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Effects Of Increasing Deciduous Shrub Litter On Ecosystem Functioning In Alpine Tundra

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EFFECTS OF INCREASING DECIDUOUS SHRUB LITTER ON ECOSYSTEM
FUNCTIONING IN ALPINE TUNDRA

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Dedication

To my parents Jesus and Maria Benhumea

EFFECTS OF INCREASING DECIDUOUS SHRUB LITTER ON ECOSYSTEM
FUNCTIONING IN ALPINE TUNDRA

by

ALEJANDRO EMMANUEL BENHUMEA, B.S.

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Abstract

Rising temperatures due to global warming have resulted in rapid environmental changes in northern environments, resulting in an increase in deciduous shrub growth which has the potential to alter soil ecosystem properties and processes. In order to address some potential mechanisms by which shrubs alter ecosystem properties and processes, we designed an experiment which separated the effects of physical shrub presence and the effects of litter quantity in a fully factorial experiment on a north facing alpine plateau in the southwest Yukon, Canada. Specifically, we asked the following questions: What are effects of shrub litter, independent of shrub presence, on (1) physical ecosystem properties, (2) soil nutrient content and availability and (3) microbial processes. I measured multiple response variables including various physical soil properties (soil moisture and temperature), measures of soil nutrient content (total C and N, available nutrients) and rates of primarily microbially controlled properties and processes (microbial biomass, litter decomposition and extracellular enzyme activity). We found shrubs increased soil temperatures in winter months and decreased them during the summer. Shrubs had few effects on soil nutrients, but their presence increased microbial biomass, and respiration rates, and reduced rates of decomposition. Litter manipulations had a stronger effect than shrubs on many variables, resulting in increased soil moisture, available nutrients, %C and %N, microbial biomass, and extracellular enzyme activity. Our results indicate shrub encroachment will influence available nutrients directly by changing litter inputs, with subsequent effects on microbial processes. Predicted longer-term impacts on carbon mineralization were not evident after 2 years of manipulations, and may require a longer time before effects are shown in the soil carbon pool.

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Introduction

Climate Change and Arctic Ecosystems

Since the 1950s, warming of the atmosphere and oceans has been observed to be occurring at an unprecedented rate (IPCC 2014), with the earth's land and ocean surface temperature warming ca 0.6°C over the past 100 years (Walther et al. 2002). This rise in temperature has been linked to an increase in greenhouse gas concentrations of methane, nitrous oxide, and carbon dioxide (CO₂), resulting from increases in anthropogenic emissions (IPCC 2014). Warming temperatures and increases in CO₂ have been linked to a multitude of effects globally, from changes in precipitation, extreme weather events, species range shifts, and ocean acidification (IPCC 2014).

While climate change is a global phenomenon, regional responses vary. The Arctic, which is warming approximately twice as fast as other areas of the globe (Richter-Menge et al. 2016), and areas of high latitudes and mountainous regions of the world are anticipated to be most affected by climate warming (Diaz and Eischeid 2007). Heat for biological use is limited in alpine and arctic tundra environments (Billings and Mooney 1968), and vegetation is adapted to an ecosystem, which has freezing conditions for much of the year, so they are particularly sensitive to variations in temperature (Bunn et al. 2007). One of the most frequently reported changes in arctic ecosystems resulting from climate warming is the reduction of sea ice, both in extent and thickness, and the impacts of this are diffuse with ramifications for the Arctic's heat allowance (Tape et al. 2006). We are also seeing rapid changes in alpine environments. Average temperature for the warmest month in alpine tundra over western areas of the U.S. were approximately 8.5°C - 9.5°C towards the beginning of the 20th century, increasing temperatures have since surpassed the 10°C boundary/classification of these environments (Diaz and Eischeid 2007). The IMAGE

(integrated model to assess the global environment) model estimates alpine tundra to have the greatest areal reduction through biome conversions compared with other ecosystem types, with potential changes to species composition and soil function (Chapin et al 2001).

Greening of the Arctic and Shrubification

These changes in climate have resulted in marked changes in the vegetation of high latitude and high altitude environments, including changes in the timing and length of growing seasons, as well as in the productivity of these communities. For example, a temporal shift in the growing season of plants has been observed with earlier spring budburst and delayed onset of autumn abscission (Lucht et al. 2002). Other responses of these temperature-limited ecosystems to warming include increased plant growth and establishment with growing seasons advancing by 5-13 days (Bunn et al. 2007). There are also spatial shifts in the establishment of plants including recorded tree establishment in alpine areas moving upward (Hughes 2000), as well as alpine grassland increasing its elevational range (Cannon et al. 2007). This change in vegetation highlights the sensitivity of these temperature limited ecosystems in response to warming.

Among the changes observed in arctic and alpine environments is a “greening of the Arctic”, that is an increase of vegetation around the circumpolar region. There are many lines of evidence for this including detection by Advanced Very High Resolution Radiometer (AVHRR) of high latitude ecosystems using normalized difference vegetation index data sets (NDVI) (Myneni et al. 1997; Jia, Epstein, and Walker 2009; Goetz et al. 2005; Verbyla 2008). A large component of this greening is suggested to be the expansion in deciduous shrub growth (termed ‘shrubification’), which has been documented via satellite and aerial photography in arctic and alpine tundra ecosystems (Jia et al. 2009). A review of research on shrubification describes observational evidence of shrub expansion over the past century in a number of areas of high

latitude or altitude including Alaska, the Canadian Arctic, Greenland, the European Arctic, the Russian Arctic, and many alpine regions (Myers-Smith et al. 2011).

The encroachment of deciduous shrubs on tundra has the potential to alter a wide variety of ecosystem properties. For example, shrubs have the potential to alter soil heat flux through changes in albedo (Williamson et al. 2016; Sturm et al. 2005). Additionally, shrubs accumulate substantially more snow in winter than the surrounding tundra due to the erect morphology of shrubs, which has potential effects on both soil hydrology and soil thermal regimes; a thicker snow layer acts as an insulator in winter increasing subnivean temperatures considerably (Sturm et al. 2000). While shrubs accumulate more snow, their long dark branches facilitate faster snow melt in the spring due to the decrease in albedo (Marsh et al. 2010). Resulting changes in soil temperature is likely to affect microbial activity under shrubs, including changes in nutrient mineralization rates (DeMarco et al. 2011). There are an increasing number of studies examining the impacts of shrub encroachment on ecosystem function reviewed in (Myers-Smith et al. 2011; Naito and Cairns 2011; Formica et al. 2014).

In addition to their influence on snow accumulation, shrubs may also affect the biophysical environment through their litter production. Deciduous shrubs produce substantially more leaf litter each year than the other dominant vegetation types in tundra, evergreen shrubs and graminoids, both, which retain leaves and litter (as standing dead) for multiple growing seasons; Shrub tundra has been demonstrated to have 2-3 times higher litter production than nearby tundra types in northern Alaska, resulting in a thick litter layer under shrub tundra (McLaren, unpublished data). This thick layer of litter may influence ecosystem properties independently of the presence of the shrubs. For example, shrub litter may insulate the soil, altering temperature and moisture regimes, which likely affect microbial processes that determine both decomposition and nutrient

cycling rates (Blok et al. 2011). In addition to changes in soil temperature and moisture, shrub litter from *Betula nana* also has a different chemical composition than the litter of other tundra species, with higher nitrogen and lignin content (McLaren et al. 2017). *Betula glandulosa* also contains a variety of compounds such as phenolics, organic acids (Prudhomme 1983), alkaloids, and volatile oils (Groot et al. 1997), which may slow decomposition. The species specific effects on changes in soil inputs, that is the quantity and quality of litter, may also influence microbial activity, including the production of extracellular enzymes (McLaren et al. 2017).

Removal Experiments

Ecosystem properties are governed by the interaction between the functional traits of the organisms within that ecosystem and abiotic factors such as climate, soil type, and geography (Hooper et al. 2005). Removal experiments allow insight into the role of different types of plants in the functioning of ecosystems (McLaren and Turkington 2010; Kotowski et al. 2013; Inouye 2006; Gundale et al. 2012). For example, shrub removal experiments can be used to assess the impacts of shrubs in arctic and alpine ecosystems. Studies conducted in continuous permafrost in Northeast Siberia, Russia found when shrubs were removed from plots the depth of the soil active layer increased (Blok et al. 2010), with elevational changes indicating soil subsidence with a deeper thaw depth (B. Li et al. 2017), resulting in a water logged depression (Nauta et al. 2014). Removal of shrubs also increased plant biomass N in the remaining plants in a boreal zone in Northern Sweden (Gundale et al. 2012). Removal of moss in a shrub understory increased evapotranspiration to a lesser degree in dense shrub plots, indicating their importance in mediating ground heat flux (Blok et al. 2011). Willow shrub removal in restoration projects increased establishment of target species such as grasses and forbs in a fen wetland (Kotowski et al. 2013).

Shrub removal experiments have highlighted their role on physical ecosystem properties, soil formation, and structure.

Litter Manipulation Experiments

Understanding shrub-litter feedbacks is critical in light of the dramatic increases in shrub abundance in arctic and alpine tundra ecosystems. Conventionally, plant litter may be defined as “dead plant material of small size lying loose on the ground” (Facelli and Pickett 1991). Plant litter, however, can encompass a variety of material from woody debris, leaves, and senesced plant tissue, such as that of perennial grasses, which remains standing when dead (Sayer 2006). The various characteristics of these different types of litter, such as their quality and quantity, affect decomposition rates and may also in turn alter soil nutrients, carbon cycling, microclimate, and soil physical properties (Sayer 2006). For example, the physical effects of accumulated litter form a barrier on the soil surface that can intercept light, reducing evaporation from the soil, as well as shade seeds and seedlings (Facelli and Pickett 1991; Sayer 2006). Litter also has the potential to alter soil physical properties such as water infiltration rates and retention of water in soils (Walsh and Voigt 1977), invariably affecting soil erosion (Sayer 2006). As plant communities are changing in response to global change (Xu, Liu, and Sayer 2013), the quantity and quality of litter inputs are changing as well, thus the need for litter manipulation experiments in assessing this change is evident.

Some of the most well-known litter manipulation experiments are the Detritus Input, Removal and Transfer (DIRT) experiments. Based off experiments started at the University of Wisconsin Arboretum in the 1960s (Nielson and Hole 1963), the DIRT network was established in the mid-1990s, focusing on effects of litter on the formation of soil organic matter via plant litter inputs above and below ground. The DIRT experiments are comprised of 4 primary treatments:

(1) doubling of leaf litter/wood inputs, (2) exclusion of litter inputs, and (3) removal of root litter inputs and (4) no inputs (above or below ground). Studies based off the DIRT framework describe multiple ecosystem impacts of the imposed litter manipulations. For example, removing root litter inputs has been shown to increase dissolved organic nitrogen and nitrate in experimental forests in Oregon (Lajtha et al. 2005) and increase soil temperatures and lower enzyme activity in an experimental forest in Hungary (Fekete et al. 2016; Fekete et al. 2011; Kotroc   et al. 2014). Complete detritus removal resulted in higher fluctuations in soil temperature (Fekete et al. 2016) as well as decreases in soil carbon (Bowden et al. 2014) in forests in Pennsylvania. Although removal of litter affected both soil C and enzyme activity, in the same studies litter additions had no effect on either variable (Bowden et al. 2014; Fekete et al. 2011; Kotroc   et al. 2014). The DIRT experiments show a dynamic relationship between litter above and below ground and soil carbon, moisture, enzyme activity, and SOM formation.

Outside of the DIRT network, other litter addition and removal experiments address the relationship between litter abundance and ecosystem function. After 16-years of experimental litter removal there was significantly less P, Mg, and Ca in the soil, and a reduction in cation exchange capacity in an oak-pine woodland ecosystem in southern Poland (Dzwonko and Gawron 2002). Similarly, removal of litter and humus had a negative effect on NH_4^+ , NO_3^- , P, and K^+ concentration in the soils in heathland in northwestern Netherlands (Baar and ter Braak 1996). Finally, litter additions increased Mg, NO_3^- and Ca in soils in a lowland tropical rainforest in Panama (Ashford et al. 2013), and increased soil moisture in some cases in grasslands in Alberta (Deutsch, Bork, and Willms 2010). Inorganic P and microbial biomass and nitrogen fixation rates all increase with added litter in a subarctic heath in Northern Sweden (Rinnan et al. 2008; Sorensen and Michelsen 2011). While litter and plant removal experiments have elucidated the relationship

of specific plant types and their litter with ecosystem properties, to the best of my knowledge there are no studies, which assess their combined role in arctic and alpine tundra.

Objectives

My overall objective is to determine the effects of increasing shrub abundance on ecosystem properties in an alpine tundra ecosystem, separating out the effects of increased litter from the other biogeochemical/biophysical impacts of shrubs. Specifically, I will ask the following questions:

Q1. What are effects of shrub litter, independent of shrub presence, on physical ecosystem properties such as soil temperature, moisture and light interception?

Q2. What are effects of shrub litter, independent of shrub presence, on soil nutrient content and availability?

Q3. Are there effects of shrub litter and shrub presence on soil microbial processes, including, microbial biomass and respiration, exoenzyme activity and litter decomposition?

Conceptual map depicting these predictions (Figure, 1-3)

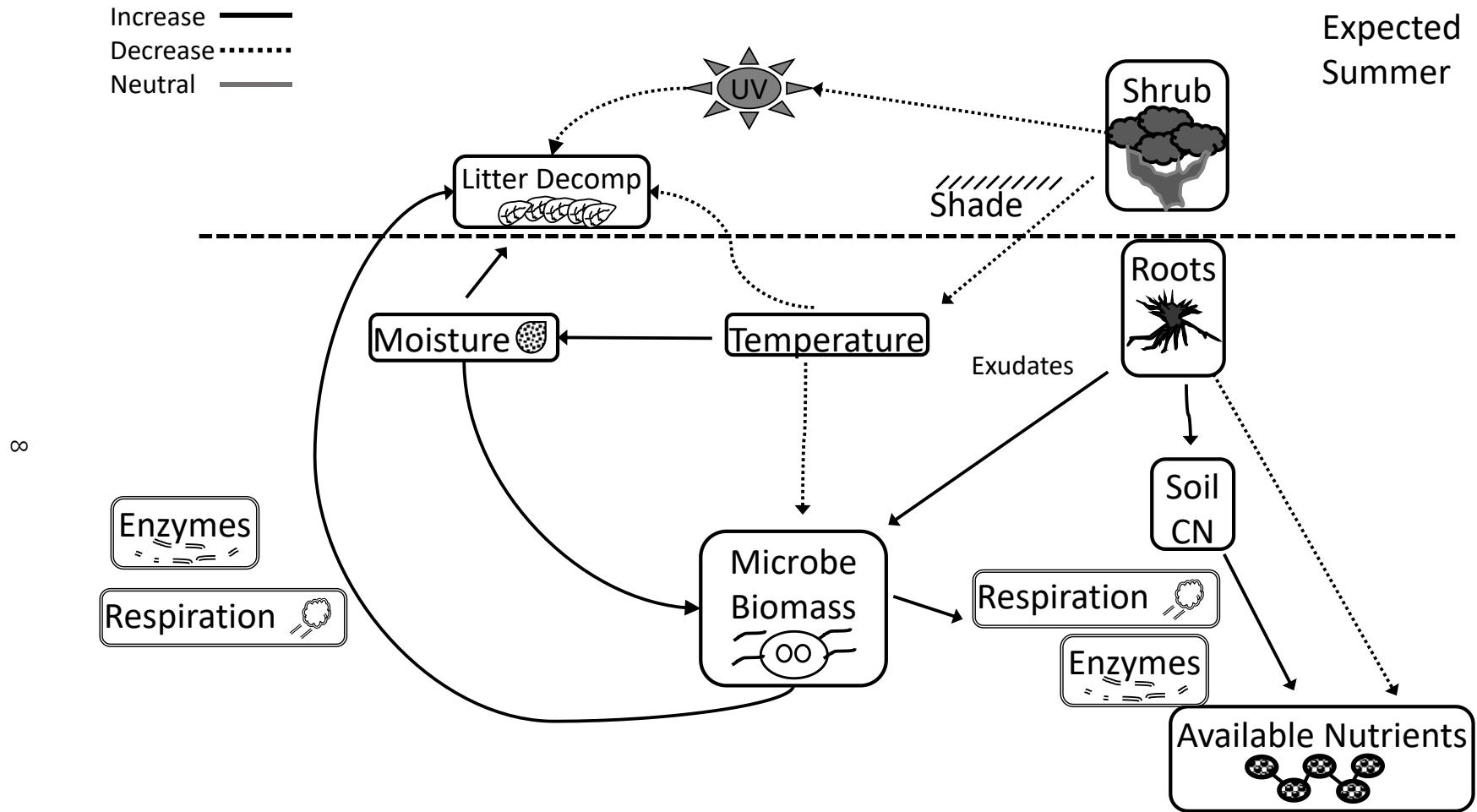


Figure 1 – Conceptual map depicting expected results for independent effect of shrubs during summer

