Received: 5 September 2023 | Accepted: 22 September 2023

DOI: 10.1002/ecs2.4743

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Coastal and Marine Ecology

Retreating coastal forest supports saltmarsh invertebrates

Emily M. Goetz | **David S. Johnson**

Biological Sciences Department, Virginia Institute of Marine Science, William & Mary, Gloucester Point, Virginia, USA

Correspondence
Emily M. Goetz
Email: emily.m.goetz@gmail.com

Present address
Emily M. Goetz, Department of Environmental Sciences, University of Virginia, Charlottesville, VA, USA.

Funding information
National Science Foundation,
Grant/Award Number: 1832221

Handling Editor: F. Joel Fodrie

Abstract

As sea-level rise converts coastal forest to salt marsh, marsh arthropods may migrate inland; however, the resulting changes in arthropod communities, including the stage of forest retreat that first supports saltmarsh species, remain unknown. Furthermore, the ghost forest that forms in the wake of rapid forest retreat offers an unknown quality of habitat to marsh arthropods. In a migrating marsh in Virginia, USA, ground-dwelling arthropod communities were assessed across the forest-to-marsh gradient, and functional use of ghost forest and high marsh habitats was evaluated to determine whether marsh arthropods utilized expanded marsh in the same way as existing marsh. Diet and body condition were compared for two marsh species found in both high marsh and ghost forest (the detritivore amphipod, *Orchestia grillus*, and the hunting spider, *Pardosa littoralis*). Community composition differed among zones along the gradient, driven largely by retreating forest taxa (e.g., Collembola), marsh taxa migrating into the forest (e.g., *O. grillus*), and unique taxa (e.g., Hydrophilinae beetles) at the ecotone. The low forest was the most inland zone to accommodate the saltmarsh species *O. grillus*, suggesting that inland migration of certain saltmarsh arthropods may co-occur with early saltmarsh plant migration and precede complete tree canopy die-off. Functionally, *O. grillus* occupied a larger trophic niche in the ghost forest than the high marsh, likely by consuming both marsh and terrestrial material. Despite this, both observed marsh species primarily consumed from the marsh grass food web in both habitats, and no lasting differences in body condition were observed. For the species and functional traits assessed, the ghost forest and high marsh did not show major differences at this site. Forest retreat and marsh migration may thus provide an important opportunity for generalist saltmarsh arthropods to maintain their habitat extent in the face of marsh loss due to sea-level rise.

KEYWORDS
functional equivalency, ghost forest, marsh migration, marsh-forest ecotone, saltmarsh arthropod, stable isotope analysis

---

INTRODUCTION

Sea-level rise threatens tidal marshes worldwide through increased erosion and drowning, but marshes may maintain their areal extent by migrating inland, if the physical and anthropogenic properties of the upland systems allow expansion (Kirwan et al., 2016; Schuerch et al., 2018). Horizontal marsh migration may be paramount to saltmarsh fauna survival in the future by allowing saltmarsh habitat, and thus both flora and fauna, to shift into undeveloped coastal forest. Although forest dieback and the inland movement of plants has been well documented by recent work (Gedan et al., 2020; Smith, 2013; Walters et al., 2022), little is known about how fauna, especially invertebrates, change as forest retreats and marsh migrates inland.

The temporal process of marsh migration into forests is represented spatially by the gradient of habitat zones that form between inland forest and salt marsh as salinity and inundation stress the forest (Fagherazzi et al., 2019; Kirwan et al., 2007), including an ecotone at the transition between forest and marsh that possesses characteristics of both ecosystems (Smith & Goetz, 2021). Ecotones may be an effective means of tracking environmental changes because they are discrete (Wasson et al., 2013) and may contain unique species (Lloyd et al., 2000; Odum, 1953). With accelerating sea-level rise, greater expanses of coastal forest are affected by marsh migration, and ghost forests, or areas of newly formed marsh where standing dead trees remain, form on the trailing edge of the ecotone (Kirwan & Gedan, 2019).

Changes in vegetation (LaSalle & de la Cruz, 1985; Torma et al., 2017), salinity (Pan et al., 2018; Pétillon et al., 2008), and inundation (Irmler et al., 2002; Widenfalk et al., 2015) that occur as forest converts to marsh likely affect arthropod community composition, resulting in a shift from forest-associated to marsh-associated arthropod species, with potential overlap at the ecotone. Changes in species composition may thus correlate with specific stages of forest retreat and marsh migration. Furthermore, zones of migrated marsh or retreating forest that support marsh arthropods may compensate for losses of salt marsh habitat caused by sea-level rise.

Environmental changes along the forest-to-marsh gradient may also affect resource availability and use. In the ghost forest, standing dead trees and remnant terrestrial shrubs likely contribute to detritus and may inhibit benthic algae growth through shading, both of which support important marsh food webs. Previous studies of constructed marshes—analogues to ghost forest, as both are newly formed salt marsh—indicate that functional equivalency of constructed and natural marshes may take longer to achieve than similar community composition (La Peyre et al., 2007; Pétillon et al., 2014). Thus, even if saltmarsh species are present in the ghost-forest ecotone, they may not use the habitat in the same way, and their fitness may be affected (Agnew et al., 2003). Assessments of community composition and functional habitat use together may therefore offer a more complete comparison of existing and migrating marsh than community composition alone.

The ability of saltmarsh arthropod communities to migrate inland is important not only for the preservation of habitat area for marsh arthropods but also for higher trophic levels, since arthropods serve as both a prey resource and a trophic link (Parker et al., 2008; Potapov et al., 2022), and the marsh as an entire ecosystem, due to arthropod contributions toward decomposition, nutrient cycling (Lopez et al., 1977; McCary & Schmitz, 2021; Zimmer et al., 2004), and herbivore population control (Denno et al., 2003; Frank et al., 2010). Thus, understanding the effects of sea-level rise, forest retreat, and marsh migration on arthropod distribution and function is essential to understanding the function of the ecosystems that result from marsh migration. Past models of horizontal salt marsh migration have not distinguished salt marsh from ghost forest when assessing upland to marshland conversion (Kirwan et al., 2016; Krause et al., 2023); however, the actual distribution of saltmarsh fauna and their use of salt marsh and ghost-forest ecotone as habitat remain unknown.

Inland marsh migration of arthropods may be especially important in areas with high rates of relative sea-level rise and low slope, where there is high potential for both marsh loss and inland expansion, such as the mid-Atlantic region of the eastern United States (Sallenger et al., 2012), where marsh migration into undeveloped uplands may equal or even exceed marsh loss (Kirwan et al., 2016; Schieder et al., 2018). Here, we use a spatial gradient along a rapidly migrating forest-to-marsh transition (Kirwan & Gedan, 2019; Smith & Kirwan, 2021), including ghost forest at the ecotone, to predict arthropod community changes caused by inland marsh migration. This work explores (1) how and when arthropod community composition changes as forest converts to marsh, with the goal of identifying the first retreating forest zone to accommodate migrating saltmarsh arthropods and leading arthropod migrant species; and (2) the functional use of newly formed ghost forest by saltmarsh arthropods as compared to existing high marsh. We hypothesized that changes in arthropod community composition occurring spatially along the forest-to-marsh gradient would represent expected compositional changes in arthropod communities as forest converts to marsh over time, with the inland extent of saltmarsh species distribution indicating the zones of retreating forest and migrating marsh serving as saltmarsh habitat. We also hypothesized that the functional characteristics of marsh arthropods would differ between ghost forest and high marsh due to differences in habitat and food availability that may affect both consumption and growth in arthropods.

METHODS

Site description

Sampling was conducted on the Eastern Shore of Virginia at Brownsville Preserve, part of the Virginia Coast Reserve long-term ecological research site and adjacent to Upper Phillips Creek (37.463, −75.835). Forest-to-marsh gradients throughout this region are characterized by low slope and high rates of relative sea-level rise, both of which contribute to this site's expanse of ghost forest at the ecotone and the predicted transition from healthy forest to high marsh within 40 years at the highest elevation of our sites (Smith & Kirwan, 2021).

Field collection and processing

Community composition

Arthropods were sampled in several zones along a gradient from healthy forest to high marsh, with the assumption that the forest will transition through multiple stages—represented by different zones along the gradient—before its complete conversion to marsh.

Twenty plots were established in the following five zones along the forest-to-marsh gradient ($n = 4$ plots/zone) based on vegetation communities and tree seedling recruitment: (1) high forest characterized by both coniferous and deciduous tree species, with ongoing seedling recruitment of all canopy species; (2) mid forest containing primarily coniferous trees and shrubs, with reduced seedling recruitment; (3) low forest, where the canopy shows partial mortality due to salt stress and minimal tree recruitment, and the understory contains primarily invasive (*Phragmites australis*) but also native shrub (*Morella cerifera*) and herbaceous (*Hydrocotyle verticillata*, *Panicum virgatum*, and *Distichlis spicata*) plant species (Gedan et al., 2022); (4) ecotone, where 50%–75% of mature trees are dead, there is no seedling recruitment, and the understory is dominated by *S. patens*, *D. spicata*, and *P. australis*; and (5) high marsh that does not contain trees and is dominated by *S. patens* and *D. spicata* (Figure 1).

