Seeing the forest for the soil: topographic controls on soil carbon dynamics in the boreal mixedwood forest

by

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

Master of Science

in

Soil Science

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University of Alberta

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Abstract

Boreal forest soils store an estimated 272 Pg of carbon. Due to a high degree of spatial heterogeneity, there is a wide range in carbon stores in this ecosystem. Changes in topography and forest structure are important to carbon distribution, influencing the soil microclimate and the chemical quality and quantity of litter inputs. With increasing pressure from a changing climate, developing our understanding of carbon dynamics and adapting our management strategies in the boreal forest is paramount. The goal of this research was to investigate how soil moisture gradients influenced soil organic carbon storage and stability, in both natural and harvested stands in the boreal mixedwood forest. I investigated the long-term (17 years) evolution of soil properties following variable retention harvest at the EMEND project, where aspen had primarily regenerated in conifer-dominated, and deciduous-dominated stands. The topographic Depth-to-Water (DTW) index was used as a proxy for soil moisture to model relationships in the forest floor and mineral soil (0-7 cm) at the stand level, and to see if harvest and aspen regeneration had altered these relationships compared to uncut control stands. In undisturbed stands, relationships between soil properties and the DTW index were more strongly expressed in the mineral soil compared to the forest floor, with increased carbon stocks, and increased carbon and nitrogen concentrations at the wet end of the gradient. Relationships between the DTW index and forest floor properties were altered to a greater extent by harvest, but these effects varied between cover types. In order to gain a deeper understanding of the topographically-driven distribution of carbon quality and stocks at the stand-scale, I performed an in-situ soil respiration study on a hillslope, which featured well-drained Orthic Gray Luvisols with an aspen dominated canopy upslope, and transitioned to poorly-drained Gleysols with a white spruce dominated canopy, at downslope positions. Measurements were taken from the surface of the forest floor, as well as from the exposed mineral soil in order to partition forest floor respiration from that of the underlying mineral profile. In addition, a controlled laboratory incubation (210 days) was conducted on forest floor materials to further investigate the linkage between soil organic carbon quality and respiration fluxes. Over the course of the in-situ experiment, mineral soil respiration was consistently lower at downslope positions due to lower temperatures and higher water content. In-situ forest floor respiration was approximately equal along the hillslope, with different microclimatic controls on fluxes. At downslope positions, respiration was controlled by temperature, while respiration upslope was related to water content. Respiration rates measured during the laboratory incubation were greater than in-situ forest floor respiration by a factor of ten. The labile carbon pool at downslope positions was nearly double upslope, suggesting that under warming, the forest floor at these lower positions may be a much larger carbon source. Both the stand-scale and hillslope scale studies indicated that topographic variation had greater influence over mineral soil properties, while the forest floor was also affected by canopy composition.

I dedicate this work to my family.

Acknowledgements

I would like to thank my supervisors, Dr. Sylvie Quideau and Dr. Miles Dyck, for your mentorship over the past three years. I would also like to thank my external examiner, Dr. Dani Degenhardt, and the chair for my defense, Dr. Derek MacKenzie. Sylvie, thank you for welcoming me into your group, I am incredibly lucky to have stumbled my way into soil science, and to have had your guidance and support throughout my studies.

To my colleagues in the Soil Biogeochemistry group, and in the Department, it has been a pleasure to get to know you, thank you for the support and thought-provoking conversation.

To my fellow researchers at the EMEND project, I am grateful to have had the opportunity to work with you; thank you all for supporting me in the field, for your love of campfires, and for your willingness to stay up for the northern lights.

I am fortunate to have made a wonderful group of friends here in Edmonton, thank you all for your encouragement, and thank you for the laughter; you made me feel at home.

I have endless gratitude for the support from my family. Thank you all for encouraging me to pursue my passions and shaping me into the person I am today.

I would like to acknowledge the laboratory and field support of Jela Burkus, Preston Sorenson, Maks Igdyrov, Laureen Echiverri, Charlotte Norris, Will Barnes, Sylyanne Foo, Zoltan Domahidi, Micki Baydack, Allan Harms, and Amy Hayden.

I would also like to acknowledge the financial support of the Natural Sciences and Engineering Research Council of Canada; The Government of Alberta, Queen Elizabeth II Scholarship (2017, 2018); The University of Alberta, Northern Research Award (2016); and The Department of Renewable Resources. I would also like acknowledge EMEND’s project partners: Daishowa Marubeni International (DMI), Canadian Forest Products (CANFOR), and Alberta Agriculture and Forestry. In addition I would like to acknowledge Dr. Jae Ogilvie and his colleagues from the University of New Brunswick, for their work developing and implementing Depth-to-Water index at the EMEND project.

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Chapter 1. Introduction

1.1 The Boreal Forest

The boreal forest is one of the largest forest ecosystems, spanning portions of North America and Eurasia. It occupies the circumpolar belt between 50°N to 65°N, covering approximately 362 million ha; it is considered one of the most important biogeoclimatic areas (Brandt, 2009). The boreal is the most northern forest ecosystem, and its climate is characterized by a short growing season with low annual mean temperatures ranging between -12 °C and 6 °C (Pan et al., 2013). The amount of precipitation is variable in this ecosystem: in the boreal plains of western Canada, annual rainfall amounts to approximately 500 mm, while in the boreal shield of eastern Canada, precipitation can exceed over 1000 mm (Price et al., 2011). The boreal forest is also considered to be one of the youngest ecosystems, established through the northward migration of coniferous species following glacial retreat 15000 years ago (Yansa, 2006). Unlike other forest ecosystems which are not acclimatized to extreme winter temperatures, tree species of the boreal are dominated by cold-tolerant species (Brandt et al., 2013). However, because of the climatic constraints, the net primary production in the boreal forest is the lowest out of all forest ecosystems (Saugier et al., 2001).

Despite its low productivity, carbon stocks of the boreal forest are second only to the tropical forest, containing an estimated 272 PgC (Pan et al., 2011). These ecosystems have widely different mechanisms governing carbon storage: while tropical forests contain larger stocks overall, the boreal forest stores a much larger proportion in the soil. In a study of carbon distributions, Pan et al., (2011) reported that 60% of the boreal forests carbon stores were contained in the soil, while only 32% of the carbon in tropical forests were sequestered in the soil (Pan et al., 2011). A large reason for this variation is due to the climate of the boreal, which hinders the decomposition of organic matter, allowing it to accumulate in the soil (Lal, 2005). In addition, the functional traits of plant species in the boreal are also resistant to decomposition. Compared to other forest ecosystems, dominant plants species of the boreal are slow growing, nutrient poor, and rich in secondary metabolites, reducing carbon losses through herbivory and decomposition (De Deyn et al., 2008).

1.2 Carbon cycling in the boreal forest under a changing climate

Forest ecosystems play an important role in the global carbon cycle, effectively sequestering carbon in biomass and soils. This role in carbon storage may be altered in the future, especially in the boreal forest, where the effects of warming are expected to be more severe (IPCC, 2007). Climate change models presented by Price et al. (2013) predict increases in temperature across the North American boreal forest. In the boreal plains mean daily minimum temperature is projected to rise by 4.5 °C during the spring, summer, and autumn, and by 6.5 °C in the winter by the year 2100. Although these models also predict an increase in precipitation across the range of the North American boreal forest, most regions are expected to face more frequent and severe droughts, due to higher temperature-induced evaporative demand. Such effects are predicted to have a negative impact on the boreal carbon stocks.

The biota of the boreal forest is well adapted to cold temperatures, and research has demonstrated that, with warming, an increase in metabolic respiration may lead to an overall decline in the fitness of many boreal plant communities (Boulanger et al., 2017). However, the impact of climate change will not be uniform among species. In a study comparing tree-ring chronology and mortality between trembling aspen and white spruce, two dominant species in the western Canadian boreal forest, Jiang et al. (2016) found that white spruce was more severely impacted under drought stress, suggesting that this mechanism may be a future driver altering boreal forest composition towards early successional species. Similarly, through long term study plots, Chen and Luo (2015) predicted that, while warming and increased drought will have negative effects on aboveground biomass across the boreal forest, the impact will be greatest for late successional species such as white spruce.

Altering soil climate conditions as well as boreal plant communities may have a profound influence on carbon stocks and cycling. The amount of soil organic carbon is controlled by the quantity and chemical quality of inputs into the soil, and the rate of output from the soil through decomposition (Lützow et al., 2006). Carbon stocks are regulated by these processes of inputs and outputs, and are subject to change until they reach a state of equilibrium (Simonson, 1959).Quantifying the multiple effects of climate change on the boreal forest poses a great challenge, especially because of the uncertainty of their interactions (Price et al., 2013). The balance governing stocks will be strongly influenced by the changing climate, in addition to changes in the soil moisture regime and shifts in vegetation communities.

Slow decomposition rates in the boreal have fostered significant soil organic carbon stocks, a large proportion of which are said to be labile (DeLuca and Boisvenue, 2012; Neff and Hooper, 2002). Soil respiration is a combination of autotrophic and heterotrophic metabolism. It is one of the most important components of carbon cycling in forest ecosystems (Davidson et al., 2006), and can serve as a proxy for carbon stability and decomposition. Because of its temperature dependence, CO_2 production via respiration may increase with warming, which could potentially create a positive feedback loop under climate change scenarios (Davidson and Janssens, 2006). Such an effect may alter the function of the boreal forest from a carbon sink, to a net source in the future (Kurz et al., 2014).

1.3 Topographic controls on carbon dynamics

In the western boreal forest , there is a high degree of physiographic variability occurring across the landscape (Beckingham et al., 1996). Topography and drainage are especially important to carbon storage in the boreal forest: carbon stocks in both the forest floor and mineral horizons have been shown to increase at lower topographic positions with poor drainage (Olsson et al., 2009; Rapalee et al., 1998; Seibert et al., 2007). While productivity in this ecosystem may be limited under higher soil moisture conditions, a widely accepted explanation for the accumulation of organic matter is through inhibited decomposition (Olsson et al., 2009; Rapalee et al., 1998).

Topography has a strong influence on soil microclimatic conditions, downslope areas in the boreal forest generally have higher water content and lower temperatures (Xu et al., 2002). While both low temperature and high soil moisture can restrict turnover, these microclimatic conditions are inversely related in soils, and their effects on in-situ respiration and decomposition are difficult to separate (Davidson et al., 1998a). While low temperature restricts the kinetic activity of soil microorganisms, high soil moisture content reduces O_2 diffusion through the soil profile, restricting the ability of microorganisms to oxidize organic matter (Davidson and Janssens, 2006). In a study comparing chemical constituents in the forest floor, Hannam et al. (2004) found that, compared to aspen stands, larger quantities of labile carbon had accumulated in spruce stands, and attributed this to poor environmental conditions restricting the breakdown of organic matter.

In the boreal forest, the soil moisture regime and vegetation communities are related: changes in topography and the water table depth are closely linked to forest cover, with wetter, low lying areas dominated by coniferous trees, and drier, upslope areas dominated by broadleaf species (Albani et al., 2005; Bartels et al., 2018; Echiverri, 2017; Nijland et al., 2015). Combined, these features are important to the distribution and stability of carbon across the boreal forest.

1.4 The role of cover type on carbon dynamics

In the western Canadian interior, the Boreal Mixedwood forest is a mosaic featuring cold-tolerant coniferous and broadleaf species (Natural Regions Committee, 2006). Boreal plant communities have a profound influence on soil biogeochemical properties. Vegetation is significant to the quantity, nutrient content, and chemical composition of both above- and belowground litter inputs; in addition, vegetation plays an important role in regulating the soil microclimate. Combined, these features have significant influence on soil organic carbon cycling (Raich and Tufekciogul, 2000).

The canopies of shade-tolerant conifer trees such as white spruce are effective at the interception of light, and shade much of the understory (Messier et al., 1998). Stands of increasing conifer composition have higher moss cover, and facilitate decreased temperatures and higher water contents (Bond-Lamberty et al., 2005; Oechel and Van Cleve, 1986). This microclimate is in contrast to stands of shade-intolerant broadleaf species, which foster brighter understory conditions, lower moss cover, and warmer soils (Bartels et al., 2018; Messier et al., 1998; Olsen and Van Miegroet, 2010).

Stands of broadleaf and conifer species also vary greatly in terms of the amount of litter inputs to the soil carbon pool. In a systematic review comparing soil properties between aspen and coniferous stands, Laganière et al. (2017) reported that forest floor stocks were larger in conifer dominated stands in the majority of studies. Although deciduous trees produce more aboveground litterfall than most conifers, bryophytes represent a large portion of the soil organic carbon pool in conifer dominated stands (O’Connel et al., 2003). In addition, conifer species have been shown to contribute a larger proportion of NPP to root biomass, enhancing soil carbon stocks through litter inputs to the forest floor (Gower et al., 1997).

Coniferous and broadleaf species also differ greatly in terms of nutrient and organic matter cycling, features owing to both to the physical and chemical properties of litter inputs as well as microbial communities present in the soil (Laganière et al., 2010). The needle litter of conifer stands typically is more resistant to herbivory and decomposition, and generally has a lower palatability, nutrient content, and pH, compared to broadleaf litter (Laganière et al., 2017). In addition, mosses are known for their rapid nutrient acquisition and slow decomposition (Oechel and Van Cleve, 1986). For these reasons soil nutrient levels in spruce stands are typically lower (Jerabkova et al., 2006), and studies have shown that low nutrient concentrations inhibit the initial stages of litter decomposition, favouring organic matter accumulation (Zhang et al., 2008). The chemical composition of soil organic matter is also an important factor to stability: for example, studies have found that forest floors in aspen dominated stands have higher lignin contents compared to spruce forest floors, which may inhibit their decomposition (Hannam et al., 2004; Laganière et al., 2013).

Combined, these abiotic and biotic features of conifer-dominated stands are thought to limit soil organic matter decomposition compared to stands of broadleaf species, and allow labile carbon to accumulate. Studies comparing in-situ respiration fluxes between these cover types have found lower CO_2 efflux under conifer-dominated stands during the growing season, supporting this notion (Buck and St. Clair, 2012; Laganière et al., 2012). However, many studies on soil respiration have occurred on relatively homogeneous terrain (Borken and Beese, 2005; Buck and St. Clair, 2012; Khomik et al., 2006; Laganière et al., 2012). While this research has been essential to our understanding of the primary controls of respiration, few inferences can be made across the landscape, because of the diverse topography and forest structure in this ecosystem (Pacific et al., 2008).

1.5 Forest management

Approximately two-thirds of the boreal forest is currently under some form of active management (Gauthier et al., 2015). Natural resource extraction is an important industry in Canada; while both forestry and oil and gas exploration have a significant role in the Canadian economy, they are also major disturbances to the boreal forest. In Alberta alone the area currently under active management spans over 13 million hectares (Alberta Agriculture and Forestry, 2017). Harvest involves the removal of biomass, and changes the soil microclimate, typically leading to losses in nutrients through mineralization and leaching (Kurz et al., 2013). Through decreases in primary production, in addition to increased mineralization, harvesting can lead to both short and long term losses in carbon sequestration (Jandl et al., 2007; Kishchuk et al., 2015).

To properly manage the boreal forest demands an understanding of the high degree of heterogeneity that occurs across the landscape. Because of the complexity of factors influencing carbon dynamics, it is important to develop new techniques for quantifying carbon stocks and soil properties at the landscape scale (Townshend et al., 1991). Remote sensing has advanced our ability to this end. The Wet-Areas mapping based Depth to water (DTW) index is a topographic index that predicts soil moisture through high resolution digital elevation models (Murphy et al., 2007). It has been used in the boreal to model site-index and soil drainage class, tree cover type and post-harvest recovery, and bryophyte and understory vegetation distributions across the boreal (Bartels et al., 2018; Echiverri, 2017; Nijland et al., 2015; Oltean et al., 2016). As of yet, it has not been used to model carbon stocks or carbon quality across the landscape.

1.6 Objectives and outline

Many studies have compared soil carbon stocks and stability among various cover types in the boreal forest (Laganière et al., 2017). In addition, the influence of soil moisture on soil carbon properties is also a well explored area (Dalsgaard et al., 2016; Kelsey et al., 2012; Rapalee et al., 1998; Seibert et al., 2007). However, the combined influence of topographically driven changes in soil moisture and vegetation gradients on soil carbon dynamics remains an understudied topic in the boreal forest. This is especially the case for soil respiration studies, which have minimized the significant natural gradients caused by topographic variability (Pacific et al., 2008).

As the body of knowledge surrounding carbon distribution and stability in the boreal continues to grow, so will our ability to manage this ecosystem. The impacts of harvesting on soil properties have been shown to extend beyond 15 years, highlighting the need for long-term studies (Kishchuk et al., 2016). Due to the topographic and structural complexity of the boreal forest, there is the need for developing tools and strategies to enhance management capabilities (Townshend et al., 1991).

The primary objective of this research was to investigate how soil moisture influenced soil carbon distribution and stability, and whether harvest altered these relationships. Specifically, the objectives of Chapter 2 were to i) compare the long-term effects of retention harvesting and stand evolution in deciduous-dominated and conifer-dominated stand types, ii) model the relationships between the DTW index and soil properties in undisturbed stands, and iii) investigate how retention harvesting had altered the relationship between soil properties and the DTW index among cover types. This study aimed to probe the long-term evolution of soil properties following harvest, and to utilize the DTW index to model carbon distributions among natural and harvested stands, in order to enhance our understanding of stand-scale soil carbon quality distribution.

Through a study at the hillslope scale, Chapter 3 focused on soil respiration fluxes and carbon stability with pronounced changes in the soil microclimate and forest structure. The objectives of Chapter 3 were to i) measure soil respiration along a hillslope transitioning from trembling aspen dominated cover upslope, to white spruce dominated cover downslope, and ii) compare these in-situ respiration fluxes with a controlled laboratory incubation of the forest floor. In-situ respiration fluxes are controlled by the combined influence of forest floor composition and the soil microclimate. By comparing these findings with a laboratory incubation where all soil materials experienced the same moisture and temperature conditions, we were able to remove the influence of climatic conditions to compare carbon quality along the hillslope. The aim of this chapter was to further our knowledge of the relationships uncovered in Chapter 2, through an enhanced understanding of the controls on carbon stability.

In Chapter 4, a summary and synthesis of the overall findings of Chapters 2 and 3 are presented, as well as some management implications of this research.

Chapter 2. Long-term harvesting effect on boreal forest soils in relation to the Depth-to-Water Index

2.1 Introduction

The boreal forest is one of the largest forest ecosystems in the world, ranging from 50°N to 60 °N in the northern hemisphere (Lorenz and Lal, 2010). This ecosystem comprises a large portion of Canada, spanning 552 million ha (Brandt, 2009); indeed, this is the largest forest ecosystem in the country. Soils are important carbon reservoirs in the boreal, comprising up to 85% of its total stocks (Dixon et al., 1994). In addition to its size and vast carbon stores, this ecosystem is also central to Canada's resource extraction based economy, both for the production of wood products and for oil and gas exploration. Combined with an intensified disturbance regime arising from climate change, management of the boreal influences stand dynamics, ultimately impacting soil organic carbon stores (Bhatti et al., 2002). As the effects of climate change, and the intensity of such disturbances continue to grow, so will the importance of understanding and managing boreal carbon stocks.

Forestry is an important component of the Canadian economy. In Alberta, the area currently under active management encompasses 13.3 million hectares. Each year the Government of Alberta sets quotas for the extraction volume; from 2014-2015, a volume of 32.4 million m^3 of coniferous and broadleaf species were allocated for harvest (Alberta Agriculture and Forestry, 2017). In addition to forestry, the oil and gas industry also has a significant role in timber extraction, where the Oil Sands represent a total 475 thousand hectares of available surface minable area, of which almost 90 thousand hectares have already been disturbed. In total, the oil sands area comprises 14 million hectares, overlaying much of the land allocated for forestry. Combined, these industries serve as a significant disturbance to the boreal forest and its carbon stores (Gauthier et al., 2015).

The boreal forest contains an estimated 471 Pg of carbon, about 23% of the global soil C (IPCC, 2001). In this ecosystem, poor climatic conditions inhibit the complete degradation of organic matter, allowing it to accumulate in the forest floor and in the mineral soil. This is a feature unique to boreal forest soils, and is defining in their significance to the global carbon cycle (DeLuca and Boisvenue, 2012). Across the range of the boreal, there is a great deal of heterogeneity, due to differences in landscape morphology and forest structure, ultimately impacting the quantity and chemical quality of carbon inputs, as well as the physical constraints on decomposition or organic matter accumulation. Stands of coniferous and broadleaf trees have vastly different soil properties arising from differences in tree morphology and the physical and chemical properties of litter inputs into the soil (Hannam et al., 2004; Laganière et al., 2017, 2013; Lindo and Visser, 2003).

In addition to biological influences on carbon dynamics, hydrological conditions also play an important role. The depth of the water table and soil moisture regime are both well-known regulators of carbon dynamics, where wetter soils typically store larger carbon stocks compared to dry sites in organic and especially mineral horizons (Dalsgaard et al., 2016; Olsson et al., 2009; Rapalee et al., 1998). Interestingly, the biological and hydrological constraints on organic matter cycling are not independent in the boreal, and stands of increasing conifer composition generally occupy wetter sites across the boreal mixedwood forest (Nijland et al., 2015).

The objectives of forest management have evolved from optimizing wood production, to viewing forests as complex ecosystems, where optimal management maintains their broad range of ecological goods and services (Lindenmayer et al., 2012). Variable retention harvest was introduced over 25 years ago, to offset the negative impacts to biodiversity brought on through clear-cutting. Variable retention involves partial stand retention during harvest in order to maintain aspects of forest structure and function, to more closely mimic natural disturbances (Fedrowitz et al., 2014). In 1999, this strategy was applied in the boreal mixedwood forest of Alberta at the Ecosystem Management Emulating Natural Disturbance (EMEND) project, where harvest was conducted at varying retention levels among stands of the dominant tree species across the landscape, with the ultimate objective of monitoring the uninterrupted evolution in vegetation and soil characteristics for the full lifespan of the forest (Spence et al., 1999). Logging operations at EMEND did well to preserve the soil through dedicated machine corridors and winter harvest, and previous reports found that changes in soil properties due to variable retention harvest by six years were limited (Kishchuk et al., 2014). In the years following harvest, trembling aspen (*Populus tremuloides* Michx.) was primarily recruited in all stand types (Echiverri, 2017; Nijland et al., 2015).

Increasing carbon storage and sequestration in the boreal has become a management objective of increasing priority due to heightened carbon emissions (IPCC, 2007). Due to the complexity of carbon dynamics in boreal forest soils, in addition to challenges in their management, it is paramount to develop better tools and strategies for more reliable information for decision making (Townshend et al., 1991). Remote sensing technologies have advanced our ability to map both topographic and vegetative features of the boreal forest (Nijland et al., 2015). The Wet Areas Mapping (WAM) based Depth-to-Water (DTW) index has been used by industry for operations planning, and prior research conducted at the EMEND project, as well as in other forested areas in Alberta, has demonstrated its utility in predicting site index, stand type, and in modeling bryophyte and understory community composition and abundance (Bartels et al., 2018; Echiverri, 2017; Murphy et al., 2007; Oltean et al., 2016). The DTW index may also be useful to model carbon storage and sequestration in the boreal, although this has yet to be demonstrated.

The EMEND project is a unique experiment offering the opportunity to observe the long-term response of soil properties to disturbance and regeneration. In this study we looked at soil properties in the forest floor and upper mineral soil (0 – 7 cm) in conifer-dominated and deciduous-dominated stands across the EMEND project, at varying degrees of retention harvesting. Our sampling was stratified along a moisture gradient modeled using the DTW index as per Echiverri (2017). Our first objective was to investigate how retention harvesting had influenced soil properties 17 years post-harvest; we were also interested to see if trembling aspen regeneration following harvest had altered differences in soil properties between the two stand types, or whether ecological legacies remained in stands formerly dominated by conifers. Our second objective was to investigate whether the DTW index was related to soil properties, including carbon stocks, in uncut stands, and to see if the relationships were altered through harvesting.