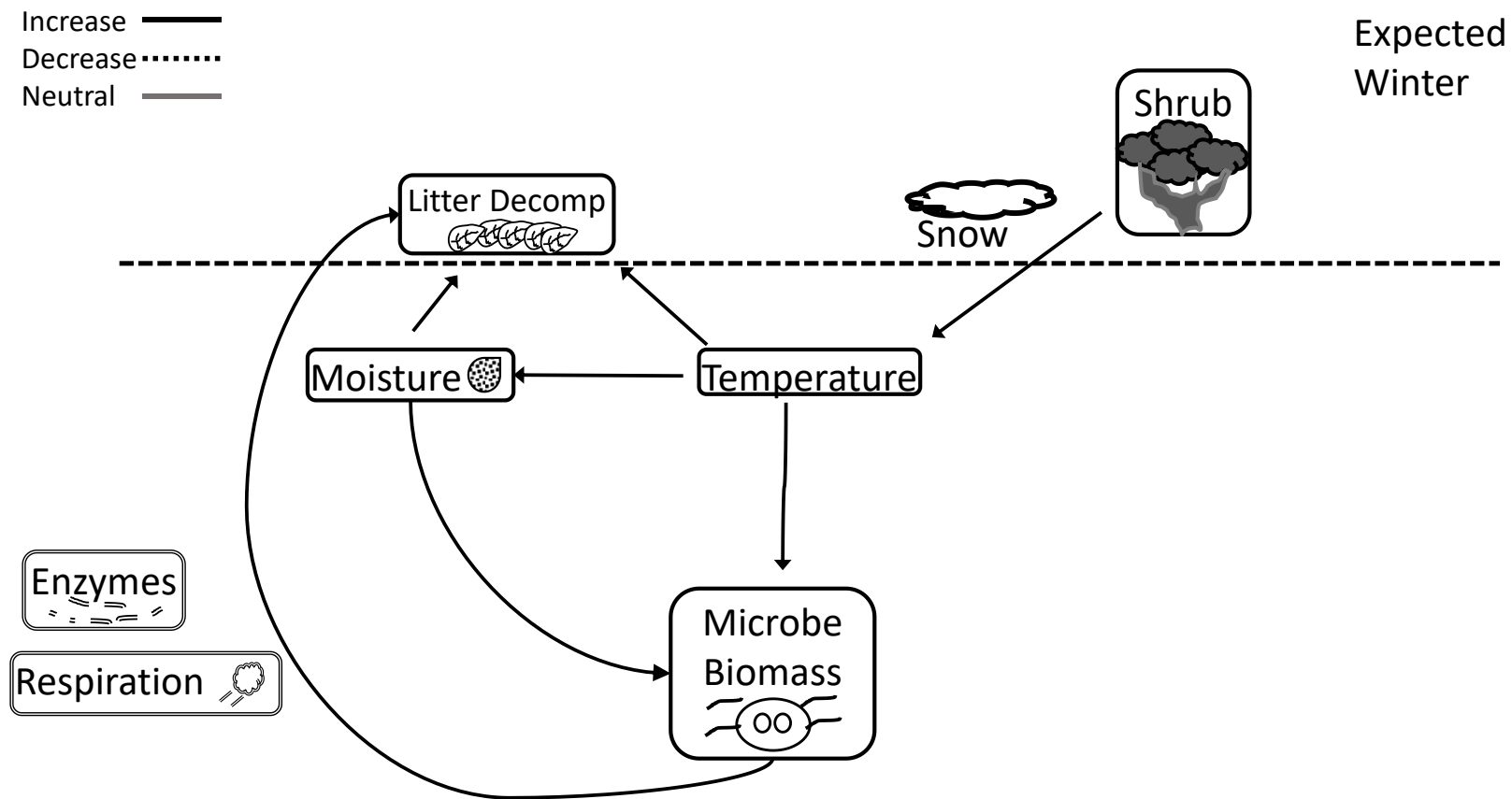


Figure 2 – Conceptual map depicting expected results for independent effect of shrubs during winter

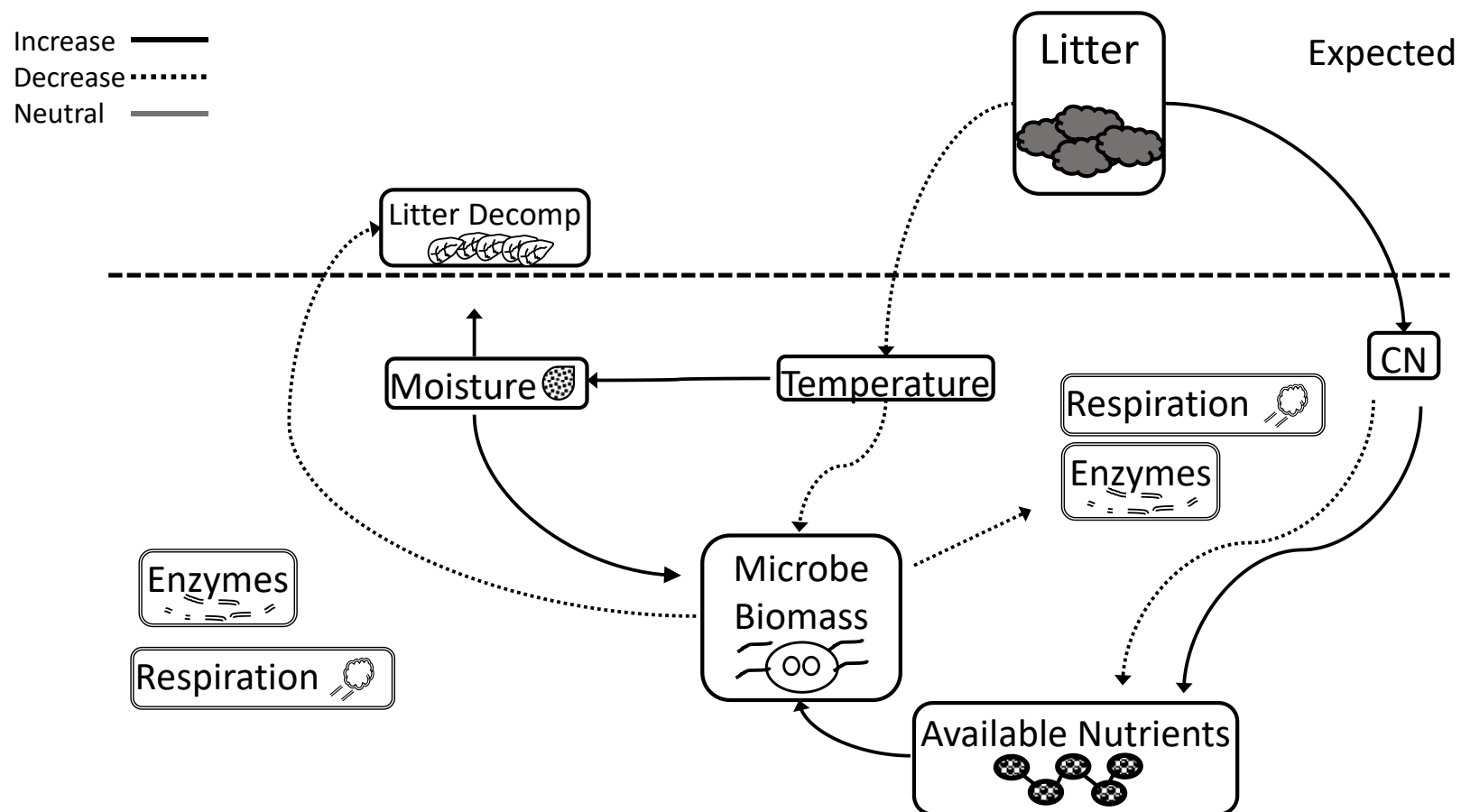


Figure 3 – Conceptual map depicting expected results for independent effect of litter

Methods and Materials

Site Description

The southwest region of the Yukon, Canada, lay geographically below the Tintina and amid the Denali fault lines (Redfield and Fitzgerald 1993; Eyles 1983), and situated in the northern part of the North American Cordillera (Israel et al., n.d.)—the western mountain chain of North America (Dickson 2004). Glaciation events of the Yukon Territory transpired over the course of the Pleistocene an estimated six times, with McConnell being the most recent 13.7.ka BP (Jackson Jr et al. 1991). Paleogeographic maps indicate the Yukon plateau, area northeast of St. Elias Mountains (Jackson Jr et al. 1991), during the middle-upper tertiary and quaternary consisted of marine sands and ultrabasic (igneous rock) intrusives and extrusives. (Ziegler 1969).

Shrub cover and abundance have been recently expanding in the southwest Yukon. For example, in a study in the Ruby Range Mountains of the southwest Yukon, alpine plant communities were shown to have increased in shrub density in over the last four decades in three out of four sites (Danby et al. 2011). This shrub density increase was accompanied by an increase in species richness and diversity, as well as an increase in graminoid cover. (Danby et al. 2011). Further, age estimates of willow species via growth ring analysis in the 12 valleys of the Kluane region indicate they have expanded to higher elevations, with six common shrubs surveyed: *Salix niphoclada*, *Salix richardsonii*, *Salix barratiana*, *Salix alaxensis*, *Salix pulchra*, and *Salix glauca* (Myers-Smith 2011).

We initiated the experiment in summer 2015 on a north facing alpine plateau near Kluane Lake Research Station in the southwest Yukon, Canada. The study site is situated in patchy shrub tundra (N°60,58.699, W°138,34.595) at 1451 m elevation, and is relatively dry receiving a mean of 230 mm annual precipitation, with approximately fifty percent as rain and the other half as snow. The

shrub tundra, located above a spruce forest composed primarily of *Picea glauca*, is composed of the dominant tall shrubs *B. glandulosa* and *Salix glauca* and has an understory primarily consisting of graminoids (dominated by *Carex consimilis*, *Festuca altaica*), forbs (dominated by *Valeriana capitata*), dwarf shrubs (dominated by *Salix reticulata* and *Dryas integrifolia*) and moss.

Experimental Design

We established treatments in order to separate the effects of increasing quantity of shrub litter from the other effects of shrubs. There were two treatments, litter addition/removal and shrub removal, established in a fully factorial split-plot design. *B. glandulosa* spreads clonally and is found in distinct patches; shrub removals were applied at the level of a single shrub patch and a full complement of litter treatments were nested within each patch. 12 patches of *B. glandulosa* (each averaging $\geq 12\text{m}^2$) were chosen ensuring that each shrub patch could fit a single 1m^2 plot for each of three litter treatments (see below), separated by a meter. The 12 shrub patches were allocated randomly to shrub removal treatments, which consisted of removal of the entire patch of *B. glandulosa*. Shrubs were removed by clipping or sawing the base of all *B. glandulosa* stems within each patch and removing the biomass. Shrubs in non-removal plots were left intact. Shrub regrowth in removal plots was minimal and was removed in subsequent years.

To assess the effects of litter quantity, we created litter manipulation plots within each shrub patch for three litter treatments: no litter (all litter removed), natural litter abundance and double natural litter abundance. Each shrub patch contained a single replicate of each litter treatment with 6 replicate patches for each shrub treatment. Plastic fences with a mesh size of 1.5 cm and a height of 20 cm, were installed along the edges of each plot to ensure litter was not redistributed between plots by wind.

For the initial litter manipulation, in July 2015 litter was collected by hand from all plots, weighed to determine average natural abundance (470g/m^2), homogenized and then redistributed according to litter treatment. In September 2015 and 2016 the recently senesced litter (both still attached and recently fallen) was collected from the no litter shrub intact plots to estimate yearly litter input (2016 litter input was an average of 171g/m^2). Using this collected litter, as well as additional litter from nearby *B. glandulosa*, litter was added to the plots according to treatments (2x natural litter fall to the double litter shrub removed plots, 1x to the double litter shrub intact plots and 1x to the natural litter abundance shrub removed plots). Litter for the natural litter fall plots within intact shrubs was not manipulated after the first litter treatment was applied in July 2015.

Response Variables

Physical Ecosystem Properties: Soil temperature was measured every 4 hours at the soil surface and 5 cm depth using soil temperature data loggers (ibuttons, model DS1921G-F5, Maxim integrated, San Jose, CA), from September 2015 to June 2017. Soil moisture to a depth of 10 cm was determined monthly during the 2016 growing season (June-August) using a water content sensor (Hydrosense Water Content measurement System, Campbell Scientific, Australia) averaging 3 randomly placed measurements in each plot. Photosynthetically active radiation (PAR) was measured mid-July 2015-16 at the soil surface and 1 m above the vegetation at the center of each plot using a quantum meter containing 6 uniformly distributed sensor heads (Apogee Instruments, Logan UT USA).

Soil collection: Soil was collected in mid-July in both 2015 and 2016 from sections of each plot reserved for destructive harvesting. A soil core approximately 5 cm in diameter and 15 cm in length was used to collect soil samples from the organic layer. The mineral layer was then cored

from within this area using a 2.5 cm diameter corer to a maximum depth of ~30cm from the soil surface, the sample depth for each plot was determined by the thickness of the organic layer. A second core was taken for the mineral layer when necessary to collect the quantity of soil necessary for all analyses. Soil samples were homogenized and large roots (> 1 mm diameter) and rocks removed. Soil was then subsampled for the following analyses, which were run independently on organic and mineral soils. All soils were frozen at -20°C until analysis with the exception of those analyzed for total C and N content, which were dried at 60°C for 48 hours.

Soil nutrients: Dried soil samples were ground and assayed for total C and N content as above. Soil available nutrients, including NH_4^+ , PO_4^{3-} , and NO_3^- , were measured once per growing season. 5 g of soil was thawed and extracted with 0.5M K_2SO_4 , shaken for 2 hours, filtered with glass filter paper, and mixed with the appropriate reagents to be assayed via colorimetric analysis using a microplate reader (BioTek, synergy HT microplate reader). The protocol for N- NH_4^+ , N- NO_3^- , and PO_4^{3-} followed the Berlethot reaction (Rhine et al. 1998), modified Griess reaction (Doane and Horwáth 2003), and the malachite green assay, (D'Angelo, Crutchfield, and Vandiviere 2001), respectively.

Microbial Properties: Microbial biomass carbon (MBC) and nitrogen (MBN) were determined using a modified chloroform fumigation method (Brookes et al. 1985). 5 g of thawed soil was fumigated with 2 ml of ethanol-free chloroform in a stoppered 250 ml Erlenmeyer flask for 24 hours. Samples were vented and then extracted with 0.5M K_2SO_4 as described above. Fumigated and non-fumigated samples were assayed for extractable organic carbon (EOC) and extractable total nitrogen (ETN), on a Shimadzu analyzer (TOC-VCPN; Shimadzu Scientific Instruments Inc., Columbia, MD, USA) with the difference in EOC and ETN between fumigated and non-fumigated samples used to calculate MBC and MBN respectively.

Extracellular enzyme activity: We measured extracellular enzyme activity using fluorescently tagged substrates via microplate fluorometry, following modified methods from Saiya-Cork, Sinsabaugh, and Zak (2002) and McLaren et al. (2017). Specifically, I measured the activity of the enzymes α -glucosidase, β -glucosidase, cellobiohydrolase, β -xylosidase, N-acetyl glucosaminidase, and phosphatase that take part in carbon, nitrogen and phosphorus cycling. 1 g of soil was thawed and blended with a modified universal buffer at a pH of 6.3, the average soil pH. Samples of the soil slurry were pipetted into black microplates, fluorescing 4-methylumbelliferone (MUB) tagged substrates added and the plates incubated at 20°C for 3.5 hours. Sample fluorescence was measured at half hour increments. The fluorescence of soils was determined using BioTek synergy HT microplate reader, at 360nm excitation, and 460 nm emission. For each substrate we measured the background fluorescence of soils and substrate and the quenching of MUB by soils and used standard curves of MUB to calculate the rate of substrate hydrolyzed.