In each 20 × 20 m plot, arthropods were sampled during a neap tide in September 2019 using both pitfall trapping and leaf litter extraction. These collection methods target different ground-dwelling arthropod communities: pitfall sampling collects mobile, surface-dwelling organisms, whereas leaf litter sampling targets soil- and litter-dwelling species, regardless of mobility. Within each plot, three pitfall traps (11-cm diameter) were installed approximately 1 m apart from each other. Marsh flooding limited pitfall trap deployment to three of the four high marsh plots. Each trap was partially filled with 25% propylene glycol preservative. After 24 h, all material in each trap was sieved through 63-μm mesh and stored in ethanol. Leaf litter was collected from two haphazardly placed 0.0625-m^2 quadrats collected approximately 1 m apart from each other and from the pitfall traps, and the two quadrats were combined into a single composite litter sample for each plot. In ecotone and high marsh zones where litter is covered by a dense layer of grass that would prevent complete detritus collection, living grass was cut and included along with detrital litter in each sample. Samples were sieved on 1.25-cm mesh in the field, and live arthropods were extracted from the finer litter over two weeks using Berlese funnels with 6-mm mesh opening size. Pitfall sampling in all five zones was repeated in September 2020 only for a leading arthropod migrant species (*Orchestia grillus*) identified from 2019 sampling. As in 2019, three pitfall traps were placed in each plot in 2020 ($n = 5$ plots/zone in high marsh and ecotone and $n = 4$ plots/zone in low forest, mid forest, and high forest).

All collected arthropods were identified to the lowest taxonomic level feasible for their order (mostly family or below; Appendix S1: Tables S1 and S2). Acari (mites and ticks) were not identified beyond superorder because of the difficulty of identifying juveniles, which comprised a large proportion of the specimens. Non-arthropods (e.g., mollusks), microcrustaceans (e.g., copepods), ant queens, insect larva, and spiderlings were excluded from analyses because they were either rare or could not be identified to the same taxonomic resolution as adults.

Functional use

To assess how marsh arthropods used migrated marsh habitat, functional characteristics (diet and body condition) of two saltmarsh species were compared between the high marsh, where salt marsh is over 40 years old, and the ghost forest, where salt marsh has formed within the last 40 years and remnants of the former forest remain in the form of standing dead trees as well as live *Juniperus virginiana* (hereafter "cedar") trees. In both

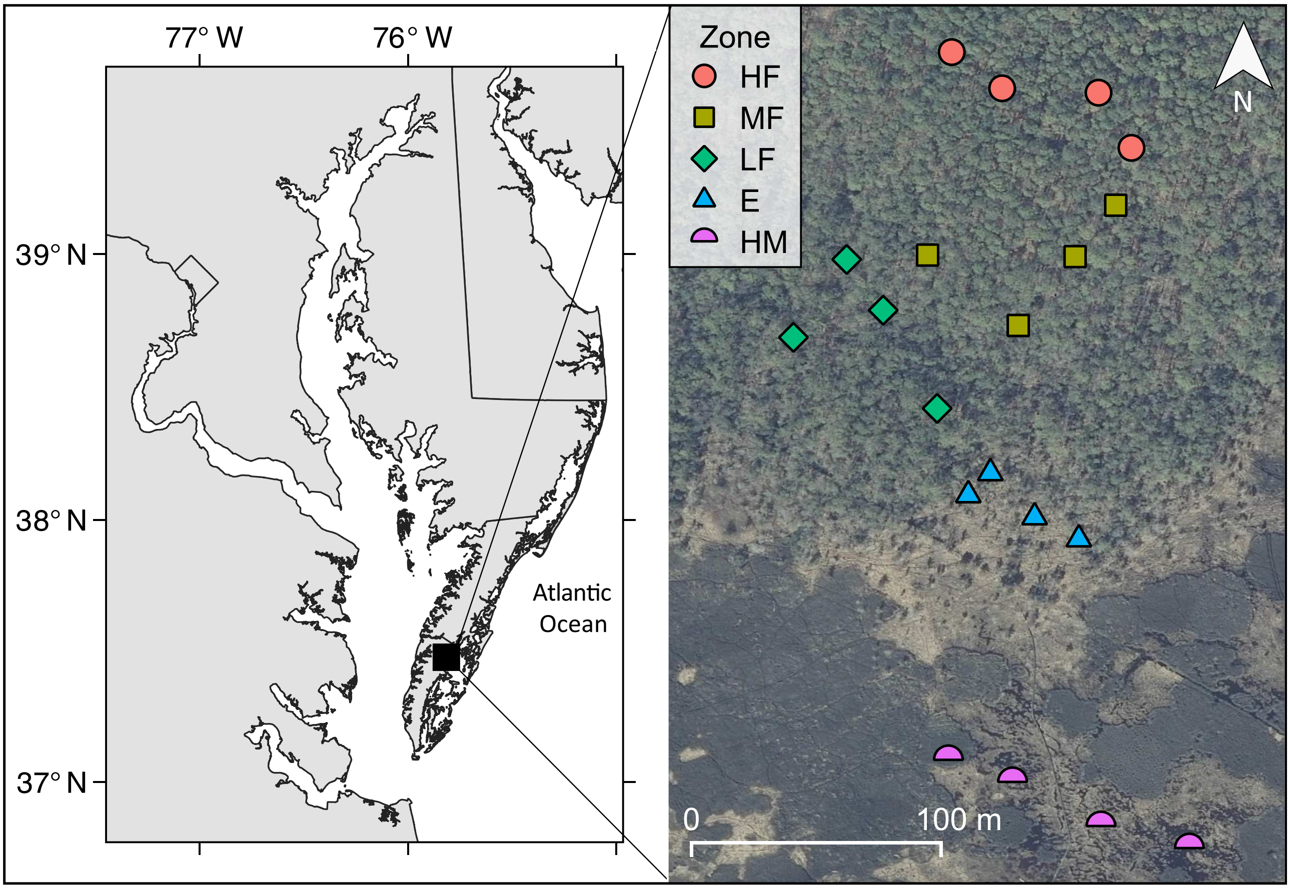

FIGURE 1 Study site (right) positioned relative to the Chesapeake Bay (left) showing plots along the marsh-forest gradient. Each point represents a plot, with shape and color corresponding to zone classification. U.S. States and Territories basemap (left) from the National Weather Service. High-resolution orthoimagery (right) courtesy of the U.S. Geological Survey via EarthExplorer. E, ecotone; HF, high forest; HM, high marsh; LF, low forest; MF, mid forest.

zones, the ground cover is dominated by the marsh grasses *S. patens* and *D. spicata*; however, the high marsh contains patches of low elevation, where ponding occurs and facilitates growth of *Spartina alterniflora* (a low marsh species) and algae, and the ghost forest contains elevated areas surrounding the trunks of both dead and live trees, where less salt-tolerant species grow. Within each of these two zones, five plots were established, spaced across an expanse of relatively homogenous marsh or ghost forest and at least 14 m apart. The ghost forest was here limited to the portion of the marsh-forest ecotone where dead and dying trees stand over high marsh grasses. Plots were deliberately placed away from areas dominated by the invasive reed *P. australis* as well as any berms or ponds found within the ghost forest or high marsh, respectively.

Diet and body condition were assessed for marsh arthropod species present in both high marsh and ghost forest (the saltmarsh amphipod *O. grillus* and the marsh hunting spider *Pardosa littoralis*). These species were selected because they were abundant in both high marsh and ghost forest and because they represent two trophic guilds with high importance in the marsh (detritivores and predators). *O. grillus* were collected using litter bags (mesh bags filled with local detritus, covered with grass, and left on the marsh surface for at least one week) and colonization of sediment cores (marsh sediment allowed to sit on the marsh surface for two weeks). *P. littoralis* were collected by netting the surface of standing pools of water, suction sampling using a modified leaf vacuum, and hand collecting using a high-sided quadrat (18.9-L [5-gallon] bucket with bottom removed). These methods were repeated for each species until an acceptable number of organisms was collected in each zone.

Diet was compared between zones using stable isotope ratios of carbon, nitrogen, and sulfur. Together, isotopic ratios can provide insight into basal producer source (δ^{13}C and δ^{34}S) and trophic position (δ^{15}N) (McCutchan et al., 2003). *O. grillus* and *P. littoralis* used for isotopic analysis were collected during September and October 2020, immediately placed on dry ice in the field to prevent cannibalism or further consumption, and kept frozen until processing. Individuals were identified to species under a dissecting microscope, thoroughly rinsed with deionized water, and dried at 60°C for 72 h. Where necessary to meet isotope analysis mass requirements (half of *O. grillus* samples and all of *P. littoralis* samples), multiple individuals were combined to create a composite sample. Samples were ground with a motorized pellet pestle and packaged in tin capsules for analysis (*O. grillus*: $n = 8$ for ghost forest and $n = 10$ for high marsh; *P. littoralis*: $n = 10$/zone).

The dominant producer species, including vascular plants and algae, and samples of detritus were collected from each zone in which they were present. Multiple stems of each vascular species were collected to form a composite sample from each plot ($n = 5$ composite samples/zone). Floating algal mats were collected from the surface of standing pools of water in the high marsh. Producer samples were transported from the field on ice and kept frozen until processing. Thick-stemmed plants were cut open and examined under a dissecting microscope to remove stem-boring arthropods, and all plants were cleaned thoroughly with deionized water. Woody plant stems were discarded. Algae samples were cleaned of debris under a dissecting microscope and repeatedly rinsed in deionized water. Primary producers were dried at 60°C for at least 5 days, then ground using either mortar and pestle (algae) or Wiley mill with 40 mesh size (plants), homogenized, and packaged in tin capsules for analysis.

All samples were analyzed at the Washington State University Stable Isotope Core Laboratory using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen). Isotopic values were reported as per mil ratios of heavy to light isotopes relative to standards of Vienna Pee Dee belemnite (δ^{13}C), atmospheric N_2 (δ^{15}N), and Vienna Cañon Diablo Troilite (δ^{34}S).

Body condition of *O. grillus* and *P. littoralis* was likewise determined for individuals of each species in each zone. Along with individuals collected as described above in fall 2020 (*O. grillus*: high marsh [HM] $n = 124$, ghost-forest ecotone [E] $n = 16$; *P. littoralis*: HM $n = 95$, E $n = 60$), additional individuals of *P. littoralis* were collected in May and June 2021 (HM $n = 50$, E $n = 31$) to target mature individuals of the same generation as juveniles collected in fall 2020. Organisms were immobilized in the field with dry ice or methyl acetate. Individuals were rinsed with deionized water, photographed through a dissecting microscope, dried at 60°C for 72 h, and weighed. Length of organisms (*O. grillus*: along dorsal edge from base of antennae 1 to tip of uropod 3; *P. littoralis*: from anterior edge of carapace to posterior edge of abdomen, excluding spinnerets) was measured in ImageJ software from photographs, and body condition was calculated as dry mass divided by length.

