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HERBIVORE EFFECTS ON LITTER QUALITY AND QUANTITY AND
INFLUENCES ON CARBON CYCLING

by

Taylor Saunders

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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ABSTRACT

Effects of Litter Quality and Quantity on Carbon Cycling in Y-K Delta Wetland

by

Taylor C. Saunders, Master of Science

Utah State University, 2024

Major Professor: Dr. Karen H. Beard
Department: Wildland Resources

Plants mediate a large component of carbon (C) and nitrogen (N) cycles in terrestrial systems, and plant litter inputs to soils influence processes such as soil microbial respiration and decomposition. Herbivores, such as geese in the Yukon Delta National Wildlife Refuge, affect these processes through their alterations to litter quality and quantity, producing measured differences in soil respiration, microbial communities, and nutrient turnover. However, because geese influence litter quality, quantity, and habitat characteristics simultaneously, it is not yet clear which of these factors most affects biogeochemical cycling within heavily grazed areas.

To study how vegetation-herbivore interactions affect C and N cycling, our field experiment investigated the potential effects of herbivores on litter decomposition, a vital process for soil organic carbon formation and nutrient turnover. Litter bags containing high and low qualities of litter were placed in ‘grazing lawn’ and *Carex* meadow habitats. Abiotic characteristics were monitored between the habitat types to account for potential habitat differences. We analyzed litter bags for carbon and nitrogen content. We also performed a fully factorial microcosm incubation experiment using soils and litter collected from the Yukon Delta National Wildlife Refuge. We manipulated levels of litter

quality and litter quantity to examine the effect of herbivore-mediated changes in litter.

We measured weekly CO₂ fluxes from the microcosms. At the end of the experiment, we sequenced microbial communities and measured soil microbial biomass carbon, dissolved carbon, inorganic nitrogen, and enzyme activity.

Our field experiment revealed strong associations between litter quality and litter decomposition rates. However, grazed habitats experienced lower decomposition rates than ungrazed *Carex* meadow habitats. In our lab experiment, quality and quantity interactively affected CO₂ fluxes. Herbivore feces produced a strong positive effect on CO₂ fluxes. Herbivore feces and low-quality senesced litter cultivated unique microbial communities, showing a strong effect of litter inputs on microbial communities in these soils. Herbivores, as ecosystem engineers, enact visible changes to their habitat in this system, but they also mediate microbial communities. Their effects on litter quality and quantity produce vegetation and soil interactions that promote CO₂ emissions from soils and promote higher turnover from litter decomposition.

(144 pages)

PUBLIC ABSTRACT

Effects of Litter Quality and Quantity on Carbon Cycling in Y-K Delta Wetland

Taylor C. Saunders

Plants are responsible for a large amount of the movement of carbon (C) and nitrogen (N) through terrestrial systems. One way that plants affect the movement of C and N is through plant litter inputs to soils. Plant litter highly influences processes such as soil microbial respiration and decomposition. Herbivores, such as geese in the Yukon Delta National Wildlife Refuge, affect these processes by changing litter quality and quantity. These changes cause differences in soil respiration, microbial communities, and nutrient turnover. However, because geese influence litter quality, quantity, and habitat characteristics simultaneously, it is not yet clear which of these factors most affects biogeochemical cycling within heavily grazed areas.

To study how these vegetation-herbivore interactions affect the movement of C and N, we performed a litter bag decomposition experiment. Our experiment investigated the potential effects of herbivores on litter decomposition, a vital process for soil organic carbon formation and nutrient turnover. Litter bags contained high and low qualities of litter, and were placed in 'grazing lawn' and *Carex* meadow habitats. 'Grazing lawn' is composed of *Carex* that geese graze, creating short-statured vegetation. *Carex* meadow is ungrazed habitat that has taller vegetation. Temperature, UV radiation, and rainfall characteristics were monitored between the two habitat types to account for potential habitat differences. We measured carbon and nitrogen content in litter bags.

We also performed a microcosm incubation experiment with soils and litter collected from the Yukon Delta National Wildlife Refuge. We manipulated levels of litter quality and litter quantity to fully examine the effect of litter associated with herbivores. We measured weekly CO₂ levels from the microcosms. At the end of the experiment, we sequenced microbial communities and measured soil microbial biomass carbon, dissolved carbon, inorganic nitrogen, and enzyme activity. These factors are associated with differences in C and N, allowing us to see how litter quality and quantity levels affected the movement of C and N.

Our field experiment showed strong associations between litter quality and litter decomposition rates. However, grazed habitats experienced lower decomposition rates than ungrazed *Carex* meadow habitats. In our lab experiment, quality and quantity affected CO₂ levels. Herbivore feces increased CO₂ levels. Herbivore feces and low-quality senesced litter cultivated unique microbial communities, showing a strong effect of litter inputs on microbial communities in these soils. Herbivore effects on litter quality and quantity produce vegetation and soil interactions that increase CO₂ emissions from soils and increase litter decomposition rates.

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In this field, it is impossible to look at the final product of any given research without acknowledging that it is not the product of just one person, but instead, the product of a community of support and mutual enthusiasm for ecology. This research represents not only my work, but hours of work others have put in to help me in this process.

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CHAPTER 1

INTRODUCTION

Abstract

Herbivores can cause large differences in litter decomposition rates, but identifying the specific mechanisms through which herbivores do this is difficult because herbivory simultaneously affects both biotic and abiotic factors. In the Yukon-Kuskokwim (Y-K) River Delta, Alaska, geese are the dominant herbivores in wet-sedge meadows, where they create ‘grazing lawns’ that have a more open structure and contain pools of more nutrient-rich litter and feces compared to ungrazed areas. To determine whether herbivores affect litter decomposition through habitat changes or litter quality changes, we tested the effects of litter type and habitat type on litter decomposition. We performed a field litter bag study in which we collected two different qualities of litter representing grazed and ungrazed conditions, then incubated them in grazed ‘grazing lawn’ and ungrazed ‘*Carex* meadow’ habitats. Litter mass loss, carbon, and nitrogen content were measured at 3, 6, 9, and 52 weeks. We monitored abiotic conditions in each habitat type. Litter type and habitat interactively affected litter decomposition; both litter types decomposed faster in ‘away’ habitats, suggesting the opposite of a home-field advantage effect. Both grazed litter-ungrazed habitat and ungrazed litter-grazed habitat combinations lost more labile materials than pairings of litter with their respective ‘home’ habitats. The combined effects of litter quality and habitat on litter decomposition in this system suggests that herbivores may affect litter decomposition through multiple pathways.

Introduction

As temperatures increase in arctic ecosystems, herbivores are projected to change their ranges in response to temperature shifts (Speed et al., 2021). This change in herbivore distribution on the landscape, particularly from geese in the Arctic, can substantially affect ecosystems (Koltz et al., 2022). Herbivores can consume up to 50% of plant material (measured in net primary production) in certain ecosystems (Chapin et al., 2002), allowing them to exert significant effects on ecosystem processes. Herbivore-plant interactions can affect ecosystems through shifts in vegetation communities (Rebollo et al., 2013; Kempel et al., 2015), changes in litter chemistry or quality (Elliott and Henry, 2011; Chollet et al., 2021; Petit Bon et al., 2022), microclimate characteristics of soils (Sjögersten et al., 2012; Frank et al., 2018), or soil microbial community composition and activity (Bardgett et al., 2001; Eldridge et al., 2017; Foley et al., 2022). These ecosystem features affect carbon (C) and nitrogen (N) cycling, making herbivores important mediators of biogeochemical processes through their impacts on plants.

However, as herbivores affect all these features simultaneously, it is not fully understood which of these impacts most substantially drives changes to C and N cycling. Differences between C and N cycling in grazed and ungrazed habitats are well documented in arctic ecosystems (Falk et al., 2015; Kelsey et al., 2016; Yläne and Stark, 2019; Koltz et al., 2022), but the underlying mechanisms behind these differences are less known. The role that animals play in nutrient cycling has potentially been previously neglected in modeling nutrient transport across ecosystems (Doughty et al., 2016). It is important to be able to properly model herbivore impacts on biogeochemical cycling to understand how potential range shifts in herbivore distributions will affect underlying ecosystem processes. To illuminate how herbivores affect biogeochemical cycling, our

studies aim to (1) examine the impact of habitat and litter quality on litter decomposition dynamics and (2) quantify the effects of litter quality and quantity on CO₂ fluxes and soil microbial community.

1.1 Herbivore-mediated litter effects on the fate of C and N

Herbivores change ecosystems through their effects on litter quality and quantity. In general, herbivores change litter quality and quantity by increasing proportions of N in litter and decreasing overall biomass through the process of grazing, often through physiological changes to plants (Elliott and Henry, 2011; Smith et al., 2012; Chollet et al., 2021; Petit Bon et al., 2022). The directionality with which herbivores alter litter quality and quantity is usually oppositional – grazed areas produce litter that is higher quality, in lower quantities. Herbivores also change litter quality and quantity by altering plant community composition through selective grazing (Rebollo et al., 2013; Kempel et al., 2015). Through these changes in plant community composition, herbivore pressure can increase the abundance of highly productive, more highly nutritious plants (Tuomi et al., 2019). Herbivore-plant interactions can therefore induce changes in plants in favor of high quality, low quantity litter combinations.

Litter quality and quantity are linked to key biogeochemical ecosystem processes regulating the transfer of C and N. Herbivory and litterfall are two ways that plants lose C they have stored through net primary production (NPP) (Chapin et al., 2002). Litterfall transfers C and nutrients to soils through decomposition, a process which can be heavily regulated by herbivore impacts on litter quality (Wardle et al., 2002; Chapman et al., 2003; Chollet et al., 2021). Net ecosystem exchange (NEE), the transfer of CO₂, is also dictated by soil microbial respiration and the photosynthetic capability of vegetation

(Chapin et al., 2002). Herbivores mediate this process by affecting plant physiological responses, changing the quantity of plant material, and stimulating soil microbial communities through nutrient-high inputs of litter and feces (Bardgett and Wardle, 2003). Understanding plant-herbivore interactions is therefore key to understanding underlying mechanisms behind C and N cycling within grazed ecosystems.

The ways that herbivores affect litter quality can ultimately influence longer-term soil processes, such as the formation or decomposition of soil organic matter (SOM). Greater litter quantity does not necessarily increase soil organic carbon (SOC) formation, given that there can be a corresponding increase in decomposition; instead, litter quality greatly determines the fate of C in soils (Man et al., 2022). Nitrogen additions can decrease decomposition of SOM through a reduction in microbial biomass (Riggs and Hobbie, 2016), as well as through greater humification (Prescott, 2010). Herbivory also changes the temperature sensitivity of SOC, making it less susceptible to decomposition with increased temperatures (Chuckran and Frank, 2013). In mineral soils in particular, higher quality litter promotes higher stabilization rates for SOM (Córdova et al., 2018). Thus, higher quality litter can both inhibit decomposition and increase stabilization of SOM in soils, affecting the balance of soil microbial respiration versus long-term C storage.

Herbivores also affect the distribution of nutrients across the landscape through digestive processes. Animals transport labile nutrients across ecosystems in the form of fecal and urine depositions on the landscape (Doughty et al., 2016). This transport of labile nutrients in the form of herbivore feces and urine can affect nutrient availability in soils (Barthelemy et al., 2015), CO₂ fluxes (Beard et al., 2023), plant primary production

(Olofsson, 2009), and litter decomposition rates (Chollet et al., 2021; Wang et al., 2023). The deposition of feces also introduces labile materials for soil microbial respiration and enzyme activity, further affecting both C and N cycling (Koltz et al., 2022; Roy et al., 2022). How herbivores alter nutrient distribution on the landscape affects larger ecosystem processes in potentially substantial ways.

1.2 Herbivore effects on soil properties and processes

In addition to affecting litter quality and quantity on the landscape, herbivores also impact soil microclimate properties that regulate ecosystem processes. By grazing and trampling, herbivores affect soil moisture (Stephan et al., 2017; Frank et al., 2018), soil temperature (Harrison and Bardgett, 2008; Gornall et al., 2009; Olofsson, 2009; Sjögersten et al., 2012), and soil compaction (Tuomi et al., 2021). Both grazing and trampling can increase soil temperatures (Olofsson, 2009; Sjögersten et al., 2012). Herbivores can affect soil moisture through grazing effects on plant transpiration, as well as increasing soil bulk density through trampling (Veldhuis et al., 2014). These effects can produce different microclimates in heavily grazed areas.

These soil microclimate properties affect soil microbial communities, constituting one possible pathway for herbivores to influence biogeochemical processes. Herbivores are known to affect microbial community composition (Bardgett et al., 2001; Eldridge et al., 2017; Foley et al., 2022), potentially through these soil microclimate effects. Soil microbial community composition changes under warmer conditions (Rinnan et al., 2009; Newsham et al., 2022). Temperature and soil moisture can also interact to affect soil microbial communities (Zhou et al., 2017). Herbivores affect both temperature and soil moisture, possibly impacting soil microbial communities in the process.

Soil microclimate properties can also change the rate of soil microbial processes, such as soil microbial respiration. Both temperature and soil moisture strongly control soil microbial respiration (Curiel Yuste et al., 2007). Increased warming is generally associated with higher rates of CO₂ release from soils because of increased soil microbial respiration (Newsham et al., 2022). Increased soil moisture also promotes decomposition (Risch et al., 2007). Decomposition is not only affected by soil moisture, but also through interactions between temperature, soil moisture, and litter quality (Petraglia et al., 2019). Because herbivores can affect all three of these factors, there are multiple possible ways that they could be affecting soil microbial processes.

It is well-documented that herbivores can alter soil microbial respiration (Rainer et al., 2021; Foley et al., 2022). However, because herbivores alter multiple components of the ecosystem simultaneously, it is not entirely clear whether soil microbial respiration is primarily affected through alterations to vegetation characteristics, microbial communities, or soil properties. Understanding which mechanisms predominantly affect soil microbial respiration is important, because in some cases, reduced biomass from grazing can shift a system that once was a net CO₂ sink to a CO₂ source due to lower net primary productivity (Sjögersten et al., 2011; Plein et al., 2022). Identifying key controls on soil microbial respiration in grazed areas can help illuminate how herbivores alter overall C cycling patterns.

1.3 Herbivores and C cycling in the Y-K Delta

The indirect alterations migratory geese make on the C cycle through litter quality, litter quantity, and habitat changes in the Yukon Kuskokwim (Y-K) River Delta provide an opportunity to study how herbivores affect C cycling feedbacks in this high

latitude ecosystem. The documented differences in gross primary productivity and greenhouse gas fluxes in ungrazed and grazed areas in this system (Kelsey et al., 2016; Leffler et al., 2019), as well as changes to microbial communities (Foley et al., 2022), show clear herbivore effects on C cycling in this system. Because we know geese produce these effects on C cycling, understanding the magnitude of effect that litter quality and quantity changes have on C cycling will help further answer the question of whether litter quality or litter quantity drives these changes in this system. There is increasing interest in modeling greenhouse gas fluxes from landscapes, making these questions of how herbivory will alter C and nutrient cycling important for informing C cycling model parameters.

1.4 Study objectives

Because scientists anticipate that migratory geese will be affected in range, distribution, and phenology due to climate change (Koltz et al., 2022), changes in their grazing ranges will likely affect ecosystem processes. Researchers expect biogeochemical cycling in Arctic ecosystems to experience major perturbances because of climate change (Bruhwiler et al., 2021). As animals are often not considered in larger biogeochemical models (Schmitz et al., 2018), fully accounting for the role of geese in biogeochemical cycling can help project changes to the ecosystem in the Y-K Delta. Within the Y-K Delta landscape, geese alter litter quality, litter quantity, and habitat simultaneously; although we know there are differences in microbial community, vegetation, and greenhouse gas fluxes in grazed versus ungrazed habitat, we do not know what alterations are affecting these differences specifically. This study builds on research into how herbivores affect C cycling by: (1) investigating the influence of litter quality and habitat on decomposition

in the Y-K Delta, (2) quantifying respiration outputs from different inputs of litter quality and quantity, and (3) tracing the effects of litter quality and quantity on microbial communities.

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TRACING HERBIVORE EFFECTS ON LITTER DECOMPOSITION¹**Abstract**

Global change drivers that modify the quality and quantity of litter inputs to soil affect greenhouse gas fluxes, and thereby constitute a feedback to climate change. Carbon cycling in the Yukon-Kuskokwim (Y-K) River Delta, a subarctic wetland system, is influenced by landscape variations in litter quality and quantity generated by herbivores (migratory birds) that create ‘grazing lawns’ of short stature, nitrogen-rich vegetation. To identify the mechanisms by which these changes in litter inputs affect soil carbon balance, we independently manipulated qualities and quantities of litter representative of levels found in the Y-K Delta in a fully factorial microcosm experiment. We measured CO₂ fluxes from these microcosms weekly. To help us identify how litter inputs influenced greenhouse gas fluxes, we sequenced soil fungal and bacterial communities, and measured soil microbial biomass carbon, dissolved carbon, inorganic nitrogen, and enzyme activity. We found that positive correlations between litter input quantity and CO₂ flux were dependent upon litter type, due to differences in litter stoichiometry and changes to the structure of decomposer communities, especially the soil fungi. These community shifts were particularly pronounced when litter was added in the form of herbivore feces, and in litter input treatments that induced nitrogen limitation (i.e., senesced litter). The sensitivity of carbon cycling to litter quality and quantity in this system demonstrates that herbivores can strongly impact greenhouse gas fluxes through their influence on plant growth and tissue chemistry.

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Introduction

Herbivores influence a variety of ecosystem features that intersect with litter decomposition dynamics, potentially driving litter decomposition rates in heavily grazed areas. Especially in Arctic and Subarctic regions, herbivores can exert an outsized effect on carbon (C) and nitrogen (N) cycling because they shape habitats, change the distribution of nutrients on the landscape, and consume vegetation (Koltz et al., 2022). While often overlooked at global scales, herbivores influence decomposition rates by affecting litter quality (Chollet et al., 2021) and by removing biomass, which in turn influences microclimates (Penner and Frank, 2019), but the relative importance of these biotic vs. abiotic changes is debated. Thus, whether herbivores positively or negatively affect decomposition rates in Arctic and Subarctic systems is dependent on multiple factors (Olofsson et al., 2002; Sjögersten et al., 2012; Tuomi et al., 2019). Identifying the main drivers behind herbivore-induced differences in litter decomposition rates will facilitate understanding of C and N cycling both within and across Arctic ecosystems.

Herbivores exert indirect effects on litter decomposition through their effects on litter quality (Saunders et al., 2023). Plants that are palatable to herbivores tend to decompose faster, with herbivores selecting vegetation with higher N concentrations (Wardle et al., 2002; Barthelemy et al., 2015). In ecosystems with abundant nutrients, plants may physiologically respond to grazing by regrowing plant tissue with higher N and lower lignin content (Wardle et al., 2002; Chapman et al., 2003). Subsequently, decomposition rates increase in litter with higher N and lower lignin content (Olofsson et al., 2002; Sjögersten et al., 2012). Herbivores can further increase plant N content in grazed areas by depositing bioavailable N to soil in the form of feces and urine (Sitters et

al., 2017a; Koltz et al., 2022). These herbivore-induced increases in litter quality can increase decomposition rates by alleviating nutrient limitations to decomposers.

Herbivores also affect soil microclimates through the act of grazing, another potential pathway through which they influence litter decomposition rates. Plant biomass loss due to herbivory exposes soils to increased solar radiation, which can influence decomposition through physical effects, such as UV exposure (Lin and King, 2014; Austin et al., 2016), as well as by increasing soil temperature (Sjögersten et al., 2012). Reduction of leaf area also decreases transpiration, which can result in higher soil moisture (Frank et al., 2018). Such changes to temperature and soil moisture could increase decomposition rates by increasing microbial respiration and activity (Chuckran and Frank, 2013; Kelsey et al., 2018) and litter leaching rates (García-Palacios et al., 2016; Petraglia et al., 2019).

Herbivores also affect microbial activity and community composition through mechanisms other than changes to microclimate. For example, herbivores may change microbial activity and community composition (Bardgett et al., 2001; Eldridge et al., 2017; Foley et al., 2022) through their changes to nutrient inputs to soils (Saunders et al., 2023). Nitrogen additions influence litter decomposition in combination with differences in abiotic characteristics because when nutrients are not the limiting factor for microbes, decomposition processes are more affected by abiotic changes (Allison et al., 2013; Creamer et al., 2015).

The home-field advantage, which describes how litter tends to decompose more quickly in soils that are typically associated with that respective vegetation type (Gholz et al., 2000; Hunt et al., 1988), can explain a substantial amount of variation in leaf litter

decomposition (Ayres et al., 2009). Although the mechanisms behind home-field advantage effects are not entirely clear, they are likely linked to microbial differences between habitats (Veen et al., 2015; Pugnaire et al., 2023). While herbivores may influence home-field advantage effects by changing litter quality and microbial communities, few studies have attempted to link home-field advantage to litter decomposition in grazed and ungrazed ecosystems (Yuan et al., 2019; Fugère et al., 2020).

We expect goose herbivory in coastal ecosystems in western Alaska to influence litter decomposition. Tens of thousands of herbivorous geese migrate to the coastal wetlands in the Y-K Delta during the summer breeding season (Sedinger et al., 1993). Geese in these ecosystems primarily feed on the abundant *Carex ramenskii*, creating short-statured *Carex* with higher litter quality (decreased C:N ratios and lignin content), which the geese prefer (Person et al., 2003; Beard et al., 2019; Ruess et al., 2019). Grazing lawns have very little aboveground vegetation, small amounts of standing dead vegetation, higher soil temperature, and greater soil moisture than ungrazed areas (Foley et al., 2022). These simultaneous shifts in vegetation and abiotic habitat features likely impact litter decomposition rates.

Our goal was to determine how biotic versus abiotic factors influence decomposition in combination with *Carex* litter of different qualities found in the Y-K Delta. We hypothesized that: 1) litter would decompose faster in grazed habitats compared to ungrazed habitats because of more favorable abiotic conditions (i.e., increased temperatures, soil moisture and UV radiation), 2) litter of higher quality (higher N, lower lignin content) would decompose faster because it provides limiting nutrients,

and 3) litter quality and habitat would interact to influence decomposition rates due to home-field advantage effects. We describe abiotic differences between grazed and ungrazed areas that may be altered by herbivores, including soil temperature, UV radiation, rainfall, and soil moisture content to determine if these variables explain differences in decomposition rates (Elliott and Henry, 2011; Frank et al., 2018; Vaieretti et al., 2018). Finally, we investigate rates of labile C and N losses from litter over the one-year study to gain insights into how these two habitat types affect litter decomposition based on interactions with litter quality.

Methods

Study Site

We conducted this study in the Y-K Delta National Wildlife Refuge along the bank of the Kashunuk River (61°19'59" N, 165°37'52" W; approximately 4 km from the coast, elevation <1 m; Fig. 1). The climate is maritime, with mean winter temperatures of -12.2°C and mean summer temperatures of 12.5°C (Palecki et al., 2021). Mean annual snowfall is 1626 mm and mean annual precipitation (rain + snow-water equivalent) is 499 mm (Palecki et al., 2021). The ground is typically covered with snow from October until around May 10 (Ely et al., 2018; Palecki et al., 2021). Soils have a typical pH between 6.8 and 7.0, and are predominantly silt and sand deposits (Tande and Jennings, 1986; Foley et al., 2021). Daytime soil temperatures are highest in early June and are higher in the heavily grazed 'grazing lawn' than in nearby ungrazed *Carex* meadow, with mean daily temperatures in grazing lawn around 13°C and *Carex* meadow around 10°C (Kelsey et al., 2016).

Within the refuge, grazing by *Branta bernicla nigricans* (black brant) and *Branta hutchinsii* (cackling geese) converts *Carex subspathacea*, the dominant vegetation in ungrazed meadows, into a short-statured vegetation type called grazing lawns (Person et al., 2003). Grazing lawn vegetation is typically 1-2 cm tall, while vegetation in *Carex* meadow is 15-16 cm tall (Kelsey et al., 2016). Grazing lawns are usually around pond margins and are patchy on the landscape and always adjacent to *Carex* meadows. At the end of the growing season, standing dead vegetation covers more than three times the amount of area in *Carex* meadow as in grazing lawn habitat (Kelsey et al., 2016). Each growing season in the meadows, living *Carex* vegetation grows through layers of senesced material from previous growing seasons.

Litter decomposition experiment

At the beginning of the growing season, we collected plant samples that best represent end-of-season litter in grazed and ungrazed habitats. More specifically, we collected senesced litter from the uppermost portion of the litter layer, because this litter most represents the litter at the end of the previous years of growth. We used green live *Carex* vegetation to represent grazed litter, because previous studies (Saunders et al. 2023) have shown its litter quality is very similar to grazing lawn vegetation and it is possible to collect large quantities of green live *Carex* at the beginning of the season, whereas collecting large quantities of grazing lawn at any time of year is not practical (Table 1). Late-season (August-collected) grazing lawn vegetation lignin:N ratios of 5.3 are very similar to early-season green live vegetation lignin:N ratios of 5.8 (Table 1) (Saunders et al., 2023).

