



Species loss and nitrogen pollution alter litter decomposition dynamics in coastal salt marshes

Tyler M. Rippel¹ · Jewel Tomasula¹ · Billie Maguire¹ · Shannon M. Murphy² · Gina M. Wimp¹

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Abstract

Litter decomposition is a central ecosystem function because dead plant biomass plays a critical role in carbon storage, the nitrogen (N) cycle, and as food/habitat for animals and microorganisms. In the face of global change, interactions between organisms that participate in litter decomposition are likely to change due to species loss and N pollution. To understand how these global change factors may interact to alter litter decomposition, we manipulated the detritivore community and N concentrations in a coastal salt marsh for 2 years. We chose to manipulate densities of a dominant, detritivorous snail (*Melampus bidentatus*) because its population size is expected to decline due to climate change, yet its impact on litter decomposition has not been tested in the field. We measured litter decomposition rates, detritivore densities, and the N concentrations of sediment and litter. We found that endogenous N enrichment (N added live plants before decomposition), exogenous N enrichment (N added to decomposing plants) and higher densities of *Melampus* increased litter decomposition rates. Linear mixed models further revealed that snails, other detritivores, and soil NH_4^+ were the best predictors of litter mass loss in the middle stages of decomposition. Notably, exogenous N added to litter already enriched with N further increased mass loss but did not increase litter %N. Our study reveals how global change in the form species loss and N pollution can have palpable impacts on carbon cycling and ecosystem function.

Keywords *Melampus bidentatus* · *Spartina alterniflora* · Species loss · Global change · Carbon cycling · Decomposers

Introduction

The decomposition of dead plant biomass is a dominant carbon flux on Earth, influencing soil carbon storage and ecosystem respiration in all vegetated ecosystems (Bradford et al. 2016). In coastal salt marshes, dead litter plays a central role in carbon storage (Kirwan and Blum 2011), the vertical accretion of the ecosystem (Rooth et al. 2003; Lovelock et al. 2014), the nitrogen (N) cycle (Valiela and Teal 1979; Zhang et al. 2018), and as food and habitat for animals and microorganisms (Gedan and Bertness 2010; McLain et al. 2020). It is generally accepted that the rate of litter

decomposition is the result of interactions between recently senesced biomass, its constituent chemical and structural parts, the environmental conditions, and the biotic decomposers of the ecosystem (Bradford et al. 2016). Although ecology has long recognized how trophic dynamics can impact the biomass, decomposition rates, and nutrient stoichiometry of litter (Lopez et al. 1977; Crawford 1979; Seastedt 1984; Wise et al. 1999), current litter decomposition studies seldom investigate the balance of biotic and abiotic interactions that occur during decomposition and how species loss can shift this balance. In the face of global change, the abundance, composition, and interactions between organisms that participate in litter decomposition are likely to change (McLain et al. 2020; Wu et al. 2021).

The role of animals in the decomposition of senesced biomass and organic matter has received considerable attention in terrestrial, coastal, and aquatic ecosystems at the local, regional, and global scale (Grandy et al. 2016; Crowther et al. 2019). Numerous studies have now demonstrated that different functional types of detritivores (shredders, grazers, scrapers, etc.) can have large top-down influences on litter

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✉ Tyler M. Rippel
tr599@georgetown.edu

¹ Department of Biology, Georgetown University, 3700 O Street NW, Washington, DC, USA

² Department of Biology, University of Denver, 2190 E. Iliff Ave, Denver, CO, USA

decomposition directly, as well as the saprotrophic microbial communities known to regulate the enzyme-mediated mineralization of plant tissues (Ingham et al. 1985; Silliman and Newell 2003; Daleo et al. 2009 reviewed in Crowther et al. 2012; A’Bear et al. 2014). However, the ability to predict the activities of detritivores under global change conditions has proven difficult as both litter quality and decomposition communities are both likely to change (Wall et al. 2008; García-Palacios et al. 2013). Further complicating the matter, detritivores change feeding behavior based on the nutrient availability or microbial decomposer communities in decomposing litter (Valiela and Rietsma 1984; Valiela et al. 1984; Price et al. 2021), which are also impacted by global change (Keiser and Bradford 2017; Raghukumar 2017). Since N is a dominant feeding cue for detritivores (Valiela and Rietsma 1984; Rietsma et al. 1988), N pollution can have a large impact on litter–detritivore interactions across ecosystems (Buchkowski et al. 2019; Yin et al. 2022).

N pollution is a ubiquitous global change driver that interrupts community assemblages, biogeochemical cycles, and ecosystem services in terrestrial, coastal, and aquatic ecosystems (Boring et al. 1988; Aber et al. 1998; Howarth 2008; Deegan et al. 2012). In addition to the N-uptake of live plants (endogenous enrichment), exogenous N can be readily absorbed by decomposing litter through microbial uptake or abiotically synthesized humic compounds (Rice 1982; White and Howes 1994; Tobias and Neubauer 2019). Notably, a few studies have compared the impacts of endogenous and exogenous enrichment on litter decomposition and detritivore dynamics (but see Hobbie 2005; Moise and Henry 2014 for terrestrial examples). Further, N pollution can alter detritivore composition and abundance (e.g., Haddad et al. 2000; Murphy et al. 2012) as well as the chemical characteristics of litter (Tobias and Neubauer 2019). Both microbial decomposers and detritivores preferentially select litter based on the nutrient stoichiometry and secondary chemical defenses present in the litter (e.g., Valiela and Rietsma 1984; Ushio et al. 2009). Thus, when N pollution is present, it can impact litter decomposition by facilitating microbial decomposition or altering detritivore abundance and behavior.