In each plot in high marsh and ghost forest, both vegetative (species composition, live and dead tree counts, ground cover biomass, and stem density) and sediment (bulk density, organic content, benthic chlorophyll, and conductivity) characteristics were quantified for three haphazardly placed 0.0625-m^2 quadrats ($n = 3$/plot = 15/zone), spaced approximately 2 m apart. Percent cover of vegetation species and bare or flooded ground was estimated in a 1-m radius, and the number of standing live and dead trees were counted within a 5-m radius. Live stem density and both live and detrital biomass were determined within each 0.0625-m^2 quadrat. Plant material was rinsed, dried at 60°C for 72 h, and weighed to determine biomass. Terrestrial contribution to detritus (e.g., cedar needles, pinecones) was weighed to determine percent contribution to total detrital biomass. Sediment cores (6.6-cm width × 5-cm depth) were dried at 60°C for at least 96 h and weighed to determine bulk density. Percent organic content of sediment cores was measured as percent of dried sample mass lost at 550°C over 6 h (loss on ignition). Benthic chlorophyll *a* was measured from the top 3 mm of sediment at each plot as in Failon et al. (2020). Conductivity was measured with a handheld meter (FieldScout EC-450).

Data analysis

All data were analyzed in R (version 4.1.2). All tests of significance were based on an alpha value of 0.05.

Community composition

Pitfall traps within each plot were combined for analyses to decrease dependence of samples. Arthropod communities were analyzed separately by trap type (i.e., pitfall trap and leaf litter collection). For both pitfall and leaf litter, community composition was analyzed visually with nonmetric multidimensional scaling (NMDS) plotting in package *vegan* (Oksanen et al., 2020). Data were automatically transformed with square root and double Wisconsin standardizations as necessary to adjust for large differences in species abundances. Community composition was further compared among zones with permutational multivariate analysis of variance (PERMANOVA) based on a Bray–Curtis matrix of dissimilarity after checking for homogeneity of variances with PERMDISP, using adonis and betadisper functions, respectively, in *vegan*. Similarity percentage (SIMPER) analysis was conducted to determine the driving taxa of observed differences (function simper in *vegan*), and taxa that consistently showed over 5% contribution to differences among zones were identified. Because SIMPER analysis can be substantially affected by taxa abundance, indicator species analysis using function multipatt in package *indicspecies* (De Cáceres & Legendre, 2009) was used to verify the most important species and to identify the taxonomic association with zone. Because of their high abundance in all zones and low taxonomic resolution, mites were not reported as a driving taxon when included in SIMPER results.

For taxa identified as drivers of differences in community composition, abundance was analyzed across zones. Where assumptions of ANOVA were met, one-way ANOVA and Tukey's honestly significant difference (HSD) post hoc test were used. Where assumptions of ANOVA were not met by raw or transformed (square root, $\log(n + 1)$, or Box Cox) data, Kruskal–Wallis and Dunn post hoc tests with Holm's method correction (function dunnTest in package *FSA*; Ogle et al., 2021) were used. For *O. grillus*, which was collected in both 2019 and 2020, sampling years were analyzed separately.

Functional use

Stable isotope values were interpreted with Bayesian mixing models using package *MixSIAR* (Stock et al., 2018; Stock & Semmens, 2016) to determine relative source contributions to consumer diets. Models were run separately for each species, with zone as a fixed effect. *D. spicata*, *S. patens*, and detritus were pooled by zone a priori because of their similar isotopic and ecological profiles. Other sources were kept separate during model runs. In addition to sources collected on site, δ^{34}S values for *Spartina* spp. and litter from the literature (Wainright et al., 2000) were included in the mixing model to account for highly enriched δ^{34}S values in *O. grillus*, possibly due to seasonal variation in δ^{34}S values. δ^{34}S values from Wainright et al. (2000) were paired with δ^{13}C and δ^{15}N values collected in situ (hereafter "Wainright *Spartina*"). All sources were pooled a posteriori into "marsh" (detritus, *D. spicata*, *S. patens*, *S. alterniflora*, algae, and Wainright *Spartina*) and "terrestrial" (cedar and *P. australis*) contributions based on their affiliation with marsh or forest habitat at this site. Models were run using either "very long" or "extreme" model parameters, the minimum necessary for model convergence based on Gelman and Geweke diagnostics (Gelman diagnostics less than 1.05 for all variables and less than 10% of Geweke diagnostics outside of ±1.96). Three chains with length of 1,000,000 (*P. littoralis*) or 3,000,000 (*O. grillus*) were run with burn-in of 500,000 (*P. littoralis*) or 1,500,000 (*O. grillus*). Uninformative priors were used and were adjusted a posteriori when unequal numbers of sources were pooled into marsh and terrestrial groups to give equal weighting to each group. Trophic enrichment factors (mean ± SD), which correct for preferential assimilation of lighter isotopes across trophic levels, were included in the model as 0.5 ± 0.13 for δ^{13}C (McCutchan et al., 2003; Pascal & Fleeger, 2013), 2.3 ± 0.28 for δ^{15}N (Graf et al., 2020; McCutchan et al., 2003), and 0.5 ± 0.5 for δ^{34}S (James et al., 2021; McCutchan et al., 2003; Nelson et al., 2019; Rezek et al., 2020). Because spiders were assumed to be at least two trophic levels above primary producers (given their diet of primary consumers as well as intra-guild predation and cannibalism; Langellotto & Denno, 2006), all trophic enrichment factors and SD were multiplied by 2.5 for the *P. littoralis* model.

Niche width was estimated from δ^{13}C and δ^{15}N distribution for each species in each zone using package *SIBER* (Jackson et al., 2011). Bayesian 95% credibility intervals of standard ellipse area (SEAb) were compared to determine differences between zones. Carbon-to-nitrogen (C/N) ratios were compared between zones for each species with Welch's independent samples *t* tests.

Individuals of *P. littoralis* collected in the fall (juveniles) were significantly smaller than individuals collected in the spring (adults); the collection periods were thus analyzed separately. All *O. grillus* were collected in fall 2020 and were analyzed together. Body condition was compared between zones with Welch's independent samples *t* tests or, when data could not be transformed to meet test assumptions, with Wilcoxon rank-sum (WRS) tests.

Habitat characteristics that may contribute to differences in functional use of habitat were compared between zones with *t* or WRS tests. For live and dead tree counts, the three counts from each plot were averaged to a single value per plot for each variable ($n = 5$/zone) before analysis to decrease dependence of samples in case of count radius overlap. *p* values from multiple habitat characteristic comparisons between zones were adjusted using the false discovery rate method.

RESULTS

Community composition

Pitfall traps: Arthropod community

NMDS plotting of arthropods collected by pitfall trap showed that community composition differed by zone, with high marsh and ecotone zones showing the greatest distinctness and low forest plots somewhat distinct from mid and high forest zones (Figure 2a). PERMANOVA showed significant differences among zones ($F_{4,14} = 3.436$,

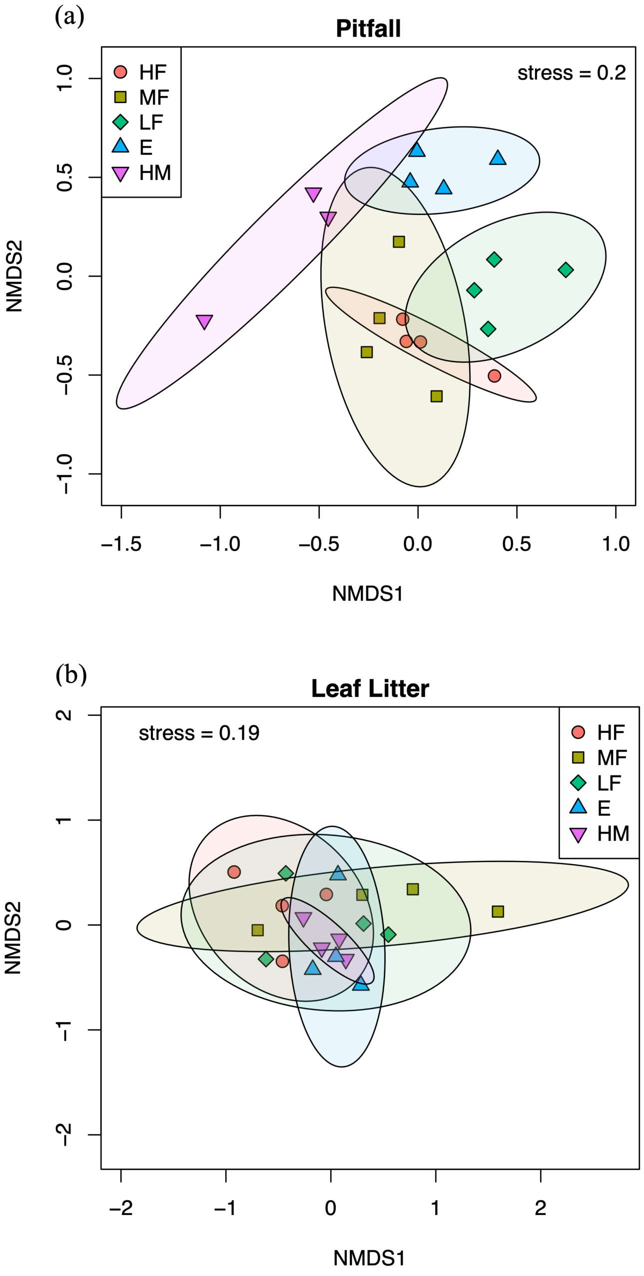

FIGURE 2 Nonmetric multidimensional scaling (NMDS) plots of communities from (a) pitfall and (b) leaf litter collections. Ellipses are 95% confidence ellipses. E, ecotone; HF, high forest; HM, high marsh; LF, low forest; MF, mid forest.

