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Invertebrates in a Migrating Salt Marsh

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William & Mary

In Partial Fulfillment

of the Requirements for the Degree of

Master of Science

by

Emily Marie Goetz

August 2022

APPROVAL PAGE

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science

Emily Marie Goetz

Approved by the Committee, July 2022

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ABSTRACT

As sea-level rise converts coastal forest to salt marsh, marsh invertebrates may migrate inland; however, the resulting changes in forest and marsh invertebrate communities, including the stage of forest retreat that first supports saltmarsh species, remain unknown. Additionally, the ghost forest that forms in the wake of rapid forest retreat offers unknown quality of habitat to marsh invertebrates. In a migrating marsh on the Eastern Shore of Virginia, USA, ground-dwelling arthropod communities were assessed across the forest-to-marsh gradient, and the ecological equivalency of ghost forest and high marsh habitats was evaluated to determine if marsh invertebrates utilized expanded marsh in the same way as existing marsh. Composition and diversity patterns were evaluated across the gradient for entire arthropod communities captured by pitfall and leaf litter samples, as well as springtail, ant, and beetle communities. Ecological equivalency was assessed by comparing community structure (composition and diversity) for epifauna and infauna as well as functional metrics (diet and body condition) 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 between zones, driven largely by retreating forest taxa (e.g., Collembola), marsh taxa migrating into the forest (e.g., the saltmarsh amphipod *O. grillus*), and unique taxa (e.g., Hydrophilinae beetles) at the ecotone. The overlap of these groups likely contributed to an observed peak in rarefied species diversity at the ecotone for pitfall samples. The composition and diversity patterns of springtails, ants, and beetles differed from entire arthropod community patterns, with springtails showing highest diversity in the high forest, and ants exhibiting peaks in diversity in high forest and ecotone. The low forest was the most inland zone to accommodate *O. grillus*, a saltmarsh species that may serve as an early indicator of marsh migration into forests.

Ghost forest habitat offered expanded variation in both community composition and *O. grillus* diet. Both forest and marsh species were present in the ghost forest, and *O. grillus* occupied a larger trophic niche width in the ghost forest from consuming both marsh and terrestrial material. Despite these differences, ghost forest habitat supported the majority of marsh species, and observed marsh species present in both habitats primarily consumed from the marsh grass food web with no lasting difference in body condition. Because of its capacity to support saltmarsh species, the ghost forest can be considered largely ecologically equivalent to high marsh at this site, which may inform evaluations of marsh spatial extent. Forest retreat and marsh migration thus provide an important opportunity for generalist saltmarsh invertebrates to maintain their habitat extent in the face of marsh loss due to sea-level rise.

Invertebrates in a Migrating Salt Marsh

1. INTRODUCTION

Sea-level rise threatens tidal marshes through increased erosion and drowning, but marshes may maintain their areal extent by migrating upland (Kirwan et al. 2016). During lateral marsh migration into forests, the press of saltwater intrusion halts tree seedling recruitment in marsh-adjacent forest, although mature trees able to withstand salt stress may survive. Eventually, storm pulses of saltwater and prolonged flooding kill even mature trees, and the resulting open space is colonized by marsh grasses (Kirwan et al. 2007; Fagherazzi et al. 2019). Depending on the local physical and hydrological characteristics and upland land use, this sequence of events may lead to successful inland marsh migration (Kirwan et al. 2016; Schieder et al. 2018; Fagherazzi et al. 2019; Farron et al. 2020). This temporal process is represented spatially by the gradient of habitat zones that form between inland forest and salt marsh, which shows the sequential stages of forest retreat. Transitional zones closest to the marsh possess characteristics of both forest and marsh habitat. The spatial gradient thus includes an ecotone, a unique ecosystem at the boundary of two adjacent ecosystems, between marsh and forest (Smith and Goetz 2021). With accelerating inland migration of the marsh and ecotone, 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 and Gedan 2019).

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 inland. This is especially apparent in areas with high rates of relative sea-level rise and low slope where there is high potential for inland migration, such as the mid-Atlantic portion of the eastern United States

(Sallenger et al. 2012). In areas conducive to upland habitat retreat, marsh migration may equal or even exceed marsh loss caused by sea-level rise (Kirwan et al. 2016; Schieder et al. 2018); however, little is known about the faunal communities, including invertebrates, supported by the different zones of habitat that form as forest transitions into marsh. Furthermore, it remains unclear if newly formed ghost forest provides the same quality of habitat for marsh invertebrates as older marsh. As sea-level rise accelerates and greater expanses of coastal forest convert to marsh (Sallenger et al. 2012; Schieder et al. 2018), a greater understanding of the invertebrate community composition of retreating forest and newly formed marsh may better inform the evaluation of migrated marsh extent for invertebrate communities. This work explores (1) how and when invertebrate community composition and diversity change as forest converts to marsh and (2) the ecological equivalency of newly formed ghost forest as compared to existing high marsh for marsh invertebrates.

Differences in vegetation (Torma et al. 2017; Pan et al. 2018), salinity (Pétillon et al. 2008; Pan et al. 2018; Aker 2020), inundation (LaSalle and de la Cruz 1985; Döbel et al. 1990; Irmeler et al. 2002; Sei 2006; Widenfalk et al. 2015), and habitat structure (van Klink et al. 2013) can influence saltmarsh invertebrate community composition. Invertebrate communities may therefore be useful indicators of forest retreat and marsh migration and offer insight into saltmarsh ecosystem function that complements other metrics (e.g., canopy cover, vegetation community composition, soil salinity) (Pennings et al. 2002; Pétillon et al. 2014). Wetland assessments have used invertebrate community composition and function to determine ecosystem condition (Weilhoefer 2011), specifically in the context of marsh restoration work (Llewellyn and La Peyre 2011; Mitchell 2012; Pétillon et al. 2014; Baumann et al. 2020; McAtee et al. 2020). Despite the likely effects of marsh migration on invertebrate communities and

invertebrates' potential benefit as marsh migration indicators, studies of migrating species have thus far focused only on plants (Smith 2013; Gedan and Fernández-Pascual 2019; Kottler and Gedan 2022) and Foraminifera (Anisfeld et al. 2017, 2019), and ghost forest habitat has been evaluated for a single marsh faunal taxon (birds: Taillie and Moorman 2019).

An ecotone may contain greater biological diversity than either adjacent ecosystem because of overlapping habitat characteristics that support species from each of the adjacent habitats as well as species specific to the ecotone itself (Odum 1953). This theory has been supported by more recent studies that show maximum species diversity at ecotones (Traut 2005; Horváth et al. 2010; Lasmar et al. 2021) and unique ecotonal communities (Lloyd et al. 2000; Wasson et al. 2013). Other studies, however, have shown either no change in invertebrate diversity across the ecotone despite compositional turnover (Martínez-Falcón et al. 2018; Martello et al. 2022) or differential responses based on species habitat specificity (Lacasella et al. 2015). Increased ecotonal diversity of invertebrates has been demonstrated specifically at the marsh-upland ecotone for invertebrate predators, as compared to adjacent marsh (Sei 2006), and spiders, as compared to both adjacent ecosystems, driven by overlap in terrestrial and saltmarsh species at the marsh-upland ecotone (Traut 2005), but patterns of diversity likely depend on vegetation composition at the ecotone relative to invertebrate habitat requirements (Wigginton et al. 2014). The hypothesis of increased ecotonal invertebrate diversity has not been tested across the marsh-upland ecotone in salt marshes of the eastern United States, where accelerated relative sea-level rise and low coastal slopes make marsh migration more prevalent and may increase movement or even expansion of the marsh-forest ecotone (Sallenger et al. 2012; Schieder et al. 2018).

In addition to the species composition of ecotone communities, it remains unknown if saltmarsh species use expanded marsh at the trailing end of the migrating ecotone (ghost forest) in the same way as existing high marsh. Just as restored marshes—an intuitive analogue to newly formed ghost forest marsh—are often not immediately equivalent to natural marshes after marsh creation efforts (La Peyre et al. 2007), new marsh formed via marsh migration may not be equivalent to older marsh. Ecological equivalency of two comparable systems, as is assessed for natural and restored marshes (La Peyre et al. 2007; Llewellyn and La Peyre 2011; Mossman et al. 2012; Rezek et al. 2017), is often considered in two parts: structural (e.g., community composition and diversity) and functional (e.g., trophic interactions and species traits) characteristics. Together, structural and functional equivalency metrics may offer a more complete comparison of two habitats than community composition alone.

Although ghost forest and high marsh often share the same ground cover species, standing dead trees and remnant terrestrial shrubs distinguish the ghost forest. The increased vertical structure likely affects habitat by contributing to the detrital pool and reducing sunlight that reaches the ground cover, possibly altering ground cover composition or characteristics (Jobe and Gedan 2021; Kottler and Gedan 2022), reducing evapotranspiration, or inhibiting benthic algae growth. These habitat differences may affect food availability for marsh and forest species within each habitat, leading to differences in not only resident species' identities, but also in how those species use each habitat. Differences in habitat and food availability may differentiate trophic behavior and growth between ghost forest and high marsh for species that occupy both zones, as seen in restored or disturbed marshes (Nordström et al. 2015; Rezek et al. 2017; Kiskaddon et al. 2019). Habitat differences may change consumption patterns for detritivores, through detrital composition and microbial growth; herbivores, through vegetation

composition; and predators, through structural complexity. Consumption behavior, in turn, may influence body condition (Agnew et al. 2003), which may affect resource availability for higher trophic levels. Previous studies have looked at invertebrate diet across the marsh-upland ecotone (Zimmer et al. 2002; Ewers et al. 2012; Hübner et al. 2015; Kiskaddon et al. 2019), but functional differences of marsh species found in both the marsh-forest ecotone and high marsh have only been studied in plants (Kottler and Gedan 2022), and ecological equivalency studies of saltmarsh invertebrates have been largely limited to restored low marsh habitats (La Peyre et al. 2007).

The ability of saltmarsh invertebrate communities to migrate inland is important not only for the preservation of habitat area for marsh invertebrates, but also for higher trophic levels, since invertebrates serve as both a prey resource and a trophic link (Parker et al. 2008), and the marsh as an entire ecosystem, due to invertebrate contributions toward decomposition, nutrient cycling (Lopez et al. 1977; Zimmer et al. 2004; McCary and Schmitz 2021), 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 invertebrate distribution and function is essential to understanding the function of the ecosystems that result from marsh migration. Although it is currently assumed that ghost forest and marsh serve the same role, and newly formed ghost forest within the ecotone may be included in spatial quantifications of marsh, the actual distribution of saltmarsh species and the functional equivalency of salt marsh and ghost-forest ecotone habitats remains unknown for saltmarsh invertebrates.

Here, a spatial gradient along the forest-to-marsh transition, including ghost forest at the ecotone, is used to predict invertebrate community changes caused by inland marsh migration and to assess ecological equivalency of ghost forest and high marsh. The first objective of this

work was to identify the zone of retreating forest in which forest invertebrate communities first change and marsh invertebrate species colonize. I hypothesized that invertebrate community composition would differ between all zones of the forest, based on observed differences in edaphic and vegetation characteristics between zones, with the different communities representing expected compositional changes as forest converts to marsh over time. I expected that some, though not all, saltmarsh species would begin to migrate inland, serving as indicators of forest conversion to marsh. The second objective was to assess if the marsh-forest ecotone supported a peak in invertebrate diversity. Based on existing ecotone theory, I hypothesized that the highest diversity would occur in the ecotone, where forest and marsh invertebrate taxa may overlap and support additional unique ecotonal species. The third objective of this work was to evaluate the ecological equivalency of the final stage of forest conversion to marsh at the ecotone (ghost forest) and existing high marsh. I hypothesized that both structural and functional characteristics would differ between ghost forest and high marsh—and thus that ghost forest would not be ecologically equivalent to marsh as invertebrate habitat—due to differences in habitat and food availability that may affect both consumption and growth in invertebrates.

2. METHODS

2.1 Site Description

Sampling was conducted on the Eastern Shore of Virginia at Brownsville Preserve, part of the Virginia Coast Reserve LTER and adjacent to Upper Phillips Creek (37.463, -75.835). Marsh-forest 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 (Smith and Kirwan 2021). In 2019, arthropod communities were sampled across the entire forest-to-marsh gradient, including multiple forest zones, ghost forest ecotone, and high marsh. In 2020, additional invertebrate sampling was conducted in the ghost forest ecotone and high marsh zones only, for a more thorough comparison of these zones.

2.2 Field Collection and Processing

2.2.1 *Forest-to-marsh Arthropod Community*

As in previous studies (Anisfeld et al. 2017; Van Allen et al. 2021), the natural spatial zonation of the marsh-forest gradient was used in a space-for-time substitution approach to assess forest conversion to marsh. To determine how invertebrate communities are predicted to change as forest dies back and marsh migrates inland, invertebrates 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 transition to marsh.

Twenty plots were established in the following five zones along the marsh-forest gradient (n=4 plots/zone) based on vegetation communities and seedling recruitment: (1) high forest characterized by both coniferous and deciduous tree species, with full seedling recruitment; (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 no tree recruitment, and the understory contains primarily invasive (*Phragmites australis*) but also salt marsh (*Spartina patens*, *Distichlis spicata*) plant species; (4) ecotone containing mostly dead and dying mature trees, with its understory 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 plot, invertebrates were sampled during a neap tide in September 2019 using both pitfall traps and leaf litter extraction methods. These collection methods target different ground-dwelling invertebrate communities: pitfall traps collect mobile, surface-dwelling organisms, whereas leaf litter collection targets soil- and litter-dwelling species. Three clear pitfall traps were installed approximately one meter apart from each other within each plot. Marsh flooding limited pitfall trap deployment to three of the four high marsh plots. Each trap was partially filled with 25% propylene glycol as a preservative. After 24 hours, all material in each trap was sieved through 63-micron mesh and stored in ethanol. Leaf litter was collected from two 0.0625m² quadrats collected approximately one meter from 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. Coarse litter that did not pass through the sifter was discarded.

Invertebrates were extracted from the remaining litter over two weeks using Berlese funnels with 6-mm mesh opening size.

All collected invertebrates were identified to the lowest taxonomic level feasible for their order (mostly family or below; Appendices A-B). 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., molluscs), microcrustaceans (e.g., copepods), ant queens, insect larva, and spiderlings were excluded from analyses.

2.2.2 *Ghost Forest Ecotone and High Marsh Ecological Equivalency*

To assess ecological equivalency of existing versus newly migrated marsh, structural (community composition and diversity) and functional (diet and body condition) characteristics were compared between the high marsh, where salt marsh has been present for over forty years, and the ghost forest, where salt marsh has formed within the last forty 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 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 meters 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.

To assess structural equivalency, epifauna arthropod sampling (pitfall trapping (n=3/plot) and leaf litter collection (n=1/plot)) was repeated in September 2020 in ghost forest and high marsh plots (n=5 plots/zone), using the same methods as in 2019. Collected arthropods were mostly identified to the same levels of taxonomic resolution as in 2019 (Appendix A), and the same taxa were excluded as described above. Additionally, macroinfauna (organisms >0.5mm that live within the sediment) were collected from 5-cm deep sediment cores (171cm³) in each zone (n=3/plot) and identified to lowest taxonomic level feasible (Appendices C and D). Taxa that were not the sampling targets (e.g., epibenthic species collected by chance) were excluded from infauna analyses (Appendix E).