Soil Respiration: We measured soil respiration using the EGM-5 CO₂ gas analyzer (PP Systems with SRC-2, Amesbury MA USA). PVC collars with a 10cm inner diameter were installed to a depth of 5cm in every plot, with the above ground portion extending 5cm. Live vegetation was removed from the inside of the collars. Volume of the SRC-2 chamber was modified to accommodate the soil collars. Processed data by the EGM-5 is calculated as the soil respiration linear rate (SRLR) in assimilation of grams (CO₂) m² Hour⁻¹.

Litter decomposition: Litter decomposition rates were determined using 5 x 10 cm litterbags constructed of 1mm nylon mesh and filled with 1 g dry weight (dried at 60°C for 48 hours) of senesced *B. glandulosa* leaf litter. Three litter bags were placed in each plot at senescence (mid-September 2015), with one bag removed in late-August of 2016 and 2017 (ca. 1 year of

decomposition). The other two bags will be removed in subsequent years. Once litter bags were collected, all foreign material such as soil particles, roots, and tiny pebbles was removed and the remaining litter dried at 60°C for 48 hours, and weighed. Litter decomposition rates were calculated as proportion mass loss: $\text{Mass Loss} = (\text{Original Mass} - \text{Mass at Collection}) / (\text{Original Mass})$. Dried litter samples were ground and assayed for total C and N content using a dry combustion CN analyzer (ElementarPyroCube®).

Analysis

All analyses were processed using the nonlinear mixed-effects model (nlme) function in the geepack package in R 5.4.1 (R Development Core Team 2004). To account for the effects of the main (shrub/removal) and sub plot (litter manipulation) factor manipulations, cluster analysis were used in the former to account for the variability and relative geographic distribution between the blocks, with the latter relevelled to the reference category of 1x litter (ambient conditions). Analysis of variance using nlme were used for each response variable. Assumptions of normality were tested with the Shapiro–Wilk test; when data was non-normal it was transformed using log or reciprocal transformation.

Results

Physical Properties

Soil pH was not affected by either litter treatments or shrub removal for any soil layer or year (2015-16) (Table 1, Figure 4). Soil moisture also showed no difference between treatments for any soil layer or year (2015-16) (Table 1, Figure 5). Soil moisture (determined gravimetrically) generally increased when litter was added in the organic layer in 2016, whereas in the mineral layer there was lower moisture in shrub removal plots with added litter and conversely in the shrub plots soil moisture was higher with added litter (Table 1, Figure 6). Light interception was lower in shrub removal plots (Data not presented). Soil temperatures at the surface and 5cm soil depth from July 2015 to August 2016 were lower in shrub plots during summer and higher over winter months (Table 1, Figure 7).

Table 1 – Summary of a multiple comparisons ANOVA on soil pH, moisture, and temperature (2015-2016). Bold values are significant at $p < 0.05$

Organic Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
pH	1,30	0.953	0.352	2,30	0.422	0.661	2,30	0.516	0.605	1,30	0.008	0.932	2,30	0.026	0.974	2,30	0.223	0.802
GSM	1,30	1.499	0.249	2,30	0.711	0.503	2,30	0.129	0.880	1,30	6.283	0.031	2,30	3.320	0.057	2,30	0.604	0.556
SM June	—	—	—	—	—	—	—	—	—	1,30	0.910	0.363	2,30	1.888	0.177	2,30	0.028	0.972
SM July	1,30	2.356	0.156	2,30	0.218	0.806	2,30	0.316	0.733	1,30	0.004	0.954	2,30	0.191	0.827	2,30	0.787	0.469
SM Aug	—	—	—	—	—	—	—	—	—	1,30	0.033	0.860	2,30	0.839	0.447	2,30	1.379	0.275
Mineral Layer																		
pH	1,30	0.508	0.492	2,30	0.444	0.647	2,30	0.676	0.520	1,30	1.341	0.274	2,30	2.441	0.113	2,30	0.061	0.941
GSM	1,30	0.326	0.581	2,30	0.395	0.679	2,30	3.223	0.061	1,30	0.075	0.790	2,30	0.763	0.479	2,30	3.357	0.055
ibutton Temperature																		
Month	0 cm									5cm								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
Jan-Aug	1,6	8.841	0.025	2,6	1.093	0.366	2,6	1.346	0.297	1,6	7.128	0.037	2,6	1.120	0.358	2,6	0.634	0.547
Dec-Mar	2,6	3.406	0.115	2,6	0.771	0.484	2,6	0.865	0.446	2,6	3.406	0.115	2,6	0.771	0.484	2,6	0.865	0.446
May-Aug	2,6	2.018	0.205	2,6	0.189	0.830	2,6	1.209	0.332	2,6	1.560	0.258	2,6	0.424	0.664	2,6	0.453	0.646

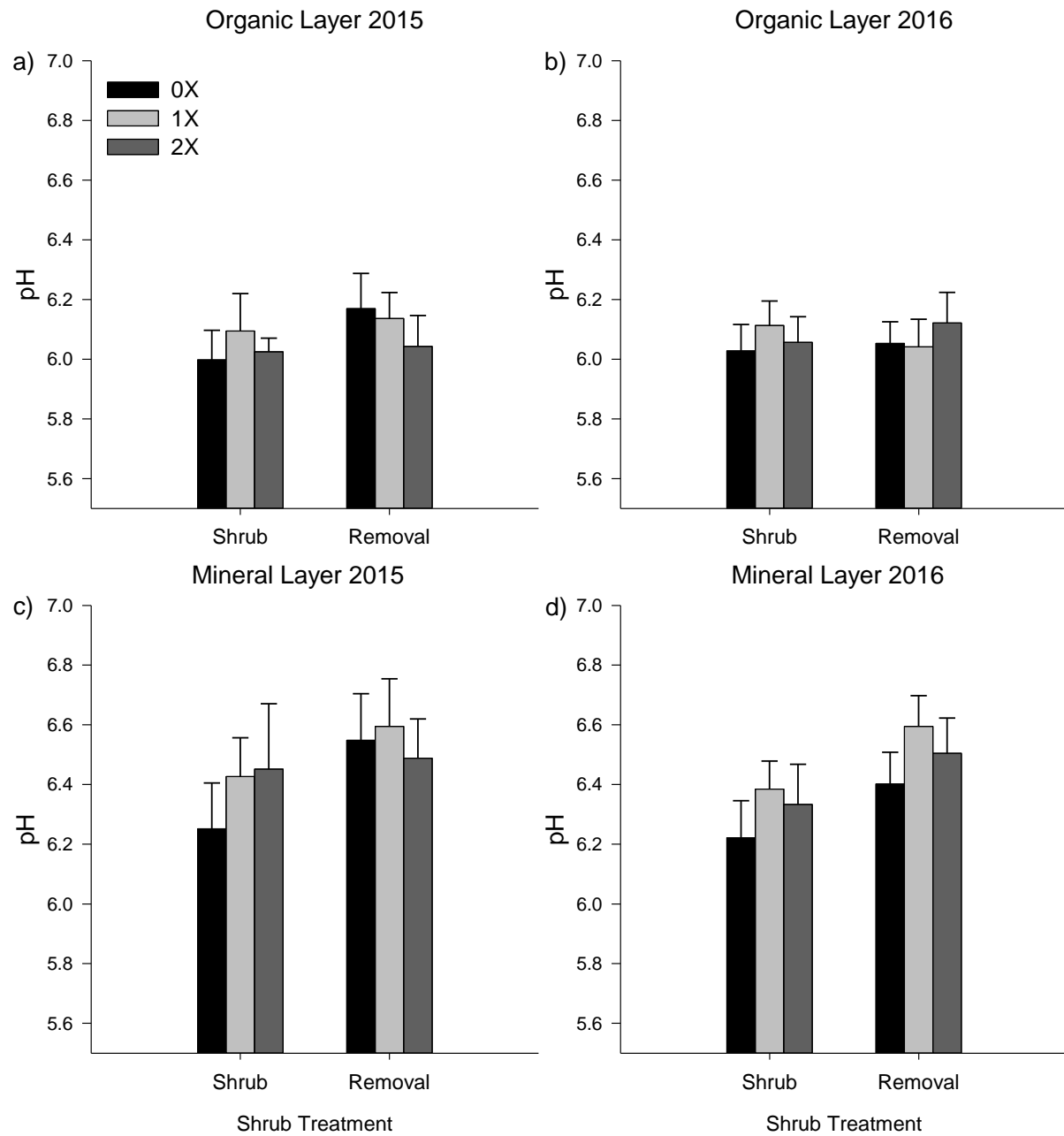


Figure 4 - Average soil pH (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015-16 growing season in alpine tundra in the SW Yukon Territory, Canada. Different colors indicate litter treatments.

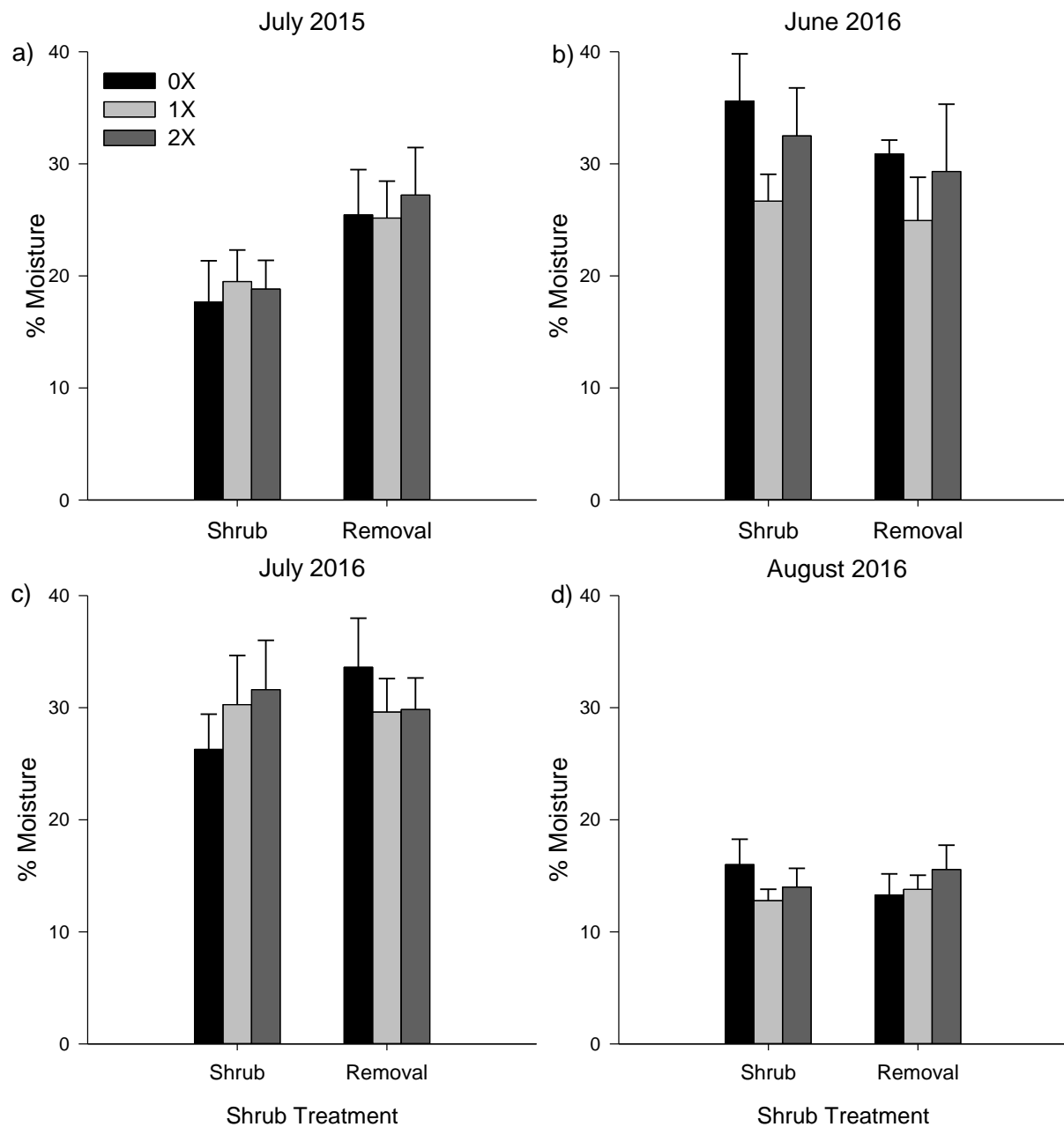


Figure 5 - Average organic layer soil moisture using a water content sensor (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015 and 2016 growing seasons in alpine tundra in the SW Yukon Territory, Canada. Different colors indicate litter treatments.

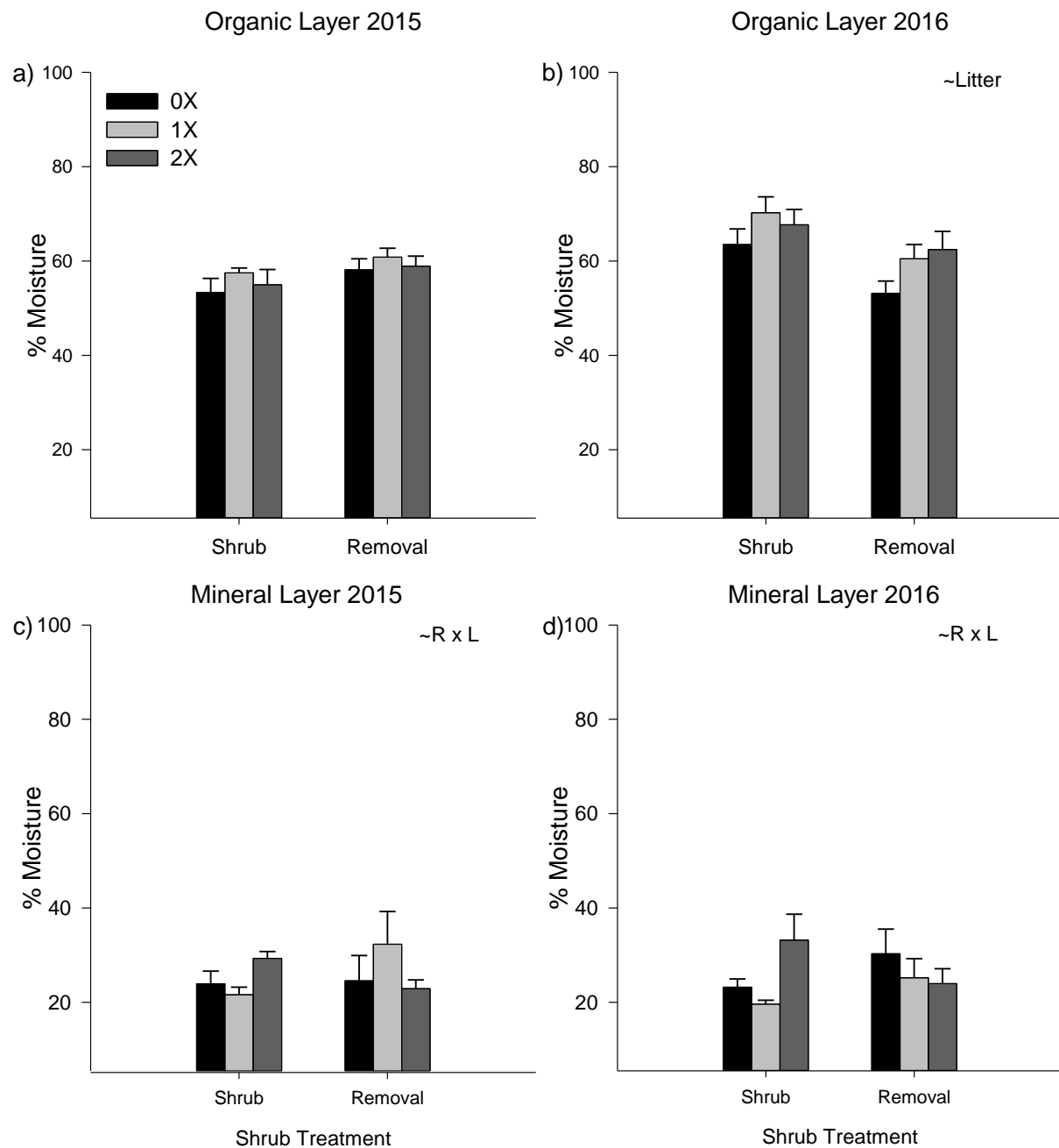


Figure 6 - Average organic layer and mineral layer soil moisture using gravimetric method (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015-16 growing season in alpine tundra in the SW Yukon Territory, Canada. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and ~ $0.1 < p < 0.05$.

