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Detritivores and exogenous nitrogen influence litter microbial communities in coastal salt marshes

Tyler M. Rippel[1,*], Alexandra L. DeCandia[1,2], Jewel Tomasula[1], Cathilyn L. McIntosh[1], Shannon M. Murphy[3], Gina M. Wimp[1]

[1]Department of Biology, Georgetown University, Washington, DC 20007, USA
[2]Smithsonian National Zoo and Conservation Biology Institute, Washington, DC 20008, USA
[3]Department of Biology, University of Denver, Denver, CO 80210, USA

ABSTRACT: Saprotrophic fungal communities and animal detritivores are known to regulate litter decomposition, yet their interaction has seldom been examined in coastal salt marshes. Such studies are important because salt marshes have some of the highest carbon storage rates of any ecosystem, and litter plays an important role in carbon cycling. Furthermore, it is currently unknown how species loss and nitrogen (N) pollution will impact the detritivore–fungi or detritivore–algae interactions that occur on litter. To test for changes in the microbial community of decaying *Spartina alterniflora* Loisel litter, we factorially altered the N concentrations of sediment surrounding the litter as well as the densities of *Melampus bidentatus* Say, 1822, an abundant but declining detritivorous snail that increases fungal abundance and litter decomposition rates. In each of 36 experimental plots, we analyzed the fungal and algal community composition of litter bundles (collected after 50 and 100 d, respectively) along with detritivore densities, plant traits, sediment and litter N, sediment chemistry, and microclimate. Notably, the densities of snails and isopods were associated with changes in the evenness and relative abundances of fungi in the litter, while amphipods influenced both fungal and algal communities. N additions further altered fungal community structure and increased the dominant saprotroph *Natantispora retorquens* at both timepoints. In sum, our novel field study revealed that N pollution and the loss of key detritivores, both of which are expected to increase in the future, will likely impact salt marsh fungi. Therefore, global change may impact the animal–microbial dynamics that influence above-ground carbon cycling.

KEY WORDS: Tidal wetlands · Litter decomposition · *Spartina alterniflora* · *Melampus bidentatus* · Nitrogen pollution · Algae · ITS2 sequencing

1. INTRODUCTION

The decomposition of litter is a fundamental ecosystem process in all vegetated ecosystems, but it plays an especially integral role in coastal ecosystems. In coastal salt marshes, plants senesce in the fall and are subsequently decomposed by microbial and animal communities while also serving as a structure on which epiphytic algal communities grow. Decomposing litter traps mineral and organic sediment, leaches carbon compounds into the soil profile, and is buried through sedimentation, which helps coastal ecosystems accrete with rising sea levels and store carbon (Rooth et al. 2003, Lovelock et al. 2014). Due to the burial of biomass and the anoxic conditions of sediments, salt marshes have among the highest carbon storage rates of any ecosystem (i.e. net ecosystem production; Chmura 2013). Fungal saprotrophs play the primary role in litter decomposition in salt marshes, representing >90% of the microbial biomass in decomposing litter (Raghukumar 2017). Invertebrate communities also play an important role by consuming litter and altering fungal communities through grazing and shredding (Valiela et

*Corresponding author: tr599@georgetown.edu

al. 1985, Newell et al. 1989, Silliman & Newell 2003). However, relatively little is known about these litter–animal–fungal interactions or how they are altered by global change factors.

Studies prior to next-generation sequencing revealed the dominance and high abundance of fungi in the decomposer community of dominant salt marsh grasses (Gessner & Kohlmeyer 1976, Newell et al. 1985, 1989, 1996a,b) as well as the impact of invertebrate detritivores on the abundance of fungal communities (Lopez et al. 1977, Valiela et al. 1985, Newell & Bärlocher 1993, Graça et al. 2000). With the advent of high-throughput sequencing, subsequent studies have revealed the extreme diversity of microbial communities (inclusive of fungal, algal, and bacterial taxa) that exist on and within decaying *Spartina* species (Buchan et al. 2002, reviewed in Raghukumar 2017). Over 130 species of fungi have been observed within the dominant salt marsh grass *Spartina alterniflora* (reclassified as *Sporobolus alterniflorus*; see Section 2.1), and these fungi are generally structured by the section of the plant they inhabit (Al-Nasrawi & Hughes 2012) and season (Newell et al. 2000). Nutrients, specifically nitrogen (N), appear to be a dominant regulator of fungal community biomass, whether it is endogenous N (internal litter; %N) or exogenous N (N external to the plant) (Valiela et al. 1985, Muhammad et al. 2020, Tan et al. 2020). However, the role of animals and exogenous N in structuring the diversity of fungi, rather than the abundance, has remained relatively unexplored. Further, the potential impact of different global change factors, such as detritivore loss and N pollution, on litter microbial communities has not yet been investigated.

Animal–fungal interactions have been shown to alter plant decomposition dynamics and nutrient cycling in many ecosystems, including salt marshes (Graça et al. 2000, Newell & Porter 2002, Hensel & Silliman 2013). Yet field studies have rarely included detritivores when examining the impact of environmental covariates on fungi, even though animals can play a central role in litter decomposition in other ecosystems (García-Palacios et al. 2013, Grandy et al. 2016). For example, detritivores can offset microbial competition through preferential grazing (Lopez et al. 1977 Crowther et al. 2012a), induce microbial inoculation (Sieg et al. 2013, Freitas et al. 2015), disperse propagules (Renker et al. 2005, Crowther et al. 2012b), and regulate exo-enzyme production of microbial communities (Crowther et al. 2011, Mueller et al. 2017). Most studies on decomposer communities in salt marshes have been observational studies examining the natural abundance (Newell et al. 1989, 2000, Graça et al. 2000, Newell 2001, Carrasco-Barea et al. 2022) or diversity of fungi (Buchan et al. 2002, Newell & Porter 2002, Van Ryckegem et al. 2007, Calado et al. 2015) across environmental gradients. When manipulative studies took place, they focused on the impact of disturbances (nutrients, fungicides, oil, sea level rise) on sediment fungal communities (e.g. Kearns et al. 2019) or on the abundance of fungi in litter (e.g. Newell et al. 1996a,b, Hensel & Silliman 2013, Lumibao et al. 2018, Zhai et al. 2020). Notably, studies examining how detritivores affect litter fungal communities have mainly occurred in mesocosms and/or focused only on fungal abundance, not diversity (Newell & Bärlocher 1993, Newell 2001, Silliman & Newell 2003). Yet these studies revealed the context-dependency of detritivore–fungi interactions, as some detritivore species decrease fungal abundance through direct consumption while others increase fungal abundance by increasing surface area via litter shredding. Thus, it is important to perform manipulative *in situ* studies that examine the impacts of detritivores on microbial community composition.