To assess functional equivalency of high marsh and ghost forest as invertebrate habitat, diet and body condition were assessed for marsh invertebrate species present in both high marsh and ghost forest (the saltmarsh amphipod *Orchestia grillus* and the marsh wolf 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, such as *O. grillus*, stimulate the base of the food web in the marsh by shredding dead material into small pieces, increasing microbial activity by producing nutrient-rich fecal pellets, and aiding nutrient cycling by reintroducing detritus to the food web (Lopez et al. 1977; Zimmer et al. 2004; Parker et al. 2008). Predators, including *P. littoralis*, exert top-down control over herbivores and detritivores in the marsh and, because they are typically larger, often function as an important trophic link between smaller invertebrates and higher trophic levels (Potapov et al. 2022). *O. grillus* were collected using litter bags (mesh bags filled with local

detritus, covered with grass, and staked into the ground 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 (five-gallon bucket with bottom removed).

Diet was compared between zones using stable isotope ratios of carbon, nitrogen, and sulfur. Together, isotopic ratios can provide insight into basal producer source ($\delta^{13}\text{C}$ and $\delta^{34}\text{S}$) and trophic position ($\delta^{15}\text{N}$) (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 hours. Where necessary to meet isotope analysis weight requirements (half of *O. grillus* samples and all of *P. littoralis* samples), multiple individuals were combined to create a composite sample. Invertebrates were ground with a motorized pellet pestle and packaged in tin capsules for analysis (*O. grillus*: n=8 for ghost forest ecotone 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 in each zone (n=5 composite samples/zone). Algal mats were collected from the surface of standing pools of water. 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 invertebrates, 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. 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 (all other producers), 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 Peedee belemnite for $\delta^{13}\text{C}$, atmospheric N_2 for $\delta^{15}\text{N}$, and Vienna Cañon Diablo Troilite for $\delta^{34}\text{S}$. Percent carbon and nitrogen were also determined for each sample.

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 hours, 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 weight divided by length.

In each plot in high marsh and ghost forest ecotone, 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-m² quadrats (n=3/plot=15/zone), spaced approximately two meters 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-m² quadrat. Plant material was rinsed, dried at 60°C for 72h, and weighed to determine biomass by species. Terrestrial contribution to detritus (e.g., cedar needles, pinecones) was weighed to determine percent contribution to total detrital biomass. Sediment cores (5-cm depth) were dried at 60°C for at least 96h and weighed to determine bulk density. Percent organic content of sediment cores was measured as percent of dried sample biomass lost at 550°C over six hours (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).

2.3 Data Analysis

For pitfall traps and infauna cores, the three samples collected within each plot were combined to ensure independence of samples. Invertebrate communities were analyzed separately by trap type (i.e., pitfall trap, leaf litter, and infauna) because of differences in targeted taxa. All data were analyzed in R (version 4.1.2). All tests of significance were based on an alpha value of 0.05.

2.3.1 Forest-to-marsh Arthropod Community

For both pitfall and leaf litter, community composition was analyzed visually with non-metric 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 statistically compared between 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 functions *adonis* and *betadisper*, respectively, in *vegan*. Post-hoc pairwise comparisons (Martinez Arbizu 2017) with Holm's method correction were conducted where PERMANOVA showed a significant difference in community composition to determine which zones showed significant dissimilarity. Similarity percentage analysis (SIMPER) was conducted to determine the driving taxa of these observed differences (function *simper* in *vegan*), and taxa that consistently showed over five percent contribution to differences between zones were identified. Because SIMPER analysis can be substantially affected by taxa abundance, indicator species analysis using function *multipatt* in package *indicspecies* (De Cáceres and Legendre 2009) was used to verify the most important species and to identify 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. Abundance data were tested for homoscedasticity (Levene's test) and independence (Durbin Watson test), and analysis residuals were tested for normality (Shapiro-Wilk test) to determine if data met the assumptions for analysis of variance (ANOVA). If raw or

transformed (square-root, $\log(n+1)$, or Box Cox) data met assumptions, abundances were assessed across zones with one-way ANOVA and, when significant, Tukey's honestly significant difference (HSD) post-hoc test. When data did not meet assumptions after transformation, the non-parametric Kruskal-Wallis test and Dunn post-hoc test with Holm's method correction (function `dunnTest` in package *FSA* (Ogle et al. 2021)) were used to compare between zones.

To compare biological diversity between zones, alpha diversity was calculated for each zone with Hill numbers of order 0 (number of taxa; hereafter "richness") and order 1 (exponential of Shannon entropy index; hereafter "Shannon diversity"), together "diversity indices." Richness is strictly a measure of the number of identified taxa, whereas Shannon diversity incorporates both the number of identified taxa as well as the proportional contribution of each taxon to the community and gives less weight to rare taxa (Jost 2006). Metrics were calculated in *vegan*. Diversity indices were compared separately between zones with either ANOVA or Kruskal-Wallis as described above.

Diversity indices based on equal sampling effort (as conducted within each plot) can be inflated for samples with high abundance, as collecting more individuals increases the likelihood of capturing additional taxa. To control for differences in sample collection abundance between zones, rarefied and extrapolated diversity indices were calculated in package *iNEXT* (Hsieh et al. 2020) based on the entire assemblage of arthropods sampled from each zone, giving a single value with bootstrapped confidence intervals for each diversity index in each zone. Diversity indices were rarefied to the lowest estimated level of sampling coverage and extrapolated to double the sample size. Sample coverage is an estimate of sampling completeness that offers a more efficient alternative to individual- or sample-based rarefaction because of its consideration

of the effect of community diversity on collection success (i.e., a less diverse community is more fully sampled after lower effort) (Chao and Jost 2012; Chao et al. 2014).

The above community composition and diversity analyses were performed for the entire sampled arthropod community, as well as for communities of three selected taxa. Diversity of the entire arthropod community provides a broad picture of diversity patterns, including overlap of broad taxa specific to different environments. Individual taxa were analyzed to reveal any patterns in community composition or diversity indices within specific taxa that would potentially be masked by combined analysis. Springtails (pitfall), ants (pitfall), and beetles (leaf litter) were selected for individual taxa analysis because they were three of the most abundant taxa and could be identified to family or lower; they belong to important trophic and functional groups; and their patterns of distribution, diversity, and function have been frequently assessed in previous work (springtails: Rusek 1998, Yang et al. 2012; ants: Canepuccia et al. 2016, Chen et al. 2016, Yusah and Foster 2016, Lasmar et al. 2021, Martello et al. 2022; beetles: Irmiler et al. 2002, Pétilion et al. 2008, Lacasella et al. 2015, Ford et al. 2017, Leonard et al. 2018). Community composition was analyzed with NMDS plots, PERMANOVA, and pair-wise comparisons, as described above. For ant and beetle analyses, a dummy variable was added before analysis to handle small sample sizes. Diversity indices were analyzed as above.

2.3.2 Ghost Forest Ecotone and High Marsh Ecological Equivalency

Structural equivalency of ghost forest and high marsh was evaluated separately by sample collection type (pitfall, leaf litter, and infauna). Community comparison was performed using NMDS, PERMANOVA, SIMPER, and indicator species analysis, as above. Diversity indices were calculated for each trap type as above and compared between zones with Welch's

independent samples t-tests. Normality was tested using Shapiro-Wilk tests, and homoscedasticity was assessed with Levene's test. Where data could not be transformed to meet test assumptions, a Wilcoxon rank sum test (WRS) was performed. Rarefaction analyses were not conducted for 2020 samples because coverage was high and relatively equal for both zones (Pitfall_{min}=0.98; Leaf litter_{min}=0.94; Infauna_{min}=0.99).

Stable isotope values were interpreted with Bayesian mixing models using package *MixSIAR* (Stock and Semmens 2016; Stock et al. 2018) 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, $\delta^{34}\text{S}$ values for *Spartina* spp. from the literature (Wainright et al. 2000) were included in the mixing model to account for highly enriched $\delta^{34}\text{S}$ values in *O. grillus* relative to observed producers, possibly due to uncaptured seasonal variation. Because $\delta^{15}\text{N}$ values from Wainright et al. (2000) were highly enriched (likely due to wastewater or livestock effluent) compared to values observed at this site, $\delta^{34}\text{S}$ values from Wainright et al. (2000) were paired with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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*) contributors 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 (three chains with chain length of 1,000,000 (*P. littoralis*) or 3,000,000 (*O. grillus*) and 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 \pm SD), which correct for preferential assimilation of lighter isotopes across trophic levels, were included in the model as 0.5 ± 0.13 for $\delta^{13}\text{C}$ (McCutchan et al. 2003; Pascal and Fleeger 2013), 2.3 ± 0.28 for $\delta^{15}\text{N}$ (McCutchan et al. 2003; Graf et al. 2020), and 0.5 ± 0.5 for $\delta^{34}\text{S}$ (McCutchan et al. 2003; Nelson et al. 2019; Rezek et al. 2020; James et al. 2021). Because spiders were assumed to be at least two trophic levels above producers (given their diet of primary consumers as well as intra-guild predation and cannibalism (Langellotto and Denno 2006)), all trophic enrichment factors and standard deviations were multiplied by 2.5 for the *P. littoralis* model.

Niche width was estimated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 ratios (C/N), a metric of the relative amounts of carbon and nitrogen, the latter of which is more digestible and palatable for organisms (Valiela and Rietsma 1984), were calculated as percent carbon divided by percent nitrogen and 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 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 tests.

Habitat characteristics were compared between zones with t-tests or Wilcoxon rank-sum tests. For live and dead tree counts, the three counts at each plot were averaged to a single value

per plot for each variable ($n=5/\text{zone}$) before analysis, to ensure independence of samples in case of count radius overlap. P values from multiple comparisons between zones were adjusted using the false discovery rate method.

3. RESULTS

3.1 Forest-to-marsh Arthropod Community

3.1.1 Community Composition

3.1.1a Pitfall Traps: Entire Arthropod Community

Non-metric multidimensional scaling (NMDS) plotting of arthropods collected by pitfall trap shows that community composition differed by zone, with high marsh and ecotone zones showing the greatest distinctness. Forest zones showed greater overlap, but low forest plots were somewhat distinct from mid and high forest zones. Permutational multivariate analysis of variance (PERMANOVA) showed significant differences between centroids of zone plot clusters ($F_{4,14}=3.436$, $R^2=0.495$, $p=0.0001$; Figure 2a); however, Holm-corrected pair-wise comparisons were not significant between any pair of zones. Similarity percentage (SIMPER) analysis showed that the primary drivers of differences in community composition were several springtail (class Collembola) families (including Hypogastruridae, Isotomidae, Entomobryidae, Sminthurididae, Sminthuridae), the saltmarsh amphipod (*Orchestia 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 taxa with significant zone associations (Table 1).

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 HSD: $p<0.05$ for all comparisons; Figure 3). *O. grillus* abundance was significantly different between zones (Kruskal-Wallis test (KW): $H_4=12.386$, $p=0.015$; Figure 3), with abundances increasing toward the marsh, but post-hoc

testing showed only a trend toward greater abundance in the ecotone than high ($p=0.090$) and mid ($p=0.081$) forest zones without any significant differences between pairs. *Monomorium* was significantly different between 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 between zones (ANOVA: $F_{4,14}=2.537$, $p=0.087$).

3.1.1b Leaf Litter Collection: Entire Arthropod Community

NMDS plotting of arthropod communities collected through leaf litter collection and Berlese extraction shows greater overlap in community composition between zones than pitfall samples, although some distinction is visible between high forest and ecotone. Nevertheless, PERMANOVA showed a significant difference between zones ($F_{4,15}=1.933$, $R^2=0.340$, $p=0.007$; Figure 2b), but Holm-corrected pair-wise comparisons were not significant between any pair of zones. SIMPER analysis showed that two sub-families 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), significantly higher than each forest zone ($p<0.01$ for each comparison) and with a trend toward higher abundance in the ecotone than in the marsh ($p=0.053$).

3.1.1c Springtail, Ant, and Beetle Communities

NMDS plots of each community indicated that springtail (order Collembola) communities were distinct in each of the forest zones and in the ecotone (Figure 4a). Ants (order Hymenoptera, family Formicidae) showed distinct communities in ecotone and high forest zones with high overlap between mid and low forest (absent in high marsh) (Figure 4b). Beetles (order Coleoptera) showed little distinction between zones (Figure 4c). PERMANOVA results corroborated the visual NMDS results for springtails and ants (springtail: $F_{4,14}=3.496$, $R^2=0.500$, $p=0.0001$; ant: $F_{4,14}=3.693$, $R^2=0.513$, $p=0.0001$) and additionally showed significant differences between zones for beetle composition ($F_{4,15}=2.267$, $R^2=0.377$, $p=0.004$). Post-hoc pair-wise comparisons did not indicate significant differences between any zone pair for any of the three taxa.

3.1.2 Diversity Patterns

3.1.2a Pitfall Traps: Entire Arthropod Community

Richness for the entire arthropod community was significantly different between zones (ANOVA: $F_{4,14}=11.56$, $p=0.0002$), overall decreasing from high forest to marsh (Figure 5). Richness was significantly lower in the marsh compared to all other zones and higher in the high forest than mid forest ($P<0.05$ for all comparisons). Shannon diversity was significantly higher in the ecotone than marsh (ANOVA: $F_{4,14}=3.698$, $p=0.030$) but not significantly different between the ecotone and any forest plots (Figure 5).

Comparison of rarefied diversity indices calculated for each zone differed from analysis of raw data. When each zone was rarefied to the lowest level of zone coverage (89% in the ecotone), both richness and Shannon diversity were significantly higher in the ecotone than all

other zones (Figure 6; Table 2). Extrapolation of diversity indices for each zone supports this, with extrapolated estimators of both indices highest in the ecotone and lowest in the marsh.

3.1.2b Leaf Litter Collection: Entire Arthropod Community

For the entire arthropod community collected in leaf litter samples, neither richness (ANOVA: $F_{4,15}=0.236$, $p=0.913$) nor Shannon diversity (ANOVA: $F_{4,15}=1.106$, $p=0.390$) differed between zones (Figure 5). Estimated coverage was low for the mid forest zone (75%), leading to overall low rarefied diversity index estimates for all zones. When rarefied, richness and Shannon diversity were highest in the mid forest, but extrapolation of richness showed a likely intersection of zone diversity metrics at higher coverage (Figure 6; Table 2).

3.1.2c Springtail, Ant, and Beetle Communities

Springtail diversity declined from high forest toward the marsh for both richness (ANOVA: $F_{4,14}=17.44$, $p=0.00003$) and Shannon diversity (ANOVA: $F_{4,14}=13.95$, $p=0.00009$) (Figure 7). When rarefied (lowest coverage=93%), springtail richness was significantly higher in the high forest than in the mid forest, low forest, or marsh, but there was no difference between high forest and ecotone (Figure 8; Table 3). Rarefied Shannon diversity was higher in the high forest than the low forest or ecotone.