In coastal salt marshes, ecosystem dynamics and litter decomposition are changing rapidly due to relative sea-level rise, nutrient pollution, species loss, and multiple other human-induced stressors (Kirwan and Blum 2011; Kirwan et al. 2013; Rippel et al. 2020). Further, coastal salt marshes serve as ideal models for investigating how N and detritivores impact litter decomposition dynamics because they: (1) are extensively impacted by N pollution (Howarth 2008), (2) can have simple plant communities (monocultures of halophyte grasses) that do not change with N addition, reducing confounding factors of shifting plant diversity (Murphy et al. 2012; Wimp et al. 2019a), (3) contain relatively simple detritivore communities (mainly snails, isopods, and amphipods)

(Wimp et al. 2011, 2019b), and (4) have one of the highest carbon storage rates on Earth (Chmura 2013). The effects of sea-level rise and the subsequent habitat fragmentation of foundation species are expected to fundamentally alter the detritivore community in salt marshes (Watson et al. 2016; Johnson and Williams 2017; Wimp et al. 2019b; Wimp and Murphy 2021). However, no field studies to date have investigated the potential impact of detritivore community alteration on litter decomposition, nor the simultaneous impact of nitrogen pollution.

To understand how multiple global change factors may interact to alter litter decomposition, we manipulated the detritivore community and N concentrations of a Mid-Atlantic salt marsh. Specifically, we aimed to generate predictions for litter decomposition under future ecological conditions in Mid-Atlantic salt marshes, where the pulmonate gastropod detritivorous snail, is declining from sea-level rise (Johnson and Williams 2017) and migrating competitors (Lee and Silliman 2006). We sought to determine if changes in the population density of *Melampus* will correspond with changes in litter decomposition, and if these changes are dependent on the N status of the environment. Therefore, we asked the following questions: (1) how does N addition, the population density of *Melampus*, and their potential interaction affect rates of litter decomposition? (2) Does the impact of *Melampus* on litter decomposition vary throughout decomposition stages? (3) Do exogenous and/or endogenous N additions impact the dominant modulators of litter decomposition and litter N? We predict that the effects of *Melampus* on litter decomposition will be density dependent given past experiments showing that *Melampus* directly consumes decomposing litter and fungi therein (Valiela and Rietsma 1984; Valiela et al. 1984; Rietsma et al. 1988; Graça et al. 2000); however, we predict that the impacts of *Melampus* on litter decomposition will be contingent on the phase of decomposition (leaching, microbial, and recalcitrant stages; see Valiela et al. (1985)) and the N status of the litter. For example, early-stage litter has high phenolic acid concentrations which *Melampus* avoids, but *Melampus* will ignore these inhibitory cues if there is a high N concentration in the litter (Valiela and Rietsma 1984; Valiela et al. 1984). Thus, this research represents one of the few studies to examine the impacts of species loss and nutrient inputs simultaneously in a field study.

Materials and methods

Study site and organisms

We conducted experimental manipulations of snail populations and N concentrations for 2 years (2018, 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 square plots (3.1 × 3.1 m; 10 m²) in an area dominated by short form *Spartina alterniflora* Loisel. at lower elevations (daily flooding) with a few surrounding patches of *S. patens* occurring at the mean high-water line. Blocks were typically 25 × 25 m and were spaced at least 25 m apart. This section of the marsh contains multiple food webs that have been previously characterized (Denno 1977; Murphy et al. 2012; Wimp et al. 2011, 2013) but here we focus on the most abundant detritivore by mass, the previously discussed snail *Melampus*, which feeds mainly on dead plant biomass. We also examined two other common detritivores that are known to be impacted by N additions (Murphy et al. 2012), the amphipod *Orchestia grillus* (Bosc.) and the isopod *Venezillo parvus* (Budde-Lund), which feed on dead *Spartina* species as well as fungal and algal resources (Lopez et al. 1977; Agnew et al. 2003; Wimp et al. 2013).

Snail and nitrogen manipulations

In a 2 × 3 factorial design, we manipulated the population density of the dominant detritivore *Melampus* and the N concentration of sediment. Each of our 6 blocks contained 6 treatments in which we either manipulated snail densities (snail reduction, ambient, or snail addition) and/or N (ambient vs. N addition). Notably, snail treatments did not involve any fencing, as *Melampus* tends to be static and has a maximum travel of 1 m over 24 h (Holle and Dineen 1957) and we did not want to potentially alter tidal flow. Prior to our experiment, we surveyed *Melampus* populations throughout a growing season and found densities ranged between 50 and 200 snails per m². Based on these numbers, we added 250–500 total snails (25–50 per m²) to ‘snail addition’ and ‘snail addition plus N’ plots 4 × per season (every 3 weeks, June–August, both field seasons), attempting to double the population density, which was mostly successful (Fig. 1). When reducing snail densities (every 3 weeks, June–August, both field seasons), we would attempt to remove the entire snail community from ‘snail reduction’ and ‘snail reduction plus N’ plots, which resulted in reductions rather than removals. On average, we removed 194 snails from snail