2.2 Materials and methods

2.2.1 Study area and selection of sites for soil sampling

The study was conducted at the EMEND Project, located in the lower foothills region of the boreal mixedwood in Alberta, Canada. EMEND is an experimental forest, where green tree variable retention (VR) harvest was conducted in 1999; for a full description of the experimental design see Luchkow et al. (2001). The mean annual temperature of the study site is 1.2 ˚C, with a mean annual precipitation of 413 mm, of which 38% accumulates as snowfall. A detailed description of the soils at EMEND can be found in Kishchuk (2004). Briefly, there are two regions of glacial-origin materials: in the southwestern portion of the research site, soils primarily developed on glacial till with overlying glaciolacustrine deposits, and in the northeastern portion, development occurred on glaciolacustrine and lacustro-till deposits. Soils are predominately fine-textured, and belong to the Luvisolic and Brunisolic orders, with Gleysols and Organic soils occurring to a smaller extent in depression or discharge areas.

Our study was based in conifer-dominated stands (CDOM; consisting of >70% conifer canopy cover) of white spruce *Picea Glauca* (Moench) Voss), and deciduous-dominated stands (DDOM; consisting of >70% broadleaf cover) of trembling aspen. We sampled across various retention levels, including clear cut (2%), 20%, 50% retention, and lastly 100 % retention, which served as uncut control stands. Each retention treatment covered 10 ha in size and is herein referred to as a “compartment”. Each compartment was replicated in triplicate across the experiment which spanned more than 1000 ha.

A moisture gradient was modelled across the experiment using the WAM-based DTW index generated from a LiDAR-derived high resolution (1 m^2) digital elevation model collected in 2008 (Nijland et al., 2015). DTW serves as a measure of the probability of soil to be saturated. Its units are in meters and it approximates the depth to the water table, with lower values predicting wetter soils, and higher values predicting drier soils (Murphy et al., 2007). DTW values are sensitive to the catchment area needed to form a flow channel, known as the flow-initiation threshold, which ranges from 0.5 ha^{-1} to 16 ha^{-1}. For example, DTW based on a 0.5 ha^{-1} flow initiation threshold will predict that a greater proportion of the landscape is wet compared to a- higher threshold (Bartels et al., 2018).

Sampling occurred within three replicate compartments of the four harvesting treatments (2%, 20%, 50%, and 100% retention) within each of the two stand types, conifer-dominated and deciduous dominated, for a total of 24 compartments. Within each compartment, 7 – 13 locations were sampled along the DTW index with increasing wetness as per Echiverri (2017).

2.2.2 Sample collection and preparation

At each selected location, nested plots had been previously established for research investigating the influence of DTW on understory vegetation and regrowth with variable retention harvest treatments (Echiverri, 2017; Nijland et al., 2015) . In general, regrowth was higher under deciduous-dominated parent stands and at the drier end of the DTW gradient due to the rapid regeneration of aspen. Conifer-dominated understory community composition was the least resilient under variable retention harvesting treatments, a feature suspected to originate from the substantial changes in understory community composition brought on by the recruitment of aspen.

Within each plot, an undisturbed and representative area was selected and cleared of live vegetation, including living (green) moss prior to soil collection. A plug of the entire forest floor was collected using a 100 cm^2 sampling frame. Forest floor morphology was described according to Green's taxonomic classification system (Green et al., 1993). A known volume of the top 0-7 cm of the mineral soil was collected using a metal core (7.3 cm internal diameter) for bulk density and chemical analysis. Samples were stored in coolers on ice until the end of the day, and then they were weighed for field moisture content and left to air dry until further laboratory analysis.

Gravimetric water content was determined on both forest floor and mineral soil samples by oven drying forest floor at 65 °C for 48 hours, and mineral soil at 105 °C for 24 hours (Carter and Gregorich, 2008). Bulk density was calculated as the quotient of oven-dry soil weight and volume of the soil material. Oven-dried forest floor was sieved to <4 mm and mineral soil to <2 mm, and the fine fractions were retained for further chemical analysis. The pH of forest floor was measured from a suspension of 5 mL of soil to 25 mL of 0.01 M $CaCl_2$ (ISO, 2005). Subsamples were ground with a ball mill at 30 Hz for 30 s (Retsch MM200). Total carbon (TC) and total nitrogen (TN) concentrations as well as the natural abundance of ^{13}C and ^{15}N isotopes were measured with a ThermoScientific Flash 2000 coupled to a Delta V Advantage IRMS. The $\delta\ ^{13}C$ values (‰) were referenced to the VPBD standard, and $\delta\ ^{15}N$ was referenced to air.

2.2.3 Data Analysis

Statistical analyses were performed using R statistical computing software (R Core Team, 2018). Differences in soil properties of the forest floor and mineral soil (0 – 7 cm) were compared among harvesting treatments with ANOVA, and followed up with pairwise comparisons using the Holm adjustment. Differences between stand types were investigated using Welch's t-tests

To investigate the relationship of the DTW index with soil properties in the control stands, we used linear mixed effect models for each stand type with the nlme package in the R statistical environment (Pinheiro et al., 2017). Because of the nested structure in the data, compartment was a random effect, and DTW was a fixed effect. The DTW index was natural log-transformed for all analyses to reduce positive skew. A weighted variance structure, varIdent, was included to account for heterogeneity of model residuals among compartments. This decision was also based on field observations: in some compartments the water table was above the forest floor-mineral soil interface.

To investigate the relationship of the DTW index with soil properties among the harvesting treatments, we used a similar approach: models were developed separately for each stand type, where compartment was a random effect, and DTW, retention level, and the interaction between DTW and retention level were fixed effects. When the interaction term was significant, post-hoc analysis was conducted to compare the slopes (between soil parameters and the DTW index) among retention harvest treatments using the lsmeans package (Lenth, 2015).

For each soil parameter, models were developed separately using DTW values computed from seven flow-initiation thresholds (0.5 ha^{-1}, 1 ha^{-1}, 2 ha^{-1}, 4 ha^{-1}, 8 ha^{-1}, 12 ha^{-1}, 16 ha^{-1}), and were compared using the second order Akaike Information Criterion AICc (Bartels et al., 2018).The optimum flow-initiation threshold was selected by comparing the ΔAICc between the thresholds, when the difference in AICc was less than two most frequently among the soil parameters (Appendix A-1).This led to the selection of 4 ha^{-1} flow initiation threshold for subsequent analysis.

2.3 Results

2.3.1 Soil properties 17 years post-harvest and the legacy of spruce

While most forest floor properties (TC, C stock, TN, C:N, $\delta^{13}C$, $\delta^{15}N$) varied between harvested and control treatments, at least under one of the two cover types, there were no differences among the variable retention harvest treatments themselves (Table 2-1). One exception was TN and the C:N ratio in deciduous-dominated stands, where the 2% and 20% retention levels significantly differed from the 50% retention treatment. Although harvest activities in conifer-dominated stands did not significantly influence the forest floor C stocks, there was a significant decrease in TC, an increase in TN, and a decrease in the corresponding C:N ratio; in addition, the natural abundance of both ^{13}C and ^{15}N decreased in these stands. Harvest in deciduous-dominated stands did not influence forest floor TC, or the δ^{13}C and δ^{15}N values, but led to an increase in C stocks and the C:N ratio, and a decrease in TN.

For most parameters examined in the mineral soils, there was no difference between harvest and control treatments (Table 2-2). However, the natural ^{13}C abundance in conifer-dominated stands decreased in the harvested treatments. The C:N ratios in deciduous-dominated stands at the 100% (control) and 50% retention levels were significantly lower than in the 20% and clearcut treatments.

Using control stands as baseline conditions, we compared the soil properties between conifer- and deciduous-dominated stands at each retention level to investigate if, 17 years post-harvest, the legacy of conifers still had an influence on forest floor and mineral soil characteristics (Figures 2-1, 2-2). In the uncut controls, forest floor TC was significantly higher, and mineral soil TC significantly lower in the conifer-dominated stands compared to the deciduous-dominated stands. Differences in forest floor TC between stand types disappeared following harvest, at all retention levels. However, in the mineral soil, the spruce legacy persisted into the 50% retention level, where the conifer-dominated stands maintained lower TC than the deciduous stands, similarly to the controls (Figure 2-2). In the control stands, forest floor C stocks (Mg ha^{-1}) were comparable under conifer- and deciduous-dominated cover type, but were lower in the mineral soils under coniferous vegetation. In terms of the mineral soil carbon stocks, these remained lower in coniferous-dominated forests at all retention levels, although in the clear cut stands the difference was not significant ($p = 0.104$).

For both the forest floor and mineral soil of the control stands, TN concentrations were lower under coniferous vegetation (Figures 2-1, 2-2). This remained true under all retention levels, including the clearcut, although this difference was not significant ($p = 0.102$). The corresponding C:N ratios were higher in conifer-dominated stands for both mineral soil and forest floor in the control stands, and remained so across all harvesting treatments. In both soil layers, the δ ^{13}C values were greater in the control stands of conifer-dominated forests. This difference was apparent in the forest floor at all retention levels. However, in the mineral soil, this was not the case in the clear-cut treatments, where the coniferous values became comparable to the ones under deciduous vegetation.

2.3.2 Modeling changes in soil properties with the Depth to Water (DTW) index

Forest Floor

In control conifer-dominated stands, carbon stocks increased with increased wetness (as evidenced by lower DTW values; Table 2-3). Increases in carbon stocks also appeared to be related to an increase in forest floor thickness, which was also significantly related to DTW in conifer-dominated stands. In addition the C:N ratio increased with lower DTW values. In control deciduous-dominated stands, there was an increase in forest floor pH, and δ ^{13}C and δ ^{15}N values with increased wetness.

Mineral Soil

In the uncut control stands of both forest types there was an increase in TC, TN, and carbon stocks, with decreasing DTW values (Table 2-4). These parameters were more strongly linked to the DTW index compared to relationships in the forest floor. In deciduous-dominated controls, natural abundance ^{15}N had a negative relationship with DTW, while in conifer-dominated stands there was a positive relationship of the same magnitude.

2.3.3 Investigating the effects of harvesting with the Depth to Water (DTW) index

Forest floor

Significant interactions between retention level and DTW indicated that the relationships between DTW and soil properties were altered through harvest (Table 2-5). Forest floor total carbon concentrations in conifer-dominated stands showed a significant interaction term; post-hoc analysis indicated a positive relationship in the harvested treatments, increasing with the degree of retention, and a negative relationship in the control. In control conifer-dominant stands there was a negative relationship between the C:N ratio and DTW, while in harvested stands there was a slight positive relationship. There was a strong negative relationship between carbon stocks and DTW in the control stands, while in the harvested treatments the increase with wetness was much more gradual (Figure 2-3). In conifer-dominated clear-cut and 50% retention treatments, natural abundance ^{15}N increased towards the dry end of the gradient, but decreased in the 20% retention and control stands (Table 2-5).

In the forest floor of harvested deciduous-dominated stands, carbon stocks were negatively related to DTW, while there was a weak positive relationship in the control stands (Table 2-5). In control stands, δ^{13}C and δ^{15}N rose at wetter sites, however in harvested stands the slopes were closer to zero.

Mineral soil

For both forest types, mineral soil TC, TN, C:N ratio, and carbon stocks were negatively related to the DTW index, meaning that all of these parameters significantly increased with increasing wetness (Table 2-6). The interaction term was significant between DTW and retention level for natural abundance ^{15}N in both stand types. In conifer-dominated stands, post-hoc analysis showed a negative slope in clear-cut stands, and positive slopes at other treatment levels, including the control. In contrast, in deciduous-dominated stands, the slopes were positive at low retention levels (2% and 20%), but were negative at high retention (50%), and the control treatments.

2.4 Discussion

2.4.1 Long-term soil response to variable retention harvest

Seventeen years post disturbance, there were few differences in the chemical properties of the forest floor and mineral soil (0-7 cm) among retention treatments (Tables 2-1, 2-2). Our results support the previous findings of Kishchuk et al. (2014), who measured carbon and nutrient levels at EMEND 10 years post-disturbance, and reported non-significant differences among the variable retention harvest treatments. However, contrary to their findings, we found significant differences between the harvested stands and uncut controls.

In the control stands, we found that forest floor and mineral soil TN levels were higher under deciduous-dominated canopies, reflecting previous reports in this forest (Jerabkova et al., 2006; Lindo and Visser, 2003). In particular, Jerabkova et al. (2006) found that TN was higher in deciduous-dominated stands, and attributed this feature to greater foliar litter inputs under aspen in terms of both mass and nitrogen content, compared to white spruce. Following the harvest of both stand types, aspen stems were quick to grow at both high and low retention levels

(Echiverri, 2017; Gradowski et al., 2010; Nijland et al., 2015). In conifer-dominated stands, this led to an increase in forest floor total nitrogen, and a decrease in total carbon concentrations, resulting in a lower C:N ratio (Table 2-1). Conversion from a conifer-dominated to a deciduous-dominated canopy likely led to these changes in forest floor properties.

Although the natural abundance of both ^{13}C and ^{15}N isotopes was not altered by retention harvest in deciduous-dominated stands, both parameters decreased in the forest floors of conifer-dominated stands (Table 2-1). Interestingly, this effect was absent four years following harvest, where there was no difference in forest floor $\delta^{13}C$ values among clear cut and control treatments in conifer-dominated stands (Hannam et al., 2005). We suspect that isotopic depletion occurred in the forest floor due to a long-term shift in the vegetation community. Since broadleaf species have larger quantities of litterfall and tend to be isotopically lighter compared to needle litter and soil organic matter, depletion in the forest floor was likely due to the larger inputs both in terms of mass and ^{12}C and ^{14}N content (Balesdent et al., 1993; Brooks et al., 1997; Laganière et al., 2017).We also suspect that harvest in conifer-dominated stands led to a decrease in ^{13}C, from the decomposition of isotopically depleted roots of harvested white spruce trees, which tend to allocate more root biomass in the forest floor compared to aspen (Benner et al., 1987; Strong and La Roi, 1983).

At EMEND, the forest floor was preserved through careful logging practices, the moss dominated forest floor remaining in conifer-dominated stands functioned as a material legacy of soil organic carbon (Hannam et al., 2005, 2004; Johnstone et al., 2016). In our study, this was evidenced through the preservation of several differences between the conifer- and deciduous-dominated stands following harvesting, including less negative $\delta^{13}C$ values in the forest floor and higher C:N ratios in both the forest floor and mineral soil under spruce in all treatments, even in the clearcuts (Figures 2-1, 2-2).

In harvested deciduous-dominated stands, aspen regeneration had the opposite effect on nitrogen levels when compared to the coniferous stands (Table 2-1). Forest floor TN decreased and the C:N ratios increased, both in the forest floor and the mineral soil. Similar effects have been reported in chronosequences of aspen stand development in both boreal and temperate forests, where decreased soil and foliar nitrogen levels were associated with younger stands (Ruark and Bockheim, 1988; Yuan and Chen, 2010). Decreases in nitrogen content could have arisen from leaching losses following harvest (Lindo and Visser, 2003). Alternatively, Miller (1995) proposed that at early successional stages there is a high nutrient demand, and once past a threshold, demand decreases and nitrogen is retranslocated from older or dying tissue, from there it eventually enters for forest floor as litterfall and recharges soil nutrient levels. In our case, harvesting led to the proliferation of young aspen trees with higher nutrient demand compared to older trees, likely contributing to the decrease in soil nitrogen content.

Harvest in deciduous-dominated stands also led to increases in forest floor carbon stocks. This may have been partly due to decreased litter nutrient concentrations at this stage of forest development, which may have slowed down decomposition, and contributed to the increase in forest floor carbon stocks (Table 2-1). Another primary driver for the increase in stocks likely originated from the preservation of the forest floor following logging activities, combined with enhanced biomass and litter production during early successional stages (Seedre et al., 2011).

2.4.2 Succession and carbon dynamics: an enhanced perspective with wet-areas mapping

Unharvested controls

The increase in mineral soil (0-7 cm) TC, TN, and carbon stocks with wetness are a well reported occurrence in boreal forest soils (Olsson et al., 2009; Rapalee et al., 1998). In addition, the relationships between most mineral soil properties and DTW were consistent among the conifer-dominated and deciduous-dominated stands, suggesting that the mineral soil was either more strongly related to the DTW index, or less influenced by the covarying factors that impacted relationships in the forest floor. Similar to our findings, Kishchuk et al. (2014) reported that most differences among harvesting treatments were exclusive to the forest floor, highlighting the forest floor responsiveness to disturbance compared to the mineral soil.

In conifer-dominated controls, the increase in forest floor thickness and carbon stocks with wetness (Table 2-3) is also a commonly reported phenomenon, and likely originates from inhibited decomposition and increased litter inputs (Olsson et al., 2009; Seibert et al., 2007). Interestingly, in deciduous-dominated stands, carbon stocks and forest floor thickness did not increase at the wet end of the gradient, instead we found that both $\delta^{13}C$ and $\delta^{15}N$ increased, suggesting higher decomposition at wetter sites or a shift in vegetation communities (Brooks et al., 1997; Natelhoffer and Fry, 1988).

A high degree of variability obscured the relationships between forest floor properties and the DTW index. In some cases, properties would only be significantly related to DTW in one stand type, such as the increase in carbon stocks with wetness in conifer-dominated, but not in deciduous-dominated stands. This could be attributed to a number of factors at both the plot and stand level including differences in drainage, as well as variation in canopy and understory vegetation, and stand age (Bergeron, 2012; Seibert et al., 2007). Echiverri (2017) also found that the relationships between understory vegetation and DTW differed between stand types, which in turn would affect soil properties. In addition, the range of DTW values differed between stand types, with conifer-dominated stands occupying wetter sites compared to deciduous-dominated stands (Nijland et al., 2015).

Harvested conifer-dominated forests

The relationship between the DTW index and forest floor properties in conifer-dominated stands was altered through harvest and aspen regeneration: in undisturbed stands, total carbon concentrations were negatively related with DTW, while in harvested stands the opposite was found and concentrations increased at drier sites (Table 2-5). Seibert et al. (2007) had similar findings, and reported increased forest floor TC at wetter locations in unharvested areas. They attributed this to an increase in primary production; whereby increased litter inputs could increase the bulk forest floor C:N ratio, compared to a more decomposed forest floor with fewer fresh inputs. Previous reports at EMEND found that there was increased canopy and shrub cover at the drier end of the gradient following harvest (Echiverri, 2017; Nijland et al., 2015), this increased cover likely reflected an increase in primary productivity, similar to Seibert et al. (2007), and would explain the increase in TC at drier sites in harvested conifer-dominated stands. In addition, carbon concentrations may have been smaller at wet sites due to increased levels of other soil nutrients such as nitrogen.

The relationship between the C:N ratio and DTW was similarly altered by harvest, where slopes were positive in the harvesting treatments, but negative in the control uncut stands (Table 2-5). In addition to the factors affecting TC, these changes may also be influenced by a decline in bryophyte cover at the wet end of the gradient in harvested stands (Samuel Bartels, personal communication), and the subsequent decomposition of moss tissue at wetter sites led to higher nitrogen concentrations in the forest floor and a decrease in the C:N ratio (Oechel and Van Cleve, 1986).

In uncut control stands, forest floor carbon stocks sharply rose at wetter sites, while in the harvested stands the increase with wetness was much more gradual (Figure 2-3). This strong negative relationship found in the uncut controls, coincides with previous findings of increased stocks at wetter soil conditions (Rapalee et al., 1998). At EMEND, Hannam et al. (2004) proposed that environmental conditions restricted turnover in conifer-dominated stands, due to the accumulation of labile carbon. The gradual slope in harvested stands may reflect enhanced decomposition of forest floor carbon at the wet end of the gradient, due to more favourable temperature conditions from disruption of the canopy. Compared to the controls, the decreased C:N ratio at wetter sites in harvested treatments also lends support to this (Preston et al., 2009). If harvest promoted decomposition at the wet end of the gradient, this would be reflected in decreases in carbon stocks and in the C:N ratio. In addition, the higher overstory and shrub cover at drier sites may have elevated the inputs to the forest floor, potentially increasing both stocks and the C:N ratio, once again leading to a more gradual slope with DTW.

Harvested deciduous-dominated forests

Unlike conifer-dominated forests, the relationships between DTW and forest floor TC and the C:N ratio were unaffected by harvest in deciduous-dominated stands (Table 2-5). Harvest did however influence the relationship between DTW and carbon stocks in this cover type, with negative slopes in the harvested treatments, and a gradual, positive slope in the control. Although the increase in carbon stocks with wetness is a well reported phenomenon (Olsson et al., 2009; Rapalee et al., 1998), we suspect that at this stage of succession, that old growth gap dynamics weakened the influence of topography in the uncut controls. In addition, clonal aspen networks are capable of nutrient and resource transfer between clones, and this property may have also confounded the influence of topography through enhanced biomass production at the dry end of the gradient (Pinno and Wilson, 2014; Saitoh et al., 2006). In the harvested deciduous-dominated treatments, increased carbon stocks with increasing wetness were likely correlated with reduced decomposition and enhanced litter inputs. Although non-significant, the slopes of the interaction for forest floor thickness mirrored the relationships observed for carbon stocks.

In control deciduous-dominated stands we saw an increase in both forest floor $\delta^{13}C$ and $\delta^{15}N$ at the wet end of the gradient, indicating a heightened degree of decomposition, while in the harvested stands, the slopes of the relationships were closer to zero (Table 2-5). The isotopic composition of the forest floor supported our hypothesis regarding carbon stocks and decomposition. Harvest and forest evolution potentially led to accumulation of organic matter and limited decomposition, decreasing the $\delta^{13}C$ and $\delta^{15}N$ values relative to controls at the wet end of the gradient.

2.5 Conclusion

While differences in both forest floor and mineral soil properties among harvesting treatments were minor, there were noticeable differences between these treatments and the uncut controls. A notable outcome of the EMEND experiment has been the pronounced regeneration of trembling aspen across all stand types (Echiverri, 2017; Nijland et al., 2015). In conifer-dominated stands, the shift towards a deciduous-dominated canopy led to a decrease in forest floor TC and an increase in TN, leading to an increased C:N ratio. In deciduous-dominated stands, harvest and aspen regeneration led instead to a decrease in forest floor TN and the C:N ratio, and to an increase in carbon stocks.

In control stands, the relationships with the topographic DTW index were more strongly expressed in the mineral soil (0-7 cm), compared to the forest floor. Mineral soil TN, TC, and carbon stocks of both cover types increased with wetness, suggesting restricted decomposition at the wet end of the gradient. Similar relationships were present in the forest floor in conifer-dominated stands: forest floor thickness, TC, and carbon stocks also rose with wetness. In contrast, forest floor decomposition was likely enhanced at the wet end of the gradient in deciduous-dominated stands, due to increases in $\delta^{13}C$ and $\delta^{15}N$ values with wetness (Natelhoffer and Fry, 1988).

Harvest altered the relationships between soil properties and the DTW index for both stand types. Most notably, we saw that harvest and aspen regeneration in conifer-dominated stands led to a decrease in forest floor TC, the C:N ratio, and carbon stocks at the wet end of the gradient, compared to undisturbed stands. While harvest in deciduous-dominated stands, led to decreases in $\delta^{13}C$ and $\delta\ ^{15}N$, and increased carbon stocks at the wet end of the gradient. Ultimately, harvest led to an accumulation of carbon that was less decomposed in conifer-dominated stands, but had the opposite effect in deciduous-dominated stands at the wet end of the DTW gradient.