Here, we manipulated the detritivore community and N concentrations of a coastal salt marsh dominated by *S. alterniflora* to examine their interactive effects on microbial communities. We altered the densities of an abundant and widespread detritivorous snail *Melampus bidentatus* Say, 1822, which has been shown to increase fungal abundance under controlled conditions (Graça et al. 2000) and litter decomposition rates in field conditions (Rippel et al. 2022). Notably, *M. bidentatus* populations are declining due to sea level rise (Johnson & Williams 2017) and migrating competitors (Lee & Silliman 2006), but it is yet unknown if *M. bidentatus* alters litter microbial communities alongside its influence on litter decomposition rates. Further, it is also currently unknown whether exogenous N alters microbial community structure, although it is likely considering its impact on litter decomposition rates (Rippel et al. 2022). Exogenous N, rather than N taken up by live plants, mimics the external inputs of N into coastal salt marshes, such as agricultural nutrient runoff or N deposition. Thus, we asked the following question: what biotic and abiotic variables correspond with changes in the diversity and composition of microbial communities in decomposing *S. alterniflora* litter? We predicted that fungal communities would change over time and be regulated by different environmental variables in different seasons. We also predicted that detritivores, specifically *M. bidentatus* and an amphipod *Speziorchestia grillus*, would impact fungal and algal communities considering past research

revealing their impact on microbial functioning and biomass (Lopez et al. 1977, Graça et al. 2000, Zimmer et al. 2004). Finally, we expected that previously discovered mechanisms that shape litter decomposition and microbial communities (season, microclimate, litter N, sediment properties) and previously unexplored variables, such as exogenous N concentrations, would also impact microbial communities.

2. MATERIALS AND METHODS

2.1. Experimental design

We experimentally manipulated snail populations and nutrient concentrations in 2019 in a vast intertidal salt marsh on the Tuckerton Peninsula in the Great Bay–Mullica River Estuary near Tuckerton, New Jersey (39° 33.2′ N, 74° 20.1′ W). We set up 36 plots (10 m^2) in a 2 × 3 factorial design within an area dominated by short-form *Spartina alterniflora*. Although the currently accepted taxonomy of *S. alterniflora* is *Sporobolus alterniflorus* (Peterson et al. 2014), we use *S. alterniflora* due to its familiarity, continued use, and support as an independent genus (Bortolus et al. 2019). We altered the densities of *Melampus bidentatus* (snail removal, ambient, snail addition [2× ambient]) and/or the N concentrations of soil (ambient, N addition), leading to 6 different treatments including control plots. Treatments were performed in 6 different blocks, and thus there were 6 treatments occurring in 6 blocks (36 plots total). Snail manipulations were performed 4× throughout the growing season and consisted of adding 250–500 snails (25–50 m^{-2}) to each snail-addition plot and removing all snails from snail-removal plots. Snail manipulations were only partly successful and snail densities varied (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m716p017_supp.pdf). Finally, we fertilized plots 3× in the early growing season (May–June) with 13.6 g N m^{-2} of urea (N:P:K = 34:0:0), similar to N inputs along the Atlantic coast as well as similar studies (McFarlin et al. 2008, Lu et al. 2018, Wimp et al. 2019).

2.2. Detritivore community sampling

We analyzed the abundance of detritivores in each plot using 2 different methods. For the detritivorous snail *M. bidentatus*, we completed 3 surveys during the course of the experiment (early August, mid-September, and mid-October). Surveys consisted of throwing a 0.047 m^2 quadrat haphazardly into plots 10 times and counting all the snails that occurred in the quadrat area. The 3 surveys (August, September, and October) were averaged to represent an average snail density per plot (Fig. S1). We also examined 2 other detritivores — *Venezillo parvus*, an isopod, and *Speziorchestia grillus* (formerly *Orchestia grillus*), an amphipod — which graze on fungi and algae and increase in abundance with N additions (Zimmer et al. 2004, Murphy et al. 2012, Pascal & Fleeger 2013). We gathered abundance data on these species only once, at peak plant biomass in mid-September. To sample, we used a D-vac suction sampler (Rincon-Vitova Insectaries) with a diameter of 21 cm. In each plot, we collected detritivores with three 5 s placements of the D-Vac on the marsh surface (Raupp & Denno 1979). We stored all arthropods in ethanol and identified and counted all detritivores within the samples.

2.3. Above-ground plant characteristics

To quantify above-ground plant characteristics, we measured total above-ground biomass at the end of the growing season in each plot. We haphazardly threw a quadrat (0.047 m^2) into each plot and removed all above-ground biomass with clippers. We dried the biomass at ~60°C for 3 d, separated live plant biomass from litter, and weighed each, respectively.

2.4. Below-ground analyses

To quantify below-ground plant and soil characteristics, we took soil samples within each plot from the same quadrat as above-ground biomass collection with a soil corer (7.5 × 15 cm) in early October. We transferred soil cores to ice for transport and froze them at −20°C until subsequent processing. Whole cores were weighed and separated into roots and sediment using 2 mm sieves. Roots were dried at ~60°C for 5 d and weighed to calculate root biomass. To determine soil pH and salinity, 10 g of dried, sieved soil was mixed with 25 ml of water (1:2.5 ratio), shaken for 20 min, and measured using a Hanna Edge Multiparameter (Hanna Instruments) using pH (HI11311) and EC/TDS/salinity (HI763100) probes, respectively. To measure NH_4^+, we extracted 4 g of wet soils with 3 successive 20 min 2 M KCl extraction shakes. Soil KCl extractions were then analyzed for NH_4^+ on a plate reader at 650 nm following a Berthelot reaction (Sims et al. 1995).