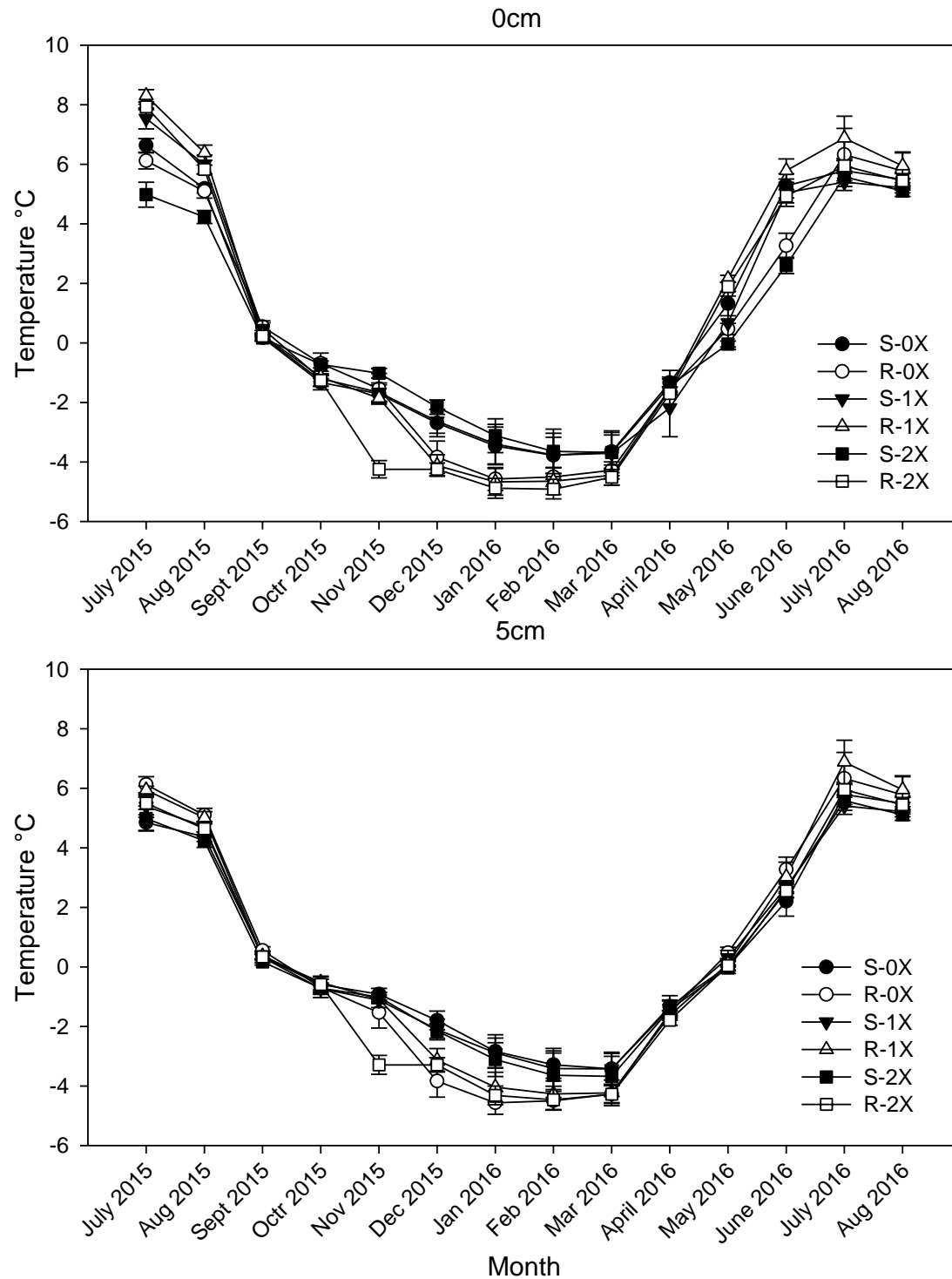


Figure 7 - Average soil temperature (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015-16 growing season in alpine tundra in the SW Yukon Territory, Canada. Different symbols indicate different treatments.

Available Nutrients

Inorganic nutrients were affected by both litter addition and shrub removal, with effects differing between soil layers and years (Table 2, Figure 8). In the organic soils in both years, NH_4^+ was significantly affected by litter treatment (Figure 8 a,b), and tended towards higher NH_4^+ in litter addition treatments than in the litter removal treatment, although post-hoc analysis did not show significant differences between individual treatments. In the mineral layer in 2015 there was a marginal increase in NH_4^+ with shrub removal (Table 2, Figure 8 c). In 2016 the NH_4^+ in the shrub removal treatment was often below minimum detectable values in the mineral layer and I did not run statistical analyses on these data. This pattern of higher NH_4^+ in shrub removal plots, however, is consistent with the pattern presented in 2015. PO_4^+ values were generally below detection or followed a non-normal distribution in the first year for both soil layers, however, the following year concentrations in the shrub removal treatment were higher than shrub present plots in the organic layer (Table 2, Figure 9). Values for NO_3^- were below detection in most cases and are not presented.

Table 2 - Summary of a multiple comparisons ANOVA on available nutrients (2015-2016). Bold values are significant at $p < 0.05$

Organic Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
NH ₄	1,29	0.066	0.803	2,29	4.614	0.023	2,29	0.397	0.678	1,30	0.910	0.363	2,30	3.716	0.042	2,30	0.967	0.397
PO ₄	—	—	—	—	—	—	—	—	—	1,29	0.059	0.814	2,29	2.294	0.127	2,29	1.100	0.352
% N	1,30	0.026	0.876	2,30	0.373	0.693	2,30	0.193	0.826	1,30	0.154	0.703	2,30	2.067	0.153	2,30	0.744	0.488
% C	1,30	0.127	0.729	2,30	0.449	0.645	2,30	0.125	0.883	1,30	0.009	0.928	2,30	3.851	0.039	2,30	1.330	0.287
Mineral Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
NH ₄	1,21	4.966	0.050	2,21	1.953	0.168	2,21	2.462	0.111	—	—	—	—	—	—	—	—	—
PO ₄	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
% N	1,30	0.094	0.766	2,30	0.209	0.813	2,30	4.513	0.024	1,30	0.422	0.531	2,30	1.841	0.185	2,30	2.065	0.153
% C	1,30	0.010	0.924	2,30	0.133	0.876	2,30	3.315	0.057	1,30	0.055	0.820	2,30	0.174	0.842	2,30	3.348	0.056

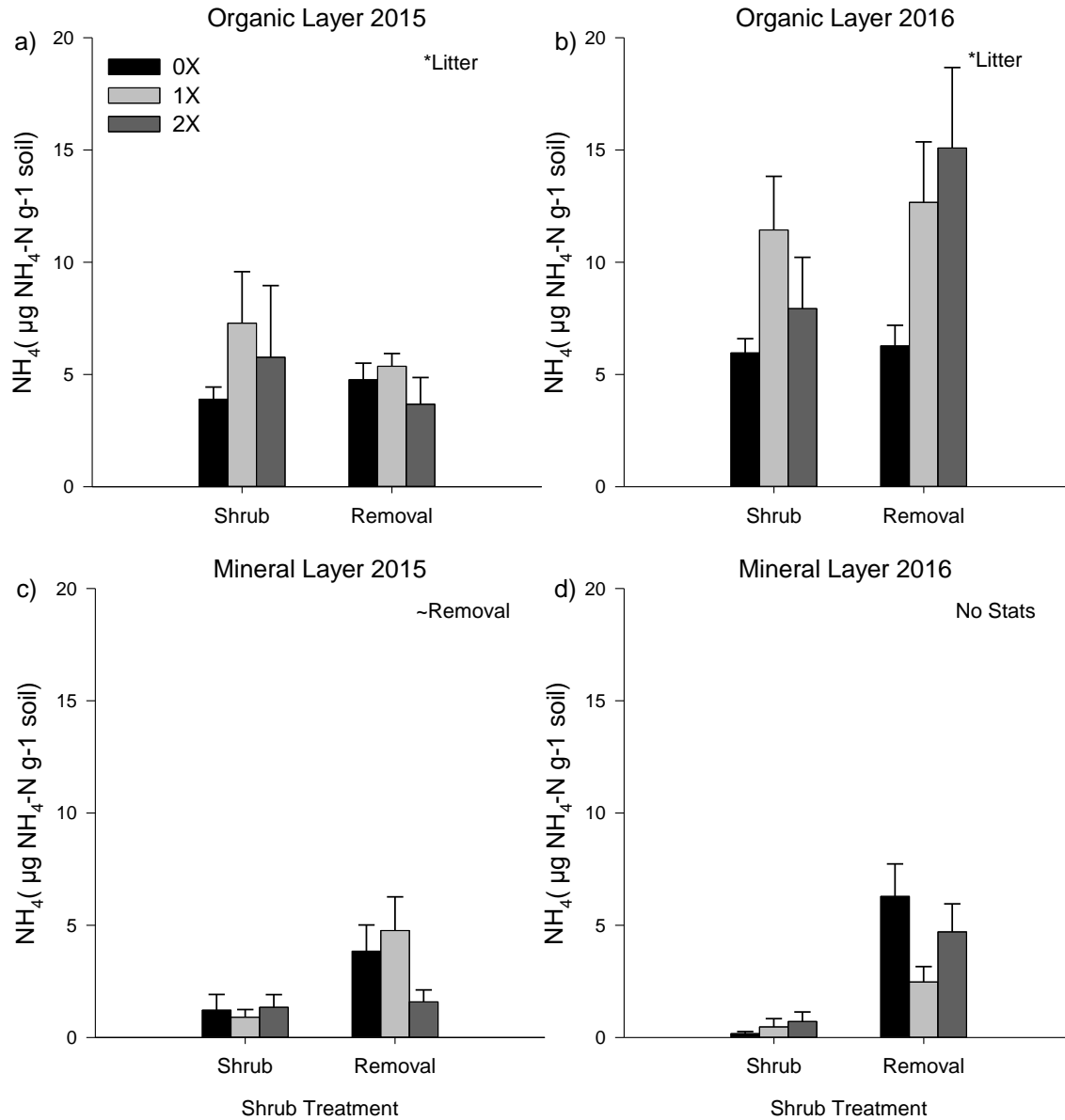


Figure 8 - Average soil available Ammonium (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015 and 2016 growing seasons in alpine tundra in the SW Yukon Territory, Canada. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and ~ $0.1 < p > 0.05$.

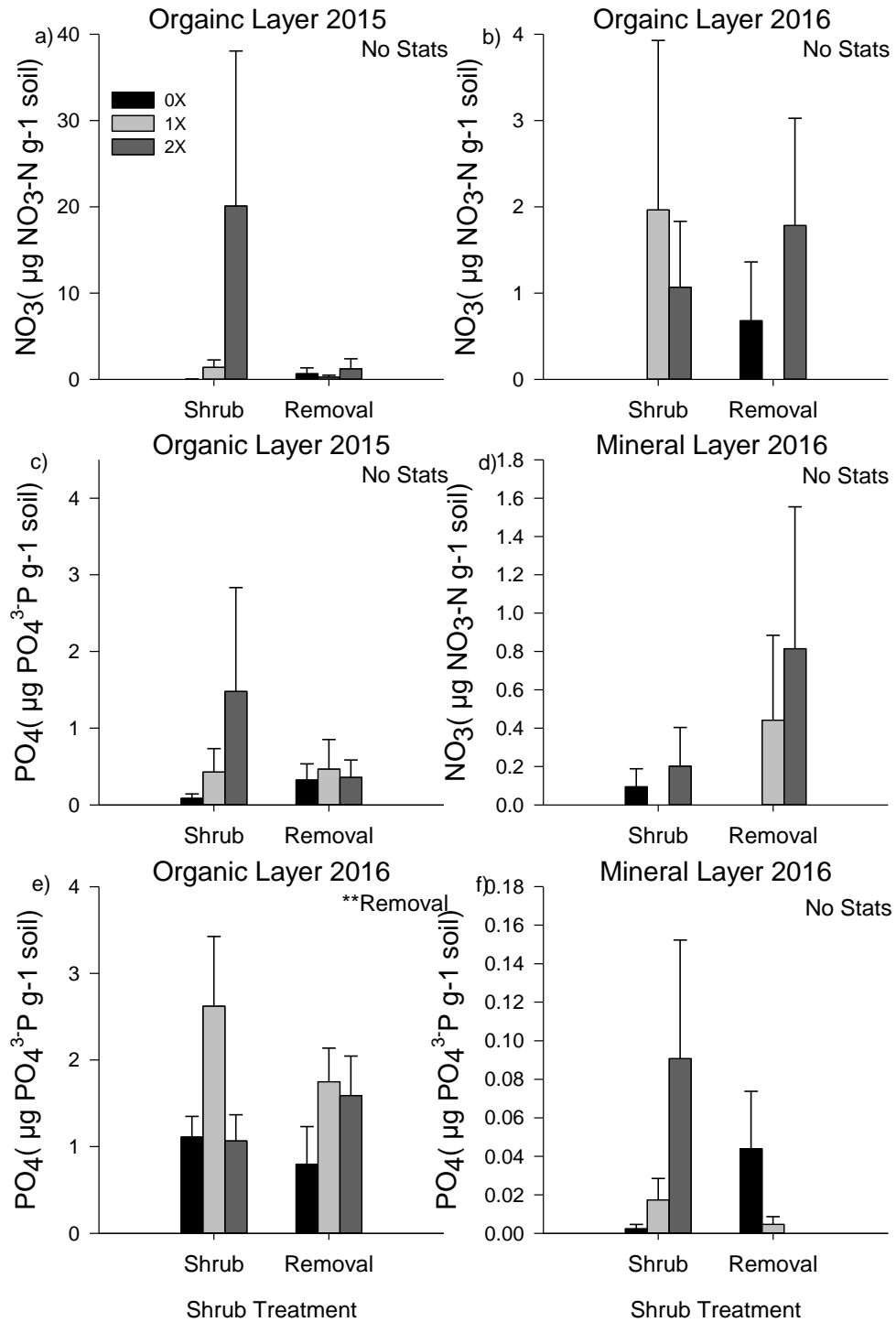


Figure 9 - Average for soil available nutrients (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015 and 2016 growing seasons in alpine tundra in the SW Yukon Territory, Canada. Scaling offset for a,d,f. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and ~ $0.1 < p < 0.05$.

CN

In 2015 there were only treatment effects on % C and % N in the mineral layer, where there was an interaction between litter and shrub removal treatments. In shrub plots, soil % C and % N were higher in the 2x litter plots than either the litter controls or litter removals. In plots where shrubs were removed, soil % C and % N were highest in plots with litter removal. There was a response in the organic layer in 2016, where % C was higher under the 1x litter treatments compared to either the litter removals or 2x addition plots. In the mineral layer, litter additions tended to increase % C in shrub plots, and decrease it in removal plots (Table 2, Figure 10).