More specifically, in late May and early June 2022, we collected random subsamples of senesced litter from the uppermost portion of the litter layer, and green, live *Carex* strands from within a 100 m x 100 m area to fill litter bags. To determine the amount of litter added to each bag, we retained air-dried subsamples of pre-decomposition litter that had been weighed in the field, dried them at 65°C to constant weight, and determined an air-dried to dry-weight conversion ($n = 10$ per litter type). We placed the equivalent of 5 g dry-weight litter material in 240, 10 cm x 10 cm litter bags with 2 mm mesh (Karberg et al., 2008).

Half of the litter bags were filled with green, standing live *Carex* and half were filled with senesced *Carex*. We placed half the litter bags of each litter type on the soil surface in *Carex* ‘grazing lawn’ and half the litter bags in ungrazed *Carex* meadow areas. We utilized 15 replicate sites where we placed four bags of each litter type (i.e., 4 in the grazing lawn and 4 in *Carex* meadow) within 5 m of each other (Fig. 1). When placing bags on the ground, if sites contained senesced litter at the soil surface, we pushed aside enough pre-existing senesced litter to be able to place the litter bags directly on the soil surface, retaining senesced litter and placing it back on the bags. We placed bags on the ground on 17 June 2022. We collected one litter bag of each type at each site after week 3, 6, 9, and 52.

We measured abiotic factors in both habitats at seven of the fifteen sites ($n = 14$). We measured rainfall using 50 mL Falcon tubes we installed into the ground, protruding 1 cm above the soil surface. We measured soil surface temperature continuously using ThermoChron iButtons (iButtonLink Technology, Whitewater, Wisconsin). We measured UV radiation in grazing lawn and *Carex* meadow habitat approximately weekly for a total

of 11 sampling days throughout the growing season using an UVA/B Light Meter 850009 at the soil surface (SPER Scientific, Arizona, USA). We measured UV radiation for approximately 5 minutes in each habitat type within 4 hours of mid-day, alternating habitat types to reduce bias from cloud cover and sun angle. We only used records where the cloud cover remained the same between alternating measurements. Soil moisture was measured hourly using EC-5 soil moisture probes in four reference grazing lawn and *Carex* meadow plots (LI-COR, Nebraska, USA). The reference plots were located within 500 m of litter bag study sites. Soil moisture measurements were taken from 4 June 2022 until 20 July 2022 because the grazing lawn instruments were flooded and unable to record data after this point.

Upon collection, we brushed litter bags of any visual soil and placed litter bag contents in paper bags to allow them to air dry. We shipped samples to Utah State University, where we dried them at 65°C until constant weight, and final weight of litter was subtracted from the initial weight to determine biomass loss to decomposition. We corrected masses by combusting a subsample of each litter bag at 550°C for 4 hours to determine ash-free dry mass (AFDM) conversions (Harmon et al., 1999). Soils at our site have a low organic matter content and a high mineral content, so combustion allowed us to correct for potential accumulation of mineral soils.

To analyze litter for C and N concentrations, we selected a subsample of the litter samples collected throughout the experiment ($n = 5$ per litter type, habitat, and collection week combination), as well as a subsample of litter collected at the beginning of the experiment ($n = 4$ per litter type). The Analytical Lab at University of Hawai'i at Hilo analyzed samples for C and N using Isotope Ratio Mass Spectrometry (ECS4010

Elemental Analyzer, Costech Analytical Technologies, Valencia, CA, USA). C and N concentrations are adjusted on a mass basis, presented throughout as percent of initial mass remaining after each time point.

Statistical Analyses

To determine decomposition rate among litter type and habitat combinations, we used the total AFDM at each time point in the following decomposition function equation (Karberg et al., 2008):

$$X_t / X_0 = e^{-kt}$$

where X_t is the AFDM at collection period, X_0 is the initial AFDM, k is the decomposition rate constant, and t is time. This equation was used to determine the litter biomass loss rate (Wieder and Lang, 1982). We used linear mixed effects models in R to determine the effect that litter quality, habitat, and collection week exerted on litter biomass loss. We used linear models to determine the effect that litter quality, habitat, and collection week had on C remaining, N remaining, and C:N ratios in litter bags. For each time period, we used linear models to analyze how litter type and habitat affected differences in litter decomposition rates. We used the package “emmeans” to perform post-hoc comparisons with Sidak adjustments (Lenth, 2022). We used the “AICcmodavg” package in R for a model selection approach to determine whether abiotic factors, UV radiation, rainfall, and soil surface temperatures, influence litter biomass loss rates (Mazerolle, 2023). We did not include soil moisture in AIC models because soil moisture data was collected in nearby reference plots instead of across litter bag sites and therefore could not be

associated with decomposition of specific litter bags. Soil moisture was instead used to examine general patterns between grazing lawn and *Carex* meadow. Modeled means (\pm standard deviations) are presented throughout.

Results

Decomposition rates

At the end of one-year, green litter in *Carex* meadow lost the most ash-free dry mass or AFDM (hereafter, biomass), and senesced litter in *Carex* meadow lost the least amount of biomass (Fig. 2). Litter type affected biomass loss independently and interacted with habitat as well as collection week to affect biomass loss (Table 2). Post-hoc tests revealed that over the whole study period, within the *Carex* meadow habitat, green litter lost 11.5% more biomass than senesced litter did (Table 3). In the grazing lawn habitat, green and senesced litter did not significantly differ in biomass loss. Green litter overall lost 9.6% more biomass in *Carex* meadow than in grazing lawn. Senesced litter overall lost 5.4% more biomass in grazing lawn than in *Carex* meadow. Between the start of the experiment and week 3, senesced litter lost 12.2% more biomass than green litter. However, by week 9 and after one-year, green litter had lost 11.4% and 25.0% more biomass than senesced litter, respectively. Whereas 61.3% of the total biomass loss occurred during the growing season (between week 0 and 9), only 38.7% occurred during the winter (between week 9 and one-year).

Litter type interacted with habitat to affect decomposition rates ($p < 0.001$). Green litter had higher decomposition rates than senesced litter, with green litter in *Carex* meadow having the highest decomposition rate overall (Table 4). Green litter in *Carex* meadow had a 13.3% higher decomposition rate than green litter in grazing lawn ($p <$

0.001). In *Carex* meadow, the decomposition rate was nearly two-fold higher for green litter than senesced litter ($p < 0.001$), but in grazing lawn, the decomposition rate did not vary between green litter and senesced ($p = 0.584$).

Litter nutrients and chemical composition

Carbon concentrations adjusted to initial proportions in litter was affected by three-way interactions among collection week and litter type, and collection week and habitat (Table 5). On week 3 in grazing lawn, green litter had 25.2% more C remaining than senesced litter (Table 6, Fig. 3). However, by week 9 in *Carex* meadow, senesced litter had 24.4% higher C remaining than green litter. At week 3, green litter lost 10.6% more C in *Carex* meadow than in grazing lawn, while senesced litter lost 8.4% more C in grazing lawn than in *Carex* meadow. By week 9, senesced litter had lost 9.0% more C in grazing lawn than in *Carex* meadow. Between week 9 and 52, senesced litter lost more C than green litter, with a 77.1% reduction in C remaining for senesced litter in *Carex* meadow and a 75.4% reduction in grazing lawn. Green litter C remaining was 67.8% lower for week 52 compared to week 9 in *Carex* meadow and 66.8% lower in grazing lawn.

Nitrogen concentration remaining in litter was affected by three-way interactions between collection week and litter type, and litter type and habitat (Table 7). Across all week and habitat combinations of the experiment, green litter proportionately lost more N than senesced litter (Table 8, Fig. 4). Senesced litter became relatively enriched with N in comparison to its initial N concentrations for some time periods, with total N for senesced litter in grazing lawns sometimes reaching values greater than its initial N mass. On week 3, senesced litter in grazing lawn had 22.4% more N remaining than senesced

litter in *Carex* meadow. After one-year, senesced litter had nearly two-fold more of its initial N mass remaining than green litter in both *Carex* meadow and grazing lawn.

The C:N ratio in remaining litter was affected by an interaction between litter type and collection week ($p < 0.001$), and not influenced by habitat (Table 9, Fig. 5). Initial C:N ratios were 79.5 % lower in green litter compared to senesced litter. Compared to senesced litter, green litter had 68.2% lower C:N on week 3, 69.4% lower C:N on week 6, 69.9% lower C:N on week 9, and 24.6% lower C:N on week 52 ($p < 0.001$, $p < 0.001$, $p < 0.001$, $p < 0.001$).

Environmental factors

Daytime soil surface temperatures were 9% higher in grazing lawn than in *Carex* meadow, approximately 1.5°C higher over the growing season ($p = 0.003$; Fig. S2). UV radiation was 32.5% higher in grazing lawn compared to *Carex* meadow ($p = 0.009$; Fig. S3). Recorded precipitation volume was 6% higher in grazing lawn compared to *Carex* meadow ($p = 0.015$; Fig. S4). Soil moisture was 27.6% higher in grazing lawn compared to *Carex* meadow ($p < 0.001$; Fig. S5). Despite these strong differences in abiotic factors, AIC model selection indicated that litter type and habitat were more strongly associated with differences in biomass remaining than were environmental factors (Table 10).

Discussion

Overall, we found that litter quality influenced decomposition rates, with higher quality litter experiencing greater biomass loss over a year, and habitat type playing a more complicated role. As we predicted, the high-quality litter lost more biomass than low-quality ungrazed litter over the whole study, but interestingly, low-quality litter lost

more biomass for the first 3 weeks. Further, the directionality of litter type and habitat interactions on litter decomposition rates did not match our predictions because higher quality litter decomposed faster in ungrazed habitat than in heavily grazed areas. This is contradictory based on our predictions that the higher temperatures, UV exposure, and lower rates of intercepted precipitation in grazing lawn would enhance decomposition, and also contradicts the expected home field advantage effects. Based on these results, we see interactive effects of litter quality and habitat affecting litter decomposition in unexpected ways.

Although litter type affected decomposition as expected, with high-quality green litter losing the most biomass over the year, we saw it affecting early-stage decomposition in unexpected ways. In the initial 3-week decomposition period only, senesced litter decomposed faster than green litter. The fact that we saw the highest decomposition overall in high-quality green litter is not surprising (Hoeber et al., 2020), and is consistent with other studies (Prieto et al., 2019; Chollet et al., 2021). However, we found higher temperatures, UV radiation, and soil moisture in grazing lawn, all factors which tend to promote decomposition (Lin and King, 2014; García-Palacios et al., 2016; Petraglia et al., 2019). The higher decomposition of green litter in *Carex* meadow as opposed to grazing lawn was surprising as we would have expected green litter to decompose faster in the habitat with favorable abiotic conditions. Results suggest that factors other than the abiotic conditions we measured were more important in influencing litter decomposition in these habitats.

On the other hand, throughout the study, low-quality senesced litter decomposed faster in grazing lawn than in *Carex* meadow, as we expected. The interactive effects of

litter quality and habitat on decomposition rates may be partially explained by the differing chemistry of the litter types. More specifically, the higher initial lignin:N ratios in senesced litter may have driven early losses of mass, given that lignin can increase biomass losses in cases where decomposition is mostly driven by abiotic sources (Austin and Ballaré, 2010). In other words, because of high lignin:N ratios found in senesced litter at the beginning of the experiment, this litter type may be particularly susceptible to temperature, soil moisture, and photodegradation found in grazing lawns (Austin et al., 2016). Therefore, high lignin:N ratios in senesced litter may have driven initial losses from photodegradation in the grazing lawn, where there was high UV radiation. This, along with the fact that green litter decomposed faster after the initial stage, suggests that perhaps abiotic factors in grazing lawn determined decomposition in the first 3 weeks, while biotic factors may drive decomposition later (García-Palacios et al., 2016).

Despite these patterns, we did not see independent habitat effects on decomposition overall. Therefore, differences in C cycling between habitat types in this region are likely primarily due to biological interactions between litter and soil (Kelsey et al., 2016; Foley et al., 2022). More specifically, we suspect that the faster decomposition of green litter in ungrazed habitats may be driven by the large microbial community differences between grazed and ungrazed habitats (Foley et al., 2022). Different microbial communities affect the loss of recalcitrant C versus labile C (Osono, 2020). Further, we know that fungal species richness is substantially greater in *Carex* meadow than in grazing lawns (Foley et al., 2022), which is perhaps in part because of the high quantities of low-quality senesced litter are found in this habitat; this litter type substantially changes fungal community composition (Saunders et al., 2023). Fungal

groups are typically the first microbes to decompose materials, and the initial colonizing community dictates decomposition rates (Cline and Zak, 2015). Thus, the highly diverse fungal community found in *Carex* meadow (Foley et al., 2022), which is already accustomed to breaking the large quantities of litter typically found in the ungrazed areas, may be more ready to break down high quality litter when it is present.

Home-field advantage effects are typically thought to be mediated by such differences in microbial communities (Palozzi and Lindo, 2018; Pugnaire et al., 2023). However, we did not see evidence of home-field advantage effects in this system. Based on home-field advantage effects, we expected senesced litter to decompose faster in *Carex* meadow and green litter to decompose faster in grazing lawn, where similar litter quality types are found. Although home-field advantage does typically cause vegetation to decompose faster in its home environment (Ayres et al., 2009; Veen et al., 2015), this does not hold true for every system (Palozzi and Lindo, 2018; Lyu et al., 2019; Chollet et al., 2021). In addition, this experiment measured decomposition over one year, and studies suggest that the home-field advantage may play a larger role in longer decomposition periods (Palozzi and Lindo, 2018). Our results support studies suggesting that home-field advantage is weaker in systems that have highly similar plant community composition (Veen et al., 2015), given that the species in grazing lawn and *Carex* meadow is the same (predominantly *Carex subspathacea*).

Decomposition was slowest for all litter and habitat combinations from week 9 (which represents the end of the growing season in this system) to one-year of the litter decomposition period. This low level of decomposition during the winter season contributed to low overall decomposition rates and high mean residence times of litter,

slowing down the breakdown of material. While diminished labile C and N likely affected decomposition over time, the effect of extremely low temperature ($< 0^{\circ}\text{C}$) and snow cover on litter decomposition potentially accounts for some of the decreased decomposition during this period (Prescott, 2010). However, greater biomass loss for green litter in *Carex* meadow relative to other litter quality and habitat combinations persisted during this time period, possibly due to differences in habitat features, like snowpack, that could not be directly observed, and to the microbial activity and community differences between the habitat types (Saccone et al., 2013). Shifts in winter abiotic conditions and seasonality due to climate change could alter these seasonal decomposition dynamics in the future (Bokhorst et al., 2010; Blok et al., 2016), making our report on decomposition rates relevant for future studies on breakdown and assimilation of litter materials in this area.

Additionally, flooding potentially affected litter decomposition during the wintertime. On 17 September 2022, Typhoon Merbok hit western Alaska, and resulted in widespread flooding in the Y-K Delta before the ground was frozen. Our study site and litterbags were underwater during this storm surge. Grazing lawns are found along pond margins, and because of their proximity to water, they can flood at monthly high tides and certainly flood more often than meadow habitats. However, these high tide events only last generally for a few hours, whereas storm surges can flood areas for nearly 14 hours (Terenzi et al., 2014). The effects of leaching or physical breakdown of litter may be relevant to these longer storm surge situations, more so than other decomposition mechanisms. The effect of cold, saline storm surge flood waters on litter decomposition could be investigated in future studies.

This is the first report that we know of investigating mean residence time of litter in a large Alaskan river delta. Our study shows that the material found in senesced litter at the end of the experiment could potentially remain aboveground for an additional six years, and for green litter, material at the end of the experiment may remain for another two years. This suggests that while much of the material in both senesced and green litter is lost over a year, around 25 to 50% of biomass remains for at least another two years. This helps explain the build-up of the senesced layers in ungrazed habitats in this ecosystem.

Further, while herbivores initially create grazing lawns, leading to two distinct habitats in the system, feedbacks between litter quality and decomposition may facilitate proportionally lower return of C and N to soils in grazed habitats (Foley et al., 2022). The relatively lower rates of decomposition in grazing lawn suggest that herbivores influence the breakdown of material in the system through their regulation of habitat in conjunction with their changes to litter quality. This could be one mechanism through which they produce known effects on microbial activity and community composition in this system (Foley et al., 2022), ultimately influencing ecosystem processes like microbial respiration (Kelsey et al., 2016) as well as decomposition. Because the rate of return of labile materials is influenced by interactions between habitat and litter quality, herbivores may spatially and temporally regulate the presence of bioavailable nutrients within this ecosystem.

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Data Accessibility

Data will be available at the NSF Arctic Data Center.

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CHAPTER 3

HERBIVORES INFLUENCE BIOGEOCHEMICAL PROCESSES BY ALTERING
LITTER QUALITY AND QUANTITY IN A SUBARCTIC WETLAND¹²**Introduction**

The quality and quantity of litter inputs to soils affect soil carbon (C) balance and, thereby, feedbacks between the terrestrial C cycle and climate change. The chemical quality of litter [i.e., its ‘palatability’ to decomposers, which is often linked to lignin content and/or carbon:nitrogen (C:N) ratios] strongly influences rates of decomposition by imposing microbial nutrient and/or energy limitations (Cotrufo et al., 2013; Cleveland et al., 2014; Castellano et al., 2015). Meanwhile, quantity of litter inputs dictates the total amount of fresh organic matter available for decomposition, and it is the balance between plant C inputs and soil C losses through decomposer respiration that determines the size of the belowground C pool (Crow et al., 2009; Chemidlin Prévost-Bouré et al., 2010). Global change drivers impact litter quality and quantity, although these parameters may exhibit divergent responses to the same environmental perturbation. Thus, identifying and separating the effects of litter quality versus quantity impacts on belowground C cycling is key, because simultaneous shifts in litter traits may amplify or suppress one another’s effects (Castellano et al., 2015; Creamer et al., 2015). For example, increasing the

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magnitude of fresh soil C inputs can either protect (Blagodatskaya and Kuzyakov, 2008) or destabilize (Shahbaz et al., 2017; X. J. A. Liu et al., 2017) native soil C stocks, with the direction and magnitude of response likely determined by C input chemistry.

There are several mechanisms by which litter input quality and quantity might interact to shape C cycling. Dissolved organic C (DOC), which is considered the most bioavailable soil C pool (Kalbitz and Kaiser, 2008), is positively correlated with the quality of decomposing litter (Kalbitz et al., 2006; Klotzbücher et al., 2011). Thus, high quality litter inputs may have a disproportionate impact on soil C cycling because of an outsized increase in labile C availability compared to low quality litter, which could lead to greater soil microbial biomass (Fanin et al., 2014). Labile C inputs may induce large losses of soil C, even at relatively low amendment rates, by priming the decomposition of native soil C. Such positive priming effects generally occur when fresh inputs increase soil microbial biomass or stimulate the co-metabolism of ‘background’ soil organic matter (Blagodatskaya and Kuzyakov, 2008). Indeed, positive priming effects have been found in N-poor subarctic soils due to the stimulation of “N-mining” in response to organic matter additions (Hicks et al., 2022; Na et al., 2022). Conversely, very high rates of labile C input can retard the decomposition of background C – a phenomenon known as ‘negative priming’ – if microbes have a strong preference for the newly added substrate (Blagodatskaya and Kuzyakov, 2008). Thus, the relationship between C input and soil C loss will depend upon the chemical composition and stoichiometry of new inputs in relation to microbial demand. In addition to priming effects, the relative concentrations of various plant compounds delivered to soil can affect total rates of decomposition by inducing or suppressing different extracellular enzyme activities. For

example, microbial production of starch-degrading enzymes is not triggered until starch is present in relatively high concentrations, potentially inducing a non-linear relationship between the magnitude of C inputs and C losses (German et al., 2011). Similarly, the production of energetically-costly lignin-degrading enzymes requires the presence of an easily available C source like DOC (Klotzbücher et al., 2011). As another example, if microbial production of extracellular enzymes is limited by the availability of N, even small amounts of N-rich litter input could trigger a burst of enzyme synthesis and thereby a dramatic acceleration of microbial decay (Schimel and Weintraub, 2003).

Finally, soil microbial communities dictate the fate and rate of litter transformation (Schimel and Schaeffer, 2012), so understanding how microbial communities respond to differences in litter quality and quantity may elucidate links between litter inputs and greenhouse gas fluxes. To this end, there have been decades-long efforts to group microbes into coherent ecological guilds with consistent effects on C cycling (Fierer et al., 2007; Malik et al., 2020; Morrissey et al., 2023). For example, the copiotroph-oligotroph framework predicts that copiotrophic microbes should predominate in the presence of high-quality substrates due to their capacity for rapid growth and generalist decomposition strategy, whereas oligotrophs should be more competitive on low-quality substrates (Fierer et al., 2007). Additionally, due to higher substrate use efficiency and resource scavenging ability, oligotrophs are expected to become more dominant when resource quantity is low (Ho et al., 2017). Therefore, this framework predicts that heterotrophic respiration per unit litter should be highest in scenarios of high-quality and high-quantity inputs due to the predominance of fast-growing, low-efficiency copiotrophs. In contrast, respiration per unit litter should be

lowest under low-quality, low-quantity inputs when slow-growing, high-efficiency oligotrophs predominate.

Herbivory is an example of a process that simultaneously alters litter quality and quantity, likely having complex effects on C cycling. Herbivory often decreases aboveground litter input quantity via plant offtake, but subsequent quality impacts are unclear. Herbivory may trigger plant responses that lead to altered tissue N or lignin content (Wardle et al., 2002; Frost and Hunter, 2008). The quality of plant litter may be further transformed via processing in the animal gut because the plant remains re-deposited as feces are often enriched in inorganic nutrients (Petkuvienė et al., 2019). Although herbivore-driven changes in litter quality and quantity often occur simultaneously in the field, current theoretical frameworks predict there could be important interactions between the two parameters (Grandy and Neff, 2008; Manzoni et al., 2012; Castellano et al., 2015), necessitating a better understanding of their individual and combined effects.

Migratory geese in the coastal wetlands of the Yukon-Kuskokwim (Y-K) Delta, Alaska, affect both above- and belowground C cycling, altering soil greenhouse gas emissions through their simultaneous impacts on litter quality and quantity (Kelsey et al., 2016). In this ecosystem, vegetation is dominated by *Carex* spp. Geese, such as *Branta bernicla nigricans* (Pacific black brant) and *Branta hutchinsii* (cackling geese), migrate to the Y-K Delta in the summer months and forage heavily to create swards of short-stature *Carex* known as ‘grazing lawns’. Grazed plant tissues have low C:N ratios and are an important source of nutritious forage for goslings (Ngai and Jefferies, 2004; Sedinger et al., 2008). These grazing lawns also have high inputs of goose fecal matter (Beard et

al., 2023). Nearby areas that are not heavily grazed have greater aboveground plant biomass, higher C:N ratios (Beard et al., 2019), and extensive accumulation of senesced *Carex* litter. Therefore, grazing increases litter nutrient content while simultaneously decreasing standing biomass, making the Y-K Delta an ideal system for examining how the quality and quantity of plant C inputs to soils jointly affect the fate of those inputs belowground.

The overall objective of this study was to determine how interactions between litter quality and quantity influence soil CO₂ fluxes, using the Y-K Delta ecosystem as a case study. Specifically, we quantified: 1) the slope of the relationship between the proportion of total C utilized by decomposers (CO₂-C flux per g C available) and the rate of C inputs, and 2) whether the sign or magnitude of these slopes depends upon the chemical characteristics (quality) of C inputs. We then assessed changes in soil nutrient availability, enzyme activities, and microbial communities to help us identify the underlying mechanisms behind litter quality-quantity interactions.

To do so, we conducted a fully factorial soil microcosm incubation experiment that separately manipulated the quality and quantity of soil C inputs. To capture variation in litter quality observed at our study site, we amended soils with inputs of varying chemical quality (as defined by litter N content and lignin:N ratios): grazed *Carex*; ungrazed, green (live) *Carex*; ungrazed, senesced *Carex*; and goose feces (which consists mainly of digested plant material, likely *Carex*). Each litter type was added at one of three rates spanning an order of magnitude which represent the range of annual litter inputs we expect that the Y-K Delta receives. We anticipated a positive relationship between the proportion of C respired and C input quantity, in line with previous studies

(e.g., Shahbaz et al., 2017b). However, we expected this correlation to be strongest in soils amended with higher-quality litters because: H1) Increasing rates of N-rich, high-quality litter addition should progressively relieve microbial N limitation and increase C bioavailability (as DOC). This should support more microbial biomass and stimulate C- and N-degrading enzyme activities, inducing priming effects. By contrast, low-quality litters should exacerbate restrictions on microbial growth. We also expected that H2) high inputs of high-quality litter should induce a shift to copiotrophic-dominant microbial communities with elevated rates of respiration.