$R^2 = 0.495$, $p = 0.0001$), and PERMDIST showed insignificant differences in dispersion ($F_{4,14} = 0.1981$, $p = 0.94$), suggesting that PERMANOVA results represent differences in community composition. SIMPER analysis showed that the primary drivers of differences in community composition were several springtail (class Collembola) families, the saltmarsh amphipod (*O. grillus*), and two genera of ant (*Monomorium* and *Aphaenogaster*). Indicator species analysis specified the associations of several springtail families with the high forest, *O. grillus* with ecotone and high marsh zones, and *Monomorium* with the ecotone and identified additional significant associations (Table 1).

O. grillus abundance was significantly different among zones in both 2019 and 2020 (Kruskal–Wallis test [KW], 2019: $H_4 = 12.386$, $p = 0.015$ and 2020: $H_4 = 14.110$, $p = 0.007$; Figure 3), with abundances increasing toward the ecotone and marsh. Although post hoc testing was insignificant in 2019, *O. grillus* was found in all but one high marsh and ecotone plot, compared to no occurrences in the high or mid forest. In 2020, abundances in the ecotone were significantly higher than both high ($p = 0.034$) and mid ($p = 0.030$) forest. In both years, *O. grillus* was collected in low abundances in the low forest. Total Collembola abundance was higher in all three forest zones than in the ecotone or marsh (ANOVA: $F_{4,14} = 16.08$, $p = 0.00004$; Tukey's HSD: $p < 0.05$ for all comparisons; Figure 3). *Monomorium* was significantly different among zones (KW: $H_4 = 15.174$, $p = 0.004$), with post hoc testing showing significantly higher abundances in the ecotone than in the high marsh, low forest, or mid forest ($p < 0.05$ for all). *Aphaenogaster* abundance was not significantly different among zones (ANOVA: $F_{4,14} = 2.537$, $p = 0.087$).

Leaf litter collection: Arthropod community

NMDS plotting of leaf litter arthropod communities showed greater overlap in community composition among zones than pitfall samples (Figure 2b), although PERMANOVA showed a significant difference among zones ($F_{4,15} = 1.933$, $R^2 = 0.340$, $p = 0.007$). PERMDIST showed insignificant differences in dispersion ($F_{4,15} = 0.931$, $p = 0.479$), but dispersion of the mid forest differed visually from other zones, and PERMANOVA results should therefore be interpreted cautiously. SIMPER analysis showed that two subfamilies of beetle (Pselaphinae and Hydrophilinae) were the primary drivers of community composition differences, and indicator species analysis identified that Hydrophilinae was associated with the ecotone (Table 1).

Pselaphinae was more abundant in the marsh than high or mid forest (ANOVA: $F_{4,15} = 4.787$, $p = 0.011$). Hydrophilinae was most abundant in the ecotone (KW: $H_4 = 16.384$, $p = 0.003$; Figure 3), higher than any forest zone ($p < 0.01$ for each comparison) and with a trend toward being higher than in the marsh ($p = 0.053$).

Functional use

Diet

Isotopic signatures showed intra-specific differences between zones, with primary producers and consumers

TABLE 1 Zone association of indicator taxa based on pitfall trap and leaf litter sampling.

Sample type	Common name	Taxon	Associated zone	*p*
Pitfall	Springtail	Isotomidae	High forest	0.003
	Springtail	Paronellidae	High forest	0.018
	Cricket	*Eunemobius*	Low forest	0.018
	Ant	*Solenopsis*	Ecotone	0.003
	True Bug	Cicadellidae	Ecotone	0.014
	Ant	*Monomorium*	Ecotone	0.005
	Amphipod	*Orchestia grillus*	Ecotone, high marsh	0.032
Leaf litter	Beetle	Hydrophilinae	Ecotone	0.003

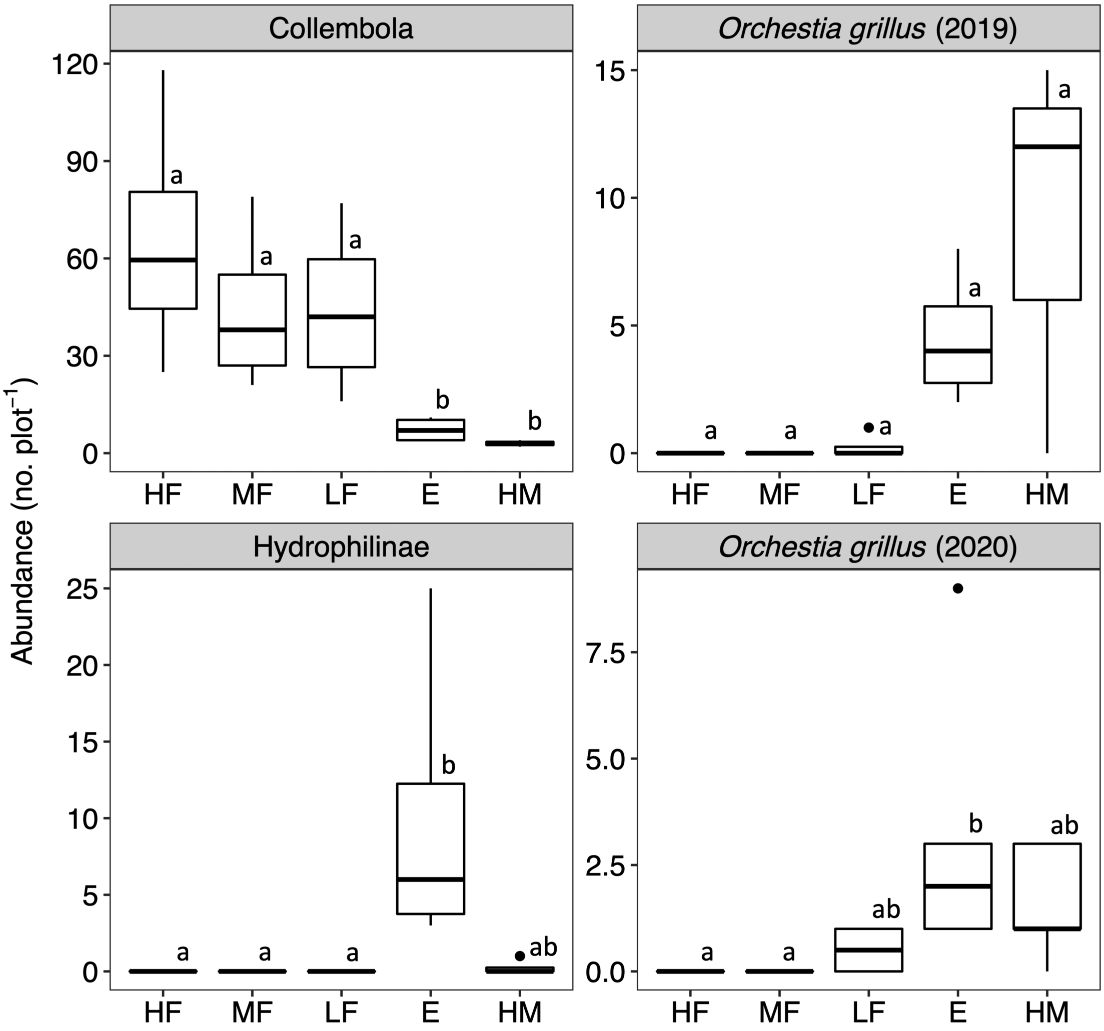

FIGURE 3 Abundance per plot of key taxa by zone for Collembola (springtails) from pitfall traps, Hydrophilinae (subfamily of Hydrophilidae beetle) from leaf litter collection, and *Orchestia grillus* (saltmarsh amphipod) from 2019 and 2020 pitfall traps. E, ecotone; HF, high forest; HM, high marsh; LF, low forest; MF, mid forest.

in the ghost forest enriched in both ^{15}N and ^{34}S relative to high marsh conspecifics (Figure 4; Appendix S1: Table S3).

Mixing models attributed the majority of *O. grillus* diet (95% credible interval) in both zones to marsh grasses and detritus with δ^{34}S values from the literature (Wainright *Spartina*) (ghost-forest ecotone [E]: 55.9%–86.7%; high marsh [HM]: 51.0%–70.7%; Table 2). In the ghost forest, cedar also contributed to diet (1.8%–29.4%), with other sources estimated to contribute only minimally. In the