These varying relationships highlight the complexity of soil organic carbon dynamics in the boreal mixedwood forest. In addition to demonstrating the utility in the DTW index for modeling soil properties, this study has shown that cover type is important to decomposition processes. Nijland et al. (2015) reported that these cover types were not randomly distributed across the boreal mixedwood landscape, and that conifer-dominated stands had a tendency to be found at lower DTW values. Since we found that decomposition was likely highest at the wet end of the gradient in deciduous-dominated stands, but lowest in conifer-dominated stands, our findings also highlight this landscape distribution of stands. In future studies, this index may perhaps be useful as a tool to track the evolution of soil properties, as suggested by Echiverri (2017), regarding understory vegetation community composition.

Tables

Table 2-1: Forest floor properties under conifer-dominated (CDOM) and deciduous-dominated (DDOM) cover type, and retention harvesting treatments, where 100% retention corresponds to uncut control stands. Differences among retention levels were evaluated through ANOVA, and pairwise t-tests with the Holm adjustment for multiple comparisons were used to compare means ($p < 0.10$). Uppercase letters indicate significant differences in soil properties among harvesting treatments within each stand type (Appendix A-2; n= 20 – 33).

Retention	TC (mg g^{-1})		C stock Mg ha^{-1}		TN (mg g^{-1})		C:N		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM
Control (100 %)	430.1 (24.7) A	419.2 (17.1) A	29.4 (14.8) A	26.5 (7.6) B	17.0 (3.7) B	24.4 (2.9) A	26.3 (5.5) A	17.4 (2.0) B	-27.1 (0.8) A	-28.1 (0.5) A	1.0 (0.8) A	0.2 (1.3) A
50 %	417.3 (22.0) AB	407.1 (28.9) A	31.7 (10.3) A	33.1 (13.1) AB	19.3 (4.5) AB	23.9 (2.6) A	22.8 (5.8) B	17.2 (1.5) B	-27.4 (0.6) AB	-27.8 (0.6) A	0.7 (0.8) AB	0.4 (0.9) A
20 %	409.3 (30.2) B	410.6 (17.5) A	32.3 (16.1) A	31.6 (10.4) AB	18.6 (3.3) AB	21.9 (1.8) B	22.6 (4.0) B	18.9 (2.0) A	-27.5 (0.6) B	-28.0 (0.7) A	0.8 (0.6) AB	0.3 (0.8) A
Clearcut (2%)	404.5 (21.8) B	407.3 (24.8) A	30.2 (16.4) A	36.6 (15.5) A	20.2 (3.7) A	21.9 (3.3) B	20.5 (3.2) B	18.9 (2.4) A	-27.4 (0.6) AB	-28.1 (0.6) A	0.5 (0.5) B	0.7 (0.6) A

Table 2-2: Mineral soil (0 – 7 cm) properties under conifer-dominated (CDOM) and deciduous-dominated (DDOM) cover type, and retention harvesting treatments, where 100% retention corresponds to uncut control stands. Differences among retention levels were evaluated through ANOVA, and pairwise t-tests with the Holm adjustment for multiple comparisons were used to compare means ($p < 0.10$). Uppercase letters indicate significant differences in soil properties among harvesting treatments within each stand type (n= 20 – 33).

Retention	TC (mg g^{-1})		C stock Mg ha^{-1}		TN (mg g^{-1})		C:N		δ^{13}C (‰)		δ^{15}N (‰)	
	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM	CDOM	DDOM
Control (100 %)	43.2 (20.9) A	54.6 (23.7) A	29.4 (8.0) A	34.2 (9.2) A	2.7 (1.6) A	4.8 (2.2) A	16.4 (2.4) A	11.7 (1.6) B	-25.4 (0.3) A	-25.7 (0.4) A	4.9 (0.8) A	4.9 (0.9) A
50 %	38.5 (19.9) A	51.4 (29.6) A	26.2 (7.4) A	31.1 (9.8) A	2.6 (1.6) A	4.4 (2.6) A	15.9 (3.1) A	11.6 (1.4) B	-25.7 (0.4) AB	-25.8 (0.4) A	4.8 (0.7) A	4.4 (0.9) A
20 %	38.0 (21.7) A	45.5 (19.5) A	26.6 (8.6) A	31.1 (7.7) A	2.7 (1.6) A	3.7 (1.8) A	14.6 (2.9) A	12.6 (1.5) AB	-25.6 (0.4) B	-25.7 (0.4) A	4.6 (0.9) A	4.7 (0.6) A
Clearcut (2%)	42.0 (19.2) A	51.6 (24.2) A	27.7 (7.9) A	32.2 (9.1) A	3.0 (1.9) A	3.8 (1.7) A	15.3 (3.1) A	13.3 (1.7) A	-25.7 (0.4) AB	-25.9 (0.5) A	4.7 (0.6) A	4.7 (0.9) A

Table 2-3: Outcome of linear mixed effect models relating forest floor properties in uncut control stands with the natural log-transformed Depth-to-Water (DTW) index (Appendix A-2). DTW values were calculated using the 4 ha^{-1} flow initiation threshold. Significant relationships (p<0.10) are denoted by an asterisk. CDOM: conifer-dominated; DDOM: deciduous dominated.

Forest floor property	Stand type	DTW slope coefficient	
-	-	-	p-value
Thickness (cm)	CDOM	-1.31 *	0.0024
	DDOM	0.26	0.2764
pH	CDOM	0.03	0.5725
	DDOM	-0.09 *	0.0011
Total Carbon (%)	CDOM	-0.25	0.2881
	DDOM	0.04	0.8336
Total Nitrogen (%)	CDOM	0.03	0.4235
	DDOM	-0.01	0.8388
C:N ratio	CDOM	-1.45 *	0.0180
	DDOM	-0.11	0.6703
Carbon stock (Mg ha^{-1})	CDOM	-6.26 *	<0.0001
	DDOM	0.23	0.7959
$\delta\ ^{13}C$ (‰)	CDOM	-0.14	0.1475
	DDOM	-0.15 *	0.0105
$\delta\ ^{15}N$ (‰)	CDOM	0.14	0.1441
	DDOM	-0.20 *	0.0655

Table 2-4: Outcome of linear mixed effect models relating mineral soil properties in uncut control stands with the natural log-transformed Depth-to-Water (DTW) index. DTW values were calculated using the 4 ha^{-1} flow initiation threshold. Significant relationships ($p<0.10$) are denoted an asterisk. CDOM: conifer-dominated; DDOM: deciduous dominated.

Soil property	Stand Type	DTW slope coefficient	
-	-	-	p-value
Total Carbon (%)	CDOM	-0.58 *	0.0106
	DDOM	-0.90 *	<0.0001
Total Nitrogen (%)	CDOM	-0.03 *	0.0923
	DDOM	-0.09 *	<0.0001
C:N ratio	CDOM	-0.39	0.1948
	DDOM	-0.15	0.5042
Carbon stock (Mg ha^{-1})	CDOM	-3.27 *	0.0018
	DDOM	-3.08 *	0.0077
$\delta\ ^{13}C$ (‰)	CDOM	0.006	0.8755
	DDOM	-0.07	0.1532
$\delta\ ^{15}N$ (‰)	CDOM	0.17 *	0.0066
	DDOM	-0.17 *	0.0537

Table 2-5: Outcome of linear mixed effect models relating forest floor properties and the natural log-transformed Depth-to-Water (DTW) index, retention level, and their interaction. DTW values were calculated using the 4 ha^{-1} flow initiation threshold (Appendix A-2). Significant differences in the interactions of the DTW index and retention level on a given forest floor soil property are indicated by different lowercase letters ($p < 0.10$). CDOM: conifer dominated; DDOM: deciduous dominated.

Forest floor parameter	Stand Type	DTW slope coefficient		Retention level	Interaction (DTW index * retention level)				
-	-	-	p-value	p-value	p-value	Clearcut Coefficient	20 % Retention Coefficient	50 % Retention Coefficient	Control Coefficient
Thickness (cm)	CDOM	-0.36	0.0045	0.8783	0.1704	-0.36	-0.46	-0.16	-1.19
	DDOM	-0.35	0.0004	0.6995	0.1032	-0.35	-0.42	-0.28	0.24
pH	CDOM	0.06	0.1271	0.0981	0.7188	0.06	0.03	0.00	0.03
	DDOM	-0.09	<0.0001	0.9817	0.6599	-0.09	-0.06	-0.04	-0.09
Total Carbon (%)	CDOM	0.36	0.0009	0.2324	0.0288	0.36 ab	0.55 ab	0.64 a	-0.23 b
	DDOM	-0.26	0.3983	0.4797	0.1865	-0.26	-0.05	0.33	0.06
Total Nitrogen (%)	CDOM	-0.06	0.2235	0.7596	0.1311	-0.06	0.00	-0.03	0.04
	DDOM	-0.05	0.0161	0.6433	0.5884	-0.05	-0.01	-0.03	-0.01
C:N ratio	CDOM	0.91	0.0537	0.4555	0.0042	0.91 a	0.01 ab	0.62 a	-1.45 b
	DDOM	0.16	0.0308	0.5748	0.5948	0.16 a	0.09 a	0.24 a	-0.11 a
Carbon stock (Mg ha^{-1})	CDOM	-0.39	0.0060	0.9786	0.0138	-0.39 a	-1.25 ab	-0.55 a	-6.14 b
	DDOM	-2.36	<0.0001	0.8168	0.0243	-2.36 ab	-3.64 b	-1.52 ab	0.01 a
$\delta\ ^{13}C$ (‰)	CDOM	0.04	0.9203	0.1021	0.4206	0.04	-0.04	0.00	-0.14
	DDOM	0.01	0.3911	0.8434	0.0520	0.01 a	0.03 ab	-0.01 ab	-0.15 b
$\delta\ ^{15}N$ (‰)	CDOM	-0.15	0.9341	0.2713	0.0056	-0.15 b	0.10 a	-0.06 ab	0.15 a
	DDOM	0.08	0.3184	0.8492	0.0161	0.08 ab	-0.02 ab	0.12 a	-0.21 b

Table 2-6: Outcome of linear mixed effect models relating mineral soil (0 – 7 cm) properties and the natural log transformed Depth-to-Water (DTW) index, retention level, and their interaction. DTW values were calculated using the 4 ha^{-1} flow initiation threshold. Significant differences in the interactions of the DTW index and retention level on a given soil property are indicated by different lowercase letters ($p < 0.10$). CDOM: conifer dominated; DDOM: deciduous dominated.

Soil property	Stand type	DTW slope coefficient		Retention level	Interaction (DTW index * retention level)				
-	-	-	p-value	p-value	p-value	Clear-cut Coefficient	20 % Retention Coefficient	50 % Retention Coefficient	Control Coefficient
Total Carbon (%)	CDOM	-0.46	<0.0001	0.635	0.475	-0.46	-0.77	-0.55	-0.60
	DDOM	-0.30	<0.0001	0.668	0.377	-0.30	-0.45	-0.54	-0.90
Total Nitrogen (%)	CDOM	-0.04	<0.0001	0.884	0.743	-0.04	-0.05	-0.04	-0.03
	DDOM	-0.03	<0.0001	0.582	0.112	-0.03	-0.03	-0.06	-0.09
C:N ratio	CDOM	-0.46	<0.0001	0.6354	0.4746	-0.46	-0.77	-0.55	-0.58
	DDOM	-0.30	<0.0001	0.6679	0.3773	-0.30	-0.45	-0.54	-0.90
Carbon stock (Mg ha^{-1})	CDOM	-2.22	<0.0001	0.479	0.252	-2.22	-3.77	-2.39	-3.15
	DDOM	-1.32	<0.0001	0.445	0.664	-1.32	-1.75	-1.65	-3.07
$\delta\ ^{13}C$ (‰)	CDOM	-0.04	0.0262	0.404	0.458	-0.04	-0.07	-0.03	0.01
	DDOM	-0.05	0.3824	0.754	0.395	-0.05	0.00	0.02	-0.08
$\delta\ ^{15}N$ (‰)	CDOM	-0.05	0.4488	0.959	0.005	-0.05 b	0.15 ab	0.02 ab	0.16 a
	DDOM	0.25	0.9567	0.802	0.002	0.25 a	0.11 a	-0.13 b	-0.17 b

Figures

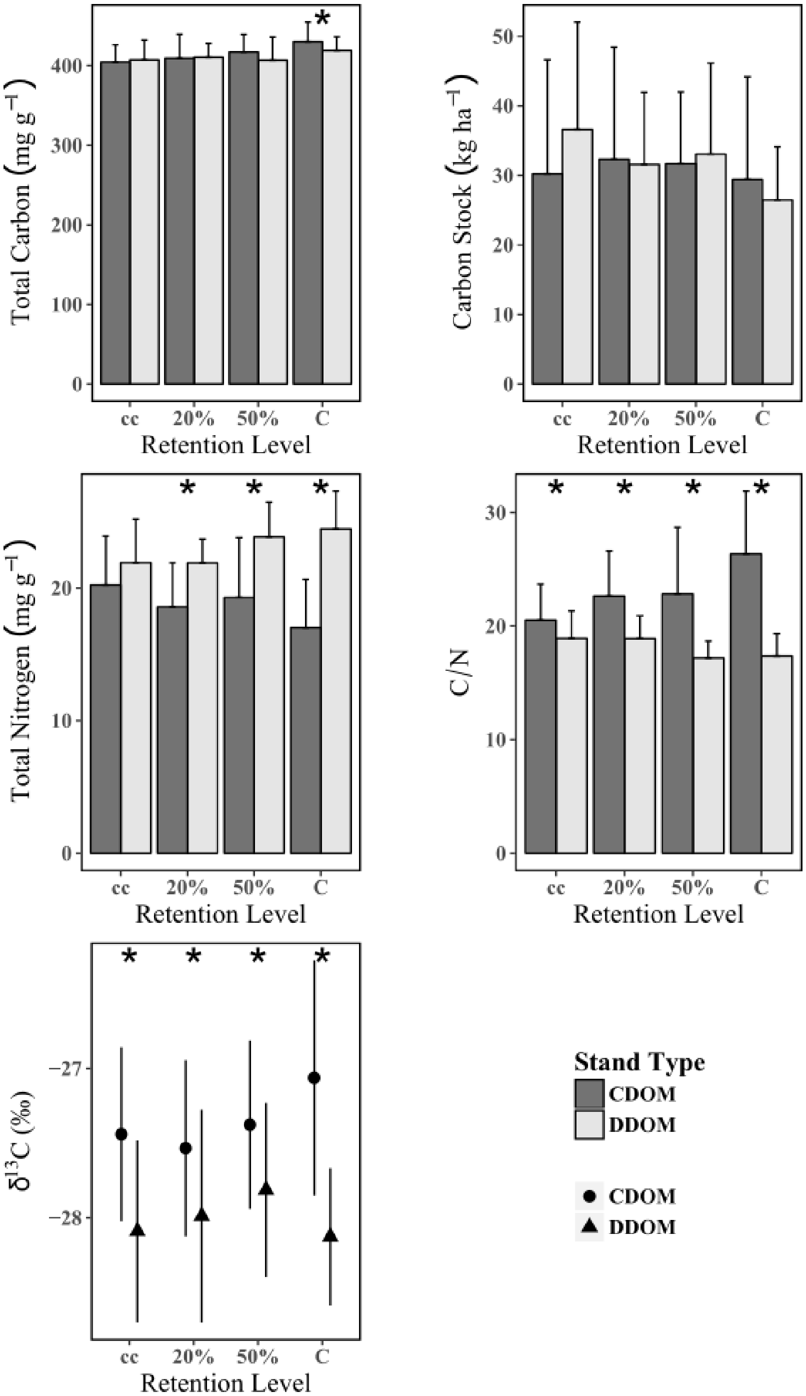

Figure 2-1: Comparison of forest floor properties between stand types (CDOM: Coniferous dominated, DDOM: Deciduous dominated) for each retention level (Appendix A-2; cc: Clearcut, C: control). Error bars represent one standard deviation, and significant differences are indicated by an asterisk ($p < 0.10$).

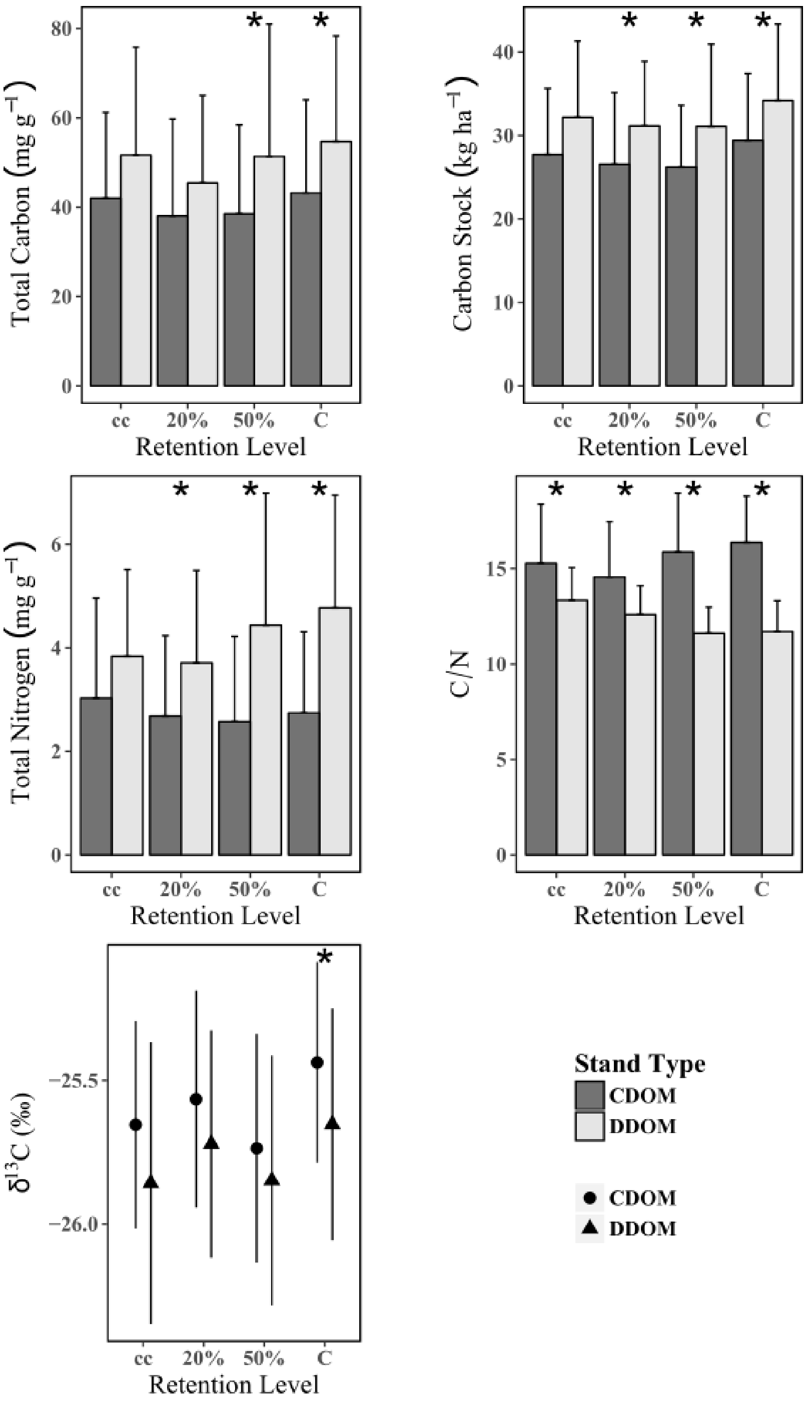

Figure 2-2: Comparison of mineral soil properties between stand types (CDOM: Coniferous dominated, DDOM: Deciduous dominated) for each retention level (cc: Clearcut, C: control). Error bars represent one standard deviation, and significant differences are indicated by an asterisk ($p < 0.10$).

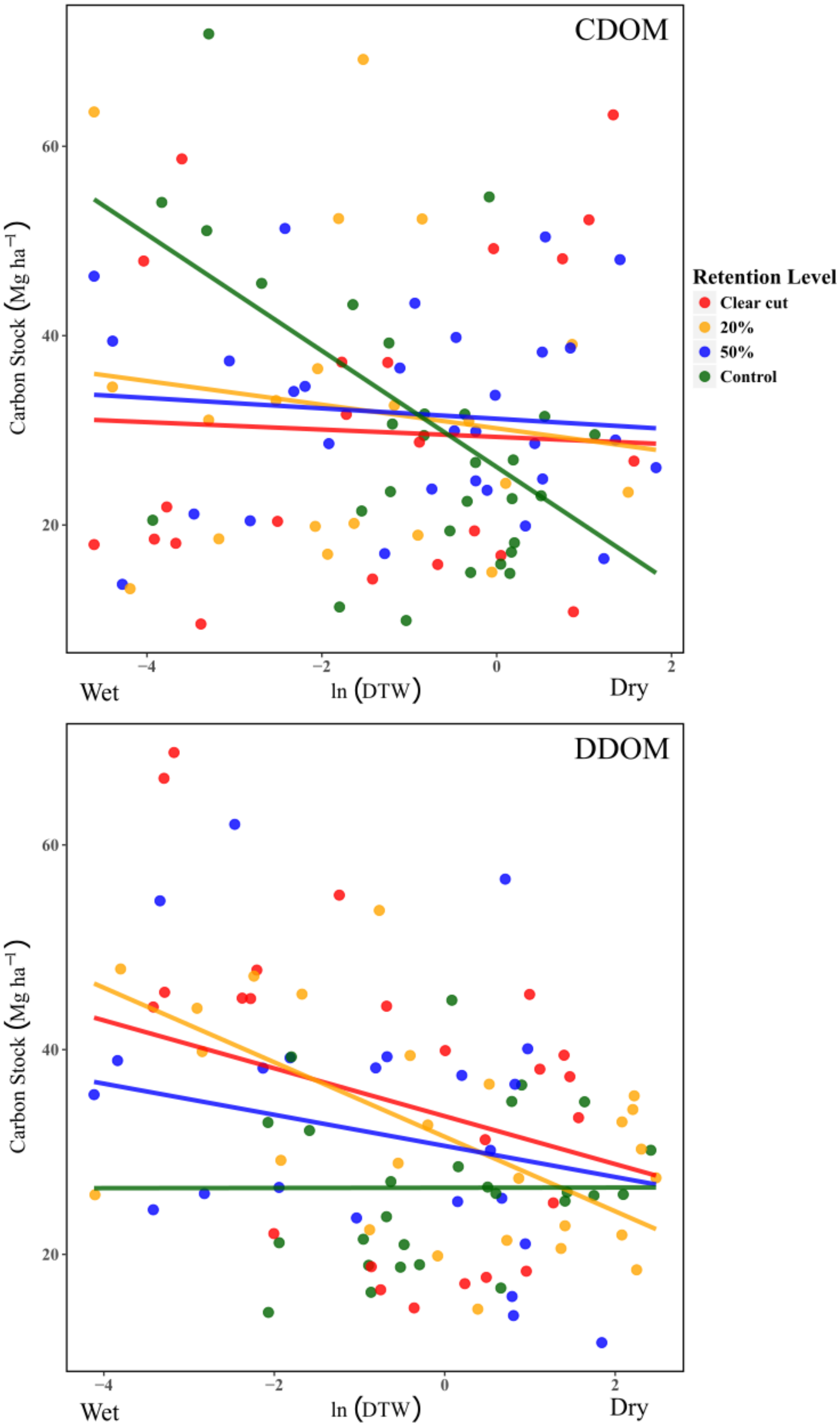

Figure 2-3: Forest floor carbon stocks (Mg ha^{-1}) in the various control and harvested treatments along the natural log of the depth-to-water gradient; CDOM: conifer-dominated, DDOM: deciduous-dominated.

Chapter 3. Topographic controls on carbon stability in boreal forest soils

3.1 Introduction

The boreal forest plays an especially important role in the global carbon cycle, storing approximately 19% of terrestrial carbon stocks worldwide (IPCC 2000). In this biome, the majority of carbon stocks are found belowground (Saugier et al., 2001). In addition, a harsh climate restricts the breakdown of organic matter, which instead accumulates on top of the mineral soil, leading to the formation of an often thick forest floor (Lorenz and Lal, 2010). The boreal forest is currently known to act as a carbon sink, sequestering carbon for the majority of its lifespan (Coursolle et al., 2012). However, with increasing pressure from a changing climate, it has been suggested that the boreal could instead function as a net source of carbon (Kurz et al., 2013).