Ant diversity metrics were also significantly different between zones for richness (ANOVA: $F_{4,14}=13.96$, $p=0.00009$) and Shannon diversity (KW: $H_4=11.991$, $p=0.017$) (Figure 7), but patterns differed from entire-community and springtail diversity patterns. Ant richness was higher in the ecotone than in mid forest, low forest, and marsh zones and higher in the high forest than low forest or marsh ($p<0.05$ for all comparisons). Post-hoc testing of Shannon

diversity was not significant for any pairing but showed an insignificant peak in the ecotone with a trend toward higher diversity in ecotone than marsh ($p=0.057$). Rarefied richness and Shannon diversity (lowest coverage=89%) were also higher in the high forest and ecotone than mid and low forest, patterns that persisted with extrapolation (Figure 8). No ants were collected in the marsh, so rarefied richness was taken to be zero in this zone, and extrapolated diversity metrics could not be estimated.

For beetles collected in leaf litter samples, neither richness (KW: $H_4=2.225$, $p=0.695$) nor Shannon diversity (ANOVA: $F_{4,15}=1.115$, $p=0.386$) differed between zones (Figure 7). Sample percent coverage was low for leaf litter traps, including beetles (lowest coverage=75%), so samples were rarefied to very low numbers of individuals for some zones. Rarefaction indicated that both beetle diversity metrics were significantly lower in low forest, ecotone, and high marsh than high and mid forest, but extrapolation showed high uncertainty (Figure 8).

3.2 Ghost Forest Ecotone and High Marsh Ecological Equivalency

3.2.1 Structural Equivalency

3.2.1a Epifauna

As in 2019, the ghost forest ecotone and high marsh comparison conducted in 2020 showed greater differences in community composition between zones in pitfall (PERMANOVA: $F_{1,8}=5.166$, $R^2=0.392$, $p=0.007$) than leaf litter (PERMANOVA: $F_{1,8}=1.950$, $R^2=0.196$, $p=0.1$) communities (Figure 9a-b). Indicator species analysis for pitfall communities showed association of several families of springtails and the ant genus *Monomorium* in the ghost forest and the spider family Araneidae in the high marsh (Table 4). Epifaunal community diversity metrics were higher in the ghost forest than high marsh for both pitfall (richness: t-test, $t_6=6.523$,

p=0.0005; Shannon diversity: t-test, $t_8=5.448$, p=0.0006) and leaf litter (richness: t-test, $t_7=2.357$, p=0.049; Shannon diversity: t-test, $t_6=2.778$, p=0.030) communities (Figure 10).

3.2.1b Infauna

Neither community composition (PERMANOVA: $F_{1,8}=1.709$, $R^2=0.176$, p=0.096) nor diversity (richness: t-test, $t_8=-0.183$, p=0.860; Shannon diversity: t-test, $t_7=0.222$, p=0.831) differed between zones for infauna samples (Figure 9c, 10). When considering abundances, however, the zones supported different taxa (Figure 11). SIMPER analysis associated Chironomidae larva (order Diptera) and Enchytraeidae (Oligochaeta) with the ghost forest and Coleoptera larva, nematodes, and Tubificidae (Oligochaeta) with the high marsh. Indicator species analysis showed that Chironomidae larva were associated with the ghost forest (Table 4).

3.2.2 Functional Equivalency

3.2.2a Diet

Isotopic signatures showed intra-specific variation between zones, with producers and consumers in the ghost forest enriched in both ^{15}N and ^{34}S relative to high marsh conspecifics (Figure 12; Table 5).

Mixing models attributed the majority of *Orchestia grillus* diet (95% credible interval) in both zones to marsh grasses and detritus with $\delta^{34}\text{S}$ values from the literature (“Wainright *Spartina*”) (ghost forest ecotone (E): 55.9-86.7%; high marsh (HM): 51.0-70.7%). In the ghost forest, cedar also contributed to diet (1.8-29.4%), with other sources estimated to contribute only minimally. In the high marsh, a small portion of the diet was attributed to both *S. 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%) (Table 6).

Pardosa 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 $\delta^{34}\text{S}$ values observed *in situ*, rather than the more enriched Wainright *Spartina* values. In the ghost forest, *Phragmites 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* were strongly negatively correlated, meaning diet contribution attributed to *P. australis* may have instead derived from algae. The algae food web thus likely contributed to a greater portion 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 confidence intervals (Table 6).

Niche width (posterior distribution mode [95% credible interval]) calculated from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ 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: $t_{16}=-4.930$, $p=0.0002$) (Figure 13). Differences in producer C/N between zones were variable, with detritus lower (higher relative nitrogen) in the high marsh and *S. patens* lower in the ghost forest. For producers specific to each zone, algae found in the high marsh had the lowest C/N, but *P. australis* found in the ghost forest was also slightly elevated in nitrogen compared to other sources.

3.2.2b Body Condition

Body condition of *O. grillus* did not differ between zones (Wilcoxon rank sum test (WRS): $W=1236$, $p=0.111$, $n=140$; Figure 14). Body condition of *P. littoralis* was significantly higher (more weight 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: $t_{75}=-0.682$, $p=0.497$).

3.2.3 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 (*Panicum virgatum*, *Schoenoplectus americanus*, *Pluchea purpurascens*, *Cyperus* sp., *Setaria parviflora*, and *Iva frutescens*) adjacent to several ghost forest plots. Within plots, there was more *D. spicata* in the ghost forest, and more *S. patens* and *S. alterniflora* in the high marsh (Figure 15). While grass species composition varied by zone, ground cover species richness was not significantly different (WRS: $W=151.5$, $p=0.075$, $n=30$; Figure 16). In addition to grass species, 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 density of live stems 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 in the ghost forest than high marsh (WRS: $W=195$, $p=0.000006$, $n=28$), in the form of cedar and pine needles, pinecones, and

bark. 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 but a trend toward more in the high marsh (t-test: $t_{28}=-2.138$, $p=0.062$). Conductivity was significantly higher in the high marsh than ghost forest (t-test: $t_{25}=-6.299$, $p=0.000006$).

4. DISCUSSION

4.1 Forest-to-marsh Arthropod Community

Total community composition differed by zone in pitfall more than leaf litter samples, with changes beginning in the low forest. Likewise, diversity indices differed by zone only in pitfall samples and showed highest rarefied diversity in the ecotone. Considering data from both trap types, three key patterns emerge that likely drove differences in composition and diversity: (1) inland migration of generalist marsh taxa (e.g., *Orchestia grillus*) into retreating forest, (2) decline in abundance of salt- and flood-intolerant taxa (e.g., Collembola) in affected zones, and (3) local endemism of unique taxa (e.g., Hydrophilinae) to specific zones within the areas of greatest habitat change (low forest and ecotone). These patterns led to overlap of marsh, forest, and ecotonal taxa at the ecotone, driving distinct community composition and a peak in diversity in pitfall communities at the boundary between forest and marsh.

4.1.1 Community Composition

The saltmarsh amphipod *O. grillus* was abundant in both the high marsh and ecotone and was also found within the low forest (Figure 3). A characteristic species of the high marsh on the United States east coast (Kneib 1982; Thompson 1984; Johnson 2011), *O. grillus* is typically found in salinities over twenty (Kneib 1982; Goetz, pers. obs.); however, here it was found in plots with salinities as low as 2.9 (Smith et al. 2021). Corresponding to an expanded salinity range, *O. grillus* was also found in zones along the marsh-forest gradient with diverse plant community characteristics. In addition to its typical high marsh habitat, where ground cover is primarily *Spartina patens* and *Distichlis spicata*, here it was collected in the ecotone and low

forest, zones that additionally contain *Phragmites australis* and dead or dying trees. This suggests that *O. grillus* may be a habitat generalist and capable of expanding its distribution into the retreating forest before the forest canopy has fully died back—an early indicator of forest transition to marsh. This follows with previous work that has identified *O. grillus* as a habitat generalist within the marsh itself, abundant in marshes dominated by the invasive *P. australis* (Angradi et al. 2001). As the most inland zone containing *O. grillus*, the low forest is the zone with earliest signs of arthropod community changes and accommodation of saltmarsh species along the marsh-forest gradient.

Collembola (springtails) showed the opposite pattern of *O. grillus*, declining in abundance from high forest plots toward the marsh, with a significant decline occurring between low forest and ecotone. Certain Collembola species live in salt marshes, but the osmotic stress of dynamic saline conditions and highly saline food reduces feeding rates and growth for even marsh-adapted species (Witteveen 1988). Within salt marshes, the diversity and density of mesofauna, including Collembola, decreases from high marsh to low marsh, attributed to an increase in inundation frequency and requirement of high levels of habitat specialization to reside in frequently inundated areas (Widenfalk et al. 2015; Haynert et al. 2017). It follows, then, that Collembola density would be greater in zones that are very rarely saturated (i.e., high forest) where individuals encounter less stress and greater numbers of species and individuals can survive. Although low relative to the marsh, the low and mid forest zones at this study site have higher soil salinity and moisture content than the high forest (Fagherazzi and Nordio 2022) and can be inundated independent of tide or storm surge (Goetz, pers. obs.). Increased inundation frequency, coupled with slightly elevated soil salinity, may make these zones less desirable habitat or preclude certain species from surviving.

Aside from taxa exhibiting linear changes along the marsh-forest gradient, certain taxa were associated with specific zones within the gradient. The presence of unique taxa in the ecotone and low forest provides additional evidence for changes in the forest beginning farther inland than the marsh or even the marsh-forest ecotone. Multiple ant genera were associated with specific zones at the marsh-forest boundary: *Aphaenogaster* in the low forest and *Monomorium* and *Solenopsis* in the ecotone. Certain ant species have been associated with distinct habitat zones in past work (Chen et al. 2015; Canepuccia et al. 2016), and drivers like salinity, ground cover, and plant diversity likely contributed to their distribution here. There was also strong ecotone association of one subfamily of beetle collected in leaf litter communities—Hydrophilinae (family Hydrophilidae), specifically *Paracymus* sp., was abundant in every ecotone plot but otherwise rare (Figure 3). Its dominant presence in the ecotone, where salinity is not spatially uniform, suggests that environmental conditions specific to the ecotone aside from salinity factored into its distribution. Hydrophilidae beetles are commonly aquatic and may be attracted to standing water or decomposing material, but they are rarely found in brackish or saline water (Van Tassell 2001). The ecotone may serve as the uniquely suitable habitat for Hydrophilinae along the marsh-forest gradient due to its frequent inundation, large volume of decaying litter, and lower soil and standing water salinities than the marsh. Martínez-Falcón et al. (2018) found that, while most beetles avoided habitat edges, some species showed a unimodal preference for a specific distance from the edge within one of the adjacent habitats, similar to the patterns seen here.

4.1.2 Diversity Patterns

Changes in species composition along the gradient also impacted diversity indices due to overlapping distributions of forest, marsh, and ecotonal taxa and changes in abundance across the marsh-forest gradient. For pitfall samples, differences in Shannon diversity across zones only partially supported my hypothesis of highest diversity in the ecotone, with dual insignificant peaks in diversity in the ecotone and high forest. Raw richness decreased from high forest to marsh. I expected taxonomic richness to be low in the marsh, as fewer species are adapted to tolerate the hostile and dynamic salinity and inundation (Pan et al. 2018), but the observed low richness at the ecotone deviated from my hypothesis. When rarefied, however, both diversity indices were highest at the ecotone. Importantly, when extrapolated, these trends persisted, with ecotone diversity indices remaining significantly higher than other zones. Here, rarefied diversity indices indicate that the ecotone has the highest richness and Shannon diversity of taxa collected by pitfall trap, consistent with my hypothesis and with previous work that has demonstrated increased arthropod diversity at the marsh-upland ecotone (Traut 2005).

At the ecotone, overlapping marsh grasses and remnants of forest canopy provide both forest and marsh habitat characteristics, likely leading to increased habitat complexity. This overlap in habitat is likely what supported the overlap in forest, marsh and ecotone arthropod taxa that led to higher ecotonal diversity. Increased vertical structural complexity may correspond to increased niche availability for taxa that can expand vertically (Lawton 1983; Brose 2003), such as spiders that may separate into ground hunters and orb weavers (Finke and Denno 2002). Indeed, arthropod species richness is positively correlated with habitat complexity (Uetz 1979; Gardner et al. 1995; Yusah and Foster 2016; Martello et al. 2022), including in salt marshes (Döbel et al. 1990; Traut 2005 (spiders); Ford et al. 2017 (spiders and beetles); Torma et

al. 2017 (true bugs)). The results of this study support previous work that has found a peak in diversity at ecotones (Traut 2005; Horváth et al. 2010) as well as work that has demonstrated that overlapping grasslands and trees offer increased niche availability and richness (Martello et al. 2022). As marsh continues to migrate inland under remnants of the forest, the expanse of ecotone with elevated habitat complexity may increase, leading to an increase in the area that can support greater arthropod diversity, although these effects may be ephemeral, depending on the rate of forest retreat and full conversion of ecotone to marsh. As it expands, the ecotone may also begin to show greater intra-ecotone variation in composition and diversity, with an additional gradient forming within the ecotone itself.

Contrary to pitfall traps, leaf litter samples did not show any differences in diversity indices between zones, and both abundance and richness were overall lower than pitfall traps. When rarefied, richness in the mid forest was significantly higher than all other zones; however, the mid forest had low coverage overall, causing the other zones to be rarefied to very low sample sizes (e.g., two individuals in the high marsh), leading to high uncertainty and making any patterns difficult to discern.

4.1.3 Springtail, Ant, and Beetle Communities

Patterns of springtail community composition and diversity suggest that fewer taxa were able to survive in the marsh, causing a shift in community composition. Springtails did not follow my hypothesis of increased diversity at the ecotone, likely due to salinity or inundation intolerances, and contributed to the secondary peak in total community diversity in the high forest. Springtail community composition and diversity likely strongly influenced total pitfall community analyses because of their high abundance. Thus, that entire community diversity

patterns deviated from springtail patterns suggests that other taxa must show greater diversity outside of the high forest.

Ants exhibited dual peaks in taxonomic richness in the high forest and ecotone compared to adjacent zones, suggesting ants may be a driving taxon behind the observed peak in ecotonal diversity indices. Changes in ant community composition as well as the peak in diversity at the ecotone can likely be attributed to the unique ant taxa found at the ecotone. These ant community results support previous studies that have found greater ant species richness in areas with overlapping grassland and forest structures (Martello et al. 2022), an increase in generalist ant species in dynamic areas (Martello et al. 2022), and greater ant richness closer to small-scale habitat edges (Lasmar et al. 2021).

Although beetle community composition and diversity did not appear to differ by zone, there were clear patterns in multiple beetle taxa (Pselaphinae and Hydrophilinae) that showed compositional changes across the gradient. Similar to the leaf litter samples as a whole, coverage for beetle communities was low, and thus the significantly higher rarefied richness in high and mid forest compared to the lower zones must be interpreted cautiously.

4.2 Ghost Forest Ecotone and High Marsh Ecological Equivalency

Overall, ghost forest habitat appeared to support saltmarsh species both structurally and functionally, despite differences in community composition due to additional terrestrial species in the ghost forest and greater variation in the diet of *O. grillus* in the ghost forest. Most marsh species were present in the ghost forest, and both observed species' diets were primarily derived from the marsh grass and detritus food webs.