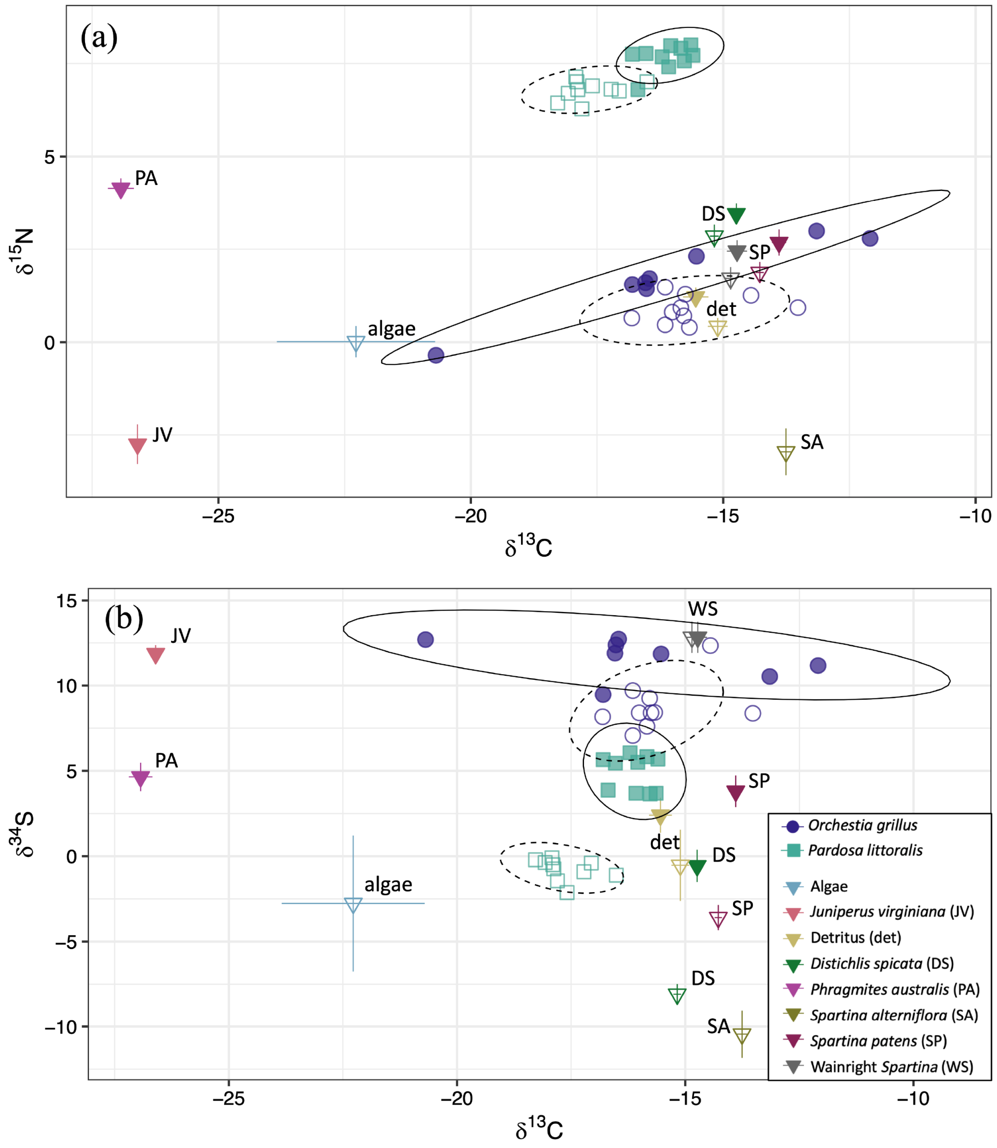

FIGURE 4 Isotope biplots for δ^{13}C, δ^{15}N, and δ^{34}S (‰). Solid symbols are ghost-forest ecotone (E), and open symbols are high marsh (HM). Inverted triangles are primary producers, squares are *Pardosa littoralis*, and circles are *Orchestia grillus*. Ellipses encompass 95% of data points (solid line, E; dashed line, HM).

high marsh, a small portion of the diet was attributed to both *Spartina alterniflora* (0.7%–22.2%) and cedar (4.0%–19.1%). When sources were combined into terrestrial and marsh groups, there was minimal difference in the probable percentage of terrestrial contribution between ghost forest (3.3%–30.2%) and high marsh (6.4%–20.1%).

P. littoralis also consumed primarily from the marsh grass and detritus food webs (E: 22.7%–77.8%; HM: 22.1%–59.3%), but best matched δ^{34}S values observed in situ, rather than the more enriched Wainright *Spartina* values. In the ghost forest, *P. australis* contributed to a small percentage of the diet (1.8%–19.8%). As with *O. grillus*, there was more overlap between potential sources in the high marsh, with proportions of the diet attributed to *P. australis* (5.0%–30.6%), *S. alterniflora* (1.0%–30.2%), and algae (1.0%–31.5%). Notably, algae and *P. australis* had similar isotopic signatures, specifically δ^{13}C (Appendix S1: Table S3), meaning diet contribution attributed to *P. australis* may have instead derived from algae. Because algae was abundant and *P. australis* largely absent from the high marsh, and algae largely absent from the ghost forest, the algae food web likely contributed to a greater proportion of the diet in the high marsh than ghost forest. A small percentage of diet in both zones was attributed to terrestrial sources, higher in the high marsh (10.7%–33.5%) than the ghost forest (5.7%–22.4%), but with much overlap between CIs.

TABLE 2 Predicted percent contributions to consumer diet in high marsh (HM) and ghost-forest ecotone (E), by individual source as well as pooled marsh and terrestrial sources.

	Orchestia grillus		*Pardosa littoralis*	
Source	**HM**	**E**	**HM**	**E**
SP, DS, det	11.7 [2.6–26.7]	4.5 [0.5–17.7]	40.6 [22.1–59.3]	53.7 [22.7–77.8]
WS	60.9 [51.0–70.7]	70.6 [55.9–86.7]	7.3 [0.9–17.4]	17.5 [0.3–39.0]
SA	10.7 [0.7–22.2]	4.5 [0.3–12.6]	14.2 [1.0–30.2]	4.7 [0.3–17.0]
Algae	1.8 [0.1–9.1]	0.9 [0–9.4]	12.0 [1.0–31.5]	5.4 [0.3–22.5]
JV	11.7 [4.0–19.1]	15.4 [1.8–29.4]	5.2 [0.3–14.6]	4.1 [0.1–15.0]
PA	1.1 [0–5.9]	0.5 [0–5.9]	18.5 [5.0–30.6]	10.7 [1.8–19.8]
Marsh	86.8 [79.9–93.6]	83.5 [69.8–96.7]	75.2 [66.5–89.3]	83.4 [77.6–94.3]
Terrestrial	13.2 [6.4–20.1]	16.5 [3.3–30.2]	24.8 [10.7–33.5]	16.6 [5.7–22.4]

Note: Values are median [95% credible interval] percent contribution.

Abbreviations: SP, DS, det, averaged *Spartina patens*, *Distichlis spicata*, and detritus; WS, Wainright *Spartina* (average of *Spartina patens*, *Spartina alterniflora*, and detritus δ^{34}S from Wainright et al., 2000, and average of *Distichlis spicata*, *Spartina patens*, and detritus δ^{13}C and δ^{15}N from this study); JV, *Juniperus virginiana* (cedar); PA, *Phragmites australis*; SA, *Spartina alterniflora*.

Niche width (posterior distribution mode [95% credible interval]) calculated from δ^{13}C and δ^{15}N was larger for *O. grillus* in the ghost forest (4.1 [1.93–8.97]) compared to the high marsh (1.0 [0.49–1.92]), largely due to an expanded range of δ^{13}C values. *P. littoralis* had the same niche width in the ghost forest (0.4 [0.21–0.81]) and high marsh (0.4 [0.20–0.79]).

C/N was higher in the high marsh for both *O. grillus* (t test: $t_{14} = -2.681$, $p = 0.018$) and *P. littoralis* (t test: $t_{16} = -4.930$, $p = 0.0002$) (Appendix S1: Figure S1).

Body condition

Body condition of *O. grillus* did not differ between zones (WRS: $W = 1236$, $p = 0.111$, $n = 140$; Figure 5). Body condition of *P. littoralis* was significantly higher (more mass per length) in the high marsh than the ghost forest for juveniles collected in the fall (WRS: $W = 2067$, $p = 0.004$, $n = 155$), but there was no difference between zones for adults collected in the spring (t test: $t_{75} = -0.682$, $p = 0.497$).

Habitat characteristics

Ground cover vegetation was primarily *S. patens* and *D. spicata* adjacent to all plots in both zones, with *S. alterniflora* present adjacent to most high marsh plots and terrestrial grasses and shrubs (*P. virgatum*, *Schoenoplectus americanus*, *Pluchea purpurascens*, *Cyperus* sp., *Setaria parviflora*, and *Iva frutescens*) adjacent to several ghost forest plots. While grass species composition varied by zone, ground cover species richness was not significantly different (WRS: $W = 151.5$, $p = 0.075$, $n = 30$; Appendix S1: Figure S2). A higher percentage of the surrounding ground was either bare or flooded in the high marsh than ghost forest (WRS: $W = 67.5$, $p = 0.014$, $n = 30$), and there were significantly more dead (WRS: $W = 25$, $p = 0.014$, $n = 10$) and live (WRS: $W = 25$, $p = 0.014$, $n = 10$) trees in the ghost forest. Within each quadrat, there was higher live stem density in the high marsh (t test: $t_{25} = 3.00$, $p = 0.014$), but no difference in either live (t test: $t_{27} = -0.848$, $p = 0.441$) or detrital (t test: $t_{28} = -0.501$, $p = 0.621$) biomass between zones. Detritus in each zone was largely reflective of the species composition, with more terrestrial contribution to detritus (e.g., cedar and pine needles, pinecones, and bark) in the ghost forest than high marsh

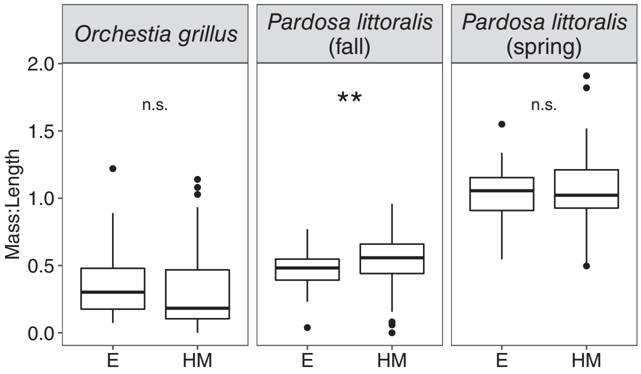

FIGURE 5 Body condition (dry mass divided by length) of *Orchestia grillus* and *Pardosa littoralis* collected in fall 2020 and spring 2021. Asterisks denote significance (n.s., $p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). E, ghost-forest ecotone; HM, high marsh.