Methods

2.1 Study site

We collected soils and litter for this study in the Yukon Delta National Wildlife Refuge along the Kashunuk River (61°19'33" N, 165°29'48" W, approximately 4 km from the coast). The climate is maritime, with 30-year mean (1991-2020) winter daily temperatures of -12.2 °C and mean summer daily temperatures of 12.5 °C. Thirty-year mean annual precipitation is 499 mm (rain + snow-water equivalent), and mean annual snowfall is 1626 mm (Palecki et al., 2021). In the winter, the ground is typically covered with snow, and the heaviest rains occur from July to September (Tande and Jennings, 1986). Soils are predominantly silt and sand deposits, with pH between 6.8 and 7.0 (Tande and Jennings, 1986; Foley et al., 2022). *Carex subspathacea* is the dominant vegetation and forms extensive wet-sedge meadows with an average vegetation height of ~15 cm (Kelsey et al., 2016). Grazing of *C. subspathacea* by Pacific black brant and cackling geese results in 'grazing lawns' in which the *C. subspathacea* is converted to a short-statured form of ~1 cm (Person et al., 2003; Kelsey et al., 2016).

2.2 Field collections and processing

On 4 August 2021, we collected 18 blocks of soil along a 100 m transect in an ungrazed *C. subspathacea* meadow. Every 20 m along the transect, we collected three 10 × 10 cm soil blocks to a depth of 15 cm using a sterile knife from the north, east, and south cardinal directions at 1 m from the transect. We collected soils from ungrazed meadows rather than grazed areas because ungrazed meadow constitutes the majority of vegetated surface area in this part of the Y-K Delta (Person et al., 2003), so soils from ungrazed meadows are most representative of the ecosystem. Additionally, because geese convert ungrazed meadow to grazing lawn over a period of several years (Person et al., 2003), soil from ungrazed meadows represent “time zero” conditions before litter quality and quantity and microbial communities are altered due to grazing pressure.

We also collected ungrazed green (live; $\geq \sim 15$ cm height) *C. subspathacea* and senesced *C. subspathacea* from ungrazed meadows near the transect, and we collected grazed *C. subspathacea* (short < 1 cm height) and goose feces from grazing lawns near the transect. We considered the tall-form *C. subspathacea* outside of grazing lawns to be ungrazed, but we cannot be absolutely certain these plants had never experienced herbivory. Nonetheless, we did not observe any evidence of recent grazing (e.g. trampling, fecal deposition) outside of the grazing lawns.

We transported soils to Utah State University on ice. Within 48 hours of collection, we subsampled a 1 cm × 1 cm × 15 cm portion of each block and stored them in a -80°C freezer for microbial community analyses. We oven-dried and homogenized litter types by grinding them, and then measured total C and N content on an elemental analyzer (ECS4010 Elemental Analyzer, Costech Analytical Technologies, Valencia, CA,

USA). Phosphorus and potassium content were measured by the Utah State University Analytical Laboratories via near-infrared spectroscopy (NIRS DS2500 F, FOSS Analytics, Hillerød, Denmark). We analyzed lignin using acid detergent fiber methods (Gessner, 2005).

2.3 Experimental design

To determine the effects of litter quality and quantity on soil C cycling, we performed a 12-week soil microcosm experiment, representing the length of the growing season on the Y-K Delta. The microcosm experiment consisted of a fully factorial manipulation of four litter quality treatments (grazed *C. subspathacea*, ungrazed green (live) *C. subspathacea*, goose feces, and senesced *C. subspathacea*) added at three C input quantity levels (0.4 mg C g⁻¹ soil, 2.4 mg C g⁻¹ soil, 4.7 mg C g⁻¹ soil, equivalent to 2.4, 14.4, and 28 g m⁻²; hereafter low, medium, and high; Table 11). To ensure C input rates ranged within the bounds observed in this ecosystem, we chose our treatment levels based upon previous measurements of aboveground biomass of three representative vegetation communities in this part of the Y-K Delta. The three reference vegetation communities (slough levee, ungrazed wet sedge meadow, and grazed wet sedge meadow) are all graminoid-dominated and have been described in detail elsewhere (Jorgenson, 2000; Kelsey et al., 2016). The three reference communities represent a gradient of standing aboveground biomass, with grazed meadows having the lowest biomass, ungrazed meadows having intermediate quantities, and slough levees having the highest biomass. We converted the standing aboveground biomass quantities of these three communities (data from Kelsey et al., 2016) to litter C inputs, assuming that 10% of litter in each habitat is incorporated into the soil per year, and that ~40% of the plant biomass

is C. The assumption of 10% litter incorporation is a conservative estimate based on our personal observations that the majority of senesced biomass remains standing aboveground through future growing seasons. In a separate experiment, we found that the ratio of standing senesced biomass to live biomass in ungrazed *Carex* meadow was ~1.13 at peak growing season (unpublished data). This indicates that most of the biomass that grew in previous years was still standing aboveground and was not yet incorporating into the soil.

The C:N ratios, lignin, and nutrient analyses of the litter informed the litter quality treatments (Table 13). We adjusted the mass of litter added within each quantity treatment to reflect the variation in C content of each litter type; therefore, all experimental units in the same litter quantity treatment received identical amounts of C, regardless of litter type. This design resulted in 12 unique treatment combinations with 10 replicates each; we also included 10 control soils with no litter additions to help us assess priming effects (see Section 4.1). Note that not all of our treatments are intended to represent actual (or potential) C input regimes at the site – for example, it is highly unlikely that 4.7 mg C cm⁻³ of feces would ever be delivered to the soil in the Yukon Delta. However, this experimental design did make it possible to directly compare slopes of the CO₂ flux-C input relationship across the different litter types.

Each microcosm consisted of 30 g dry weight of homogenized soil in a 250 mL glass jar fitted with a septum. We adjusted soil moisture content in microcosms to 60% of water holding capacity, which maximizes soil heterotrophic respiration (Zhou et al., 2014). At the beginning of the experiment, we adjusted microcosms for moisture content using a solution with a salinity of 28 g L⁻¹ total dissolved sodium salts (Instant Ocean

SeaSalt, Spectrum Brands, Blacksburg, VA, USA) (Person and Ruess, 2003) to represent the brackish water these soils are typically exposed to. We weighed microcosms weekly to determine water loss and maintained soil moisture levels by adding deionized water when necessary (to avoid continuous increases in soil salt content). We incubated microcosms in the dark at 10 °C to simulate mean temperatures during the growing season in the field (Jorgenson and Ely, 2001).

2.4 Laboratory analyses

Once per week over the incubation period, we sealed the microcosms and allowed gas to accumulate in the headspace over 24 hrs. We used gas chromatography to analyze concentrations (μmol) of carbon dioxide (CO_2) that accumulated in the headspace (GC-2014 Greenhouse Gas Analyzer, Shimadzu, Kyoto, Japan; 8610C Gas Chromatograph, SRI Instruments, Las Vegas, Nevada). At the start of the experiment and following each headspace sampling, we randomized microcosm locations within the incubator.

At the end of the incubation, we stored soil subsamples from each microcosm at -80°C for analysis of enzyme activity and microbial DNA. In addition, we determined total inorganic nitrogen (TIN) as the sum of ammonium (NH_4) and nitrate (NO_3) N content in each microcosm, measured through colorimetric analysis of 2 M KCl extracts.

2.5 Microbial analyses

At the conclusion of the incubation, we measured microbial biomass in each microcosm using the direct chloroform fumigation and extraction method (Witt et al., 2000), and analyzed the resulting extracts for total dissolved C content on a TOC-L (Shimadzu, Kyoto, Japan). We determined microbial biomass carbon (MBC) as the

difference between C content in K₂SO₄ fumigated and unfumigated soil extracts. We determined extracellular enzyme activities of cellobiase (CB), N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), acid phosphatase (AP), and β -glucosidase (BG) with p-nitrophenol linked substrates (German et al., 2011).

Following manufacturer protocols, we extracted DNA from each of the 130 microcosm soil samples and five subsamples of pre-incubation soils using a DNeasy PowerSoil Kit (Qiagen, Hilden, Germany). DNA extracts were pooled in equimolar concentrations and pair-ended sequenced (2×250) using the Illumina MiSeq platform at the USU Center for Integrated Biosystems. Following Earth Microbiome project protocols, 16S-rRNA regions were amplified with 515F-806R primers, and ITS regions were amplified using ITS1f-ITS2 primers (Caporaso et al., 2011, 2012; Thompson et al., 2017). We used the QIIME 2 bioinformatics pipeline to process and assign taxonomy to soil bacterial and fungi communities (Bolyen et al., 2019). We determined amplicon sequence variants (ASVs) using the DADA2 algorithm (Callahan et al., 2016). We separated taxonomic units of bacterial and fungal sequences using the Greengenes database to train a Naïve Bayesian classifier (DeSantis et al., 2006). We identified fungal groups using the UNITE database (Nilsson et al., 2019) in combination with the BLAST+ algorithm (Camacho et al., 2009). We rarefied each sample for a total of 25,000 sequences for fungal communities and 40,000 sequences for bacterial communities. We used the rrnDB database (Stoddard et al., 2015) to predict *rrn* gene copy number for each bacterial ASV according to the method of (Li et al., 2021), and we calculated community-weighted mean abundance of *rrn* gene copies for each soil sample following the approach of (Nemergut et al., 2016). Community-weighted *rrn* copy number is a

community-aggregated indicator of bacterial ecological strategies, where higher *rrn* copy number indicates a more copiotrophic lifestyle (Klappenbach et al., 2000; Fierer et al., 2007).

2.6 Statistical analyses

We used linear mixed-effects models to determine the effects of litter input quantity (in g C), quality (litter type), incubation day and their interactions on CO₂ fluxes, and included microcosm identifiers as a random effect to control for the non-independence of CO₂ measurements taken from the same microcosm over time. All C fluxes were standardized to the total amount of C available in each microcosm, including litter inputs (i.e., flux units were mg C g⁻¹ C h⁻¹). In effect, this means that we tested whether the *proportion of soil/litter C that is utilized* increases with the total quantity of C available. To further assess how different litter input treatments elevated soil respiration rates against the ‘background rate’ of soil respiration, we performed separate mixed effects models to assess treatment effects relative to no-litter controls. These models included a fixed effect for litter treatment (quantity or quality), incubation day, and a random effect for microcosm identity. Finally, we note that treatment-related differences in respiration rates would cause the ‘bioavailable’ C pool to exhibit different temporal dynamics in each treatment group. Therefore, we also employed a first-order exponential decay model to explore how the litter quality and quantity treatments affected respiration after controlling for C availability (Kuzyakov, 2011).

To determine whether priming effects (i.e. enhanced decomposition of pre-existing soil C with litter additions) impacted the CO₂ fluxes we observed, we calculated

a conservative estimate of priming effect as follows (Blagodatskaya and Kuzyakov, 2008):

$$PE = C_{treatment} - C_{control} - C_{litter}$$

Where $C_{treatment}$ is the cumulative C respired in a microcosm receiving litter amendments, $C_{control}$ is the cumulative C respired in the microcosms receiving no litter inputs, and C_{litter} is the quantity of litter C added.

We used general linear models to analyze post-incubation measurements, including cumulative CO₂ fluxes, microbial biomass, dissolved organic C, inorganic-N pools, bacterial weighted-mean *rrn* copy number, and enzyme activities. All models included litter quality and quantity as main effects, and their interaction. We removed outliers greater than 3.5 standardized residual variances above the mean. When significant main effects of a treatment were found, we performed post-hoc pairwise comparisons with a Tukey adjustment. We also determined the relative contribution of quality, quantity, and their interaction to the model R² value using the *lmg* metric with the R package “relaimpo” (Groemping and Matthias, 2021).

All statistical analyses were performed in the R statistical computing environment (R Core Team, 2023). Linear and non-linear mixed models were performed in the R package “nlme” (Pinheiro et al., 2019). General linear models were performed using the *lm* command in base R, and post-hoc comparisons were performed in the R package “emmeans” (Lenth, 2022).

We determined variation in microbial communities among treatment types by performing non-metric multidimensional scaling (NMDS) and Permutational Analysis of

Variance (PERMANOVA) on Bray-Curtis distance matrices using the R package “vegan” (Oksanen et al., 2019). We followed the recommendations of (Nearing et al., 2022) to determine which microbial taxa contributed to community differences among treatments by performing differential abundance analysis using four separate differential abundance tools. We used the R packages “ANCOMBC” (Lin and Peddada, 2020), “Maaslin2” (Mallick et al., 2021), “ALDEx2” (Fernandes et al., 2013), and “microbiomeStat” (Zhou et al., 2022) for these analyses. We considered a taxon differentially abundant if at least three of the tools identified it as such. We performed post-hoc pairwise comparisons for taxa that were significantly affected by treatments using Benjamini-Hochberg adjusted Wilcoxon rank sum tests on centered log-ratio (clr) transformed abundance data. The clr transformation is the log-ratio of abundance of a single taxon to the mean abundance of all taxa in a sample. A positive clr value therefore indicates that the taxon is more abundant than average, and a negative clr value indicates the taxon has less than average abundance.

Results

3.1 *CO₂ fluxes*

Litter quality and quantity interacted to affect soil respiration (Fig. 6, Table 12). *CO₂ fluxes* (expressed per g C available in each microcosm) always increased with C input quantity: on average, microcosms in the high-quantity and medium-quantity litter treatments produced *CO₂ fluxes* 75% and 35% higher than microcosms in the low-quantity treatments, respectively (Fig. 8). However, the positive influence of C input quantity on respiration was most pronounced when C was added in the form of grazed *Carex* or feces, and least evident when C was added as ungrazed, senesced *Carex* (Fig. 6).

Moreover, litter quality and quantity effects on CO₂ flux varied with time (Fig. 7, Table 12). Microcosms amended with the largest amounts of grazed litter exhibited the highest CO₂ fluxes through day 36 of the experiment; thereafter, microcosms amended with feces exhibited the highest respiration rates (Fig. 7, Fig. S7). As a result, cumulative CO₂ flux across the 12-week incubation was greatest in microcosms receiving the highest quantity of C inputs, in the form of feces (Table S7, Table S5). Cumulative fluxes were smallest in microcosms receiving the lowest quantity of C inputs, regardless of the quality of litter added. In fact, in post-hoc tests, CO₂ fluxes in microcosms receiving the lowest rates of litter addition were not significantly different from no-input controls. These patterns were robust even after accounting for differences in the bioavailable C pool's depletion rate using an exponential decay model (Table S7). Overall, our linear model predicted 94.3% of the variation in cumulative respiration, with 72.3% explained by the quantity treatment, 14.4% by the quality treatment, and 7.5% by their interaction.

For all microcosms, the calculated priming effect was negative, and litter quality and quantity interacted to influence the priming effect ($p < 0.001$). There were no significant differences in priming among litter types within the low quantity treatments. Within the medium quantity treatments, the magnitude of the priming effect mirrored the respiration response, following the order: feces > grazing lawn = green live > senesced litter; the priming effect within high quantity treatments also mirrored respiration response, following the order: feces > grazing lawn > green live > senesced litter (data not shown).

3.2 Soil biogeochemistry

Litter quality, quantity, and their interaction all significantly affected soil TIN after the 12-week incubation (Fig. 8a, Table S4). Averaged across all litter types, high-quantity treatments resulted in 18% higher TIN than low-quantity treatments, but the pattern was more pronounced for N-rich litters. In general, soil TIN concentrations across the litter quality treatments reflected the N content of each litter type. The largest amounts of inorganic N accumulated in microcosms amended with N-rich grazed *Carex*, whereas TIN concentrations were lowest – indeed, 20% lower than in no-input control treatment – in microcosms amended with N-poor senesced *Carex*.

Neither litter quality nor quantity treatments significantly affected MBC after 12 weeks of incubation (Fig. 8b, Table S4). However, compared to no-addition controls, medium- and high-quantity litter addition treatments produced 20-24% higher MBC, and soils amended with litter from grazing lawn treatments produced 25% higher MBC than microcosms with no C inputs (Fig 8b, Table S6). Meanwhile, DOC responded to the independent effects of litter quality and quantity (Figs. 8c-d, Table S4). High-quantity and medium-quantity litter additions resulted in 29% and 21% more DOC than low-quantity additions, respectively, and feces additions resulted in 15-25% more DOC than other litter types. All litter treatments elevated DOC concentrations above those seen in microcosms without C inputs (Table S6). Finally, NAG was the only enzyme to respond to the litter input treatments: activity was 18-22% greater in the low- and medium-quantity litter addition treatments compared to high-quantity additions ($p = 0.03$ and $p = 0.01$, respectively) (Fig. S8).

3.3 Microbial communities

Litter quality and quantity interacted to affect bacterial community-weighted mean *rrn* copy number ($p < 0.001$; Fig. S9). High quantity treatments tended to result in higher weighted mean *rrn* copy numbers than low quantity treatments, except within the senesced litter treatments, where quantity did not affect copy number. The impacts of litter quality on mean *rrn* copy number varied slightly with quantity. Within medium and high quantity treatments, feces and green live additions had the highest weighted mean copy numbers; within the low quantity treatments, feces and senesced litter additions had higher weighted mean copy numbers than grazed *Carex* additions.

The quality and quantity of litter inputs significantly interacted to affect microbial community structure (Figs. 9 and 10), although litter quality explained more of the variance in bacterial and fungal community structure than litter quantity. Differential abundance analysis indicated that litter quality and quantity interacted to affect the abundance of nine bacteria phyla (Figs. S10-S18). Among the most abundant bacteria, *Firmicutes* and *Bacteroidetes* exhibited the strongest treatment responses as indicated by large differences in clr transformed abundance. Within the medium- and high-quantity treatments, differences in *Firmicutes* abundance were primarily driven by senesced litter additions, which resulted in *Firmicutes* abundance that was 0.09-0.58 clr units lower than other litter types. Within the low-quantity treatment, *Firmicutes* abundance in the senesced treatment was 0.48 clr units higher than in the grazing lawn treatment. Differences in *Bacteroidetes* abundance were driven by senesced litter and feces. Feces additions increased *Bacteroidetes* abundance within the medium and high quantity treatments. Senesced litter additions decreased *Bacteroidetes* abundance within the

medium quantity treatments. In addition to responding to litter treatments, post-incubation bacterial communities differed markedly from field-fresh pre-incubation communities (Fig. 10a). *Firmicutes* abundance exhibited the largest change, increasing from a clr abundance of 1.36 in field-fresh soils to 6.63 in post-incubated no-addition soils. Post-incubation *Bacteroidetes* and *Planctomycetes* abundance also increased, whereas *Acidobacteria* and *WS3* abundance decreased.

Differential abundance analysis indicated that litter quality and quantity also interacted to affect the abundance of seven fungal classes (Figs. S19-S25).

Pezizomycetes, *Dothideomycetes*, and *Tremellomycetes* exhibited the strongest treatment responses. The responses to quality treatments for these classes tended to be strongest within the high- and medium-quantity treatments. *Pezizomycetes* clr abundance in feces treatments increased to 6.61 and 5.91 within the medium and high quantity treatments, respectively, compared to an average of -0.26 for the other litter types. *Dothideomycetes* clr abundance in grazing lawn treatments was 1.37-3.42 units higher than other litter types within the medium- and high-quantity treatments. Within the medium- and high-quantity treatments, *Tremellomycetes* abundance was higher in the grazing lawn and green live treatments than in the feces and senesced treatments. Similar to bacteria, post-incubation fungal communities differed from field-fresh pre-incubation communities irrespective of litter treatments (Fig. 10b). Specifically, fungal communities shifted from predominately unidentified fungal classes in pre-incubated soils to a composition with substantial representations from *Saccharomycetes*, *Dothideomycetes*, *Sordariomycetes*, and *Eurotiomycetes* classes in post-incubated, no-litter addition soils.

Discussion

Our results suggest that both the quality and quantity of litter are important determinants of litter decomposition. In line with our expectations, higher quantities of litter addition resulted in higher cumulative CO₂ efflux per unit C added, as found in other studies (G. Liu et al., 2017; Shahbaz et al., 2017). This phenomenon may be attributable to ‘hotspots’ of organic matter availability in soils under high rates of litter amendment, which alleviate spatial constraints on microbial litter access (Schnecker et al., 2019). However, the degree to which elevated C input stimulated CO₂ flux depended on the type of litter added. This result is important, as it suggests that the effects of increased plant productivity on soil C balance will hinge on the chemistry of those plant C inputs. The mechanisms underlying this pattern may relate to differences in the chemical recalcitrance or stoichiometry of the plant inputs; additionally, litter quality-quantity interactions may emerge from shifts within decomposer microbe communities. Below, we consider support for each of our hypotheses in turn.

4.1 Effects of litter quality on respiration across a gradient of litter input quantity: the role of plant tissue chemistry

We expected soil respiration to correlate more strongly with C input rate in ‘high-quality’ (high-N, low lignin:N) litter treatments, because these inputs should alleviate N limitation and allow for increased decomposition of both fresh and native soil organic matter (Blagodatskaya and Kuzyakov, 2008). In fact, microcosms amended with senesced *Carex*—which exhibited the lowest rates of respiration—had less TIN than control soils with no litter inputs, indicating net N immobilization and (potentially) aggravation of N limitation. Additionally, we found that the activity of the extracellular enzyme NAG –

which targets N-rich chitin – was suppressed when litter was added at high rates, suggesting high quantity additions alleviated the need to invest in N-acquisition.

However, N cycle parameters did not perfectly correlate with patterns of CO₂ flux across the different treatments. Concentrations of TIN at the end of the incubation paralleled the N content of litter inputs, but cumulative CO₂ flux did not follow the same pattern, suggesting that litter characteristics other than N-content were most important for dictating the respiration response. For example, cumulative respiration rates were highest in microcosms amended with feces, even though this type of litter input had a relatively low N content, a high lignin:N ratio, and somewhat smaller TIN pools at the conclusion of the incubation. Instead, other limiting factors, such as the amounts of bioavailable C or inorganic nutrients could have affected decomposition dynamics. For example, the high CO₂ flux from feces-amended microcosms could be due to the greater C availability (suggested by high DOC), which could have fueled lignin degradation (Klotzbücher et al., 2011). Additionally, high respiration in microcosms receiving feces could have been driven by P availability, as feces had the lowest C:P ratio of all litters by a large margin. Overall, we were able to demonstrate partial support for our hypothesis that the N content of litter influences its decomposition along gradients of C availability; however, this was primarily evident when litter quality was very low (i.e. high lignin:N and C:N). In the case of higher quality litters, it appears that other limiting resources (labile C, P) play an outsized role in dictating decomposition.

To what extent did priming effects contribute to the patterns we observed?

Because we standardized respiration rates to the quantity of C added to each microcosm, our findings reflect greater C utilization with higher rates of C input, especially for high-

quality litter. This could represent ‘true’ priming effects (enhanced decomposition of pre-existing soil C), or ‘apparent’ priming (more complete decomposition of the added litter), so we calculated priming effect to distinguish between these phenomena. For all microcosms, priming effect values were negative, indicating that the magnitude of C inputs exceeded litter-induced C losses (i.e., all soils accumulated C throughout the incubation). Without isotopic labelling, we cannot precisely quantify the source of C respired in each treatment (background soil organic matter vs. new litter input). However, ‘true’ priming effects – if they occurred – were not large enough to trigger a net soil C loss, in any litter quantity or quality treatment. Despite this, it is clear that the total magnitude of C loss from each individual microcosm was dependent on both the amount and chemical composition of C added.

4.2 Effects of litter quality on respiration across a gradient of litter input quantity: the role of microbial community shifts

Because the size of the microbial biomass did not vary among the different litter quantity or quality treatments, changes in microbial C use efficiency or biomass turnover rate – both of which could be associated with community shifts – likely drove the changes in C cycling we observed (Fierer et al., 2007; Malik et al., 2020; Morrissey et al., 2023). We found evidence in support of our hypothesis that greater C respiration was associated with more copiotrophic microbial communities. Specifically, we found that mean weighted *rrn* copy number of bacterial communities was highest for feces addition treatments and tended to increase with litter quantity. *rrn* copy number has been shown to associate with putative copiotrophic traits like high maximum growth rate and low C use efficiency (Klappenbach et al., 2000; Roller et al., 2016), and copiotrophic microbes are

thought to exhibit faster biomass turnover rates (Fierer et al., 2007), all of which could have contributed to the higher respiration rates in the feces amended soils. Contrary to our hypothesis, however, the litters with the lowest lignin:N ratios did not result in the most copiotrophic bacterial communities, indicating that community shifts toward copiotrophy were driven by something other than litter N and lignin. In fact, community weighted *rrn* copy number was positively correlated with soil DOC at the end of the experiment ($p = 0.001$, $r = 0.28$). This could indicate that greater C availability promoted more copiotrophic bacterial communities, although it is also possible that higher DOC concentrations resulted from faster biomass turnover rates in these communities.

It is important to note that community-weighted *rrn* copy number does not consider fungal communities, which also contribute to the degree of copiotrophy vs oligotrophy within soils (Ho et al., 2017). In fact, fungal communities exhibited more dramatic compositional shifts to our litter treatments than bacterial communities. These strong fungal responses may suggest that fungi were more functionally distinct than bacteria in this system, and therefore potentially more important for driving differences in decomposition among treatments. In contrast, bacterial communities differentiated more strongly from pre-incubated soils than they did among litter addition treatments. This indicates that bacterial community turnover was primarily driven by successional dynamics. However, as we did not directly manipulate microbial communities, we cannot say definitively whether fungi or bacteria played a more important role in driving differences in litter decomposition.