2.5. Microclimate

To measure abiotic environmental variables, we measured microclimate air temperature and relative humidity in each plot 6 times throughout the growing season (June–October) using a HOBO MX1101 temperature/RH data logger (Onset Computer Corporation). We calculated the microclimate temperature and relative humidity of each plot by comparing ambient air temperatures and relative humidity taken at chest height with measurements taken within vegetation at the soil surface. To calculate each plot's temperature and relative humidity (M_{temp}, M_{rh}), we subtracted ambient temperature and relative humidity measurements (A_{temp}, A_{rh}) from soil surface temperature and relative humidity measurements (S_{temp}, S_{rh}): $M_i = S_i - A_i$.

2.6. Litter bundles

To assess the fungal and algal communities, we constructed litter bundles similar to those described in Hensel & Silliman (2013). We first collected standing-dead biomass from an otherwise unused *S. alterniflora* patch. We then removed any live or heavily decomposed material and washed and dried the plant material at ~60°C for 3 d. Bundles were constructed by combining 3.00 g of standing dead *S. alterniflora* stems with zip-ties. Two litter bundles were haphazardly placed in each plot on the soil surface in early August 2019 and were collected after ~50 (September) and ~100 d (November). We originally planned on leaving the second litter bundle until the following growing season; however, bundles decomposed rapidly, and several were found to be missing. Therefore, we collected the second bundles in November. To analyze the N concentration of litter, we subsampled bundles by taking 5–10 clips of all bundles and ground them in a MM 400 model mixer mill (Retsch), weighed them using an XP6 microbalance (Mettler-Toledo), and rolled them into tin capsules (Elementar Americas). Prepared samples were sent to the Cornell Stable Isotope Laboratory for %N analysis using an elemental analyzer–stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS).

2.7. Fungal DNA extraction and sequencing

We extracted DNA from 40 mg of a mixture of dead stems and leaves subsampled from litter bundles using Qiagen DNeasy Plant Mini Kits. We followed the manufacturer's protocol and used a Qiagen TissueLyser II (Hilden). We then used a Qubit 2.0 fluorometer (Invitrogen) to quantify extracted DNA. Extracted DNA was amplified using ITS86(F)/ITS4(R) primer sets (F: GTG AAT CAT CGA ATC TTT GAA; R: TCC TCC GCT TAT TGA TAT GC) to confirm the presence of fungal DNA (Op De Beeck 2014). Once confirmed, 10 µg of genomic DNA was sent to the Integrated Microbiome Resource (IMR) at Dalhousie University for paired-end sequencing of the internal transcribed spacer 2 (ITS2) amplicon using the Illumina MiSeq platform and the same primers described above. The ITS2 region has successfully been used to characterize both fungal and algal communities, although there are fewer reference sequences for algae, which may lead to an underestimated algal diversity (Lutz et al. 2019). Of the 61 samples sent, 60 had sufficient read depth (>1300 reads) for subsequent analyses.

2.8. Microbial DNA processing and classification

We followed the QIIME 2 pipeline (Kuczynski et al. 2012), with modifications specific for ITS2 (Kõljalg et al. 2013), for sequence assembly and comparison. These steps include denoising, singleton and doubleton filtering, phylogeny construction, and amplicon sequence variant (ASV) binning (Caparosa et al. 2010, Bolyen et al. 2019). ASVs are used as a common approximation for fungal diversity as they provide the highest resolution for analysis, allow for better comparison across studies, and provide a more accurate and precise method for microbial diversity compared to traditional operational taxonomic unit-based methods (Jeske & Gallert 2022, Tipton et al. 2022). Following processing, we retained 1 490 255 reads, containing 639 unique ASVs with an average sampling depth of 24 837. We analyzed multiple metrics of alpha diversity and community composition to capture the change of litter microbial communities among treatments. For alpha diversity, we measured fungal richness (ASV richness), Pielou's evenness (ASV equitability), and Shannon's diversity index, which accounts for both richness and evenness. Before we examined alpha diversity metrics, we used the alpha-rarefaction function in QIIME2 to generate rarefaction curves to control for differences in sequencing depths among samples. Finally, we examined community composition metrics for differences in ASV presence–absence using unweighted UniFrac (Lozupone et al. 2011) and ASV abundance using Bray-Curtis dissimi-

larity (Faith et al. 1987). We generated unweighted UniFrac and Bray-Curtis dissimilarity measures for statistical analysis using the 'core-metrics-phylogenetics' function in QIIME 2. ASVs were taxonomically assigned using a pre-trained naïve Bayes classifier (UNITE database, 99% similarity) with the 'fit-classifier-naive-bayes' function (Nilsson et al. 2019).

2.9. Statistical analysis

2.9.1. Treatment effects on microbial alpha diversity metrics

To assess the effect of collection time, snail manipulations, fertilizer additions, and the interaction between snails and fertilizer on ASV richness, Pielou's evenness, and Shannon's diversity, we used linear mixed models with the 'lmer' function in the R package 'lme4' (Bates et al. 2015). We first visually inspected residual plots to check for a normal distribution of residuals and analyzed studentized residual plots to check for homogeneity of variance. We input collection timepoints (September, November), snail manipulations (ambient, added, removed), N manipulations (fertilizer added, no fertilizer added), and the interaction between snails and N as the fixed factors. Blocks (1–6), as described in Section 2.1, were input as random factors for all the tests. Thus, our models had the following structure: Alpha Diversity Metric ~ Time + Snails × Fertilizer+(1|Block). If a model showed a significant difference among the treatments ($p < 0.05$), we implemented Tukey's HSD using the 'emmeans' function in the R package 'lsmeans'. Analyses were performed in R (version 4.0.5) (R Core Team 2021).