(WRS: $W = 195$, $p = 0.000006$, $n = 28$). Organic content did not vary between zones (t test: $t_{28} = 1.838$, $p = 0.092$), but bulk density was higher in the ghost forest than high marsh (t test: $t_{27} = 6.557$, $p = 0.000006$). There was no significant difference in benthic chlorophyll a between zones (t test: $t_{28} = -2.138$, $p = 0.062$). Conductivity was significantly higher in the high marsh than ghost forest (t test: $t_{25} = -6.299$, $p = 0.000006$).

DISCUSSION

The low forest, where stressed forest canopy overlaps with both terrestrial and saltmarsh groundcover, was the first zone observed to exhibit changes in arthropod community composition and to accommodate an endemic saltmarsh species (*O. grillus*). This zone, which already experiences frequent inundation and partial sediment salinization, is thus at the vanguard of marsh migration for both saltmarsh plants and arthropods. A later stage of marsh development, the ghost-forest ecotone, supported most of the high marsh arthropods observed at this site.

Along with the inland migration of generalist marsh taxa (e.g., *O. grillus*) into retreating forest, two other key patterns of compositional change across the forest-to-marsh gradient are evident: (1) local endemism of unique taxa (e.g., Hydrophilinae) to specific zones within the areas of greatest habitat change (low forest and ecotone) and (2) decline in abundance of salt- and flood-intolerant taxa (e.g., Collembola) in affected zones. These patterns led to overlap of marsh, forest, and unique taxa at the ecotone, driving distinct community composition at the boundary between forest and marsh and providing evidence for changes in arthropod community composition beginning farther inland than the marsh or even the marsh-forest ecotone.

Although certain Collembola species live in salt marshes, the osmotic stress of dynamic saline conditions and highly saline food may increase specialization requirements and reduce Collembola density moving toward the marsh (Haynert et al., 2017; Widenfalk et al., 2015; Witteveen, 1988). Although low relative to the marsh, the low forest at this study site has higher soil salinity and moisture content than the high forest (Fagherazzi & Nordio, 2022) and can be inundated independent of tide or storm surge (E. Goetz, & D. Johnson, personal observation). Increased inundation frequency, coupled with slightly elevated soil salinity, may make this zone a less desirable habitat or preclude certain forest species from surviving. Decreases in abundance and changes in species composition of this critical group of soil detritivores may influence rates of litter decomposition as forest converts to marsh (McCary & Schmitz, 2021), which may in turn affect habitat and resource availability in the changing forest.

Decreases in forest detritivores, such as Collembola, may be compensated by increases in a saltmarsh detritivore, however. The saltmarsh amphipod *O. grillus* was abundant in both the high marsh and ecotone but was also found within the low forest (Figure 3). A characteristic species of the high marsh on the US east coast (Johnson, 2011; Kneib, 1982; Thompson, 1984), *O. grillus*, is typically found in soil salinities over 20 (Kneib, 1982; E. Goetz, & D. Johnson, personal observation); however, here it was found in plots with soil salinities as low as 2.9 (Smith et al., 2021). Corresponding to this broad salinity range, *O. grillus* was also found in zones along the forest-to-marsh gradient with differing plant communities. In addition to the typical saltmarsh grasses (*Spartina patens* and *D. spicata*) of the high marsh, *O. grillus* was found as far inland as the low forest, which is primarily comprised of *P. australis* and salt-stressed trees, but also contains shrubs, wetland plants, and small distributions of native saltmarsh grasses (Gedan et al., 2022). These habitat characteristics suggest that *O. grillus* is a habitat generalist and capable of expanding its distribution into the retreating forest concurrently with native marsh grasses and small increases in soil salinity. *O. grillus* is migrating into the low forest while it still more closely resembles a forest rather than a marsh (i.e., before the tree canopy and salt-intolerant plant assemblage has fully died back), making it one of the first biotic saltmarsh colonizers of forest transitioning to marsh. Its presence suggests that retreating forest may provide habitat for saltmarsh generalists before complete conversion to marsh. Given that the low forest accommodates *O. grillus*, it may likewise support other marsh species, including plant or animal species that depend on *O. grillus* for nutrient cycling or as prey (Buchsbaum et al., 2009).

Although community compositions of the ghost-forest ecotone and existing high marsh were distinct, differences were driven largely by the addition of terrestrial species in the ghost forest rather than the absence of marsh species. Furthermore, for the observed species present in both ghost-forest ecotone and high marsh (*O. grillus* and *P. littoralis*), differences in diet and body size between zones were small. For both *O. grillus* and *P. littoralis*, the majority of their diet in both ghost forest and high marsh was derived from the marsh grass and detritus food web. In the ghost forest, however, *O. grillus* occupied a greater niche width, likely driven by the presence of cedar in ghost forest detritus. Similar to its ability to move into habitats distinct from its typical high marsh distribution (i.e., low forest), *O. grillus* incorporated new types of available detritus into its diet in its expanded marsh habitat, the ghost forest, suggesting that it is both a diet and habitat generalist (Angradi et al., 2001; Pascal & Fleeger, 2013) and thus that its distribution may not be limited by either food resources or habitat composition. The diet of *P. littoralis* differed minimally between zones, although individuals in the high marsh may have consumed more prey from the algae food web than those in the ghost forest, where algae availability may be slightly reduced (Table 2; Appendix S1: Figure S2). *P. littoralis* may preferentially consume saltmarsh prey species rather than terrestrial prey, which may limit its ability to move farther inland than the ghost-forest ecotone.

Interestingly, although there was no major difference in diet between zones, juveniles of *P. littoralis* collected in the fall had a higher mass-to-length ratio (i.e., more robust body condition) in the high marsh. This difference in body condition may have resulted from a variety of possible factors, including greater access to an algae-based food web in the salt marsh, although effects of increased producer nitrogen content, such as is seen in algae, are contingent on prey identity for *P. littoralis* (Wimp et al., 2021), and C/N values of both *O. grillus* and *P. littoralis* were higher (i.e., lower relative nitrogen) in the marsh (Appendix S1: Figure S1). When body condition was reassessed for the same generation of spiders as adults, however, there was no significant difference in body condition, suggesting that any differences in diet are limited to juveniles and do not have long-term effects on body condition. Although additional species and characteristics (e.g., growth and survival) must be considered before concluding that high marsh and ghost-forest ecotone are functionally equivalent, these results suggest that the ghost-forest ecotone is able to support at least certain generalist saltmarsh arthropods.

Forest retreat and marsh migration thus provide an important opportunity for saltmarsh arthropods, especially generalists, to migrate inland with, and even in advance of, changes in vegetation. As existing high marsh drowns, marsh that is allowed to form in place of retreating upland becomes even more essential for arthropod communities. Furthermore, species that rely on marsh arthropods may be better able to colonize migrating marsh zones once marsh arthropods are established. Fish and birds that consume marsh arthropods (Buchsbaum et al., 2009; Vince et al., 1976) and infauna that rely on developed marsh sediments (Craft & Sacco, 2003) may be more likely to migrate inland once saltmarsh arthropods are present or have stimulated ecosystem function in the newly formed marsh. This may include several bird species whose high marsh habitat is expected to decline with sea-level rise (e.g., rails and marsh sparrows; Hunter et al., 2015), most notably the saltmarsh sparrow, which has been predicted to go extinct by 2060 in the absence of effective marsh migration (Field et al., 2017). Certain saltmarsh bird species, however, are known to use newly migrated marsh less than existing high marsh (Taillie & Moorman, 2019). Because this study demonstrates the presence of saltmarsh arthropod prey in the ghost forest, previously observed differences in bird occupancy may be driven by differences in habitat structure between zones (Benoit & Askins, 1999), rather than arthropod prey availability.

As larger areas of forest convert to ghost forest and more existing marsh is lost to drowning (Kirwan & Gedan, 2019), the community composition and species function of both arthropods and their predators will be important to consider when evaluating the maintenance and expansion of the spatial extent of marshes. Future studies should consider the applicability of the patterns observed here to other rapidly migrating marshes, especially those in which ghost forest ground cover is dominated by invasive grasses (e.g., *P. australis*; Kirwan & Gedan, 2019; Smith, 2013), which may lead to greater differences in arthropod community composition and function between marsh and ghost forest (Agnew et al., 2003; Angradi et al., 2001). Future studies should also compare the occupancy and functional use of ghost forest and high marsh by additional taxonomic groups and consider additional functional and behavioral characteristics to determine the overall equivalency of ghost forest and high marsh. Although both saltmarsh species observed here used ghost forest habitat in approximately the same way as high marsh, specialist saltmarsh species may be incapable of migrating into new habitat or unable to use ghost forest habitat as effectively as existing marsh (Taillie & Moorman, 2019). More comprehensive knowledge of the response of critical marsh faunal groups to marsh migration is necessary for accurate evaluation of marsh extent. Finally, additional work should consider the effects of inland arthropod migration on ecosystem function, as saltmarsh arthropods may aid in ecosystem development, including through decomposition and energy flow, and contribute to the retreating forest's functional transition to marsh.

ACKNOWLEDGMENTS

The authors would like to thank Manisha Pant, Andrew Nemeth, Catherine Wilhelm, Esther Harper-Smith, Leah Scott, Dr. Serina Wittyngham, Kayla Martinez-Soto, and Jonah Morreale for help collecting and processing samples; Dr. Arthur Evans, Dr. Xuan Chen, Dr. Gina Wimp, Curt Harden, Dr. Richard Heard, Jenny Dreyer, and many BugGuide contributors for assistance with specimen identification; Dr. Jimmy Nelson and Ben Harlow for assistance with stable isotope sample preparation; and the reviewers of this manuscript for their helpful feedback and suggestions. This work was funded by the National Science Foundation (grant number 1832221).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Goetz & Johnson, 2022; Johnson & Goetz, 2022) are available from the Environmental Data Initiative data portal: https://doi.org/10.6073/pasta/859252320b7300eb78215663820f8466 and https://doi.org/10.6073/pasta/234adaf63d9de7601c0feb84271f0022.