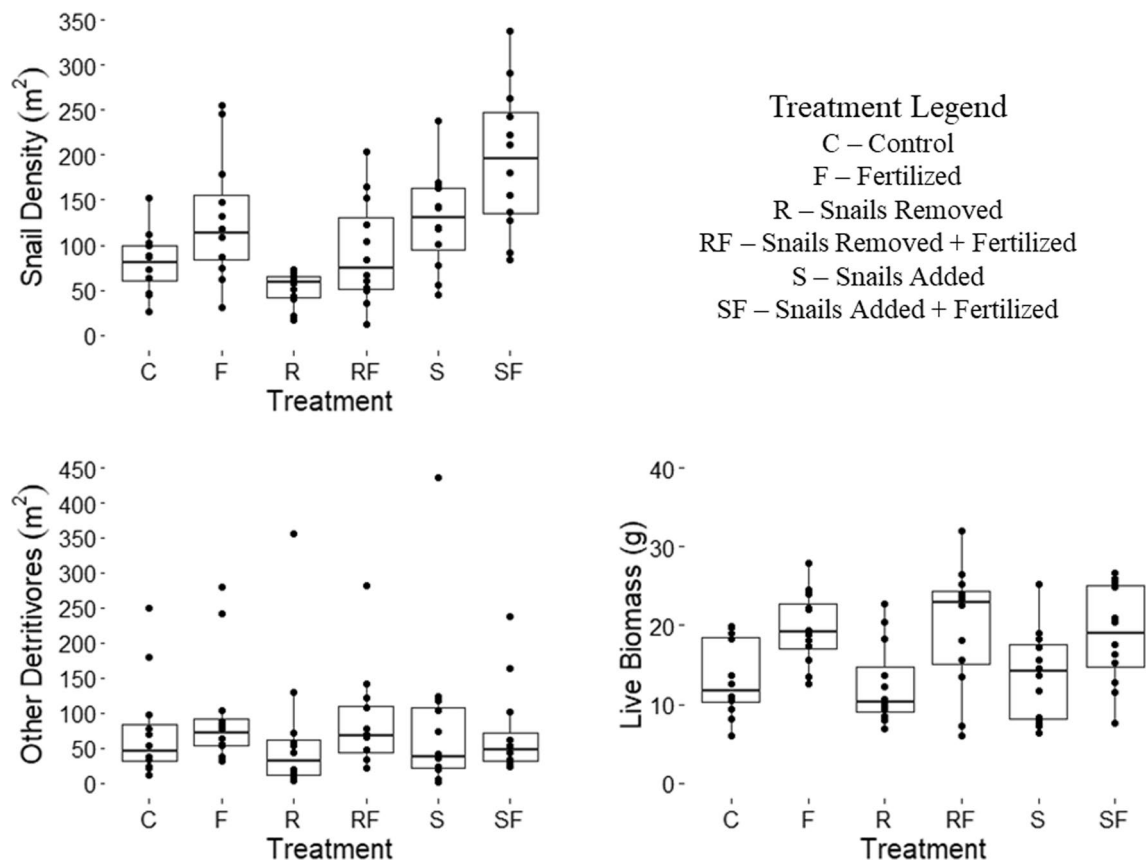


Fig. 1 The effects of fertilization and snail manipulations on snail density (counts), detritivore density (D-Vac), and live biomass (grams of dry biomass/quadrat). Boxplots contain median values, quartiles, and 95% confidence intervals

reduction plots and 222 snails from snail reduction plus N plots, with a range of 35–> 1500 snails. We surveyed snail populations in each plot four times per season starting in July by haphazardly throwing a 0.047 m² quadrat into plots ten times and counting all snails found in the quadrat. Snail densities used in analyses represent the averages from all surveys. Further, we fertilized plots 3 × early in the growing season (May–June, both field seasons) during peak plant uptake by adding 13.6 g N/m² each time in the form of granular urea, an amount reflective of N inputs along the Atlantic coast and other studies examining the impacts of N in salt marshes (Boyer and Zedler 1998; Bertness et al. 2002; Wimp et al. 2019a).

Plant characteristics

In all plots, we measured the above-ground plant biomass at the end of the growing season (October) during both field seasons. We collected all the above-ground biomass from within a haphazardly thrown 0.047 m² quadrat and transported samples to the lab. We dried all biomass at ~60 °C, and then separated and weighed live and dead biomass.

Litter decomposition

To quantify rates of decomposition within plots, we used litter bags filled with *S. alterniflora* litter in decomposition assays. In 2018, we tested the decomposition rate of unmanipulated, ‘control’ litter. In 2019, we examined the impact of endogenous N via ‘enriched litter’ as well as control litter. In late July each year, we collected living biomass from an unmanipulated *S. alterniflora* patch that was not otherwise used in the study. Using live biomass before natural senescence is a common method in salt marsh litter decomposition studies but may overestimate decomposition rates (Menéndez and Sanmartí 2007). In late July of 2019, in addition to the control litter collections, we collected living biomass from a *S. alterniflora* patch (otherwise not used in the study) that had previously been fertilized with the same N concentrations as our experimental N manipulations. From our biomass collections, we selected only previously living, green culms, and washed and dried it at ~60 °C. We made litter bags from fiberglass screens (2 mm mesh) loosely sewn together with fishing line to form 10 cm² square-shaped bags with 2 cm long openings on all sides, and we filled each bag with 4.00 g of dry *S. alterniflora* biomass. In the beginning of August 2018, we placed three replicate control litter bags haphazardly distributed in each plot (108 control litter bags in 36 plots) as close to the soil surface as possible. In the beginning of August 2019, we placed three replicate control litter bags and three replicate fertilized litter bags haphazardly in each plot (108 control and 108 fertilized litter bags in 36 plots). We removed one bag from each plot ~30, ~75,

and ~150 days after being deployed. After harvesting the litterbags from the field, we removed remaining litter from each bag, rinsed it with water, dried it at ~60 °C, and weighed it. We calculated the percent mass remaining (PMR) for each bag by dividing the litter mass in each bag by its original mass. We calculated litter decomposition rates (k) using simple exponential models (Olson 1963).