4.2.1 Structural Equivalency

Community composition was different in pitfall, but not leaf litter or infauna, communities between ghost forest and high marsh. As in 2019, the primary drivers were additional species of ants and springtails found in the ghost forest pitfall community. These additional species are reflected in the greater richness and diversity observed in the ghost forest compared to the high marsh. Although the ghost forest contained additional species, there were very few taxa in the marsh that were not also found in the ghost forest. Where communities differed (i.e., pitfall communities), it was largely driven by the addition of forest species rather than the absence of marsh species. Ghost forest and high marsh invertebrate communities were not the same; however, when considering the ghost forest's ability to provide habitat for marsh species as they migrate inland, the ghost forest appears to be sufficient and to effectively serve as expanded marsh. The additional (terrestrial) species found in the ghost forest may create novel community interactions via predation or competition, however, which may affect marsh species abundance, behavior, or fitness.

Although infauna community composition was not significantly different between zones, the abundances of certain taxa differed (Figure 11), which may have been due to differences in sediment structure, food availability, and physical characteristics. Bulk density was higher in the ghost forest, and the more compact sediment may be less desirable for certain infauna. Although organic content measured through loss on ignition did not differ between zones, results may have been confounded by increased root matter in the ghost forest compared to high marsh, which may have masked differences in the detrital organic material on which infauna rely (Craft and Sacco 2003) and which is typically higher in older marshes (Craft et al. 2002).

4.2.2 Functional Equivalency

Of the two invertebrate species assessed, *O. grillus* showed more substantial differences in basal carbon source between zones. In both zones, the majority of its diet was comprised of marsh grasses and detritus. In the ghost forest, however, *O. grillus* exhibited increased variability in $\delta^{13}\text{C}$ and thus greater niche width, likely driven by its consumption of cedar detritus. This supports previous work that has identified *O. grillus* as a diet opportunist under varying food source abundances (Pascal and Fleeger 2013). Similar to its ability to move into different habitats (i.e., low forest), *O. grillus* exhibited generalist behavior by incorporating new types of available detritus into its diet in its expanded marsh habitat, the ghost forest.

Despite this diet expansion, the majority of the *O. grillus* diet in both zones was comprised of marsh producers and detritus. Even in the ghost forest, the contribution of terrestrial sources to assimilated body mass was small, reflective of the overall small percentage of detritus with terrestrial origins (Figure 16). *O. grillus* may have greater capacity to process litter from marsh species or may preferentially select marsh grasses with low C/N over terrestrial species with more structural compounds. Zimmer et al. (2002) found that terrestrial-sourced detritus was better digested by terrestrial detritivores that had higher tolerances for the cellulose and phenolics specific to terrestrial detritus than their marsh counterparts. Bottom-up effects of detrital composition may alter consumer feeding behavior or growth, depending on the species' digestive ability and preference (Zimmer et al. 2002, 2004; Hübner et al. 2015); however, observed differences in diet did not lead to a significant difference in body size for *O. grillus*, although sample size for body condition comparison was low in the ghost forest, and subtle differences in size or variation may not have been captured by sampling efforts.

There were limited differences in diet for the predator *Pardosa littoralis*, for which differences in isotopic signatures between zones largely corresponded to intra-specific producer species' variation between zones and did not reflect a major difference in carbon source or trophic level. *P. littoralis* in the high marsh may have consumed more prey from the algae food web than those in the ghost forest, but most of its diet in both zones came from the marsh grass and detritus food webs. Interestingly, although there was no major difference in diet, there was a significant difference in body condition. *P. littoralis* had a higher dry weight-to-length ratio (i.e., more robust body condition) in the high marsh when juveniles were collected in the fall. This difference in body condition may have resulted from greater access to an algae-based food web, 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 (lower relative nitrogen) in the marsh (Figure 13).

Alternatively, differences in body condition may have stemmed from differences in foraging ability due to differences in habitat structure. The high marsh contains both dense thatch and vegetation, as well as open (bare or flooded) areas (Figure 16). In the high marsh, open areas caused by ponding may serve as efficient hunting grounds, similar to the interstitial space between plants in the low marsh, which increases foraging efficiency (Lewis and Denno 2009). Increased vegetation density and complexity can reduce ground predator hunting ability (Brose 2003) but also offers protection. In the drowning high marsh, *P. littoralis* may be able to hunt in the open but also escape into dense vegetation surrounding open hunting grounds, where they can seek refuge from their own predators (Jeffries and Lawton 1984; Brose 2003; Moran et al. 2010), including larger conspecifics (Langellotto and Denno 2004). The patchiness in the drowning high marsh likely resembles habitat edges between *S. patens* and *S. alterniflora*, which

P. littoralis have been shown to favor (Wimp et al. 2019). Greater hunting efficiency caused by open space bordered by refuge habitat may lead to more rapid weight gain in young spiders that may otherwise spend more time hiding or hunting in less optimal habitat (i.e., homogeneous dense vegetation). When body condition was re-assessed for the same generation of spiders in the spring after they had reached maturity, however, there was no significant difference in body size. This suggests that any differences in foraging behavior are specific to juveniles and do not have long-term effects on body condition.

5. SUMMARY AND CONCLUSIONS

Beginning in the low forest, differences in arthropod community composition were driven by indicator taxa that were the first to appear in forest converting to marsh (*Orchestia grillus* and Pselaphinae), taxa that decreased in abundance toward the marsh (Collembola), and taxa unique to specific zones undergoing rapid change between ecosystems (*Monomorium*, *Aphaenogaster*, and Hydrophilinae). In pitfall samples, the marsh-forest ecotone supported both unique taxa and higher diversity. Ghost forest, the final stage of forest conversion to marsh, showed expanded variability in both invertebrate community composition and diet of the detritivore *O. grillus*; however, it supported almost all species found in the high marsh, and neither primary diet contribution nor mature body condition differed between zones for *O. grillus* or *P. littoralis*, indicating that the ghost forest is largely ecologically equivalent to the high marsh for the observed species at this study site.

Based on these results, I determined that forest retreat and marsh migration provide an important opportunity for saltmarsh invertebrates, especially generalists, to migrate inland with, and even in advance of, marsh vegetation. As habitat in the high marsh begins to drown and become unsuitable for high marsh species, marsh that replaces retreating upland becomes even more essential as habitat for invertebrate communities. Additionally, the dynamic zone between forest and marsh is a critical ecotone, providing opportunity for not only early inland migration of generalist marsh species but also potentially elevated arthropod diversity. The abundance of indicator species of marsh migration, such as *O. grillus*, may offer insight into the status of forest conversion to marsh. Similar species may show comparable patterns at other sites, and

assessments of other converting forests may consider using the taxa that exhibited the strongest patterns in this study (i.e., amphipods and springtails) as indicators of forest retreat.

As more ghost forest forms with accelerating sea-level rise, its ecological equivalency should be considered during spatial quantification of marsh. Both species observed here utilized ghost forest in approximately the same way as high marsh, but saltmarsh species that are specialists may not thrive in the same way, by being either incapable of migrating into new habitat or unable to utilize ghost forest habitat as effectively. Observed overlap in marsh and forest species may lead to novel interactions between invertebrates throughout the marsh-forest ecotone, with unknown consequences for saltmarsh species' fitness. Physiological and biotic stressors will likely affect invertebrate species differently as they migrate inland, as has been observed for plants (Jobe and Gedan 2021).

This work presents the first data on invertebrate communities in a retreating forest and migrating marsh and indicates many future directions of study. Additional work should be done to determine if the taxonomic patterns observed here hold true across multiple sites, especially those where ghost forest does not share ground cover species with adjacent marsh (e.g., *Phragmites australis* ghost forest), and how observed patterns deviate with both intra- and interannual variation. Future studies should also incorporate assessment of environmental characteristics of the ecotone and adjacent systems to determine the drivers of changes in community composition and diversity across the ecotone. Despite the presence of marsh invertebrates in the ghost forest known from this study, consumers of invertebrates do not always utilize ghost forest as frequently as high marsh (Taillie and Moorman 2019). Future studies should consider trophic dynamics between invertebrates and higher trophic levels in the ghost

forest to better understand any discrepancy in habitat use between trophic levels and the implications for the overall ecosystem.

TABLES AND FIGURES

Table 1. Indicator taxa and zone association from pitfall trap and leaf litter communities (2019).

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

Table 2. Estimated coverage, observed richness, and coverage-based rarefied richness and Shannon diversity values for each zone [confidence interval] for pitfall and leaf litter communities (2019).

		High forest	Mid forest	Low forest	Ecotone	Marsh
Pitfall						
	Coverage	0.971	0.967	0.960	0.893	0.930
	Observed	40	32	37	34	18
	Rarefied richness	18.09 [16.5-19.7]	15.77 [14.0-17.6]	14.23 [12.6-15.9]	34 [25.5-42.5]	15.27 [12.7-17.9]
	Rarefied Shannon	9.69 [8.7-10.7]	7.65 [6.6-8.7]	7.34 [6.5-8.2]	16.65 [13.3-20.0]	7.04 [5.3-8.8]
Leaf Litter						
	Coverage	0.912	0.752	0.866	0.939	0.940
	Observed	21	17	18	16	14
	Rarefied richness	1.4 [1.3-1.5]	17 [12.0-22.0]	3.04 [2.5-3.5]	3.73 [3.4-4.1]	1.89 [1.8-2.0]
	Rarefied Shannon	1.32 [1.2-1.4]	9.08 [5.0-13.2]	2.29 [1.8-2.8]	3.18 [2.8-3.5]	1.72 [1.6-1.9]

Table 3. Estimated coverage, observed richness, and coverage-based rarefied richness and Shannon diversity values for each zone [confidence interval] for springtail, ant, and beetle communities (2019).

	High forest	Mid forest	Low forest	Ecotone	Marsh
Springtail					
Coverage	0.992	0.989	1	0.933	1
Observed	9	9	6	5	4
Rarefied richness	5.8 [5.4-6.2]	4.8 [4.3-5.3]	4.5 [4.1-4.8]	5 [2.8-7.2]	3.9 [3.0-4.8]
Rarefied Shannon	4.5 [4.1-4.9]	3.8 [3.4-4.2]	3.8 [3.5-4]	2.4 [1.3-3.4]	3.7 [2.8-4.6]
Ant					
Coverage	0.892	1	1	0.925	NA
Observed	6	2	2	6	NA
Rarefied richness	6 [3.4-8.6]	1.8 [1.6-2.0]	1.7 [1.5-1.8]	3.8 [2.7-4.9]	NA
Rarefied Shannon	3.6 [2.1-5.0]	1.7 [1.5-1.8]	1.5 [1.4-1.7]	2.7 [2-3.4]	NA
Beetle					
Coverage	0.746	0.801	0.831	1	0.955
Observed	7	9	5	5	4
Rarefied richness	7 [4.6-9.4]	8.1 [6-10.1]	2.4 [1.5-3.3]	1.9 [1.7-2.1]	1 [1-1]
Rarefied Shannon	5.7 [3.4-8.1]	7 [4.9-9.1]	2 [1.0-2.9]	1.8 [1.6-2.0]	1 [1-1]

Table 4. Indicator taxa and zone association from pitfall trap, leaf litter, and infauna communities (2020).

	Common name	Taxon	Associated zone	p-value
Pitfall	Springtail	Entomobryidae	Ecotone	0.009
	Springtail	Hypogastruridae	Ecotone	0.009
	Springtail	Sminthuridae	Ecotone	0.009
	Ant	<i>Monomorium</i>	Ecotone	0.009
	Spider	Araneidae	High marsh	0.045
Infauna	Fly larva	Chironomidae larva	Ecotone	0.033

Table 5. Stable isotope values (‰) for all consumers and sources collected from high marsh (HM) and ghost forest ecotone (E). Values are mean \pm standard deviation (sample size). OG=*Orchestia grillus*; PL=*Pardosa littoralis*; det=detritus; DS=*Distichlis spicata*; SP=*Spartina patens*; SA=*Spartina alterniflora*; JV=*Juniperus virginiana* (cedar); PA=*Phragmites australis*; Wainright *Sp*=average of *Spartina patens*, *Spartina alterniflora*, and detritus $\delta^{34}\text{S}$ from Wainright et al (2000) and average of *Distichlis spicata*, *Spartina patens*, and detritus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from this study.

Consumer/source	Zone	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
OG	HM	-15.6 \pm 0.9 (10)	0.9 \pm 0.4 (10)	8.8 \pm 1.5 (10)
OG	E	-16 \pm 2.6 (8)	1.8 \pm 1 (8)	11.6 \pm 1.1 (8)
PL	HM	-17.6 \pm 0.5 (10)	6.8 \pm 0.3 (10)	-0.8 \pm 0.6 (10)
PL	E	-16.1 \pm 0.4 (10)	7.7 \pm 0.4 (10)	4.9 \pm 1 (10)
det	HM	-15.1 \pm 0.4 (5)	0.4 \pm 0.5 (5)	-0.5 \pm 4.7 (5)
det	E	-15.5 \pm 0.6 (5)	1.2 \pm 0.6 (5)	2.4 \pm 2.3 (5)
DS	HM	-15.2 \pm 0.2 (5)	2.9 \pm 0.7 (5)	-8.1 \pm 1.3 (5)
DS	E	-14.7 \pm 0.1 (5)	3.5 \pm 0.6 (5)	-0.6 \pm 2.1 (5)
SP	HM	-14.3 \pm 0.2 (5)	1.9 \pm 0.6 (5)	-3.6 \pm 1.7 (5)
SP	E	-13.9 \pm 0.3 (5)	2.7 \pm 0.8 (5)	3.8 \pm 2.1 (5)
SA	HM	-13.8 \pm 0.2 (5)	-3 \pm 1.4 (5)	-10.4 \pm 3.1 (5)
algae	HM	-22.3 \pm 3.5 (5)	0 \pm 0.9 (5)	-2.8 \pm 8.9 (5)
JV	E	-26.6 \pm 0.1 (5)	-2.8 \pm 1.2 (5)	11.9 \pm 1.1 (5)
PA	E	-26.9 \pm 0.6 (5)	4.1 \pm 0.6 (5)	4.6 \pm 1.9 (5)
Wainright <i>Sp</i>	HM	-14.9 \pm 0.5 (15)	1.7 \pm 1.2 (15)	12.8 \pm 3.8 (17)
Wainright <i>Sp</i>	E	-14.7 \pm 0.8 (15)	2.5 \pm 1.1 (15)	12.8 \pm 3.8 (17)

Table 6. 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. SP, DS, det=averaged *Spartina patens*, *Distichlis spicata*, and detritus; SA=*Spartina alterniflora*; PA=*Phragmites australis*; JV=*Juniperus virginiana* (cedar); Wainright Sp=Wainright *Spartina*. Values are median [95% credible interval] percent contribution.