Due to a high degree of spatial variability, carbon stocks are heterogeneously distributed across the boreal forest. Landscape morphology and soil drainage both have a pronounced effect on soil climate and organic carbon storage, with wet areas storing vastly more carbon due to inhibited decomposition (Trumbore et al., 1998). Drainage is also related to forest structure, which can further modify carbon storage through its influence on soil microclimatic conditions, as well as the chemical quality and quantity of litterfall of various tree and understory species (Berg et al., 1995; Laganière et al., 2013; Nijland et al., 2015; Olsson et al., 2009; Trofymow et al., 2002). In addition, soils of the boreal forest feature a wide vertical distribution of organic matter, with approximately 25% of the ecosystem carbon stocks stored in the forest floor. Because of its position at the air-soil interface, the forest floor is exposed to intense atmospheric fluctuations and is known for its rapid carbon turnover compared to the underlying mineral horizons (Trumbore et al., 1998).

Carbon stored in the boreal is particularly vulnerable to climate change, since this ecosystem is predicted to have greater exposure to warming compared to other terrestrial ecosystems (Price et al., 2013). It is therefore essential to further our understanding of carbon cycling in the boreal forest. Soil respiration is a combination of autotrophic and heterotrophic processes; it is a key component of the carbon cycle and reflects carbon turnover as well as primary productivity (Davidson et al., 2006). Soil respiration also serves as a proxy for soil carbon stability, although its sensitivity to soil moisture and temperature regimes can obscure our understanding to this end. With increased temperature, soil respiration and carbon turnover are expected to increase (Lloyd and Taylor, 1994), however there remains uncertainty regarding the extent of these changes, especially across complex terrain in ecosystems such as the boreal forest (Pacific et al., 2008).

In the boreal mixedwood forest of Western Canada, there is a high degree of physiographic variability and diverse topography occurring over the landscape (Beckingham et al., 1996). Toposequences predominately transition from Luvisolic or Brunisolic soils at upslope positions to Gleysolic and Organic orders at lower slope positions with reduced drainage (Bedard-Haughn, 2011; Lavkulich and Arocena, 2011). Trembling aspen and associated understory vegetation are likely to dominate on concave slopes and ridges that are drier, while channels and depression areas are more likely to consist of spruce trees and a forest floor largely composed of moss mats (Albani et al., 2005). These landscape features are important in a broader context since they are analogous to ongoing shifts in the boreal forest's composition and microclimatic conditions across its entire range. This aspen-spruce interface is expected to shift northward in coming years due to reduced fitness of spruce trees with a changing climate (Jiang et al., 2016). Both soil temperature and moisture regimes are important to carbon turnover in the soil profile. However, due to the forest floor's unique position, it is also influenced by changes in relative humidity which can lead to decoupling of the forest floor respiration from the total soil profile respiration (Berryman et al., 2014; Kelliher et al., 2004). For these reasons, in addition to vastly different properties between the forest floor and mineral soil, research has emphasized the vertical partitioning of soil respiration fluxes (Berryman et al., 2014; E.A. Davidson et al., 2006; Goffin et al., 2014; Pumpanen et al., 2008).

Changes in forest structure and soil climate are closely linked to topography and are important to soil organic carbon dynamics in both the mineral soil and forest floor. In this study, we measured soil respiration along a boreal hillslope, partitioning forest floor respiration from the total soil profile, and compared fluxes with a controlled, laboratory incubation of the forest floor. We were interested in how soil temperature and moisture conditions, and carbon quality influenced respiration in-situ, and how removal of these abiotic effects impacted turnover in the laboratory. Our specific objectives were to: partition the mineral soil respiration from the total soil profile efflux to assess whether topographically induced variation affected forest floor respiration; and to assess the linkage between soil organic matter quality and in-situ respiration fluxes through laboratory incubation of forest floor materials. Such hillslope transitions with pronounced natural gradients provide ideal conditions to compare the effect of soil microclimate and vegetation controls on soil respiration and soil organic carbon quality.

3.2 Materials and methods

3.2.1 Study area and site selection

This study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance; Spence et al., 1999) site (56° 46' 13" N, -118° 22' 28" W), located in the lower foothills regions of the boreal mixedwood forest of Alberta (Beckingham et al., 1996). The EMEND project is a fully replicated, long-term experiment investigating the effects of anthropogenic and natural disturbance on boreal forests. Soils of the study site primarily originated from glacial till or glacial lacustrine deposits; the majority are Luvisols, with a more limited presence of Gleysols and Brunisols (Kishchuk, 2004). The mean annual temperature of the region is 1.2 °C, and mean annual precipitation is 413 mm, 38% of which accumulates as snow (Kishchuk, 2004).

For our study, we selected a representative hillslope (56° 45' 50" N, -118° 22' 40" W) with seven distinct topographic positions, four upslope (summit, shoulder, upper and lower backslope), and three downslope (footslope, toeslope and depression). The slope was south-west facing and was located within a 140 year-old boreal mixedwood stand (Bergeron, 2012). Elevation on the slope ranged from 729 masl to 762 masl, and the incline was 31° at its steepest. At upslope positions, the canopy was dominated by trembling aspen (*Populus tremuloides* Michx.), with a sparse sub canopy consisting of white spruce (*Picea Glauca* (Moench) Voss) and balsam fir (*Abies Balsamea (L.) Mill*). Downslope, the canopy was dominated by white spruce with some balsam poplar (*Populus balsamifera L.*). Plots (5 m by 5 m) were established in triplicate at each of the seven topographic positions along the hillslope. Further characterization at each plot included slope, elevation, vegetation and soil description.

3.2.2 Soil and vegetation characterization and sampling

Soils at each position were characterized morphologically as per Watson (2014) including a description of colour, structure, coarse fragments, mottling, effervescence, and rooting for each morphological horizon. The forest floor itself was characterized morphologically as per Green et al. (1993). Soils were classified using the Canadian System of Soil Classification (Soil Classification Working Group, 1998). Samples of each mineral horizon were collected and brought back to the laboratory for chemical and physical analyses.

Forest floor materials were collected for bulk density determination by excavating a 100 cm^2 area to the surface of the mineral soil, and the forest floor thickness was recorded to calculate the volume of the forest floor plug sampled. Additional forest floor samples were taken for chemical analysis. Lastly, a set of forest floor samples was taken for a laboratory incubation in triplicate from each plot using a 10 cm by 10 cm sampling frame. These samples were stored in a cooler on ice until the end of the day, and then transferred to a freezer at -20 °C until the start of the incubation experiment.

Vegetation metrics were characterized in August 2016. Within each 5 m by 5 m plot, canopy cover was estimated using a spherical convex densitometer, where the mean of each cardinal direction was calculated. Tree height was calculated as the mean of two measurements using a Haglof Vertex IV, and DBH (1.3 m) was recorded. In a nested 2 m by 2 m plot, percent cover of tall (1 m - 5 m) shrubs and short (15 cm - 1 m) shrubs was estimated and the most abundant species were recorded. In a 1 m by 1 m plot percent cover of forbs, trailing woody plants (<15 cm), graminoids, moss, and lichen, as well as needle, and broadleaf cover were estimated (Kershaw, J., Mackinnon, 1995; Appendix A-3).

3.2.3 Soil respiration

At the center of each plot, two PVC soil collars (20 cm diameter, 11 cm high) were spaced 0.5 m apart and installed into the soil to a depth of 7 cm. One collar was installed directly into the forest floor and live vegetation was cleared from the inside. The second collar was installed into exposed mineral soil where the forest floor had been removed. The purpose of the collar installed in the forest floor was to measure respiration from the entire soil profile, herein referred to as Total Soil Respiration. The collar installed in the mineral soil was to measure the contribution of the mineral soil to respiration fluxes, herein referred to as Mineral Soil Respiration. Collars were left for 2 weeks to allow soil to equilibrate. Prior to any measurements, live vegetation was cleared from inside both soil collars, and any fresh litter fall was removed from the Mineral Soil Respiration collar.

Soil respiration was measured using a Li-Cor Li-8100a soil gas flux system equipped with a 8100-103 survey chamber (Li-Cor, Nebraska, NE). To bring chamber conditions to ambient, a 30 s pre-purge period occurred prior to each measurement. A 30 s deadband preceded the 120 s observation period to allow for adequate mixing of gases. The rate of CO_2 efflux was fitted using a linear relationship between the rise in CO_2 concentration with time. A 30 s post-purge period followed each measurement to remove moisture from the gas lines. Soil temperature (at a depth of 8 cm from the surface of the forest floor for Total Soil Respiration measurements, or (8 cm) from the surface from the mineral soil for Mineral Soil Respiration measurements) was logged each second over the 120 s efflux measurement using a peripheral 6000-09TC Omega probe, and the mean was computed. Forest floor moisture was determined gravimetrically by collecting samples in triplicate around each plot at each time of sampling. In order to reduce the effect of diurnal variation on respiration fluxes, measurements occurred from 7:30 to 14:00 using a complete randomized block design. In the event of rainfall >1 mm, the experiment was terminated. In addition to the discrete sampling events, soil temperature and moisture content (10 cm below the forest floor surface) were logged hourly over the course of the study using Decagon 5TM moisture and temperature probes connected to a Em50 datalogger, and daily means were calculated. Mean daily air temperature and daily precipitation were acquired from a nearby weather tower (56° 44' 39" N, 118° 20' 35" W) obtained through the University of Alberta Enviro-Net (Enviro-Net, 2018).

3.2.4 Laboratory analyses and incubation

Moisture content was determined gravimetrically on forest floor subsamples by recording the field moist weight, oven drying at 65 °C for 48 hours, and measuring the final mass. Moisture content of mineral soil subsamples was determined by drying samples at 105 °C for 24 hour (Carter and Gregorich, 2008). Bulk density of the forest floor was determined using the same drying procedure, and was calculated as the quotient of the oven dry weight by the volume of the forest floor plug sampled.

Mineral soil and forest floor subsamples were air-dried, and sieved to <2 mm and <4 mm, respectively. The pH of the mineral and forest floor samples was measured from a suspension of 5 mL of soil to 25 mL of 0.01 M $CaCl_2$ (ISO, 2005). Particle size distribution was determined with the Bouyoucos hydrometer method (Scrimgeour, 2008). One modification of this method included physical separation of the sand fraction; following the 7 hour measurement, samples were sieved to 53 µm and washed, the coarse fraction was oven dried at 105 °C overnight and the weight was recorded to determine the sand content. For elemental analysis, the fine fractions were oven dried using the same procedure as before, and ground with a ball mill at 30 Hz for 30 s (Retsch MM200). TOC and TN concentrations were measured with a Costech Model EA 4010 Elemental Analyzer. Prior to analysis samples were treated with 5% HCl to remove inorganic carbon.

Prior to the start of the laboratory incubation, forest floor samples were thawed at 4 °C for 24 hours. Materials were then sieved to <6 mm, and within-plot replicates were homogenized; 100 g subsamples from each plot replicate were pooled and homogenized by topographic position. Moisture content and pH were determined on subsamples as described before. Field capacity of the forest floor was determined on subsamples using pressure plates (Carter and Gregorich, 2008). Briefly, subsamples were saturated with water for 24 hours, transferred to plates and into pressure chambers, which were sealed and a pressure of 10 kPa was applied for 24 hours. Samples were weighed and then the moisture content was determined. Water content at this pressure was an approximation for field capacity, which was the water content used during the incubation experiment.

Thawed Forest floor samples had been stored at 4 °C for one week while measuring pH, water content, and determining field capacity. Following this period, subsamples were brought to field capacity by adding deionized water, and were left to equilibrate in sealed ziplock bags for 24 hours at 4 °C. Following this period, 5 g oven dry equivalent forest floor subsamples were weighed into microcosms and placed in 1 L mason jars. Our microcosm design was similar to that of (Laganière et al., 2015), except forest floor material was suspended on a layer of 50 um litterbag mesh to prevent samples from sitting at the base of the mason jar. A 20 mL aliquot of tap water was added to the bottom of each jar to maintain 100 % relative humidity and the mass was recorded. Each topographic position was incubated in triplicate. For every sampling event 20 mL of headspace was collected and injected into a HP 5890 Series II gas chromatograph coupled to a thermal conductivity detector. Sampling originally occurred 3 times per week, but as rates of CO_2 efflux decreased so did the frequency of sampling. At the end of each sampling event, mason jars were opened for 10 minutes to return CO_2 concentrations to atmospheric levels, and water was added to return the container to its original mass. Cumulative respiration was calculated as the sum of each sampling event. Respiration rates were calculated by dividing the concentration of CO_2 evolved by the time between each respiration measurement. The incubation experiment continued for a total of 210 days, and included a total of 35 individual respiration measurements.

3.2.5 Data Analysis

To compare in-situ respiration between upslope and downslope positions for each sampling event we used a mixed effect modeling approach with the nlme package in R statistical software (Pinheiro et al., 2017). Forest floor respiration, mineral soil respiration, and total soil respiration fluxes were square-root transformed for normality. Respiration measurements occurred from the same soil collar for the duration of the experiment and our results were likely affected by repeated measures. To address this, soil collar ID was used as a random effect, while sampling event, topographic position, and their interaction were fixed effects. Orthogonal contrasts of significant interactions were investigated using the lsmeans package using the Holm adjustment for multiple comparisons (Lenth, 2015). We only compared orthogonal contrasts to avoid making unnecessary comparisons and also to prevent inflation of type II errors. The coefficients of variation of soil respiration and soil moisture and temperature were used to investigate the degree of spatial and temporal variability between flux measurements.

The temperature dependence of in-situ respiration was modelled using linear regressions for both the Total Soil and Mineral Soil Respiration. The moisture dependence of Total Soil Respiration was modelled using both linear and quadratic regressions with the gravimetric water content of the forest floor (Zhang et al., 2010). However, for Mineral Soil Respiration, the mean daily volumetric water content determined from nearby data loggers was used to model the moisture dependence of respiration.

We investigated differences in forest floor thickness and chemical properties among the topographic positions using Permutation al ANOVA followed by Tukey's HSD multiple comparison test to test for differences between means ($p<0.10$). For the laboratory incubation, the gas chromatogram measured the peak area of CO_2; this was converted to concentration with a calibration curve that was prepared using CO_2 standards for each respiration measurement. The concentration of CO_2 was converted to grams using the headspace volume of each Mason jar and the ideal gas law. The concentration of CO_2 per gram of total carbon was determined by dividing this mass by the total carbon concentration in each forest floor material. A first order kinetic exponential model was then used to describe the cumulative C mineralized (in mg C-CO_2 g^{-1} Total C) at time *t* using the function:

$$C_t = C_o (1 - e^{-kt})$$

Where C_t is the total carbon mineralized at time *t*; C_o is the labile, or active, carbon pool; and *k* is the rate of mineralization (Pare et al., 2005). In addition to this one pool model, we also determined the proportion of fast carbon, which was defined as the amount of cumulative carbon mineralized during the first 100 days of incubation (Laganière et al., 2013). Model parameters and the final respiration rates were compared using Permutation al ANOVA followed by Tukey's HSD multiple comparison test ($p < 0.10$). The package lmPerm was used for permutation procedures (Wheeler, 2010).

In-situ forest floor respiration fluxes were calculated by subtracting mineral soil respiration from total soil respiration as per Jonard et al. (2007). Due to spatial variability between soil collars, the calculation sometimes led to negative forest floor respiration values; in this we set the respiration equal to zero. We also converted forest floor respiration (μmol-CO_2 m^{-2} s^{-1}), to units comparable to our laboratory incubation (mg C-CO_2 g^{-1} Total C), by dividing fluxes by forest floor depth and bulk density, and the total organic carbon concentrations.

3.3 Results

3.3.1 Soil and vegetation properties along the hillslope

Lessivage, or translocation of clay particles from the surficial (Ae) to clay-enriched subsoil (Bt) horizons was the apparent dominant soil process upslope, indicating a high degree of water percolation through the soil profiles at these positions (Figure 3-1). Soils at the summit, shoulder and backslope positions were classified as Orthic Gray Luvisols (Appendices A-4, A-5). Overall soil development was most pronounced at the footslope position, with a solum thickness over 70 cm, which was the deepest on the hillslope. At this position there was a drastic decrease in slope angle, from 26° to 12°. In addition, gleying became an important process, with prominent mottles common in the profile starting at a depth of 20 cm, and the soil was classified as a Gleyed Gray Luvisol (Figure 3-1). Prominent mottles were also common at depths > 20 cm at the toeslope position, along with faint mottling in the Bt horizon at a depth of 9 cm, indicating seasonal water table fluctuations. The toeslope soil was classified as an Orthic Luvic Gleysol. Mottling was even more obvious at the depression area, where many prominent mottles were found at a depth of 7 cm, and the soil, an Orthic Gleysol, was the shallowest described along the hillslope.

The hillslope featured a trembling aspen canopy with a white spruce understory at the summit, a predominantly aspen canopy along the slope, and a transition into spruce at the base (Figure 3-1). Bryophyte cover was highest at the downslope positions under the white spruce canopy, and lowest on the steep portions of the slope. Forest floor morphology varied greatly along the hillslope, and followed changes in vegetation composition (Appendix A-5). In addition, from upslope to downslope, there was an increase in canopy cover, coinciding with an increase in forest floor thickness (Table 3-1). The forest floor at the toeslope and depression area was formed from white spruce needles and thick moss mats (Figure 3-1). At these positions, the fibric F horizons consisted primarily of partially decomposed moss tissue and fungal mycelia and were classified as Fs and Fsm, and the humus forms as Sphagnomores (Green 1997). The F horizons of the other soils were composed of dense, partially decomposed root fabric with an abundance of fungal hyphae and were classified as Fr and Frm, and the humus forms as either Hemimors or Resimors. The forest floor was largely Hemic, dominated by the F horizon and lacking a fully decomposed H horizon. Upslope soils had a thin H layer (<0.4 cm), while the H layers at the footslope was thicker at 1.8 cm. Some sites at the depression area also had a thick H layer (>1cm); this area was a transitional zone between Orthic Gleysols, Humic Gleysols, and Terric Organic soils.

3.3.2 Abiotic conditions

The mean daily air temperature over the course of the study was 13.6 °C, ranging from a maximum temperature of 19.7 °C on July 18th to a minimum of 4.1 °C on September 11th (Figure 3-2). Over the course of the study there were two temperature trends: 1. an overall warming period from the beginning of the experiment to August 20th, where the mean daily temperature fluctuated between 12.4 °C and 19.7 °C; and 2. from August 20th onward, a decline in mean daily temperature from 16.1 °C to 4.1 °C. There were several precipitation events each month over the course of the study period with a total accumulation of 143 mm. With the exception of a large rain event, the latter halves of August and September were drier, while more frequent rainfall occurred at the beginning of the experiment

Through hourly logging in the mineral soil, we found that the mean daily mineral soil temperatures at the summit, shoulder, upper-, and lower backslope positions were notably similar and warmer compared to the other positions (Figure 3-2). Mean daily mineral soil temperatures at the footslope and toeslope positions were comparable and consistently cooler, while the depression area was the coldest position. Mean daily mineral soil water content was greatest at the depression area, toeslope, and footslope positions, while upslope was consistently drier (Figure 3-2).

On each soil respiration sampling event, upslope forest floor temperature (8 cm) was warmer than downslope, and ranged from 10.5 to 12.9 °C, while downslope ranged from 8.3 to 11.0 °C (Table 3-2). In addition, the forest floors at downslope positions consistently had higher water contents ranging from 2.0 to 2.7 g g^{-1}, while upslope ranged from 1.1 to 1.9 g g^{-1}. While the seasonal coefficient of variation in forest floor temperature fluxes was approximately equal along the hillslope, the variation in forest floor moisture content was larger at upslope positions (Table 3-3).

3.3.3 In-situ soil respiration fluxes

Total soil respiration measured over the course of the study ranged from 1.8 to 12.1 μmol-CO_2 m^{-2} s^{-1}, and was higher across the study site during the warming period, from July to mid-August (Figure 3-3a). The median respiration rate of upslope positions ranged from 5.7 to 6.8 μmol-CO_2 m^{-2} s^{-1} over that period, and was significantly higher than downslope respiration on July 14th and August 12th; median downslope respiration ranged from 1.8 to 6.6 μmol-CO_2 m^{-2} s^{-1} over the same period (Figure 3-3a). When temperature declined later in the summer, respiration fluxes decreased, especially at the upslope positions (summit, shoulder, and upper- and lower backslope), which responded earlier and more drastically compared to downslope (footslope, toeslope, depression area). As a result, the temporal coefficient of variation of total soil respiration was larger for upslope positions compared to downslope (Table 3-3).

Mineral soil respiration of upslope positions was significantly higher than downslope for every sampling event (Figure 3-3b). Upslope fluxes ranged between 0.85 and 4.04 μmol-CO_2 m^{-2} s^{-1}, while downslope fluxes ranged from 0.32 to 2.77 μmol-CO_2 m^{-2} s^{-1}. Mineral soil respiration fluctuated less over the course of the growing season than total soil respiration and had smaller temporal coefficients of variation (Table 3-3).

Downslope forest floor respiration fluxes varied little over the first four sampling events, with median fluxes ranging from 3.4 to 3.7 μmol-CO_2 m^{-2} s^{-1}. On the last sampling event there was a sharp decrease to a median of 2.15 μmol-CO_2 m^{-2} s^{-1} (Figure 3-3c). Upslope forest floor respiration increased from the start of the experiment to early August, with median fluxes climbing from 3.3 to 4.2 μmol-CO_2 m^{-2} s^{-1}. Fluxes then decreased to 1.9 and 1.3 μmol-CO_2 m^{-2} s^{-1}, on the last two sampling events. There was no difference between upslope and downslope respiration fluxes until the last two sampling events, when upslope forest floor respiration significantly decreased.

For both the total soil- and the partitioned mineral soil respiration fluxes, temperature was a better predictor in modeling respiration fluxes than moisture content based on the coefficient of determination (Table 3-4). Mineral soil respiration had a higher correlation coefficient with both moisture and temperature than total soil respiration. Temperature was positively correlated with both mineral soil and total soil respiration fluxes. Increased moisture content led to a decrease in the mineral soil respiration; however for total soil respiration we found a weak quadratic relationship: where increases in moisture content from 1.0 to 1.7 g g^{-1} led to an increase in respiration, and beyond that led to a decrease in fluxes.

3.3.4 Laboratory incubations and forest floor carbon quality

Forest floors from the toeslope and depression area had the significantly highest C:N ratios (> 30) along the hillslope, followed by the summit and footslope positions, with ratios of 22, and 25, respectively (Table 3-1). The other upslope positions had significantly lower ratios of approximately 20. An increase in the C:N ratio was associated with a decrease in total nitrogen concentrations. There was also a significant decrease in the $\delta^{13}C$ values from the summit to the footslope, and an increase from the footslope to depression area (Table 3-1).

From our laboratory incubation, we found that upslope positions had much larger fast carbon pools. However, as the incubation continued, upslope rates decreased significantly and were eventually surpassed by downslope positions (Figure 3-4). Albeit the depression area had the lowest cumulative respiration, its rate of efflux also surpassed the upslope positions by the end of the experiment (Table 3-5). Through the first order kinetic model, we found that the toeslope and footslope positions had the largest labile carbon pools, containing 290.7 mg C-CO_2 g^{-1} Total C, and 180.5 mg C-CO_2 g^{-1} Total C, respectively, while other positions had labile pools of approximately 130 mg C-CO_2 g^{-1} Total C.