Sediment and litter nitrogen concentrations

To examine the impacts of N fertilization on litter decomposition, we evaluated the N concentration of sediment and of litter from decomposition bags. Considering sediment nitrate is in very low abundance at these sites (Windham and Ehrenfeld 2003), we focused on sediment ammonium (NH₄⁺), the dominant N form. To analyze the NH₄⁺ concentrations of sediment, we took sediment cores (7.5 × 15 cm) in the same location and date as plant biomass collections (at peak biomass). After quadrats were clipped of all above-ground biomass, we took sediment cores in the center of quadrat locations and transferred them to ice and subsequently froze them at –20 °C until processing. Whole cores were separated into roots and sediment and then dried at ~60 °C. We subsampled sediment samples from each plot for KCl extraction, where 4.00 g of dried sediment were extracted for NH₄⁺ using three successive 2 M KCl extraction shakes for 20 min. Sediment KCl extractions were then analyzed for NH₄⁺ on a plate reader at 650 nm following a modified Berthelot reaction (Weatherburn 1967; Sims et al. 1995). We subsampled litter samples by taking 5–10 clips of litter from each collection and then ground them in a Retsch MM 400 model mixer mill (Retsch GmbH), weighed them using a Mettler-Toledo XP6 microbalance (Mettler-Toledo), and rolled them into tin capsules (Elementar Americas). We then sent these prepared samples to the Cornell Stable Isotope Laboratory to be analyzed for percent N (%N) using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA Systems).

Microclimate measurements

We gathered microclimate data from plots as the relatively heterogeneous microclimate in salt marshes is known to be a modulator of litter decomposition and animal populations (Reice and Stiven 1983). We calculated microclimate air temperatures and relative humidity six times per season on hot, cloudless days in each plot and averaged these measurements across seasons. Ambient air temperatures and relative humidity were taken at chest height, followed by the microclimate air temperature and relative humidity in plots on the soil surface using a HOBO MX1101 temperature/RH data logger (Onset Computer Corporation). To identify the

temperature and relative humidity of a patches' microclimate (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}): $M_i = S_i - A_i$.

Detritivore sampling

Although we only intended to manipulate the densities of *Melampus*, nutrient manipulations are known to increase the abundance of detritivores in salt marshes, particularly *V. parvus* and *O. grillus* (Murphy et al. 2012). Therefore, we analyzed the detritivore food web in each season (September) using a D-vac suction sampler (Rincon-Vitova Insectaries) with a diameter of 21 cm. We collected all arthropods in plots by taking 3, 5-s placements of the D-Vac on the marsh surface (Wimp et al. 2019a). We stored all arthropods in ethanol, identified them to species, and counted detritivores in samples. We refer to isopod and amphipods together as “other detritivores.”

Statistical analysis

Effects of nitrogen addition and snail manipulation

We first statistically evaluated how our treatment effects impacted the following variables: litter decomposition rates (control and enriched separately), percent mass remaining (PMR; each control and enriched bag separately), and litter %N (each control and enriched bag separately). We used repeated-measures linear mixed models to evaluate whether N and snail manipulation treatments altered the response variables listed above. Our random effects were year and block nested within year, with plot considered as the repeated-measures unit in an autoregressive 1 covariance structure. For enriched litter, we only included block as the random variable. To test the impact of endogenous N, we constructed four linear mixed models containing litter decomposition rates or PMR (each collection separately) as the response variable, litter type (control or enriched) as the fixed effect, and block, treatment, and plot as random effects. Significant models were subsequently analyzed using Tukey's HSD to examine which treatments differed from one another. Prior to analysis, we visually inspected residual plots to check for a normal distribution of residuals and analyzed studentized residual plots to check for homogeneity of variance. Due to violations of one or both assumptions, we subsequently transformed multiple variables (Table S1). Since snail density varied within treatments, we evaluated whether using continuous snail density as a predictor variable was associated with decomposition rates and PMR of

litter using simple linear regressions. Similarly, we evaluated the relationship between %N and PMR of litter bags.

Modulators of litter decomposition

To determine the drivers of litter decomposition, we used linear mixed models to determine which variables were best associated with litter decomposition rates and PMR. In each model, we included the following fixed factors as potential predictors: snail density (/m²), other detritivore density (/m²), %N (of each respective bag), soil NH₄⁺ (PPM), and the relative humidity of each plot. We used the same random-effects structure as above. We avoided model selection procedures as there is little agreement on optimal selection procedures and our full models contain typical regulators of litter decomposition known in the literature (Bradford et al. 2017). Instead, we compared full models to null models using the ‘anova’ function in R, and models with lower AIC scores ($\Delta\text{AIC} < 2$) were considered significantly better. To evaluate multicollinearity, we used the “vif” function in R (version 3.6.1) with a cutoff of $\text{VIF} < 3$. Assumptions for normality and homogeneity of variance were visually examined as in the prior section. Models and parameters are interpreted with beta-values, pseudo- R^2 values, F -statistics, and p values. Due to the range of scales inherent in our fixed factors, we standardized beta-values using the “std_beta” function in the “sjstats” package in R (version 3.6.1) which standardizes beta estimates between -1 and 1 (Lüdtke 2019). Pseudo- R^2 values were calculated using the “r.squaredGLMM” function in the “MuMIn” package (Barton and Barton 2015).

Modulators of litter nitrogen

We used a similar linear mixed model approach as above to determine the variables that are best associated with the %N of litter. For each bag, we included the following fixed factors as potential predictors of %N: snail density, detritivore density, and sediment NH₄⁺. We used the same random-effects structure as in the previous sections.

Results

Effects of nitrogen addition and snail manipulation

Of the 18 response variables evaluated, 10 variables were significantly impacted by treatment effects (Table S1). For control litter, fertilizer and snails significantly impacted decomposition rates (k) relative to control plots and plots where snails were removed ($F_{5,60} = 7.97$, $p < 0.001$, Fig. 2). Notably, fertilized plots had 33% higher decomposition rate than control plots and plots with snails added had 25% higher