Source	<i>Orchestia grillus</i>		<i>Pardosa littoralis</i>	
	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]
Wainright Sp	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]

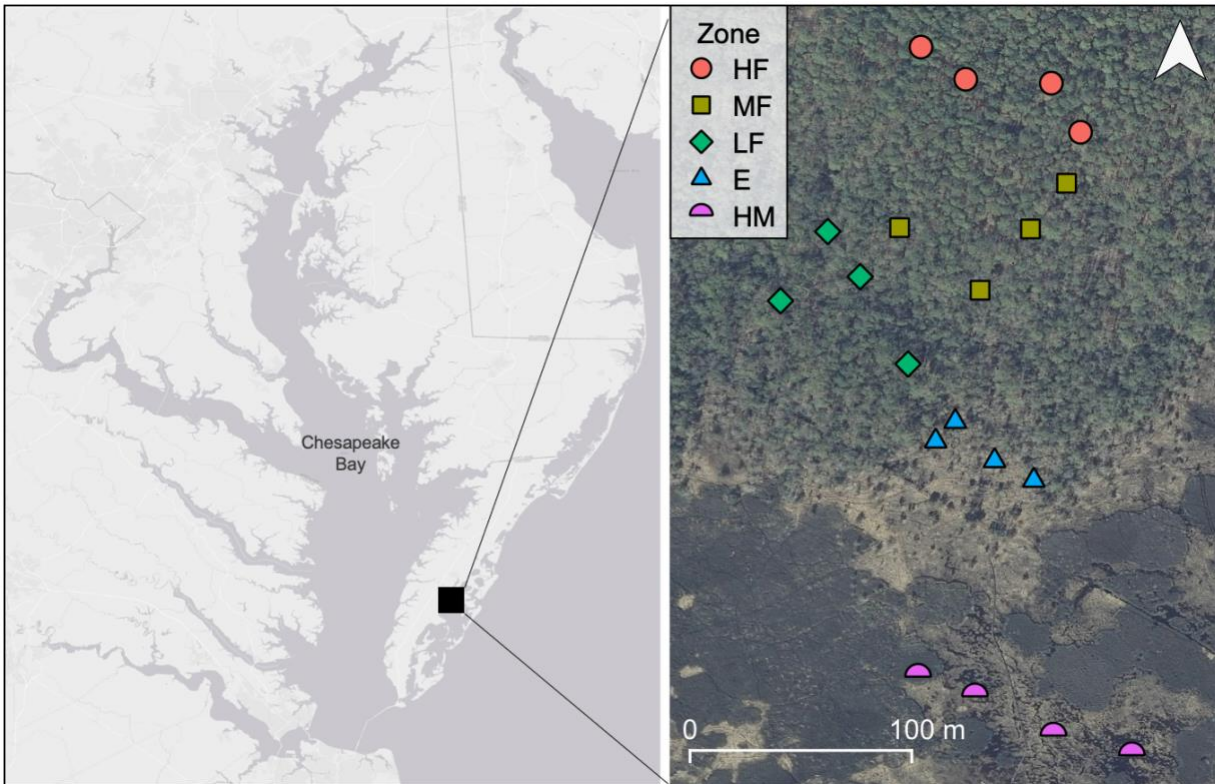


Figure 1. Study site (right) positioned relative to the Chesapeake Bay (left) showing plots along the forest-to-marsh gradient. Each point represents a plot, with shape and color corresponding to zone classification. HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh. Chesapeake Bay map (left) courtesy of Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS user community. High resolution orthoimagery (right) courtesy of the U.S. Geological Survey via EarthExplorer.

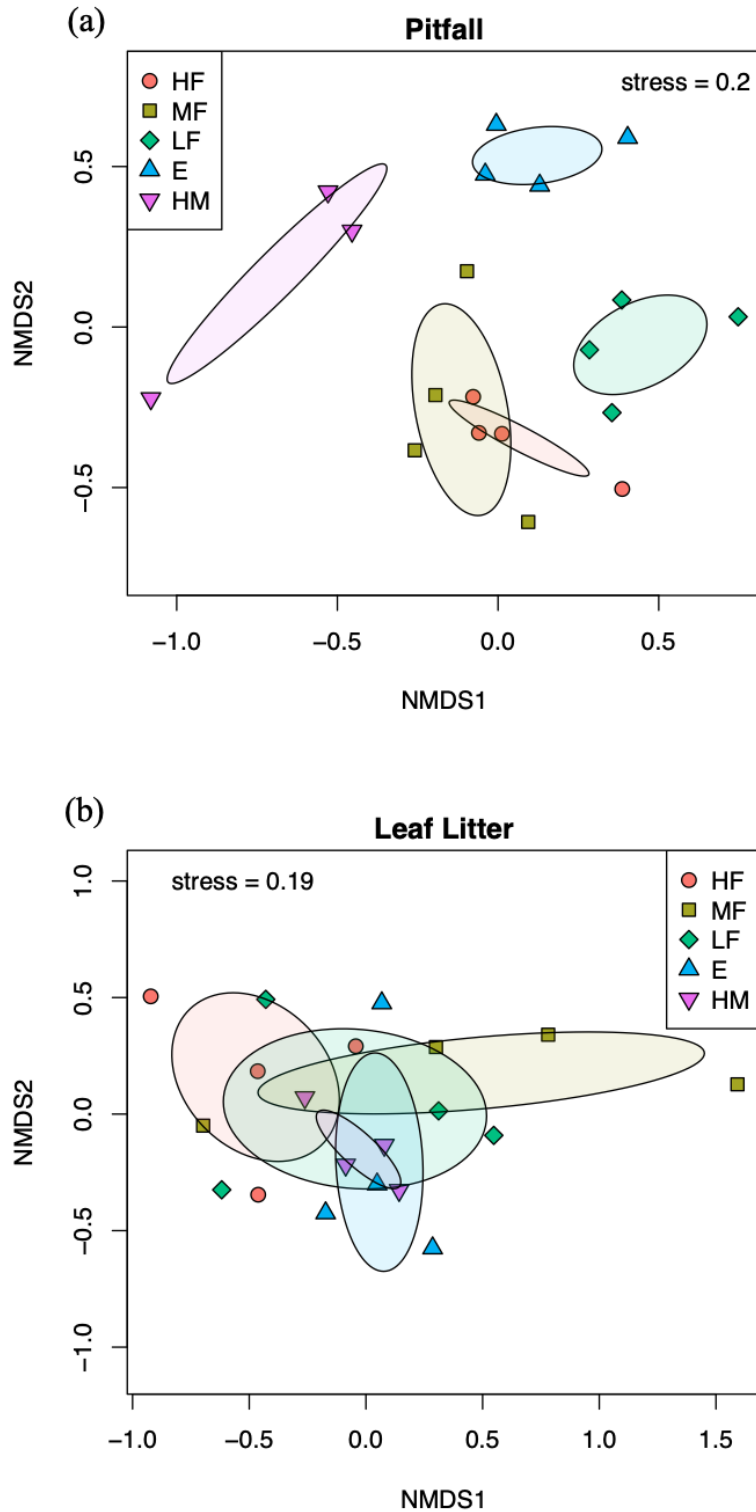


Figure 2. NMDS plots of communities from (a) pitfall and (b) leaf litter collections (2019). Ellipses are 40% confidence ellipses. HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

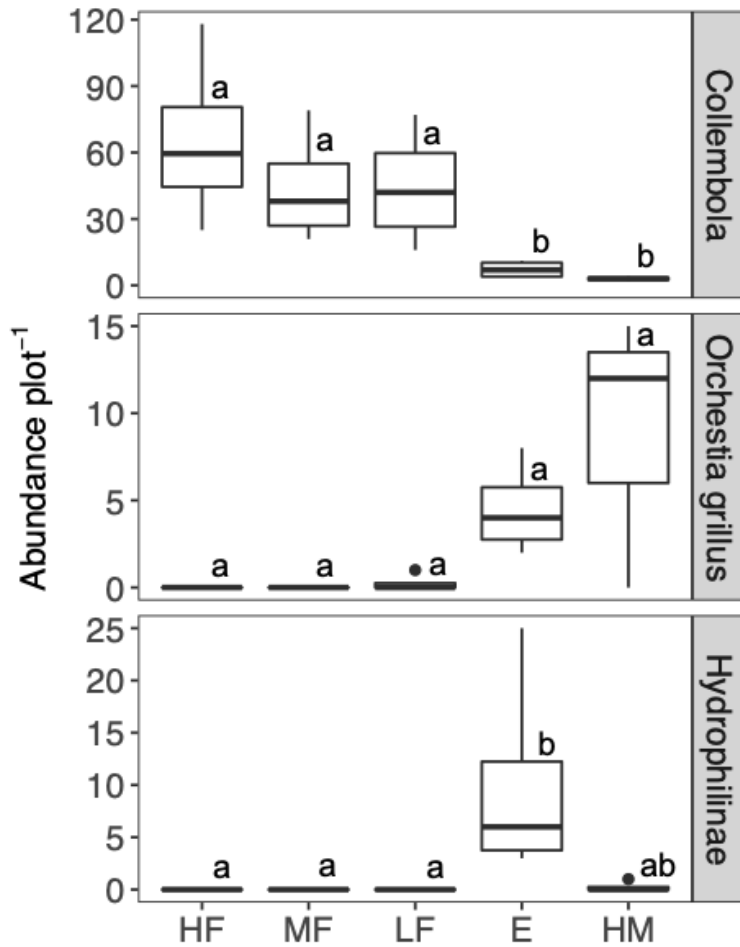


Figure 3. Abundance per plot of key taxa by zone for Collembola (springtails) from pitfall traps, *Orchestia grillus* (saltmarsh amphipod) from pitfall traps, and Hydrophilinae (subfamily of Hydrophilidae beetle) from leaf litter collection (2019). HF=high forest; MF=mid forest; LF=low forest; E=ecotone;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

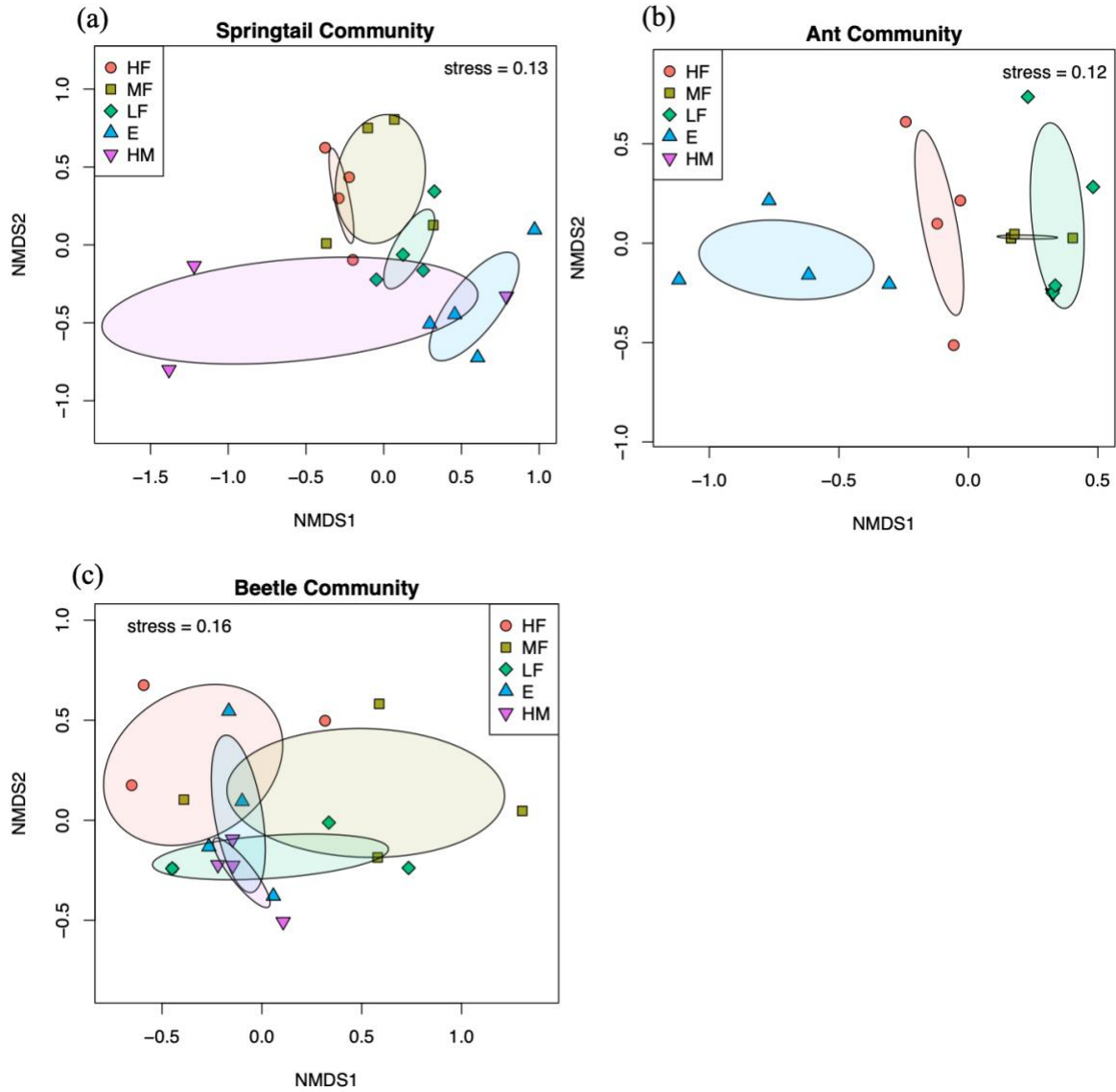


Figure 4. NMDS plots of individual communities of (a) springtails from pitfall traps, (b) ants from pitfall traps, and (c) beetles from leaf litter collection (2019). Ellipses are 40% confidence ellipses. HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