3.4 Discussion

3.4.1 Vertical partitioning of respiration fluxes and the contribution of the forest floor

We found that mineral soil respiration fluxes were lower at downslope positions for the duration of the study, likely due to the consistently low temperatures and high water content (Figures 3-2, 3-3b, Table 3-2). Temperature is the most commonly studied factor in respiration studies, and previous research has established a non-linear positive relationship between temperature and soil respiration (Reichstein and Janssens, 2009). Lower mineral soil temperatures likely occurred downslope partly due to the increased forest floor thickness and moss cover, which serves as a filter for heat transport, cooling mineral horizons (Oechel and Van Cleve, 1986). Increased water content may result in increased or decreased respiration. Depending on the soil pore-size distribution, and matric potential, increased water content can reduce CO_2 and O_2 diffusion through the soil profile (Davidson et al., 1998a). In a study of soil respiration on an agricultural hillslope, Wiaux et al. (2015) found that higher water content at downslope positions reduced soil respiration, even when there were minimal differences in soil temperature. It was likely the case that upslope mineral soil respiration fluxes were unaffected by moisture, but downslope was inhibited by the high water content, resulting in lower fluxes.

Compared to mineral soil, total soil respiration was more variable over the course of the season (Table 3-3). Across the study site, the temporal coefficients of variation for total soil respiration were higher compared to the partitioned mineral soil fluxes. This was especially the case for upslope positions where the seasonal coefficient of variation for total soil respiration was more than double that of mineral soil respiration. A large degree of the disparity between mineral and total soil fluxes appeared to be driven by the forest floor.

The temporal coefficient of variation for forest floor respiration was also much higher at upslope positions. We found that these positions had a more variable gravimetric water content relative to downslope positions, indicating a degree of insulation downslope due to topographically driven trends in forest structure and forest floor morphology (Table 3-2, Table 3-3). By comparing total soil to mineral soil respiration, we observed a disproportionate decrease in fluxes originating from the forest floor on our last two sampling events, indicating different controls on fluxes between the organic and mineral horizons (Figures 3-3a, b). Moisture content is an important factor to forest floor decomposition: in a laboratory incubation of forest soils, Kelliher et al. (2004) reported a 500 fold increase in forest floor respiration and a 3 fold increase in mineral soil respiration upon wetting to 60% water holding capacity. Similar effects have been reported in field studies, Berryman et al. (2014) compared the partitioned forest floor respiration to the total soil profile, and found that relative humidity was an important driver of forest floor respiration, while total soil respiration fluxes were dominated solely by temperatures.

On the last two events, upslope forest floor respiration fell sharply (Figure 3-3c). This decrease appeared to be linked to soil temperature as well as forest floor moisture content, which alone decreased by nearly 25% on the last two events (Table 3-2). Since water content at downslope positions was consistently greater than upslope, the smaller temperature appeared to limit respiration fluxes. The influence of moisture content at upslope positions paralleled the findings of Kelsey et al., 2012: once above a threshold temperature, water content was an important variable in controlling respiration in soil with thick organic horizons in Alaska, however below this threshold, moisture content was not a driving feature, as we observed downslope. Although forest floor respiration was approximately equal between slope positions for the duration of the study, soil temperature downslope was consistently lower, inhibiting decomposition (Figure 3-3c, Table 3-2). This suggests that much of the carbon stored in the forest floor at downslope positions is a result of temperature restriction on decomposition, and could be mineralized under future warming scenarios.

3.4.2 Linking in-situ respiration and soil organic carbon quality

We found an increase in the C:N ratios at downslope positions (Table 3-1). Values were similar to previous reports in this ecosystem for trembling aspen-, mixedwood, and coniferous-dominated canopies (Jerabkova et al., 2006). The chemical properties of the forest floor were influenced by litter inputs: where the toeslope and depression area had the highest C:N ratios due to the presence of conifer dominated canopies and forest floor composed of moss mats. The shoulder and backslope positions had the lowest C:N ratios since the litter inputs originated primarily from aspen trees and associated understory vegetation, and the summit and footslope positions had intermediate C:N ratios, due to the inputs of both conifer and broadleaf species. The summit did not have any coniferous trees within the plots, however conifers were adjacent and likely contributed some litter to the forest floor at this position (Figure 3-1).

By incubating forest floor materials under laboratory conditions, we were able to compare carbon quality along the hillslope, while removing the confounding influence of soil microclimate. Initially upslope positions had rapid carbon turnover, but rates of production decreased sharply over the course of the experiment compared to downslope positions (Figure 3-4). From the first-order kinetic model, we saw that with the exception of the depression area, labile carbon pools at downslope positions were much larger, reaching stages of slow decay later than upslope positions (Table 3-5). In a litter decomposition study comparing the mass loss of various litters, Berg et al. (1995) reported that litters that had lower initial decay rates took longer to decompose, but did so more fully and with much larger proportions of mass loss. They attributed this difference to variation in the nutrient content of litters, especially nitrogen, which enhanced decomposition initially, but inhibited mass loss at late decay stages. In our study, we found that downslope positions generally had lower total nitrogen concentrations, which was likely a dominating factor in the slower, but more complete, decomposition that we observed in the laboratory incubations (Table 3-1).

In an incubation study on forest floors from trembling aspen and black spruce stands, (Laganière et al., 2013) similarly reported larger initial production and fast carbon pools under aspen stands, and attributed this to difference to nitrogen content. Contrary to our findings, they found that this difference was shorted lived, and that the proportions of labile carbon were equal between the two stands. In a long-term litter decomposition study, Trofymow et al. (2002) compared the mass loss of numerous litter types at upland boreal sites across Canada. They found that litter nutrient content best described loss over the first year, and decomposition was positively correlated to total nitrogen in addition to other quality variables. However, climate was more important to long-term decomposition, and loss was positively related to increases in temperature and precipitation. Our results contrast those of Laganière et al. (2013) possibly due to the more drastic microclimatic gradient observed in our study, and to the fact that downslope positions had restricted turnover due to the combined effects of poor litter quality and an unfavourable microclimate.

Differences in the labile carbon pools would also be influenced by the chemical composition of the forest floor. In a previous study on forest floors from this research area, Hannam et al. (2004) found that the forest floor from aspen stands had a higher lignin content compared to spruce forest floors. They also found that while there was more aromatic carbon in forest floors of spruce stands, it was due to the accumulation of condensed tannins, which are not resistant to decomposition. They proposed that environmental conditions limited decomposition in spruce forest floors, allowing these structures to accumulate.

We observed a similar phenomenon in comparing the labile carbon pools at the summit and footslope positions. Although there was no significant difference in the C:N ratio between these positions, the footslope had a much larger labile carbon pool (Tables 3-1, 3-5). We suspect that this difference originated from environmental limitations, where low temperatures restricted decomposition at the footslope position. This is also supported by studies of boreal climosequences where a decrease in mean annual temperature is correlated with an increase in the mineralizable carbon pool (Hilli et al., 2008; Tian et al., 2016). In addition, we found a decrease in the $\delta^{13}C$ signature from the summit to the footslope position (Table 3-1), which is a feature indicating limited decomposition associated with colder temperatures (Kohl et al., 2017; Preston et al., 2006; Tian et al., 2016).

Interestingly, the carbon quality at the depression area varied drastically from other downslope positions, having a much smaller active carbon pool in addition to a high $\delta^{13}C$ signature (Table 3-1, Table 3-5), suggesting a heightened degree of decomposition relative to other downslope positions. The forest floor also had an uncharacteristically thick H layer, which also suggests a greater degree of decomposition. (Table 3-1; Appendix A-5). Initially we suspected sampling error was to blame for the small active carbon pool, however given that the forest floor total organic carbon concentration and pH were comparable to other downslope positions, this is likely not the case. The soils at the depression area transitioned between gleysols and organic soils; there were likely distinct soil processes at this position compared to the rest of the hillslope. Because this position was in a local depression and close to a nearby stream, we suspect that it may not have burned as intensely in the past as other topographic positions, allowing the forest floor more time to develop. Groundwater fluctuations also affected soil properties at the depression area, evidenced by the high base status in the mineral soil, yet the absence of carbonates. It is likely that either the fire history, or the influence of groundwater, or a combination of the two distinguished the depression area forest floor from the rest of the hillslope. While having unique properties, this position is an important outlier that highlights the extent of spatial variability in carbon storage and sequestration in the boreal forest.

In our in-situ study, we expected the combined influence of cold soil temperatures and poor forest floor quality to impede decomposition, leading to smaller respiration fluxes at the lower slope positions. However, we found that forest floor respiration rates were approximately equal between hillslope positions for the duration of the in-situ study (Figure 3-3c). Compared to the laboratory results, in-situ fluxes along the entire hillslope were impeded by a factor of ten, and may be potentially large sources of carbon under future warming (Figure 3-3d, Table 3-5). Furthermore, from our laboratory incubation, we found that once rates stabilized, downslope respiration rates were nearly double upslope positions, hence may constitute an even larger source of labile carbon with a changing climate (Table 3-5). While our study focused primarily on changes in fluxes and carbon stability along a hillslope, these results could be extended to the boreal at large, where broadleaf species have a tendency to occupy drier- and conifers occupy wetter and colder upland soils (Nijland et al., 2015).

3.5 Conclusion

Soils of the boreal forest play a critical role in the global carbon cycle. This is especially the case for the forest floor, which has been estimated to contain nearly 25% of the ecosystem carbon stocks. However, because of the high degree of spatial variability in the boreal, there is a wide range in the distribution and stability of soil organic carbon. By studying soil respiration and carbon stability along a hillslope, we were able to compare changes linked to soil microclimate and vegetation, while minimizing environmental factors varying at the broader landscape level. With this study we aimed to investigate the influence of topographically induced variation on total soil respiration and on the partitioned forest floor. In addition, we sought to compare these fluxes with a controlled laboratory incubation to investigate the linkage between our in-situ observations and soil organic carbon quality.

From our in-situ study we found that there were different controls governing soil respiration in the forest floor. At downslope positions respiration appeared to be inhibited by low temperatures, and fluctuated to a smaller extent because of this limitation. Instead, at upslope positions we found that forest floor water content was important to respiration, and forest floor desiccation reduced fluxes. From our laboratory incubation we found that carbon turnover was affected by forest floor nutrient content as well as soil microclimate. Because of limitations in-situ, downslope positions had a larger labile carbon pool as well as higher rates of CO_2 production that were nearly double upslope positions by the end of the laboratory incubation.

For the majority of the study, in-situ forest floor respiration fluxes were approximately equal along the hillslope, contrary to our initial hypothesis of downslope producing less carbon. However, our laboratory experiment demonstrated that downslope rates of production were almost double upslope. Albeit in-situ fluxes were limited along the entire hillslope, this suggests that the proportion of mineralizable carbon is much higher at downslope positions and may serve as a significant source of carbon under warming scenarios. While our findings are constrained to a hillslope, they are important in a broader context across the boreal, representing landscape changes in forest structure and drainage.

Tables

Table 3-1: Main properties of the forest floor and top mineral soil horizon for each topographic position. Values represent the mean (n=3) with the standard deviation in parenthesis. Forest floor thickness and chemical properties were evaluated through Permutation ANOVA, and Tukey's HSD multiple comparison test was used to compare means ($p < 0.10$; Appendix A-6). The two backslope positions were pooled for mineral soil characterization. (TOC: Total organic carbon (mg g^{-1})).

Position	Forest Floor										Mineral Soil			
	Thickness (cm)		pH p <0.10		TOC p <0.10		C:N Ratio p <0.10		δ^{13}C (‰) p <0.10		pH	TOC	C:N	Texture Class
Summit	7.4 (1.4)	b	4.98 (0.03)	e	455.5 (33.6)	a	22.0 (1.8)	b,c	-27.1 (0.5)	a,b	4.29 (0.01)	11.9	17.0	SiL
Shoulder	7.0 (0.8)	b	5.22 (0.0)	d	476.0 (7.9)	a	19.5 (0.1)	c	-27.5 (0.1)	a,b,c	4.66 (0.01)	12.3	13.7	SL
Upper Backslope	6.0 (1.1)	b	5.35 (0.03)	c	459.1 (26.2)	a	19.5 (0.5)	c	-27.8 (0.2)	b,c	5.85 (0.02)	12.4	12.4	L
Lower Backslope	6.2 (0.4)	b	5.48 (0.02)	b	480.2 (7.4)	a	20.2 (0.7)	c	-27.8 (0.4)	b,c				
Footslope	9.0 (0.2)	a,b	6.10 (0.01)	a	486.0 (9.6)	a	25.4 (2.9)	b	-27.9 (0.2)	c	4.46 (0.03)	15.0	13.6	L
Toeslope	8.2 (0.5)	b	4.28 (0.02)	g	499.3 (4.9)	a	31.4 (4.0)	a	-27.4 (0.2)	a,b,c	4.11 (0.01)	7.3	10.4	SiL
Dep. Area	13.1 (4.0)	a	4.42 (0.02)	f	466.3 (45.0)	a	33.4 (1.1)	a	-26.8 (0.2)	a	6.15 (0.03)	41.0	16.4	SiCL

Table 3-2: Mean forest floor temperature and gravimetric water content for upslope (n=12) and downslope positions (n=9), coinciding with each soil respiration measurement. Standard deviations are reported in parentheses.

Date	Forest floor temperature		Forest floor moisture content	
	Upslope	Downslope	Upslope	Downslope
-	(°C)	(°C)	(g^1 g^{-1})	(g^1 g^{-1})
14/07/2016	12.92 (0.34)	9.43 (0.60)	1.47 (0.16)	2.03 (0.39)
25/07/2016	12.44 (0.36)	9.62 (0.41)	1.86 (0.20)	2.06 (0.36)
12/08/2016	14.13 (0.50)	11.01 (0.46)	1.92 (0.16)	2.68 (0.28)
25/08/2016	13.35 (0.29)	10.50 (0.44)	1.05 (0.15)	2.17 (0.30)
15/09/2016	10.45 (0.37)	8.13 (0.33)	1.30 (0.21)	2.30 (0.39)

Table 3-3: Summary statistics of the seasonal variation of soil respiration, forest floor temperature and water content, and mineral soil temperature and water content, for upslope and downslope topographic positions. The mean values are reported below with the coefficients of variation (CV) in parenthesis (n=5).

Slope position	Total soil respiration	Forest Floor Respiration	Forest floor temperature	Forest floor water content
Upslope Downslope	5.25 (0.22) 4.23 (0.17)	3.03 (0.37) 3.04 (0.19)	12.7 (0.11) 9.6 (0.11)	1.52 (0.24) 2.25 (0.12)
Slope position	Mineral soil Respiration	-	Mineral soil temperature	Mineral soil water content
Upslope Downslope	2.21 (0.10) 1.19 (0.14)	-	12.5 (0.11) 9.3 (0.12)	0.18 (0.05) 0.24 (0.11)

Table 3-4: Regression analysis relating soil moisture and temperature with total and mineral soil respiration. Parameters were measured concurrently with each efflux measurement. Soil temperature was measured with in the forest floor and mineral soil for total soil respiration and mineral soil respiration, respectively. Gravimetric water content of the forest floor was used for modelling total soil respiration, while moisture content from permanently installed em50 probes at time of sampling was used to model mineral soil respiration. LFH: Forest floor (8 cm); MS: upper mineral soil (8 cm from the exposed mineral soil.

Substrate	Parameter	*m*		b	R^2	AIC	RMSE	p-value
Total Soil	LFH temperature	0.91		0.41	0.35	105.1	1.00	<0.001
Mineral Soil	MS temperature	0.25		-1.03	0.49	56.5	0.50	<0.001
Function				**Rs = *m*T + b**				
Total Soil	LFH water content	-0.12		5.00	0.00	121.2	1.25	0.79
Mineral Soil	MS water content	-10.3		3.9	0.3	67.6	0.58	<0.001
Function				**Rs = *m W* + b**				
Substrate	Parameter	a	b	c	R2	AIC	RMSE	p-value
Total Soil	LFH water content	-0.29	6.16	-1.73	0.06	118.9	1.18	0.14
Function				$\mathbf{Rs} = a + bW + cW^2$				

Table 3-5: Forest floor carbon pools determined through laboratory incubations and final respiration rates, representing the mean mineralization rates of the final three measurements. Fast carbon consists of the cumulative CO_2 generated per gram of total carbon over the first 100 days of the experiment, and active carbon is the maximum mineralizable carbon determined through a first order kinetic model. Differences between carbon pools and rates were evaluated through Permutation ANOVA, and Tukey's HSD multiple comparison test was used to compare means ($p < 0.10$; Appendix A-6).

Position	Fast Carbon (mg $C\text{-}CO_2$ g^{-1} Total C) $p < 0.10$			Active Carbon (mg $C\text{-}CO_2$ g^{-1} Total C) $p < 0.10$			Final respiration rate (mg $C\text{-}CO_2$ g^{-1} Total C h^{-1}) $p < 0.10$		
Summit	97.0	(3.4)	a	124.7	(4.0)	c	0.89	(0.08)	c
Shoulder	94.6	(2.0)	a,b	134.2	(3.6)	c	0.98	(0.12)	c
Upper Backslope	98.1	(1.8)	a	134.3	(0.8)	c	0.94	(0.10)	c
Lower Backslope	88.0	(2.0)	c	116.8	(3.9	c	0.79	(0.09)	c
Footslope	90.7	(0.6)	b,c	180.5	(0.5)	b	2.0	(0.12)	a
Toeslope	75.7	(0.9)	d	290.7	(25.2)	a	2.0	(0.10)	a
Depression Area	50.1	(0.8)	e	124.4	(9.2)	c	1.4	(0.13)	b

Figures

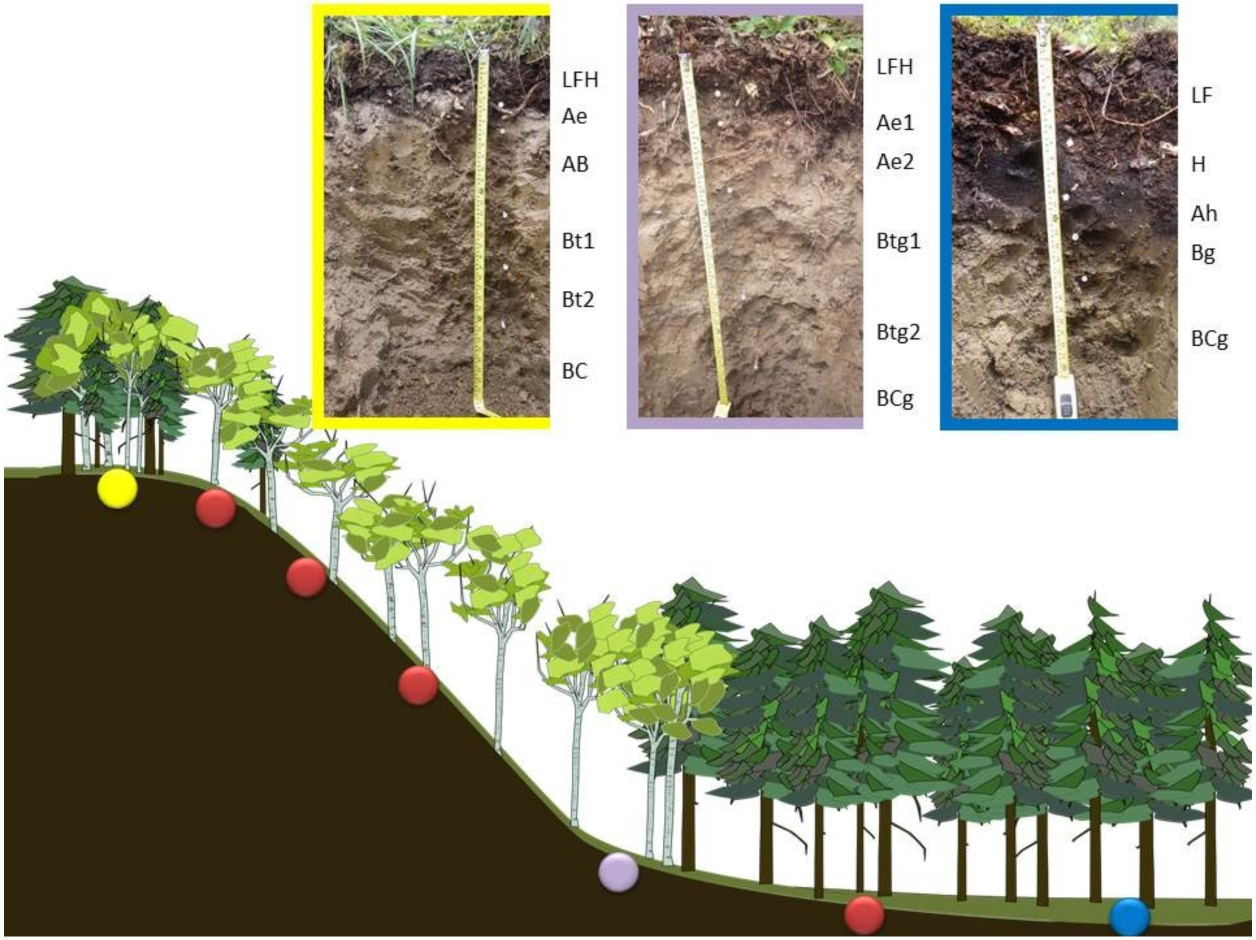

Figure 3-1: Diagram of the study site and key soil profiles. Topographic positions are indicated by red closed circles, where upslope positions included the summit, shoulder, upper backslope, and lower backslope; and downslope featured the footslope, toeslope and depression area (from upper left to bottom right). Noteworthy topographic positions including the summit (yellow), footslope (purple), and depression area (blue) were highlighted and the corresponding soil profile was included.

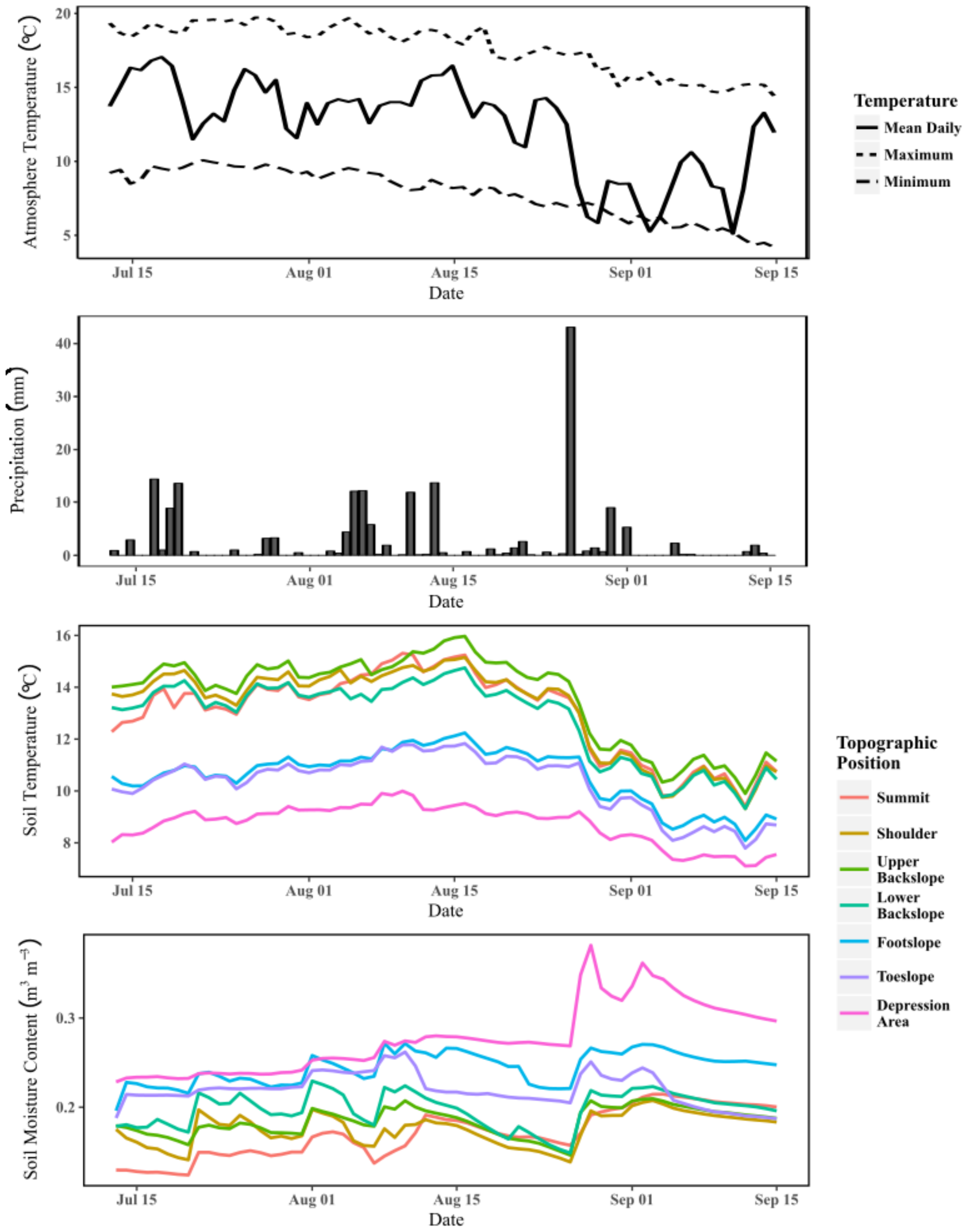

Figure 3-2: Meteorological conditions spanning the respiration experiment, including: mean daily air temperature, 20 year maximum daily and minimum daily temperatures (˚C), daily precipitation (mm), and mean daily mineral soil temperature and volumetric water content for each topographic position along the hillslope. Soil measurements were taken at a depth of 10 cm below the forest floor surface, while atmospheric values were obtained from a nearby weather station. Over this period in 2016, there was 143 mm of precipitation, which exceeded the 20 year average of 117 mm.

