<i>Agarophyton</i> vs. <i>Spartina</i>	35	7.21	0.712	34	40.03	0.001	32	13.79	0.107	33	9.47	0.467
<i>Agarophyton</i> vs. Control	38	125.36	0.001	37	28.30	0.007	35	12.33	0.093	36	10.23	0.335
<i>Spartina</i> vs. Control	35	106.38	0.001	34	35.62	0.003	32	10.53	0.072	33	19.17	0.076

A. vermiculophyllum and *S. alterniflora* (Fig. 4a; Table S2). *A. valida* also showed a response to collection day, with more amphipods present on Day 5. Another amphipod, *Gammarus mucronatus*, and mud crabs (Xanthidae, both juvenile and megalopa stages) were also highly abundant, respectively accounting for 30.74 and 17.34% of all individuals. Like *A. valida*, these invertebrates demonstrated significantly greater colonization in *A. vermiculophyllum* and *S. alterniflora* than in the controls but showed no difference in colonization between the

2 macrophytes (Fig. 4b–d; Tables S2 & S3). Finally, the polychaete *Alitta succinea*, which accounted for 6.76% of individuals, showed significantly different colonization between wrack treatments and days, with more *A. succinea* colonizing *A. vermiculophyllum* and *S. alterniflora* than the control litter bags and increasing in abundance over time (Fig. 4e; Tables S2 & S3). The remaining species were present in low densities and had variable responses to both treatment and collection day (Fig. 4f–i; Tables S2 & S3).