2.9.2. Biotic and abiotic modulators of microbial alpha diversity

To determine which abiotic and biotic variables impacted fungal and algal alpha diversity metrics, we used a linear mixed-model selection procedure. We selected the best predictors for fungal and algal ASV richness, Pielou's evenness, and Shannon's diversity for each taxonomic group at each timepoint separately, and thus performed this analysis 12 times. We separated the 2 timepoints, as fungal communities can be regulated by different factors in different seasons and throughout fungal succession (Van Ryckegem et al. 2007, Malloch et al. 2022) and we were interested in exploring which environmental factors influenced fungal communities in each timepoint separately. For each model, we included block as the random factor and the following 9 fixed factors: snail density (counts m^{-2}), amphipod density (counts m^{-2}), isopod density (counts m^{-2}), soil NH_4^+ (ppm), soil pH, soil salinity (mS m^{-1}), litter percent N (%), live biomass (g), and plot humidity (%). We compared Akaike's information criterion adjusted for small sample size (AICc) scores for all possible model combinations using the 'dredge' function in the 'MuMin' package (Barton 2019), with a selection criterion of >2 ΔAICc points. To evaluate multicollinearity, we used the 'vif' function in the 'car' package in R with a cutoff of VIF < 3 (Fox et al. 2019). Assumptions for normality and homogeneity of variance were visually examined as in the prior section, and no transformations were needed. Full models are interpreted with AICc values, chi-squared (χ^2) values, and p-values. χ^2 and p-values were produced by comparing best-fit models with null models using the 'anova' function in R. Parameters are interpreted with *F*-statistics, p-values, and beta values. Due to the range of scales of our fixed factors, we standardized beta values with 'std.coef' function in the R package 'MuMin'.

2.9.3. Treatment effects on microbial community composition

To assess differences in fungal and algal beta diversity and community composition among treatments, we implemented permutational multivariate analysis of variance (PERMANOVA) using the 'diversity adonis' function in QIIME 2 (Oksanen et al. 2019). We used PERMANOVA to test for differences in ASV presence (unweighted UniFrac) and ASV abundance (Bray-Curtis dissimilarity) for fungi and algae across timepoints and treatments. We first analyzed if the 2 collection timepoints (September, November) differed in fungal communities for fungi and algae separately, which had the following structure: Community Composition Metric ~ Time + (1|Block). Next, we separated the timepoints to determine whether fertilizer, snail manipulations, and/or fertilizer and snail interactions impacted fungal and/or algal communities in litter bundles, which had the following structure: Community Composition Metric ~ Snails × Fertilizer + (1|Block). We produced NMDS plots with Bray-Curtis dissimilarity represented as Euclidean distances in the 'vegan' package in R (Oksanen et al. 2019). We conducted a vector analysis using the 'envfit' function in the 'vegan' package, inputting the same 9 factors as used in linear mixed-

model selection as well as plot temperature and dead plant mass. Only significant ($p < 0.05$) vectors are shown in NMDS plots, which are interpreted with R^2 values. To determine which species drove the differences between groups, we used Bray-Curtis similarity percentage (SIMPER) analysis using the 'simper' function in the 'vegan' package in R (Clarke 1993).

3. RESULTS

3.1. Collection day and fertilizer impact fungal alpha diversity metrics

Fungal and algal alpha diversity metrics differed between timepoints, but only fungi was impacted by exogenous N (Fig. 1, Tables S1 & S2). According to linear mixed models, fungal ASV richness ($F_{1,48} = 7.5$, $p < 0.01$) and Shannon's diversity ($F_{1,48} = 12.8$, $p < 0.001$) decreased by 17 and 15%, respectively, from September to November (Table S1). Algal ASV richness (percent change [PC]: −12%, $F_{1,48} = 4.9$, $p < 0.05$), Pielou's evenness (PC: −18%, $F_{1,48} = 43.4$, $p < 0.001$), and Shannon's diversity (PC: −23%, $F_{1,48} = 53.7$, $p < 0.001$) also decreased from September to November. In September, unfertilized plots had 10% higher fungal Pielou's evenness ($F_{1,48} = 9.8$, $p < 0.01$) and 8.8% higher Shannon's diversity ($F_{1,48} = 6.02$, $p < 0.05$) than fertilized plots. Notably, fertilizer treatments did not impact algae (Fig. 1), and snail treatments did not affect any metric of fungal or algal alpha diversity (Tables S1 & S2).