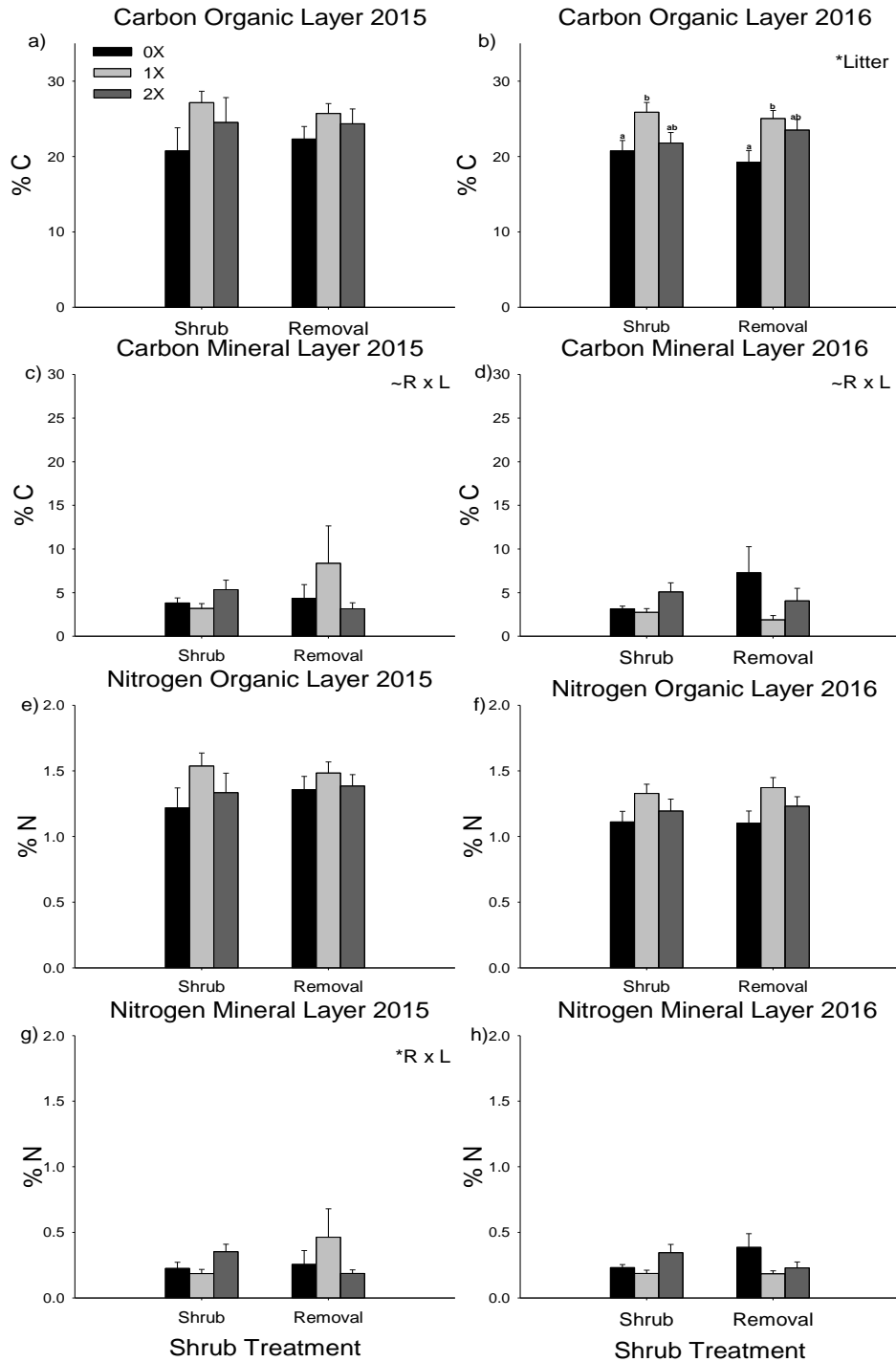


Figure 10 - Average soil %C and %N (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015 and 2016 growing season in alpine tundra in the SW Yukon Territory, Canada. Note that %C and %N are presented on different scales. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and $\sim 0.1 < p > 0.05$.

Microbial Biomass Carbon and Nitrogen

In 2015 MBN in the organic layer decreased with both litter addition and removal, with no effect of shrub removal (Table 3, Figure 11). Although results are not statistically significant, the pattern of response of MBC to litter removal was similar to that of MBN, with the highest levels under the natural abundance of litter. Similar to MBN, there was no effect of shrub removals on MBC. In the soil mineral layer, neither MBC nor MBN responded to any experimental treatment. In 2016 organic layer MBC decreased with shrub removal, with litter having no effect; MBC in the mineral layer were not affected by either treatment (Table 3, Figure 12). MBN samples could not be analyzed for this year.

Table 3 - Summary of a multiple comparisons ANOVA on microbial biomass C and N (2015-2016). Bold values are significant at $p < 0.05$

Organic Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
MBN	1,30	0.345	0.570	2,30	4.251	0.029	2,30	0.757	0.482	—	—	—	—	—	—	—	—	—
MBC	1,30	0.022	0.885	2,30	2.202	0.137	2,30	0.626	0.545	1,30	7.458	0.021	2,30	1.063	0.364	2,30	0.148	0.863
Mineral Layer																		
MBN	1,30	0.009	0.925	2,30	0.822	0.454	2,30	1.869	0.180	—	—	—	—	—	—	—	—	—
MBC	1,30	0.006	0.938	2,30	1.703	0.208	2,30	1.217	0.317	1,30	13.175	0.005	2,30	1.278	0.301	2,30	2.526	0.105

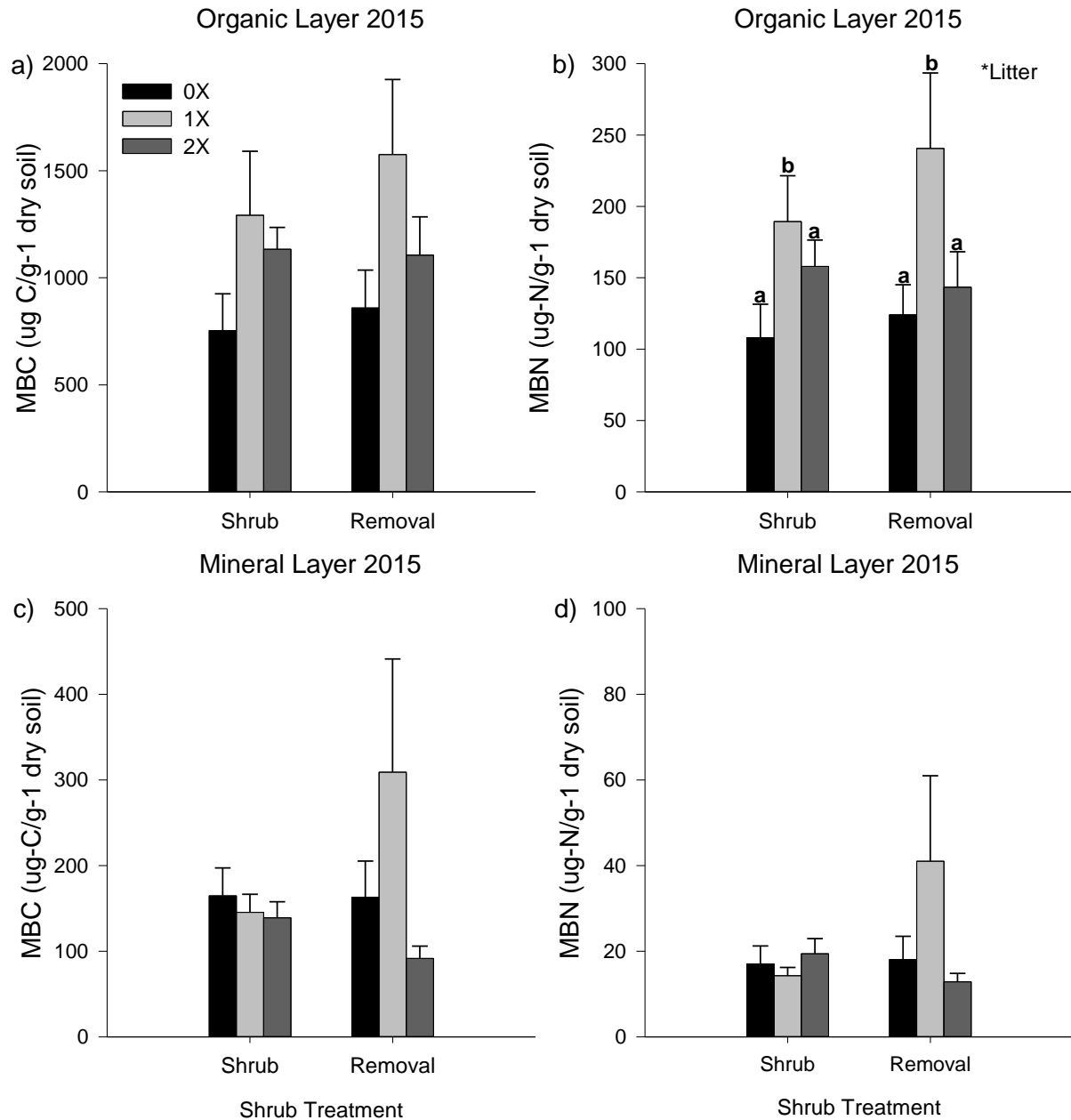


Figure 11 - Average microbial biomass C and N (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015 growing season in alpine tundra in the SW Yukon Territory, Canada. When there is no significant interaction between shrub and litter treatments, Tukey's comparisons are presented without regard to shrub treatment. Scaling offset for all figures. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and $\sim 0.1 < p > 0.05$.

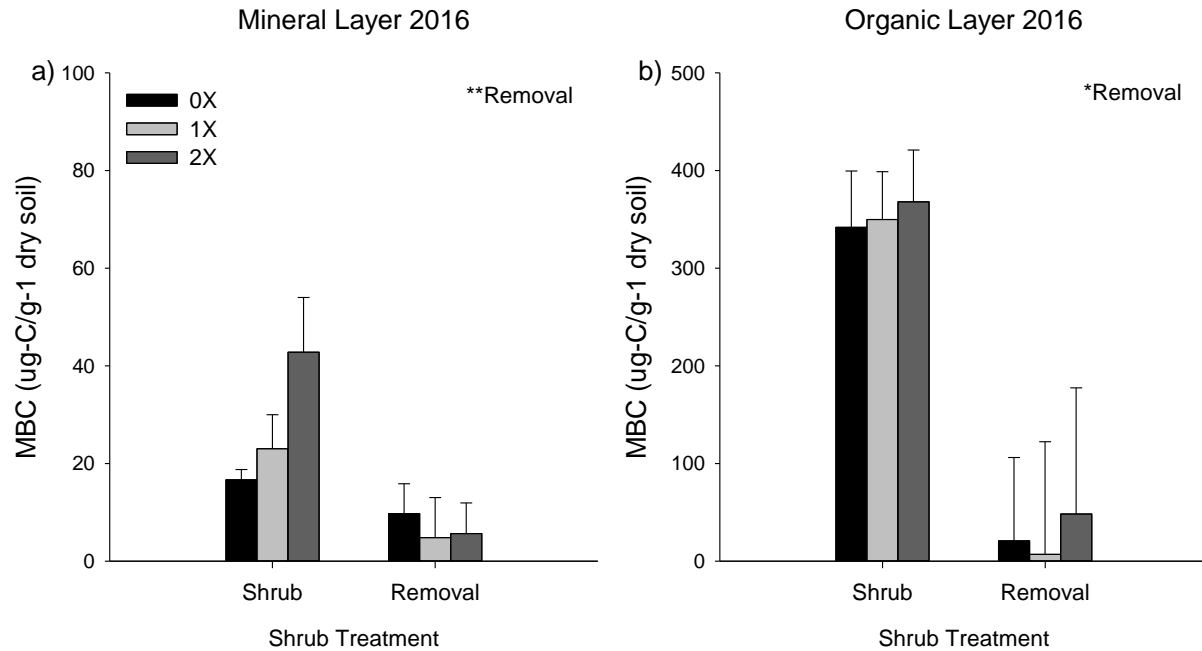


Figure 12 - Average microbial biomass C and N (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2016 growing season in alpine tundra in the SW Yukon Territory, Canada. When there is no significant interaction between shrub and litter treatments, Tukey's comparisons are presented without regard to shrub treatment. Scaling offset for all figures. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and $\sim 0.1 < p > 0.05$.

Enzymes

In the organic layer, extracellular enzymes, particularly phosphatase and β -glucosidase, responded to shrub removal in the first year (2015) and in the second year (2016) litter additions tended to increase those enzymes in shrub removal plots and decrease them in shrub plots. (Table 4, Figure 13). In the mineral layer 2015 there was no effect of either treatment, the following year (2016) enzymes responded to litter X removal treatments for phosphatase, β -glucosidase, N-acetyl glucosaminadase, and Cellobiohydrolase (Table 4, Figure 14), because enzyme activity tended to be low without litter in shrub present plots and high without litter in shrub removal plots.

Table 4 - Summary of a two-way ANOVA on extracellular enzymes (2015-2016). Bold values are significant at $p < 0.05$

Organic Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Phosphatase	1,30	16.254	0.002	2,30	0.832	0.450	2,30	0.474	0.630	1,30	1.708	0.221	2,30	6.318	0.008	2,30	1.496	0.248
B-gluc	1,30	4.469	0.061	2,30	0.182	0.835	2,30	0.769	0.477	1,30	0.010	0.923	2,30	8.381	0.002	2,30	3.803	0.040
NAG	1,30	3.160	0.106	2,30	0.353	0.707	2,30	0.398	0.677	1,30	0.257	0.624	2,30	1.543	0.238	2,30	0.473	0.630
B-cello	1,30	0.670	0.432	2,30	0.566	0.577	2,30	0.120	0.888	1,30	0.743	0.409	2,30	2.300	0.126	2,30	1.003	0.385
a-gluc	—	—	—	—	—	—	—	—	—	1,30	0.125	0.731	2,30	1.629	0.221	2,30	1.294	0.296
Mineral Layer																		
Variable	2015									2016								
	Removal			Litter			Removal x Litter			Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Phosphatase	1,30	0.108	0.749	2,30	0.150	0.862	2,30	0.113	0.894	1,30	0.492	0.499	2,30	1.528	0.241	2,30	3.861	0.038
B-gluc	—	—	—	—	—	—	—	—	—	1,30	0.889	0.368	2,30	0.403	0.674	2,30	4.124	0.032
NAG	1,30	0.796	0.393	2,30	0.139	0.871	2,30	1.425	0.264	1,30	0.320	0.584	2,30	0.464	0.636	2,30	2.913	0.078
B-cello	—	—	—	—	—	—	—	—	—	1,30	1.599	0.235	2,30	0.114	0.893	2,30	6.029	0.009

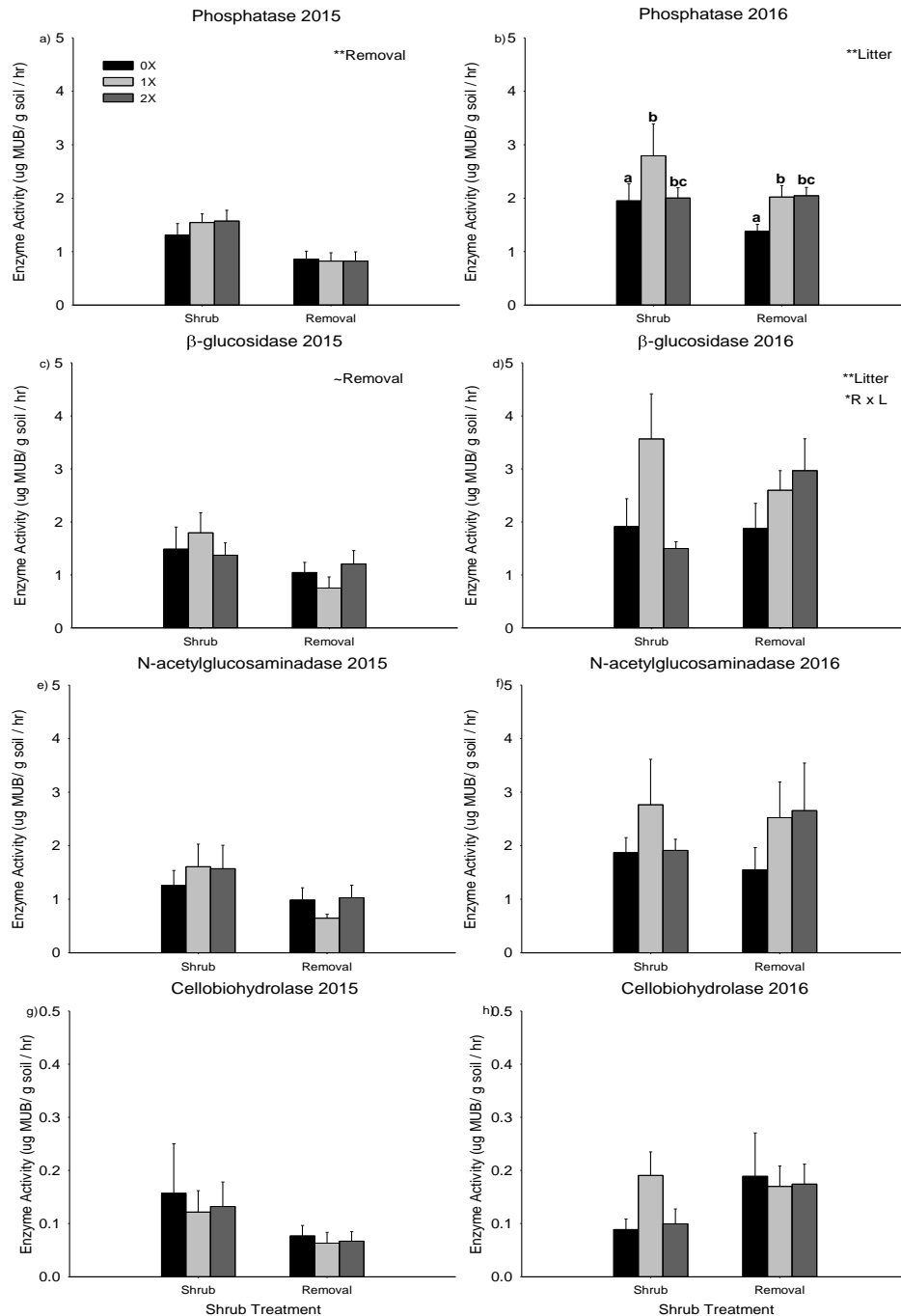


Figure 13 - Average organic layer extracellular enzyme activity in the organic layer: phosphatase, β-glucosidase, N-acetyl glucosaminadase, and cellobiohydrolase (± SE) in a factorial shrub removal x litter manipulation experiment in the 2015 and 16 growing season in alpine tundra in the SW Yukon Territory, Canada. Tukey's comparisons in b are for analysis conducted across shrub removal treatments. Different colors indicate litter treatments. Significant effects from the mixed effects model are indicated by * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ and ~ $0.1 < p > 0.05$.