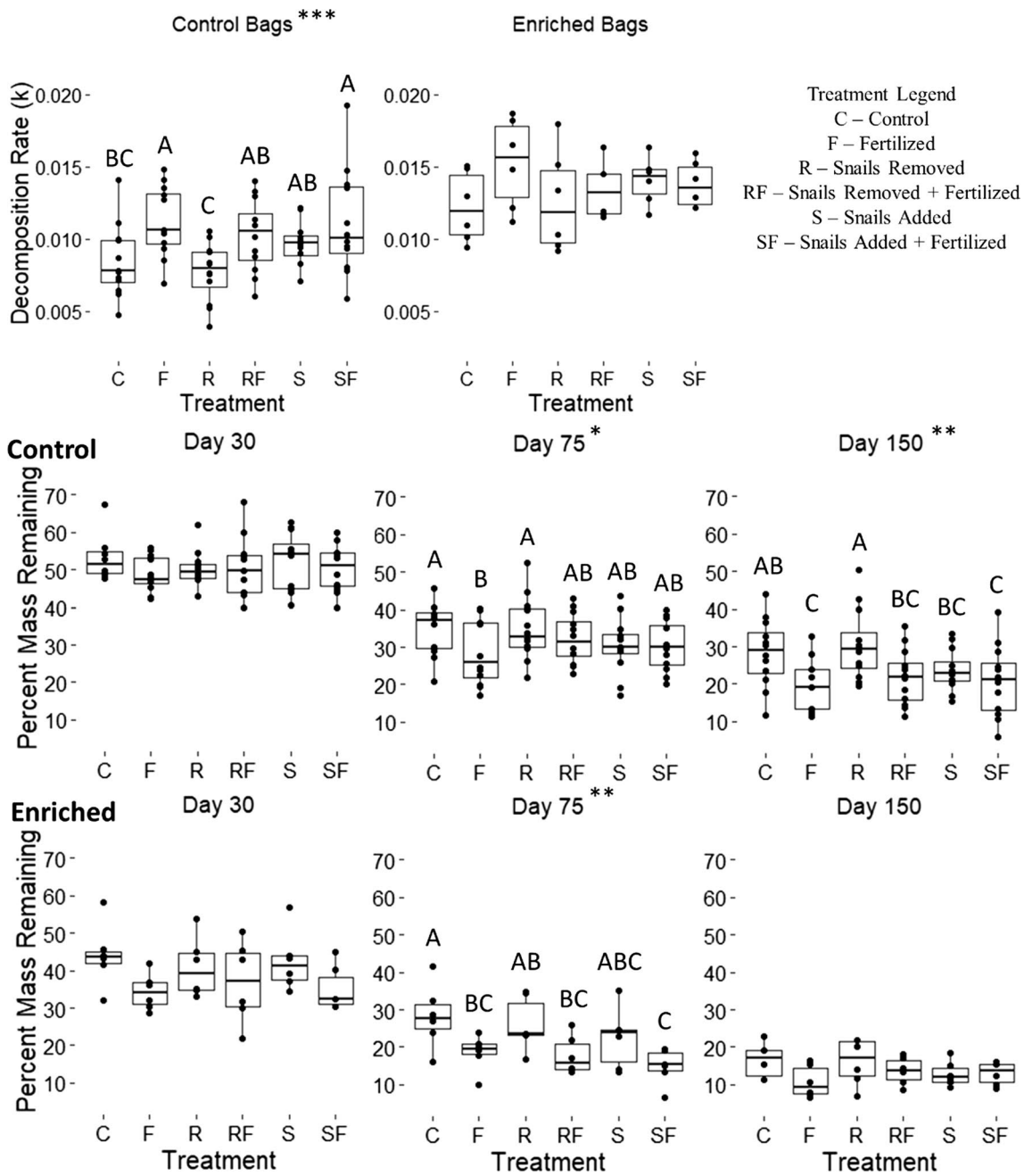


Fig. 2 The effects of fertilization and snail manipulations on litter decomposition rates (k) as well as percent mass remaining (PMR) of control and enriched litter according to the day collected from the

field. Boxplots contain median values, quartiles, and 95% confidence intervals. Significance: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

decomposition rates than plots where snails were removed. All treatment effects disappeared for endogenously enriched litter ($F_{5,25} = 1.54$, $p = 0.21$, Fig. 2). However, endogenous N significantly ($p < 0.001$) increased litter decomposition rates by 64% on average and mass loss at every collection point (Day 30: 20%, Day 75: 40%, Day 150: 53%) relative to control litter (Table S1). Treatment effects on mass loss were more apparent at later collection dates for control litter:

percent mass remaining (PMR) did not differ by treatment at Day 30, began to differ at Day 75 ($F_{5,60} = 3.85$, $p = 0.01$, Fig. 2), and at Day 150, we found higher mass loss (lower PMR) in plots with added N and either ambient or increased snail densities ($F_{5,60} = 8.98$, $p < 0.001$, Fig. 2). Notably, for bags collected at Day 150, plots with snails added had 23% less litter than plots with snails removed, further revealing the importance of *Melampus* on litter removal. However,

the pattern was different for enriched litter: while we did not find any effects of snail manipulation or N additions on mass loss at Day 30 or Day 150, we found treatment effects at Day 75 ($F_{5,25} = 5.58$, $p = 0.001$, Fig. 2). Relative to control plots, there was a 48% increase in mass loss in plots where we added both snails and N and a 34% increase in plots where we added N. Notably, while treatment effects on mass loss occurred at later decomposition stages for control litter, %N differed by treatment at earlier decomposition stages (Fig. S1). N additions affected litter %N at Day 30 ($F_{5,60} = 4.66$, $p = 0.001$, Fig. S1) and Day 75 ($F_{5,60} = 2.41$, $p = 0.047$, Fig. S1), but not at Day 150. Again, these patterns were different for the enriched litter. We did not find any differences in litter %N for the enriched litter at Day 30 or Day 75 but did find peculiar differences at Day 150 ($F_{5,25} = 4.29$, $p = 0.006$) (Fig. S1).