ORCID

Emily M. Goetz https://orcid.org/0000-0003-3794-2045
David S. Johnson https://orcid.org/0000-0002-7898-4893

REFERENCES

Agnew, A. M., D. H. Shull, and R. Buchsbaum. 2003. "Growth of a Salt Marsh Invertebrate on Several Species of Marsh Grass Detritus." *Biological Bulletin* 205(2): 238–39. https://doi.org/10.2307/1543273.

Angradi, T. R., S. M. Hagan, and K. W. Able. 2001. "Vegetation Type and the Intertidal Macroinvertebrate Fauna of a Brackish Marsh: *Phragmites* vs. *Spartina*." *Wetlands* 21(1): 75–92. https://doi.org/10.1672/0277-5212(2001)021[0075:VTATIM]2.0.CO;2.

Benoit, L. K., and R. A. Askins. 1999. "Impact of the Spread of *Phragmites* on the Distribution of Birds in Connecticut Tidal Marshes." *Wetlands* 19(1): 194–208. https://doi.org/10.1007/BF03161749.

Buchsbaum, R. N., L. A. Deegan, J. Horowitz, R. H. Garritt, A. E. Giblin, J. P. Ludlam, and D. H. Shull. 2009. "Effects of Regular Salt Marsh Haying on Marsh Plants, Algae, Invertebrates and Birds at Plum Island Sound, Massachusetts." *Wetlands Ecology and Management* 17: 469–487. https://doi.org/10.1007/s11273-008-9125-3.

Craft, C., and J. Sacco. 2003. "Long-Term Succession of Benthic Infauna Communities on Constructed *Spartina alterniflora* Marshes." *Marine Ecology Progress Series* 257: 45–58. https://doi.org/10.3354/meps257045.

De Cáceres, M., and P. Legendre. 2009. "Associations between Species and Groups of Sites: Indices and Statistical Inference." *Ecology* 90(12): 3566–74. https://doi.org/10.1890/08-1823.1.

Denno, R. F., C. Gratton, H. Döbel, and D. L. Finke. 2003. "Predation Risk Affects Relative Strength of Top-Down and Bottom-up Impacts on Insect Herbivores." *Ecology* 84(4): 1032–44. https://doi.org/10.1890/0012-9658(2003)084[1032:PRARSO]2.0.CO;2.

Fagherazzi, S., S. C. Anisfeld, L. K. Blum, E. V. Long, R. A. Feagin, A. Fernandes, W. S. Kearney, and K. Williams. 2019. "Sea Level Rise and the Dynamics of the Marsh-Upland Boundary." *Frontiers in Environmental Science* 7: 25. https://doi.org/10.3389/fenvs.2019.00025.

Fagherazzi, S., and G. Nordio. 2022. "Groundwater, Soil Moisture and Weather Data in Brownsville Forest, Nassawadox, VA, 2019-2021 Ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/27b067eb7fcae65c8a4237a408f4d1c6.

Failon, C. M., S. S. Wittyngham, and D. S. Johnson. 2020. "Ecological Associations of *Littoraria irrorata* with *Spartina cynosuroides* and *Spartina alterniflora*." *Wetlands* 40: 1317–25. https://doi.org/10.1007/s13157-020-01306-4.

Field, C. R., T. S. Bayard, C. Gjerdrum, J. M. Hill, S. Meiman, and C. S. Elphick. 2017. "High-Resolution Tide Projections Reveal Extinction Threshold in Response to Sea-Level Rise." *Global Change Biology* 23(5): 2058–70. https://doi.org/10.1111/gcb.13519.

Frank, S. D., P. M. Shrewsbury, and R. F. Denno. 2010. "Effects of Alternative Food on Cannibalism and Herbivore Suppression by Carabid Larvae." *Ecological Entomology* 35(1): 61–68. https://doi.org/10.1111/j.1365-2311.2009.01156.x.

Gedan, K., J. MacGregor, R. Mohammadi, and A. Khan. 2022. "Forest Transition Experiment – Vegetation Monitoring on a Coastal Virginia Forest, 2019-2022 Ver 6." Environmental Data Initiative. https://doi.org/10.6073/pasta/a7de61660e2fa73ce1899200cc64744b.

Gedan, K. B., R. Epanchin-Niell, and M. Qi. 2020. "Rapid Land Cover Change in a Submerging Coastal County." *Wetlands* 40: 1717–28. https://doi.org/10.1007/s13157-020-01328-y.

Goetz, E. M., and D. S. Johnson. 2022. "Comparison of High-Marsh and Ghost-Forest Invertebrates in Virginia, 2020 Ver 2." Environmental Data Initiative. https://doi.org/10.6073/pasta/859252320b7300eb78215663820f8466.

Graf, N., K. P. Battes, M. Cimpean, M. H. Entling, K. Frisch, M. Link, A. Scharmüller, et al. 2020. "Relationship between Agricultural Pesticides and the Diet of Riparian Spiders in the Field." *Environmental Sciences Europe* 32(1): 1–12. https://doi.org/10.1186/s12302-019-0282-1.

Haynert, K., M. Kiggen, B. Klarner, M. Maraun, and S. Scheu. 2017. "The Structure of Salt Marsh Soil Mesofauna Food Webs—The Prevalence of Disturbance." *PLoS One* 12(12): e0189645. https://doi.org/10.1371/journal.pone.0189645.

Hunter, E. A., N. P. Nibbelink, C. R. Alexander, K. Barrett, L. F. Mengak, R. K. Guy, C. T. Moore, and R. J. Cooper. 2015. "Coastal Vertebrate Exposure to Predicted Habitat Changes Due to Sea Level Rise." *Environmental Management* 56: 1528–37. https://doi.org/10.1007/s00267-015-0580-3.

Irmler, U., K. Heller, H. Meyer, and H. D. Reinke. 2002. "Zonation of Ground Beetles (Coleoptera: Carabidae) and Spiders (Araneida) in Salt Marshes at the North and the Baltic Sea and the Impact of the Predicted Sea Level Increase." *Biodiversity and Conservation* 11: 1129–47. https://doi.org/10.1023/A:1016018021533.

Jackson, A. L., A. C. Parnell, R. Inger, and S. Bearhop. 2011. "Comparing Isotopic Niche Widths among and within Communities: SIBER – Stable Isotope Bayesian Ellipses in R." *Journal of Animal Ecology* 80: 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x.

James, W. R., R. O. Santos, J. S. Rehage, J. C. Doerr, and J. A. Nelson. 2021. "E-Scape: Consumer-Specific Landscapes of Energetic Resources Derived from Stable Isotope Analysis and Remote Sensing." *Journal of Animal Ecology* 91: 381–390. https://doi.org/10.1111/1365-2656.13637.

Johnson, D. S. 2011. "High-Marsh Invertebrates Are Susceptible to Eutrophication." *Marine Ecology Progress Series* 438: 143–152. https://doi.org/10.3354/meps09306.

Johnson, D. S., and E. M. Goetz. 2022. "Invertebrates in a Retreating Coastal Forest near Nassawadox, VA, 2019-2020 Ver 3." Environmental Data Initiative. https://doi.org/10.6073/pasta/234adaf63d9de7601c0feb84271f0022.

Kirwan, M. L., and K. B. Gedan. 2019. "Sea-Level Driven Land Conversion and the Formation of Ghost Forests." *Nature Climate Change* 9: 450–57. https://doi.org/10.1038/s41558-019-0488-7.

Kirwan, M. L., J. L. Kirwan, and C. A. Copenheaver. 2007. "Dynamics of an Estuarine Forest and Its Response to Rising Sea Level." *Journal of Coastal Research* 2007(232): 457–463. https://doi.org/10.2112/04-0211.1.

Kirwan, M. L., D. C. Walters, W. G. Reay, and J. A. Carr. 2016. "Sea Level Driven Marsh Expansion in a Coupled Model of Marsh Erosion and Migration." *Geophysical Research Letters* 43: 4366–73. https://doi.org/10.1002/2016GL068507.

Kneib, R. T. 1982. "Habitat Preference, Predation, and the Intertidal Distribution of Gammaridean Amphipods in a North Carolina Salt Marsh." *Journal of Experimental Marine Biology and Ecology* 59: 219–230. https://doi.org/10.1016/0022-0981(82)90117-4.

Krause, J. R., A. J. Oczkowski, and E. B. Watson. 2023. "Improved Mapping of Coastal Salt Marsh Habitat Change at Barnegat Bay (NJ, USA) Using Object-Based Image Analysis of High-Resolution Aerial Imagery." *Remote Sensing Applications: Society and Environment* 29: 100910. https://doi.org/10.1016/j.rsase.2022.100910.

La Peyre, M. K., B. Gossman, and J. A. Nyman. 2007. "Assessing Functional Equivalency of Nekton Habitat in Enhanced Habitats: Comparison of Terraced and Unterraced Marsh Ponds." *Estuaries and Coasts* 30: 526–536. https://doi.org/10.1007/BF03036518.

Langellotto, G. A., and R. F. Denno. 2006. "Refuge from Cannibalism in Complex-Structured Habitats: Implications for the Accumulation of Invertebrate Predators." *Ecological Entomology* 31(6): 575–581. https://doi.org/10.1111/j.1365-2311.2006.00816.x.

LaSalle, M. W., and A. A. de la Cruz. 1985. "Seasonal Abundance and Diversity of Spiders in Two Intertidal Marsh Plant Communities." *Estuaries* 8(4): 381–393. https://doi.org/10.2307/1351876.

Lloyd, K. M., A. A. M. McQueen, B. J. Lee, R. C. B. Wilson, S. Walker, and J. B. Wilson. 2000. "Evidence on Ecotone Concepts from Switch, Environmental and Anthropogenic Ecotones." *Journal of Vegetation Science* 11(6): 903–910. https://doi.org/10.2307/3236560.

