

Research

Detrital traits affect substitutability of a range-expanding foundation species across latitude

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Climate-driven range shifts of foundation species could alter ecosystem processes and community composition by providing different resources than resident foundation species. Along the US Atlantic coast, the northward expanding foundation species, black mangrove *Avicennia germinans*, is replacing the dominant salt marsh foundation species, marsh cordgrass *Spartina alterniflora*. These species have distinct detrital attributes that ostensibly provide different resources to epifauna. We experimentally examined how detritus of these species affects decomposition and community composition in different habitat contexts at regional and local scales. First, we manipulated detritus identity (*Avicennia*, *Spartina*) at 13 sites across a 5° latitudinal gradient spanning mangrove, mixed marsh-mangrove and salt marsh habitats. Across latitude, we found that *Avicennia* detritus decomposed 2–4 times faster than *Spartina* detritus, suggesting that detrital turnover will increase with mangrove expansion. Epifaunal abundance and richness increased 2–7 times from south to north (mangrove to salt marsh) and were equivalent between *Avicennia* and *Spartina* detritus except for crabs, a dominant taxonomic group that preferred *Spartina* detritus. Second, to examine the whether changing habitat context affected regional patterns, we manipulated detritus identity and surrounding habitat type (mangrove, salt marsh) at a single mixed site, also including inert mimics to separate structural and nutritional roles of detritus. Epifaunal richness was similar between the two detrital types, but crabs were 2–7 times more abundant in *Spartina* detritus due to its structural attributes. Surrounding habitat type did not influence decomposition rate or community patterns, which suggests that latitudinal influences, not surrounding habitat, drove the regional community patterns in the first experiment. Overall, mangrove expansion could alter epifaunal communities due to the lower structural value and faster turnover of mangrove detritus. As species shift with changing climate, understanding foundation species substitutability is critical to predict community change, but we must account for concomitant environmental changes that also modify communities.

Keywords: *Avicennia*, benthic macrofauna, biogenic habitat, climate change, detritus, ecosystem engineer, foundation species, mangrove, range expansion, salt marsh, *Spartina*



Introduction

Foundation species provide physical habitat structure for other species and mediate ecosystem processes (Dayton 1972, Ellison et al. 2005). However, it is unclear how community and ecosystem dynamics change when one foundation species replaces another and whether expanding foundation species can provide substitutable functions in recipient systems. As foundation species expand into new environments during species range expansions or invasions (Hoegh-Guldberg and Bruno 2010), they can either complement or replace resident foundation species, with different outcomes for associated species at different spatial scales (Angelini et al. 2011). At a regional scale, increased habitat heterogeneity in areas with mixed assemblages of foundation species could increase the species pool relative to more homogeneous habitat in pure stands of foundation species (Yakovis et al. 2008, Stein et al. 2014, Angelini et al. 2015). At a local scale, resident and expanding foundation species can differentially affect associated species if each foundation species provides resources of varying quality or quantity. Empirical examination of ecosystem processes and communities associated with shifting foundation species at different spatial scales is essential to understand mechanisms of community change in species expansions and to assess whether expanding foundation species can provide substitutable community and ecosystem functions.

At a local scale, morphological differences in the physical structure provided by resident and expanding foundation species can alter associated abiotic factors, with cascading effects on biotic communities (Jones et al. 1994, Byers et al. 2006, Jones et al. 2010). For example, plasticity in shrub morphology in response to increasing Arctic temperatures enables expanding shrub foundation species to replace native tundra species by creating dense canopies that limit light availability to other species (Bret-Harte et al. 2001). This expansion and structural change has altered local communities, leading to declines in lichens and mosses (Walker et al. 2006) and increases in resource availability for herbivores (Post and Pedersen 2008). Because differences in morphology between resident and expanding foundation species can affect the resources available to other species, it is essential to consider how the identity and attributes of surrounding habitat affect the community composition of associated species.

Expanding foundation species can also change key resources, such as detritus, in recipient systems. Differences in detrital quality between foundation species can affect decomposition, and detritus with greater nutrient and lower lignin levels are often associated with faster decomposition rates (Melillo et al. 1982, Taylor et al. 1989, Cornelissen and Thompson 1997, Cornwell et al. 2008). Decomposition rate influences other ecosystem properties such as carbon sequestration, productivity and nutrient cycling (Cornelissen et al. 1999, Prescott 2010). Detritus also provides both nutrition and structure for associated species (Cebrian and Kingsolver 1999, Moore et al. 2004, Ince et al. 2007), so differences

in detrital attributes between resident and expanding foundation species could lead to differences in associated community composition. Differences in detrital inputs following species expansion can lead to community 'trophic shifts' (Whitcraft et al. 2008); for example, after the invasion of marsh cordgrass *Spartina alterniflora* in San Francisco Bay, dominant native food webs shifted from algae-based to detritus-based (Levin et al. 2006, Grosholz et al. 2009). In addition to its nutritional importance, detritus also provides physical structure for many species – as refuge to minimize predation risk, for breeding or oviposition, or for alleviating stressful abiotic conditions (Bultman and Uetz 1984, Harmon et al. 1986, Reice 1991). Despite widespread evidence that organisms use detritus for its structure, few studies have examined how structural differences in detritus between resident and expanding species affect associated community composition. In this study, we examine how differences in both the nutritional and structural value of detritus provided by resident and expanding foundation species affect the composition of associated communities.

Research system and questions

The ongoing climate-driven range expansion of mangroves into salt marshes in northern Florida provides an opportunity to examine how ecosystem processes and associated biota respond to shifting distributions of foundation species. Along the Atlantic coast of Florida, mangrove area doubled from 1984 to 2011 at the expense of salt marsh habitat (Cavanaugh et al. 2014), and there is a distinct latitudinal vegetation shift from homogeneous mangrove stands in south Florida, to heterogeneous salt marsh-mangrove mixed habitat along the central Florida coast, and then to homogeneous salt marsh stands in northernmost Florida and beyond. Here, we compare how detrital resources provided by the dominant salt marsh species, marsh cordgrass *Spartina alterniflora*, and the fastest expanding mangrove species in Florida (Williams et al. 2014, Cavanaugh et al. 2015), black mangrove *Avicennia germinans*, affect detrital turnover and associated epifaunal community composition in different habitat contexts at regional and local spatial scales.

Spartina alterniflora and *Avicennia germinans* (hereafter *Spartina* and *Avicennia*) are morphologically distinct. *Spartina* (0.3–1 m tall) is clonal, grassy and herbaceous, with multiple flat leaves that extend from a central stem; *Avicennia* (1–5 m tall at our field sites) has woody trunks and branches, leafy canopies and dense pneumatophores (pencil-sized aerial roots) (Simpson et al. 2017). These physical differences could directly affect the composition of epifaunal invertebrate communities by altering refuge availability, or indirectly, through changes to the abiotic environment (e.g. altered hydrodynamic, light, salinity, temperature, oxygen regimes) (Nagelkerken et al. 2008, Gutiérrez et al. 2011). For example, the significant aboveground structure created by *Avicennia* canopies increases shading relative to *Spartina*, leading to decreased sediment chlorophyll a levels

and decreased food availability for some epifaunal invertebrates (R. Smith, unpubl.). Recent work examining the relative abundance of nekton and infaunal communities in salt marsh, mixed salt marsh–mangrove, and mangrove habitats has shown mixed but distinct preferences for these different habitats by different species (Caudill 2005, Lunt et al. 2013, Johnston and Caretti 2017, Scheffel et al. 2017, Smee et al. 2017). However, no previous work has compared epifaunal invertebrate communities among these habitats or across a latitudinal mangrove expansion gradient.

Avicennia and *Spartina* also differ in the nutritional and structural resources of their detritus. Although the detritus of both species contain phenolic chemical compounds (Hedges and Mann 1979, Wilson et al. 1986, McKee 1995), *Avicennia* detritus has a lower C:N ratio (47–55) (Twilley et al. 1986, Lawton-Thomas 1997) than *Spartina* detritus (65–92) (Breteler et al. 1981, White and Howes 1994), which indicates that it has greater nutritional value. *Avicennia* and *Spartina* litter have different structural attributes that likely provide different quality refuge to epifauna. *Avicennia* leaves are flat, whereas *Spartina* detritus has a hollow, straw-like structure (Supplementary material Appendix 1 Fig. A1). *Spartina* stems and *Avicennia* leaves were the primary detrital components of the litter present at our field sites, and we expected that *Spartina* stems would provide greater refuge quality than *Avicennia* leaves. Although the composition of epifaunal invertebrate communities associated with *Spartina* detritus has previously been documented (Reice and Stiven 1983, Angradi et al. 2001, Brusati and Grosholz 2006, Levin et al. 2006), to our knowledge, epifaunal communities associated with *A. germinans* detritus have seldom, if ever, been examined (Morrisey et al. 2010).