The most conspicuous effects of litter quality on fungal communities occurred within the feces treatments, which became strongly dominated by the *Pezizomycetes*

fungal class, and the grazing lawn treatments, which became strongly dominated by the order *Pleosporales* from the *Dothideomycetes* class. *Pezizomycetes* are well-documented dung-associated fungi (Pfister and Healy, 2021), and *Pleosporales* have previously been observed to strongly predominate during the decomposition of a *Carex* species (Ma et al., 2020). Therefore, the fast decomposition rates in the feces and grazing lawn treatments, especially under the highest rates of litter amendment, could be due to the development of functionally distinct fungal communities that were well matched to the available litter type.

In general, microbial communities differentiated across the litter quality treatments only at medium and high levels of C input, paralleling trends observed for respiration. One notable exception to this pattern was observed for fungal communities receiving low inputs of senesced litter: these strongly differed from the assemblages found in all other treatments. Perhaps this is a signal of the accentuated N limitation in the senesced litter treatment. Moreover, we note that the pre-incubation microbial community composition differed greatly from all post-incubation microbial communities, including those not amended with litter. Therefore, although we cannot directly extrapolate our data from the experimental microcosms to the field, our findings strongly suggest that differences in litter quality have the potential to affect C utilization patterns via their effects on bacterial and fungal communities.

4.3 Implications for C cycling on the Y-K Delta

Plants influence soil C cycling through their litter inputs quantity and chemical composition, and herbivores can strongly impact both traits. Here we show that three known effects of herbivory can modify greenhouse gas fluxes from wetland soils through

multiple mechanisms (1) by dramatically reducing the quantity of aboveground plant tissue available for decomposition, (2) by enhancing the nutrient content of vegetation, (3) by further modifying litter chemistry before re-deposition as feces. Each of these changes, in turn, was associated with significant shifts in the composition of soil microbial communities. Thus, a complex interaction among animals, plants, bacteria, and fungi ultimately governs ecosystem carbon balance in this high-latitude wetland.

Herbivores strongly influence both litter quality and quantity on the Y-K Delta, with opposing effects on overall CO₂ flux. Our results suggest that herbivores—which create grazing lawns and feces—accelerate soil organic matter cycling by altering litter quality. At the same time, by reducing C inputs, herbivores may strongly suppress soil C fluxes. Which effect predominates *in situ*? Field studies in the Y-K Delta imply that the latter effect may play a stronger role in determining overall soil C balance: field-measured ecosystem respiration is higher in ungrazed habitats than grazed habitats (Kelsey et al., 2016), likely because of the much larger inputs of litter in ungrazed areas. However, field-measured ecosystem respiration in the ungrazed *Carex* meadows is only ~1.5 times greater than in grazing lawns, despite litter inputs being up to six-fold greater (Kelsey et al., 2016). This suggests that soil C accumulation is higher in ungrazed meadows, and that goose herbivory decreases the strength of the ecosystem C sink by reducing litter quantity.

Additionally, grazing-induced alterations in litter type and quantity are both associated with changes in microbial communities, providing further context for previously observed differences in microbial communities between grazed and ungrazed meadows in the Y-K Delta (Foley et al., 2022). In that study, grazing lawn soils incubated

without external C amendments exhibited higher respiration rates than ungrazed soils, suggesting the soil microbes associated with grazing lawns have an inherently higher rate of metabolism, and that more labile C is found in grazing lawn soils, perhaps due to enhanced root exudation (Sun et al., 2017). This indicates that microbial communities in grazing lawns are more copiotrophic than in ungrazed soils, a pattern that our findings suggest may be partially driven by feces deposition favoring copiotrophic bacteria. This effect may explain why field-measured ecosystem respiration in grazing lawns is so much higher than would be expected based on the quantity of litter inputs relative to ungrazed *Carex* meadows (Kelsey et al., 2016). In addition to impacting soil CO₂ flux, more copiotrophic communities in grazing lawns may also influence soil C persistence. The lower C use efficiency of copiotrophic communities leads to less accumulation of microbial necromass, which may be preferentially stabilized in soil compared to plant-derived inputs (Liang et al., 2017, 2019). Determining how grazing influences soil C persistence in sub-arctic and arctic ecosystems is an important avenue for future research.

This study can also inform our understanding of how CO₂ fluxes may change in this system with potential shifts in vegetation quality and quantity, due to changes in herbivore distributions. Black brant populations in the Y-K Delta have been experiencing declines over several decades (Fondell et al., 2011), and our results suggest that the subsequent decline in grazing meadows could alter the C source strength of the region (Leffler et al., 2019). In our experiment, heterotrophic respiration in treatments typical of ungrazed meadows (high quantity, senesced and green live *Carex*) was ~50% higher than in treatments typical of grazed meadows (low quantity, grazed *Carex* and goose feces). Our experiment also shows a surprising effect of herbivory on microbial communities,

with unique fungal communities associated with feces addition, alongside unexpectedly high respiration rates. Similar effects on soil microbial communities could occur in other systems with high densities of animals, with consequences for soil functioning and climate change feedbacks. Although there have been several studies of the effects of herbivory on C cycling (Sjögersten et al., 2010; Kelsey et al., 2016; Penner and Frank, 2019; Koltz et al., 2022), the role of microbial communities in mediating these changes is not well known (Andriuzzi and Wall, 2017). We suggest that herbivory studies that explicitly account for microbial community effects will improve our understanding of how herbivory influences climate change.

Conclusions

We show that the proportion of organic matter utilized increases with the rate of fresh C addition, and that the strength of this relationship is dependent upon the type of litter added. The nutrient content of litter only partially explains this phenomenon; shifts in microbial communities also play an important role. Moreover, our results demonstrate that animals have complex and far-reaching impacts on soil biogeochemistry through their impacts on litter chemistry and abundance, which to date, are not incorporated into predictive ecosystem models (Schmitz et al., 2018).

Author Contributions

BWG, KHB, and TBA designed the experiments. TS, JA, and KHB performed the experiments. All authors analyzed the data. TS and JA wrote the original draft, KHB, BWG and TBA revised the manuscript.

Data Accessibility

Data is available at the NSF Arctic Data Center, accessible at:
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CHAPTER 4

CONCLUSIONS

Our studies add to the body of research showing that herbivores can exert strong effects on C and N cycling in the Y-K Delta. Our litter bag study found that litter quality does interact with habitat to produce different litter decomposition rates. As ecosystem engineers, geese create differences in habitat that were further supported by this study as well, with clear abiotic differences measured in grazing lawn habitats. This litter bag study affirms the role of geese in structuring vegetation communities on the landscape, as lower litter turnover in grazing lawns shows a clear difference in how this habitat processes inputs to soils.

Additionally, our soil microcosm experiment shows the unique effect that herbivore feces produces on both CO₂ fluxes and microbial communities. Given this unique effect, further insights into CO₂ fluxes and microbial communities in these soils may be gathered by studying how fecal chemistry, including phosphorus composition (Sitters et al., 2017), affects C and nutrient cycling. Linking microbial communities to variations in CO₂ fluxes is an increasingly important topic in soil microbial ecology, and this study adds to the body of research investigating how differences in microbial communities affect greenhouse gas emissions from soils.

Beyond herbivores, we might expect litter quality, abiotic characteristics, and vegetation communities to change in the Y-K Delta. Many pathways for potential further perturbances to this system exist, including atmospheric carbon fertilization decreasing overall litter quality (Cotrufo et al., 1994), flooding possibly affecting vegetation

communities (Terenzi et al., 2014), and changes in goose distribution and phenology (Beard et al., 2019; Koltz et al., 2022). It is worth investigating whether these changes to litter quality, vegetation communities, and habitat might change C cycling in the future as well. These studies provide an herbivore-focused approach toward asking questions about how litter quality, quantity, and habitat affect C cycling in this region, but these results may inform how broader ecosystem changes in the Y-K Delta affect litter decomposition and CO₂ fluxes.

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TABLES

Table 1

Chemistry of litter collected at the end of the growing season from Saunders et al. (2023), and chemistry of pre-decomposition litter used in litter bags collected at the beginning of the growing season.

Collected	Litter Type	C%	N%	Lignin %	Lignin:N	C:N
End of season	Grazing lawn	45.12	3.35	17.63	5.26	13.47
Early season	Green	40.53	2.39	14.58	6.10	16.94
End of season	Green	45.10	2.15	12.55	5.84	21.01
Early season	Senesced	37.45	0.45	11.33	25.18	82.76
End of season	Senesced	40.91	0.61	13.68	23.38	67.56

Table 2

Linear mixed effects model results with biomass remaining in each litter bag as a response variable. Site was included as a random effect.

Factor	χ^2	<i>df</i>	<i>p</i>
Litter type	3.98	1	0.046
Habitat	1.24	1	0.265
Collection week	544.40	3	<0.001
Litter type x Habitat	17.99	1	<0.001
Litter type x Collection week	53.22	3	<0.001
Habitat x Collection week	1.82	3	0.610
Litter type x Habitat x Collection week	3.05	3	0.383

Table 3

Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat and week collected effects on biomass remaining. Results based on linear mixed effects models.

Week Collected	Condition	contrast	t.ratio	p.value
3	Senesced	<i>Carex</i> meadow - Grazing lawn	2.35	0.020
	Green	<i>Carex</i> meadow - Grazing lawn	-1.84	0.067
6	Senesced	<i>Carex</i> meadow - Grazing lawn	-0.28	0.783
	Green	<i>Carex</i> meadow - Grazing lawn	-1.34	0.180
9	Senesced	<i>Carex</i> meadow - Grazing lawn	0.97	0.332
	Green	<i>Carex</i> meadow - Grazing lawn	-2.85	0.005
52	Senesced	<i>Carex</i> meadow - Grazing lawn	1.34	0.180
	Green	<i>Carex</i> meadow - Grazing lawn	-1.63	0.106
3	<i>Carex</i> meadow	Senesced – Green	-1.28	0.202
	Grazing lawn	Senesced – Green	-5.18	<0.001
6	<i>Carex</i> meadow	Senesced – Green	0.94	0.350
	Grazing lawn	Senesced – Green	-0.08	0.938
9	<i>Carex</i> meadow	Senesced – Green	4.26	<0.001
	Grazing lawn	Senesced – Green	0.44	0.663
52	<i>Carex</i> meadow	Senesced – Green	5.16	<0.001
	Grazing lawn	Senesced – Green	1.83	0.068

Table 4

Decomposition constant (k), mean residence time (MRT), and time to 95% decomposition (3/k) for collection periods, habitat, and litter type combinations.

Habitat	Litter Type	K (days ⁻¹)	MRT (days)	3/k (days)
CM	Green	0.00236 ± 0.00016	424.34 ± 28.13	1273.02
	Senesced	0.00118 ± 0.00015	847.46 ± 104.93	2542.37
GL	Green	0.00208 ± 0.00016	480.91 ± 36.52	1442.72
	Senesced	0.00132 ± 0.00016	757.58 ± 94.18	2272.73

Table 5

Linear model results with fraction of initial C remaining as a response variable (n = 5 per litter and habitat combination per collection week).

Factor	<i>F</i>	<i>df</i>	<i>p</i>
Litter type	0.03	1	0.875
Habitat	0.26	1	0.610
Collection week	701.18	3	<0.001
Litter type x Habitat	8.67	1	0.004
Litter type x Collection week	20.33	3	<0.001
Habitat x Collection week	1.25	3	0.293
Litter type x Habitat x Collection week	3.47	3	0.017

Table 6

Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat, and collection week effects on fraction of initial C remaining. Results based on linear models.

Condition		Contrast	<i>t</i> ratio	<i>p</i>
Green	<i>Carex</i> meadow	Week 3 - Week 6	5.277	< 0.001
		Week 3 - Week 9	7.572	< 0.001
		Week 3 - Week 52	22.743	< 0.001
		Week 6 - Week 9	2.296	0.102
		Week 6 - Week 52	16.723	< 0.001
		Week 9 - Week 52	14.136	< 0.001
Green	Grazing lawn	Week 3 - Week 6	9.828	< 0.001
		Week 3 - Week 9	9.149	< 0.001
		Week 3 - Week 52	22.282	< 0.001
		Week 6 - Week 9	-0.101	1.000
		Week 6 - Week 52	14.134	< 0.001
		Week 9 - Week 52	13.514	< 0.001
Senesced	<i>Carex</i> meadow	Week 3 - Week 6	2.546	0.056
		Week 3 - Week 9	0.993	0.753
		Week 3 - Week 52	22.329	< 0.001
		Week 6 - Week 9	-1.414	0.492
		Week 6 - Week 52	19.192	< 0.001
		Week 9 - Week 52	19.908	< 0.001
Senesced	Grazing lawn	Week 3 - Week 6	1.193	0.632
		Week 3 - Week 9	0.981	0.761
		Week 3 - Week 52	19.006	< 0.001
		Week 6 - Week 9	-0.169	0.998
		Week 6 - Week 52	17.833	< 0.001
		Week 9 - Week 52	17.372	< 0.001
Week 3	Green	<i>Carex</i> meadow - Grazing lawn	-3.150	0.002
	Senesced	<i>Carex</i> meadow - Grazing lawn	2.186	0.030
Week 6	Green	<i>Carex</i> meadow - Grazing lawn	1.402	0.162
	Senesced	<i>Carex</i> meadow - Grazing lawn	0.845	0.399
Week 9	Green	<i>Carex</i> meadow - Grazing lawn	-1.056	0.292
	Senesced	<i>Carex</i> meadow - Grazing lawn	1.989	0.048
Week 52	Green	<i>Carex</i> meadow - Grazing lawn	-0.522	0.603
	Senesced	<i>Carex</i> meadow - Grazing lawn	-0.195	0.845
Week 3	<i>Carex</i> meadow	Green - Senesced	1.334	0.184
	Grazing lawn	Green - Senesced	6.372	< 0.001
Week 6	<i>Carex</i> meadow	Green - Senesced	-1.347	0.179
	Grazing lawn	Green - Senesced	-1.927	0.055
Week 9	<i>Carex</i> meadow	Green - Senesced	-4.884	< 0.001
	Grazing lawn	Green - Senesced	-1.822	0.070
Week 52	<i>Carex</i> meadow	Green - Senesced	1.123	0.263
	Grazing lawn	Green - Senesced	1.351	0.178

Table 7

Linear model results with fraction of initial N remaining as a response variable (n = 5 per litter and habitat combination per collection week).

Factor	<i>F</i>	<i>df</i>	<i>p</i>
Litter type	899.27	1	<0.001
Habitat	4.71	1	0.031
Collection week	232.39	3	<0.001
Litter type x Habitat	17.80	1	<0.001
Litter type x Collection week	10.64	3	<0.001
Habitat x Collection week	2.34	3	0.075
Litter type x Habitat x Collection week	6.34	3	<0.001

Table 8

Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat, and collection week effects on fraction of initial N remaining. Results derived from linear models.

Condition		contrast	<i>t</i> ratio	<i>p</i>
Green	<i>Carex</i> meadow	Week 3 - Week 6	5.88	< 0.001
		Week 3 - Week 9	6.14	< 0.001
		Week 3 - Week 52	16.81	< 0.001
		Week 6 - Week 9	-0.50	0.958
		Week 6 - Week 52	8.24	< 0.001
		Week 9 - Week 52	9.93	< 0.001
Green	Grazing lawn	Week 3 - Week 6	6.07	< 0.001
		Week 3 - Week 9	4.76	< 0.001
		Week 3 - Week 52	13.25	< 0.001
		Week 6 - Week 9	-0.99	0.755
		Week 6 - Week 52	8.20	< 0.001
		Week 9 - Week 52	8.66	< 0.001
Senesced	<i>Carex</i> meadow	Week 3 - Week 6	3.59	0.002
		Week 3 - Week 9	-0.93	0.787
		Week 3 - Week 52	7.80	< 0.001
		Week 6 - Week 9	-4.20	< 0.001
		Week 6 - Week 52	4.11	< 0.001
		Week 9 - Week 52	8.10	< 0.001
Senesced	Grazing lawn	Week 3 - Week 6	7.55	< 0.001
		Week 3 - Week 9	3.54	0.003
		Week 3 - Week 52	13.74	< 0.001
		Week 6 - Week 9	-3.73	0.001
		Week 6 - Week 52	6.54	< 0.001
		Week 9 - Week 52	9.85	< 0.001
Week 3	Green	<i>Carex</i> meadow - Grazing lawn	1.66	0.098
	Senesced	<i>Carex</i> meadow - Grazing lawn	-6.24	< 0.001
Week 6	Green	<i>Carex</i> meadow - Grazing lawn	0.73	0.464
	Senesced	<i>Carex</i> meadow - Grazing lawn	-1.82	0.070
Week 9	Green	<i>Carex</i> meadow - Grazing lawn	0.43	0.669
	Senesced	<i>Carex</i> meadow - Grazing lawn	-1.28	0.200
Week 52	Green	<i>Carex</i> meadow - Grazing lawn	-0.09	0.927
	Senesced	<i>Carex</i> meadow - Grazing lawn	0.64	0.525
Week 3	<i>Carex</i> meadow	Green - Senesced	-5.53	< 0.001
	Grazing lawn	Green - Senesced	-12.40	< 0.001
Week 6	<i>Carex</i> meadow	Green - Senesced	-7.10	< 0.001
	Grazing lawn	Green - Senesced	-11.32	< 0.001
Week 9	<i>Carex</i> meadow	Green - Senesced	-11.35	< 0.001
	Grazing lawn	Green - Senesced	-12.83	< 0.001
Week 52	<i>Carex</i> meadow	Green - Senesced	-13.30	< 0.001
	Grazing lawn	Green - Senesced	-11.58	< 0.001

Table 9

Linear mixed effects model results with C:N of measured replicates as a response variable. Site was included as a random effect.

Factor	χ^2	<i>df</i>	<i>p</i>
Litter type	113.16	1	<0.001
Habitat	5.39	1	0.2021
Collection week	116.06	3	<0.001
Litter type x Habitat	0.03	1	0.874
Litter type x Collection week	190.41	3	<0.001
Habitat x Collection week	1.29	3	0.731
Litter type x Habitat x Collection week	4.30	3	0.231

Table 10

Candidate linear model results for AIC with biomass remaining as a response variable. Biomass remaining from all litter type, habitat, and collection period combinations are included in each of these models.

Candidate models	K	AICc	Δ AIC
Litter * Habitat	5	-268.41	0
Habitat	3	-261.84	6.57
Litter	3	-261.44	6.97
Litter * Temperature	5	-175.89	92.52
Litter * UV	5	-153.94	114.47
Litter * Water	5	-126.85	141.56
Litter * (Water + UV)	7	-100.62	167.79
Litter * (Water + Temperature)	7	-86.07	182.34
Litter * (Temperature + UV)	7	-66.75	201.66
Litter * (Water + Temperature + UV)	9	-60.53	207.88

Table 11

Chemistry of litter used for treatments. Lignin:N determined quality ranking. ADF = acid detergent fiber.

Litter type	C%	N%	P%	K%	Lignin %	ADF %	Lignin:N	C:N	C:P
Grazing lawn	45.12	3.35	0.37	1.93	17.63	48.73	5.26	13.47	121.96
Green live	45.10	2.15	0.30	2.50	12.55	36.07	5.84	21.01	150.57
Feces	26.74	1.62	0.42	2.30	13.68	47.30	8.45	16.51	63.68
Senesced	40.91	0.61	0.17	0.69	13.68	57.85	23.38	67.56	242.42

Table 12

Denominator degrees of freedom (*df*), χ^2 statistics and *p*-values for the effect of quality, quantity, and incubation day of litter on CO₂ fluxes (in units of mg CO₂-C g⁻¹ C h⁻¹).

Statistics are derived from a Type II ANOVA performed on linear mixed-effects models, which included microcosm identity as a random effect.

	<i>df</i>	χ^2	<i>p</i>
Quality	3	45.35	<0.001
Quantity	2	257.42	<0.001
Incubation Day	1	1196.13	<0.001
Quality x Quantity	6	21.15	<0.001
Quality x Incubation Day	3	76.24	<0.001
Quantity x Incubation Day	2	57.54	<0.001
Quality x Quantity x Incubation Day	6	34.00	<0.001

FIGURES

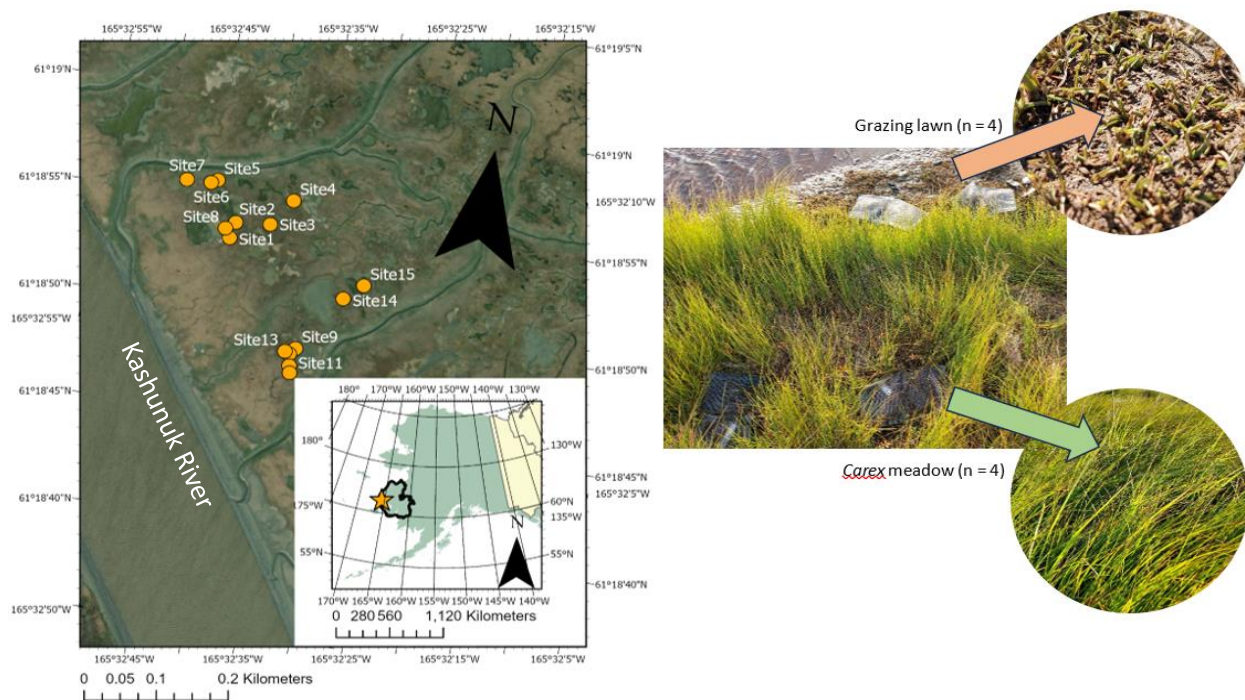


Figure 1. Site location and study design. Photo is representative of each replicate site, with four bags in each of the two habitats at each site.

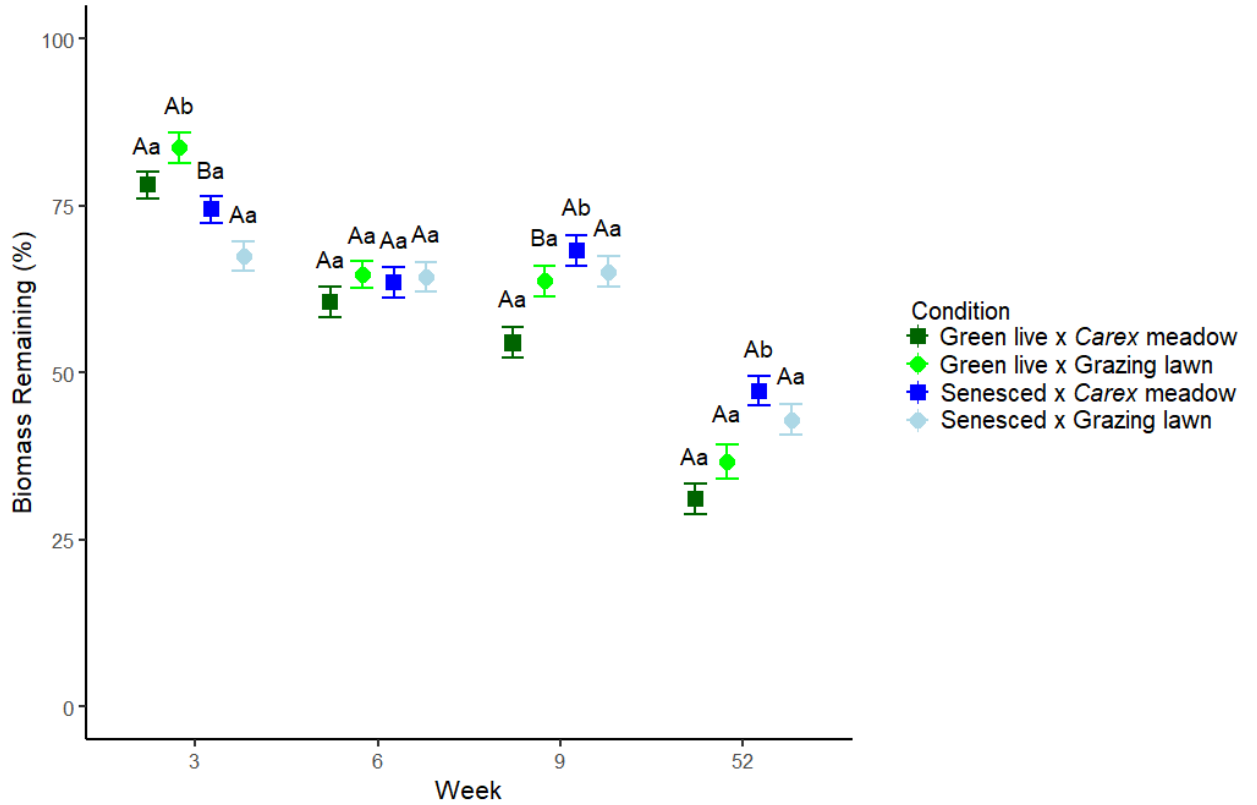


Figure 2. Biomass remaining (%) for each time period. Capital letters denote significant differences among habitats within litter groups, while lowercase letters denote significant differences among litter types within habitats ($\alpha = 0.05$).