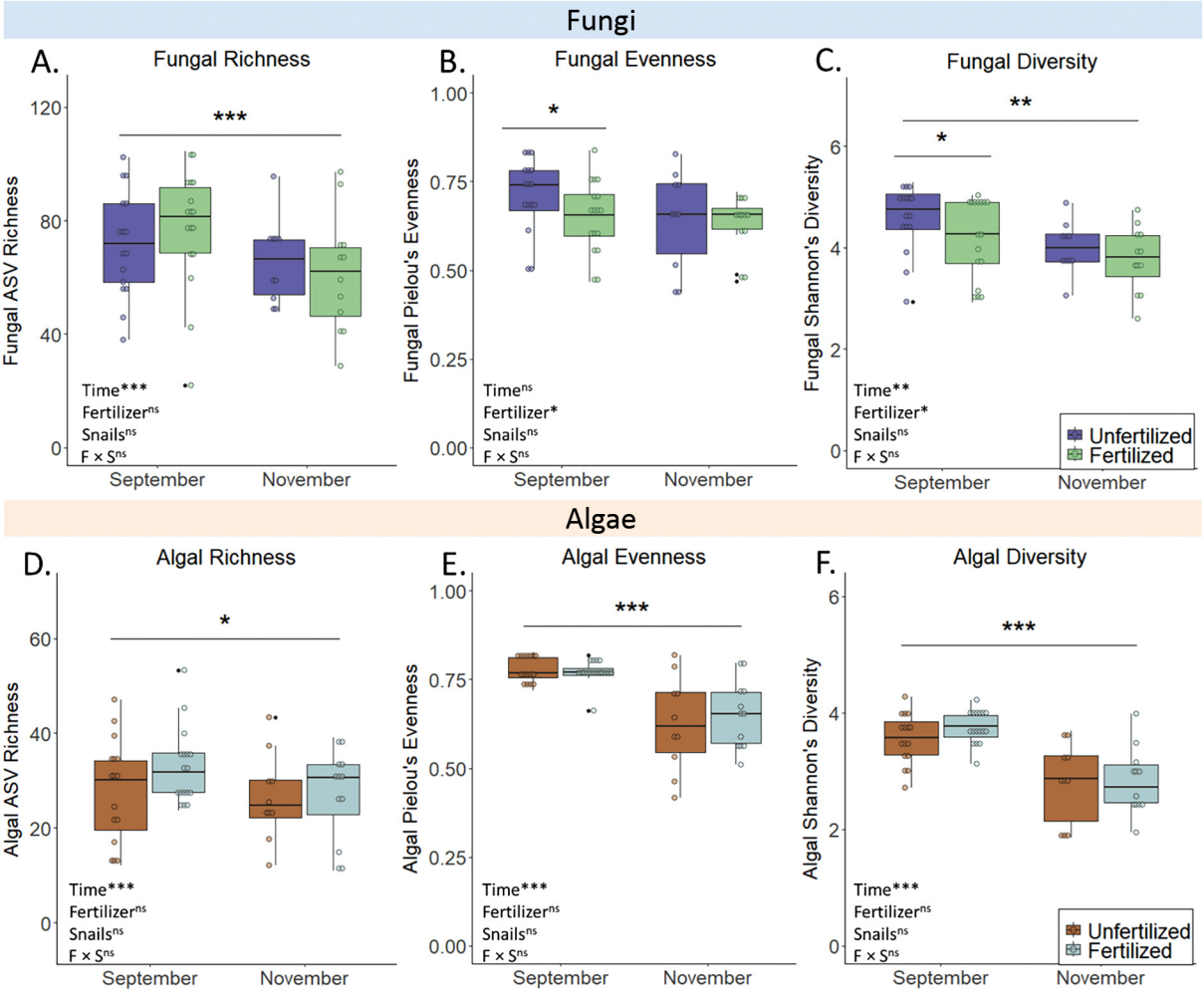

Fig. 1. Comparisons of (A,B,C) fungal and (D,E,F) algal alpha diversity metrics between fertilized and unfertilized plots that were sampled in September and November. Statistics displayed are from linear mixed models evaluating the impact of collection time, fertilizer, snail manipulations, and fertilizer × snail (F × S) interactions. Because snail effects were insignificant, we only display the differences between timepoints and fertilizer manipulations. ASV: amplicon sequence variant; Boxplots: centre line = median, box limits = inter-quartile range, whiskers = 95% confidence interval; ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns: not significant

3.2. Detritivores and the environment alter fungal and algal alpha diversity

Of the 12 linear mixed models constructed, 8 were superior to null models after model selection (Table 1), with 4 for fungal communities and 4 for algal. Best-fit models typically had competing models that were within 2 AICc points (Tables S3 & S4). Notably, 4 models included significant impacts of detritivores. The best-fit model for fungal ASV richness at timepoint 1 (September) revealed a negative association with amphipods ($\beta = -0.53 \pm 0.15$, $F_{1,30} = 12.3$, $p < 0.01$). The best-fit models for fungal Pielou's evenness contained snails ($\beta = 0.46 \pm 0.18$, $F_{1,30} = 6.2$, $p < 0.05$) and isopods ($\beta = 0.51 \pm 0.18$, $F_{1,30} = 8.1$, $p < 0.01$) along with a negative influence of live biomass (Table 1). For timepoint 2 (November), the best-fit model for fungal evenness contained positive influences from litter %N and sediment pH and NH_4^+ (Table 1).

For models of algal ASV richness and Shannon's diversity in September, both had amphipods (richness: $\beta = -0.44 \pm 0.17$, $F_{1,30} = 7.3$, $p < 0.05$; diversity: $\beta = -0.53 \pm 0.15$, $F_{1,30} = 8.3$, $p < 0.01$) as their sole fixed factor (Table 1). In November, only algal richness outcompeted its null model, with salinity as the sole factor ($\beta = 0.51 \pm 0.18$, $F_{1,30} = 4.3$, $p < 0.05$).

3.3. Collection day and fertilizer impact fungal community composition

The relative compositional abundance (Bray-Curtis dissimilarity) and ASV presence (unweighted UniFrac) of fungal and algal communities differed between timepoints and N manipulations, according to PERMANOVA analysis. Fungal presence ($F_{1,53} = 2.3$, $R^2 = 0.043$, $p < 0.05$) and relative abundance ($F_{1,53} = 2.9$, $R^2 = 0.051$, $p < 0.05$; Fig. 2) both differed between timepoints (Fig. 2, Tables S5 & S6). SIMPER analysis revealed that *Natantispora retorquens*, which decreased in abundance from September to November, was the dominant driver of community differences between timepoints. Other species that differed between timepoints were *Phaesphaeria halima*, *Lulworthia* spp., *Talaromyces helicus*, and *Lignicola laevis* (Fig. 3, Table S7). Algal presence ($F_{1,53} = 6.4$, $R^2 = 0.1$, $p < 0.001$) and relative abundance ($F_{1,53} = 16.4$, $R^2 = 0.24$, $p < 0.001$) also differed between collection dates (Tables S5 & S6). The abundance of *Pseudendoclonium submarinum* was drastically reduced in November while *Chlorothrix* spp. appeared and dominated (Fig. 3, Table S8). Finally, N additions led to changes in the relative abundances of fungal ASV in September ($F_{1,32} = 4.13$, $R^2 = 0.12$, $p < 0.01$) and November ($F_{1,20} = 2.84$, $R^2 = 0.12$,

Table 1. Best-fit models from linear mixed-model selection on fungal and algal alpha diversity metrics. **Bold** depicts best-fit models that outcompeted null models containing only random variables. AIC: Akaike's information criterion; $^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$