We conducted two field experiments to examine how detrital attributes of resident and expanding foundation species affect decomposition rate and epifaunal community composition in different habitat contexts across a latitudinal gradient. First, at a regional scale, we manipulated detritus identity (*Avicennia*, *Spartina*) within three regional habitat types (mangrove, mixed salt marsh–mangrove and salt marsh) along a 5° latitudinal expansion gradient, and documented associated changes in decomposition and epifaunal community composition. We expected that epifaunal abundance and taxonomic richness would be greatest in mixed salt marsh–mangrove habitats in the central region of our domain where habitat heterogeneity is greatest, compared to homogeneous stands of either mangrove or salt marsh vegetation. Second, at a local scale at a single mixed vegetation site, we manipulated detritus identity (*Avicennia*, *Spartina*) in different surrounding habitat types (mangrove, salt marsh) to examine changes in decomposition rate and epifaunal community composition, while holding latitudinal influences constant. We also included artificial detritus mimics to separate the structural and nutritional role of detrital inputs on epifaunal community composition.

At both regional and local scales, we expected that decomposition rates would be higher for *Avicennia* detritus compared to *Spartina* detritus because *Avicennia* has a lower

C:N ratio. We also expected that if epifauna use detritus primarily for structural refuge, they would be more abundant and taxa-rich in *Spartina* detritus than *Avicennia* detritus because it is more persistent over time and its hollow structure could provide greater refuge value. Conversely, if epifauna use detritus primarily as a food resource, we expected that they would be more abundant and taxa-rich in *Avicennia* detritus because it is more nutritious and biologically available. Together, these experiments allow us to assess whether the detrital attributes of expanding species can substitute for the ecosystem and community functions of resident species detritus, including parsing out whether regional patterns are driven by latitudinal factors, local differences in surrounding habitat, or the distinct nutritional and structural attributes of detritus.

Methods

Experiment 1. Regional effects of detritus identity and habitat heterogeneity

Study sites

We selected 13 sites that were systematically spaced ~100 km apart along the SE Atlantic seaboard from West Palm Beach, FL to Savannah, GA to capture habitat variability across a latitudinal gradient (27–32°) of mangrove expansion into salt marshes (Fig. 1, Supplementary material Appendix 1 Table A1). To focus on community differences among broad habitat types, we chose the gradient to include a southern region of pure mangrove habitat (four sites from West Palm Beach, FL, to Sebastian Inlet, FL), a central region of interspersed salt marsh and mangrove habitat (four sites from Cape Canaveral, FL, to St. Augustine, FL), and a northern region of pure salt marsh habitat (five sites from Ponte Vedra, FL to Savannah, GA) (Fig. 1, Supplementary material Appendix 1 Table A1). Eight of the sites (south, $n=4$; central, $n=4$) coincided with permanent vegetation plots established by Simpson et al. 2017, and we divided each site into waterward fringe and landward interior sections (Fig. 1) to encompass a diversity of abiotic conditions at each site, and in the case the of central region, a mix of both habitat types (Simpson et al. 2017). Within each region, these sections exhibited different inundation regimes, edaphic conditions and vegetation types. In the north salt marsh region, tall-form *Spartina alterniflora* dominated the fringe section and a mix of high marsh species composed the interior, including short-form *Spartina alterniflora*, *Batis maritima* and *Salicornia depressa* (Fig. 1). In the central mixed region, the fringe section was comprised of high marsh species and the black mangrove, *Avicennia germinans*, with a few red mangrove, *Rhizophora mangle*, interspersed. The interior section resembled the north region interior (Fig. 1). In the south mangrove region, *R. mangle* dominated both fringe and interior sections; interior trees were shorter (~3 m tall) and denser than fringe trees (~5 m tall). *Avicennia* and white mangrove, *Laguncularia racemosa*, were also intermittently present at

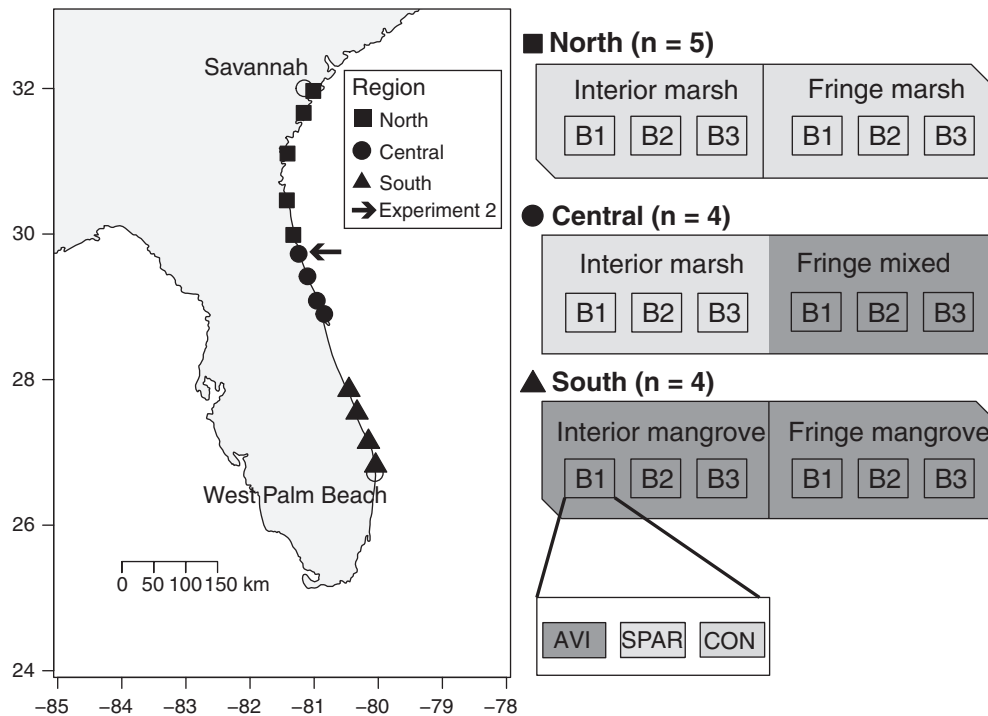


Figure 1. Experiment 1 sites span a mangrove density gradient from West Palm Beach, FL to Savannah, GA. Mangrove vegetation dominated the south region, mixed (mangrove/salt marsh) vegetation characterized the central region, and salt marsh vegetation dominated the north region. A replicate of each detritus treatment (*Avicennia*=AVI, *Spartina*=SPAR, empty control=CON) was placed in three blocks (B1–3) in both the waterward fringe and landward interior sections at each site in a randomized block design. Dominant vegetation in fringe and interior sections varied by region. Experiment 2 was performed at one central region site.

most southern sites (Fig. 1). Although salt marsh and mangrove stands are each composed of a mixture of species, we focused on *Spartina* and *Avicennia* because these two species dominate mixed environments at the leading edge of the mangrove expansion front.

Experimental set-up

To examine whether epifaunal community composition and detrital breakdown vary with detritus identity across this latitudinal gradient, we established three detritus identity treatments. We filled polypropylene litterbags (0.0225 m²; 0.635 cm mesh) with either *Spartina* or *Avicennia* detritus. To focus on epifaunal responses to structure, we also included an empty bag treatment as a procedural control for the structure provided by the bag. We collected *Spartina* and *Avicennia* detritus from the field in late June 2015 from a central mixed habitat site in Crescent Beach, FL (29°76'12.33"N, 81°26'69.17"W). We picked yellow, fully senescent *Avicennia* leaves directly from adult trees and gathered dead *Spartina* from the wrack line. These collections correspond to the respective plant parts of each species that typically enter the benthic detrital pool (i.e. *Avicennia* leaves, *Spartina* stem and sheath) and these were the dominant detrital components at our field sites (Wilson et al. 1986, White and Howes 1994, Coronado 2001, Proffitt and Devlin 2005). To maintain uniformity in initial detritus mass, we air-dried both detritus types for a week prior to litterbag addition. We then cut

Spartina wrack into 9 cm pieces to fit inside the litterbags. We added 7 g of detritus to each litterbag; on average, each treatment contained 30 mangrove leaves or 11 pieces of *Spartina* wrack. Additionally, we oven-dried samples of air-dried *Spartina* and *Avicennia* detritus that were not placed in the field so that we could create a standard curve to estimate initial starting dry masses.