When we examined snail density as a continuous variable, we found that litter decomposition rates increased with increasing snail densities for control litter ($R^2 = 0.13$, $p = 0.0022$, Fig. S2), with k values increasing around 50% from 12 snails/m² to 338 snails/m². Notably, we did not find a relationship between snail densities and decomposition rates for enriched litter ($R^2 = 0.06$, $p = 0.15$). When we examined mass loss across time for control litter, we found that there was no relationship between snail density and mass loss at Day 30 ($R^2 = 0.014$, $p = 0.33$), but mass loss increased 31% from lowest to highest snail densities at Day 75 ($R^2 = 0.092$, $p = 0.0096$) and 44% at Day 150 ($R^2 = 0.093$, $p = 0.0091$). For enriched litter, there was no effect of snail density on mass loss at Day 30 ($R^2 = 0.022$, $p = 0.39$), but a marginal effect at Day 75 ($R^2 = 0.086$, $p = 0.083$) and Day 150 ($R^2 = 0.078$, $p = 0.098$).

When we examined %N as a continuous variable, we found that the %N of litter at Day 75 was negatively associated with the PMR at for control litter ($R^2 = 0.14$, $p = 0.0014$, Fig. S3). There were no other significant relationships between litter bags and %N; however, the positive associations between %N and PMR at Day 30 for enriched litter ($R^2 = 0.093$, $p = 0.07$), %N and PMR at Day 75 for enriched litter ($R^2 = 0.11$, $p = 0.052$), and %N and PMR at Day 150 for enriched litter ($R^2 = 0.087$, $p = 0.081$) were all nearly significant.

Modulators of litter decomposition

We used linear mixed models to evaluate the influence of snail density, other detritivore density, plant tissue N, soil NH_4^+ , and relative humidity on the decomposition of control and N-enriched litter. When we compared full models to null models containing only random effects, five out of eight models outcompeted null models (Table 1). When we modeled the decomposition rate (k) of control litter, the full model (AIC = -673.9) outcompeted the null model

(AIC = -654.8, $\chi^2 = 29.2$, $p < 0.001$). The parameters driving this relationship were NH_4^+ ($F_{1,65} = 15.2672$, $p < 0.001$, $\beta = 0.34$) and snail density ($F_{1,65} = 11.92$, $p < 0.001$, $\beta = 0.31$), which both increased decomposition rates. For the PMR on Day 75, our full model (AIC = 487.8) outcompeted the null model (AIC = 482.8, $\chi^2 = 14.6$, $p = 0.01$). Both snail density ($F_{1,65} = 6.96$, $p = 0.01$, $\beta = -0.26$) and other detritivore density ($F_{1,65} = 5.08$, $p = 0.028$, $\beta = -0.24$) were negatively associated with the PMR at Day 75. Similarly, for our model of PMR on Day 150, the full model (AIC = 486.2) outcompeted the null model (AIC = 498.7, $\chi^2 = 24.5$, $p < 0.001$), and snail density ($F_{1,65} = 10.99$, $p = 0.002$, $\beta = -0.28$) and soil NH_4^+ ($F_{1,65} = 7.5$, $p = 0.009$, $\beta = -0.23$) were significantly negatively associated with the PMR. Finally, the only model the PMR of enriched litter that outcompeted the null model (AIC = 258) was on Day 75 (AIC = 247.5, $\chi^2 = 28.5$, $p < 0.001$, Table 2). Snail density ($F_{1,30} = 7.41$, $p = 0.01$, $\beta = -0.25$) and other detritivore density ($F_{1,30} = 7.33$, $p = 0.01$, $\beta = -0.28$) were negatively associated with PMR, and %N ($F_{1,30} = 4.89$, $p = 0.01$, $\beta = 0.3$) and relative humidity ($F_{1,30} = 13.35$, $p = 0.01$, $\beta = 0.4$) were positively associated.

Modulators of litter nitrogen

We used linear mixed models to evaluate the influence of snails, other detritivores, and sediment NH_4^+ on the %N concentrations of control and enriched litter. Of the six candidate models, only two outcompeted null models, all being related to control litter (Table S2). The full model for %N of litter at Day 30 (AIC = -69.56) outcompeted its null model (AIC = -63.47, $\chi^2 = 12.091$, $p = 0.007$). Other detritivores ($F_{1,65} = 5.12$, $p = 0.03$, $\beta = -0.15$) were significantly negatively associated with %N, while sediment NH_4^+ ($F_{1,65} = 4.69$, $p = 0.03$, $\beta = 0.13$) was positively associated. Further, the model for %N at Day 150 for control litter (AIC = -1.31) outcompeted its null model (AIC = 8.9, $\chi^2 = 16.21$, $p = 0.001$), with other detritivores ($F_{1,65} = 19.42$, $p < 0.001$, $\beta = -0.46$) being the only significant parameter.

Discussion

Our results demonstrate that global change in the form species loss and N pollution can have palpable impacts on carbon cycling and ecosystem function. We found that exogenous and endogenous N additions and higher snail densities increased rates of litter decomposition in coastal salt marshes. To our knowledge, this is the first experiment that has factorially altered detritivore densities and type of N addition (endogenous vs. exogenous) to examine litter decomposition in a coastal salt marsh to simulate future conditions. We found a causative relationship between the

Table 1 Results from linear mixed models examining the biotic and abiotic factors regulating litter decomposition for control bags