Lopez, G. R., J. S. Levinton, and L. B. Slobodkin. 1977. "The Effect of Grazing by the Detritivore *Orchestia grillus* on *Spartina* Litter and Its Associated Microbial Community." *Oecologia* 30: 111–127. https://doi.org/10.1007/BF00345415.

McCary, M. A., and O. J. Schmitz. 2021. "Invertebrate Functional Traits and Terrestrial Nutrient Cycling: Insights from a Global Meta-Analysis." *Journal of Animal Ecology* 90(7): 1714–26. https://doi.org/10.1111/1365-2656.13489.

McCutchan, J. H., Jr., W. M. Lewis, Jr., C. Kendall, and C. C. McGrath. 2003. "Variation in Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur." *Oikos* 102: 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x.

Nelson, J. A., J. Lesser, W. R. James, D. P. Behringer, V. Furka, and J. C. Doerr. 2019. "Food Web Response to Foundation Species Change in a Coastal Ecosystem." *Food Webs* 21: e00125. https://doi.org/10.1016/j.fooweb.2019.e00125.

Odum, E. P. 1953. *Fundamentals of Ecology*. Philadelphia, PA: Saunders.

Ogle, D. H., J. C. Doll, P. Wheeler, and A. Dinno. 2021. "FSA: Fisheries Stock Analysis." R Package Version 0.9.1. https://github.com/droglenc/FSA.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, et al. 2020. "vegan: Community Ecology Package." R Package Version 2.5-7. https://CRAN.R-project.org/package=vegan.

Pan, C., Q. Feng, J. Liu, Y. Li, Y. Li, and X. Yu. 2018. "Community Structure of Grassland Ground-Dwelling Arthropods along Increasing Soil Salinities." *Environmental Science and Pollution Research* 25: 7479–86. https://doi.org/10.1007/s11356-017-1011-1.

Parker, J. D., J. P. Montoya, and M. E. Hay. 2008. "A Specialist Detritivore Links *Spartina alterniflora* to Salt Marsh Food Webs." *Marine Ecology Progress Series* 364: 87–95. https://doi.org/10.3354/meps07504.

Pascal, P. Y., and J. W. Fleeger. 2013. "Diverse Dietary Responses by Saltmarsh Consumers to Chronic Nutrient Enrichment." *Estuaries and Coasts* 36: 1115–24. https://doi.org/10.1007/s12237-013-9624-1.

Pétillon, J., A. Georges, A. Canard, J. C. Lefeuvre, J. P. Bakker, and F. Ysnel. 2008. "Influence of Abiotic Factors on Spider and Ground Beetle Communities in Different Salt-Marsh Systems." *Basic and Applied Ecology* 9(6): 743–751. https://doi.org/10.1016/j.baae.2007.08.007.

Pétillon, J., S. Potier, A. Carpentier, and A. Garbutt. 2014. "Evaluating the Success of Managed Realignment for the Restoration of Salt Marshes: Lessons from Invertebrate Communities." *Ecological Engineering* 69: 70–75. https://doi.org/10.1016/j.ecoleng.2014.03.085.

Potapov, A. M., F. Beaulieu, K. Birkhofer, S. L. Bluhm, M. I. Degtyarev, M. Devetter, A. A. Goncharov, et al. 2022. "Feeding Habits and Multifunctional Classification of Soil-Associated Consumers from Protists to Vertebrates." *Biological Reviews* 97: 1057–1117. https://doi.org/10.1111/brv.12832.

Rezek, R. J., J. A. Massie, J. A. Nelson, R. O. Santos, N. M. Viadero, R. E. Boucek, and J. S. Rehage. 2020. "Individual Consumer Movement Mediates Food Web Coupling across a Coastal Ecosystem." *Ecosphere* 11(12): e03305. https://doi.org/10.1002/ecs2.3305.

Sallenger, A. H., Jr., K. S. Doran, and P. A. Howd. 2012. "Hotspot of Accelerated Sea-Level Rise on the Atlantic Coast of North America." *Nature Climate Change* 2(12): 884–88. https://doi.org/10.1038/nclimate1597.

Schieder, N. W., D. C. Walters, and M. L. Kirwan. 2018. "Massive Upland to Wetland Conversion Compensated for Historical Marsh Loss in Chesapeake Bay, USA." *Estuaries and Coasts* 41: 940–951. https://doi.org/10.1007/s12237-017-0336-9.

Schuerch, M., T. Spencer, S. Temmerman, M. L. Kirwan, C. Wolff, D. Lincke, C. J. McOwen, et al. 2018. "Future Response of Global Coastal Wetlands to Sea-Level Rise." *Nature* 561: 231–34. https://doi.org/10.1038/s41586-018-0476-5.

Smith, A. J., and E. M. Goetz. 2021. "Climate Change Drives Increased Directional Movement of Landscape Ecotones." *Landscape Ecology* 36(7): 3105–16. https://doi.org/10.1007/s10980-021-01314-7.

Smith, A. J., M. Kirwan, and T. Messerschmidt. 2021. "Carbon Stocks in Forests Transitioning to Salt Marsh at Four Sites in the Chesapeake Bay Region, 2019 Ver 1." Environmental Data Initiative. https://doi.org/10.6073/pasta/4524c22708628eb7f06d174edae89ff2.

Smith, A. J., and M. L. Kirwan. 2021. "Sea Level-Driven Marsh Migration Results in Rapid Net Loss of Carbon." *Geophysical Research Letters* 48: e2021GL092420. https://doi.org/10.1029/2021GL092420.

Smith, J. A. M. 2013. "The Role of *Phragmites australis* in Mediating Inland Salt Marsh Migration in a Mid-Atlantic Estuary." *PLoS One* 8(5): e65091. https://doi.org/10.1371/journal.pone.0065091.

Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. "Analyzing Mixing Systems Using a New Generation of Bayesian Tracer Mixing Models." *PeerJ* 6: e5096. https://doi.org/10.7717/peerj.5096.

Stock, B. C., and B. X. Semmens. 2016. "MixSIAR GUI User Manual, Version 3.1." https://github.com/brianstock/MixSIAR. https://doi.org/10.5281/zenodo.1209993.

Taillie, P. J., and C. E. Moorman. 2019. "Marsh Bird Occupancy along the Shoreline-to-Forest Gradient as Marshes Migrate from Rising Sea Level." *Ecosphere* 10: e02555. https://doi.org/10.1002/ecs2.2555.

Thompson, L. S. 1984. "Comparison of the Diets of the Tidal Marsh Snail, *Melampus bidentatus* and the Amphipod, *Orchestia grillus*." *The Nautilus* 98(1): 44–53.

Torma, A., M. Bozsó, C. Tölgyesi, and R. Gallé. 2017. "Relationship of Different Feeding Groups of True Bugs (Hemiptera: Heteroptera) with Habitat and Landscape Features in Pannonic Salt Grasslands." *Journal of Insect Conservation* 21: 645–656. https://doi.org/10.1007/s10841-017-0007-y.

Vince, S., I. Valiela, and J. M. Teal. 1976. "Predation by the Salt Marsh Killifish *Fundulus heteroclitus* (L.) in Relation to Prey Size and Habitat Structure: Consequences for Prey Distribution and Abundance." *Journal of Experimental Marine Biology and Ecology* 23(3): 255–266. https://doi.org/10.1016/0022-0981(76)90024-1.

Wainright, S. C., M. P. Weinstein, K. W. Able, and C. A. Currin. 2000. "Relative Importance of Benthic Microalgae, Phytoplankton and the Detritus of Smooth Cordgrass *Spartina alterniflora* and the Common Reed *Phragmites australis* to Brackish-Marsh Food Webs." *Marine Ecology Progress Series* 200: 77–91. https://doi.org/10.3354/meps200077.

Walters, D. C., J. A. Carr, A. Hockaday, J. A. Jones, E. McFarland, K. E. Kovalenko, M. L. Kirwan, D. R. Cahoon, and G. R. Guntenspergen. 2022. "Experimental Tree Mortality Does Not Induce Marsh Transgression in a Chesapeake Bay Low-Lying Coastal Forest." *Frontiers in Marine Science* 8: 782643. https://doi.org/10.3389/fmars.2021.782643.

Wasson, K., A. Woolfolk, and C. Fresquez. 2013. "Ecotones as Indicators of Changing Environmental Conditions: Rapid Migration of Salt Marsh-Upland Boundaries." *Estuaries and Coasts* 36: 654–664. https://doi.org/10.1007/s12237-013-9601-8.

Widenfalk, L. A., J. Bengtsson, A. Berggren, K. Swiggelaar, E. Spijkman, F. Huyer-Brugman, and M. P. Berg. 2015. "Spatially Structured Environmental Filtering of Collembolan Traits in Late Successional Salt Marsh Vegetation." *Oecologia* 179: 537–549. https://doi.org/10.1007/s00442-015-3345-z.

Wimp, G. M., D. Lewis, and S. M. Murphy. 2021. "Prey Identity but Not Prey Quality Affects Spider Performance." *Current Research in Insect Science* 1: 100013. https://doi.org/10.1016/j.cris.2021.100013.

Witteveen, J. 1988. "The Impact of the Salinity of Soil-Water and Food on the Physiology, Behaviour, and Ecology of Salt-Marsh Collembola." *Functional Ecology* 2(1): 49–55. https://doi.org/10.2307/2389459.

Zimmer, M., S. C. Pennings, T. L. Buck, and T. H. Carefoot. 2004. "Salt Marsh Litter and Detritivores: A Closer Look at Redundancy." *Estuaries* 27(5): 753–769. https://doi.org/10.1007/BF02912038.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Goetz, Emily M., and David S. Johnson. 2024. "Retreating Coastal Forest Supports Saltmarsh Invertebrates." *Ecosphere* 15(1): e4743. https://doi.org/10.1002/ecs2.4743