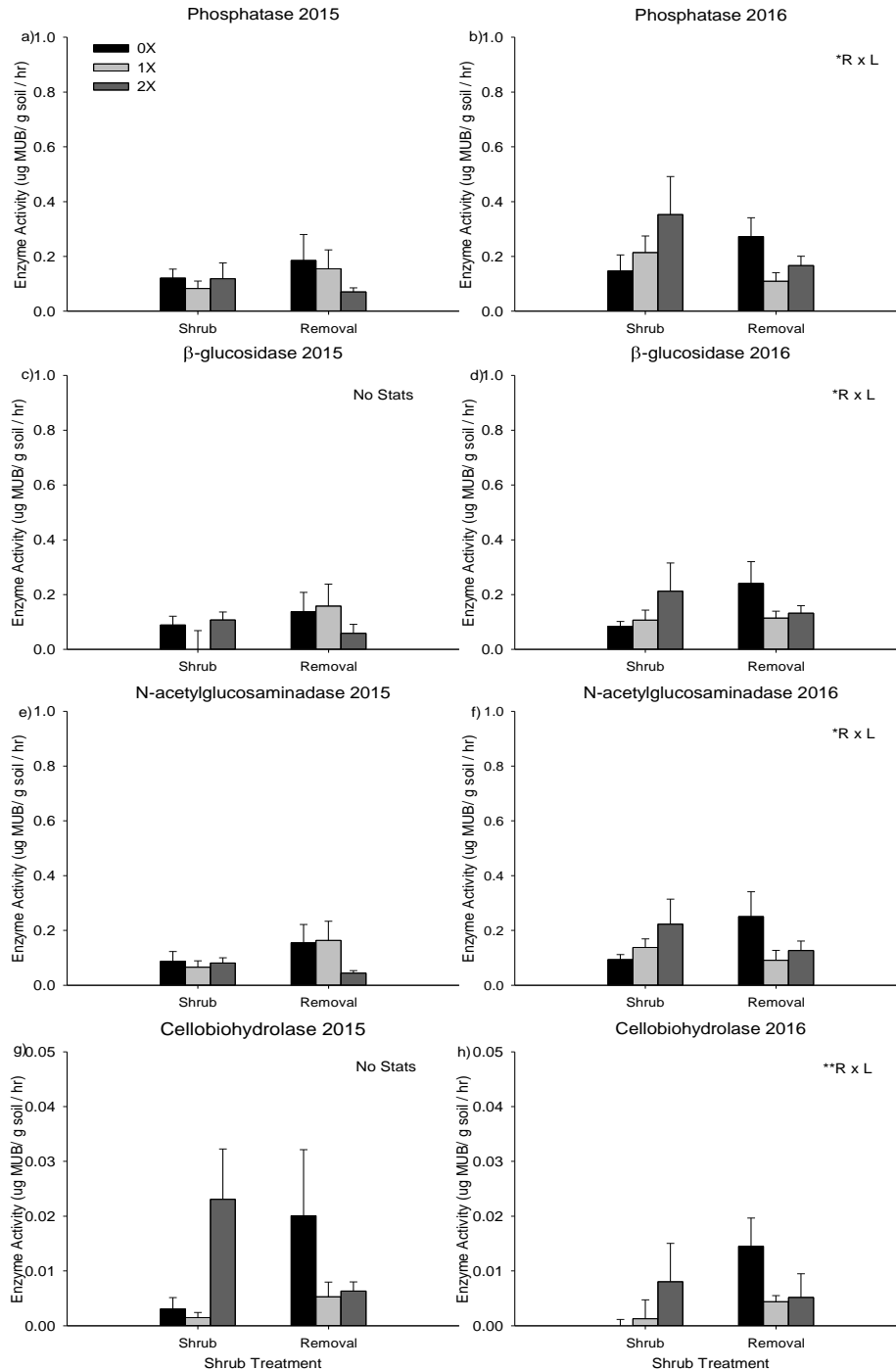


Figure 14 - Average for mineral layer extracellular enzymes: phosphatase, β -glucosidase, N-acetyl glucosaminadase, and cellobiohydrolase (\pm SE) in a factorial shrub removal x litter manipulation experiment in the 2015-16 growing season in alpine tundra in the SW Yukon Territory, Canada. Note scale is different for Cellobiohydrolase. Scaling for **e**, **f** is offset from the other graphs depicted. Significant effects from the mixed effects model are indicated by * p < 0.05, ** p < 0.01, *** p < 0.001 and ~ 0.1 < p > 0.05.

Respiration

SRLR showed no response to either treatment in either June or July 2016 (Table 5, Figure 15).

Table 5 - Summary of a multiple comparisons ANOVA on soil respiration (2016). Bold values are significant at $p < 0.05$

2016 Respiration									
Variable	Removal			Litter			Removal x Litter		
	df	F	P	df	F	P	df	F	P
June	1,30	0.007	0.937	2,30	0.879	0.431	2,30	0.601	0.558
July	1,30	0.002	0.962	2,30	0.393	0.680	2,30	0.939	0.408

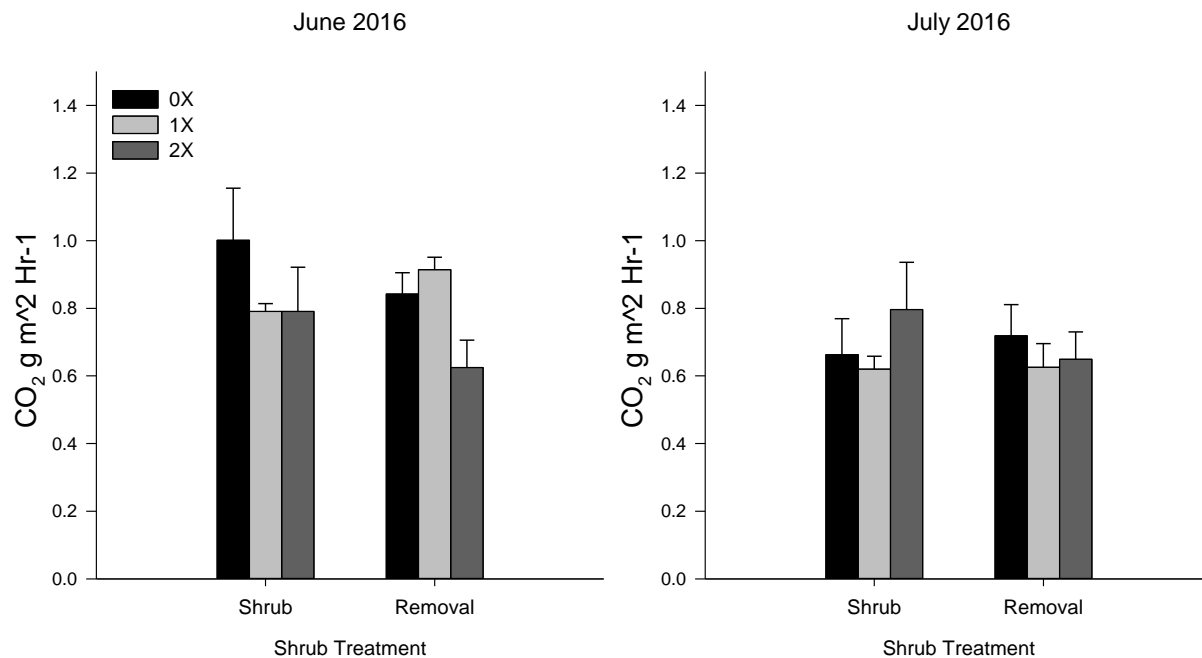


Figure. 15 - Average soil respiration (SRL (\pm SE)) in a factorial shrub removal x litter manipulation experiment in the 2015-16 growing season in alpine tundra in the SW Yukon Territory, Canada. Different colors indicate litter treatments.

Litter Mass Loss

Litter mass loss was not affected by any litter treatment after either 1 or 2 years of decomposition. In contrast, shrub removal increased decomposition rates after both one year and 2 years of decomposition (Table 6, Figure 16). After two years of decomposition there was a marginal interaction between the shrub removal and litter addition treatments, where litter addition decreased decomposition rates in shrub removal plots and to a lesser extent in the shrub plots (Table 6, Figure 16).

Table 6 - Summary of a multiple comparisons ANOVA on litter decomposition (2015-2016).
Bold values are significant at $p < 0.05$

Organic Layer									
		Removal			Litter			Removal x Litter	
Variable	df	F	P	df	F	P	df	F	P
1 year	1,30	13.912	0.004	2,30	0.249	0.782	2,30	0.008	0.992
2 year	1,30	27.477	0.004	2,30	2.525	0.105	2,30	3.100	0.067

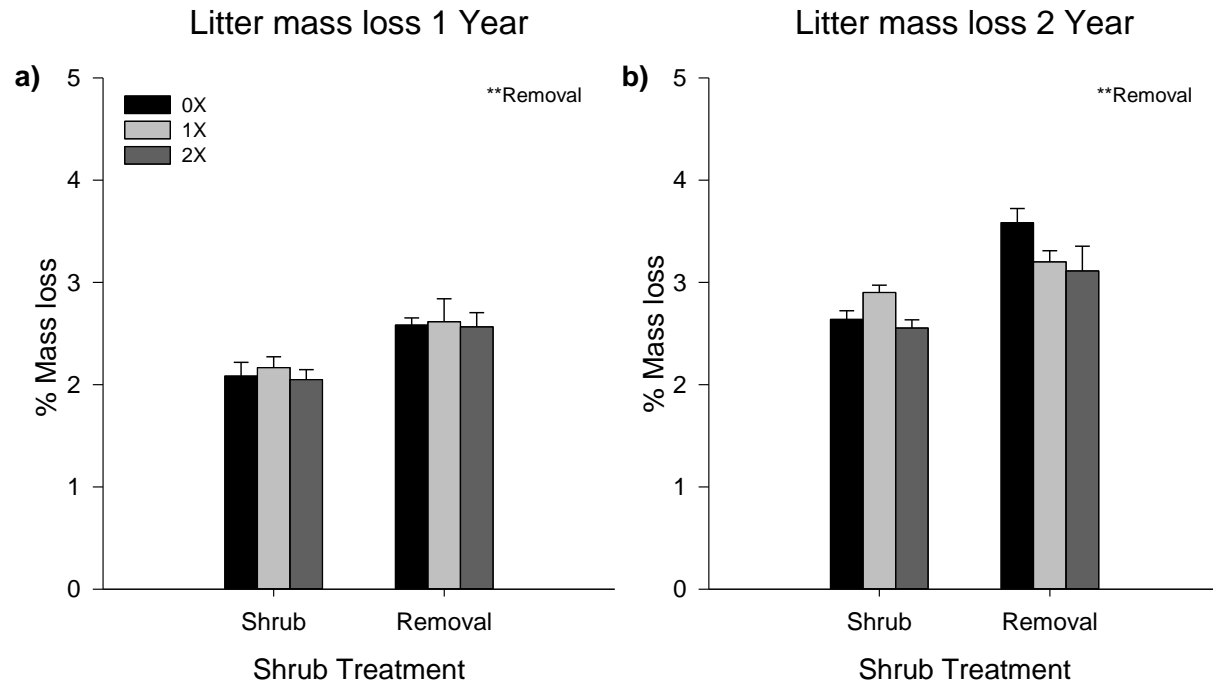


Figure 16 - Average litter mass loss (Initial - Final Mass)/Initial Mass (\pm SE) in a factorial shrub removal x litter manipulation experiment in 2015-16 in alpine tundra in the SW Yukon Territory, Canada.

Discussion

The present study sought to address the relative impact of increasing deciduous shrubs on ecosystem properties in alpine tundra. The effects of increased litter were separated from the biogeochemical/biophysical impacts of shrubs, treatments of shrub litter and shrub presence affected physical ecosystem properties, available nutrients, and microbial processes. Effects of treatments differed between years, with litter being stronger. Our results highlight the mechanisms through, which shrubs are affecting ecosystem properties in alpine tundra.

Q1: Physical Soil Properties

Temperature

Surface and 5cm soil depth temperatures from July 2015 to August 2016 were lower in shrub plots during summer and higher in shrub plots over winter months. Opposite to our winter results, removal of the understory (*Dicranopteris dichotoma*) increased soil temperatures in subtropical forest south China for December-January (Wu et al. 2011). The shrub canopy may have affected temperature through 2 mechanisms. Firstly albedo can increase with shrub (*B. glandulosa*) presence via its canopy, thus potentially affecting ground heat flux, where short wave radiation reflected reduces soil temperatures and radiative feedback to climate (Williamson et al. 2016). Other studies, however, have shown shrub cover to decrease albedo (Sturm et al. 2005). Secondly soil temperatures in our study were higher in shrub plots during snow cover months; these results support the snow-shrub hypothesis where tall shrubs retain snow transported by the wind, generating a thicker snow layer, insulating the soil during winter (Demarco et al. 2014; Sturm et al. 2001; Pomeroy et al. 2006). While the addition of snow has been recorded to increase soil temperatures in mesic tundra site in West-Greenland (Blok et al. 2015) we would need to measure snow depth at our sites to fully support this hypothesis. Our results suggest the shrub

canopy will have opposite effects on soil temperature in summer and winter months, however, it is not clear the extent of influence this will have on soil moisture, available nutrients and microbial processes.

While litter manipulation had no effect on soil temperature, A meta-analysis found temperature in mostly temperate and sub-tropical forests generally increased with the removal of litter, with its addition having the opposite effect (Xu, Liu, and Sayer 2013; Sayer 2006) although this meta-analysis did not consider seasonal variation in temperature. Others have reported the same effects of litter in a tropical forest in Costa Rica (Wood and Lawrence 2008), a pine plantation in China (Fan et al. 2015), and a coniferous forest in Oregon (Sulzman et al. 2005). Alternatively, others reported soil temperature in litter addition plots to be lower, such as in a in a neotropical savanna in Brazil (Villalobos-vega et al. 2011) and deciduous forest in northeastern Hungary (Fekete et al. 2016). Changes in soil temperature in response to external influences of climate is partially mitigated by litter as it serves as a protective barrier (Sayer 2006), as well as moss (Blok, Heijmans, et al. 2011). We may not have found an effect of litter on soil temperatures because not enough litter was added to exceed the buffering capacity of these soils to temperature change during summer months.