Response variable	Predictor variables	Standardized β estimate	F	P value	R^2 (fixed)	R^2 (fixed + random)
Control K				< 0.001	0.18	0.67
	Soil NH₄⁺	0.34 ± 0.088	15.26	< 0.001		
	Snail density	0.31 ± 0.089	11.92	< 0.001		
	Other detritivores	0.38 ± 0.097	0.75	0.39		
	Bag 1%nitrogen	-0.078 ± 0.17	0.21	0.66		
	Relative humidity	0.0062 ± 0.12	0.0026	0.96		
Control bag 1 PMR				0.84	0.059	0.26
	Snail density	-0.12 ± 0.13	0.78	0.38		
	Other detritivores	-0.13 ± 0.13	0.96	0.33		
	Bag 1%nitrogen	-0.061 ± 0.21	0.083	0.78		
	Soil NH ₄ ⁺	-0.25 ± 0.13	0.95	0.85		
	Relative humidity	0.16 ± 0.16	0.038	0.33		
Control bag 2 PMR				0.012	0.16	0.43
	Snail density	-0.26 ± 0.1	6.96	0.01		
	Other detritivores	-0.24 ± 0.11	5.08	0.028		
	Bag 2%nitrogen	-0.11 ± 0.14	0.68	0.41		
	Soil NH ₄ ⁺	-0.033 ± 0.13	0.12	0.74		
	Relative humidity	0.36 ± 0.13	0.077	0.041		
Control bag 3 PMR				< 0.001	0.16	0.63
	Snail density	-0.28 ± 0.86	10.99	0.0018		
	Soil NH₄⁺	-0.23 ± 0.085	7.5	0.0086		
	Bag 3%nitrogen	-0.11 ± 0.11	1.07	0.31		
	Other detritivores	-0.12 ± 0.11	1.37	0.25		
	Relative humidity	0.041 ± 0.12	0.11	0.74		

Bold response variables signify full models that outcompeted null models ($\Delta\text{AIC} < 2$)

dominant detritivorous snail, *Melampus*, and litter decomposition in a natural field setting. This finding confirms previous mesocosm and laboratory experiments which suggested that *Melampus* may play a substantial role in litter decomposition (Valiela et al. 1985; Graça et al. 2000; Hines and Eisenhauer 2021). Further, we found that exogenous N additions are readily absorbed into decomposing litter, which increased litter decomposition rates by 33%, while endogenous N increased litter decomposition rates by 64%. This is notable because most past studies examining the effects of N fertilization on litter decomposition in salt marshes have only examined endogenous N. Here, we found that N inputs, both during live plant uptake (endogenous N) and during decomposition (exogenous N), can increase rates of litter decomposition. Finally, we found that other detritivores present in plots, isopods (*V. parvus*) and amphipods (*O. grillus*), were also associated with increases in mass loss and decreases in litter N in the middle stages of decomposition. These results demonstrate that future global change in salt marshes, due to N pollution and altered detritivore populations, is likely to alter current litter decomposition dynamics. Considering *Melampus* is expected to decline as

sea levels rise (Johnson and Williams 2017) and competitors move northward (Lee and Silliman 2006), these results suggest that species declines will impact litter decomposition dynamics.

When analyzed as a categorical variable (snails added, removed, or ambient), *Melampus* increased decomposition rates overall for control litter, likely through direct grazing on dead litter and facilitating fungal decomposers (Rietsma et al. 1988; Zimmer et al. 2004). However, for enriched litter, we did not find an impact of these snails on overall decomposition rates, which is surprising considering %N has been reported as the dominant feeding cue for *Melampus* (Valiela and Rietsma 1984; Valiela et al. 1984). Further, both univariate regressions and linear mixed models confirmed that higher snail densities led to faster litter decomposition rates for control litter, but not enriched litter. These results only partially support our first hypothesis that faster litter decomposition rates are associated with higher densities of *Melampus*, as we expected snails to have a large impact on enriched litter. Although some studies using similar densities of snails found no direct relationships between *Melampus* and litter mass loss (Treplin et al. 2013), our results provide field data

Table 2 Results from linear mixed models examining the biotic and abiotic factors regulating litter decomposition for N-enriched bags

Response variable	Predictor variables	Standardized β estimate	<i>F</i>	<i>P</i> value	<i>R</i> ² (fixed)	<i>R</i> ² (fixed + random)
Enriched K	Snail density	0.12 ± 0.17	0.56	0.45	0.16	0.2
	Other detritivores	0.29 ± 0.18	2.66	0.11		
	Bag 3%nitrogen	−0.2 ± 0.17	1.38	0.25		
	Relative humidity	−0.065 ± 0.19	0.12	0.73		
	Soil NH ₄ ⁺	−0.39 ± 0.18	0.046	0.83		
Enriched bag 1 PMR	Snail density	−0.19 ± 0.15	1.59	0.21	0.13	0.43
	Other detritivores	−0.044 ± 0.18	0.059	0.81		
	Bag 1%nitrogen	−0.27 ± 0.17	2.43	0.13		
	Soil NH ₄ ⁺	−0.27 ± 0.17	2.46	0.46		
	Relative humidity	−0.16 ± 0.21	0.57	0.13		
Enriched bag 2 PMR				< 0.001	0.41	0.66
	Relative humidity	0.4 ± 0.15	7.41	0.011		
	Bag 2%nitrogen	0.33 ± 0.12	7.33	0.011		
	Snail density	−0.25 ± 0.11	4.89	0.036		
	Other detritivores	−0.28 ± 0.14	4.19	0.049		
	Soil NH ₄ ⁺	−0.29 ± 0.12	3.38	0.077		
Enriched bag 3 PMR	Snail density	−0.16 ± 0.17	0.95	0.34	0.19	0.22
	Soil NH ₄ ⁺	0.085 ± 0.18	0.022	0.96		
	Bag 3%nitrogen	0.23 ± 0.17	1.85	0.19		
	Other detritivores	−0.27 ± 0.17	2.35	0.14		
	Relative humidity	−0.096 ± 0.19	0.26	0.61		

Bold response variables signify full models that outcompeted null models ($\Delta\text{AIC} < 2$)

that supports mesocosm studies showing that *Melampus* increases litter decomposition (Valiela et al. 1984; Hines and Eisenhauer 2021). Although the impact of *Melampus* on litter decomposition rates was relatively modest, the slowing of litter decomposition rates by the reduction of *Melampus* densities could have palpable impacts on carbon cycling in salt marshes, especially in areas that currently have densities of *Melampus* exceeding 1000/m² (Zajac et al. 2017).