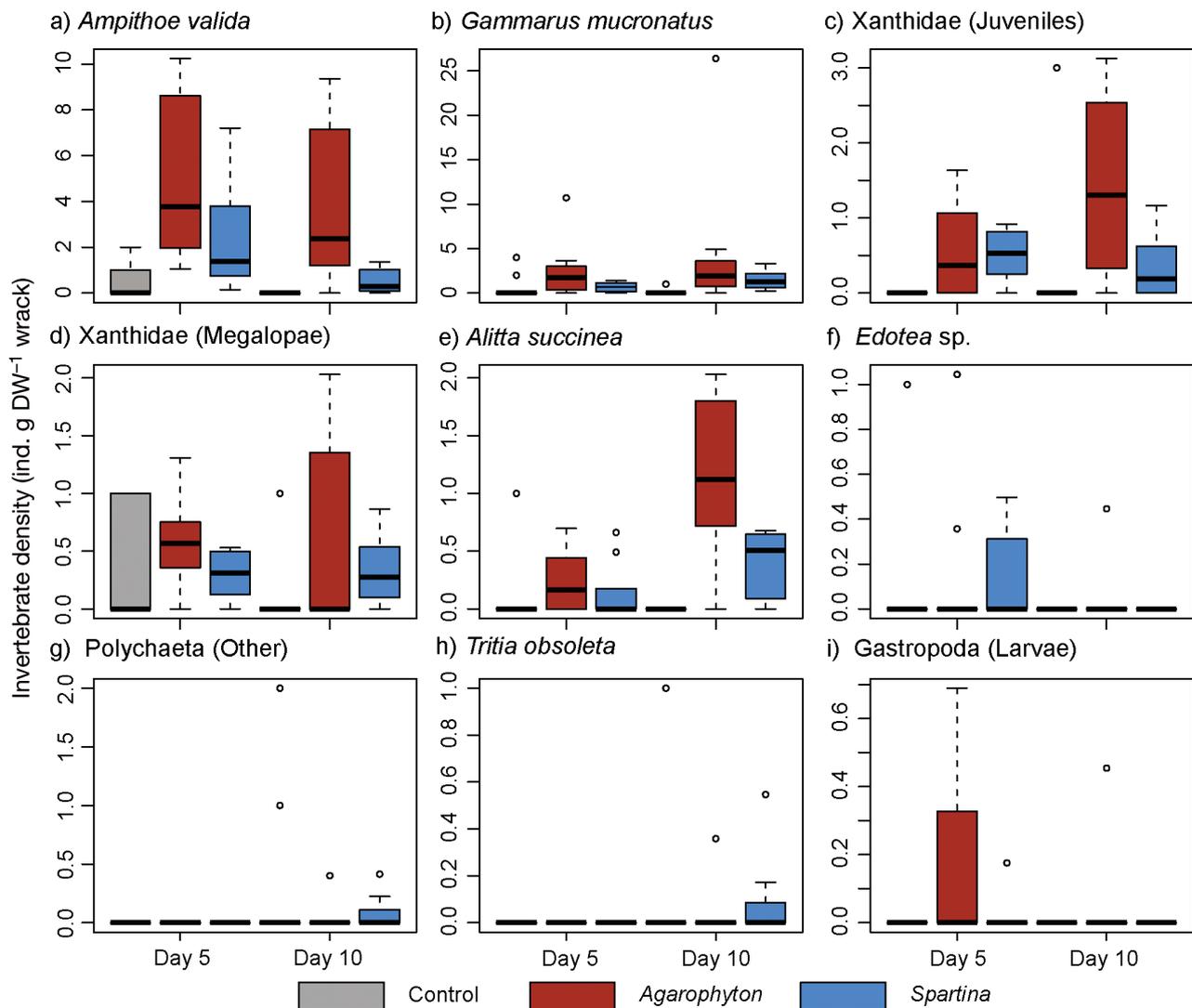


Fig. 4. Median invertebrate density (individuals per g dry weight [ind. g DW⁻¹] of remaining wrack) across wrack treatments (control [empty litter bag, n = 10], *Agarophyton vermiculophyllum* [n = 10], and *Spartina alterniflora* [n = 9]) and collection days (5 and 10). Taxa depicted include (a) amphipod *Ampithoe valida*; (b) amphipod *Gammarus mucronatus*; (c) mud crab Xanthidae juveniles; (d) mud crab Xanthidae megalopae; (e) polychaete *Alitta succinea*; (f) isopod *Edotea* sp.; (g) other Polychaeta; (h) mud snail *Tritia obsoleta*; (i) Gastropoda larvae. Taxa with fewer than 5 individuals across the colonization experiment were excluded. To allow for better visualization and to account for the lack of wrack biomass present in the controls, 1 g DW was added to all wrack treatments. See Fig. 1 for definition of boxplots

4. DISCUSSION

Our study found that despite marked differences in decomposition between the native and non-native species, whether buried or on the surface, both macrophytes supported similar invertebrate assemblages, suggesting an interesting effect of detrital identity on ecosystem function and community structure. As predicted, *Agarophyton vermiculophyllum* decomposed much more rapidly than *Spartina alterniflora*. Similarly slow decomposition of *S. alterniflora* has been observed in other areas of the eastern USA, due largely to its high refractory carbon and nitrogen content (White & Howes 1994, Smith et al. 2019). For *A. vermiculophyllum*, similar rapid decomposition has been reported in the southeastern USA, with $38 \pm 39\%$ biomass loss within 6 d in Virginia and up to 100% biomass loss upon burial within 2 wk in Georgia and South Carolina (Thomsen et al. 2009, Byers et al. 2012). Because macroalgae often lack highly recalcitrant compounds like those of vascular plants, decomposition is relatively fast, and labile carbon and nutrients can quickly be incorporated into the sediment, seawater, and even surrounding macrophytes (Tyler & McGlathery 2006, Gonzalez et al. 2013, Gulbransen & McGlathery 2013). Thus, *A. vermiculophyllum* may present a pulse of highly concentrated nitrogen in a nitrogen-limited system (Hopkinson & Schubauer 1984, Dai & Wiegert 1997).

Differences in rate of decomposition following burial of the macrophytes further highlight inherent differences between the 2 sources of detritus. *A. vermiculophyllum* decomposed almost twice as rapidly when buried than when deposited on the sediment surface, with buried *A. vermiculophyllum* virtually gone by Day 20, while *S. alterniflora* decomposed at the same slow rate across deposition treatments, losing relatively little biomass over the 30 d period (Fig. 1). However, for *A. vermiculophyllum*, our observed rate of decay on the sediment surface was approximately 5 times slower than that observed in Conover et al. (2016) during the same time of year. This disparity between results is likely due to the seaweed preparation method and exposes a key mechanism of our observed rapid decay upon burial. Conover et al. (2016) froze their *A. vermiculophyllum* prior to deployment, which kills the seaweed, while we did not. In Georgia and South Carolina, high tide stranding and burial of fresh seaweed are more realistic causes of mortality yet may not mean immediate mortality for *A. vermiculophyllum*. In fact, *A. vermiculophyllum* can survive and continue photosynthesizing under harsh conditions, such as UV stress

and desiccation (Roleda et al. 2012), which may slow decay of thalli deposited in the marsh. These traits may thus contribute to *A. vermiculophyllum* decaying more rapidly when buried than when on the sediment surface. The similar response of *S. alterniflora* to burial and surface deposition was unexpected, given that previous literature demonstrated slower decay in anaerobic burial conditions (e.g. Hackney 1987). However, the similarities observed in the present study may be the result of our relatively short experimental window.