Soil Moisture

Soil moisture (as determined by either a water content sensor or gravimetrically) was not significantly affected by either shrub removal or litter treatments for any soil layer or year. In 2016, however, after a full year of treatments there were trends ($p < 0.1$) towards effects of both litter and shrub removals on gravimetric soil moisture. In the organic soil layer, moisture tended to decrease when litter was removed, possibly due to the protective barrier provided by the litter layer mediating soil water content (Sayer 2006). Whereas in the mineral layer moisture increased when

litter was removed (but only when shrubs were also removed). Similar to our findings, in many studies, soil moisture did not vary across litter treatments including litter removal/addition in deciduous forest in northeastern Hungary (Fekete et al. 2016), an old growth coniferous forest in Oregon (Sulzman et al. 2005), a rain forest in Costa Rica (Wood and Lawrence 2008), and artificial forest in China (Fan et al. 2015), although the latter did show an effect on soil moisture when litter removal was combined with root trenching (similar to our interaction between litter and shrub removal for mineral soils). When litter manipulations have affected soil moisture in other experiments, the effects have not been in a consistent direction with litter addition increasing gravimetric soil moisture in a lowland tropical rainforest in Costa Rica (Wieder et al. 2012), and a wet tropical forest in Costa Rica (Leff et al. 2012) but declining in response to litter removal in a lowland wet tropical forest in Costa Rica (Weintraub et al. 2013), the subtropics in China (Xiong et al. 2008), and in a neotropical savanna in Brazil (Villalobos-vega et al. 2011).

There are many reasons why we did not find an effect of litter on soil moisture - a meta-analysis found litter addition to overall have no effect on soil moisture (Xu et al. 2013). However, comparing across studies may provide useful information; there are multiple factors, which contribute to soil moisture that change based on ecosystem type, making the potential response to litter manipulations at different sites really different from each other. These differences include regional climate, which may affect soil moisture as increases in temperature increase rates of evapotranspiration (Dai et al. 2004). Vegetation type also influences soil light interception and albedo (McLaren and Turkington 2010) affecting rates of transpiration as well. Other possibilities include that the ground heat flux is mediated by the thick layer of moss present in many of my plots, and effects of litter manipulation on temperature may not exceed that buffer. Our two sampling methods may have yielded different results because soil moisture content may vary from

day to day due to the timing of rainfall events. Lastly, shrub removals increased soil temperatures during the summer relative to shrub present plots, indicating the effects on soil moisture maybe limited due to the buffering capacity of moss to changes in soil temperature. Based on our results, increasing deciduous shrub will most likely increase soil water content as well.

Q2: Soil Nutrients

Soil Total Carbon and Nitrogen

%C increased with litter addition in the organic layer after 2 years of experimental treatment. Similar to our results, litter addition increased soil C concentrations in a wet tropical forest in Costa Rica (Weintraub et al. 2013), a lowland tropical rainforest in Panama (Ashford et al. 2013) and a sub-arctic heath northern in Sweden (Rinnan et al. 2008). However, a 20 yr. litter addition experiment detected no increase in C concentrations, although removal of litter lowered soil C in sclerophyll forest in Pennsylvania (Bowden et al. 2014). Additionally the increase or removal of litter had no effect on carbon in the mineral soil in a temperate deciduous forest in Tennessee (Garten 2009).

In order to put our results into perspective, it is important to consider factors that contribute to soil C. Litter addition may have directly add Organic C to the organic layer. The soil carbon pool is supplied by above- and belowground carbon inputs with their own chemical properties that may influence decomposition of this carbon (Bowden et al. 2014). . The positive response of soil C to litter addition suggests that the encroachment of deciduous shrubs will increase these values at least over the short term.

In our experiment, aboveground inputs of litter increased %C, however, shrub removals may have an effect on belowground inputs as well through the breakdown of roots. Rasse, Rumpel, and Dignac (2005) in fact maintain that the contribution of belowground inputs to the soil carbon

pool may be greater than that of aboveground litter fall. While there was no impact of shrubs in our study, this may be due to mechanisms that preserve root derived C. The lignification of roots is generally greater than that of litter limiting its access to soil microbes via chemical recalcitrance (Goering and Van Soest 1970). Additionally the root exudations of labile C into the rhizosphere (Merckx et al. 1985), may be protected due to physical isolation via aggregates of soil polymers (Rasse et al. 2005). It thus may be some time before our shrub removal plots exhibit an increase in %C through the decomposition of roots.

Soil % N responded to an interaction between treatments in the deeper mineral soils in the first year after treatments were applied, where litter addition increased %N in shrub plots but decreased %N in removal plots. Congruent with our results for %N, studies found litter addition elevated total N concentrations (Ashford et al. 2013), a deciduous forest in Germany (Cullings et al. 2003; Kalbitz et al. 2007), and in an experiment that combined warming via open top chambers with litter addition (Rinnan et al. 2008). Alternatively, litter addition had no effect in a pine stand in Yellowstone national park (Cullings et al. 2003). The removal of litter had no effect on %N in an oak-pine woodland in southern Poland (Dzwonko and Gawron 2002).

Soil N pools are determined by inputs through plant litter and root exudates along with atmospheric N deposition, with N loss due to plant uptake or leaching (Marty et al. 2017). While there was an interaction between treatments in the mineral layer 2015, this effect was transient and currently we have no evidence that increased litter from shrubs or uptake will affect soil N pools.

Available Nutrients

Litter addition increased inorganic nitrogen (NH_4^+) the soil organic layer, (nitrate was generally too low in our plots to measure in our experiment). Litter addition has frequently been shown to increase soil available N: litter addition increased NO_3^- , in lowland tropical rainforest in

Panama (Ashford et al. 2013; Sayer et al. 2012) and Costa Rica (Wieder et al. 2012) and a forest understory in southern China (Lu et al. 2016), and increased NH_4^+ in a lowland tropical forest in Costa Rica (Wieder et al. 2012). Other litter manipulation experiments have shown litter removal treatment where to lower soil nutrients (NO_3^- , Ca, Mg, and P) in a forest understory in Northern China (Lu et al. 2016) and in a tropical forest in Panama (NH_4^+ ; Sayer et al. 2012) although others have found no effect of litter removal on available N (Fuentes et al. 2014) in a sclerophyll forest or nutrient cycling in tropical wet forest in Costa Rica (Wood et al. 2009).

NH_4^+ may have been affected by litter addition in our plots for a variety of reasons. First, increases in plant uptake with litter addition would explain the decrease in nutrients. However, we also found decreased ammonium when shrubs (and thus the majority of vegetation in the plots) were removed in the first year of the study, particularly in the mineral layer, and thus changes in uptake are probably not the mechanism for our litter effects. Second, soil microbes could be taking up, or immobilizing, the nitrogen while they access the new carbon source from the added litter. The added litter may be nitrogen poor and so the microbes could be using N from the soil to access the C in the litter (Schmidt et al. 1997; Schaeffer et al. 2003). This may be less important in removal plots as decomposing roots provide a source for N (see the tendency towards an interaction in NH_4^+ results in 2016 where NH_4^+ does not decline with added litter). However, an increase in immobilization would also result in an MBN increase, which is not reflected by our results.

Nutrients (NH_4^+ , PO_4^-) in deeper mineral soils were more affected by the shrub removal treatments than by litter manipulations, with both nutrients increasing with shrub removal. Other removal experiments have shown nutrient availability to increase with shrub removal in moist tussock tundra in Toolik Lake, Alaska, (Bret-harte et al. 2004) and in other non-shrub removal

experiments where the forest understory was removed in southern china (Wu et al. 2011). It's possible that increasing nutrients are a result of decomposing roots remaining from plant removals (Bret-Hart et al., 2004) or decreasing uptake resulting from shrub removals is also likely, particularly in deeper soils where shrub roots predominate over the more shallowly rooted grasses (McLaren, Wilson, and Peltzer 2004). If the increase in nutrients was a result of increased mineralization of decaying root tissue we would expect these effects to diminish over time (McLaren and Turkington 2010) and thus in future years we may be able to distinguish between the two mechanisms.

Q3: Soil Microbial Properties and Processes

pH

The pH of soil can directly affect microbial communities as it typically limits growth between a pH of 4-9, however, soil microbes can also influence pH via the oxidation of NH_4^+ ions (Bardgett 2005). Soil pH in our plots was not affected by either litter or shrub removal treatments for any soil layer in either year (2015-16). Litter manipulations have resulted in varying effects on soil pH in studies in other ecosystems. Similar to our results, pH was not altered by litter treatments in a sub-arctic heath in Northern Sweden (Rinnan et al. 2008), a lodgepole pine stand in Yellowstone National Park (Cullings et al. 2003), or a rain forest in Costa Rica (Wood and Lawrence 2008). However, in contrast to our results, litter removal has been shown to both decrease soil pH in a mixed oak-woodland in southern Poland (Dzwonko and Gawron 2002) and a deciduous forest in northern Hungary (Kotroczó et al. 2014) but also in some cases to increase it, such as in converted grassland in China (Xiong et al. 2008). Litter addition has also had mixed effects, for example soil pH was higher in litter addition plots in a lowland tropical rainforest (Ashford et al. 2013) and forest in northern Hungary (Kotroczó et al. 2014), but lower in a

temperate deciduous forest in Bavaria, Germany (Huang and Spohn 2015) and neotropical savanna south of Brasilia, Brazil (Villalobos-vega et al. 2011).

The stability of soil pH to litter manipulations depends on a variety of factors such as: vegetation composition, initial soil pH, and soil composition (Sayer 2006). Vegetation at our site in the open alpine tundra consisted mostly of deciduous and evergreen shrubs, graminoids, forbs, and moss, making comparisons with other studies difficult as a majority of litter manipulation studies have been done in temperate, deciduous, or tropical forests (Sayer 2006). Our site had a neutral soil pH (ca.6.6), while the other sites that showed effects of litter manipulation on soil pH were generally more acidic (pH of 4 (Dzwonko and Gawron 2002), 5.2 (Kotroczó et al. 2014), 5.3 (Ashford et al. 2013), 4.2 (Huang and Spohn 2015), and 4.1 (Villalobos-vega et al. 2011). Acidic soils are less buffered than neutral soils. Soils at our site had a large amount of soil organic matter as well as a clay dominated layer beginning 15~20 cm from the soil surface; this type of soil composition may create negative binding sites that can eliminate hydrogen and aluminium ions creating buffered soils with near neutral or alkaline pH (Sayer 2006). Given the suggested buffering capacity of these soils as they are rich in organic matter and clay, it may take a longer period of time before litter and/or shrub manipulations will alter this threshold.

Microbial Biomass Carbon and Nitrogen

Litter additions or removals had no effect on MBC in either year of the experiment, but increased MBN in the first year. Litter effects on microbial biomass have been previously reported, although the direction of the effect has been dependent on the study and ecosystem. Other studies found removal of litter to lower MBC in wet tropical forest in Cost Rica (Leff et al. 2012), and a tropical forest in Puerto Rico (Y. Li et al. 2004). However, in contrast with our results litter removal increased MBC in some cases in a temperate deciduous forest in Germany (Huang and

Spohn 2015). Litter addition above ambient generated higher MBC in a wet tropical forest (Leff et al. 2012), although there was no effect of litter addition (combined with warming) in a sub-arctic heath northern Sweden (Rinnan et al. 2008). Similar to our findings the absence of litter lowered MBN in lowland tropical forest in Costa Rica (Wieder et al. 2012). While litter addition only increased MBN in the first year of the study MBC did show similar patterns, and so the encroachment of deciduous shrubs may then increase carbon pools altering microbial biomass as they are generally C-limited (Xu et al. 2013). While litter did not increase MBC in our plots, this contrasts the idea that microbial C relies on litter production (Zak et al. 1994). Microbial C can also be affected by soil moisture, which we did see increase with litter addition, however the effects may not have been strong enough to alter MBC. Based on our results increasing deciduous shrub litter will most likely increase MBN, although it may take some time for the indirect effects of litter on soil moisture to change MBC.

Concerning plant exclusions, in could be the drastic reduction of MBC in removal plots could have altered soil microbial activity as C availability decreased through root mortality (Zak et al. 1994). Other possibilities are that soil microbial carbon can be altered via a host of environmental variables such as temperature, SM, and rainfall (Feng et al. 2009). Temperature can affect carbon transformations and thus microbial biomass (Nicolardot et al. 1994), however, shrub removals had lower MBC even though those plots had higher temperatures and so it probably was not a factor. The effects of shrubs will most likely increase soil microbial C via root exudation relative to bare ground, potential increasing carbon mineralization.

Respiration

The soil respiration linear rate (SRLR) showed no response to either experimental manipulations in June or July of 2016 (the only year in, which it was measured). A meta-analysis

including arctic, boreal, temperate and tropical regions showed soil respiration rates decline with litter removal and increase with its addition (Xu et al. 2013). Other studies confirm this observation as litter addition increases soil respiration in a neotropical savanna in Brazil (Villalobos-vega et al. 2011), a subtropical forest southern China (Fang et al. 2015), temperate deciduous forest in Tennessee (Garten 2009), a pine plantation China (Fan et al. 2015), a temperate deciduous forest in Germany (Huang and Spohn 2015; Park and Matzner 2003), and in an old growth coniferous forest in Oregon (Sulzman et al. 2005). There have been mixed responses reported for litter removal where soil respiration decreased in some cases such as in a pine plantation in China (Fan et al. 2015), a wet tropical forest in Puerto Rico (Y. Li et al. 2004), a subtropical forest in China (WenDe et al. 2013), and a sclerophyll forest in Chile (Fuentes et al. 2014), while it increased in a temperate deciduous forest in Germany (Huang and Spohn 2015).

The main factors governing soil respiration are soil moisture, temperature (Sayer 2006), and fertility (Singh and Gupta 1977). As decomposition and nutrient cycling rates are determined by temperature and moisture (Blok et al. 2011), we would have expected an increase in soil respiration for shrub removal plots or litter addition, respectively. Additionally, litter manipulation can alter soil microbial biomass through an increase in available C spurring microbial growth (Feng, Zou, and Schaefer 2009). Total C in our plots was increased by litter addition in the organic layer, however, it could be that the soil microbes are N limited and therefore cannot access it. Furthermore, estimations of microbial biomass C were substantially lower in shrub removal plots as compared to shrub present plots and we expect soil respiration to correlate with microbial biomass (Wang et al. 2003). However we are measuring the sum of all soil metabolic functions including microbial respiration, root respiration, and faunal respiration (Singh and Gupta 1977) and not just microbial respiration. While temperature is an underlying factor affecting soil

respiration, the destruction of roots in our removal plots may outweigh this, inhibiting direct comparison with shrub present plots as root exudates are supplying labile C to microorganisms. As litter addition and shrub removal had no effect on soil respiration, further time may be required to assess the role of increasing deciduous shrubs on soil C cycling in alpine tundra.

Enzymes

Extracellular enzyme activity (EEA) in the soil organic layer decreased with shrub removal in the first year of the study for phosphatase (aP) and β -glucosidase (BG) with patterns of activity for (NAG) and β -Cellobiosidase (CBH) tending in the same direction. This decrease in activity may result from the decrease in exudate production by shrubs once removed, removing this labile C source for the microbes (Kotroczo et al. 2014).

In the second year of the study aP and BG increased with litter addition with NAG and CBH exhibiting similar (non-significant) patterns. Parallel to our findings, litter addition increased enzyme activity in temperate deciduous forest in Hungary (β -glucosidase, phosphatase; Kotroczo et al. 2014), a wet tropical forest in Cost Rica (NAG, acid phosphatase, β -Glucosidase, b-Xylosidase, b-Cellobiosidase; Weintraub et al. 2013) and Harvard forest in Massachusetts (Lajtha et al. 2014).

EEA is regulated by organic matter inputs to the soil, nutrient limitations of microbes, and pH (Sinsabaugh et al. 2008). The model of “optimal allocation” states that based on the stoichiometry of the substrate, soil microbes will produce EEA relative to the resource most limited (Sinsabaugh and Moorhead 1994). As litter addition increased the relative amounts of aP, BG, NAG, and CBH in the soil organic layer, it provides evidence that the microbes were substrate limited in C, N, P. Total C increased in our ambient litter plots and so further production of EEA by soil microbes may have responded to this increase in C and N sources. Additionally, NH_4^+

increased with litter addition in our plots in 2016, likely indicating mineralization, rather than immobilization, by microbes of the nitrogen in this newly added substrate. Therefore if N is limiting soil biota may not be able to change enzyme concentrations as they might be blocked by physiological or metabolic limitations (Weintraub et al. 2013). Aside from substrate input, the end product of extracellular degradation and current nutrient pools may also suppress enzyme production (Geisseler and Horwáth 2009), this may be why we saw no increase in activity for α -glucosidase and β -Xylosidase. Concerning soil pH, there were no significant variations across treatment, however, it has direct effects on soil EEA as well as the composition of the microbial community (Sinsabaugh et al. 2008). Our results suggest increasing litter from shrub encroachment will increase the production of EEA and subsequent mineralization of organic compounds.