At each site within each region, we established three complete blocks of the detritus treatments (*Avicennia*, *Spartina*, control) in each fringe and interior section (Fig. 1). Blocks were located at least 10 m apart within a section, and sections within a site were separated by 30–80 m. Within each block, we attached one replicate of each detritus treatment to a single 40 cm PVC pole with fishing line and secured each litterbag to the ground with a garden staple to keep bags in contact with the sediment and to prevent them from washing away. We did not place bags in the interior section of two sites (Avalon State Park and John D. MacArthur State Park, Supplementary material Appendix 1 Table A1) because these sites were located on small islands that did not grade into interior stature trees. Thus, we deployed a total of 216 litterbags across all sites. Initial placement occurred between 9 July 2015 and 30 July 2015, and we left the bags in the field for 90 days. We collected bags in the same order that we placed them in the field from 5 October 2015 to 22 October 2015 to maintain uniformity in experiment duration.

Collection and post-processing

Upon collection, we removed each litterbag from its associated PVC stake and placed each bag in an individually labeled clear plastic bin. In some cases, associated external sedimentation or detritus was also collected with each bag. We then added seawater to each bin to prevent desiccation during transport to the lab and post-processing. At the lab, we first rinsed and removed any external detritus that had collected on the outside of each litterbag sample to separate it from the treatment detritus. We dried the external detritus in a drying oven at 60°C for three days until it reached a constant weight, so that we could use these values as a covariate in our models to account for the fact that associated external detritus could potentially serve as additional substrate for invertebrates in our treatment samples.

Next, we cleaned and removed the treatment detritus from each bag and set it aside for dry mass processing. We then removed the invertebrates from each litterbag by passing each sample through a 500 µm sieve with seawater. We placed the sample remaining on the sieve into a clear plastic bin and examined the contents under a magnifying lamp. We counted, photographed, and preserved all invertebrates in 90% ethanol, and identified taxa to the lowest taxonomic group possible. Lastly, we placed the treatment detritus in a drying oven at 60°C for three days, until the samples reached a constant weight. We then measured detritus dry mass to determine losses in percent dry mass across region for each detritus type.

Statistical analysis

Epifaunal community composition. We used R ver. 3.1.3 (<www.r-project.org>) for all statistical analyses. To examine differences in the structural role of the litter treatments over time, for all community analyses we used invertebrate counts per litterbag because bags began with the same initial substrate mass for the detritus treatments (*Avicennia*, *Spartina*). This approach quantifies litter habitat value to invertebrates in a way that incorporates the influence of the differential persistence of the litter types, and also allows comparison among all litter treatments, including the controls that had no substrate mass. First, we explored how overall community abundance and composition varied across region and detritus identity. A test of community composition dispersion with the betadisper function in the 'vegan' package revealed uneven dispersion between predictor levels, which violates the PERMANOVA assumption of homogeneity of variance (Oksanen et al. 2013). Thus, we performed a multivariate analysis of invertebrate community composition using a model-based approach (Warton et al. 2012, 2015), where we fit a generalized linear mixed model using the 'lme4' package (Bates et al. 2015). We created a model to examine the effects of region (south, central, north), detritus identity (*Avicennia*, *Spartina*, empty control), and their interaction on invertebrate taxa abundance. We also included a random slopes term in the model that allowed each main effect (region, detritus identity) to vary by taxa identity, which enabled us to

examine how much community composition changed based on both region and detritus identity. We also included site as a random intercept and block as a fixed effect and fit the model with a Poisson distribution and a log link function. We did not include section (fringe, interior) as a predictor in the model because this variable confounds multiple factors (e.g. tidal elevation, inundation, vegetation type) that are not orthogonal across region. Rather, we considered litterbag placement within both fringe and interior sections in each region to capture the full range of habitat (i.e. local scale) variability present in each region. We also initially included the external detritus dry mass as a covariate in the model, but its effect was negligible and was excluded from the final model. This analysis only included taxa that had at least ten observed individuals across the entire study to reduce zero-inflation issues during model fitting (Zuur et al. 2009), which reduced the number of taxa in the analysis from 72 to 25.

Second, we investigated how community metrics and individual taxonomic group abundances varied across region and with detritus identity. We performed separate univariate analyses for total individuals, for taxonomic richness, and for dominant taxonomic groups that showed strong patterns in the multivariate analysis (e.g. amphipods, crabs, polychaetes). All observed taxa were included in these analyses. We also performed separate univariate analyses for the most abundant individual taxa ($n \geq 10$ across sites). We constructed generalized linear mixed models for each of these measures as a function of the interactive effect of region (south, central, north) and detritus identity (*Avicennia*, *Spartina*, empty control), including site as a random intercept. We fit all models with a Poisson distribution and a log link function, checking for overdispersion and re-fitting overdispersed models with negative binomial distributions and log links. Block and external detritus were initially included in the models, but were removed if they did not account for significant variation. We used Bonferroni corrections to account for the family-wise error inherent in multiple univariate tests. We performed Tukey's post hoc tests for significant univariate models to examine differences in detritus identity across region, using an interaction term that combined both detritus identity and region.

Decomposition. To examine whether detrital breakdown differed by detritus identity treatments across region, for each detritus type in each region we calculated the percent dry mass remaining (% DMR) at the end of the experiment as the final measured dry mass divided by the initial estimated dry mass for *Avicennia* and *Spartina* detritus. Because we collected *Avicennia* and *Spartina* detritus at different stages in their decomposition trajectory (senescent *Avicennia* leaves from the tree versus *Spartina* stems from the wrack line), we compared within each detritus type across regions. For each detritus type, we constructed a linear mixed model in which we examined the effect of region (south, central, north) on the % DMR at the end of experiment 1. We also included site as a random intercept and fit the models with a Gaussian

distribution, checking residual plots to ensure that model assumptions were met. We initially included block as a fixed effect in the model for each detritus type, but it did not account for significant variation in either model and was ultimately excluded.

Experiment 2. Local effects of detritus identity and surrounding habitat

Study site

We performed an additional detritus manipulation in the fringe section of a single mixed site in Crescent Beach, Florida (29°76'19.33"N, 81°26'75.81"W) to examine effects of surrounding habitat type on epifaunal community composition, while keeping latitudinal and tidal factors constant. At this site, *Avicennia* was naturally interspersed within a *Spartina*-dominated salt marsh, creating local scale (1 m²) patches of mangrove and salt marsh habitat. Salt marsh and mangrove habitat were present at the same tidal height, and we used a randomized block design to create replicated detritus treatments across ten blocks of paired mangrove and salt marsh habitat. Each block contained an isolated adult mangrove (136.90 ± 24.30 cm, mean height ± SD) located a minimum of 2 m from the next closest adult mangrove. *Spartina* (32.98 ± 2.65 cm, mean height ± SD) in the block surrounded each target mangrove and we chose paired salt marsh habitat to be within 2 m of each target mangrove. All blocks were separated by at least 2 m, and there was no difference in tidal elevation between blocks (Real-time Kinetic GPS, 1.40 ± 0.037 m, mean ± SD).

Experimental set-up

To examine how both surrounding habitat type and the structural and nutritional differences between *Avicennia* and *Spartina* detritus affect epifaunal community composition, we deployed detritus treatments in litterbags as in experiment 1 (*Avicennia*, *Spartina*, empty control litterbags). We also included two plastic detritus mimic treatments in each block to isolate the structural effects of each detritus type. For the *Avicennia* structural mimic, we used plastic leaves cut from a decorative plant that approximated the dimensions of natural *Avicennia* leaves (4–6 cm long), adding 30 plastic leaves to each litterbag (Supplementary material Appendix 1 Fig. A1a–b). For the *Spartina* structural mimic, we cut hollow, plastic exterior airline piping (0.9 cm diameter) into 9 cm lengths and added eleven pieces to each litterbag (Supplementary material Appendix 1 Fig. A1c–d). We deployed litterbags in a randomized block design (n = 10 blocks), crossing detritus identity (*Avicennia*, *Avicennia* mimic, *Spartina*, *Spartina* mimic, empty control) and surrounding habitat type (mangrove, salt marsh) for a total of 100 bags. To keep the timing and duration of deployment consistent with experiment 1, we placed litterbags in the field on 5 July 2015 and collected them on 2 October 2015 (87 days). We collected and processed litterbags as described above.

Decomposition

To measure decomposition rate over multiple time points in the two habitats, we created litterbags with *Avicennia* and *Spartina* detritus as described above, making 60 bags of each detritus type. We placed three bags each of the two detritus types (n = 6 total) in the 10 paired habitat blocks (mangrove, salt marsh) alongside experiment 2 on 5 July. We then collected one bag of each detritus type from each block at 30, 149 and 214 days and used the natural *Spartina* and *Avicennia* detritus treatments from experiment 2 as the 87-day time point. At each time point, we measured the change in detritus dry mass as described above using the initial estimated dry masses.