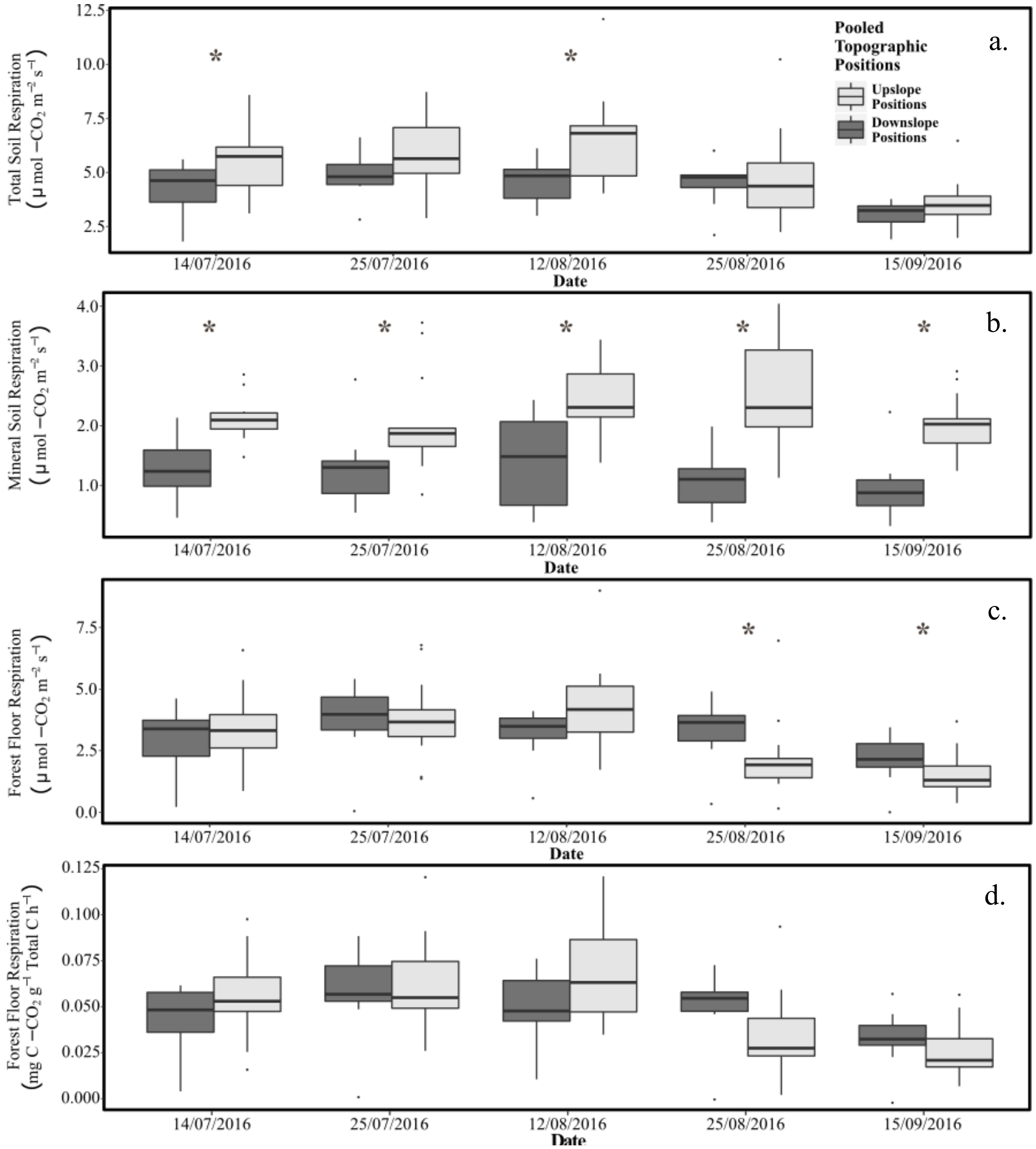

Figure 3-3: Box plots of a. total in-situ soil respiration; b. mineral soil respiration, and c. partitioned forest floor respiration (µmol-CO$_2$ m^{-2} s^{-1}), and; d. the partitioned forest floor respiration, with units relativized to the laboratory incubation (mg C-CO$_2$ g^{-1} Total C). Upslope positions include the summit, shoulder, and upper and lower backslope, while downslope positions include the footslope, toeslope and depression area. Horizontal lines represent median values, boxes represent the inter-quartile ranges, whiskers represent the 10th and 90th percentiles, and solid circles represent outliers. Upslope and downslope respiration fluxes were compared using linear mixed effect models, followed by post-hoc comparisons using the Holm adjustment ($p < 0.10$).

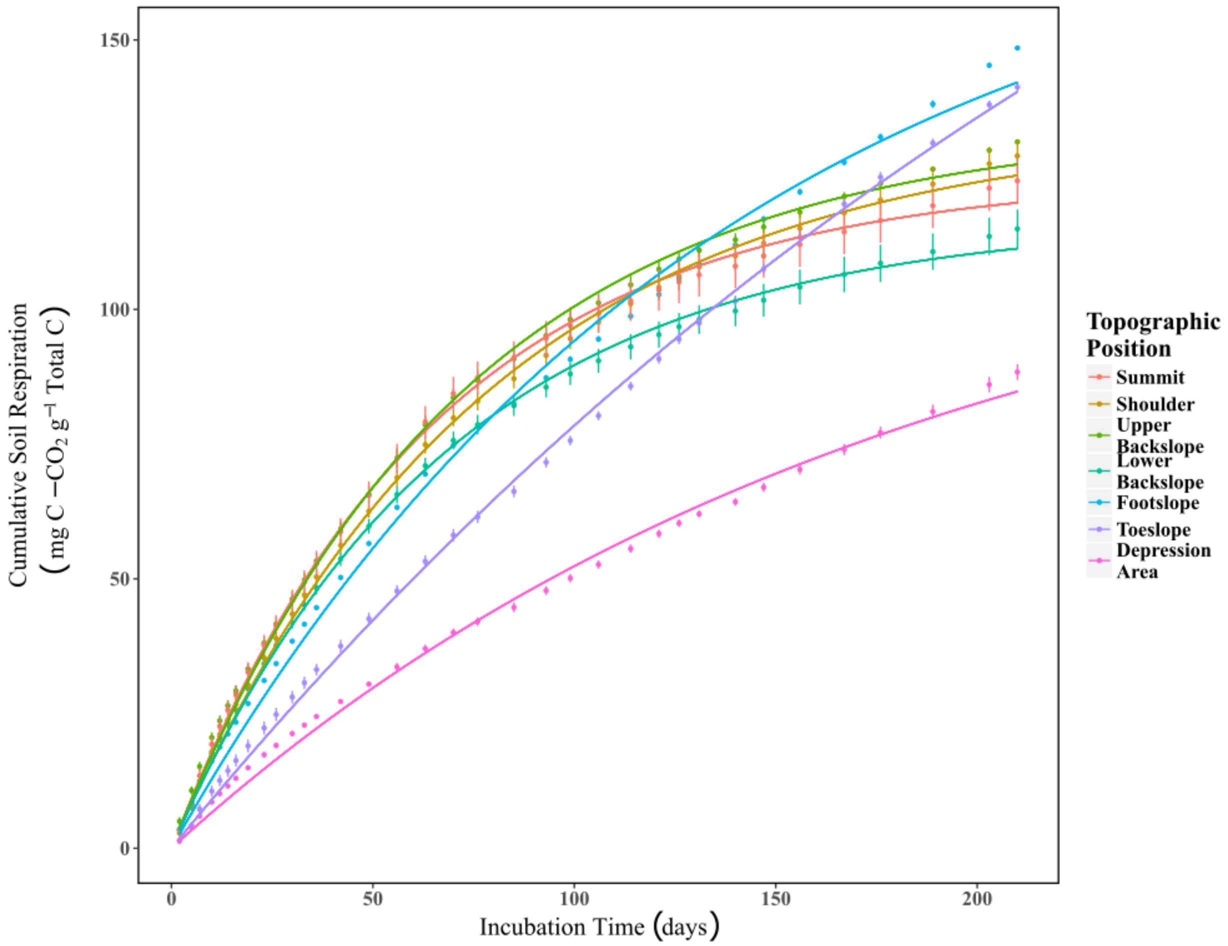

Figure 3-4: Cumulative soil respiration (mg C- CO_2 g^{-1} Total C) of forest floor materials collected from each topographic position and incubated in the laboratory at field capacity and 20˚C over a period of 210 days). Error bars represent one standard deviation (n = 3). The cumulative respiration of each position was fitted to the first-order kinetic model, $C_t = C_o(1 - e^{-kt})$, where C_t is the total carbon mineralized at time *t*; C_o is the labile carbon pool; and *k* is the rate of mineralization.

Chapter 4. Synthesis and Discussion

4.1 Research Summary

The overall goal of this research was to investigate how moisture gradients influenced soil organic carbon dynamics, among natural and harvested stands that were dominated by trembling aspen and white spruce. The specific objectives of Chapter 2 were to use a topographic index to model soil properties between conifer-dominated and deciduous-dominated stands. This study focused on the evolution and comparison of these soil parameters between cover types, 17 years post-harvest. In addition, we were interested to see if aspen regeneration following retention harvesting had altered soil properties between these cover types, and whether the relationships with the topographic index varied based on the degree of retention.

The objectives of Chapter 3 were to develop a finer understanding of the processes governing soil organic carbon properties uncovered in Chapter 2. Soil organic carbon is a balance between soil inputs and outputs (Simonson 1959), and the objective of this chapter was to focus on the controls governing the output, or turnover of carbon. Specifically, the objectives were to measure soil respiration along a hillslope that transitioned from upslope positions featuring well-drained luvisols and a trembling aspen dominated canopy, to poorly drained gleysols dominated by white spruce cover at lower slope positions. We were interested in how topographically-induced changes in forest structure, soil microclimate, and forest floor composition influenced soil respiration and carbon stability. We paired our in-situ study with a laboratory incubation, where all soil materials were kept at equal soil moisture and temperature conditions in order to directly compare carbon stability. Such landscape features are common in the boreal, and serve as important interfaces that are analogous to stands of aspen and spruce occurring across the landscape.

4.2 Landscape scale controls on carbon distribution

Trembling aspen regeneration dominated in the years following harvest at EMEND (Echiverri, 2017; Nijland et al., 2015). In disturbed stands, there were multiple factors influencing soil properties that originated from the combined effects of retention harvesting, aspen regeneration, and in conifer-dominated stands, the legacy of spruce in the soil. Harvest in deciduous-dominated stands led to decreased forest floor TN content, which potentially was lost through leaching following harvest, or through the proliferation of young aspen trees, which have higher nutrient demand (Lindo and Visser, 2003; Miller, 1995). In contrast, harvest in conifer-dominated stands led to increased forest floor TN content, and decreased TC, and the C:N ratio. This gain in nitrogen likely originated from aspen recruitment, which may have compensated for leaching losses through incorporating nitrogen-rich litterfall into the soil. The decrease in forest floor $\delta^{13}C$ values in harvested conifer-dominated stands also reflects the conversion to a deciduous-dominated canopy (Brooks et al., 1997). Interestingly, this effect has taken years to manifest, and was absent up to four years following harvest (Hannam et al., 2005).

The relationships between the DTW index and soil properties were more strongly expressed in the mineral soil layer of uncut control stands, compared to the forest floor. In the mineral soil, we observed increases in TN and TC content, and carbon stocks, with increased moisture. These findings indicate limited decomposition at the wet end of the gradient, and aligns with previous reports of carbon distribution in the boreal (Olsson et al., 2009; Rapalee et al., 1998). While relationships in the forest floor were more variable, we found similar patterns in conifer-dominated stands, where carbon stocks and forest floor depth increased at wetter sites. In contrast, we found that the natural abundance of ^{13}C and ^{15}N rose at wetter sites in deciduous-dominated stands, which suggests that there was an increase in decomposition at the wet end of the DTW gradient (Natelhoffer and Fry, 1988).

While there was virtually no relationship between forest floor carbon stocks and DTW in control deciduous-dominated stands, harvest led to large increases in stocks and forest floor thickness at wetter sites. In addition, we found that in control stands there was an increase in $\delta^{13}C$ and $\delta^{15}N$ values at wetter sites, while the relationships in harvested stands were closer to zero. Both the increase in stocks, and the decrease in natural isotopic abundances, suggests reduced decomposition in harvested deciduous-dominated stands at the wet end of the gradient. We found the opposite in conifer-dominated stands, where decomposition appeared to increase. Compared to the controls, there was an decrease in carbon stocks, and the C:N ratio at the wet end of gradient in harvested stands.

4.3 Hillslope scale controls on carbon stability

From our in-situ study, we found that there were different controls governing mineral soil respiration and forest floor respiration fluxes. We found that mineral soil respiration fluxes were dominated by the soil microclimate, with downslope positions consistently respiring less than upslope because of lower temperatures and higher water contents. Forest floor respiration was more variable: at downslope positions, respiration was limited from consistently low temperatures, while upslope was mainly limited through desiccation.

In our laboratory incubation, we found that upslope positions initially had fast rates of respiration, but declined later in the experiment, and were eventually surpassed by most downslope positions. In addition, the first-order kinetic models predicted that downslope positions had larger labile carbon pools compared to upslope. The rapid initial turnover was likely due to the higher nitrogen content upslope, while downslope positions had larger labile carbon pools overall, because of poor conditions in-situ favouring the accumulation of partially decomposed organic matter. Although the rates at the end of the incubation were greater than our in-situ fluxes by a factor of ten, downslope rates were nearly double upslope positions, and are a potentially larger long-term carbon source under warming scenarios.

4.4 Linking carbon stability and stocks

Based on temporal coefficients of variation, we found that forest floor respiration and total soil respiration fluxes were more variable compared to mineral soil respiration. In addition, through regression analysis, we found that mineral soil was most strongly related to soil temperature and moisture. The higher degree of variability in forest floor respiration originated from confounding variables that we did not measure. In an in-situ respiration study conducted in the rocky mountains, Berryman et al. (2014) found that litter respiration was strongly influenced by relative humidity, while total soil respiration was linked to temperature. Similarly, Goffin et al. (2014) found that wind turbulence was also an important driver of respiration solely in the forest floor. Since the forest floor is at the air-soil interface, it is more intensely affected by atmospheric fluctuations compared to the mineral soil, and this feature distinguishes its respiration activity from the rest of the soil profile.

In our stand-scale study of carbon stocks, a similar phenomenon occurred by relating the DTW index to soil properties in uncut control stands. Mineral soil TC and carbon stocks were more strongly related to DTW compared to the forest floor; stocks increased at wetter sites, where respiration fluxes would have been smallest. This suggests that decomposition processes are more strongly correlated with topography in the mineral soil. In their study of landscape-scale carbon distribution, Rapalee et al. (1998) had similar findings: mineral soil carbon stocks were strongly related to soil drainage, while the distribution in the organic horizons was dominated by the disturbance regime.

We found that the relationships between the DTW index, and indictors of forest floor stability, varied between stand types. At wetter sites there was increased forest floor decomposition in undisturbed deciduous-dominated stands, while in conifer dominated stands, accumulation of organic matter suggested the opposite. A notable feature of the in-situ respiration study was that upslope forest floor respiration was limited by desiccation events, which supports our observation that decomposition was most hampered at drier sites in deciduous-dominated stands. At downslope positions with dense white spruce cover, temperature limitations restricted soil respiration. This may also parallel our findings of larger stocks at wetter sites in conifer-dominated stands, since soil temperature and moisture are negatively related in soils (Davidson et al., 1998; Xu et al., 2002).

4.5 Project limitations and future research

Research of carbon stability and distribution was constrained by a number of limitations. In Chapter 2 we demonstrated the utility of DTW as a tool in modeling the distribution and quality of soil organic carbon. Future research should incorporate other predictor variables to improve the strength of relationships. From Chapter 3, I learned that both the soil microclimate and soil respiration are strongly influenced by changes in forest structure. In a study on the controls of soil temperature and moisture in temperate forest, Xu et al. (2002), reported that in addition to topography, canopy height, and cover type were important controls on soil microclimate. Including canopy parameters will likely enhance modeling efforts; this information is also available with LiDAR data, and would be a next step towards improving model performance. Including soil parameters as explanatory variables may also improve modeling efforts. While DTW predicts soil moisture, it does so based on changes in elevation

(Murphy et al., 2007). Including soil texture, soil order, or great group may have strengthen relationships, since these features are important to soil drainage and carbon distribution (Dalsgaard et al., 2016).However a drawback of incorporating soil properties could be more intensive sampling with limited improvement to modeling efforts. With this in mind, future work should possibly be limited to other remote sensing tools.

In Chapter 3, seven topographic positions were established along the hillslope, to investigate how incremental changes in soil moisture and temperature influenced in-situ soil respiration and carbon stability. However, this high sampling effort reduced my opportunities to collect data, and because of equipment failure and poor weather conditions, led to five sampling events that could be used for analysis. In addition, a high degree of spatial heterogeneity and diurnal variation during sampling, limited my ability to relate these incremental changes in the soil microclimate to soil respiration. This led to coarser-scale comparisons between upslope and downslope positions along the hillslope. Reducing the number of topographic positions would have simplified both analysis and interpretation of the data. However, I believe that the hillslopes are important and understudied interfaces, and future work at this scale should involve long-term continuous monitoring of respiration fluxes in order to better understand how both incremental changes in microclimate and various seasons (especially snowmelt) influence soil respiration and carbon stability.

Forest floor removal to measure mineral soil respiration fluxes is an approach that has been used in previous studies (Jonard et al., 2007; Rey et al., 2002). However removal of the forest floor may have led to altered microclimatic conditions compared to undisturbed soils, influencing respiration fluxes. Calculation of forest floor respiration may have also been skewed, given that forest floor thickness varied along the slope. With very thick forest floors, CO_2 released from the mineral soil would have to diffuse a greater distance through the forest floor to be detected, this may have led to a decrease in respiration rates relative to thin forest floors, where the distance was much smaller.

Hillslopes transitioning from trembling aspen to white spruce are important landscape features in the boreal; they contain transitions in a small area that are analogous to changes across its range. We found that forest structure, soil microclimate, and forest floor composition were important drivers of soil respiration and carbon stability. Future work should compare several hillslopes featuring single cover types to attempt to isolate the effects of soil microclimate on respiration fluxes at this scale. Lastly, we focused on carbon stability in the forest floor; mineral soil is a longer-term store of carbon, and including an investigation of its stability along topographic gradients will enhance our understanding of carbon cycling in forest soils.

4.6 Management Implications

Drawing management recommendations for these findings is a challenge since they correlate to 17 years following harvest of a forest nearing approximately 140 years in age: the relationships observed may be isolated to this point and time, and differ in various timeframes.

If the objective of foresters is to manage for carbon storage in the boreal mixedwood forest, without engaging in any silvicultural activities following harvest, then our findings may help to meet these goals with the use of the DTW index. Our results suggest that under the EMEND framework and aspen regeneration, harvesting at the wet end of the DTW gradient may lead to an increase in forest floor carbon stocks of deciduous-dominated stands, but a decrease in conifer-dominated stands. Harvest at the dry end of the gradient is a preferable option in conifer-dominated stands, since TC and the C:N ratio will increase, and potentially reduce the decomposability of the forest floor. A caveat of these recommendations however, is that these strategies reflect carbon storage solely in the forest floor. The forest floor is a temporary store of carbon, and sensitive to changes in canopy as well as the disturbance regime (Kurz et al., 2013). In addition, our study does not account for changes that will immediately occur following harvesting. However, the potential for DTW has been demonstrated, and future work should seek to understand how the relationships between this tool and soil parameters change with time following disturbances.

References

Albani, M., Andison, D.W., Kimmins, J.P., 2005. Boreal mixedwood species composition in relationship to topography and white spruce seed dispersal constraint. For. Ecol. Manage. 209, 167–180.

Balesdent, J., Girardin, C., Mariotti, A., 1993. Site-related δ13C of tree leaves and soil organic matter in a temperate forest. Ecology 74, 1713–1721.

Bartels, S.F., Caners, R.T., Ogilvie, J., White, B., Macdonald, S.E., 2018. Relating Bryophyte Assemblages to a Remotely Sensed Depth-to-Water Index in Boreal Forests. Front. Plant Sci. 9, 1–11.

Beckingham, J.D., Archibald, J.H., Corns, I.G.W., 1996. Field guide to ecosites of northern Alberta, Natural Resources Canada. Canadian Forestry Service, Edmonton.

Bedard-Haughn, A., 2011. Gleysolic soils of Canada: Genesis, distribution, and classification. Can. J. Soil Sci. 91, 763–779.

Benner, R., Fogel, M.L., Sprague, E.K., Hodson, R.E., 1987. Depletion of 13C in lignin and its implications for stable carbon isotope studies. Nature 329, 708–710.

Berg, B., McClaugherty, C., De Santo, A.V., Johansson, M.B., Ekbohm, G., 1995. Decomposition of litter and soil organic matter—can we distinguish a mechanism for soil organic matter buildup? Scand. J. For. Res. 10, 108–119.

Bergeron, C., 2012. Fire history, landscape biodiversity and indicators for sustainable management of the boreal mixedwood forest. Ph.D. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

Berryman, E.M., Marshall, J.D., Kavanagh, K., 2014. Decoupling litter respiration from whole-soil respiration along an elevation gradient in a Rocky Mountain mixed-conifer forest. Can. J. For. Res. 44, 432–440.

Bhatti, J.S., Apps, M.J., Jiang, H., 2002. Influence of nutrients, disturbances and site conditions on carbon stocks along a boreal forest transect in central Canada. Plant Soil 242, 1–14.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2005. Spatiotemporal measurement and modeling of stand-level boreal forest soil temperatures. Agric. For. Meteorol. 131, 27–40.

Borken, W., Beese, F., 2005. Soil respiration in pure and mixed stands of European beech and Norway spruce following removal of organic horizons. Can. J. For. Res. 35, 2756–2764.