Response variable	AIC (Marginal)	R^2 (Conditional)	R^2	χ^2	Predictor variables and standardized β estimates (±SE) of best-fit model
September					
Fungal richness	284.6	0.28	0.28	5.9*	**Amphipods**** (−0.53 ± 0.15)
Fungal evenness	−49.7	0.46	0.58	23.1***	**Snails*** (0.46 ± 0.18) + **isopods**** (0.51 ± 0.18) + **live biomass***** (−1.23 ± 0.23)
Fungal diversity	29.4	0.13	0.45	18.5***	**Live Biomass***** (−1.19 ± 0.24)
Algal richness	93.7	0.19	0.19	6.1*	**Amphipods*** (−0.44 ± 0.16)
Algal evenness	91.4	0.26	0.4	4.6*	**Litter %N*** (0.33 ± 0.16)
Algal diversity	89.3	0.23	0.32	6.9**	**Amphipods*** (−0.47 ± 0.16)
November					
Fungal richness	113.7	–	–	–	Null model
Fungal evenness	31.9	0.23	0.29	6.7*	**Sediment NH_4^+*** (0.51 ± 0.18) + **litter %N*** (0.55 ± 0.25) + **sediment pH** (0.39 ± 0.22)
Fungal diversity	17.6	–	–	–	Null model
Algal richness	61	0.13	0.52	4.3*	**Salinity*** (0.36 ± 0.18)
Algal evenness	65.9	–	–	–	Null model
Algal diversity	64.2	–	–	–	Null model

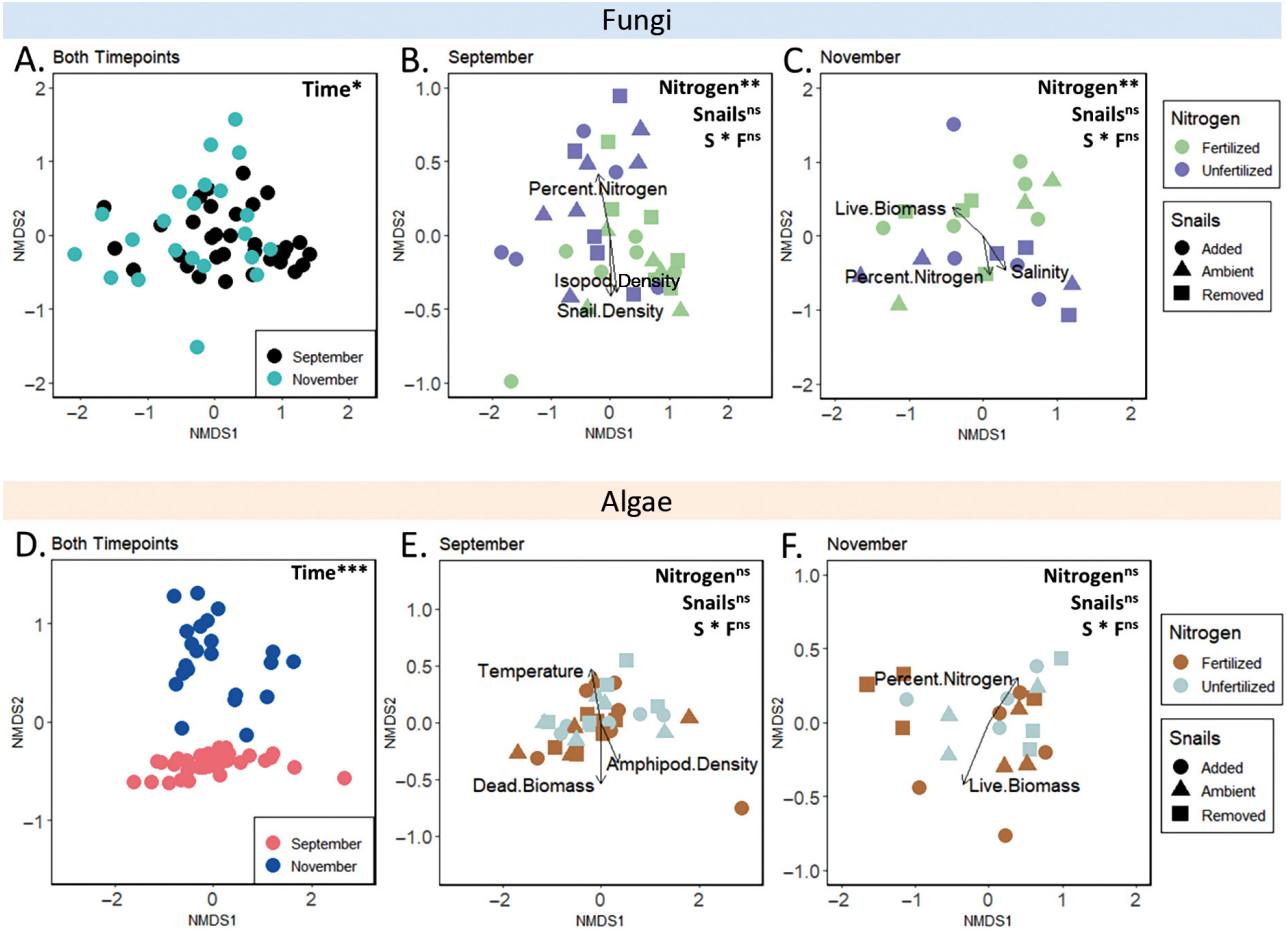

Fig. 2. Community composition of fungi and algae in our experimental plots. Euclidean distances via nonmetric multidimensional scaling (NMDS) plots that best display Bray-Curtis dissimilarities of (A,B,C) fungal and (D,E,F) algal communities between timepoints (A,D) and treatments in September (B,E) and November (C,F). Points represent microbial communities from a single litter bundle collection at a single timepoint. Statistics displayed are from PERMANOVA analysis. Vectors represent significant correlations between environmental variables and fungal or algal composition. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns: not significant

$p < 0.01$). These changes were driven by increases in *N. retorquens* in fertilized plots and decreases in *P. halima*, *T. helicus*, unassigned Ascomycota, and unassigned fungi at both timepoints (Table S7).

Vector analyses on Bray-Curtis distances revealed the influence of environmental drivers on fungal and algal community composition (Fig. 2). In September, snail (*M. bidentatus*) density ($R^2 = 0.17$, $p < 0.05$), isopod density ($R^2 = 0.16$, $p < 0.05$), and %N ($R^2 = 0.21$, $p < 0.05$) influenced fungal communities. In November, fungal communities were structured by salinity ($R^2 = 0.3$, $p < 0.05$), live biomass ($R^2 = 0.33$, $p < 0.05$), and litter %N ($R^2 = 0.29$, $p < 0.05$). For algal communities in September, amphipod density ($R^2 = 0.25$, $p < 0.05$), microclimate temperature ($R^2 = 0.26$, $p < 0.01$), and dead plant mass ($R^2 = 0.29$, $p < 0.01$) were strongly associated with changes in algal community composition. Finally, algal communities in November were structured by live biomass ($R^2 = 0.29$, $p < 0.05$) and litter %N ($R^2 = 0.25$, $p < 0.05$).