Statistical analysis

Epifaunal community composition. First, we examined how overall community abundance and composition varied with surrounding habitat type and detritus identity. As in experiment 1, we performed a multivariate analysis using a generalized linear mixed model to examine how invertebrate taxa abundance varied as a function of habitat type (mangrove, salt marsh), detritus identity (*Avicennia*, *Avicennia* mimic, *Spartina*, *Spartina* mimic, empty control), and their interaction, and we fit the model with a Poisson distribution and a log link. As above, we also included a random slopes term that allowed each of the main effects (habitat type, detritus identity) to vary by epifaunal taxon. The model initially included external detritus dry mass as a covariate and experimental block as a fixed effect, but neither of these variables accounted for significant variation in the data, and we removed them from the final model. This analysis only included taxa that had at least ten observed individuals, which reduced the final taxa count from 36 to 11.

Second, as above, we also performed univariate analyses for total individuals, taxa richness, and dominant taxonomic groups, including all observed taxa. We also performed univariate analyses for the most abundant individual taxa (n ≥ 10 across blocks), constructing generalized linear mixed models with the same main effects as the multivariate analysis. For all models, we initially included the external detritus dry mass as a covariate and block as a fixed effect in the models, and removed them from models for response variables in which they were not significant. We used Bonferroni corrections to account for the family-wise error inherent in multiple univariate tests. We then performed Tukey's post hoc tests for significant univariate models to examine differences among detritus treatments between habitat types, using an interaction term that combined both detritus identity and habitat type.

Decomposition. To determine the decomposition rate for each detritus and habitat type combination, we calculated the percent dry mass remaining (% DMR) of detritus for each block (n = 10) at each time point (days 30, 87, 149, 214). We then log-transformed the % DMR values and performed a linear regression of the log (% DMR) versus time in the field (days), with the slope of each regression

providing the decomposition rate (k) over time (d) for each block (Conover et al. 2016). Although the two litter types were presumably collected at different time points in their decomposition trajectories (senescent *Avicennia* leaves versus *Spartina* stems from the wrack line), we captured the exponential decline of both curves over the experimental duration of seven months. There was no evidence of non-linearities in our data, confirming that an exponential decay model was appropriate and that decay rates would be the same for each litter type regardless of when we collected the plant material. Similarly, *Spartina* litter in southern marshes does not exhibit the non-linearities (Burkholder and Bornside 1957, Kirby and Gosselink 1976, Kruczynski et al. 1978, White et al. 1978, Reice and Stiven 1983) that have been observed in some northern marshes (Frasco and Good 1982, Valiela et al. 1985, Wilson et al. 1986). To analyze differences in k (day^{-1}) between detritus identity and habitat type, we used a linear model to examine k as a function of detritus identity (*Avicennia*, *Spartina*), habitat (mangrove, salt marsh), and their interaction. We fit the model with a Gaussian distribution and checked residual plots to ensure that model assumptions were met.

Data deposition

Data are available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.g60vv21>> (Smith et al. 2019).

Results

Experiment 1. Regional effects of detritus identity and habitat heterogeneity

Epifaunal community composition

We collected 4156 individuals across 72 taxa (Supplementary material Appendix 1 Table A2). In the multivariate analysis, invertebrate community composition varied significantly with both region ($\chi^2=7.27$, $df=2$, $p=0.026$) and detritus identity ($\chi^2=14.09$, $df=2$, $p=0.00087$), and there was no significant interaction between region and detritus identity ($\chi^2=6.81$, $df=4$, $p=0.15$). The direction and magnitude of the effects of both region and detritus identity varied by taxa (Supplementary material Appendix 1 Fig. A2, A3, Table A3, A4). Most epifaunal invertebrate taxa differed in abundance by region. Grouping across all taxa, the mean number of individuals increased 4.5–7 times from south to north along the latitudinal gradient (Fig. 2a). Abundance was lowest in the south region (mangrove), and highest in the north region (salt marsh) (Fig. 2a, Supplementary material Appendix 1 Table A6a). Relative taxonomic richness was also nearly two times greater in the north region compared to the south (Fig. 2b, Supplementary material Appendix 1 Table A6b).

Several taxonomic groups, including crabs, polychaetes, snails and ostracods, drove community differences across the latitudinal gradient (Supplementary material Appendix 1 Fig. A3, Table A4). Crab mean abundance increased along

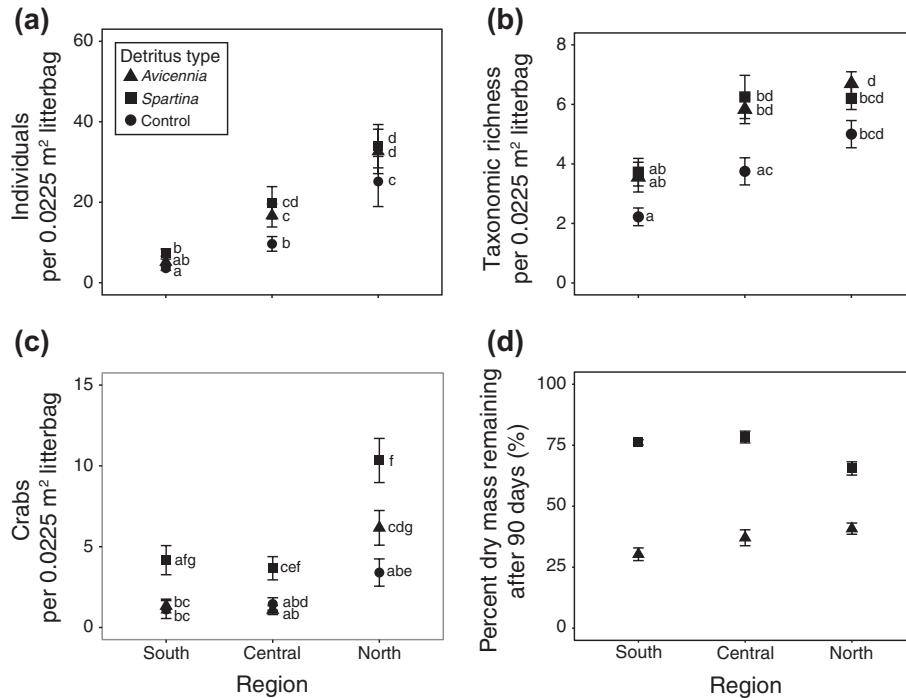


Figure 2. Mean \pm SE for (a) number of individuals, (b) taxonomic richness, and (c) number of crabs collected within 0.0225 m² litterbags, and (d) percent dry mass remaining (% DMR) after 90 days across three geographic regions (south, central, north) in the three detritus treatments (*Avicennia*, *Spartina*, control) of experiment 1 ($n = 216$ litterbags total). Non-control litterbags started with 7 g of each litter type. Letters reflect significant post hoc tests ($\alpha < 0.05$). Supplementary material Appendix 1 Fig. A3 shows abundance data for other taxonomic groups.

the latitudinal gradient, and we observed 2.5–4.5 times more crabs in the north salt marsh region compared to the south mangrove region (Fig. 2c, Supplementary material Appendix 1 Table A6d). Fiddler crabs (*Uca* spp.) and the square-backed marsh crab *Armases cinereum* were the primary drivers of these patterns (Supplementary material Appendix 1 Fig. A2, Table A3, A5i, m). Polychaete abundance was significantly higher in the north region relative to the other two regions (Supplementary material Appendix 1 Fig. A3i, Table A4, A6h), a pattern that was driven primarily by *Capitellidae* spp. 1, *Nereididae* spp. 1 and *Streblospio benedicti* (Supplementary material Appendix 1 Fig. A2, Table A3, A5c, e, f). Ostracod and snail abundance was also greater in the north region compared to the other regions (Supplementary material Appendix 1 Fig. A3h, k, Table A4, A6g, i). In contrast, amphipods, insect larvae and tanaids were present in negligible numbers in the north and south regions, but we observed greater numbers of all three groups in the central region (Supplementary material Appendix 1 Fig. A3a, f, l, Table A3, A6c, e, j). The tanaid *Leptocheilia rapax*, amphipods *Grandidierella bonnieroides* and *Gammarus mucronatus*, and insect larvae Odonata spp. and *Chironomidae* spp. primarily drove these patterns (Supplementary material Appendix 1 Fig. A2, Table A3, A5).