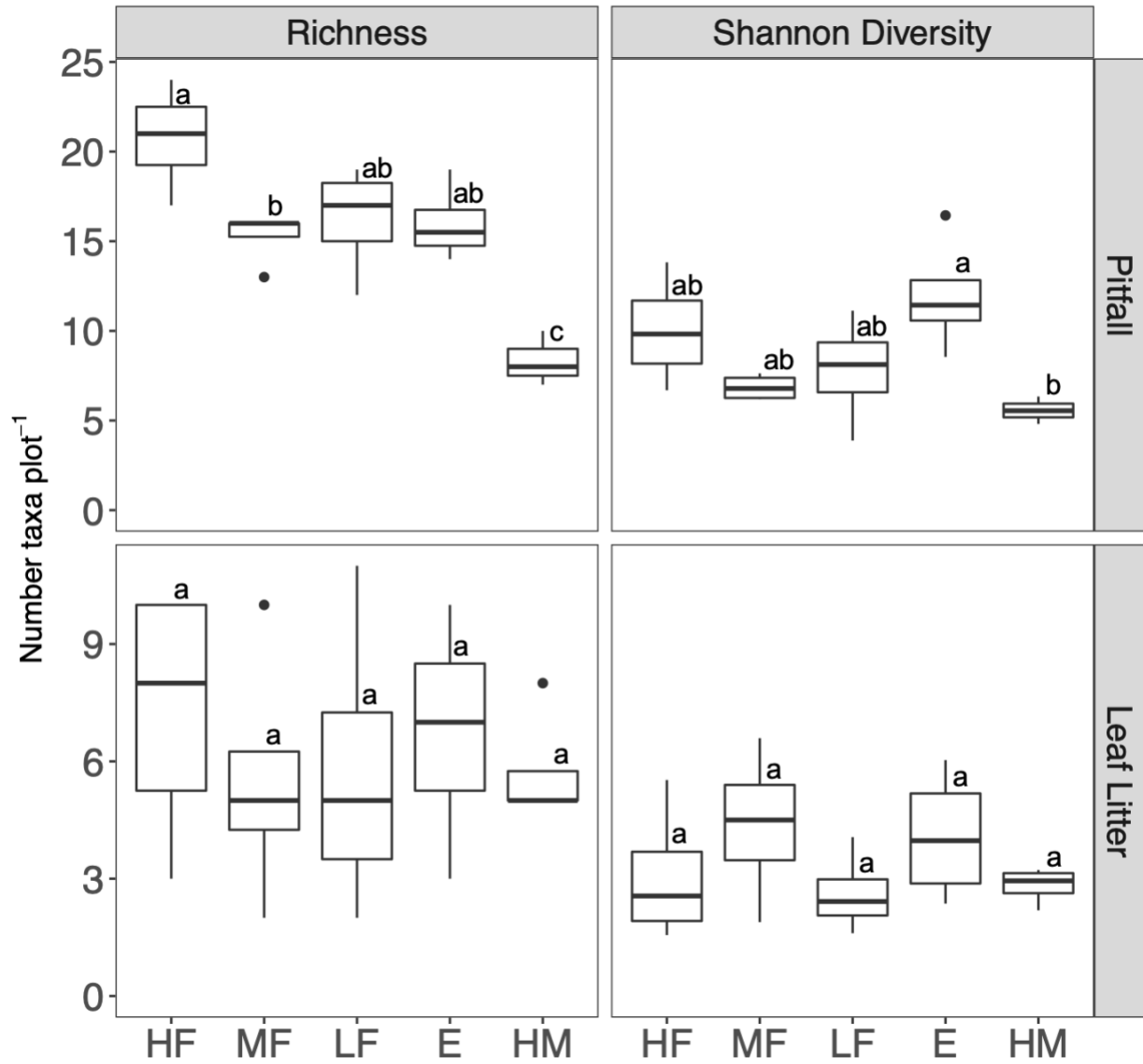


Figure 5. Richness (Hill numbers $q=0$) and Shannon diversity (Hill numbers $q=1$) for communities in pitfall and leaf litter collections (2019). HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

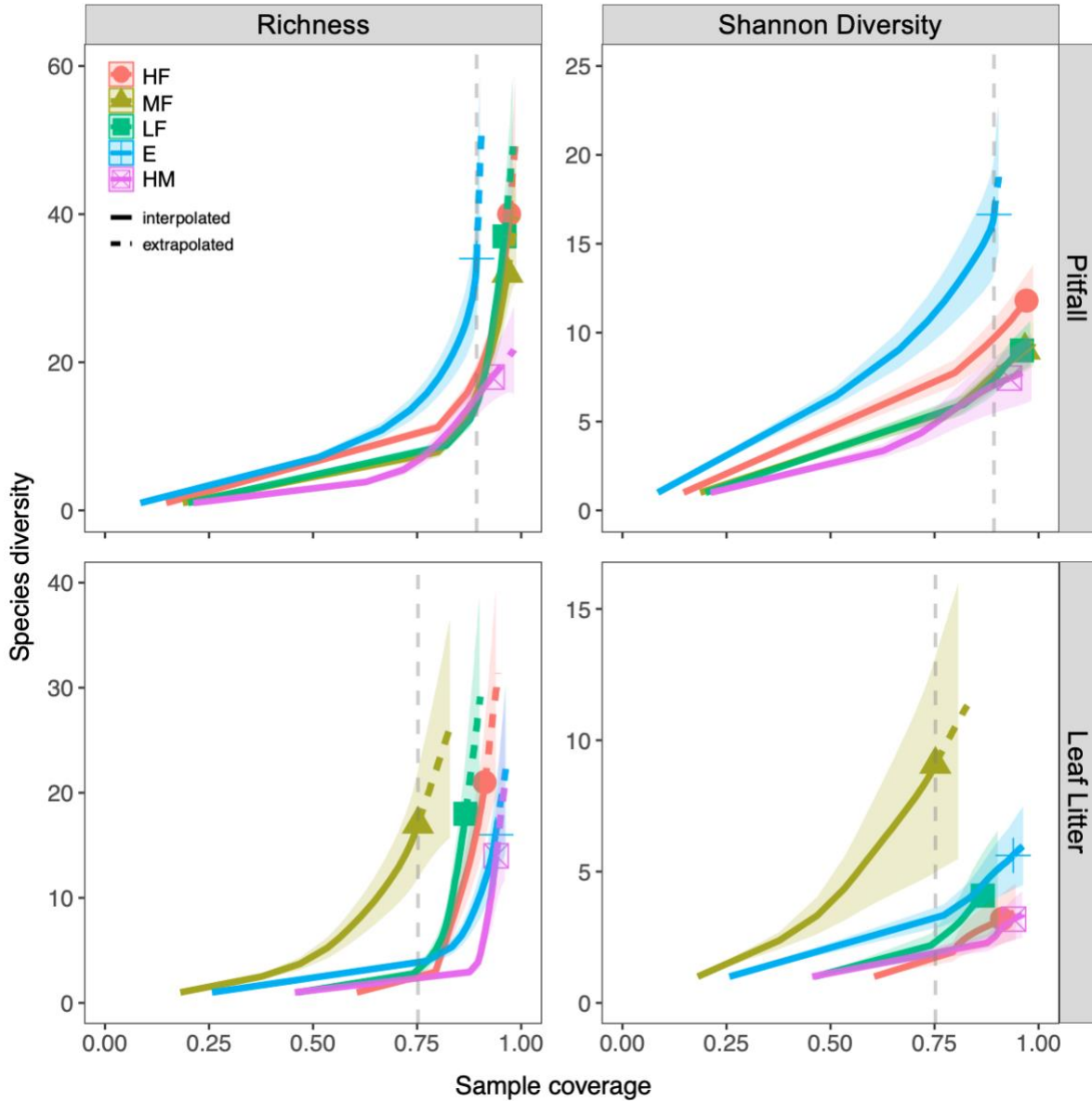


Figure 6. Coverage-based rarefaction (solid line) and extrapolation (dashed line) with 95% confidence intervals (shaded area) of richness (Hill numbers $q=0$) and Shannon diversity (Hill numbers $q=1$) for pitfall and leaf litter communities. Dashed gray vertical lines show the minimum zone coverage, or the coverage level to which richness was rarefied (2019). HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

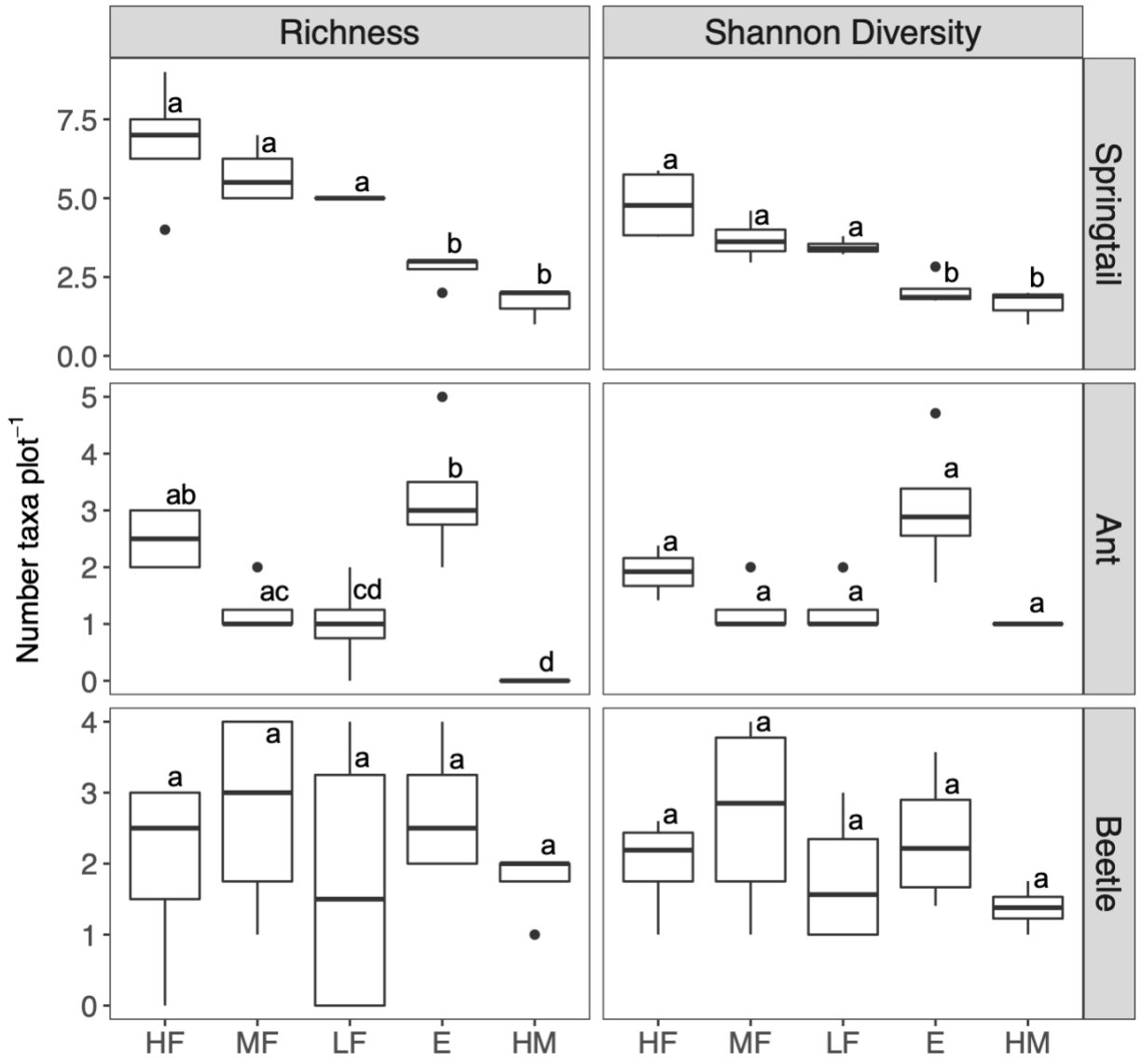


Figure 7. Richness (Hill numbers $q=0$) and Shannon diversity (Hill numbers $q=1$) for communities of springtails from pitfall traps, ants from pitfall traps, and beetles from leaf litter collection (2019). HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

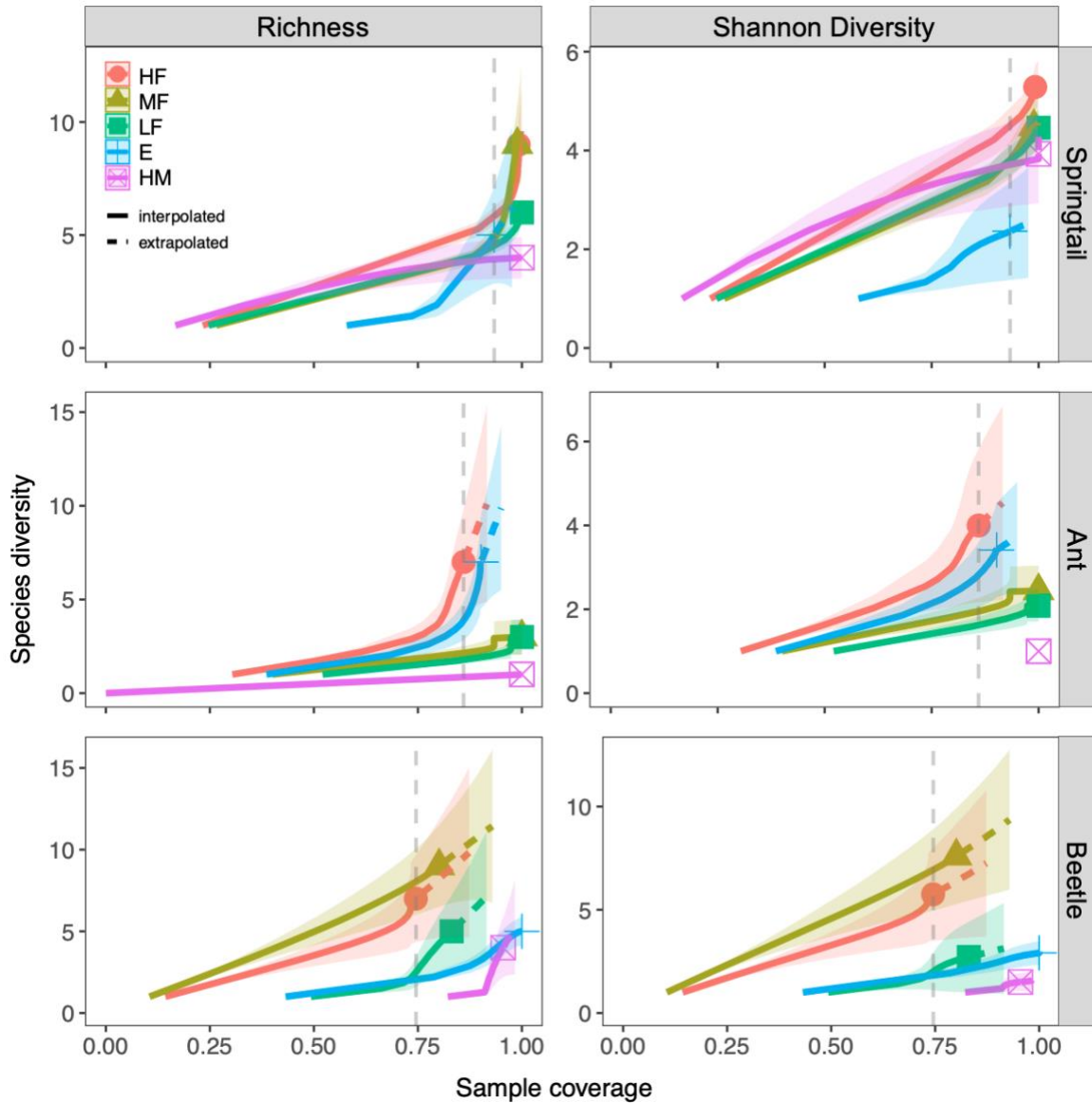


Figure 8. Coverage-based rarefaction and extrapolation with 95% confidence intervals (shaded area) of richness (Hill numbers $q=0$) and Shannon diversity (Hill numbers $q=1$) for communities of springtails from pitfall traps, ants from pitfall traps, and beetles from leaf litter collection. Dashed gray lines show the minimum zone coverage, or the coverage level to which richness was rarefied (2019). HF=high forest; MF=mid forest; LF=low forest; E=ecotone; HM=high marsh.