4. DISCUSSION

Detritivores can drive litter decomposition dynamics throughout the world (Heděnec et al. 2022), but their influence on fungal communities has been relatively unexplored, especially in coastal salt marshes. Along with other detritivores, we found that a key detritivorous snail *Melampus bidentatus* altered the evenness and relative abundances of fungal communities residing within litter at the 50th day of litter decomposition. Thus, detritivores in this study influenced the composition of fungal communities resid-

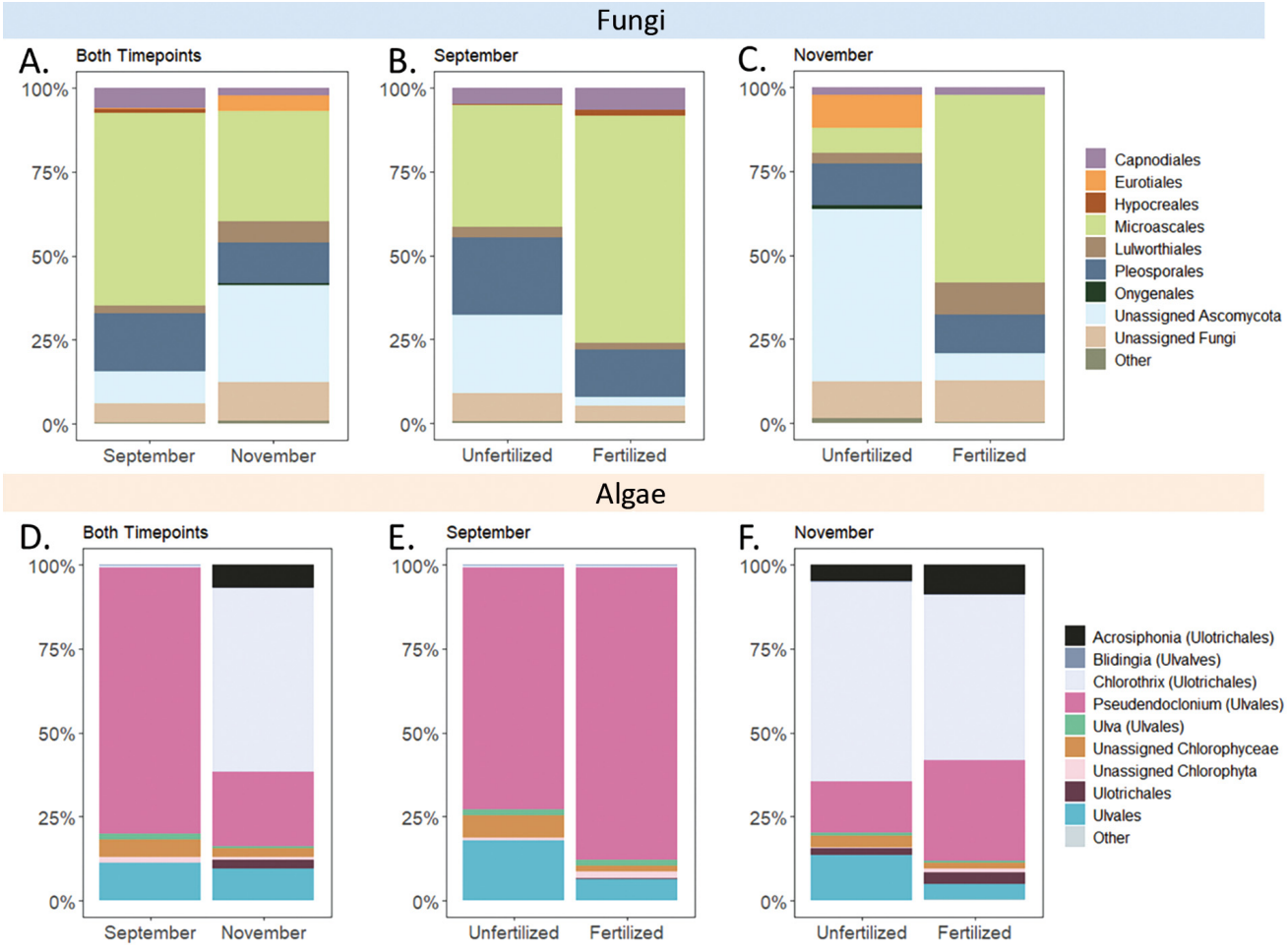

Fig. 3. The average taxonomic composition for (A,B,C) fungi and (D,E,F) algae in our experimental plots. The first column compares the average fungal (A) and algal (D) taxonomic composition of litter bundles collected in September and November, respectively. The second and third columns compare the average taxonomic composition of fungi and algae between fertilized and unfertilized plots for litter bundles collected in September (B,E) and November (C,F), respectively. Colors represent different taxonomic groups of either fungi or algae

ing in decomposing litter, similar to terrestrial ecosystems (Crowther et al. 2011, 2012b, Moghadam & Zimmer 2016). We also found that exogenous N additions, meant to simulate a nutrient pulse coming from agricultural runoff or N deposition, restructured the community composition of fungi by favoring a competitively dominant ascomycete saprotroph. While litter decomposition rates are known to increase with N additions, we demonstrate a potential mechanism for this pattern. Our results suggest that the global change factors that currently threaten coastal salt marshes, including N pollution and species loss, are likely to alter litter microbial communities, which may impact carbon cycling in these ecosystems.