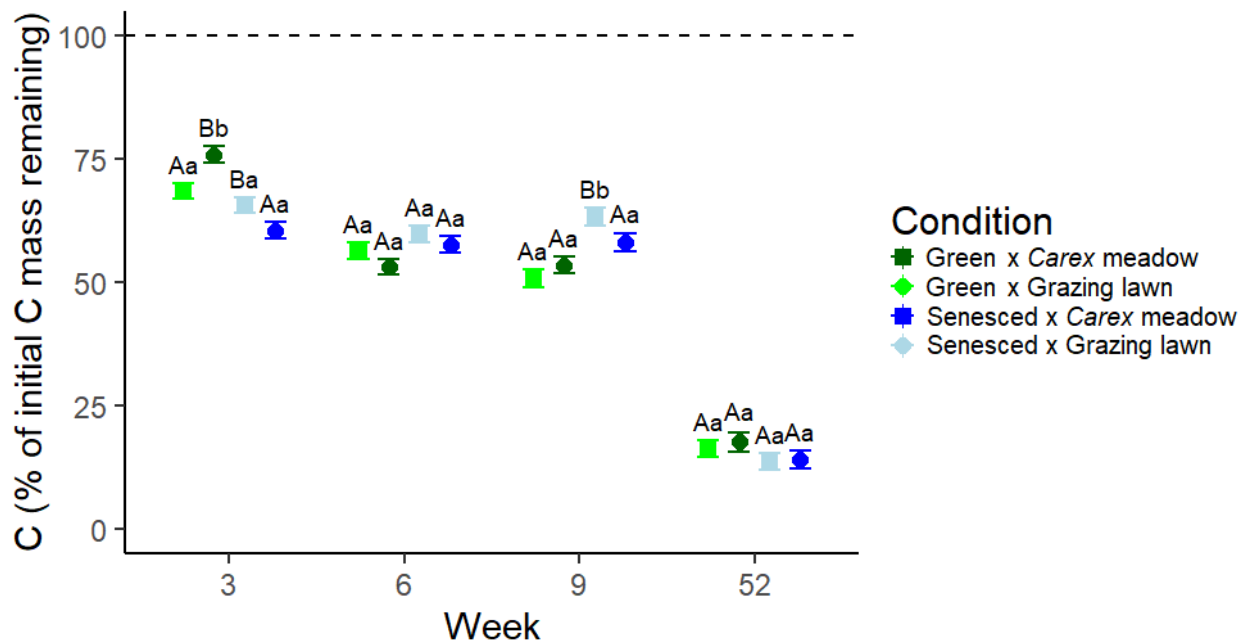


Figure 3. a) C as a percent of initial concentration based on litter type and habitat combinations. Capital letters denote group differences within litter types, and lowercase letters denote group differences among habitats ($\alpha = 0.05$).

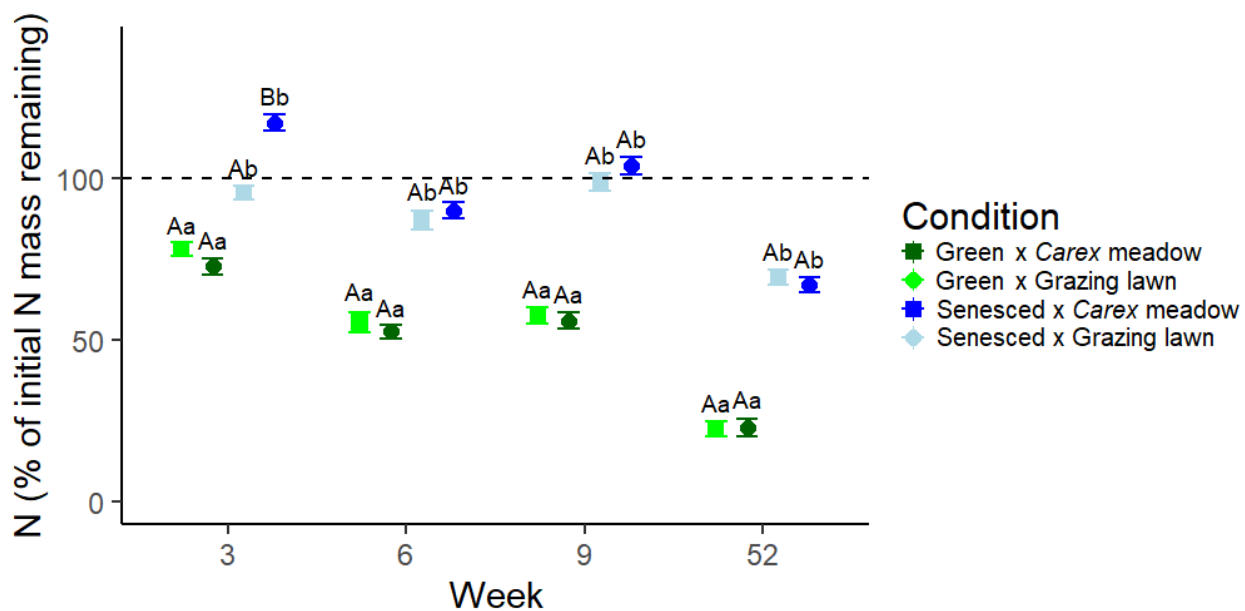


Figure 4. a) N as a percent of initial concentration based on litter type and habitat combinations. Capital letters denote differences within litter types, and lowercase letters denote differences among habitats ($\alpha = 0.05$).

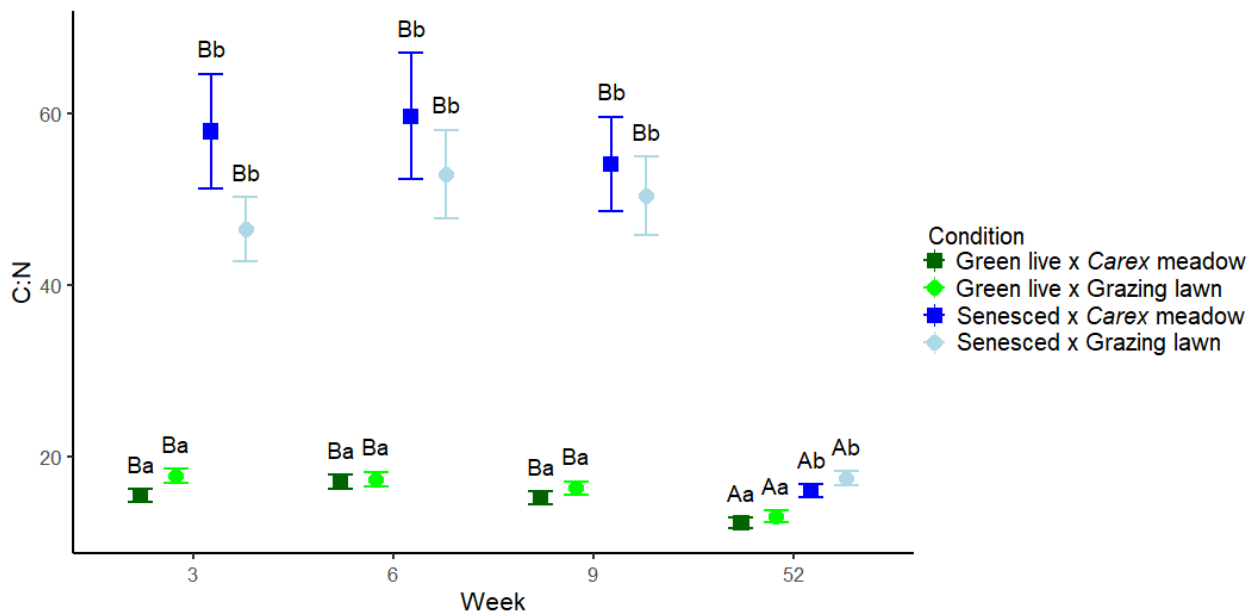


Figure 5. C:N ratio on each decomposition week by litter type and habitat combinations. Capital letters denote significant differences between different litter types within collection weeks, while lowercase letters denote significant differences within litter groups on different collection weeks ($\alpha = 0.05$).

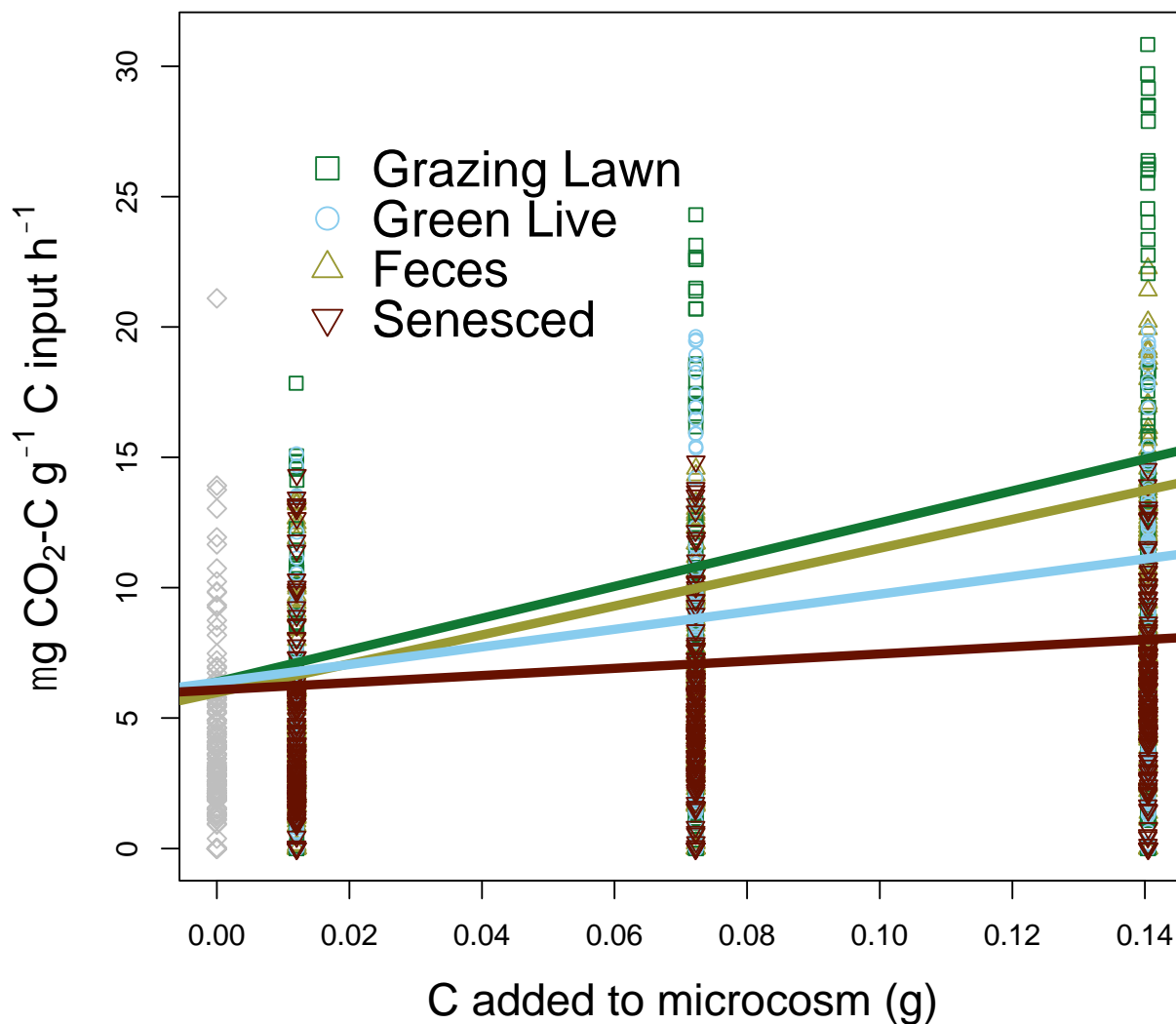


Figure 6. The relationship between C input rate (litter quantity) and soil respiration for microcosms in each litter quality treatment: grazed *Carex* sampled from *C. subspathacea* grazing lawns, ungrazed live (green) *Carex* sampled outside the grazing lawns, goose feces, and senesced *Carex*, also sampled outside the grazing lawns. Slopes and intercepts are taken from a linear mixed effects model performed on weekly CO₂ fluxes, standardized to the total quantity of litter and soil C available in each microcosm.

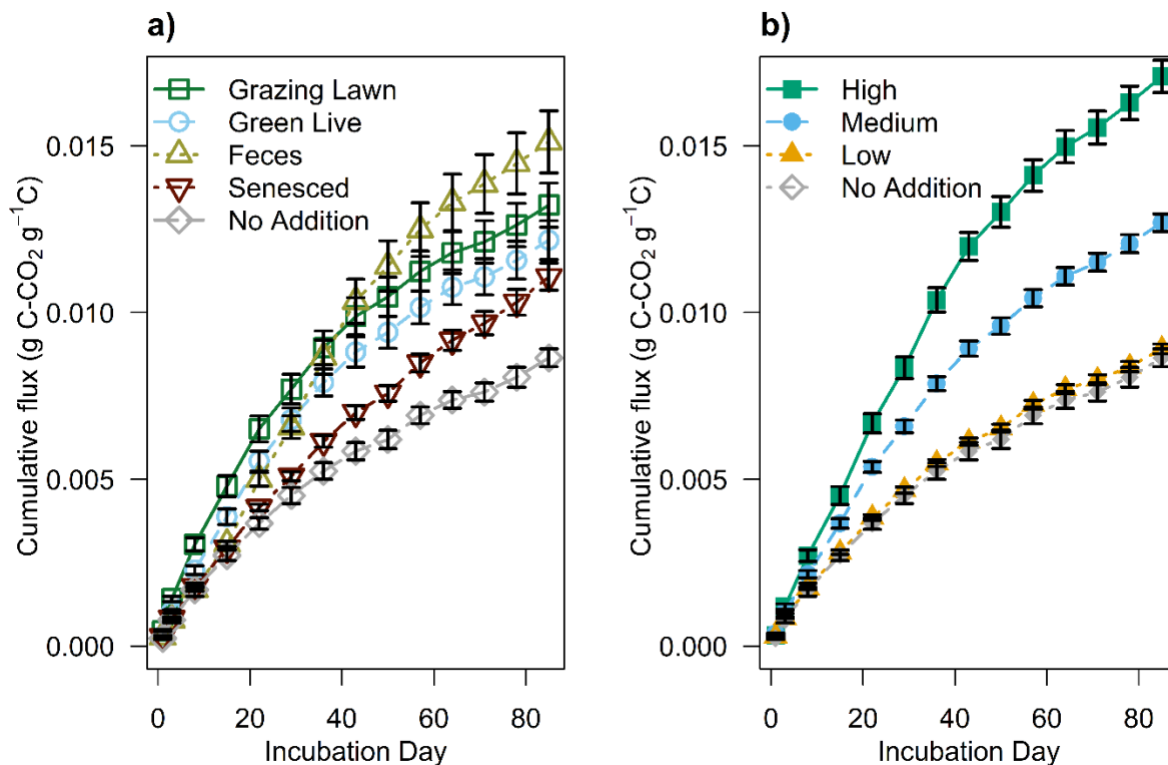


Figure 7. Mean cumulative CO₂ fluxes (\pm SE) for treatment types a) by litter quality and b) by litter quantity. Microcosms with no additions were not included in linear models for cumulative fluxes, but are included in the figures for comparison. These values are standardized to the g C contained in each microcosm, inclusive of the C added from treatments.

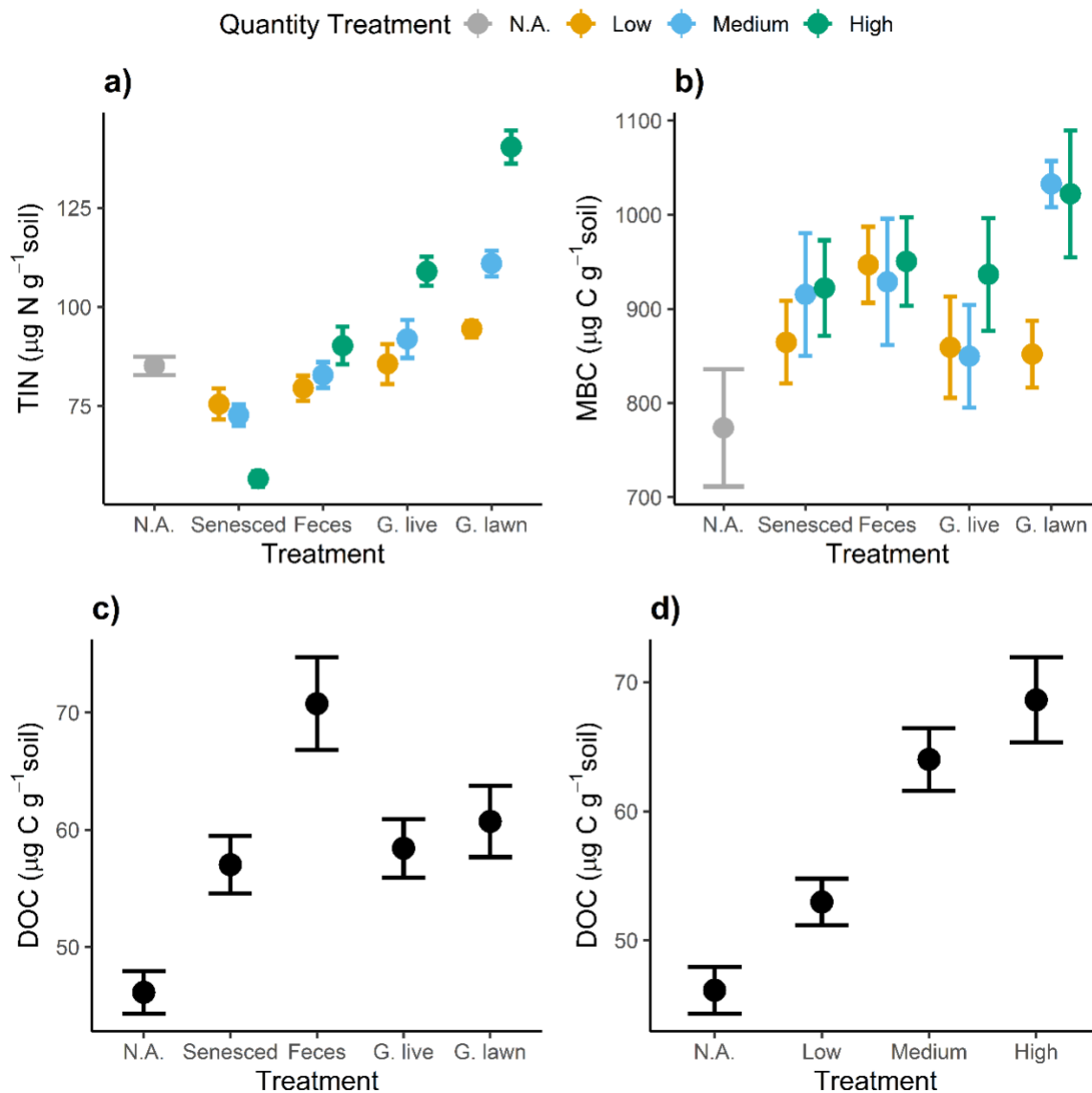


Figure 8. Mean (\pm SE) a) Total Inorganic Nitrogen, b) Microbial Biomass Carbon, c) Dissolved Organic Carbon by quality treatment, and d) Dissolved Organic Carbon by quantity treatment. Microcosms with no additions were not included in linear models. “N.A.” are no-addition, “G. live” are green live, and “G. lawn” are grazing lawn treatments.

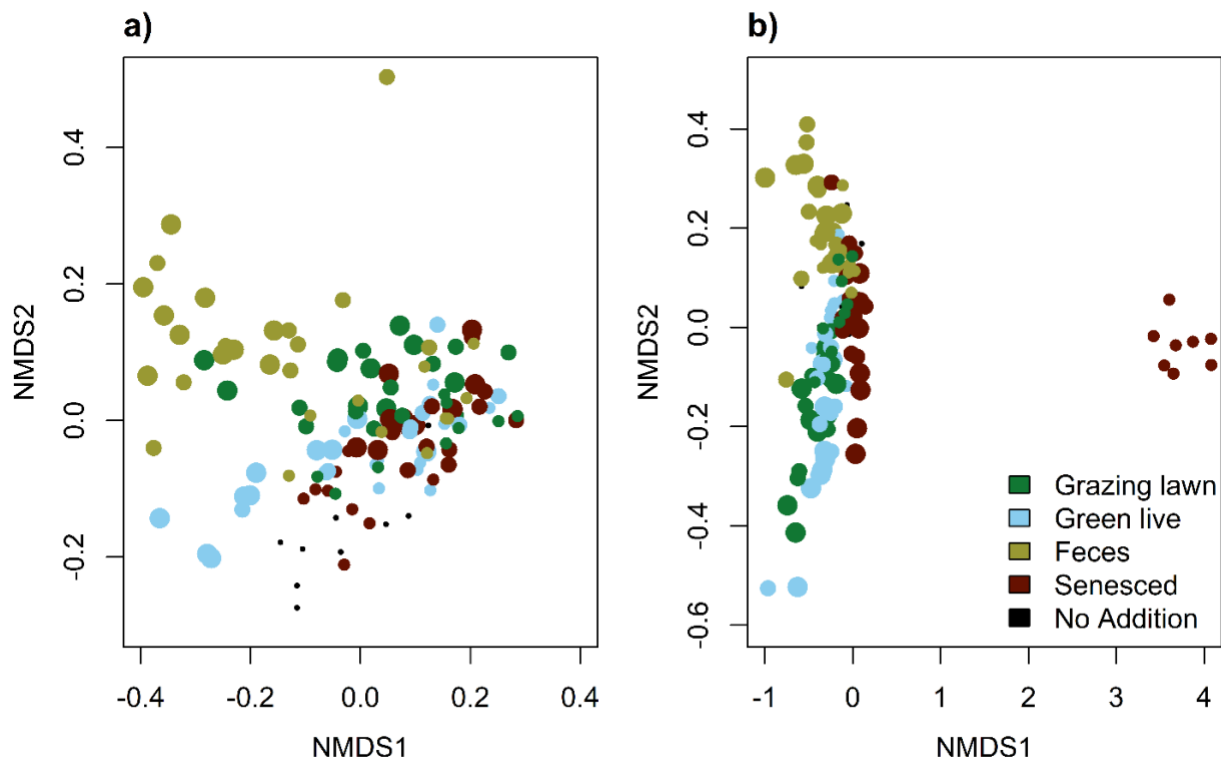
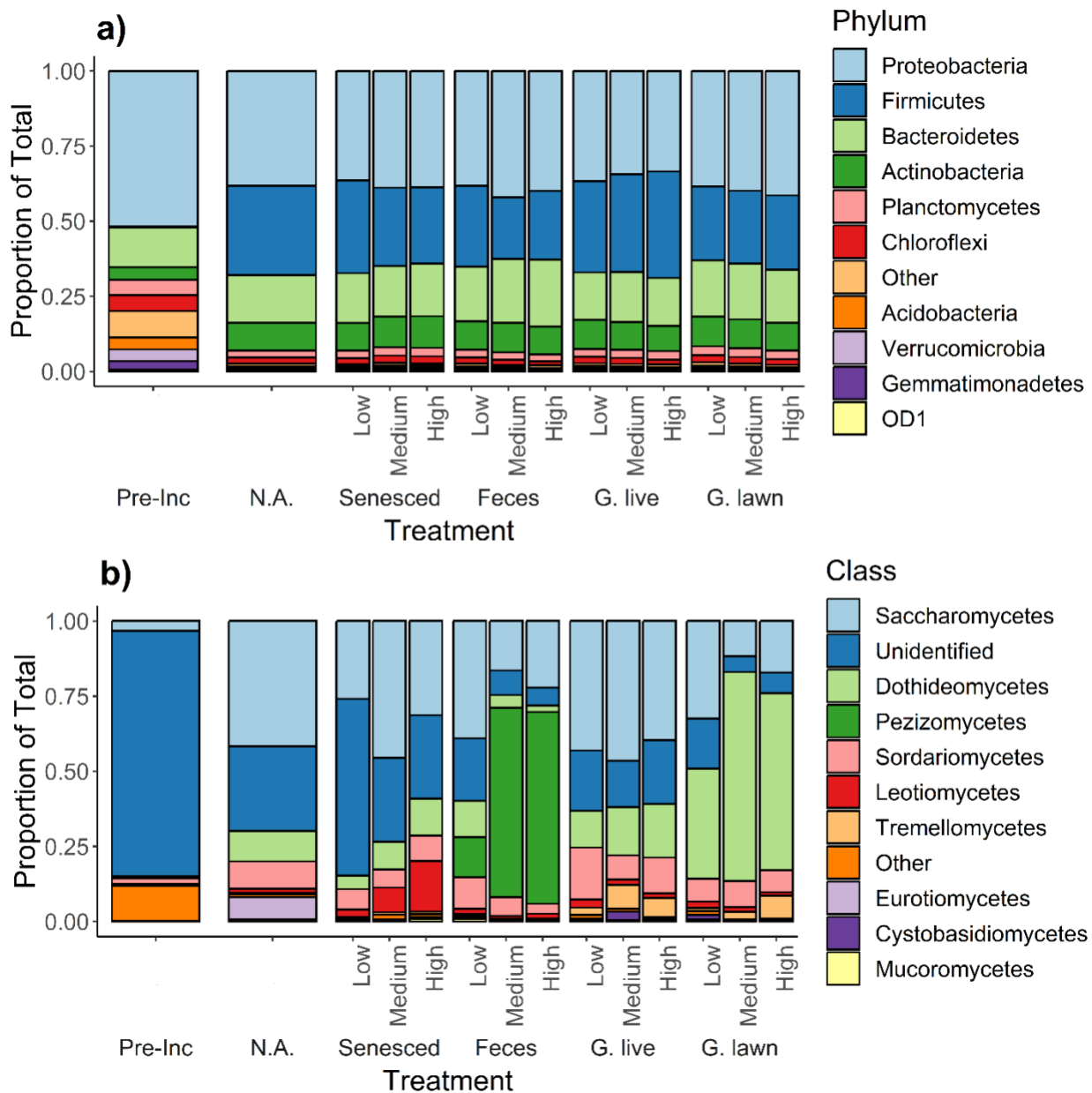


Figure 9. a) Non-metric multidimensional scaling plots conducted on Bray-Curtis distance matrices for bacterial (stress = 0.12; Quality $p = 0.001$, $R^2 = 0.310$; Quantity $p = 0.001$, $R^2 = 0.076$; Quality x Quantity $p = 0.001$, $R^2 = 0.105$) and b) fungal communities (stress = 0.07; Quality $p = 0.001$, $R^2 = 0.283$; Quantity $p = 0.001$, $R^2 = 0.038$, Quality x Quantity $p = 0.001$, $R^2 = 0.098$) based on treatments. Microcosms with no additions were not included in PERMANOVA analysis. Point size denotes different quantity treatments, with larger dots corresponding to higher quantity additions.