Despite their differences in decomposition and apparent chemistry, *A. vermiculophyllum* and *S. alterniflora* had similar positive effects on invertebrate colonization, diversity, and community structure. The magnitude of the colonization effect varied by invertebrate taxa. For example, amphipods were the most abundant colonizers, composing over 70% of the invertebrate community. High densities of amphipods in non-native *A. vermiculophyllum* are commonly observed in temperate estuaries of the southeastern USA and Europe (Nyberg et al. 2009, Thomsen et al. 2009, Byers et al. 2012, Kollars et al. 2016). In our study, the high abundance of amphipods relative to other organisms and their preference for colonizing *A. vermiculophyllum* over bare substrate reflect similar observations of amphipods and the non-native seaweed on mudflats. In our study, the amphipod *Ampithoe valida* was the most abundant amphipod in the low marsh; however, in Georgia, *Gammarus mucronatus* dominates the lower elevation mudflat community (Byers et al. 2012, Wright et al. 2014), suggesting that macrophytic detritus may expand available niche space across the landscape. Similar responses in other invertebrate taxa (namely crabs and the polychaete *Alitta succinea*) and diversity metrics suggest that *A. vermiculophyllum* provides a novel resource, attractive across invertebrate species.

Possible mechanisms of greater invertebrate colonization on *A. vermiculophyllum* and *S. alterniflora* than within control litter bags may be a combination of benefits from the macrophytes' provision of physical structure or food, but currently, evidence points to structure as more influential (Wright et al. 2014, L. E. Haram unpubl. data). On mudflats, *A. vermiculophyllum*'s structure provides refugia, protecting small invertebrates from desiccation and predation (Johnston & Lipcius 2012, Wright et al. 2014, Bishop & Byers 2015). Native *S. alterniflora* similarly attracted a sizable invertebrate community, also likely because of its refugia quality. Indeed, in Georgia and Florida salt marshes, crabs preferen-

tially utilize *S. alterniflora* wrack over other estuarine vascular plant species because of its high value as habitat rather than food (Smith et al. 2019). Given the similarity in invertebrate response to both non-native *A. vermiculophyllum* and native *S. alterniflora*, the introduction of *A. vermiculophyllum* boosts the quantity of wrack habitat and likely extends this habitat to lower tidal elevations than does *S. alterniflora* alone, as *A. vermiculophyllum* is deposited at lower tidal elevations given its lower buoyancy.

Although *A. vermiculophyllum* may provide additional habitat, it is important to consider how wrack duration and density may accentuate the differences between, and complementarity of, these 2 macrophytes. *A. vermiculophyllum* decayed an order of magnitude faster than *S. alterniflora*, making *S. alterniflora* a more durable, stable detrital habitat. Colonizers of *A. vermiculophyllum* detritus will presumably have to migrate more frequently, as their wrack habitat disappears more quickly, although the consistent, year-round input of live and detrital *A. vermiculophyllum* versus the annual cycle of *S. alterniflora* senescence in the fall may enhance the stability of wrack resources overall. It is also important to note that the positive association of invertebrates with *A. vermiculophyllum* wrack may change with wrack density. In areas with high densities of bloom algae and/or eutrophic conditions, rapid decomposition can lead to anoxic or toxic sediment conditions, which in turn may have different, even negative, outcomes on decomposition, nutrient cycling, and invertebrate community assemblage (Boyer & Fong 2005, Bishop & Kelaher 2013a, Gonzalez et al. 2013, Watson et al. 2015). Though we did not find evidence of negative effects on invertebrate colonization in our experiment (which utilized relatively low biomass to mimic natural conditions in Georgia low marsh habitats), other regions of *A. vermiculophyllum*'s introduced range experience much higher densities of the invasive seaweed (e.g. Thomsen et al. 2006, Keller et al. 2019) and may see different biogeochemical and ecological responses as a result.

In conclusion, our study shows that *A. vermiculophyllum* may provide a complementary source of detritus in southeastern salt marshes. *A. vermiculophyllum* provides a quick pulse of detrital nutrients and organic matter both above- and belowground compared to the traditional steady, slow release by *S. alterniflora*, altering a fundamental ecosystem property of the recipient system. The differences in structure between *A. vermiculophyllum* and *S. alterniflora* may also diversify habitat for invertebrates that rely on wrack for refuge. Despite the seemingly

enhancing effect of *A. vermiculophyllum* on these processes, further research should investigate density-dependent and mixed-wrack assemblage effects of *A. vermiculophyllum* subsidies on ecosystem function and community structure. Future research should also investigate these relationships over longer time periods to inform the seasonality of the observed effects. Invasions by non-native macrophytes are a primary focus for changes to ecosystem functions, in part because these non-natives can interact with novel systems through multiple pathways. Not only do they supply primary productivity, but they also provision detritus and habitat (even as wrack). Thus, a non-native species' death does not signal the end of its impact; rather, in some systems, death can initiate new and different influences for both native and non-native macrophytes.

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