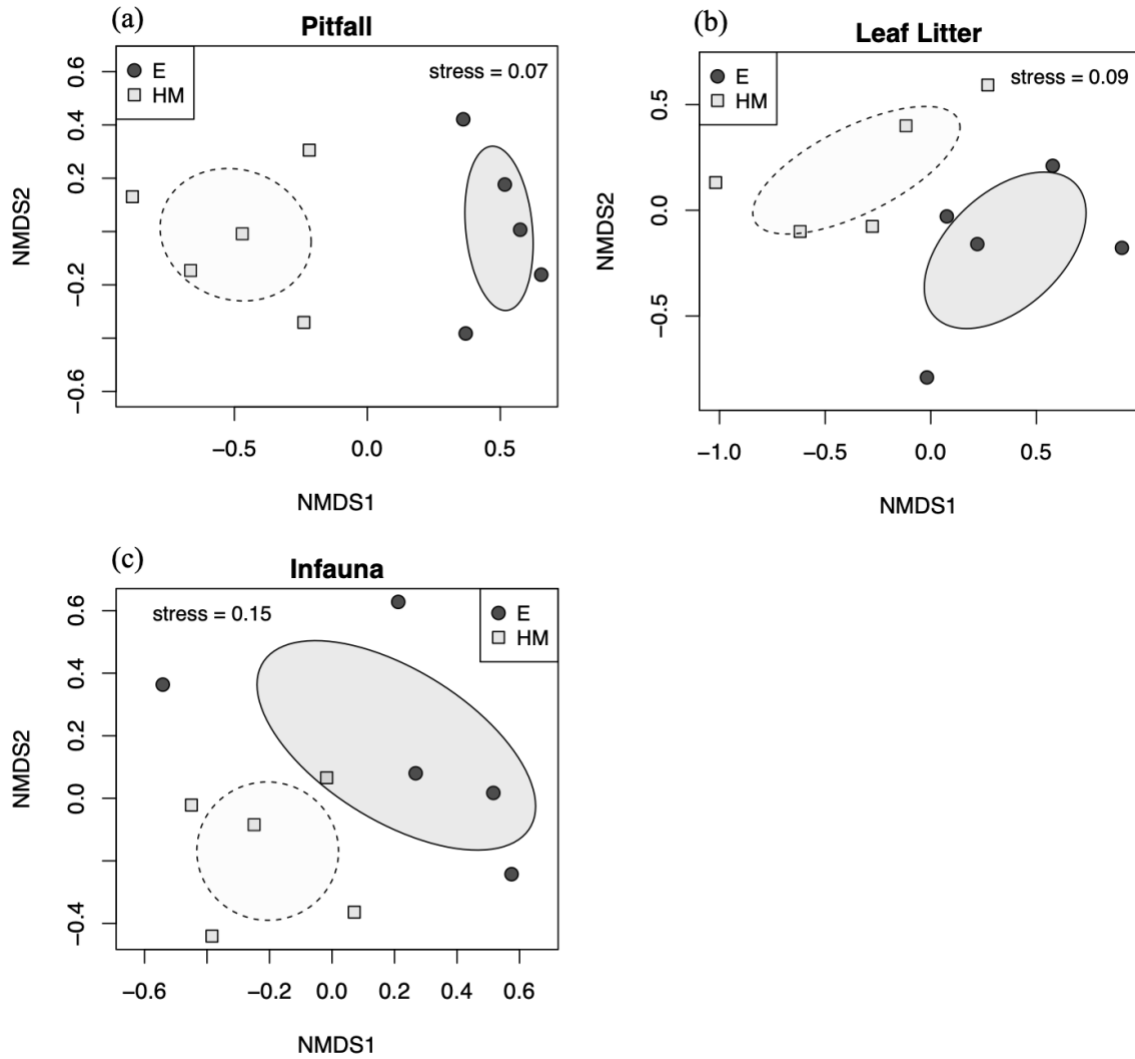


Figure 9. NMDS plots for (a) pitfall, (b) leaf litter, and (c) infauna communities (2020). Dark circles and solid ellipses are ghost forest ecotone (E). Pale squares and dashed ellipses are high marsh (HM). Ellipses are 40% confidence ellipses.

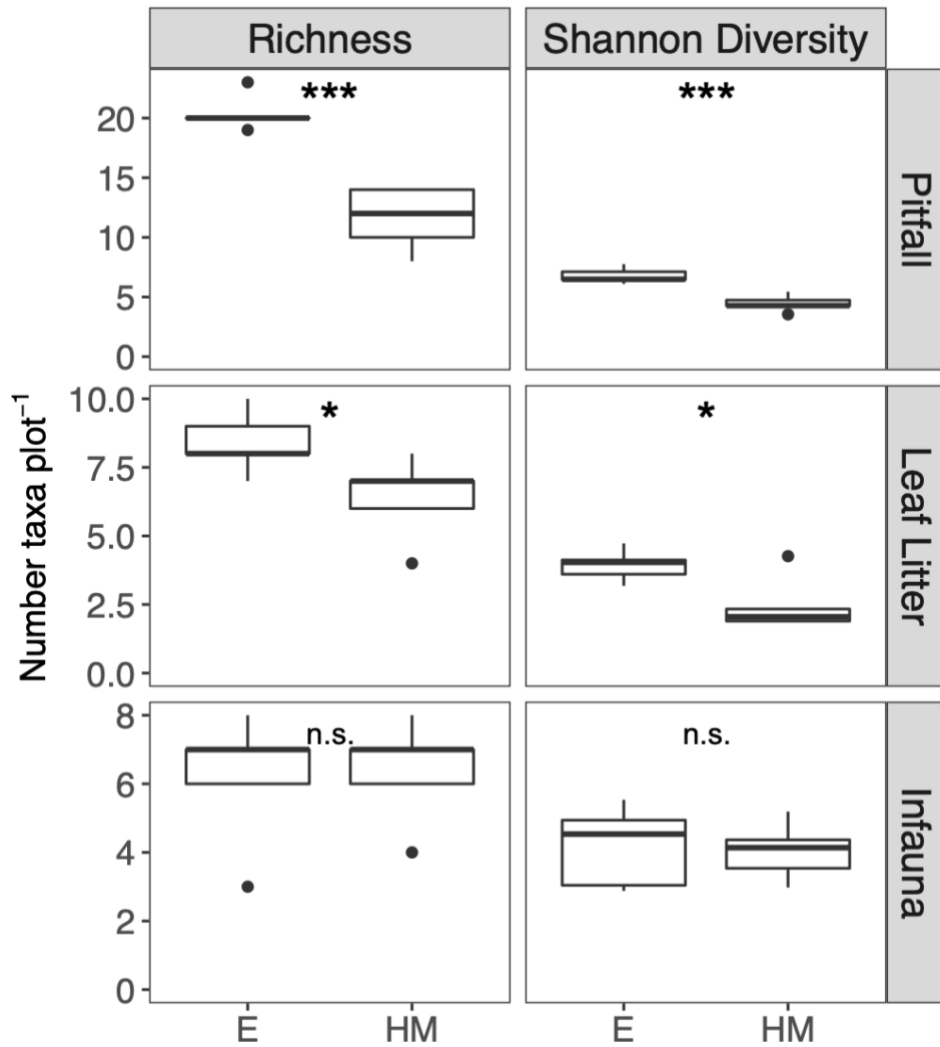


Figure 10. Richness (Hill numbers $q=0$) and Shannon diversity (Hill numbers $q=1$) for pitfall, leaf litter, and infauna communities in the ghost forest ecotone (E) and high marsh (HM) (2020). Asterisks denote significance (n.s. > 0.05, * < 0.05, ** < 0.01, *** < 0.001).

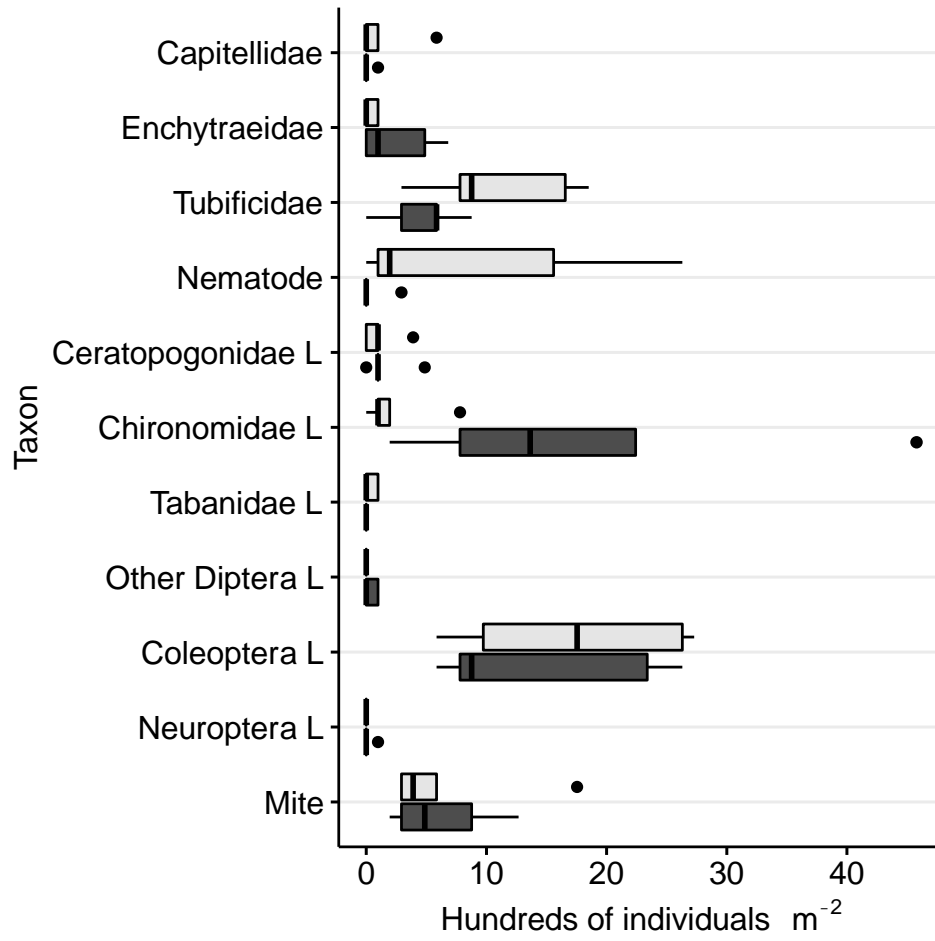


Figure 11. Abundance of infauna taxa in each zone (2020). Dark bars are ghost forest ecotone, and pale bars are high marsh. L indicates larva.

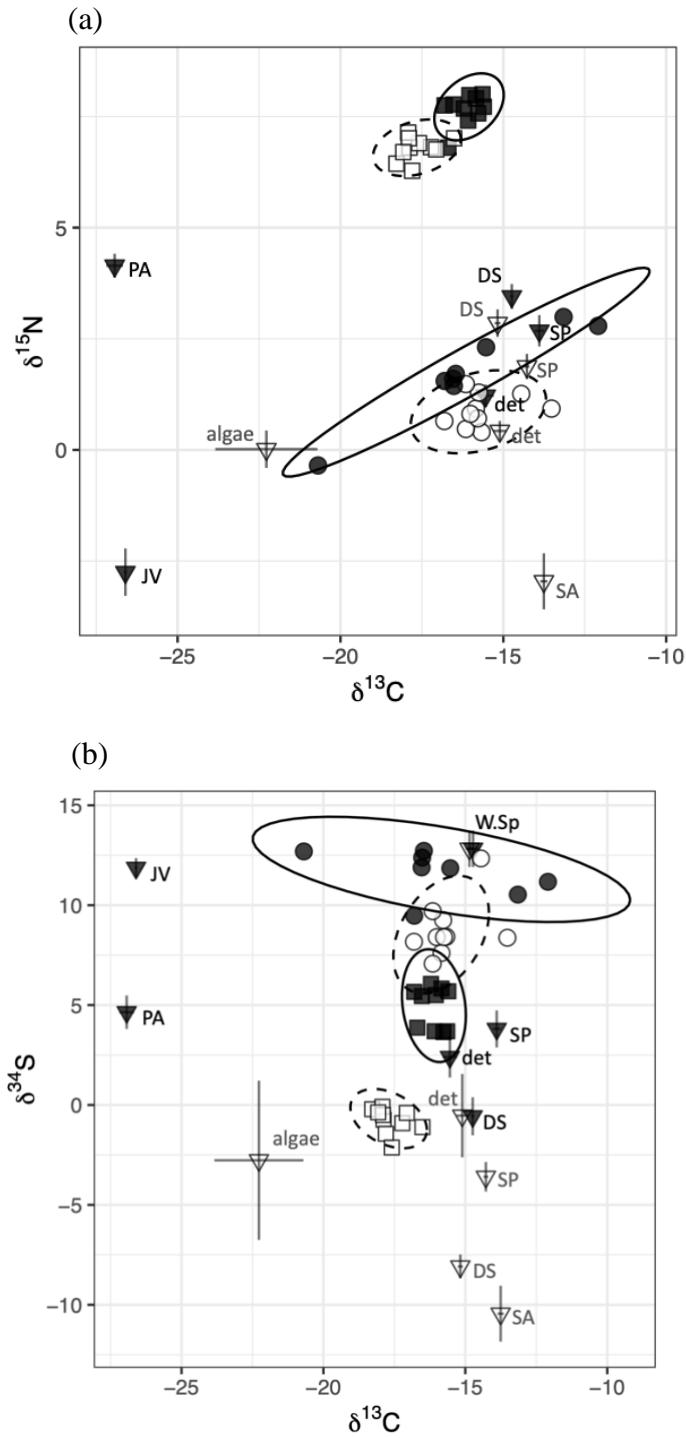


Figure 12. Isotope biplots for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ (‰) (2020). Filled shapes are ghost forest ecotone (E), and open shapes are high marsh (HM). Inverted triangles are producers, squares are *Pardosa littoralis*, and circles are *Orchestia grillus*. Ellipses encompass 95% of data points (solid line=E; dashed line=HM). SP=*Spartina patens*; DS=*Distichlis spicata*; SA=*Spartina alterniflora*; W.Sp=Wainright *Spartina*; det=detritus; JV=*Juniperus virginiana* (cedar); PA=*Phragmites australis*.

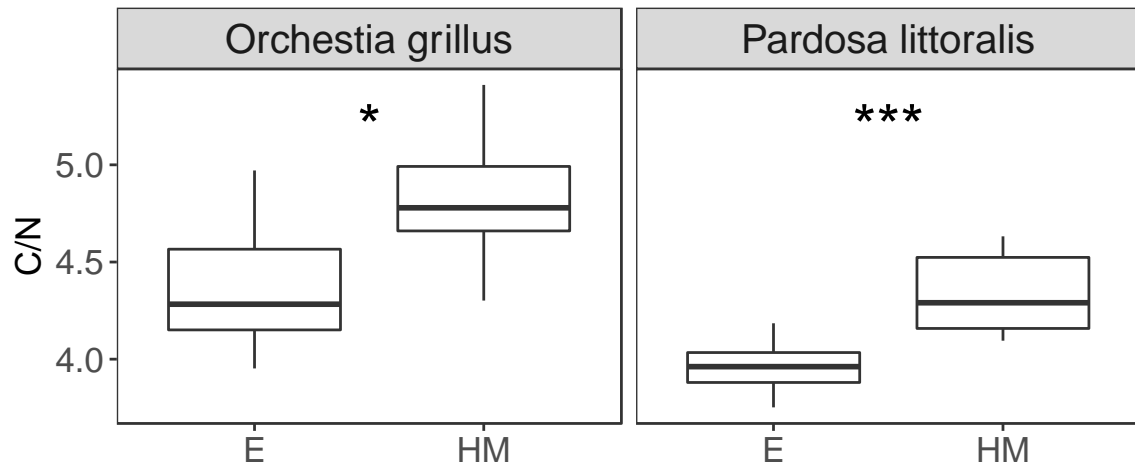


Figure 13. Carbon-to-nitrogen ratio (C/N) of consumers collected in fall 2020. E=ghost forest ecotone; HM=high marsh. Asterisks denote significance (n.s. > 0.05, * < 0.05, ** < 0.01, *** < 0.001).