APPENDICES

SUPPLEMENTAL TABLES

Table S1. Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat and week collected effects on C mass remaining. Results based on linear models.

Week Collected	Condition	Contrast	t.ratio	p.value
3	<i>Carex</i> meadow	Senesced - Green	-3.82	< 0.001
3	Grazing lawn	Senesced - Green	-7.96	< 0.001
6	<i>Carex</i> meadow	Senesced - Green	-0.35	0.723
6	Grazing lawn	Senesced - Green	0.20	0.842
9	<i>Carex</i> meadow	Senesced - Green	3.27	0.001
9	Grazing lawn	Senesced - Green	0.25	0.801
52	<i>Carex</i> meadow	Senesced - Green	-1.49	0.138
52	Grazing lawn	Senesced - Green	-1.69	0.093
3	Senesced	<i>Carex</i> meadow - Grazing lawn	1.58	0.117
3	Green	<i>Carex</i> meadow - Grazing lawn	-3.09	0.002
6	Senesced	<i>Carex</i> meadow - Grazing lawn	0.77	0.440
6	Green	<i>Carex</i> meadow - Grazing lawn	1.38	0.170
9	Senesced	<i>Carex</i> meadow - Grazing lawn	1.98	0.049
9	Green	<i>Carex</i> meadow - Grazing lawn	-1.04	0.300
52	Senesced	<i>Carex</i> meadow - Grazing lawn	-0.18	0.858
52	Green	<i>Carex</i> meadow - Grazing lawn	-0.51	0.609

Table S2. Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat and week collected effects on N mass remaining. Results based on linear models.

Week Collected	Habitat	Contrast	t.ratio	p.value
3	<i>Carex</i> meadow	Senesced - Green	-35.49	< 0.001
	Grazing lawn	Senesced - Green	-27.24	< 0.001
6	<i>Carex</i> meadow	Senesced - Green	-21.92	< 0.001
	Grazing lawn	Senesced - Green	-20.04	< 0.001
9	<i>Carex</i> meadow	Senesced - Green	-20.15	< 0.001
	Grazing lawn	Senesced - Green	-19.15	< 0.001
52	<i>Carex</i> meadow	Senesced - Green	-4.88	< 0.001
	Grazing lawn	Senesced - Green	-5.00	< 0.001
3	Senesced	<i>Carex</i> meadow - Grazing lawn	-2.29	0.023
	Green	<i>Carex</i> meadow - Grazing lawn	3.10	0.002
6	Senesced	<i>Carex</i> meadow - Grazing lawn	-0.63	0.527
	Green	<i>Carex</i> meadow - Grazing lawn	2.19	0.030
9	Senesced	<i>Carex</i> meadow - Grazing lawn	-0.20	0.841
	Green	<i>Carex</i> meadow - Grazing lawn	0.80	0.426
52	Senesced	<i>Carex</i> meadow - Grazing lawn	0.44	0.662
	Green	<i>Carex</i> meadow - Grazing lawn	-0.17	0.865

Table S3. Post-hoc pairwise comparisons (Sidak tests) for litter type, habitat and week collected effects on lignin mass remaining. Results based on linear mixed effects models.

Week	Collected	Condition	Contrast	t.ratio	p.value
3		<i>Carex</i> meadow	Senesced - Green	-5.15	< 0.001
		Grazing lawn	Senesced - Green	-2.41	0.017
6		<i>Carex</i> meadow	Senesced - Green	-4.72	< 0.001
		Grazing lawn	Senesced - Green	-3.95	< 0.001
9		<i>Carex</i> meadow	Senesced - Green	6.71	< 0.001
		Grazing lawn	Senesced - Green	7.54	< 0.001
52		<i>Carex</i> meadow	Senesced - Green	-13.95	< 0.001
		Grazing lawn	Senesced - Green	1.57	0.119
3		Senesced	<i>Carex</i> meadow - Grazing lawn	-4.06	< 0.001
		Green	<i>Carex</i> meadow - Grazing lawn	-1.66	0.098
6		Senesced	<i>Carex</i> meadow - Grazing lawn	0.46	0.649
		Green	<i>Carex</i> meadow - Grazing lawn	1.45	0.148
9		Senesced	<i>Carex</i> meadow - Grazing lawn	-0.50	0.619
		Green	<i>Carex</i> meadow - Grazing lawn	0.34	0.737
52		Senesced	<i>Carex</i> meadow - Grazing lawn	-4.41	< 0.001
		Green	<i>Carex</i> meadow - Grazing lawn	10.29	< 0.001

Table S4

Type II ANOVA results for denominator degrees of freedom (*df*), *F*-statistics and *p*-values for the effect of quality and quantity of litter on cumulative greenhouse gas fluxes (in units of mg CO₂-C g⁻¹ C h⁻¹) and end-of-incubation nutrients. TIN = Total Inorganic Nitrogen; MBC = Microbial Biomass Carbon; DOC = Dissolved Organic Carbon

	Quality			Quantity			Quality x Quantity		
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>
Cumulative CO ₂	3	94.20	<0.001	2	544.96	<0.001	6	23.03	<0.001
TIN	3	85.93	<0.001	2	17.43	<0.001	6	14.22	<0.001
MBC	3	1.70	0.171	2	2.25	0.111	6	0.92	0.488
DOC	3	5.13	0.002	2	11.42	<0.001	6	1.41	0.218

Table S5

Post-hoc pairwise comparisons (Tukey tests) for quality and quantity effects on cumulative CO₂ fluxes, derived from linear models.

Treatment		<i>t</i> -ratio	<i>p</i> -value
Grazing lawn	High - medium	11.97	<0.001
	High - low	17.26	<0.001
	Low - medium	-5.98	<0.001
Green live	High - medium	7.44	<0.001
	High - low	10.84	<0.001
	Low - medium	-5.22	<0.001
Feces	High - medium	26.83	<0.001
	High - low	14.80	<0.001
	Low - medium	-12.42	<0.001
Senesced	High - medium	6.32	<0.001
	High - low	6.05	<0.001
	Low - medium	-2.21	0.074
High	Grazing lawn – Green live	4.73	<0.001
	Feces - Grazing lawn	8.19	<0.001
	Feces - Green live	12.92	<0.001
	Grazing lawn - Senesced	9.42	<0.001
	Green live - Senesced	4.69	<0.001
	Feces - Senesced	17.62	<0.001
Medium	Grazing lawn – Green live	0.20	0.997
	Feces - Grazing lawn	5.36	<0.001
	Feces - Green live	5.56	<0.001
	Grazing lawn - Senesced	3.51	0.004
	Green live - Senesced	3.31	0.007
	Feces - Senesced	8.87	<0.001
Low	Grazing lawn – Green live	0.56	0.945
	Feces - Grazing lawn	-0.98	0.764
	Feces - Green live	-0.22	0.996
	Grazing lawn - Senesced	0.28	0.992
	Green live - Senesced	-0.20	0.977
	Feces - Senesced	-0.43	0.973

Table S6

χ^2/F statistics and p -values for the effect of litter quality and quantity, respectively, on soil biogeochemical parameters. These models included data from microcosms to which no litter was added. Statistics for cumulative CO₂ flux are derived from a Type II ANOVA performed on linear mixed-effects models, including day of incubation as a fixed effect, and microcosm identity as a random effect. All other responses were analyzed with one-way ANOVAs. TIN = Total Inorganic Nitrogen; MBC = Microbial Biomass Carbon; DOC = Dissolved Organic Carbon

	Quality			Quantity		
	<i>df</i>	χ^2/F	<i>p</i>	<i>df</i>	χ^2/F	<i>p</i>
Cumulative CO ₂	4	28.07	<0.001	3	251.68	<0.001
TIN	4	3.42	0.019	3	35.06	<0.001
MBC	4	3.03	0.020	3	3.85	0.011
DOC	4	5.56	<0.001	3	10.24	<0.001

Table S7

Parameter results for decomposable C pool (C_a), decay constant (k), Mean Residence Time (MRT), and percent of total microcosm C that decomposed (C %) based on single-carbon pool model.

Treatment		C _a (mg C g ⁻¹ added C)	k (d ⁻¹)	MRT (d)	C (%)
Grazing lawn	High	18.98 ± 0.53	0.029 ± 0.0001	33.49	1.04
	Medium	13.78 ± 0.54	0.026 ± 0.0001	37.39	0.79
	Low	10.90 ± 0.54	0.022 ± 0.0001	44.95	0.64
Green live	High	18.81 ± 0.56	0.022 ± 0.0001	45.93	1.03
	Medium	14.02 ± 0.53	0.025 ± 0.0001	40.15	0.80
	Low	10.05 ± 0.54	0.021 ± 0.0001	47.91	0.59
Feces	High	47.49 ± 4.78	0.008 ± 0.0001	132.51	2.61
	Medium	22.95 ± 0.92	0.013 ± 0.0001	77.23	1.01
	Low	11.92 ± 0.55	0.018 ± 0.0001	56.28	0.70
Senesced	High	23.48 ± 0.76	0.010 ± 0.0001	98.81	1.29
	Medium	16.17 ± 0.63	0.013 ± 0.0001	74.59	0.92
	Low	10.43 ± 0.55	0.019 ± 0.0001	51.39	0.62

SUPPLEMENTAL FIGURES

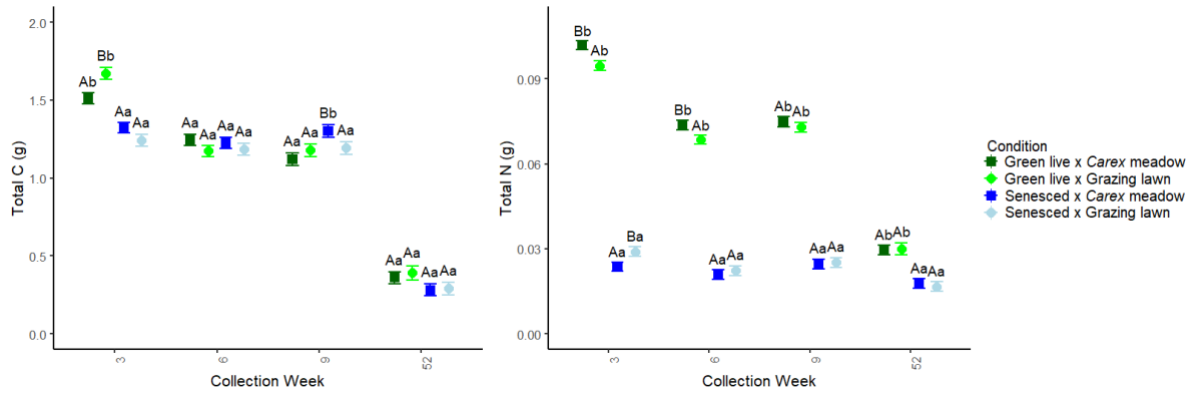


Figure S1. a) Total amount of C remaining and b) total amount of N remaining on each decomposition day by treatment type. Capital letters denote significant differences among habitats within litter groups, while lowercase letters denote significant differences among litter types within habitats.

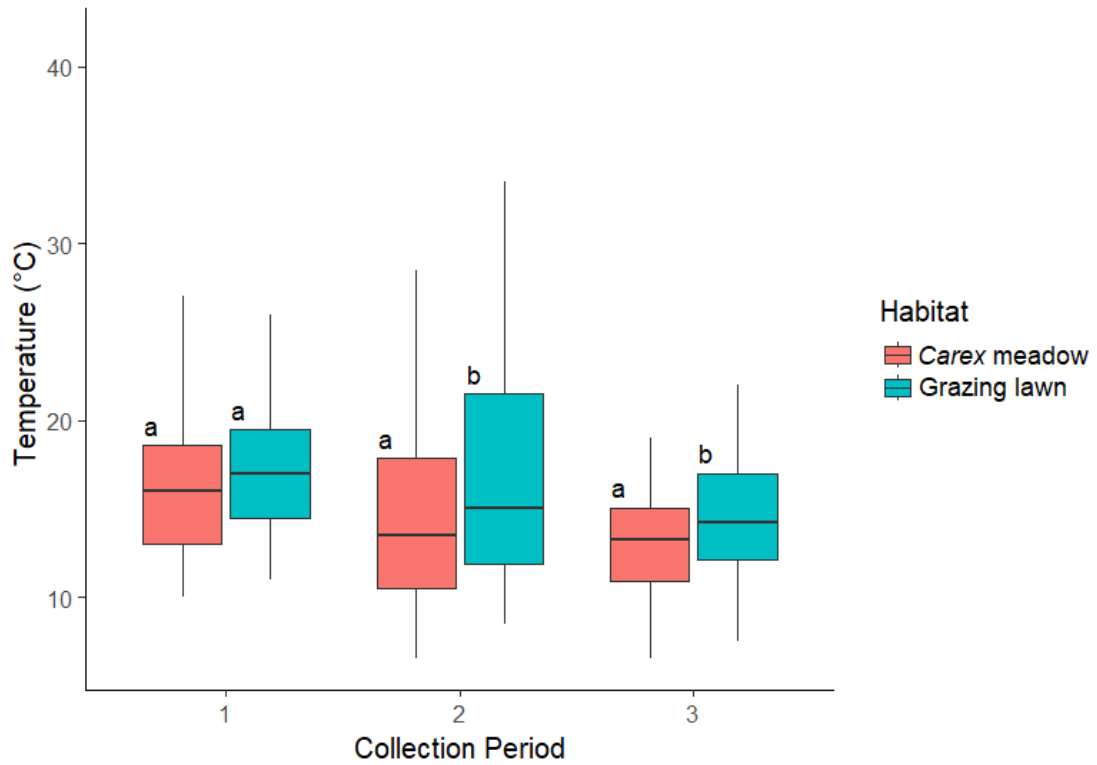


Figure S2. Daily temperature at solar noon for each habitat type during each collection period. Letters denote habitat groups that are significantly different within each collection period.

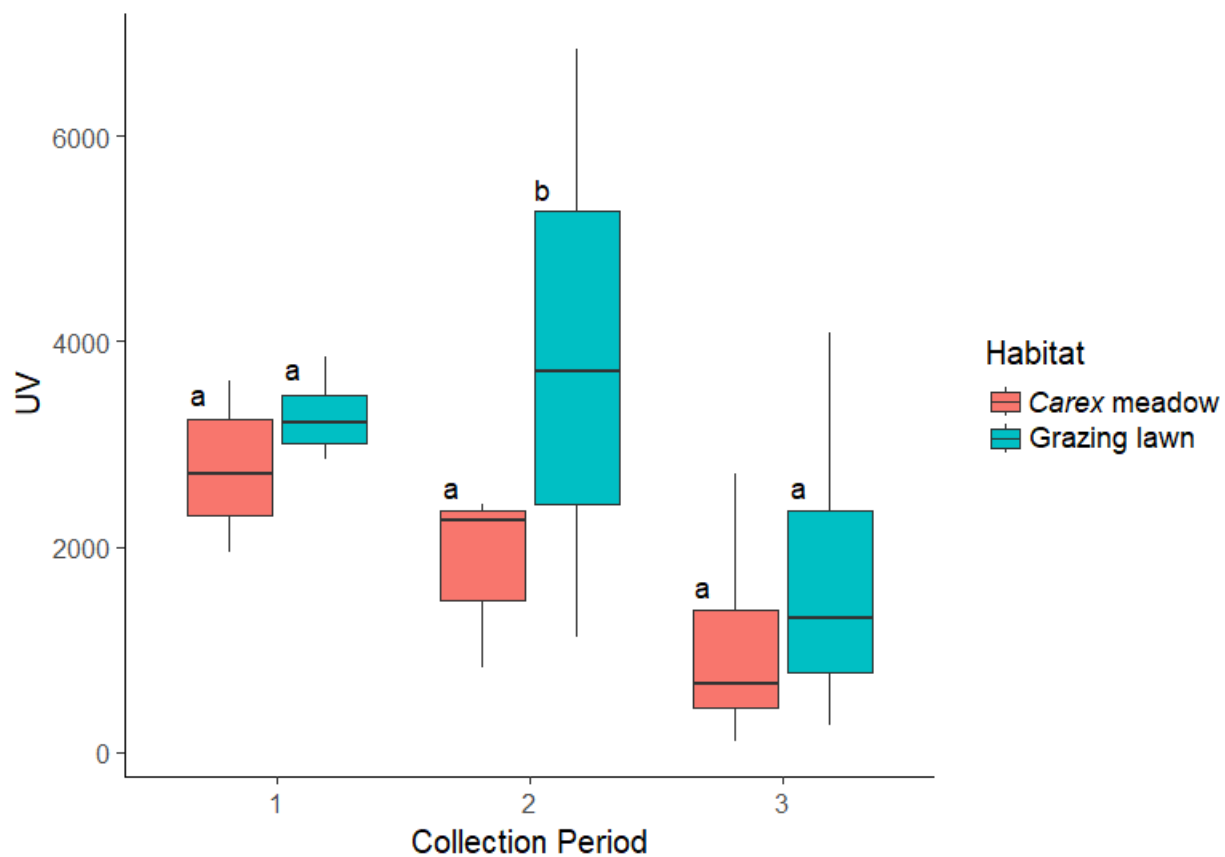


Figure S3. UV radiation for each habitat type during each collection period. Letters denote habitat groups that are significantly different within each collection period.

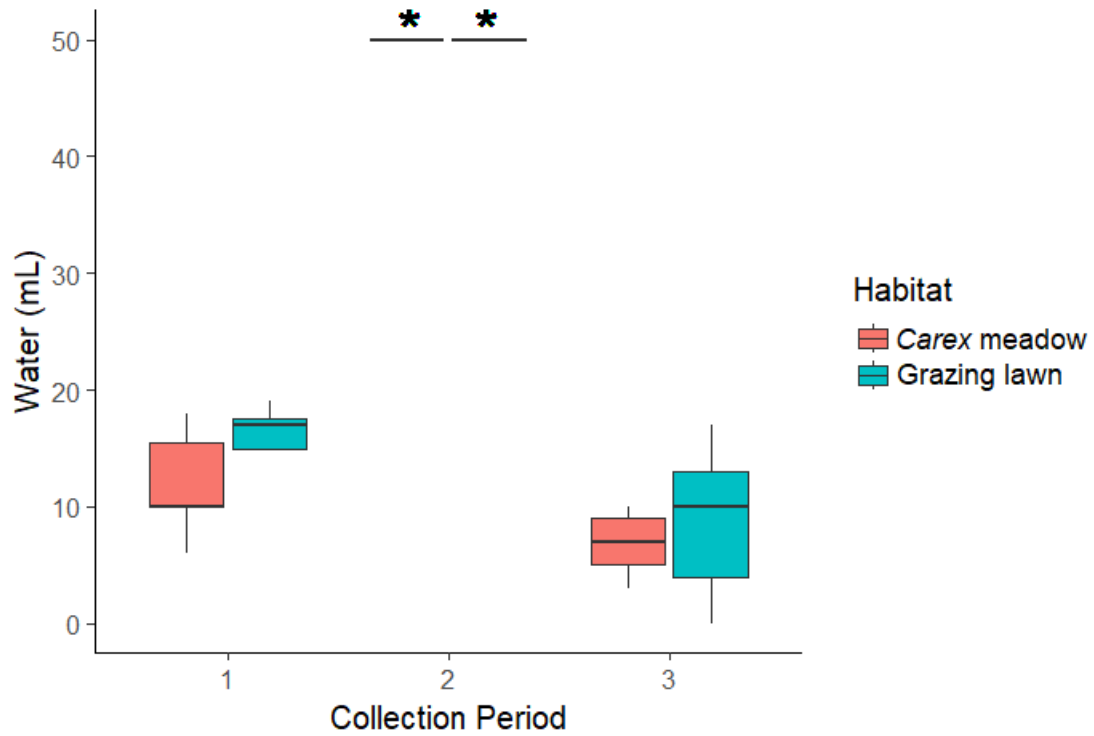


Figure S4. Water volume recorded in Falcon tubes installed below the ground. *For collection period 2, water volume exceeded the capacity of many tubes, and therefore water volume was recorded at maximum tube capacity (50 mL) if the tube overflowed.

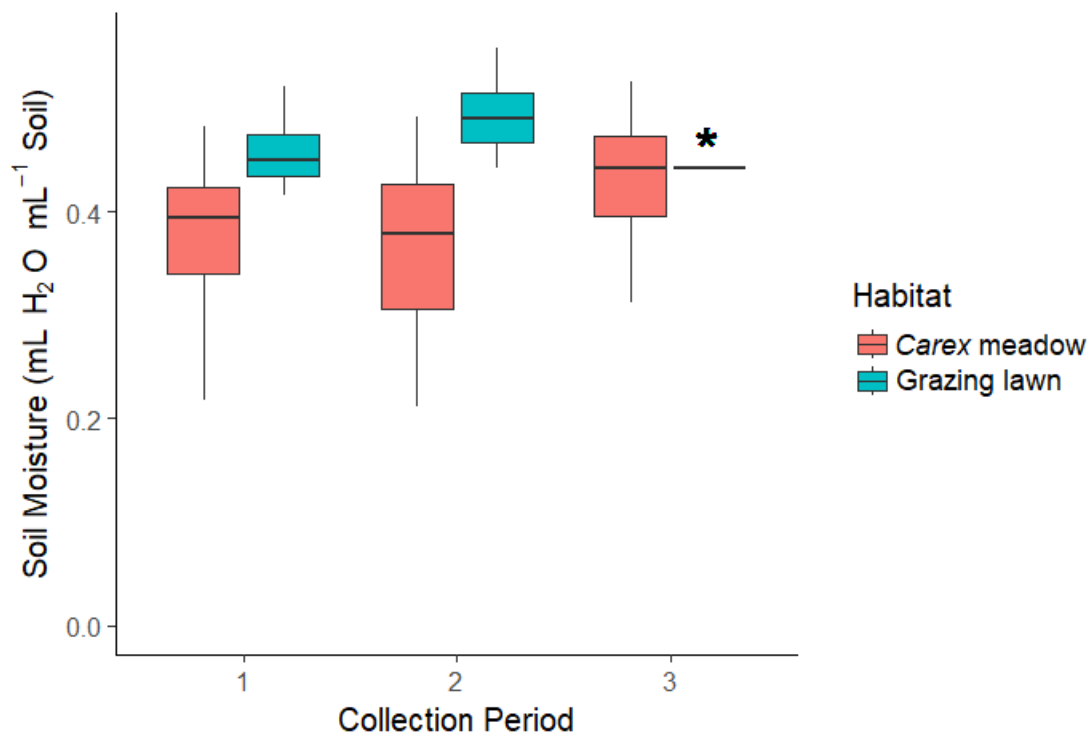


Figure S5. Soil moisture recorded in nearby reference plots during each collection period. *No data was collected for grazing lawns in collection period 3 due to inundation of measurement instruments.