We observed significantly more individuals and greater taxonomic richness in detritus treatments compared to control litterbags (Fig. 2a–b), and there were no significant differences between *Avicennia* and *Spartina* detritus within any of the three regions (Fig. 2a–b). In contrast, across all regions, crabs were 1.5–4 times more abundant in *Spartina* detritus compared to either *Avicennia* detritus or the control (Fig. 2c, Supplementary material Appendix 1 Table A4, A6d). As above, fiddler crabs and the square-backed marsh crab were the primary drivers of these patterns. No other taxonomic groups showed differences in abundance between *Spartina* and *Avicennia* detritus, although several groups (e.g. annelids, amphipods) were more abundant in natural detritus compared to controls (Supplementary material Appendix 1 Fig. A3, Table A4, A6).

Decomposition

There was not a significant effect of region on percent dry mass remaining (% DMR) after 90 days for either *Avicennia* ($\chi^2=2.21$, $df=2$, $p=0.33$) or *Spartina* detritus ($\chi^2=4.74$, $df=2$, $p=0.093$) (Fig. 2d).

Experiment 2. Local effects of detritus identity and surrounding habitat

Epifaunal community composition

Overall, we collected 1029 individuals across 36 taxa (Supplementary material Appendix 1 Table A7). In the multivariate analysis, invertebrate community composition did not differ significantly with habitat type ($\chi^2=0.88$, $df=1$, $p=0.35$), detritus identity ($\chi^2=7.049$, $df=4$, $p=0.13$), or their interaction ($\chi^2=5.41$, $df=4$, $p=0.25$), and most

taxa showed no preference for either habitat type or detritus identity (Supplementary material Appendix 1 Fig. A4, Table A9, A11).

The total number of individuals varied significantly with detritus identity, and there was not a significant effect of habitat or an interaction between detritus or habitat (Fig. 3a, Supplementary material Appendix 1 Table A11a). There were nearly two times more individuals in natural and mimic *Spartina* detritus compared to natural and mimic *Avicennia* detritus and nearly three times as many individuals compared to the empty control bag in both habitat types (Fig. 3a). Total individual abundance did not vary between natural and mimic detritus for either *Avicennia* or *Spartina* in either habitat type (Fig. 3a). Taxonomic richness did not vary based on either habitat type or detritus identity (Fig. 3b, Supplementary material Appendix 1 Table A11b).

Crabs were the most abundant taxonomic group (74% of all observed individuals) and were primarily responsible for the observed patterns for total individuals. Indeed, when we removed crabs from the total individuals group and re-ran the model, the remaining taxa did not show significant effects of detritus ($\chi^2=4.65$, $df=4$, $p=0.32$), habitat ($\chi^2=0.11$, $df=1$, $p=0.74$), or their interaction ($\chi^2=6.83$, $df=4$, $p=0.15$). Crabs were 2–3.5 times more abundant in natural and mimic *Spartina* detritus compared to natural and mimic *Avicennia* detritus and 5–7 times more abundant compared to the empty control bags (Fig. 3c). Again, there was no difference in crab mean abundance between natural and mimic detritus treatments of either detrital type (Fig. 3c), and crabs were more abundant in salt marsh habitat compared to mangrove habitat for natural and mimic *Spartina* detritus (Fig. 3c, Supplementary material Appendix 1 Table A9, A11f). As observed at the regional scale, fiddler crabs *Uca* spp. and the square-backed marsh crab *Armases cinereum* drove these patterns (Supplementary material Appendix 1 Fig. A4e–f, Table A8, A10e–f). Most other taxonomic groups were not abundant enough to have strong trends. However, snails were more abundant in salt marsh habitat compared to mangrove habitat (Supplementary material Appendix 1 Fig. A5k, Table A9, A11k), a pattern primarily driven by the snail *Assiminea succinea* (Supplementary material Appendix 1 Fig. A4d, Table A8, A10d).

Decomposition

Avicennia detritus decomposed significantly faster than *Spartina* detritus ($F_{3, 36}=43.56$, $p<0.0001$, $R^2=0.77$) in both mangrove and salt marsh habitats; there was not a significant effect of habitat or the interaction between detritus identity and habitat (Fig. 4). The decay rate, k (d^{-1}), of *Avicennia* was -0.0082 ± 0.0005 in mangrove habitats and -0.0097 ± 0.0007 in salt marsh habitats (mean \pm SE). The decay rate of *Spartina* was -0.0047 ± 0.0005 in mangrove habitats and -0.0032 ± 0.0003 in salt marsh habitats (mean \pm SE).

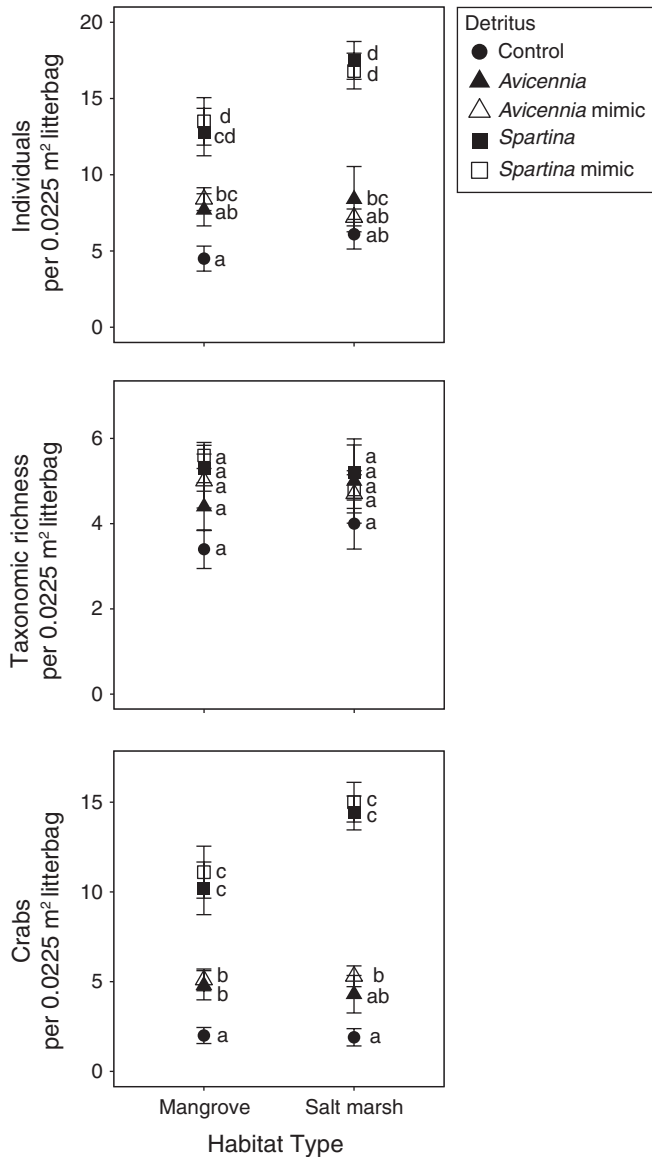


Figure 3. Mean \pm SE for (a) number of individuals, (b) taxonomic richness, and (c) number of crabs collected within 0.0225 m² litterbags, based on detritus treatment (*Avicennia*, *Avicennia* mimic, *Spartina*, *Spartina* mimic, empty control) and the surrounding habitat (mangrove, salt marsh) at a central region, mixed site in experiment 2 (n = 100 litterbags total). Mimics are plastic representations that approximate the dimensions and density of *Avicennia* and *Spartina* detritus included in the natural litterbags. Letters reflect significant post hoc tests ($\alpha < 0.05$). Supplementary material Appendix 1 Fig. A5 shows abundance data for other taxonomic groups.

Discussion

When foundation species shift into new environments, differences in species traits, habitat context, and large-scale environmental factors can affect whether expanding foundation species can substitute for the ecosystem and community functions of resident foundation species. In our study, we

compared detrital attributes of resident and expanding foundation species in different habitat contexts across a latitudinal gradient to determine how the detritus of expanding foundation species alters decomposition and associated epifaunal community composition. We found that the detritus of the expanding foundation species, *Avicennia germinans*, decomposed 2–4 times faster than that of the dominant resident foundation species, *Spartina alterniflora*, at both regional and local spatial scales (Fig. 2d, 4). Although epifaunal abundance and taxonomic richness increased across a regional gradient from south to north (mangrove to salt marsh), most epifaunal taxa did not differ in abundance based on detrital identity at either spatial scale (Fig. 2a–b, 3a–b). The exception was crabs, a dominant taxonomic group, which were significantly more abundant in *Spartina* detritus compared to *Avicennia* detritus across all habitats at both spatial scales (Fig. 2c, 3c). Our inert mimic treatments suggest that the structural attributes of *Spartina* detritus relative to *Avicennia* detritus are sufficient to increase crab abundance. At a local scale, surrounding habitat type did not affect decomposition rate or community patterns. This result suggests that the epifaunal community patterns that we measured at a regional scale are more likely due to large-scale environmental factors that vary across latitude and not habitat context. Overall, these differences in detrital structure and decomposition rate suggest that detritus from the two foundation species is non-substitutable due to differences in detrital attributes. As mangroves expand into salt marshes, the lower refuge value and faster turnover of mangrove detritus compared to salt marsh detritus could lead to changes in crab abundance and shifts in community dominance.