Boulanger, Y., Taylor, A.R., Price, D.T., Cyr, D., McGarrigle, E., Rammer, W., Sainte-Marie, G., Beaudoin, A., Guindon, L., Mansuy, N., 2017. Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landsc. Ecol. 32, 1415–1431.

Brandt, J.P., 2009. The extent of the North American boreal zone. Environ. Rev. 17, 101–161.

Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D., Volney, W.J. a., 2013. An introduction to Canada’s boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ. Rev. 21, 207–226.

Brooks, J.R., Flanagan, L.B., Buchmann, N., Ehleringer, J.R., 1997. Carbon isotope composition of boreal plants: functional groupings of life forms. Oecologia 110, 301–311.

Buck, J.R., St. Clair, S.B., 2012. Aspen Increase Soil Moisture, Nutrients, Organic Matter and Respiration in Rocky Mountain Forest Communities. PLoS One 7, 1–6.

Chen, H.Y.H., Luo, Y., 2015. Net aboveground biomass declines of four major forest types with forest ageing and climate change in western Canada's boreal forests. Glob. Chang. Biol. 21, 3675–3684.

Coursolle, C., Margolis, H.A., Giasson, M.A., Bernier, P.Y., Amiro, B.D., Arain, M.A., Barr, A.G., Black, T.A., Goulden, M.L., McCaughey, J.H., Chen, J.M., Dunn, A.L., Grant, R.F., Lafleur, P.M., 2012. Influence of stand age on the magnitude and seasonality of carbon fluxes in Canadian forests. Agric. For. Meteorol. 165, 136–148.

Dalsgaard, L., Lange, H., Strand, L.T., Callesen, I., Borgen, S.K., Liski, J., Astrup, R., 2016. Underestimation of boreal forest soil carbon stocks related to soil classification and drainage [1]. Can. J. For. Res. 46, 1413–1425.

Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob. Chang. Biol. 4, 217–227.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Davidson, E.A., Janssens, I.A., Lou, Y., 2006. On the variability of respiration in terrestrial ecosystems: Moving beyond Q10. Glob. Chang. Biol. 12, 154–164.

Davidson, E.A., Savage, K.E., Trumbore, S.E., Borken, W., 2006. Vertical partitioning of CO 2 production within a temperate forest soil. Glob. Chang. Biol. 12, 944–956.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531.

DeLuca, T.H., Boisvenue, C., 2012. Boreal forest soil carbon: Distribution, function and modelling. Forestry. 85, 161–84.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., Brown, S., Houghton, R.A., Trexier, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. Science. 263, 185–190.

Echiverri, L., 2017. Identifying understory diversity and resilience patterns with the depth- to-water index in boreal mixedwood forests. M.Sc. Thesis, Department of Renewable Resources, University of Alberta, Edmonton, AB.

Enviro-net, 2018. University of Alberta. http://www.enviro-net.org/Default.aspx. Accessed on March 2017

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. J. Appl. Ecol. 51, 1669–1679.

Government of Alberta, 2017. Sustainable Forest Management. https://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/formain15744/$FILE/2201-AAC-Fact-Sheet.pdf. Accessed on June 10, 2018.

Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. Science 349, 819–822.

Goffin, S., Aubinet, M., Maier, M., Plain, C., Schack-Kirchner, H., Longdoz, B., 2014. Characterization of the soil CO2 production and its carbon isotope composition in forest soil layers using the flux-gradient approach. Agric. For. Meteorol. 188, 45–57.

Gower, S.T., Vogel, J.G., Norman, M., Kucharik, C.J., Steele, S.J., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102, 29–41.

Gradowski, T., Lieffers, V.J., Landhäusser, S.M., Sidders, D., Volney, J., Spence, J.R., 2010. Regeneration of Populus nine years after variable retention harvest in boreal mixedwood forests. For. Ecol. Manage. 259, 383–389.

Green, R.N., Trowbridge, R.L., Klinka, K., 1993. Towards a taxonomic classification of humus forms. For. Sci. Monogr. 39, 1–49.

Hannam, K.D., Quideau, S. a., Oh, S.-W., Kishchuk, B.E., Wasylishen, R.E., 2004. Forest floor composition in aspen- and spruce-dominated stands of the Boreal mixedwood forest. Soil Sci. Soc. Am. J. 68, 1735.

Hannam, K.D., Quideau, S. a, Kishchuk, B.E., Oh, S.-W., Wasylishen, R.E., 2005. Forest-floor chemical properties are altered by clear-cutting in boreal mixedwood forest stands dominated by trembling aspen and white spruce. Can. J. For. Res. 35, 2457–2468.

Hilli, S., Stark, S., Derome, J., 2008. Carbon quality and stocks in organic horizons in boreal forest soils. Ecosystems 11, 270–282.

IPCC, 2007. IPCC fourth assessment report: climate change 2007. www.ipcc.ch/ publications_and_data/publications_and_data_reports.shtml. Accessed on January 2017.

IPCC, 2001. IPCC third assessment report: climate change 2001. www.ipcc.ch/ publications_and_data/publications_and_data_reports.shtml. Accessed on January 2017.

ISO, 2005. ISO 10390 Soil quality - Determination of pH. https://www.sis.se/api/document/preview/905787/. Accessed on December 2016.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268.

Jenny, H., 1941. Factors of Soil Formation. New York: McGraw-Hill. 130

Jerabkova, L., Prescott, C.E., Kishchuk, B.E., 2006. Nitrogen availability in soil and forest floor of contrasting types of boreal mixedwood forests. Can. J. For. Res. 36, 112–122.

Jiang, X., Huang, J.G., Stadt, K.J., Comeau, P.G., Chen, H.Y.H., 2016. Spatial climate-dependent growth response of boreal mixedwood forest in western Canada. Glob. Planet. Change 139, 141–150.

Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L.W., Schoennagel, T., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ.

Jonard, M., Andre, F., Jonard, F., Mouton, N., Proces, P., Ponette, Q., 2007. Soil carbon dioxide efflux in pure and mixed stands of oak and beech. Ann. For. Sci. 64, 141–150.

Kelliher, F.M., Ross, D.J., Law, B.E., Baldocchi, D.D., Rodda, N.J., 2004. Limitations to carbon mineralization in litter and mineral soil of young and old ponderosa pine forests. For. Ecol. Manage. 191, 201–213.

Kelsey, K.C., Wickland, K.P., Striegl, R.G., Neff, J.C., 2012. Variation in soil carbon dioxide efflux at two spatial scales in a topographically complex boreal forest. Arctic, Antarct. Alp. Res. 44, 457–468.

Kershaw, J., Mackinnon, P., 1995. Plants of the western Boreal forest and aspen parkland.

Khomik, M., Arain, M.A., McCaughey, J.H., 2006. Temporal and spatial variability of soil respiration in a boreal mixedwood forest. Agric. For. Meteorol. 140, 244–256.

Kishchuk, B.E., 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment, northwestern Alberta. Can. For. Serv. Info. Rep. NOR-X-397.

Kishchuk, B.E., Morris, D.M., Lorente, M., Keddy, T., Sidders, D., Quideau, S., Thiffault, E., Kwiaton, M., Maynard, D., 2016. Disturbance intensity and dominant cover type influence rate of boreal soil carbon change: A Canadian multi-regional analysis. For. Ecol. Manage. 381, 48–62.

Kishchuk, B.E., Quideau, S., Wang, Y., Prescott, C., 2014. Long-term soil response to variable-retention harvesting in the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment, northwestern Alberta. Can. J. Soil Sci. 94, 263–279.

Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., Sidders, D., 2015. Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. Can. J. For. Res. 45, 141–152.

Kohl, L., Philben, M., Edwards, K.A., Podrebarac, F.A., Warren, J., Ziegler, S.E., 2017. The origin of soil organic matter controls its composition and bioreactivity across a mesic boreal forest latitudinal gradient. Glob. Chang. Biol. 458–473.

Kurz, W.A., Shaw, C.H., Boisvenue, C., Stinson, G., Metsaranta, J., Leckie, D., Dyk, A., Smyth, C., Neilson, E.T., 2013. Carbon in Canada’s boreal forest — A synthesis. Environ. Rev. 21, 260–292.

Laganière, J., Boča, A., Van Miegroet, H., Paré, D., 2017. A tree species effect on soil that is consistent across the species’ range: the case of aspen and soil carbon in North America. Forests 8, 113.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.Y.H., 2012. The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. Soil Biol. Biochem. 53, 18–27.

Laganière, J., Paré, D., Bergeron, Y., Chen, H.Y.H., Brassard, B.W., Cavard, X., 2013. Stability of Soil Carbon Stocks Varies with Forest Composition in the Canadian Boreal Biome. Ecosystems 16, 852–865.

Laganière, J., Paré, D., Bradley, R.L., 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Can. J. For. Res. 40, 465–475.

Laganière, J., Podrebarac, F., Billings, S.A., Edwards, K.A., Ziegler, S.E., 2015. A warmer climate reduces the bioreactivity of isolated boreal forest soil horizons without increasing the temperature sensitivity of respiratory CO<inf>2</inf> loss. Soil Biol. Biochem. 84, 177–188.

Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manage. 220, 242–258.

Lavkulich, L.M., Arocena, J.M., 2011. Luvisolic soils of Canada: Genesis, distribution, and classification. Can. J. Soil Sci. 91, 781–806.

Lenth, R., 2015. Package ‘ lsmeans .’ J. Stat. Softw. 69, 1–33.

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., Gustafsson, L., 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. 5, 421–431.

Lindo, Z., Visser, S., 2003. Microbial biomass, nitrogen and phosphorus mineralization, and mesofauna in boreal conifer and deciduous forest floors following partial and clear-cut harvesting. Can. J. For. Res. 33, 1610–1620.

Lloyd, J., Taylor, J., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315-323

Lorenz, K., Lal, R., 2010. Carbon Sequestration in Forest Ecosystems. Springer: New York, 289.

Luchkow, S., Forester, C., River, P., 2001. EMEND final harvest layout and extraction pattern. http://www.emendproject.org/public/Emend/Controller/Page/downloads/emend_final_harvest_lalayo.pdf Accessed on Feburary 2016.

Lützow, M. V., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: Mechanisms and their relevance under different soil conditions - A review. Eur. J. Soil Sci. 57, 426-445.

Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9, 511.

Miller, H.G., 1995. The influence of stand development on nutrient demand, growth and allocation. Plant Soil 168–169, 225–232.

Murphy, P.N.C., Ogilvie, J., Connor, K., Arp, P.A., 2007. Mapping wetlands: A comparison of two different approaches for New Brunswick, Canada. Wetlands 27, 846–854.

Natelhoffer, K.J., Fry, B., 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Sci. Soc. Am. J. 52, 1633- 16340.

Natural Regions Committee. 2006. Natural Regions and Subregions of Alberta. https://www.albertaparks.ca/media/2942026/nrsrcomplete_may_06.pdf . Accessed on

August 10 2018.

Neff, J.C., Hooper, D.U., 2002. Vegetation and climate controls on potential CO2, DOC and DON production in northern latitude soils. Glob. Chang. Biol. 8, 872–884.

Nijland, W., Coops, N.C., Macdonald, S.E., Nielsen, S.E., Bater, C.W., White, B., Ogilvie, J., Stadt, J., 2015. Remote sensing proxies of productivity and moisture predict forest stand type and recovery rate following experimental harvest. For. Ecol. Manage. 357, 239–247.

O'Connel, K.E., Gower, S.T., Norman, J.M., 2003. Net ecosystem production of two contrasting boreal black spruce communities. Ecosystems 6, 248–260.

Oechel, W.C., Van Cleve, K., 1986. The role of bryophytes in nutrient cycling in the Taiga. In *Forest Ecosystems in the Alaskan Taiga.* Springer: New York. 121-137 pp.

Olsen, H.R., Van Miegroet, H., 2010. Factors affecting carbon dioxide release from forest and rangeland soils in northern Utah. Soil Sci. Soc. Am. J. 74, 282.

Olsson, M.T., Erlandsson, M., Lundin, L., Nilsson, T., Nilsson, Ake, Stendahl, J., 2009. Organic carbon stocks in swedish podzol soils in relation to soil hydrology and other site characteristics. Silva Fenn. 43, 209–222.

Oltean, G.S., Comeau, P.G., White, B., 2016. Carbon isotope discrimination by *Picea glauca* and *Populus tremuloides* is related to the topographic depth to water index and rainfall. Can. J. For. Res. 46, 1225–1233.

Pacific, V.J., McGlynn, B.L., Riveros-Iregui, D.A., Welsch, D.L., Epstein, H.E., 2008. Variability in soil respiration across riparian-hillslope transitions. Biogeochemistry 91, 51–70.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993.

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The structure, distribution, and biomass of the world's forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622.

Pare, D., Boutin, R., Larocque, G., et Raulier, F., Paré, D., Boutin, R., Larocque, G., Raulier, F., 2005. Effect of temperature on soil organic matter decomposition in three forest biomes of eastern Canada. Can. J. Soil Sci. 7, 247–256.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, R.-C., 2017. nlme: Linear and nonlinear mixed effects models. R Package version 3.1-131.

Pinno, B.D., Wilson, S.D., 2014. Nitrogen translocation between clonal mother and daughter trees at a grassland–forest boundary. Plant Ecol. 215, 347–354.

Preston, C.M., Bhatti, J.S., Flanagan, L.B., Norris, C., 2006. Stocks, chemistry, and sensitivity to climate change of dead organic matter along the Canadian boreal forest transect case study. Clim. Change 74, 233–251.

Preston, C.M., Nault, J.R., Trofymow, J.A., & Smyth, C.E., 2009. Chemical Changes During 6 Years of Decomposition of 11 Litters in Some Canadian Forest Sites. Part 1. Elemental Composition, Tannins, Phenolics, and Proximate Fractions. Ecosystems, 12, 1053-1077.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., Mckenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J. a, Venier, L. a, 2013. Anticipating the consequences of climate change for Canada's boreal forest ecosystems. Environ. Rev. 21, 322–365.

Price, D.T., McKenney, D.W., Joyce, L.A., Siltanen, R.M., Papadopol, P. and Lawrence, K.,

2011. High-resolution interpolation of climate scenarios for Canada derived from general circulation model simulations. Information Report NOR-X-421. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre: Edmonton. 104 pp

Pumpanen, J., Ilvesniemi, H., Kulmala, L., Siivola, E., Laakso, H., Kolari, P., Helenelund, C., Laakso, M., Uusimaa, M., Hari, P., 2008. Respiration in boreal forest soil as determined from carbon dioxide concentration profile. Soil Sci. Soc. Am. J. 72, 1187–1196.

R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2018.

Raich, J.W., Tufekciogul, A, 2000. Vegetation and soil respiration: correlations and controls. Biogeochemistry 48, 71–90.

Rapalee, G., Trumbore, S.E., Davidson, E.A., Harden, J.W., Veldhuis, H., 1998. Soil carbon stocks and their rate of accumulation and loss in a boreal forest landscape. Global Biogeochem. Cycles 12, 687–701.

Reichstein, M., Janssens, I.A., 2009. Semi-empirical modelling of the response of soil respiration to environmental factors in laboratory and field conditions. In *Soil Carbon Dynamics: An integrated methodology.* Cambridge University Press: Cambridge, 207–220.

Rey, A., Pegoraro, E., Tedeschi, V., De Parri, I., Jarvis, P.G., Valentini, R., 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. Glob. Chang. Biol. 9, 851- 866.

Ruark, G.A., Bockheim, J.G., 1988. Biomass, net primary production, and nutrient distribution for an age sequence of Populus tremuloides ecosystems. Can. J. For. Res. 18, 435–443.

Saitoh, T., Seiwa, K., Nishiwaki, A., 2006. Effects of resource heterogeneity on nitrogen translocation within clonal fragments of Sasa palmata: An isotopic (15N) assessment. Ann. Bot. 98, 657–663.

Saugier, B., Roy, J., Mooney, H. a., 2001. Estimations of global terrestrial productivity: Converging towards a single number? In *Terrestrial Global Productivity.* Academic Press: New York, 543–558.

Scrimgeour, C., 2008. Soil Sampling and Methods of Analysis (Second Edition). CRC Press: Boca Raton , 1224 pp.

Seedre, M., Shrestha, B.M., Chen, H.Y.H., Colombo, S., Jõgiste, K., 2011. Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. J. For. Res. 16, 168–183.

Seibert, J., Stendahl, J., Sørensen, R., 2007. Topographical influences on soil properties in boreal forests. Geoderma 141, 139–148.

Simonson, R.W., 1959. Outline of a Generalized Theory of Soil Genesis 1. Soil Sci. Soc. Am. J., 23, 152-156.

Soil Classification Working Group, 1998. *The Canadian System of Soil Classification* (3rd ed.). Agric. And Agri-Food Can.

Spence, J., Volney, W., Lieffers, V., Weber, M., Luchkow, S., Vinge, T., 1999. The Alberta EMEND project: Recipe and cooks' argument. *The Sustainable Forest Managment Network Conference Science and Practice: Sustaining the Boreal Forest Edmonton, Alberta*. 583–591.

Strong, W.L., La Roi, G.H., 1983. Root-system morphology of common boreal forest trees in Alberta Canada. Can. J. For. Res. 13, 1164–1173.

Tian, Q., He, H., Cheng, W., Bai, Z., Wang, Y., Zhang, X., 2016. Factors controlling soil organic carbon stability along a temperate forest altitudinal gradient. Sci. Rep. 6, 1–9.

Townshend, J., Justice, C., Li, W., Gurney, C., McManus, J., 1991. Global land cover classification by remote sensing: present capabilities and future possibilities. Remote Sens. Environ. 35, 243–255.

Trofymow, J.A., Moore, T.R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M., Trofymow, S.V., 2002. Rates of litter decomposition over 6 years in Canadian forests : influence of litter quality and climate 804, 789–804.

Trumbore, E., Davidson, A., Harden, W., 1998. Nx 12, 687–701.

Watson, K., 2014. Soils Illustrated - Field Descriptions Third Edition. International Remote Sensing Surverys Limited: Kamloops. 174 pp.

Wheeler, R.E., 2010. Permutation Tests for Linear Models in R. R Doc. https://cran.r-project.org/web/packages/lmPerm/vignettes/lmPerm.pdf. Accessed on July 11, 2018.

Wiaux, F., Vanclooster, M., Van Oost, K., 2015. Vertical partitioning and controlling factors of gradient-based soil carbon dioxide fluxes in two contrasted soil profiles along a loamy hillslope. Biogeosciences 12, 4637–4649.

Xu, M., Chen, J., Qi, Y., 2002. Growing-season temperature and soil moisture along a 10km transect across a forested landscape. Clim. Res. 22, 57–72.

Yansa, C.H., 2006. The timing and nature of Late Quaternary vegetation changes in the northern Great Plains, USA and Canada: A re-assessment of the spruce phase. Quaternary Science Reviews. 25, 263-281.

Yuan, Z.Y., Chen, H.Y.H., 2010. Changes in nitrogen resorption of trembling aspen (Populus tremuloides) with stand development. Plant Soil 327, 121–129.

Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93.

Zhang, L.H., Chen, Y.N., Zhao, R.F., Li, W.H., 2010. Significance of temperature and soil water content on soil respiration in three desert ecosystems in Northwest China. J. Arid Environ. 74, 1200–1211.

Appendices

Appendix A-1 Flow initiation threshold selection.

Table A-1.1: Summary of the best-supported flow-initiation thresholds for modeling soil properties where the ΔAICc < 2.0 in conifer-dominated and deciduous-dominated stands.

Soil layer	Flow initiation threshold						
-	0.5 ha^{-1}	1 ha^{-1}	2 ha^{-1}	4 ha^{-1}	8 ha^{-1}	12 ha^{-1}	16 ha^{-1}
	Number of models where ΔAICc < 2.0						
Forest floor	5	7	8	9	3	2	4
Mineral Soil	4	3	6	10	3	2	2

Table A-1.2: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor thickness (cm) under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	579.6	3.2	472.4	11.5
1	577.0	0.6	466.8	5.9
2	576.5	0.1	461.8	1.0
4	576.4	0.0	460.8	0.0
8	576.6	0.2	463.8	2.9
12	577.5	1.1	471.2	10.3
16	578.8	2.4	473.0	12.2

Table A-1.3: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor pH under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	165.7	5.6	121.3	9.8
1	165.2	5.1	118.9	7.4
2	165.3	5.2	116.3	4.8
4	165.5	5.4	111.5	0.0
8	163.1	3.0	121.8	10.3
12	162.9	2.8	121.7	10.3
16	160.1	0.0	125.5	14.1

Table A-1.4: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor total carbon (%) under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	1003.8	5.4	921.5	3.9
1	1000.0	1.6	922.9	5.3
2	998.4	0.0	917.6	0.0
4	1000.0	1.6	920.7	3.1
8	1003.6	5.2	918.8	1.2
12	1003.2	4.7	922.9	5.3
16	1001.9	3.5	919.2	1.6

Table A-1.5: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor total nitrogen (%) under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	467.3	0.0	578.5	0.0
1	471.3	4.0	578.7	0.2
2	467.7	0.5	582.2	3.7
4	469.5	2.2	581.8	3.3
8	470.8	3.5	581.3	2.8
12	468.3	1.0	580.9	2.4
16	470.1	2.8	582.5	4.0

Table A-1.6: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor C:N ratio under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	641.6	5.7	414.1	0.0
1	636.0	0.0	417.4	3.3
2	642.3	6.4	425.3	11.2
4	642.0	6.0	425.4	11.3
8	643.1	7.1	424.4	10.3
12	642.4	6.5	422.7	8.6
16	644.8	8.8	421.6	7.5

Table A-1.7: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor carbon stocks (Mg ha^{-1}) under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	2397.7	2.6	2206.8	15.7
1	2395.0	0.0	2202.2	11.2
2	2395.4	0.3	2194.3	3.2
4	2395.1	0.0	2191.1	0.0
8	2399.8	4.7	2196.4	5.3
12	2400.0	5.0	2207.3	16.2
16	2400.7	5.6	2209.2	18.1

Table A-1.8: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor δ ^{13}C abundance under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	236.0	1.1	176.7	1.4
1	234.9	0.0	175.3	0.0
2	236.1	1.2	177.7	2.3
4	236.1	1.2	175.7	0.4
8	237.8	2.8	179.2	3.9
12	237.8	2.8	179.0	3.7
16	236.5	1.5	178.2	2.9

Table A-1.9: Comparison of AICc and ΔAICc of linear mixed effect models for forest floor δ ^{15}N abundance under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	253.5	14.2	243.7	7.5
1	249.1	9.8	242.3	6.0
2	245.6	6.3	236.2	0.0
4	245.2	5.9	236.3	0.1
8	239.3	0.0	241.2	5.0
12	241.3	2.1	240.3	4.1
16	240.7	1.5	239.9	3.7

Table A-1.10: Comparison of AICc and ΔAICc of linear mixed effect models for mineral soil total carbon (%)under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	472.5	1.0	460.9	6.7
1	472.4	0.8	461.4	7.2
2	473.2	1.7	457.6	3.4
4	471.6	0.0	454.2	0.0
8	487.2	15.6	469.6	15.4
12	487.5	15.9	474.6	20.3
16	489.0	17.4	474.2	19.9

Table A-1.11 Comparison of AICc and ΔAICc of linear mixed effect models for mineral soil total nitrogen (%)under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	-98.7	0.0	-10.3	11.8
1	-95.5	3.3	-12.2	9.9
2	-94.4	4.3	-17.9	4.2
4	-95.5	3.2	-22.2	0.0
8	-81.6	17.1	-7.2	14.9
12	-81.2	17.6	-0.7	21.5
16	-78.8	19.9	-1.1	21.0

Table A-1.12: Comparison of AICc and ΔAICc of linear mixed effect models for mineral soil C:N ratio under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	549.5	1.4	392.0	11.3
1	549.7	1.5	394.5	13.7
2	548.6	0.4	392.4	11.6
4	549.9	1.7	392.5	11.7
8	548.3	0.1	381.9	1.2
12	548.1	0.0	387.3	6.5
16	552.4	4.3	380.8	0.0

Table A-1.13: Comparison of AICc and ΔAICc of linear mixed effect models for mineral carbon stocks under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	2347.0	2369.1	2080.2	11.2
1	2348.2	2370.4	2079.5	10.4
2	-17.9	4.2	2075.0	5.9
4	-22.2	0.0	2069.1	0.0
8	2372.7	2394.8	2084.3	15.2
12	2373.3	2395.4	2088.9	19.8
16	2377.4	2399.5	2090.6	21.5

Table A-1.14: Comparison of AICc and ΔAICc of linear mixed effect models for mineral soil δ ^{13}C abundance under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	112.4	0.0	139.6	20.8
1	115.4	3.0	141.5	22.8
2	114.4	2.0	141.7	23.0
4	114.3	1.9	141.9	23.1
8	118.0	5.6	141.2	22.5
12	117.7	5.3	133.8	15.0
16	118.7	6.3	118.7	0.0

Table A-1.15 Comparison of AICc and ΔAICc of linear mixed effect models for mineral soil δ ^{15}N abundance under CDOM and DDOM cover types, CDOM: conifer-dominated; DDOM: deciduous-dominated.