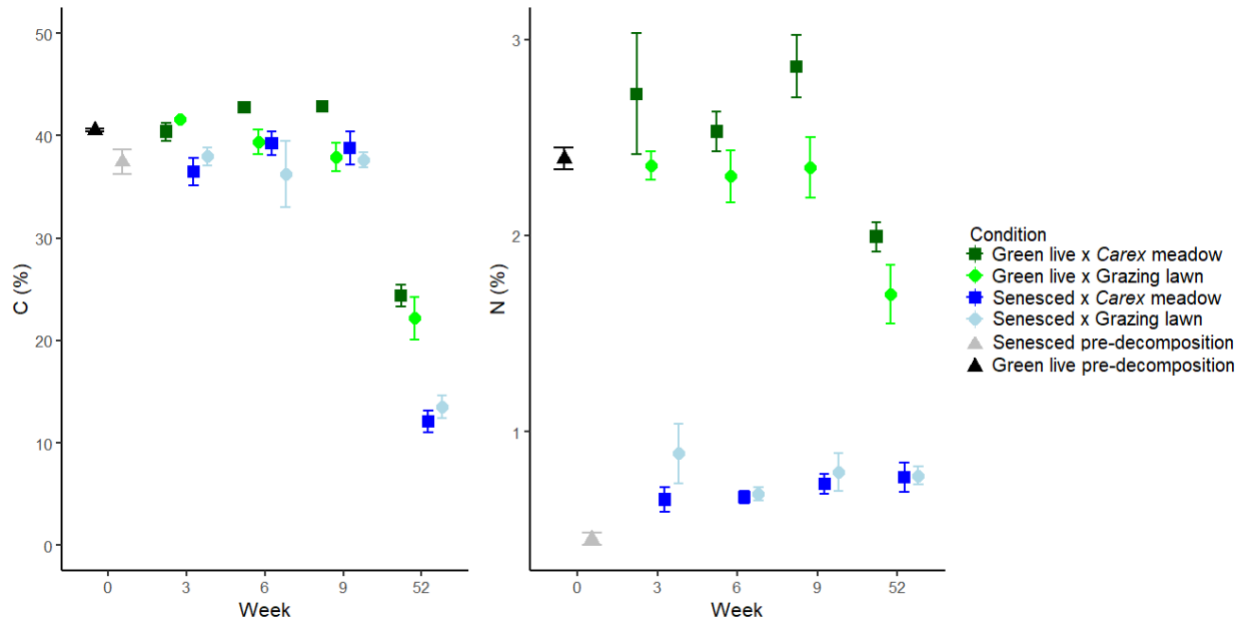


Figure S6. a) Percent C and b) percent N differences among habitat and litter type combinations.

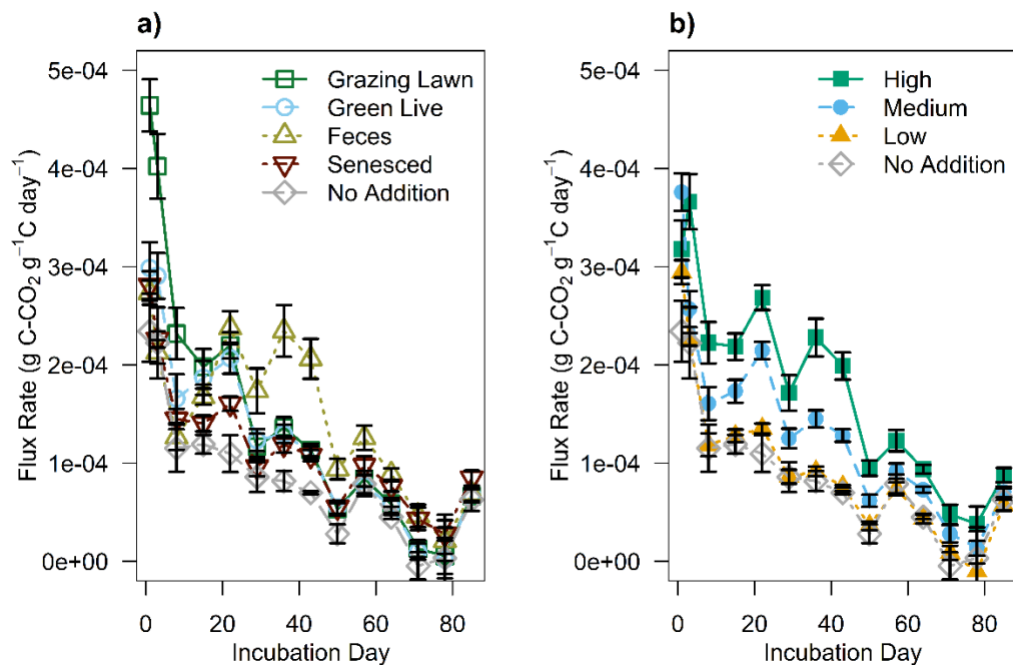
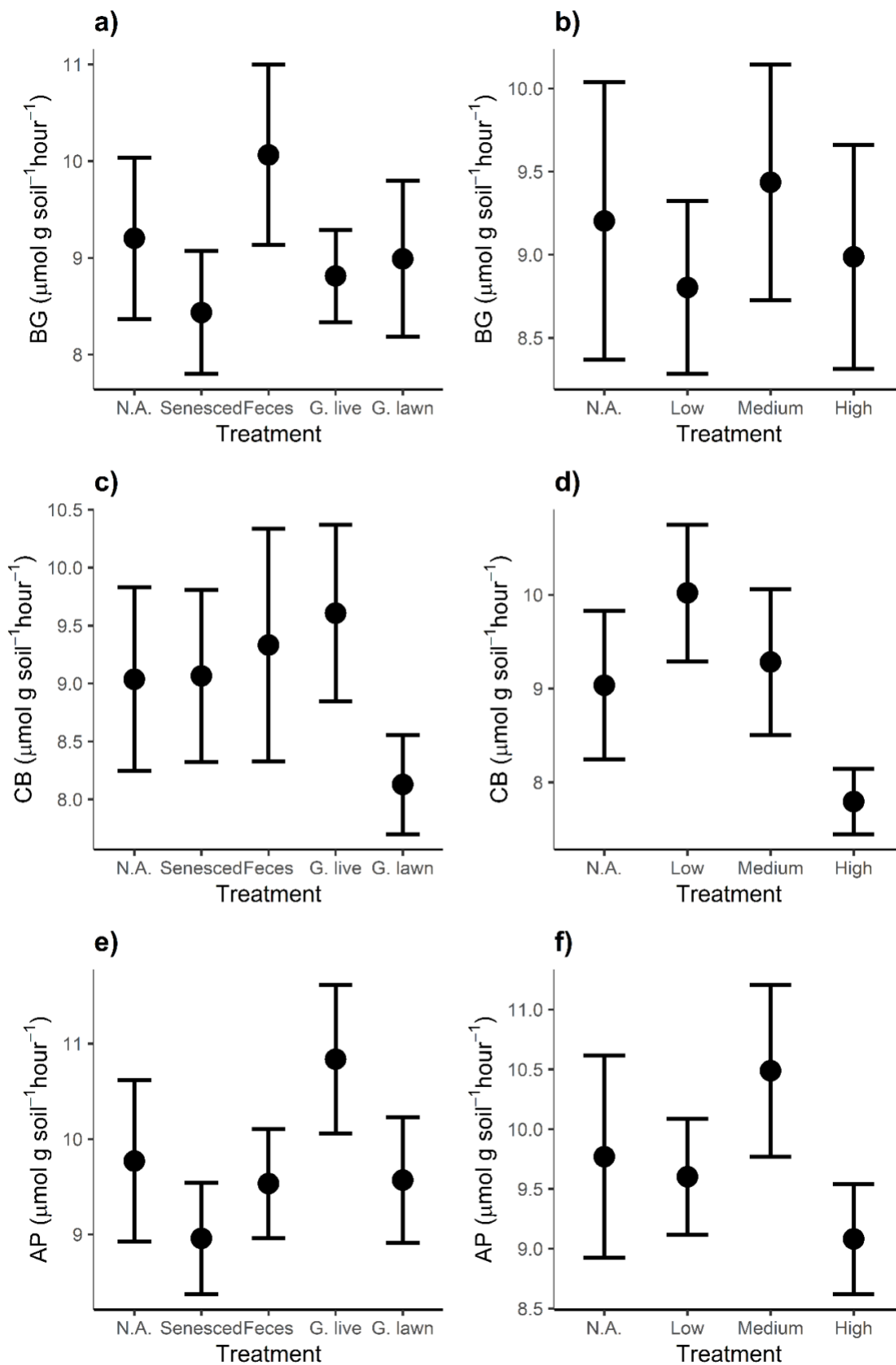


Figure S7. Mean CO₂ flux rates (\pm SE) for treatment types a) by litter quality and b) by litter quantity over time. Microcosms with no additions were not included in linear mixed effects modeling for fluxes, but are included in the figures for comparison. These values are standardized to the g C contained in each microcosm, inclusive of the C added from treatments.



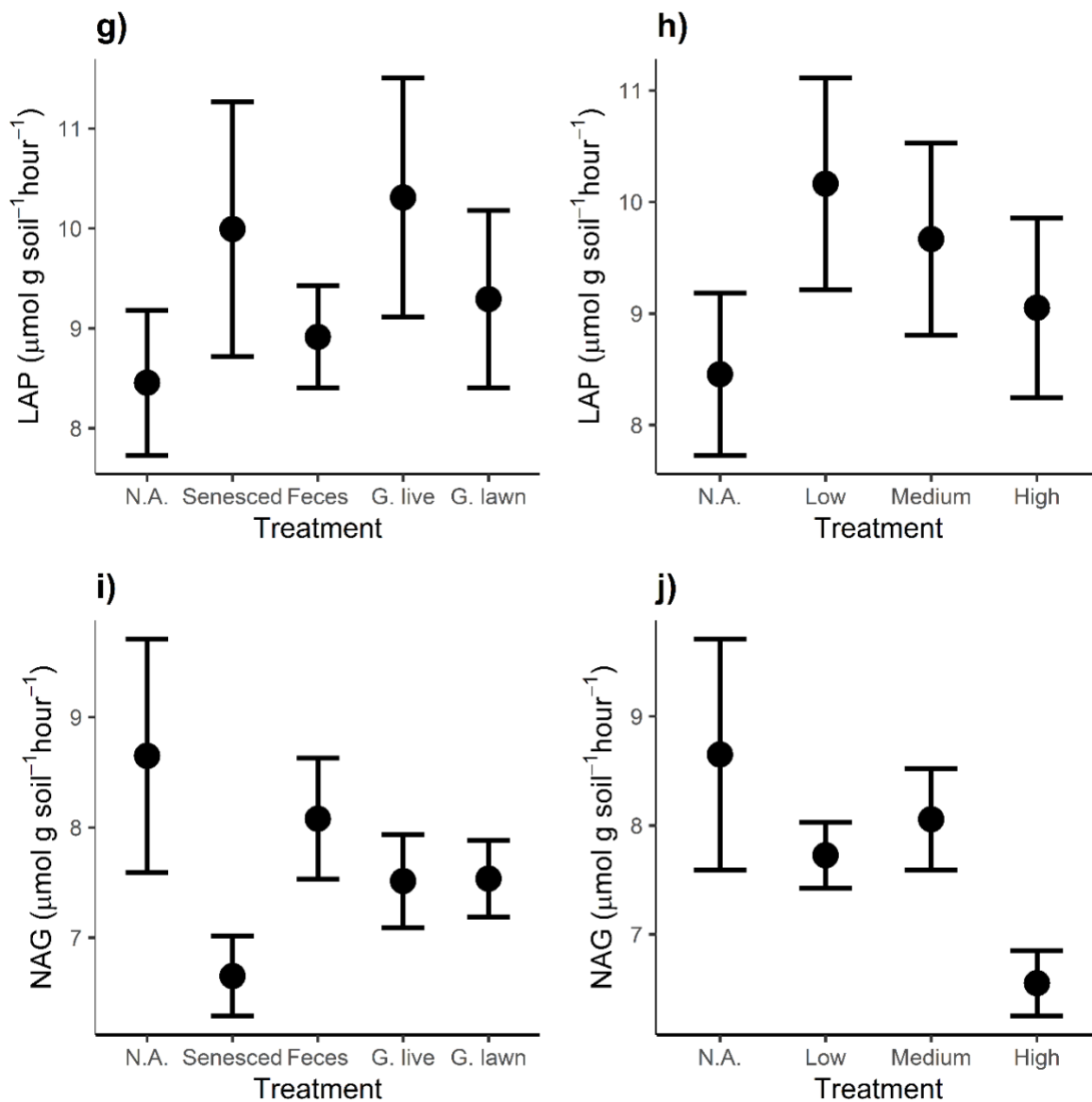


Figure S8. Mean enzyme activities (\pm SE) for quality and quantity treatments. Microcosms with no additions were not included in linear models for enzyme activities, but are included in the figures for comparison.

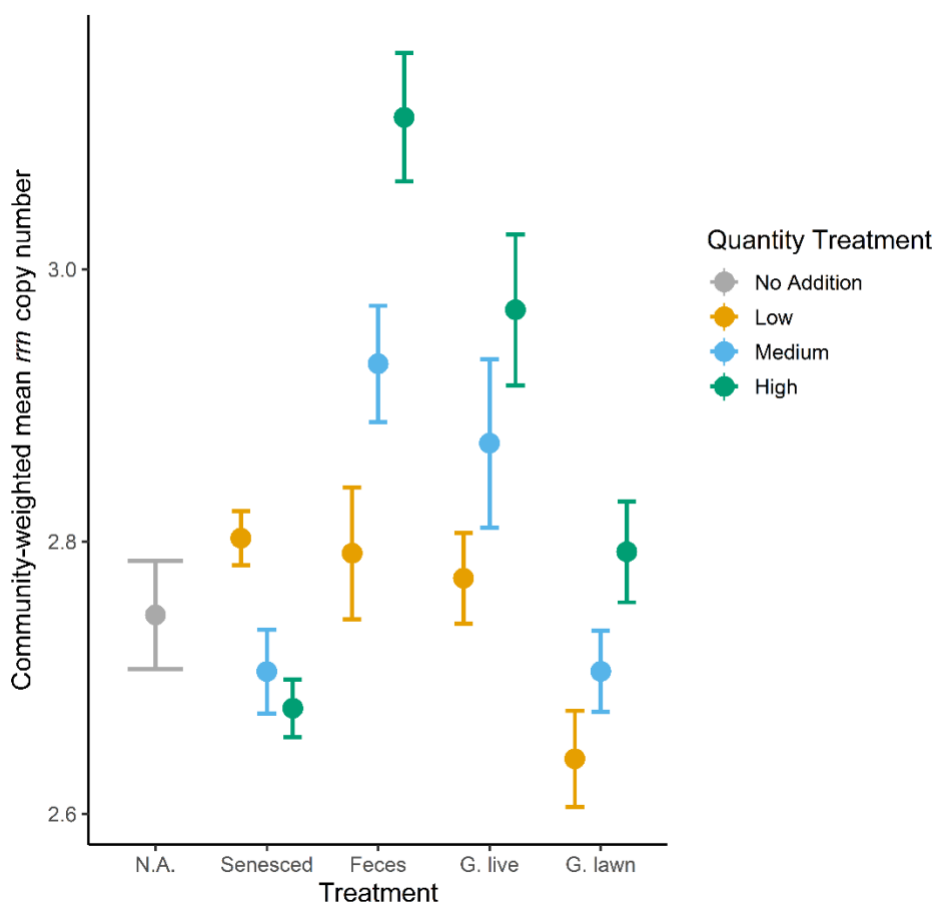


Figure S9. Community-weighted mean *rrm* copy numbers (\pm SE) for quality and quantity treatments. Microcosms with no additions were not included in linear models, but are included in the figure for comparison.

Figures S10-S18. Transformed abundance of bacterial phyla that differential abundance analysis revealed to be significantly affected by litter quality and quantity treatments. Data is center log-ratio transformed. Statistically significant phyla were *Bacteroidetes*, *Firmicutes*, *Proteobacteria*, *Acidobacteria*, *Planctomycetes*, *Gemmatimonadates*, *FBP*, *ODI*, and *WS3*. Points represent abundance measured in each sample and boxplots represent their distribution. Uppercase letters denote pairwise significant differences between treatment combinations within each sub-panel. Pairwise differences were assessed using Wilcoxon rank sum tests. Pairwise differences were considered significant at $\alpha=0.05$ after a Benjamini-Hochberg adjustment for multiple comparisons.