As hypothesized, *Avicennia* detritus decomposed faster than *Spartina* detritus. Our values for *Spartina* detritus decay constants (-0.0032 to -0.0047 day⁻¹) are comparable to literature values from along the Atlantic east coast that range between k (day⁻¹) values of -0.002 and -0.006 (Burkholder and Bornside 1957, Kruczynski et al. 1978, Marinucci 1982, Wilson et al. 1986, White and Howes 1994). Similarly, our calculated k values for *Avicennia* litter (-0.0082 to -0.0097 day⁻¹) fall within the range of literature values, from -0.004 to -0.022 (Twilley et al. 1986, Middleton and McKee 2001, Proffitt and Devlin 2005, Perry and Mendelssohn 2009). The rapid decomposition rate of *Avicennia* detritus relative to *Spartina* detritus likely stems from the higher lignin values and C:N ratios of *Spartina* as compared to *Avicennia* (Hedges and Mann 1979, Taylor et al. 1989, Henry and Twilley 2013). However, the influence of factors like inundation regime and temperature could account for the wide variation of literature values for *Avicennia* decomposition rate (Kruczynski et al. 1978, Valiela et al. 1985, Twilley et al. 1986). In fact, because detritus decomposition rates are temperature-dependent (Chapin et al. 2011), we expected that temperature differences within and among sites would affect our measurements of detrital turnover. Surprisingly, there were not differences in % DMR based on region or surrounding habitat type (Fig. 2d, 4). Examination of decomposition

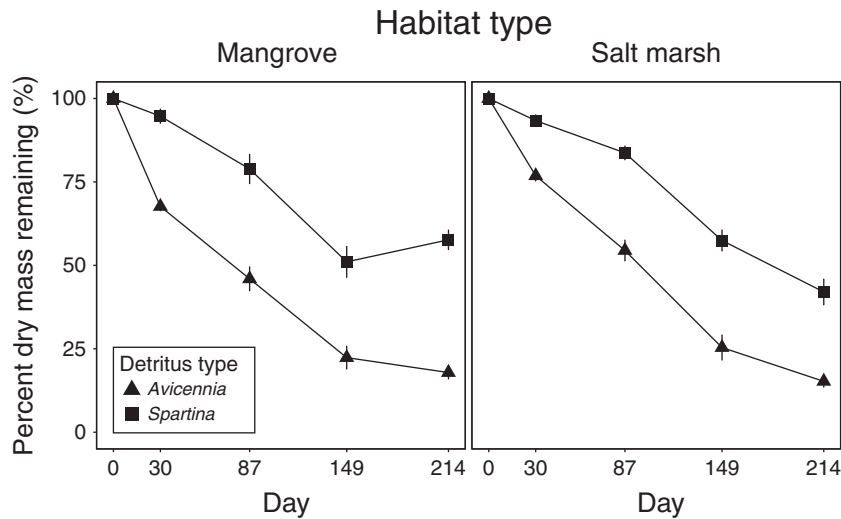


Figure 4. Mean \pm SE percent dry mass remaining (% DMR) of the initial dry mass for *Spartina* and *Avicennia* over time (0, 30, 87, 149, 214 days after deployment; $n = 40$ litterbags per time point) at a central region, mixed site in experiment 2.

over a longer time period that includes winter months when a larger temperature gradient is apparent across latitude could reveal differences in decomposition rate across region.

Although most taxonomic groups showed changes in abundance across the regional gradient, only crabs responded strongly to detritus identity and consistently preferred *Spartina* detritus to *Avicennia* detritus at both regional and local scales. *Spartina* detritus decomposes more slowly than *Avicennia* detritus, which indicates that, on average, it has a lower nutritional value and also persists longer in the environment as a structural refuge for invertebrates. There was no difference in crab abundance between natural and mimic detritus for either *Spartina* or *Avicennia* detritus, which suggests that crabs primarily use both detritus types for their structural attributes. Additionally, the appreciable colonization of control litterbags in our experiments suggests that structural refuge is limiting to epifauna in these systems, which supports the important structural role of detritus. The greater refuge value of *Spartina* detritus relative to *Avicennia* detritus for crabs is also evident from observations of crab behavior during sample processing. Crabs took refuge inside both natural and mimic *Spartina* detritus, and we had to slice open natural and mimic detritus tubes to extract the crabs. In comparison, we easily displaced crabs from the other treatments with seawater. Thus, the increased structural value and persistence of *Spartina* detritus relative to *Avicennia* detritus likely drives this pattern of increased crab abundance.

It is unclear why crabs were the only taxa to respond to detritus identity. In our experiments, crabs represented 21% of all individuals observed in the regional scale experiment (experiment 1) and 74% of all individuals observed at our single mixed site in the local scale experiment (experiment 2). Thus, due to their high relative abundance (especially in experiment 2), crabs provide the best resolution of any taxonomic group for detecting significant treatment effects (Supplementary material Appendix 1 Fig. A5). The high and

differential abundance of crabs in *Spartina* detritus is also biologically important, and crabs have influential functional roles in these ecosystems (Bertness 1985, Lee 1998). In salt marsh ecosystems, marsh crabs (e.g. *Uca* spp., *A. cinereum*) are dominant, highly connected species with high food web importance relative to other species (McCann et al. 2017). Although *Uca* spp. are detritivorous (Haines 1976), *A. cinereum* is omnivorous and is known to consume various other epifaunal species (Buck et al. 2003). In general, the crabs in our study were <2 cm in carapace width, which suggests that detritus is primarily harboring juvenile and female crabs. Marsh crabs hide from xanthid crab predators (e.g. *Eurytium limosum*, *Panopeus herbstii*) in the structure of salt marsh habitat (Lee and Kneib 1994), and *Spartina* detritus likely acts as an additional refuge from these predators. Structural refuge decreases predator capture efficiency in these environments (Vince et al. 1976, Gotceitas and Colgan 1989, Lewis and Eby 2002), and decreased structural refuge availability in expanded habitats could have further cascading effects on multiple trophic levels (Grabowski 2004, Byers et al. 2017) – for example, for nekton that have distinct habitat preferences between mangrove and salt marsh habitats (Caudill 2005, Smee et al. 2017). Replacement of *Spartina* by *Avicennia* could deprive dominant crab species of preferred salt marsh habitat and essential detritus structural refuge or facilitate novel competitor species, such as the mangrove tree crab, *Aratus pisonii*, which is already expanding into salt marshes ahead of the mangrove expansion front (Riley et al. 2014).

These detrital effects were consistent at regional and local scales and did not vary with habitat context. For both detritus types, epifaunal community abundance and taxonomic richness increased with latitude across a regional expansion gradient from south (pure mangrove) to north (pure salt marsh) (Fig. 2a–b), and crab, annelid, snail and ostracod taxa drove this pattern (Supplementary material Appendix 1

Fig. A3, Table A4). However, aside from crabs, taxa abundances were roughly equivalent for *Spartina* and *Avicennia* detritus. The overall observed northward increase in epifaunal community abundance is contrary to our hypothesis that species abundance and richness would be greatest in the central region, where mixed assemblages of both salt marsh and mangrove species provide heightened habitat heterogeneity relative to pure vegetation stands. Although habitat heterogeneity is correlated with increased species abundance and diversity in many systems (Kerr and Packer 1997, Tews et al. 2004, Stein et al. 2014), it is likely that additional environmental factors influenced the observed regional pattern, especially since we made our observations across a 5° latitudinal gradient. The observed pattern also contradicts classic latitudinal diversity gradient patterns that predict that species diversity and abundance should be greater at lower latitudes (Willig et al. 2003, Hillebrand 2004), although it is possible that our taxonomic resolution was not high enough to capture true diversity differences across the gradient or that our latitudinal range was too small to resolve true biogeographic trends. Latitudinal gradients in abundance and diversity are often correlated with gradients of other abiotic variables such as temperature, precipitation, or insolation (Rohde 1992, Hawkins et al. 2003). In this case, an important abiotic factor that could influence community patterns is the fact that our sites span the South Atlantic Bight, which exhibits an extreme gradient in tidal amplitude (Dame et al. 2000, Byers et al. 2015). At the southern mangrove sites, the tidal range is substantially lower (1 m) than at the northern salt marsh sites (3 m) (NOAA 2018), which could affect community composition by increasing nutrient loading or propagule delivery in northern areas with larger tidal ranges (Childers 1994, Schoch et al. 2006).