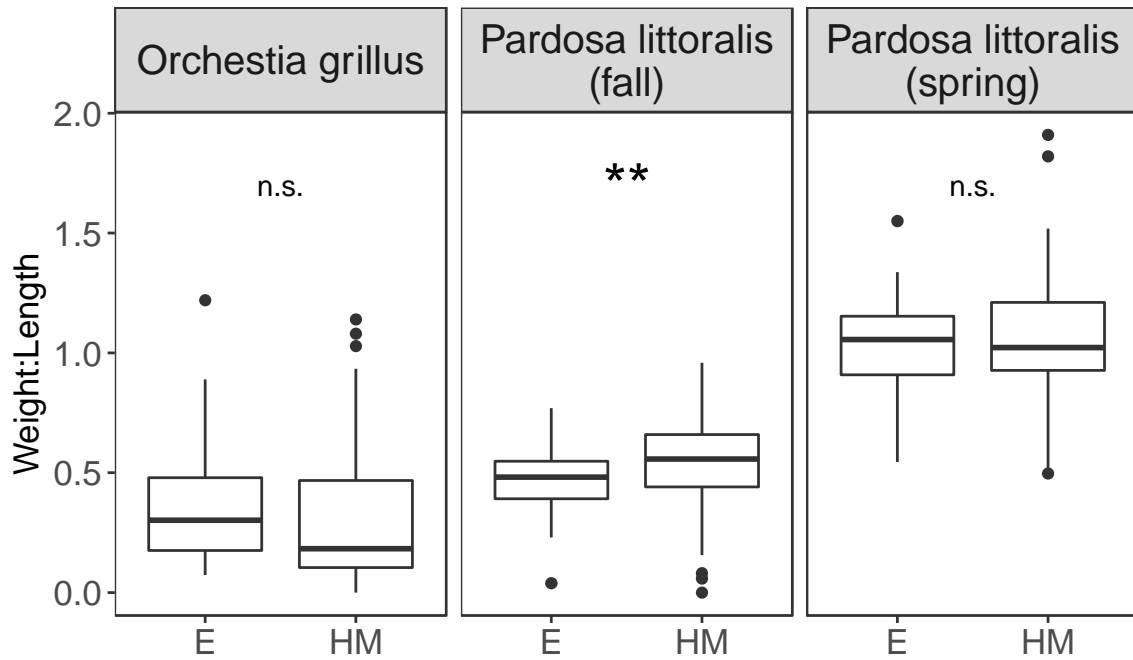


Figure 14. Body condition (dry weight divided by length) of *Orchestia grillus* and *Pardosa littoralis* collected in fall 2020 and spring 2021. E=ghost forest ecotone; HM=high marsh. Asterisks denote significance (n.s. > 0.05, * <0.05, ** < 0.01, *** < 0.001).

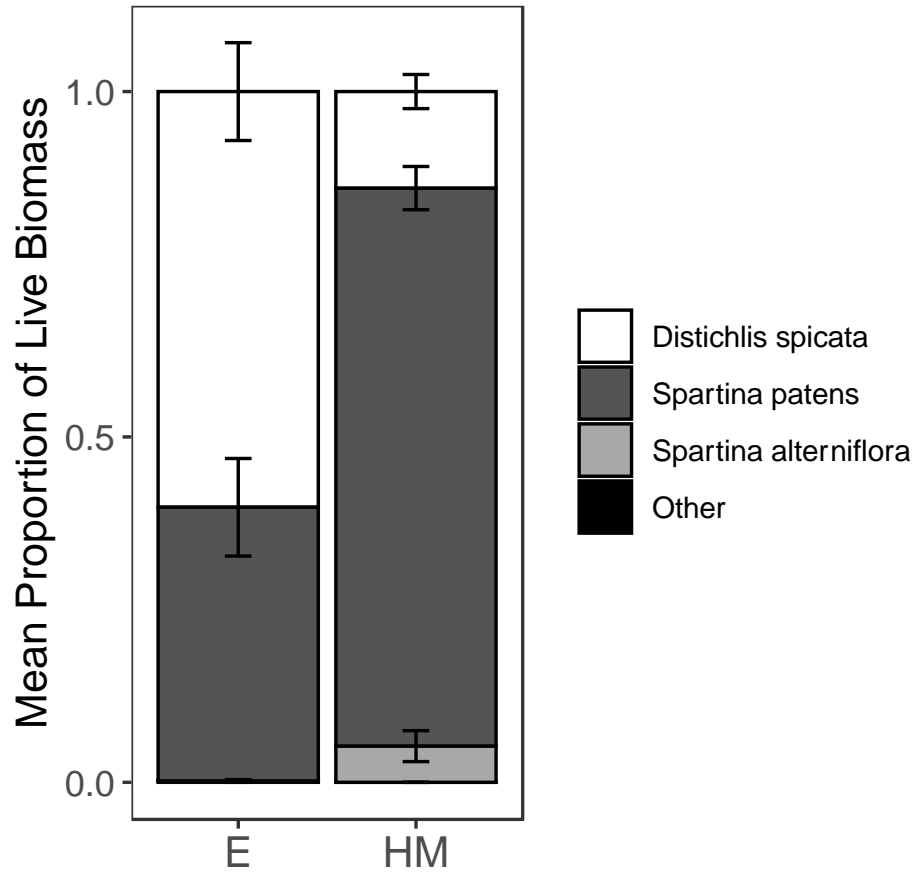


Figure 15. Mean proportion contribution to ground cover live biomass by plant species. Error bars are one standard error. E=ghost forest ecotone; HM=high marsh.

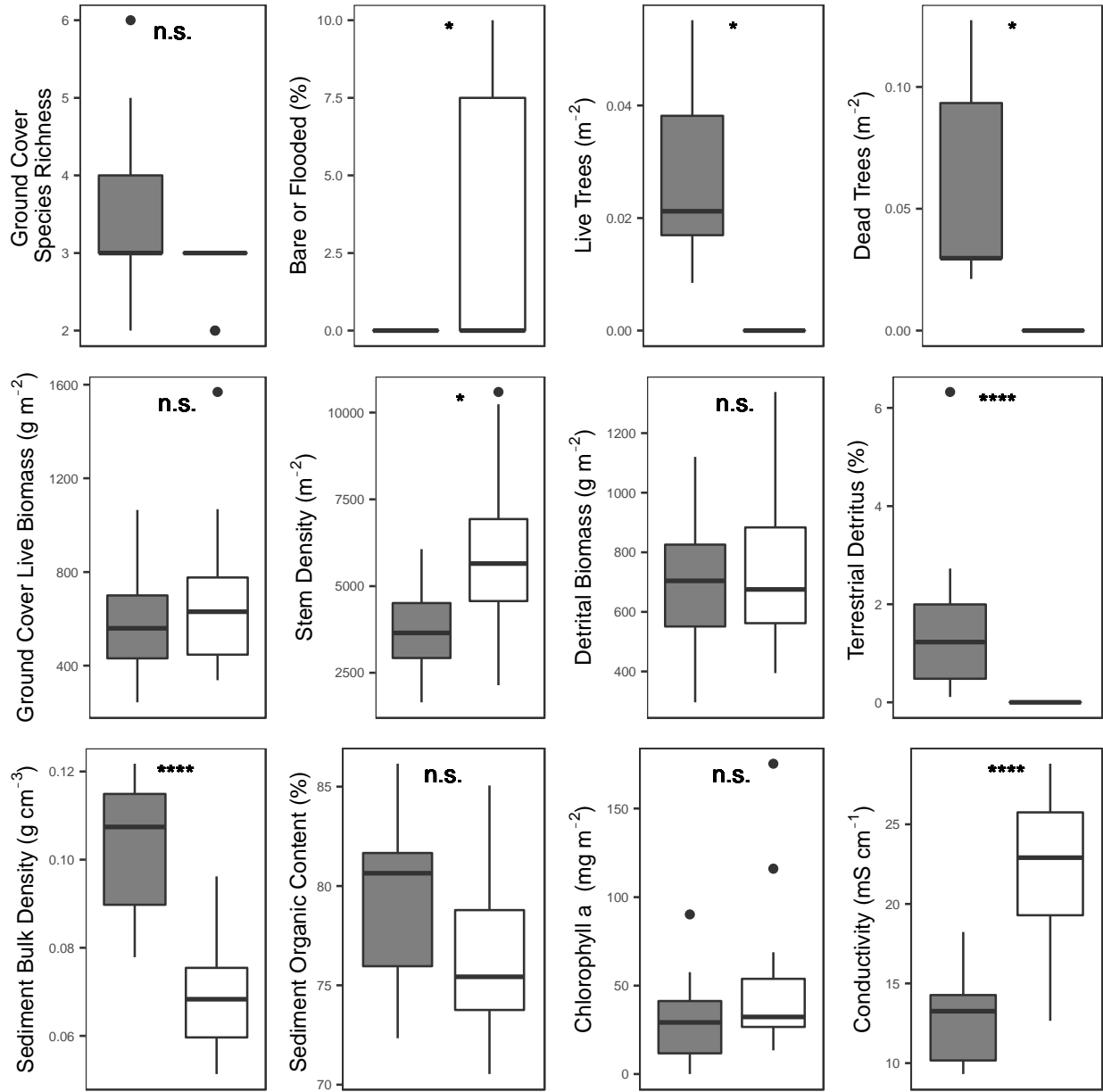


Figure 16. Habitat characteristics compared between zones. Gray bars are ghost forest ecotone, and white bars are high marsh. Asterisks denote significance (n.s. > 0.05, * < 0.05, ** < 0.01, *** < 0.001, **** < 0.0001).

APPENDIX A. Taxonomic resolution for pitfall and leaf litter collections (2019 and 2020).

Class	Order/superorder	Resolution
Arachnida	Acari	superorder
	Araneae	family
	Pseudoscorpiones	family
Collembola	Collembola	family
Malacostraca	Amphipoda	species
	Isopoda	species
Insecta	Archaeognatha	species
	Blattodea	family
	Coleoptera	sub-family
	Diptera	family (2019) or suborder (2020)
	Hemiptera	family
	Hymenoptera, Formicidae	genus
	Hymenoptera, other	family
	Orthoptera	genus
	Psocoptera	order
	Thysanoptera	order
Myriapoda	Polyxenida	order

APPENDIX B. List of all included taxa from pitfall and leaf litter samples (2019 and 2020).

Class	Order/superorder	Lowest Taxon		
Arachnida	Acari	Agelenidae		
		Araneidae		
	Araneae	Clubionidae		
		Cybaeidae		
		Dictynidae		
		Hahniidae		
		Linyphiidae		
		Lycosidae		
		Oxyopidae		
		Salticidae		
		Segestriidae		
		Thomisidae		
		Pseudoscorpiones	Cheliferidae	
			Neobisiidae	
Collembola	Collembola	Dicyrtomidae		
		Entomobryidae		
		Hypogastruridae		
		Isotomidae		
		Neanuridae		
		Onychiuridae		
		Paronellidae		
		Poduridae		
		Sminthuridae		
		Sminthurididae		
		Tomoceridae		
		Malacostraca	Amphipoda	<i>Gammarus palustris</i>
				<i>Orchestia grillus</i>
<i>Uthlorchestia uhleri</i>				

	Isopoda	<i>Caecidotea</i> sp. <i>Littorophiloscia vittata</i>
Insecta	Archaeognatha	<i>Machiloides banksi</i>
	Blattodea	Ectobiidae
	Coleoptera	Acrotrichinae Aleocharinae Copelatinae Corticariinae Corylophidae Dryophthorinae Enochrinae Euaesthetinae Hydrophilinae Hydroporinae Lamiinae Leiodinae Nitidulinae Noteridae Oxytelinae Paederinae Phloeocharinae Pselaphinae Scirtidae Scymninae Steninae Trechinae Xenoscelinae
	Diptera	Brachycera (sub-order) Cecidomyiidae Ceratopogonidae Chironomidae Culicidae

	Drosophilidae
	Empididae
	Nematocera (sub-order)
	Phoridae
	Sarcophagidae
	Sciaridae
Hemiptera	
	Aphididae
	Blissidae
	Cicadellidae
	Coccomorpha
	Coreidae
	Delphacidae
	Hebridae
	Lygaeidae
	Miridae
	Pachygronthidae
	Veliidae
Hymenoptera, Formicidae	
	<i>Aphaenogaster</i>
	<i>Camponotus</i>
	<i>Crematogaster</i>
	<i>Monomorium</i>
	<i>Myrmecina</i>
	<i>Myrmecosystus</i>
	<i>Nylanderia</i>
	<i>Pheidole</i>
	<i>Solenopsis</i>
	<i>Temnothorax</i>
Hymenoptera, other	
	Aphelenidae
	Bethylidae
	Braconidae
	Ceraphronidae
	Diapriidae
	Encyrtidae
	Mymaridae

		Platygastridae
		Pompilidae
		Pteromalidae
		Scelionidae
	Orthoptera	
		<i>Allonemobius</i>
		<i>Cycloptilum</i>
		<i>Eunemobius</i>
		<i>Gryllus</i>
		<i>Neonemobius</i>
		Tetrigidae sp.
	Psocoptera	
	Thysanoptera	
Myriapoda		
	Polyxenida	

APPENDIX C. Taxonomic resolution for infauna collection (2020).

Phylum		Resolution
Arthropoda	Acari	superorder
	Coleoptera larva	order
	Diptera larva	family
	Neuroptera larva	order
Nematoda		phylum
Annelida	Oligochaeta	family
	Polychaeta	family

APPENDIX D. List of all taxa identified in infauna samples (2020).

Phylum	Broad Taxon	Lowest Taxon
Arthropoda	Acari	
	Coleoptera larva	
	Diptera larva	Ceratopogonidae Chironomidae Tabanidae Unknown Diptera larva
	Neuroptera larva	
Nematoda		
Annelida	Oligochaeta	Enchytraeidae Tubificidae (=Naididae)
	Polychaeta	Capitellidae

APPENDIX E. Abundances of organisms identified in infauna cores from each zone that are not considered infauna, were not the target of the sampling method, and were not included in infauna analysis.

	Ghost forest ecotone	High marsh
Amphipod	1	10
Ant	6	1
Beetle	60	25
Centipede	1	0
Copepod	7	3
Culicidae larva	1	2
Flatworm	0	3
Hemiptera	10	22
Hymenoptera	4	4
Isopod	7	1
Ostracod	23	27
Psocoptera	1	1
Mollusca	0	17
Spider	3	20
Springtail	2	13
Thysanoptera	1	0

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