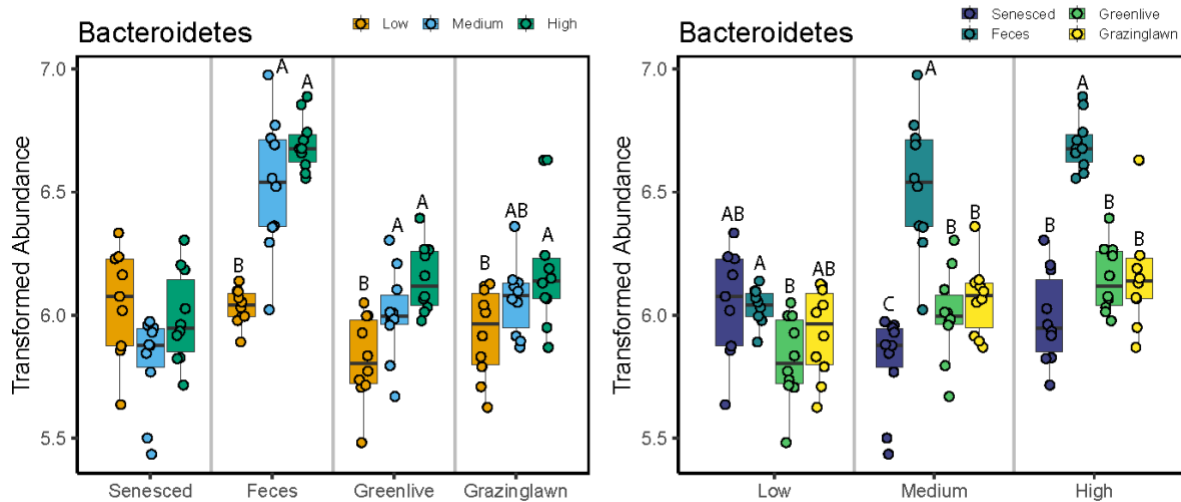


Figure S10

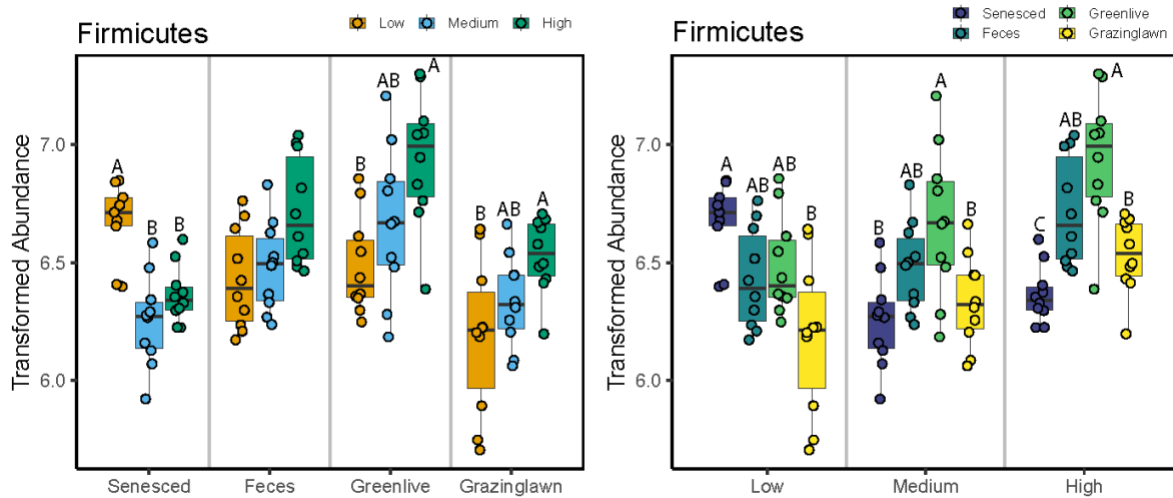


Figure S11

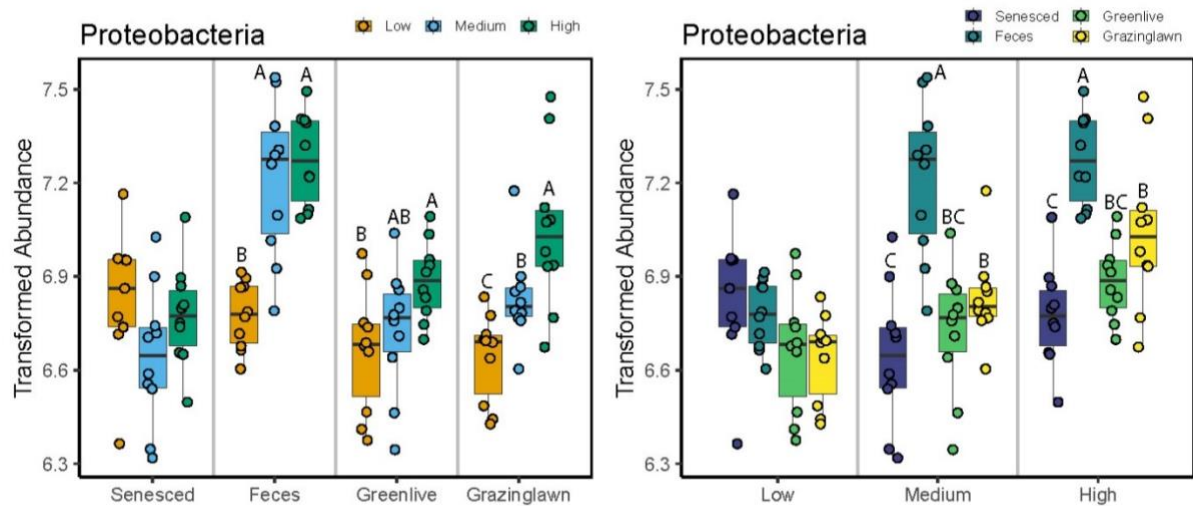


Figure S12

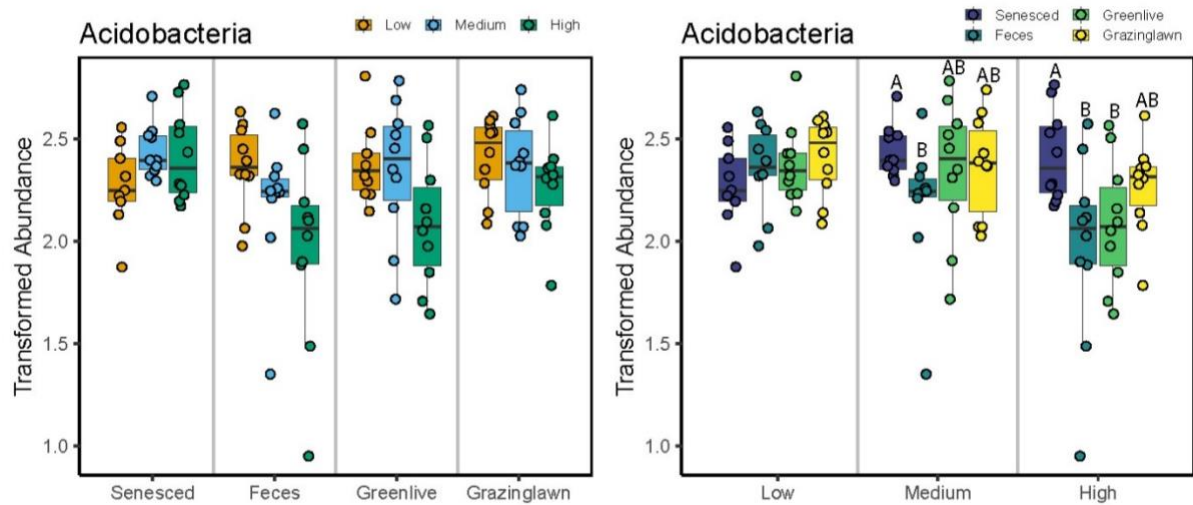


Figure S13

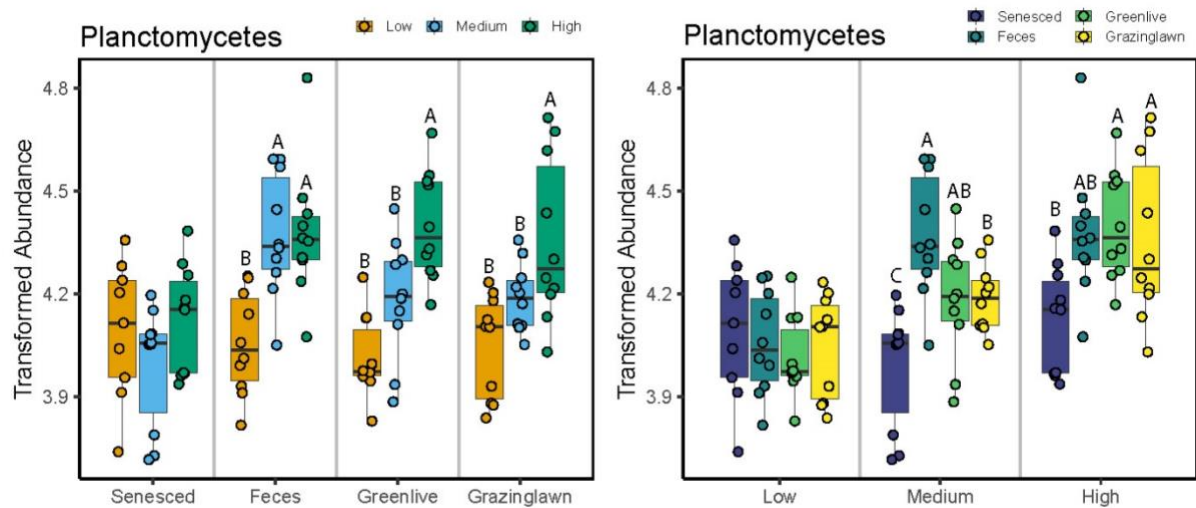


Figure S14

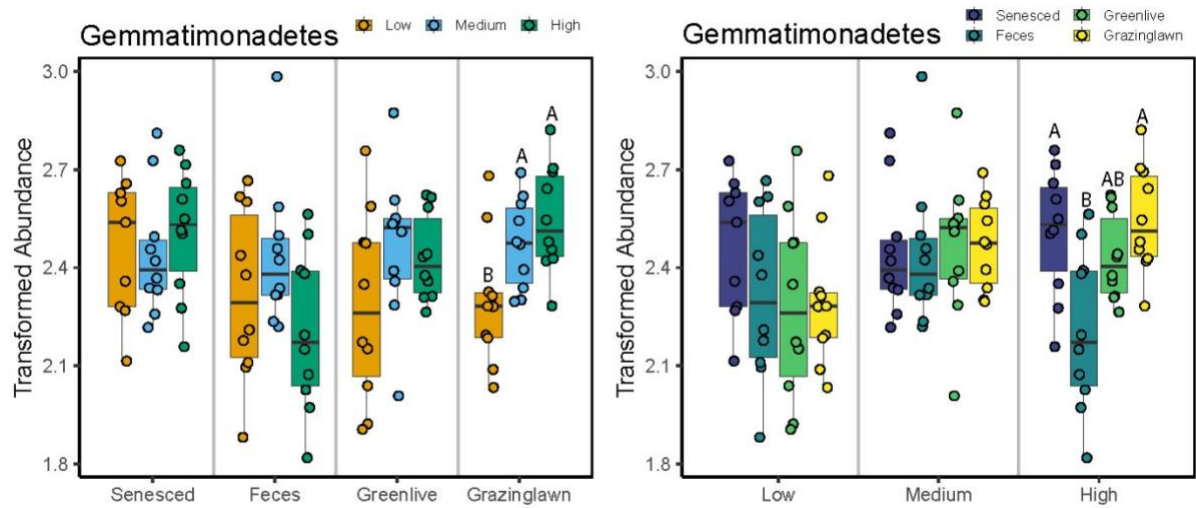


Figure S15

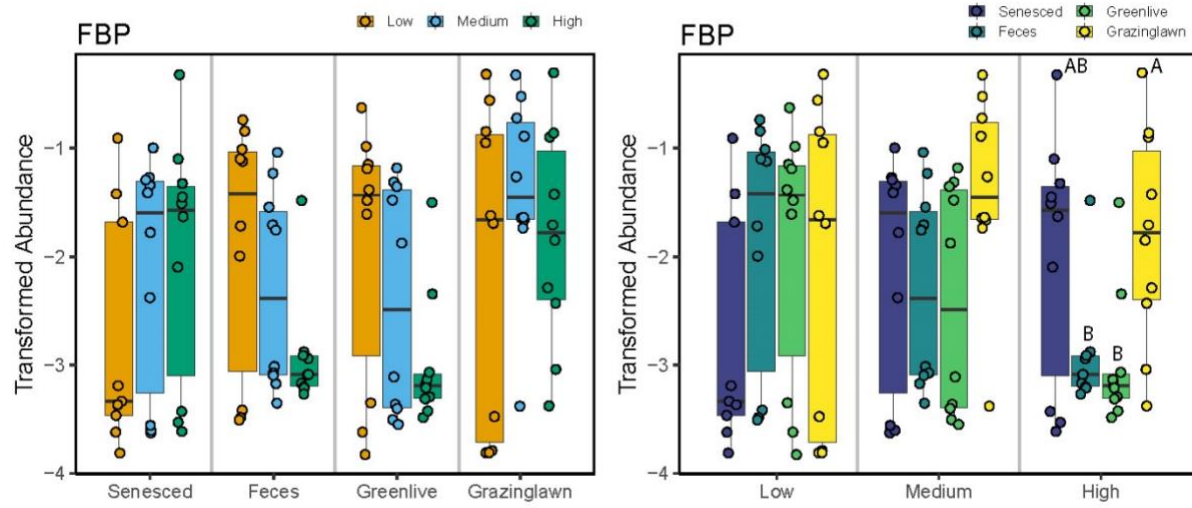


Figure S16

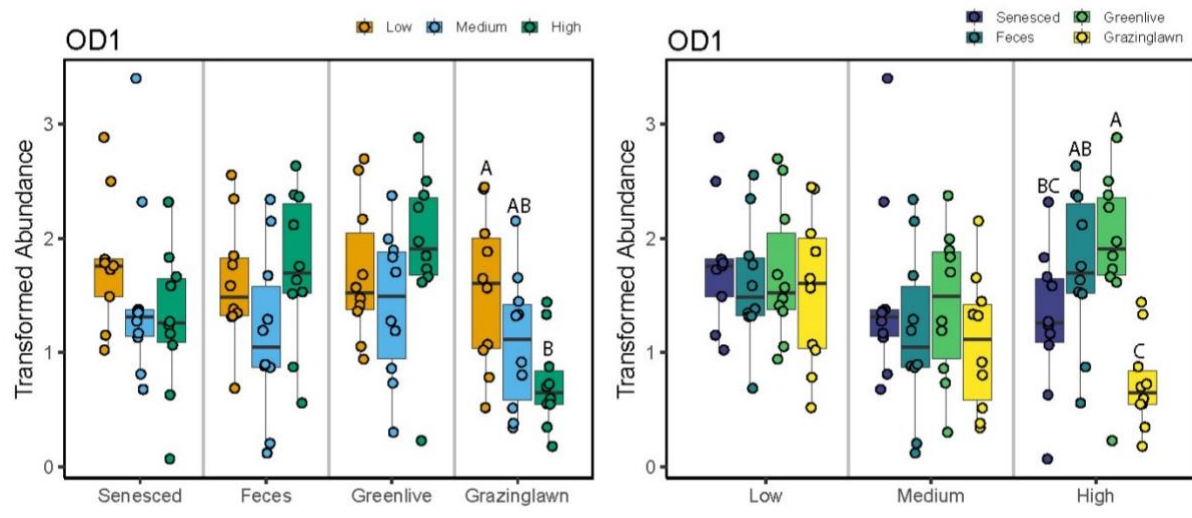


Figure S17

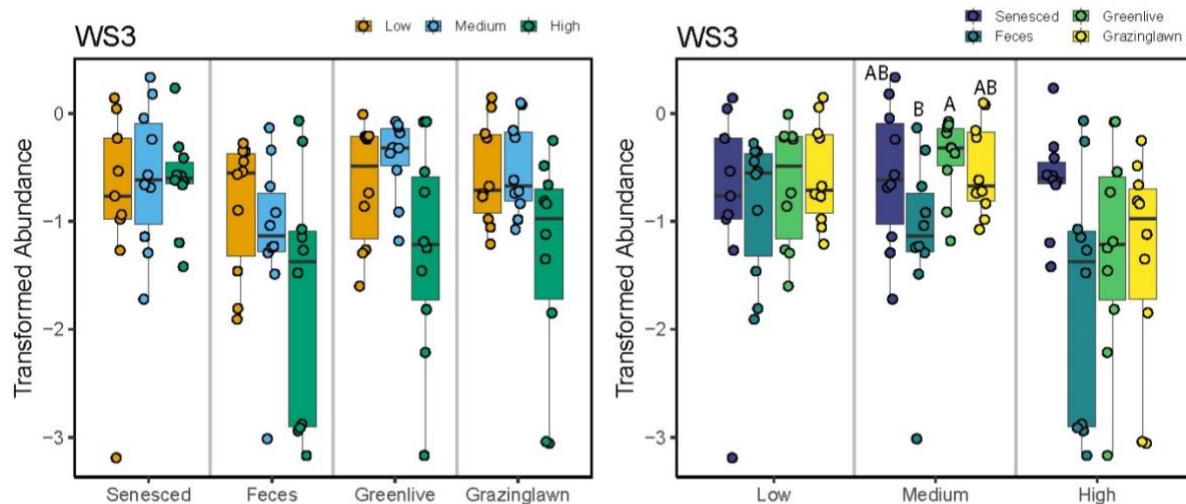


Figure S18

Figures S19-S25. Transformed abundance of fungal classes that differential abundance analysis revealed to be significantly affected by litter quality and quantity treatments. Data is center log-ratio transformed. Statistically significant classes were *Peizomyces*, *Dothideomyces*, *Tremellomyces*, *Microbotryomyces*, *Agaricostilbomyces*, *Mucoromyces*, and *Sordariomyces*. Points represent abundance measured in each sample and boxplots represent their distribution. Uppercase letters denote pairwise significant differences between treatment combinations within each sub-panel. Pairwise differences were assessed using Wilcoxon rank sum tests. Pairwise differences were considered significant at $\alpha=0.05$ after a Benjamini-Hochberg adjustment for multiple comparisons.

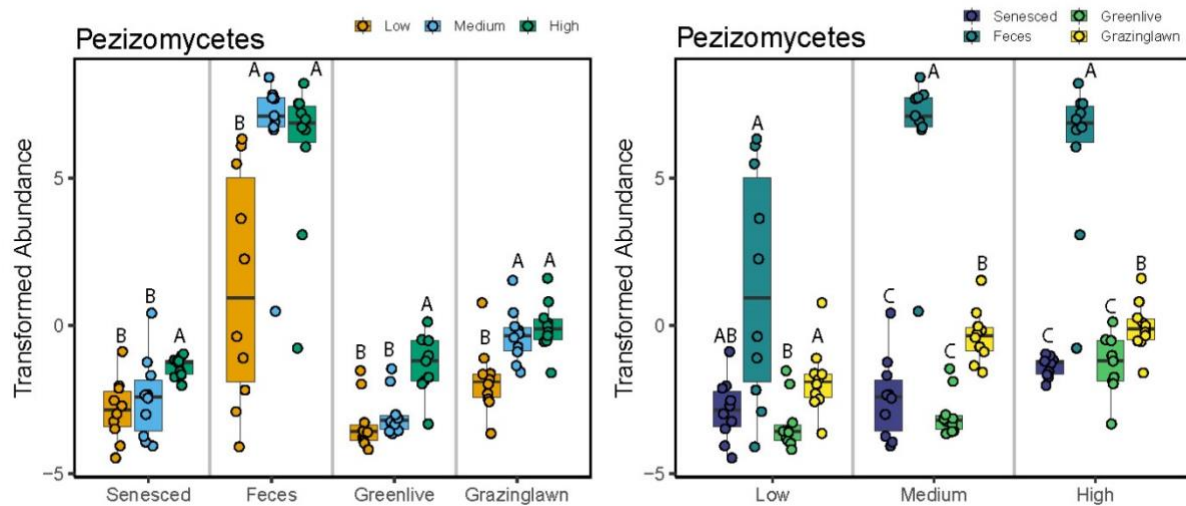


Figure S19

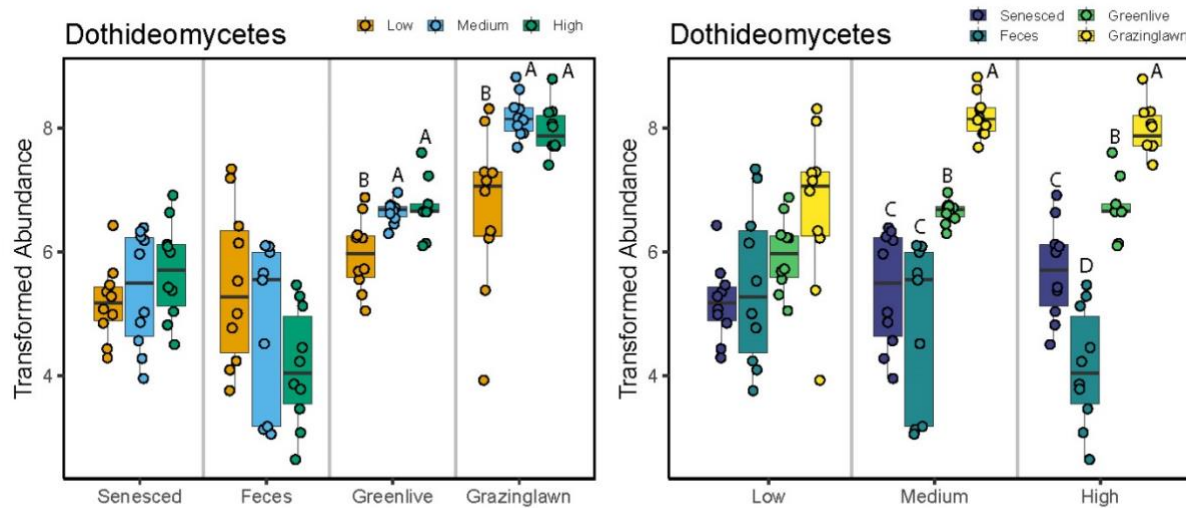


Figure S20

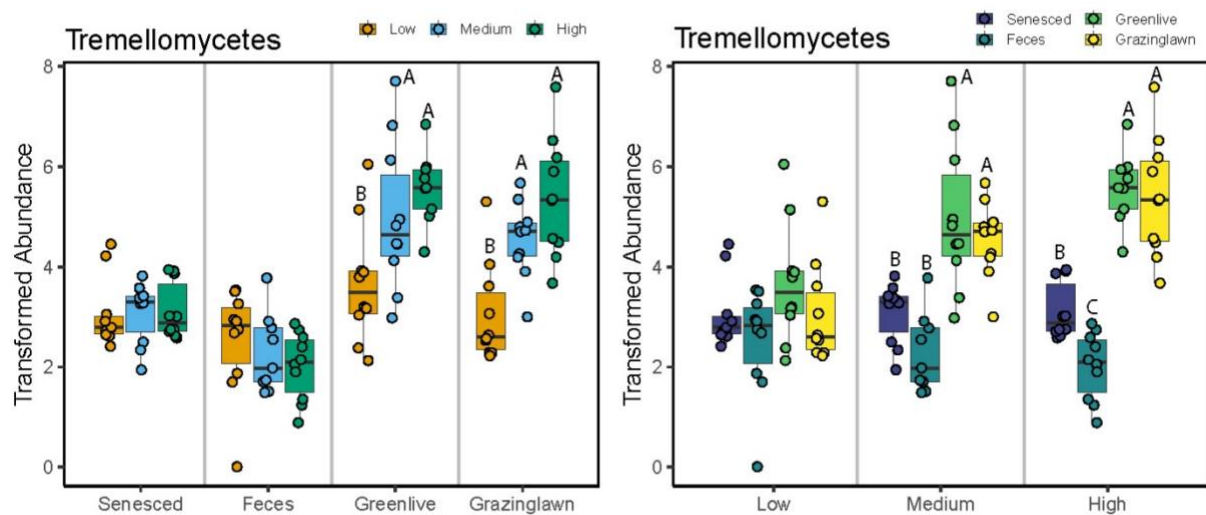


Figure S21

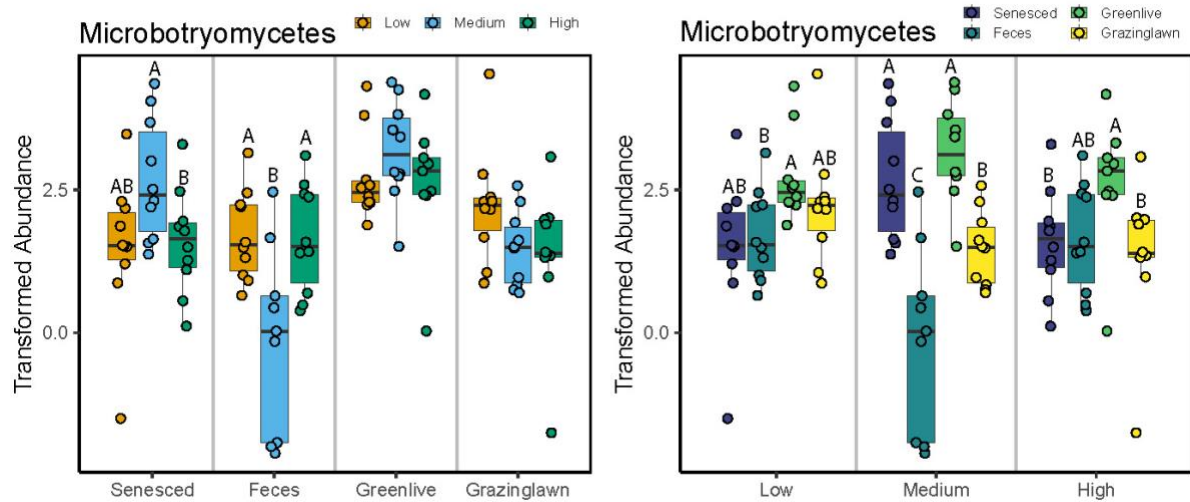


Figure S22

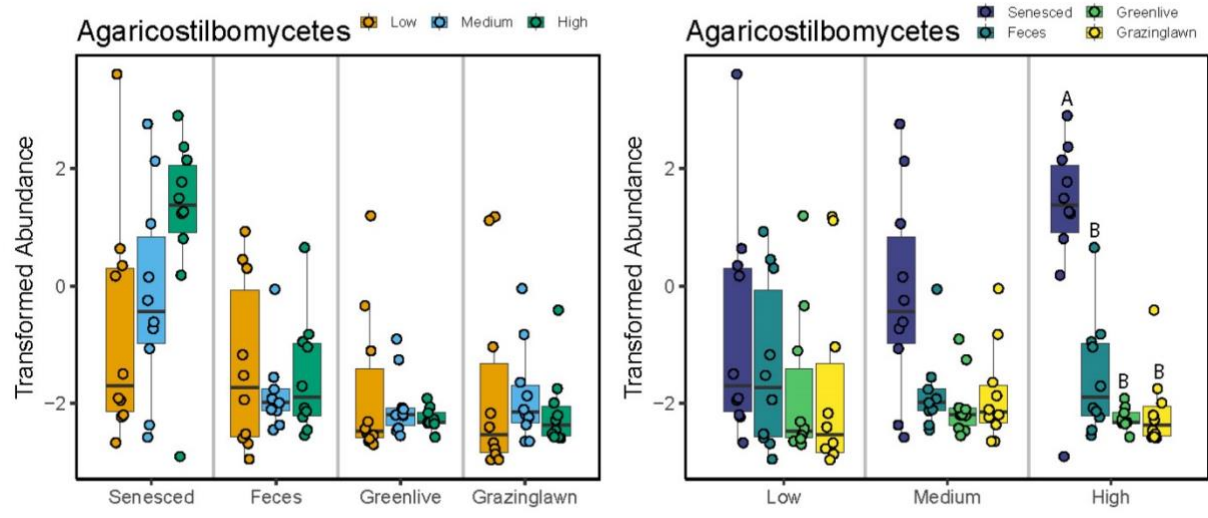


Figure S23

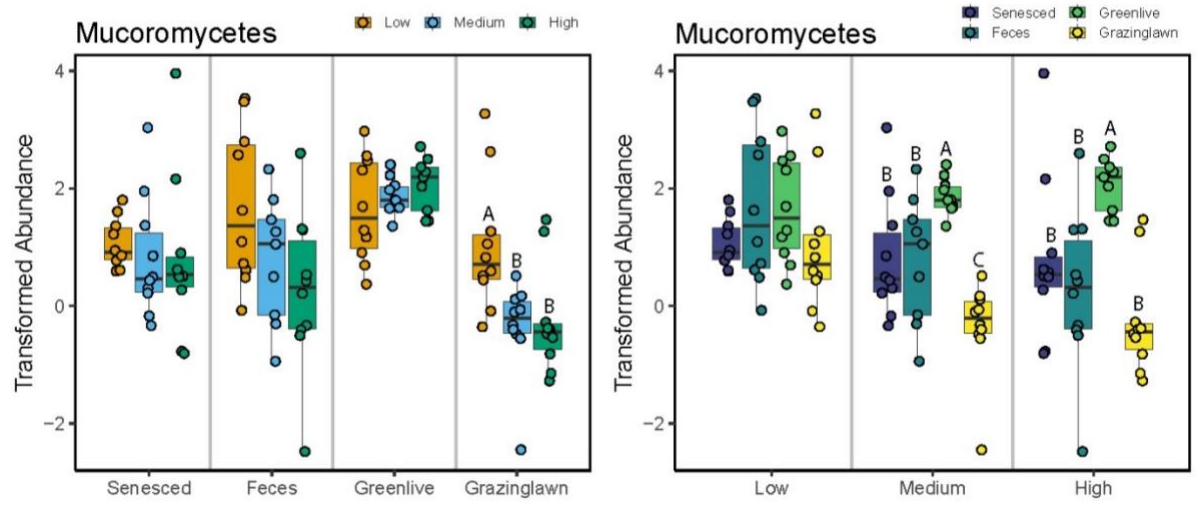


Figure S24

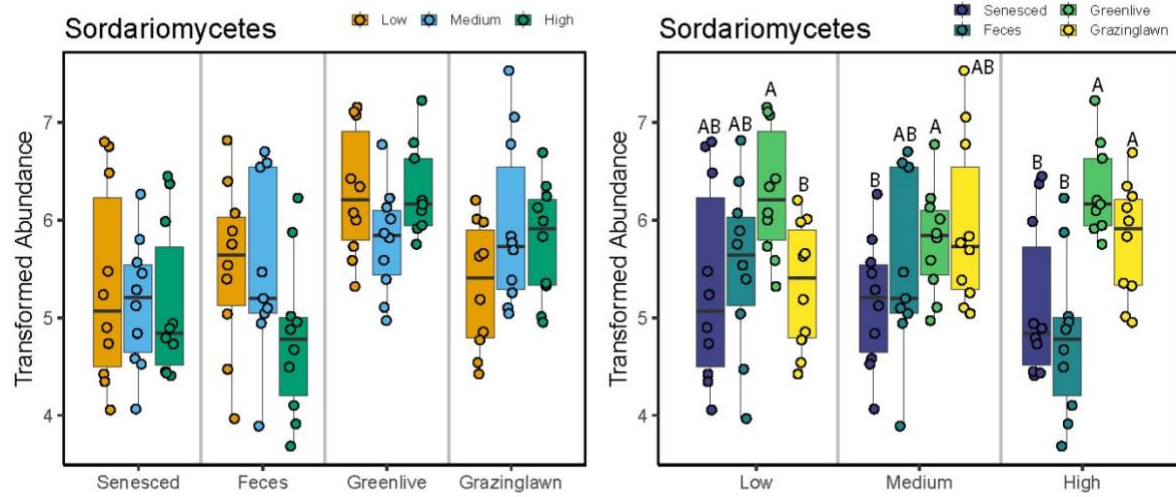


Figure S25