At a local scale, we did not see a difference in community composition based on surrounding habitat type (mangrove, salt marsh) at a single, mixed site where latitude and tidal elevation were fixed (Fig. 3, Supplementary material Appendix 1 Table A4, Fig. A4). Thus, the observed regional abundance patterns are not likely due to underlying differences in the identity of surrounding habitat. This result contrasts with other studies that show local scale differences in epifaunal invertebrate abundance based on surrounding vegetation type (Angradi et al. 2001, Wang et al. 2008, Chen et al. 2015). In our study, overall epifaunal abundance was low at the local scale, which could have prevented us from detecting differences in abundance between habitats (Supplementary material Appendix 1 Fig. A5). However, our epifaunal abundances are comparable to other studies in salt marsh habitats (Reice and Stiven 1983, Netto and Lana 1999, Chen et al. 2015), with some exceptions (Angradi et al. 2001). The fact that we did not see significant effects of local surrounding habitat context or regional habitat heterogeneity on community abundance and richness suggests that other large-scale environmental factors (e.g. temperature, tidal amplitude) that vary across latitude could drive observed regional community patterns.

To our knowledge, our regional study is the first documentation of epifaunal detrital communities in this area, and we provide a valuable and robust baseline data set of epifaunal community composition for the Atlantic coast of Florida and Georgia. The range limit of black mangrove *A. germinans*, is predicted to continue moving northward at a rate of 2.2–3.2 km year⁻¹ over the next 50 years (Cavanaugh et al. 2015). By characterizing communities in uninvaded salt marsh habitat, our data can be used for future comparisons following predicted mangrove expansion and environmental change in these areas.

In summary, our work highlights that shifts in foundation species distributions can lead to accompanying changes in ecosystem processes and community composition based on specific foundation species traits. We showed that differences in detrital attributes between the expanding foundation species, *A. germinans*, and the resident foundation species, *S. alterniflora*, altered epifaunal community composition and ecosystem processes, which suggests that these detrital resources are non-substitutable. Crabs, a dominant and functionally important taxonomic group in these communities, were significantly more abundant in *Spartina* detritus compared to *Avicennia* detritus across all habitats at both regional and local scales. This pattern is strongly tied to the structural attributes of *Spartina* detritus. As mangroves expand into salt marshes, shifts in detritus decomposition rate and structural value could lead to accompanying shifts in crab abundance and community dominance. We also observed a pattern of increasing community abundance and richness from south to north across the mangrove expansion gradient, yet neither regional habitat heterogeneity nor local surrounding habitat identity had strong effects on overall epifaunal community composition. Instead, these findings point to the important role of covarying latitudinal factors in driving community patterns during climate-driven range expansions. Studies of ecosystem and community effects of shifting foundation species are essential to understand whether expanding foundation species can provide substitutable ecosystem and community functions relative to resident species. However, it is also important to account for the role of concomitant environmental changes that also directly alter community and ecosystem processes.

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References

- Angelini, C. et al. 2011. Interactions among foundation species and their consequences for community organization, biodiversity and conservation. – *BioScience* 61: 782–789.
- Angelini, C. et al. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. – *Proc. R. Soc. B.* 282: 20150421.
- Angradi, T. R. et al. 2001. Vegetation type and the intertidal macroinvertebrate fauna of a brackish marsh: *Phragmites* vs *Spartina*. – *Wetlands* 21: 75–92.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – arXiv:1406.5823 [stat.CO] 67: 48.
- Bertness, M. D. 1985. Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. – *Ecology* 66: 1042–1055.
- Bret-Harte, M. S. et al. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. – *Ecology* 82: 18–32.
- Breteler, R. et al. 1981. Trace element enrichments in decomposing litter of *Spartina alterniflora*. – *Aquat. Bot.* 11: 111–120.
- Brusati, E. D. and Grosholz, E. D. 2006. Native and introduced ecosystem engineers produce contrasting effects on estuarine infaunal communities. – *Biol. Invas.* 8: 683–695.
- Buck, T. L. et al. 2003. Diet choice in an omnivorous salt-marsh crab: different food types, body size and habitat complexity. – *J. Exp. Mar. Biol. Ecol.* 292: 103–116.
- Bultman, T. L. and Uetz, G. W. 1984. Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. – *Am. Midland Nat.* 111: 165–172.
- Burkholder, P. R. and Bornside, G. H. 1957. Decomposition of marsh grass by aerobic marine bacteria. – *Bull. Torrey Bot. Club* 84: 366–383.
- Byers, J. E. et al. 2006. Using ecosystem engineers to restore ecological systems. – *Trends Ecol. Evol.* 21: 493–500.
- Byers, J. E. et al. 2015. Geographic variation in intertidal oyster reef properties and the influence of tidal prism. – *Limnol. Oceanogr.* 60: 1051–1063.
- Byers, J. E. et al. 2017. Contrasting complexity of adjacent habitats influences the strength of cascading predatory effects. – *Oecologia* 185: 107–117.
- Caudill, M. C. 2005. Nekton utilization of black mangrove (*Avicennia germinans*) and smooth cordgrass (*Spartina alterniflora*) sites in southwestern Caminada Bay, Louisiana. *Oceanography and Coastal Sciences*. – Louisiana State Univ.
- Cavanaugh, K. C. et al. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. – *Proc. Natl Acad. Sci. USA* 111: 723–727.
- Cavanaugh, K. C. et al. 2015. Integrating physiological threshold experiments with climate modeling to project mangrove species' range expansion. – *Global Change Biol.* 21: 1928–1938.
- Cebrian, J. and Kingsolver, J. G. 1999. Patterns in the fate of production in plant communities. – *Am. Nat.* 154: 449–468.
- Chapin, F. S. et al. 2011. *Principles of terrestrial ecosystem ecology*. – Springer.
- Chen, H. et al. 2015. Invasive cordgrass facilitates epifaunal communities in a Chinese marsh. – *Biol. Invas.* 17: 205–217.
- Childers, D. 1994. Fifteen years of marsh flumes: a review of marsh–water column interactions in southeastern USA estuaries. – *Global Wetlands*.
- Conover, J. et al. 2016. Biomass decay rates and tissue nutrient loss in bloom and non-bloom-forming macroalgal species. – *Estuar. Coast. Shelf Sci.* 178: 58–64.
- Cornelissen, J. and Thompson, K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. – *New Phytol.* 135: 109–114.
- Cornelissen, J. H. et al. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. – *New Phytol.* 143: 191–200.
- Cornwell, W. K. et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. – *Ecol. Lett.* 11: 1065–1071.
- Coronado, M. C. 2001. Litterfall dynamics and nutrient cycling in mangrove forests of southern Everglades, Florida and Terminos Lagoon, Mexico. – Louisiana State Univ.
- Dame, R. et al. 2000. Estuaries of the south Atlantic coast of North America: their geographical signatures. – *Estuaries* 23: 793–819.
- Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. – In: *Proceedings of the colloquium on conservation problems in Antarctica*, pp. 81–96.
- Ellison, A. M. et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. – *Front. Ecol. Environ.* 3: 479–486.
- Frasco, B. A. and Good, R. E. 1982. Decomposition dynamics of *Spartina alterniflora* and *Spartina patens* in a New Jersey salt marsh. – *Am. J. Bot.* 69: 402–406.
- Gotceitas, V. and Colgan, P. 1989. Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. – *Oecologia* 80: 158–166.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. – *Ecology* 85: 995–1004.
- Grosholz, E. D. et al. 2009. Changes in community structure and ecosystem function following *Spartina alterniflora* invasion of Pacific estuaries. – In: Silliman, B. R. et al. (eds), *Human impacts on salt marshes: a global perspective*. Univ. of California Press, pp. 23–40.
- Gutiérrez, J. et al. 2011. Physical ecosystem engineers and the functioning of estuaries and coasts. – *Treatise Estuar. Coast. Sci.* 7: 53–81.
- Haines, E. B. 1976. Relation between the stable carbon isotope composition of fiddler crabs, plants and soils in a salt marsh. – *Limnol. Oceanogr.* 21: 880–883.
- Harmon, M. E. et al. 1986. Ecology of coarse woody debris in temperate ecosystems. – *Adv. Ecol. Res.* 15: 133–302.
- Hawkins, B. A. et al. 2003. Energy, water and broad scale geographic patterns of species richness. – *Ecology* 84: 3105–3117.