Our results suggest that *M. bidentatus* and other detritivores affect the fungal and algal communities in coastal salt marshes. However, the interpretation of our results is limited by the partial success of our snail manipulations, as snail additions were more successful than snail removals (Fig. S1). This led to the categorical analysis of snails showing no impact on fungal properties, while the continuous measurement of snail densities corresponded with impacts on fungal properties. Nonetheless, *M. bidentatus* (snails) and *Venezillo parvus* (isopods) appeared to influence the composition of fungal communities, while *Speziorchestia grillus* (amphipods) influenced algal communities. Previous studies have revealed that both *M. bidentatus* and *V. parvus* can impact litter decomposition (Zimmer et al. 2004, Rippel et al. 2022), microbial respiration (Zimmer et al. 2002, 2004), and fungal abundance (Graça et al. 2000), but no prior study has examined their impact on fungal community composition. The snail *M. bidentatus* is

an active shredder of decomposing litter (Zimmer et al. 2004) and can increase fungal productivity by 2-fold (Graça et al. 2000). Other shredding detritivores have been shown to significantly alter the composition of fungal communities, with some detritivores increasing fungal richness (Colas et al. 2016) and others decreasing it (Domingos et al. 2015). Here, *M. bidentatus* increased fungal evenness and altered relative abundances, but the exact mechanisms (e.g. grazing specific fungal communities, avoiding fungal species, increasing surface area via shredding, etc.) through which these changes were achieved remain unclear.

When species such as *M. bidentatus* are lost from ecosystems, not only is biodiversity lost, but all the interactions and ecosystem services linked to this species are lost as well (Bascompte & Stouffer 2009). Due to sea level rise and the loss of high marsh habitat, this detritivore is projected to decrease in abundance and perhaps become extirpated or extinct (Johnson & Williams 2017, Zajac et al. 2017). Our results showed that *M. bidentatus* plays a role in structuring the fungal communities in decomposing litter, as it explained 17% of the variation in fungal community composition in September. The fact that *M. bidentatus*, as well as other detritivores, only impacted microbial communities in September is likely the byproduct of our second collection of litter bundles having occurred in late November. By late November, it is possible that detritivores were dormant, and their impacts were therefore not apparent. Nonetheless, it is still notable that *M. bidentatus* has an influence on litter fungal communities, even if it only occurs early in litter decomposition. Recently, Rippel et al. (2022) found that litter decomposition rates are, in part, proportional to the densities of *M. bidentatus* and the N concentrations of sediment and litter. Our results here suggest that the changes in litter decomposition rates associated with *M. bidentatus* discovered by Rippel et al. (2022) may very well be caused by alterations in fungal communities. Thus, the reduction of *M. bidentatus* due to sea level rise may alter litter decomposition rates (Johnson & Williams 2017, Rippel et al. 2022) and the litter fungal communities that regulate decomposition.

Alongside species loss, N pollution is expected to alter litter decomposition dynamics (Rippel et al. 2022) and detritivore communities (Murphy et al. 2012, Wimp et al. 2019) in coastal salt marshes. Past studies have shown that N fertilization can alter fungal biomass in coastal salt marshes (Newell et al. 1996b, McFarlin et al. 2008) and fungal community composition in sediments (Kearns et al. 2019), but no studies to our knowledge have examined the impact of N on fungal community diversity in plant litter. We found that N addition alters fungal communities by favoring competitively dominant species. The dominant fungal species altered by N was the ascomycete *Natantispora retorquens*, which is known to be one of the most common and dominant decomposers of *S. alterniflora* species (Calado et al. 2015, Devadatha et al. 2021). The abundance of *N. retorquens* increased in plots that received fertilization treatments relative to other species. Thus, it is possible that *N. retorquens* has a competitive advantage in salt marshes that have high inputs of N, as *N. retorquens* appears to be capable of assimilating exogenous N. This result has not been previously discussed in any literature to our knowledge and represents a major insight into the influence of exogenous N on fungal dynamics during litter decomposition in salt marshes. Whether an increase in *N. retorquens* corresponds with specific variations in the physicochemical breakdown of litter should be further considered. Although N taken up by live plants impacts litter fungal community composition (Allison et al. 2007, Jabiol et al. 2018, 2019), our finding that exogenous N (external, non-plant-tissue N assimilated by fungi) alters the community composition of fungal decomposers is notable.

Finally, our results demonstrate that the amphipod *S. grillus* has large impacts on the composition of algal communities. This finding complements past studies that revealed the impact of *S. grillus* on fungal and algal abundance (Lopez et al. 1977, Morrison & White 1980, Pascal & Fleeger 2013) and litter decomposition rates (Rippel et al. 2022). Although there are contrasting reports of whether *S. grillus* directly consumes litter (Rietsma et al. 1982) or only grazes microbial communities (Lopez et al. 1977), we can be reasonably certain that it significantly impacts litter decomposition rates, microbial abundance, and microbial diversity. Algal communities have been known to increase litter decomposition rates indirectly through a priming effect that is dependent on the carbon, N, and phosphorus concentrations in the environment and algal exudates (Halvorson et al. 2019a, 2019b). Whether this priming effect is apparent in our system and how *S. grillus* alters litter decomposition remains unknown and should be further explored. Contrary to past studies, N additions did not appear to impact algal community composition (Sullivan & Currin 2002). However, in agreement with past studies, algal communities were heavily influenced by seasonality and time-of-collection (Sullivan & Currin 2002, van Hulzen et al. 2006), with new species

appearing and dominating at later collection dates when there is decreased competition for light between algae and *S. alterniflora* (Sullivan & Daiber 1975, Sullivan 1977). Thus, our results reveal that algal communities, like fungal communities, are structured by both biotic and abiotic forces.

5. CONCLUSIONS

We found that detritivore communities and exogenous N structure the diversity and community composition of litter fungal communities in coastal salt marshes. Our finding that common marsh detritivores (*Melampus bidentatus*, *Venezillo parvus*, *Speziorchestia grillus*) impact fungal communities represents the first indication that detritivores influence litter fungal communities in the field. As *M. bidentatus* populations decline due to sea level rise and habitat loss, its impacts on litter fungal communities could be altered. Furthermore, we revealed that N pulses influence fungal communities by favoring the dominant ascomycete saprotroph *Natantispora retorquens*. The impact of exogenous N on microbial communities may serve as a future avenue for determining how N impacts biological communities and ecosystem processes. Future research should delineate whether these changes in microbial communities relate to shifts in ecosystem processes such as litter decomposition.

Data availability. Data are available on Dryad: https://doi.org/10.5061/dryad.8cz8w9gvv

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