Litter Decomposition

Removal

Litter mass loss increased with shrub removal in both 2015 and 2016. Contrasting to our results, understory removal reduced litter mass loss in a subtropical forest in China (Wu et al. 2011). The decomposition of litter is regulated by components of climate, leaf litter chemical composition, and the microbial community (Coûteaux et al. 1995). Litter decomposition during winter months maybe due to physical degradation (fragmentation by freeze/thaw conditions; Hobbie and Chapin 1996) or microbial activity under the snow layer (McLaren et al. 2017). As shrubs accumulate more snow, subnivean temperatures increase (Sturm et al. 2000), and so microbial activity is likely to be affected (DeMarco et al. 2011). While temperature was higher in our plots during winter months, rates of decomposition was not and so maybe summer had a greater influence. To address this another set of litter decomposition bags have been deployed independently for summer and winter and thus in future years we will be able to test the relative

differences in decomposition as temperatures in shrub removal plots were higher during summer months and intercepted a greater amount of light, possibly leading to higher microbial activity (McLaren et al. 2017) and photodegradation (Austin and Vivanco 2006) respectively.

Litter

While we had no response of decomposition to our litter manipulations, others have found litter addition to increase mass loss in a neotropical savanna in Brazil (Villalobos-vega et al. 2011), a forest in Puerto Rico (Ostertag et al. 2003), with its removal decreasing it in a subtropical forest southern china (Fang et al. 2015). Soil moisture (a primary component of decomposition) at our site was higher in litter addition plots in 2016, with an interaction among treatments occurring in the soil mineral layer over both years, and so it may have had a small effect, however, the rate of decomposition was higher in shrub removal plots. Chemical composition of the litter is unlikely to have an effect as all decomposition bags contained homogenized litter of the same species, although litter addition treatments of *B. glandulosa* may increase the amount of toxic compounds in the surrounding litter (Groot et al. 1997). Concerning microbial activity, MBC increased with litter addition during the first year and was reduced greatly by shrub removal plots in the second year and so you would expect the reduction of soil microbes would reduce decomposition rates, however, this was not the case.

Based on our results the expansion of deciduous shrubs will slow the decomposition of organic material as rates were higher in shrub removal plots indicating physical degradation by light interception and climate. However, as litter addition increased with soil moisture, this may have a larger effect on decomposition with the accumulation of litter over time.

Synthesis

In assessing the relative impact of shrub encroachment, the employment of a fully factorial experimental design allowed for the effects of shrubs and their litter on ecosystem properties to be determined independently and in combination with each other.

Our results support current ideas that shrub expansion will affect soil temperatures, which may influence other ecosystem properties via physical effects. However, these temperature effects did not always cause the predicted changes in associated soil variables. For example, although cooler summer temperatures under the shrub canopy was predicted to decrease microbial biomass and EEA, there was no response by these variables. These variables may be less responsive to temperature and more to the other positive effects of shrub presence (i.e., root exudates). The decrease in temperature during summer months with shrubs should have also decreased C mineralization, although we found no effect on soil C; effects on total soil C may take years to become evident. Effect on soil nutrients by shrubs are likely less due to changes in soil temperature (which would have decreased nutrients) and more likely due to increases in both plant uptake and root when shrubs are present. Lastly, shrub presence reduced decomposition rates indicating overall nutrient turnover and carbon mineralization will most likely be slowed by increasing shrubs, although the higher decomposition rates of shrub litter specifically may mitigate these effects (Figure, 17-18).

In addition to the other direct effects of shrubs, changes in litter quantity appears to be an important mechanisms through which shrubs influence physical properties, available nutrients and microbial activity. Litter addition increased soil moisture, which is known to affect a number of microbial processes. This increase in soil moisture, may be at least partially responsible for the corresponding increase in microbial biomass and enzyme activity. As litter treatments did not

affect soil temperature, temperature was not a driving mechanism behind these changes in microbial activity. Additionally, the additional substrate (i.e., the added litter) may also be driving these microbial effects; litter addition treatments were shown to have higher microbial biomass, soil CN and soil available nutrients, all of, which may increase with increased substrate availability. Given the positive effects of litter on both nutrient availability and microbial processes, we can conclude that increased litter abundance is an important mechanism through, which shrub encroachment will affect tundra ecosystem properties (Figure, 19).

One of the challenges of this experiment, and of many ecosystem studies particularly those in arctic and alpine ecosystems, are that short term responses may not be reflective of those on the long term. Some variables (such as available nutrients and microbial activity) may change day to day, whereas others (such as soil carbon) may only change on the order of years or decades. We project that on the long term physical properties like soil temperature and light interception will continue to be governed by the physical structure of shrubs, while soil moisture will likely continue increasing with litter addition. While shrubs had no independent effect on soil CN yet, this variable may take several years to change from root and leaf litter inputs. We also predict that litter addition will remain a dominant factor in increasing soil nutrient content and availability. Lastly, we will likely continue to see higher microbial activity in litter addition plots due to the positive effect of litter on soil moisture and CN pools. In predicting long term effects, we must balance contradicting influences, such as plant uptake and root exudates increasing nutrient mineralization, as well as larger background influences (i.e., increasing global temperatures and length of seasons).

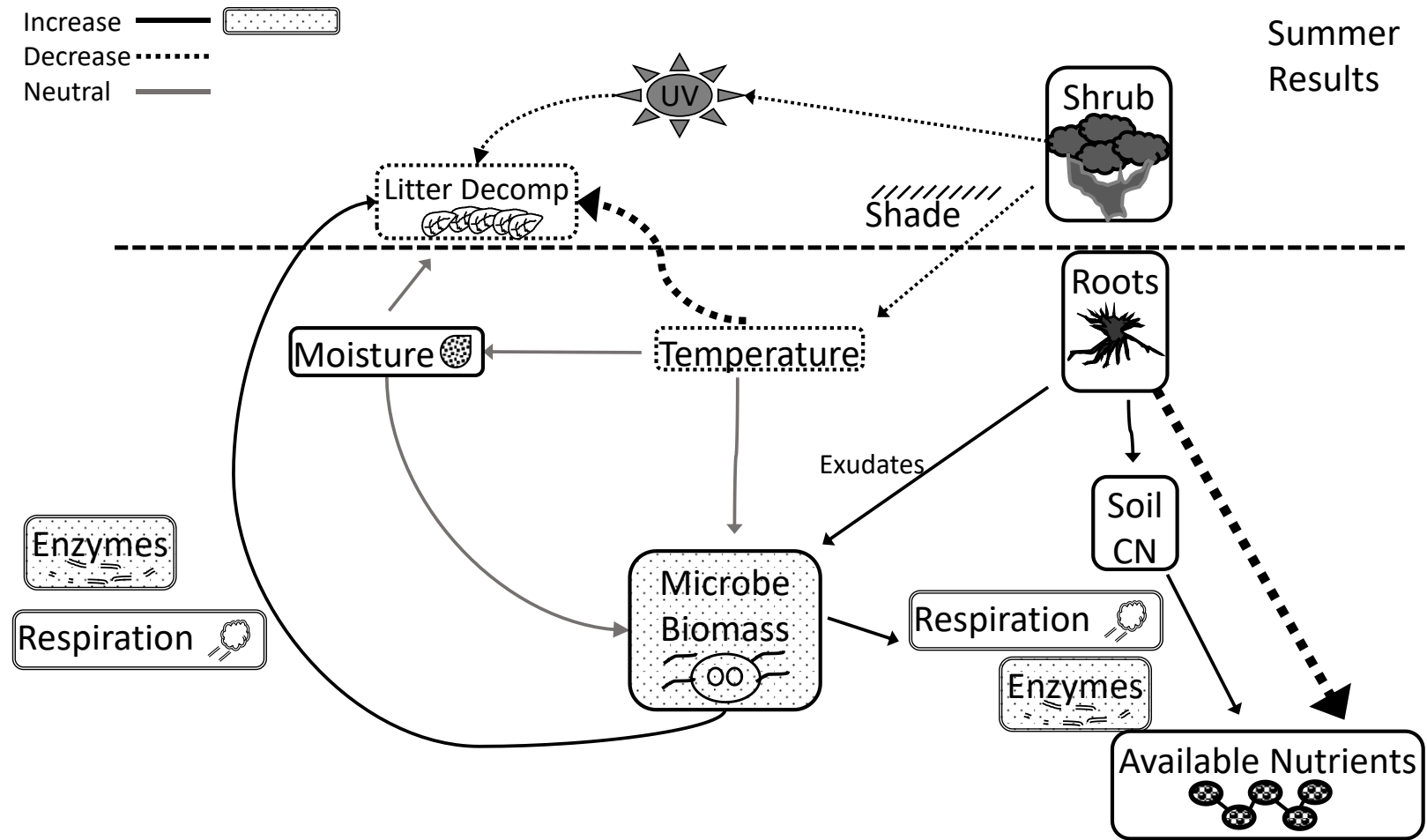


Figure 17 – Conceptual map depicting results for independent effect of shrubs during summer. Thicker lines represent the dominant mechanisms.

Increase ——— [dotted box]
 Decrease
 Neutral ———

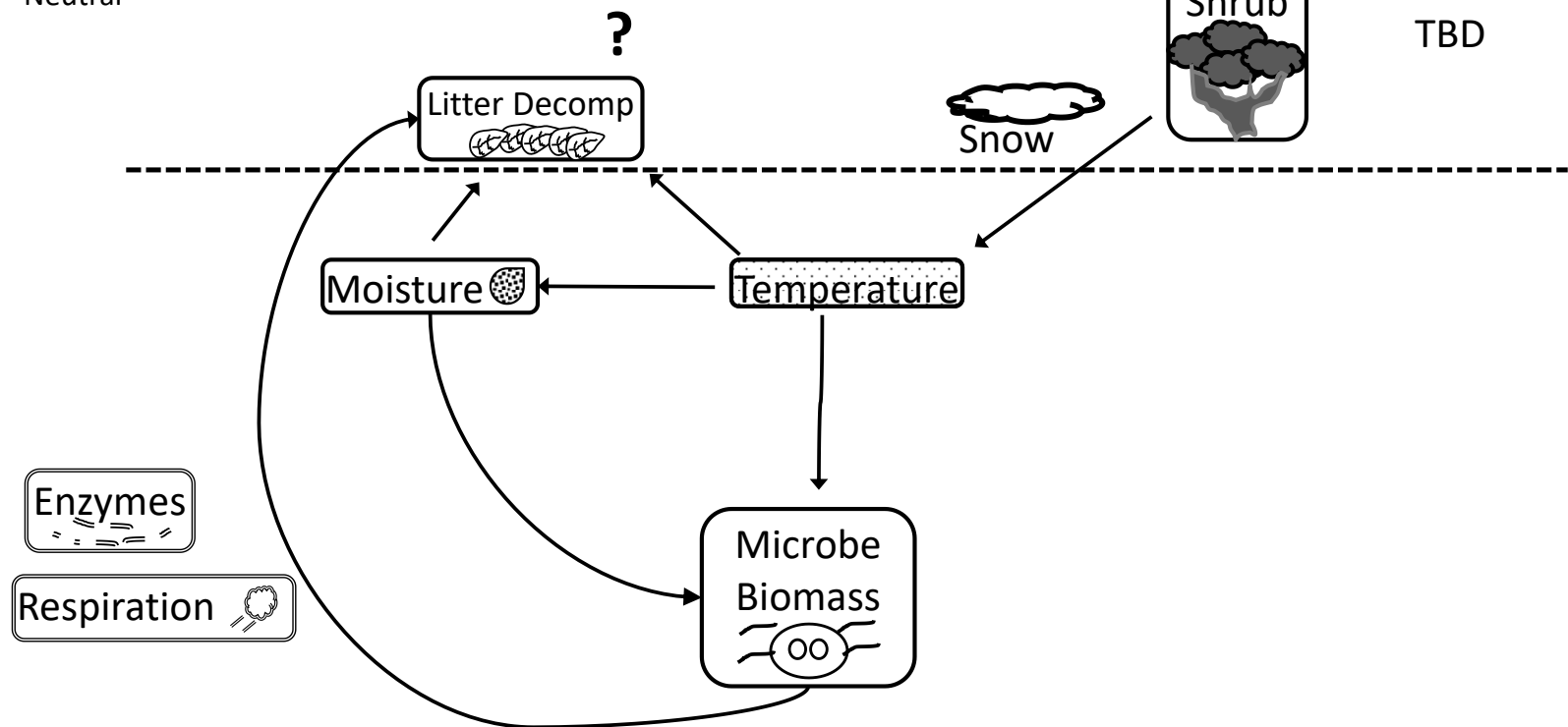


Figure 18 – Conceptual map depicting results for independent effect of shrubs during winter

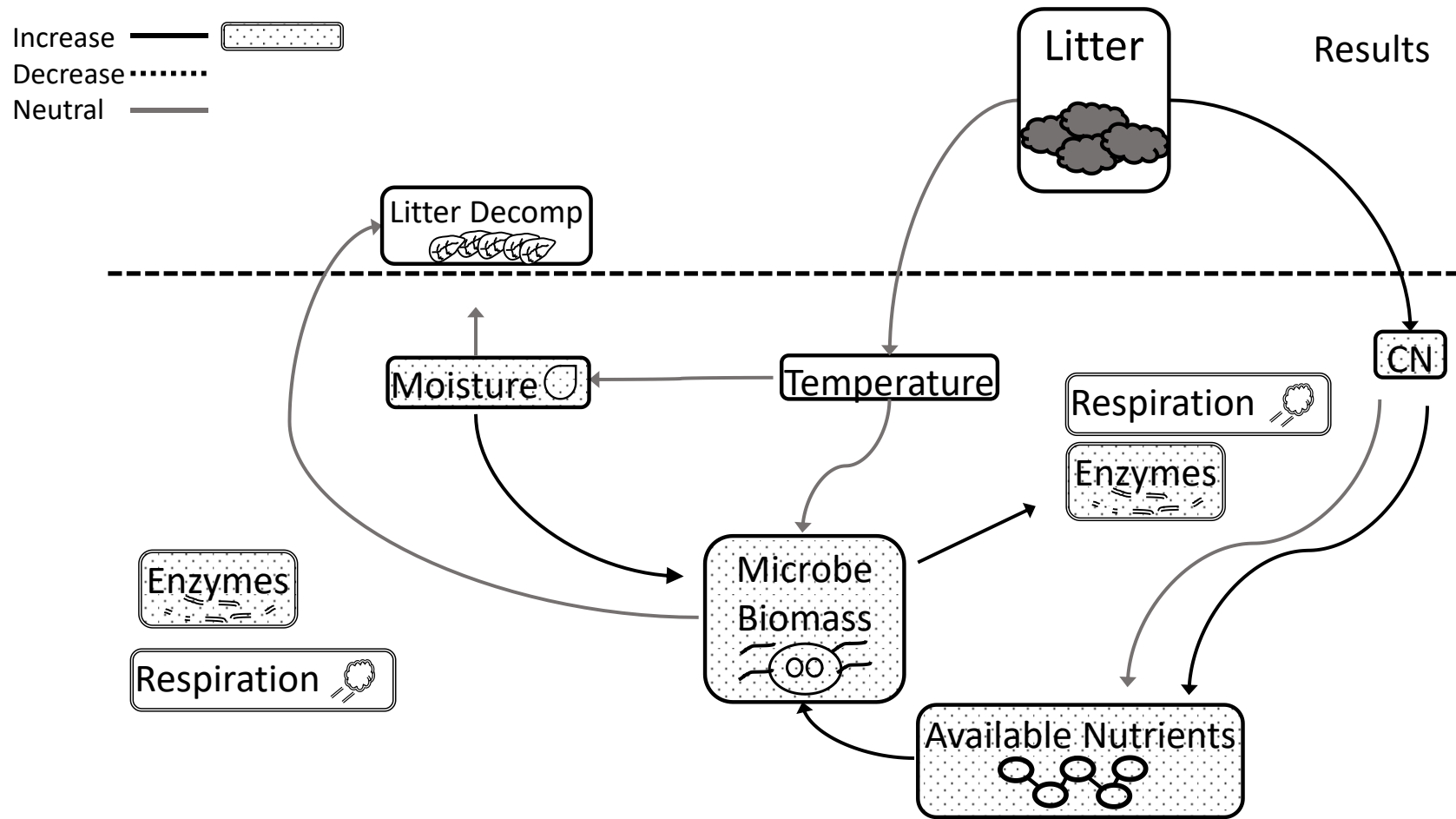


Figure 19 – Conceptual map depicting results for independent effect of litter

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Vita

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