- Hedges, J. I. and Mann, D. C. 1979. The characterization of plant tissues by their lignin oxidation products. – *Geochim. Cosmochim. Acta* 43: 1803–1807.
- Henry, K. M. and Twilley, R. R. 2013. Soil development in a coastal Louisiana wetland during a climate-induced vegetation shift from salt marsh to mangrove. – *J. Coast. Res.* 29: 1273–1283.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – *Am. Nat.* 163: 192–211.
- Hoegh-Guldberg, O. and Bruno, J. F. 2010. The impact of climate change on the world's marine ecosystems. – *Science* 328: 1523–1528.
- Ince, R. et al. 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. – *Estuar. Coast. Shelf Sci.* 74: 77–86.
- Johnston, C. A. and Caretti, O. N. 2017. Mangrove expansion into temperate marshes alters habitat quality for recruiting *Callinectes* spp. – *Mar. Ecol. Prog. Ser.* 573: 1–14.
- Jones, C. G. et al. 2010. A framework for understanding physical ecosystem engineering by organisms. – *Oikos* 119: 1862–1869.
- Jones, C. G. et al. 1994. Organisms as ecosystem engineers. – *Ecosyst. Manage.* 69: 130–147.
- Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. – *Nature* 385: 252–254.
- Kirby, C. J. and Gosselink, J. G. 1976. Primary production in a Louisiana Gulf Coast *Spartina alterniflora* marsh. – *Ecology* 57: 1052–1059.
- Kruczynski, W. et al. 1978. Studies on the plant community of a North Florida salt marsh. Part II. Nutritive value and decomposition. – *Bull. Mar. Sci.* 28: 707–715.
- Lawton-Thomas, L. L. 1997. Canopy retranslocation and litter immobilization of nitrogen and phosphorus in three mangrove species along the Shark River estuary, Florida. – Univ. of Southwestern Louisiana.
- Lee, S. 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. – *Mar. Freshwater Res.* 49: 335–343.
- Lee, S. and Kneib, R. 1994. Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh. – *Mar. Ecol. Prog. Ser.* 104: 39–47.
- Levin, L. A. et al. 2006. Invasive cordgrass modifies wetland trophic function. – *Ecology* 87: 419–432.
- Lewis, D. B. and Eby, L. A. 2002. Spatially heterogeneous refugia and predation risk in intertidal salt marshes. – *Oikos* 96: 119–129.
- Lunt, J. et al. 2013. Effects of black mangrove (*Avicennia germinans*) expansion on saltmarsh (*Spartina alterniflora*) benthic communities of the south Texas Coast. – *Gulf Caribbean Res.* 25: 125–129.
- Marinucci, A. C. 1982. Trophic importance of *Spartina alterniflora* production and decomposition to the marsh-estuarine ecosystem. – *Biol. Conserv.* 22: 35–58.
- McCann, M. J. et al. 2017. Key taxa in food web responses to stressors: the Deepwater Horizon oil spill. – *Front. Ecol. Environ.* 15: 142–149.
- McKee, K. L. 1995. Interspecific variation in growth, biomass partitioning and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. – *Am. J. Bot.* 82: 299–307.
- Melillo, J. M. et al. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. – *Ecology* 63: 621–626.
- Middleton, B. and McKee, K. 2001. Degradation of mangrove tissues and implications for peat formation in Belizean island forests. – *J. Ecol.* 89: 818–828.
- Moore, J. C. et al. 2004. Detritus, trophic dynamics and biodiversity. – *Ecol. Lett.* 7: 584–600.
- Morrisey, D. J. et al. 2010. The ecology and management of temperate mangroves. – *Oceanogr. Mar. Biol. Annu. Rev.* 48: 43–160.
- Nagelkerken, I. et al. 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. – *Aquat. Bot.* 89: 155–185.
- Netto, S. A. and Lana, P. C. 1999. The role of above- and below-ground components of *Spartina alterniflora* (Loisel) and detritus biomass in structuring macrobenthic associations of Paranaguá Bay (SE, Brazil). – *Hydrobiologia* 400: 167–177.
- NOAA. 2018. NOAA tides and currents. – Center for Operational Oceanographic Products and Services.
- Oksanen, J. et al. 2013. Package 'vegan'. Community ecology package, ver. 2. – <<https://cran.r-project.org/web/packages/vegan/index.html>>.
- Perry, C. L. and Mendelssohn, I. A. 2009. Ecosystem effects of expanding populations of *Avicennia germinans* in a Louisiana salt marsh. – *Wetlands* 29: 396–406.
- Post, E. and Pedersen, C. 2008. Opposing plant community responses to warming with and without herbivores. – *Proc. Natl Acad. Sci. USA* 105: 12353–12358.
- Prescott, C. E. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? – *Biogeochemistry* 101: 133–149.
- Proffitt, C. E. and Devlin, D. J. 2005. Grazing by the intertidal gastropod *Melampus coffeus* greatly increases mangrove leaf litter degradation rates. – *Mar. Ecol. Prog. Ser.* 296: 209–218.
- Reice, S. R. 1991. Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. – *J. N. Am. Benthol. Soc.* 10: 42–56.
- Reice, S. R. and Stiven, A. E. 1983. Environmental patchiness, litter decomposition and associated faunal patterns in a *Spartina alterniflora* marsh. – *Estuar. Coast. Shelf Sci.* 16: 559–571.
- Riley, M. E. et al. 2014. Range expansion of *Aratus pisonii* (mangrove tree crab) into novel vegetative habitats. – *Southeast. Nat.* 13: N43–N48.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. – *Oikos* 65: 514–527.
- Scheffel, W. A. et al. 2017. Effect of habitat complexity on predator-prey relationships: implications for black mangrove range expansion into northern Gulf of Mexico salt marshes. – *J. Shellfish Res.* 36: 181–188.
- Schoch, G. C. et al. 2006. Fifteen degrees of separation: latitudinal gradients of rocky intertidal biota along the California Current. – *Limnol. Oceanogr.* 51: 2564–2585.
- Simpson, L. T. et al. 2017. Carbon storages along a climate induced coastal wetland gradient. – *Wetlands* 37: 1023–1035.
- Smee, D. L. et al. 2017. Mangrove expansion into salt marshes alters associated faunal communities. – *Estuar. Coast. Shelf Sci.* 187: 306–313.
- Smith, R. S. et al. 2019. Data from: detrital traits affect substitutability of a range-expanding foundation species across latitude. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.g60vv21>>.
- Stein, A. et al. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. – *Ecol. Lett.* 17: 866–880.

- Taylor, B. R. et al. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. – *Ecology* 70: 97–104.
- Tews, J. et al. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. – *J. Biogeogr.* 31: 79–92.
- Twilley, R. W. et al. 1986. Litter production and turnover in basin mangrove forests in southwest Florida. – *Ecology* 67: 670–683.
- Valiela, I. et al. 1985. Decomposition in salt marsh ecosystems: the phases and major factors affecting disappearance of above-ground organic matter. – *J. Exp. Mar. Biol. Ecol.* 89: 29–54.
- Vince, S. et al. 1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. – *J. Exp. Mar. Biol. Ecol.* 23: 255–266.
- Walker, M. D. et al. 2006. Plant community responses to experimental warming across the tundra biome. – *Proc. Natl Acad. Sci. USA* 103: 1342–1346.
- Wang, J. et al. 2008. Exotic *Spartina alterniflora* provides compatible habitats for native estuarine crab *Sesarma dehaani* in the Yangtze River estuary. – *Ecol. Eng.* 34: 57–64.
- Warton, D. I. et al. 2012. Distance-based multivariate analyses confound location and dispersion effects. – *Methods Ecol. Evol.* 3: 89–101.
- Warton, D. I. et al. 2015. Model-based thinking for community ecology. – *Plant Ecol.* 216: 669–682.
- Whitcraft, C. R. et al. 2008. Utilization of invasive tamarisk by salt marsh consumers. – *Oecologia* 158: 259–272.
- White, D. A. et al. 1978. Productivity and decomposition of the dominant salt marsh plants in Louisiana. – *Ecology* 59: 751–759.
- White, D. S. and Howes, B. L. 1994. Nitrogen incorporation into decomposing litter of *Spartina alterniflora*. – *Limnol. Oceanogr.* 39: 133–140.
- Williams, A. A. et al. 2014. Record northernmost endemic mangroves on the United States Atlantic Coast with a note on latitudinal migration. – *Southeast. Nat.* 13: 56–63.
- Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. – *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.
- Wilson, J. O. et al. 1986. Decomposition in salt marsh ecosystems: phenolic dynamics during decay of litter of *Spartina alterniflora*. – *Mar. Ecol. Prog. Ser.* 29: 177–187.
- Yakovis, E. L. et al. 2008. Multiple foundation species shape benthic habitat islands. – *Oecologia* 155: 785–795.
- Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.

Supplementary material (available online as Appendix oik-06149 at www.oikosjournal.org/appendix/oik-06149). Appendix 1.