The impact of snails and other detritivores were most apparent, for both control and enriched litter, at intermediate stages of decomposition (Day 75 and Day 150). This supports the finding that detritivores play little-to-no role in the early, leaching phase of litter decomposition, wherein soluble compounds are lost from litter (Valiela et al. 1985). However, we expected that fertilized plots and litter previously enriched with N would be impacted by snails regardless of decomposition stage, which did not occur. Rather, *Melampus* and other detritivores only increased the decomposition of enriched litter between Day 30 and Day 75. Thus, fertilization did not increase snail feeding in early decomposition stages, as was the case in mesocosm and laboratory studies (Valiela and Rietsma 1984; Valiela et al. 1984; Rietsma et al.

1988). Nevertheless, the fact that higher *Melampus* densities were associated with greater mass loss for litter collected at Day 75 and Day 150 for control litter, and at Day 75 for enriched litter, clearly demonstrates that detritivores play an important role in decomposition after the initial leaching phase. These findings from the field confirm laboratory and microcosm studies that demonstrate *Melampus* prefers detritus that has been partially decomposed (Valiela and Rietsma 1984; Valiela et al. 1984; Graça et al. 2000), and that litter decomposition at different decomposition stages is regulated by different environmental variables (Valiela et al. 1985; Calado et al. 2019).

Notably, exogenous and endogenous N both had substantial impacts on litter decomposition, with exogenous inputs increasing litter decomposition by 33% and endogenous inputs increasing decomposition by 64%. Consistent with past studies, N-enriched litter had markedly faster litter decomposition rates than control litter (Marinuccia et al. 1983; Hines et al. 2006; García-Palacios et al. 2013), and N added to plots as exogenous N was taken up by decomposing litter (Tobias and Neubauer 2019). However, we show these effects can be additive, as enriched litter in fertilized

plots collected at Day 75 had the highest mass loss (Fig. 2), 43% higher than control litter in control plots. The fact that exogenous N additions increased the %N of control litter early in the experiment (Day 30) is counter to past studies in salt marshes which showed that N is incorporated into decomposing litter at later stages of decomposition (White and Howes 1994). However, studies in grasslands and forests have also shown that exogenous N can be incorporated into litter in early stages of decomposition (Li et al. 2019), although these results are variable (Hobbie 2005; Zhang et al. 2018). Notably, although exogenous inputs did not typically increase the %N of decomposing litter, they did increase overall decomposition rates of control litter, as well as mass loss at Day 75 for control and enriched litter and at Day 150 for control litter. This is likely due to direct influences on litter microbial communities (Li et al. 2019). Further, in plots with added snails and N, %N sharply decreased from Day 75 to Day 150. This goes against past studies, which have shown that *Melampus* can increase the N content of litter at lower densities than used in this study (Zimmer et al. 2004). Thus, knowing the identity of the microorganisms and N compounds within the litter may be essential for interpreting our results, as most of the factors that were found to be modulators of litter decomposition had relatively low predictive power.

The probable interaction between N compounds and fungi is further exemplified by the differences that emerged from linear mixed models examining the modulators of decomposition in the middle stages of decomposition. For control litter, mass loss increased with snail density, other detritivore, and soil NH_4^+ , while mass loss for enriched litter increased with the same factors but decreased with increasing humidity and litter %N. Notably, N-enriched litter collected at Day 75 was the only collection where all putative litter decomposition modulators were influential. Although microclimate has been shown to have context-dependent impacts on litter decomposition (Bradford et al. 2017), it is notable that increasing litter %N slowed mass loss for N-enriched bags. Both field studies and meta-analyses have shown that excessive N can have variable impacts on litter decomposition depending upon the microorganisms present, amount of biologically available N, and the amount of complex N-containing compounds within the litter (Hobbie 2005; Zhang et al. 2018). It is likely that endogenously enriched litter had a higher concentration of phenolic compounds which slowed decomposition. However, N-enriched litter (endogenous treatment) still had 64% higher decomposition rates than control litter and thus, N inputs generally increased litter decomposition. Further, it is also notable that rather than litter %N, soil NH_4^+ was consistently a strong predictor of mass loss and litter decomposition rates for control litter.

Thus, exogenous N inputs did not just impact litter decomposition by increasing the N content of litter, but through some other process, such as altering microbial communities within litter. This was also revealed by the fact that enriched litter in fertilized plots did not have significant increases in %N but did have increases in mass loss relative to control plots. Thus, endogenous and exogenous N can have relatively similar impacts on litter decomposition, but exogenous N does not appear to alter decomposition by simply increasing the %N of litter.

Conclusion

Coastal salt marshes face a plethora of global change factors which interact to alter ecosystem processes and species assemblages. Our field study showed that higher densities of *Melampus* and other detritivores were associated with faster litter decomposition. Considering the potential loss or reduction of *Melampus* population densities, as is predicted in the face of sea-level rise and increased competition, litter decomposition dynamics might be impacted in areas with declining densities of *Melampus*. Further, since *Melampus* is a widespread and abundant detritivore that can directly interact with microbial communities, changes in *Melampus* densities may also impact microbial structure and function in decomposing litter. Finally, although it is known that higher N contents of litter can increase litter mass loss, our study demonstrates that exogenous N can further increase the decomposition rate of litter that already has a high N content. In sum, our results reveal that detritivores have palpable impacts on litter decomposition and litter N dynamics, which may be altered in the face of global change and species loss.

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Author contribution statement TMR and GMW conceived and designed the experiments. TMR, JT, BM, and GWM performed the experiments. TMR and SMM did the laboratory analyses. TMR analyzed the data. TMR wrote the manuscript and all the authors provided substantive edits.

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Declaration

Conflict of interest The authors have not disclosed any competing interests.

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