	CDOM		DDOM	
Flow Initiation Threshold (ha^{-1})	AICc	ΔAICc	AICc	ΔAICc
0.5	248.6	4.0	252.8	6.1
1	244.9	0.3	248.4	1.7
2	244.6	0.0	246.7	0.1
4	244.8	0.2	246.6	0.0
8	251.8	7.2	250.2	3.6
12	252.6	8.1	250.9	4.3
16	253.7	9.1	251.6	5.0

Appendix A-2 Chapter 2 statistics summary

Table A-2.1: Results of one-way ANOVA testing for differences in forest floor δ^{13}C values among retention levels in conifer-dominated stands (From Table 2-1).

Variable	Degrees of freedom	F-value	p-value
Retention Level	3	2.792	0.0442

Table A-2.2: Results of pairwise t-tests comparing differences in the mean forest floor δ^{13}C values among retention levels in conifer dominated stands, with the Holm adjustment for multiple comparisons (from Table 2-1).

	Clearcut	20 %	50 %
20 %	1.000	-	-
50 %	1.000	1.000	-
Control	0.165	0.0072	0.235

Table A-2.3: Results of linear mixed effect model relating forest floor thickness in uncut conifer-dominated stands with the natural logarithm-transformed DTW index (from Table 2-3).

Variable	Degrees of freedom	F-value	p-value
Ln(DTW)	29	10.975	0.0025

Table A-2.4: Results of linear mixed effect model relating forest floor total carbon concentrations to the natural logarithm-transformed DTW index, retention level, and the DTW*retention interaction (from Table 2-5).

Variable	Degrees of freedom	F-value	p-value
Ln(DTW)	91	11.856	0.0009
Retention level	8	1.759	0.2324
Ln(DTW) * Retention level interaction	91	3.150	0.0288

Table A-2-5: Results of Welch's t-tests comparing differences in mean forest floor $\delta^{13}C$ values between CDOM and DDOM stands types at each retention level. CDOM: Conifer-dominated; DDOM: Deciduous-dominated.

Retention level	Degrees of freedom	t-value	p-value
Control	53.006	6.4859	<0.0001
50 %	50.604	2.8043	0.0071
20 %	43.703	2.3626	0.0227
Clearcut	45.905	3.7787	0.0005

Appendix A-3 Hillslope-based vegetation assessments

Table A-3.1: Canopy characteristics, and understory and forest floor cover determined for each topographic position (n=3).

Position	Canopy Cover	Tree Density				Understory Cover							Forest Floor Cover	
		Trembling Aspen	Balsam Poplar	White Spruce	Balsam Fir	Tall Shrub	Short Shrub	Graminoids	Forb	Woody Plant	Lichen	Bryophytes	Needle	Leaf
-	(%)	(mean tree count per position)				(%)							(%)	
Summit	80.5	1.3	0.0	0.0	0.0	1.0	23.8	4.8	8.5	4.0	1.3	11.5	0.1	48.8
Shoulder	80.9	2.7	0.0	0.7	0.0	3.7	15.0	2.2	9.3	2.7	0.5	2.0	0.1	68.3
Upper Backslope	68.6	2.0	0.3	0.0	0.0	1.0	12.7	3.7	2.7	4.7	0.1	0.7	0.1	60.0
Lower Backslope	69.6	1.3	0.0	0.7	0.0	4.3	17.3	2.7	8.0	3.7	0.4	1.2	0.1	38.3
Footslope	81.4	0.7	0.0	1.7	1.0	1.7	12.7	0.9	15.3	3.3	0.1	10.0	0.2	48.3
Toeslope	91.7	0.0	0.0	4.7	0.3	0.0	3.3	0.4	7.0	1.7	0.7	40.0	6.3	16.3
Depression Area	87.3	0.0	0.0	4.3	0.0	0.0	2.2	0.0	9.7	0.7	0.1	52.7	5.7	3.7

Appendix A-4 Soil morphological description sheets

Site description codes:

Soil Classification	
Orthic Gray Luvisol	OGL
Orthic Luvic Gleysol	OLG
Orthic Gleysol	OG

Soil description codes (Watson, 2014):

Texture	
Class	Code
Clay	C
Silty clay	SiC
Clay loam	CL
Silty loam	SiL
Sandy Clay Loam	SCL
Silty Clay Loam	SiCL
Sandy loam	SL
Loam	L

Moisture	
Class	Code
Wet	W
Moist	M
Dry	D

Horizon Boundary			
Distinctness		Form	
Class	Code	Class	Code
Abrupt	A	Smooth	S
Clear	C	Wavy	W
Gradual	G	Irregular	I
Diffuse	D	Broken	B

Structure							
Grade		Size		Type		Consistence	
Class	Code	Class	Code	Class	Code	Class	Code
Weak	W	Very fine	VF	Massive	MA	Loose	1
Moderate	M	Fine	F	Single grain	SGR		
Strong	S	Medium	M	Subangular blocky	SBK	Very friable	2
		Coarse	C	Angular blocky	ABK	friable	3
						Firm	4
						Very firm	5

Coarse fragments				Rooting			
Size		Shape		Abundance		Orientation	
Class	Code	Class	Code	Class	Code	Class	Code
Gravels	G	Rounded	R	Very few	VF	Vertical	V
Cobbles	C	Subrounded	SR	Few	F	Horizontal	H
Stones	S	Subangular	SA	Plentiful	P	Oblique	O
Boulders	B	Angular	A	Abundant	A	Random	R

Mottles				Effervescence	
Abundance		Size		Class	Code
Class	Code	Class	Code	Very weak	VW
Few	F	Fine	F	Weak	W
Common	C	Medium	M	Moderate	M
Many	M	Coarse	C	Strong	S

Soil Profile Description								
Site: Summit		Date: 26 Aug 2016		Will and Paul				
GPS Coordinates	N 56.76519							
	W 118.37820							
Horizon			LFH	Ae	AB	Bt1	Bt2	BC
Depth (cm)			10-0	0-7	7-27	27-40	40-56	56-
Colour in field			NA	10YR7/2	10YR5/4	10YR4/4	10YR4/2	10YR4/1
Colour (dry)			NA	10YR7/2	10YR7/3	10YR6/3	10YR6/3	10YR6/3
Moisture			M	D	M	M	M	M
Horizon Boundary	Distinctness		A	C	C	G	G	
	Form		W	W	W	W	W	
Structure	Primary	Grade	NA	W	M	MS	MS	W
		Size	NA	F	M	F	M	M
		Type	NA	GR	GR	SBK	SBK	SBK
		Consistence	NA	1	4	4	4	5
	Secondary	Grade	NA					
		Size	NA					
		Type	NA					
		Consistence	NA					
Coarse Fragments (>2mm)	Primary	%	NA					
		Size	NA					
		Shape	NA					
Rooting	Abundance	Very fine	A	F	P	V	V	-
		Fine	A	F	V	V	V	V
		Medium	F	F	V	F	V	V
		Coarse	V	F	V	-	V	-
	Orientation	Very fine	R	O	O	O	O	-
		Fine	R	O	O	O	O	O
		Medium	R	O	O	O	O	O
		Coarse	R	O	H	-	H	-
Mottles	Abundance		NA					
	Size		NA					
	Contrast		NA					
	Colour in field		NA					
Effervescence (10%)			NA	-	-	-	-	
Depth to carbonates (cm)			NA					

Soil Profile Description						
Site: Shoulder		Date: 26 Aug 2016		Will and Paul		
GPS Coordinates	N 56.76499					
	W 118.37792					
Horizon			LFH	Ae	Bt	Ck
Depth (cm)			8-0	0-8	8-37	37+
Colour in field			NA	7.5YR4/4	7.5YR4/6	10YR4/4
Colour (dry)			NA	7.5YR5/3	7.5YR4/4	10YR4/4
Moisture						
Horizon Boundary	Distinctness		C	C	C	
	Form		W	W	W	
Structure	Primary	Grade	NA	W	WM	W
		Size	NA	F	F	F
		Type	NA	SBK	SBK	SBK
		Consistence	NA	2	4	1
	Secondary	Grade	NA			
		Size	NA			
		Type	NA			
		Consistence	NA			
Coarse Fragments (>2mm)	Primary	%	NA			
		Size	NA			
		Shape	NA			
Rooting	Abundance	Very fine	A	V	F	V
		Fine	A	F	F	F
		Medium	F	F	P	F
		Coarse	P	V	-	-
	Orientation	Very fine	R	O	O	O
		Fine	R	O	O	O
		Medium	O	O	O	O
		Coarse	O	O	-	-
Mottles	Abundance		NA			
	Size		NA			
	Contrast		NA			
	Colour in field		NA			
Effervescence (10%)			NA	-	-	M
Depth to carbonates (cm)			NA			37

Soil Profile Description						
Site: Backslope			Date: 26 Aug 2016	Will and Paul		
GPS Coordinates	N 56.76483					
	W 118.37818					
Horizon			LFH	Ae	Bt	Ck
Depth (cm)			11-0	0-10	10-42	42+
Colour in field			NA	7.5YR4/4	7.5YR5/6	10YR4/4
Colour (dry)			NA	7.5YR5/4	7.5YR4/4	10YR4/4
Moisture			M	M	M	D
Horizon Boundary	Distinctness		C	C	C	
	Form		W	W	W	
Structure	Primary	Grade	NA	W	WM	W
		Size	NA	F	M	F
		Type	NA	SBK	SBK	SBK
		Consistence	NA	2	4	2
	Secondary	Grade	NA			
		Size	NA			
		Type	NA			
		Consistence	NA			
Coarse Fragments (>2mm)	Primary	%	NA			
		Size	NA			
		Shape	NA			
Rooting	Abundance	Very fine	A	F	V	F
		Fine	A	F	V	F
		Medium	P	F	F	V
		Coarse	F	V	F	-
	Orientation	Very fine	R	O	O	O
		Fine	R	O	O	O
		Medium	O	O	O	O
		Coarse	O	O	O	-
Mottles	Abundance		NA			
	Size		NA			
	Contrast		NA			
	Colour in field		NA			
Effervescence (10%)			NA	-	-	M
Depth to carbonates (cm)			NA			42

Soil Profile Description								
Site: Footslope		Date: 26 Aug 2016		Will and Paul				
GPS Coordinates	N 56.76445							
	W 118.37779							
Horizon			LFH	Ae1	Ae2	Btg1	Btg2	BCg
Depth (cm)			9-0	0-6	6-20	20-50	50-70	70+
Colour in field			NA	10YR6/3	10YR4/3	10YR5/2	10YR5/1	10YR4/1
Colour (dry)			NA	10YR6/2	10YR6/2	10YR7/3	10YR7/2	10YR6/2
Moisture			M	M	M	M	M	M
Horizon Boundary	Distinctness		A	C	C	G	G	
	Form		W	W	W	W	W	
Structure	Primary	Grade	NA	W	W	MS	WM	WM
		Size	NA	M	M	C	C	M
		Type	NA	SBK	SBK	WEG	SBK	SBK
		Consistence	NA	2	2	5	4	4
	Secondary	Grade	NA			M	M	
		Size	NA			C	M	
		Type	NA			SBK	SBK	
		Consistence	NA			4	4	
Coarse Fragments (>2mm)	Primary	%	NA					
		Size	NA					
		Shape	NA					
Rooting	Abundance	Very fine	P	F	F	V	-	-
		Fine	P	P	P	V	V	-
		Medium	P	F	F	F	V	V
		Coarse	V	-	F	-	V	-
	Orientation	Very fine	R	O	O	O	-	-
		Fine	R	O	O	O	O	-
		Medium	O	O	O	O	O	O
		Coarse	O	-	O	-	O	-
Mottles	Abundance		NA			C	C	C
	Size		NA			M	M	M
	Contrast		NA			P	P	P
	Colour in field		NA			7.5YR5/8	7.5YR5/8	7.5YR5/8
Effervescence (10%)			NA	-	-	-	-	-
Depth to carbonates (cm)			NA					

<table>
<tr><td colspan="8">Soil Profile Description</td></tr>
<tr><td colspan="2">Site: Toeslope</td><td colspan="2">Date: 26 Aug 2016</td><td colspan="4" rowspan="3">Will and Paul</td></tr>
<tr><td rowspan="2">GPS Coordinates</td><td colspan="3">N 56.76416</td></tr>
<tr><td colspan="3">W 118.37805</td></tr>
<tr><td colspan="3">Horizon</td><td>LFH</td><td>Ae</td><td>Bt</td><td>Btg</td><td>BCg</td></tr>
<tr><td colspan="3">Depth (cm)</td><td>12-0</td><td>0-9</td><td>9-21</td><td>21-45</td><td>45+</td></tr>
<tr><td colspan="3">Colour in field</td><td>NA</td><td>10YR6/2</td><td>10YR5/2</td><td>10YR4/1</td><td>10YR4/1</td></tr>
<tr><td colspan="3">Colour (dry)</td><td>NA</td><td>10YR7/1</td><td>10YR7/2</td><td>10YR6/3</td><td>10YR6/4</td></tr>
<tr><td colspan="3">Moisture</td><td>M</td><td>M</td><td>M</td><td>M</td><td>M</td></tr>
<tr><td rowspan="2">Horizon Boundary</td><td colspan="2">Distinctness</td><td>A</td><td>C</td><td>C</td><td>G</td><td></td></tr>
<tr><td colspan="2">Form</td><td>W</td><td>W</td><td>W</td><td>W</td><td></td></tr>
<tr><td rowspan="8">Structure</td><td rowspan="4">Primary</td><td>Grade</td><td>NA</td><td>WM</td><td>M</td><td>WM</td><td>W</td></tr>
<tr><td>Size</td><td>NA</td><td>M</td><td>C</td><td>M</td><td>M</td></tr>
<tr><td>Type</td><td>NA</td><td>PL</td><td>SBK</td><td>PR</td><td>SBK</td></tr>
<tr><td>Consistence</td><td>NA</td><td>3</td><td>5</td><td>5</td><td>4</td></tr>
<tr><td rowspan="4">Secondary</td><td>Grade</td><td>NA</td><td></td><td></td><td>M</td><td>M</td></tr>
<tr><td>Size</td><td>NA</td><td></td><td></td><td>C</td><td>F</td></tr>
<tr><td>Type</td><td>NA</td><td></td><td></td><td>SBK</td><td>GR</td></tr>
<tr><td>Consistence</td><td>NA</td><td></td><td></td><td>5</td><td>4</td></tr>
<tr><td rowspan="3">Coarse Fragments (>2mm)</td><td rowspan="3">Primary</td><td>%</td><td>NA</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Size</td><td>NA</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Shape</td><td>NA</td><td></td><td></td><td></td><td></td></tr>
<tr><td rowspan="8">Rooting</td><td rowspan="4">Abundance</td><td>Very fine</td><td>A</td><td>V</td><td>V</td><td>-</td><td>-</td></tr>
<tr><td>Fine</td><td>A</td><td>F</td><td>V</td><td>V</td><td>V</td></tr>
<tr><td>Medium</td><td>P</td><td>F</td><td>F</td><td>F</td><td>-</td></tr>
<tr><td>Coarse</td><td>P</td><td>V</td><td>-</td><td>-</td><td>-</td></tr>
<tr><td rowspan="4">Orientation</td><td>Very fine</td><td>R</td><td>O</td><td>O</td><td>-</td><td>-</td></tr>
<tr><td>Fine</td><td>R</td><td>O</td><td>O</td><td>O</td><td>O</td></tr>
<tr><td>Medium</td><td>R</td><td>O</td><td>O</td><td>O</td><td>-</td></tr>
<tr><td>Coarse</td><td>R</td><td>O</td><td>-</td><td>-</td><td>-</td></tr>
<tr><td rowspan="4">Mottles</td><td colspan="2">Abundance</td><td>NA</td><td></td><td>F</td><td>M</td><td>M</td></tr>
<tr><td colspan="2">Size</td><td>NA</td><td></td><td>F</td><td>M</td><td>C</td></tr>
<tr><td colspan="2">Contrast</td><td>NA</td><td></td><td>F</td><td>PR</td><td>P</td></tr>
<tr><td colspan="2">Colour in field</td><td>NA</td><td></td><td></td><td>7.5YR5/8</td><td>7.5YR5/8</td></tr>
<tr><td colspan="3">Effervescence (10%)</td><td>NA</td><td>-</td><td>-</td><td>-</td><td>-</td></tr>
<tr><td colspan="3">Depth to carbonates (cm)</td><td>NA</td><td></td><td></td><td></td><td></td></tr>
</table>

Soil Profile Description							
Site: Depression Area			Date 26 Aug 16		Will and Paul		
GPS Coordinates	N 56.76343						
	W 118.37713						
Horizon			LF	H	Ah	Bg	BCg
Depth (cm)			26-10	10-0	0-7	7-17	17+
Colour in field			NA	10YR2/1	10YR3/1	10YR5/2	10YR5/1
Colour (dry)			NA	10YR4/2	10YR6/4	10YR6/4	2.5YR6/4
Moisture			M	M	M	M	M
Horizon Boundary	Distinctness		C	C	C	G	
	Form		W	W	W	W	
Structure	Primary	Grade	NA	W	W	W	WM
		Size	NA	M	M	M	F
		Type	NA	SBK	SBK	SBK	GR
		Consistence	NA	3	3	3	3
	Secondary	Grade	NA	WM	WM	WM	
		Size	NA	F	M	M	
		Type	NA	GR	GR	GR	
		Consistence	NA	3	3	3	
Coarse Fragments (>2mm)	Primary	%	NA				
		Size	NA				
		Shape	NA				
Rooting	Abundance	Very fine	A	P	F		
		Fine	A	V	F		
		Medium	P	V	V	F	V
		Coarse	P	F			
	Orientation	Very fine	R	O	O		
		Fine	R	O	O		
		Medium	R	O	O	O	O
		Coarse	R	O			
Mottles	Abundance		NA			M	M
	Size		NA			M	Cg
	Contrast		NA			P	P
	Colour in field		NA			1OYR5/8	10YR5/8
Effervescence (10%)			NA	-	-	-	-
Depth to carbonates (cm)			NA				

Appendix A-5 Summary of soil and forest floor properties

Table A-5.1 Morphological soil properties

Position	Horizon	Depth		Colour	Structure	Coarse Frag.	Mottles		Effervesence
		Upper Bound	Lower Bound	(Dry)		(>2 mm)	Abund.	Colour	(Y/N)
		(cm)				(%)			
Summit	LFH	7	0	-	-	-	-	-	-
Summit	Ae	0	7	10YR7/3	GR	<5	-	-	N
Summit	AB	7	27	10YR7/2	GR	<5	-	-	N
Summit	Bt1	27	40	10YR6/3	SBK	<5	-	-	N
Summit	Bt2	40	56	10YR6/3	SBK	<5	-	-	N
Summit	BC	56	+	10YR6/3	SBK	<5	-	-	N
Shoulder	LFH	7	0	-	-	-	-	-	-
Shoulder	Ae	0	8	7.5YR5/3	SBK	50	-	-	N
Shoulder	Bt	8	37	7.5YR4/6	SBK	50	-	-	N
Shoulder	Ck	37	+	10YR4/4	SBK	50	-	-	Y
Backslope	LFH	6	0	-	-	-	-	-	-
Backslope	Ae	0	10	7.5YR5/4	SBK	50	-	-	N
Backslope	Bt	10	42	7.5YR4/4	SBK	50	-	-	N
Backslope	Ck	42	+	10YR4/4	SBK	50	-	-	Y
Footslope	LFH	9	0	-	-	-	-	-	-
Footslope	Ae1	0	6	10YR6/2	SBK	<5	-	-	N
Footslope	Ae2	6	20	10YR6/2	SBK	<5	-	-	N
Footslope	Btg1	20	50	10YR7/3	BK	<5	C	7.5YR5/8	N
Footslope	Btg2	50	70	10YR752	SBK	<5	C	7.5YR5/8	N
Footslope	BCg	70	+	10YR6/2	SBK	<5	C	7.5YR5/8	N
Toeslope	LFH	8	0	-	-	-	-	-	-
Toeslope	Ae	0	9	10YR7/1	PL	<5	-	-	N
Toeslope	Bt	9	21	10YR7/2	SBK	<5	F	-	N
Toeslope	Btg	21	45	10YR6/3	PR	<5	M	7.5YR5/8	N
Toeslope	BCg	45	+	10YR6/4	SBK	<5	M	7.5YR5/8	N
Depression Area	LFH	13	0	-	-		-	-	-
Depression Area	Ah	0	7	10YR4/2	SBK	<5	-	-	N
Depression Area	Bg	7	17	10YR6/4	SBK	<5	P	10YR5/8	N
Depression Area	BCg	17	+	10YR6/4	GR	<5	P	10YR5/8	N

Table A-5.2 Physical and chemical soil properties

Position	Horizon	Depth		Particle size description				Chemical Properties		
		Upper Bound	Lower Bound	Sand	Silt	Clay	Texture Class	pH_{CaCl2}	TOC	TN
-	-	(cm)		(%)			-	-	(g g^{-1} %)	
Summit	LFH	7	0	-	-	-	-	4.98 (0.03)	45.55	1.81
Summit	Ae	0	7	37.9	48.3	13.9	SiL	4.29 (0.01)	1.19	0.07
Summit	AB	7	27	22.4	37.9	39.6	CL	4.17 (0.02)	1.12	0.09
Summit	Bt1	27	40	18.3	38.0	43.7	C	3.93 (0.01)	0.62	0.07
Summit	Bt2	40	56	20.2	34.9	44.9	C	3.95 (0.01)	0.61	0.07
Summit	BC	56	+	20.3	37.4	42.3	C	4.09 (0.01)	0.61	0.07
Shoulder	LFH	7	0	-	-	-	-	5.22	47.60	2.21
Shoulder	Ae	0	8	65.6	30.6	3.8	SL	4.66 (0.01)	1.23	0.09
Shoulder	Bt	8	37	60.6	17.7	21.7	SCL	5.51 (0.01)	1.21	0.10
Shoulder	Ck	37	+	78.0	9.8	12.1	SL	7.48 (0.01)	0.73	0.07
Backslope	LFH	6	0	-	-	-	-	5.48 (0.02)	48.02	2.21
Backslope	Ae	0	10	51.3	37.3	11.4	L	5.85 (0.02)	1.24	0.10
Backslope	Bt	10	42	30.3	28.6	41.1	C	5.94 (0.02)	1.22	0.13
Backslope	Ck	42	+	60.7	20.0	19.2	SL	7.37 (0.01)	0.94	0.09
Footslope	LFH	9	0	-	-	-	-	6.10 (0.01)	48.60	1.72
Footslope	Ae1	0	6	40.8	46.6	12.6	L	4.46 (0.03)	1.50	0.11
Footslope	Ae2	6	20	40.5	45.7	13.8	L	4.28 (0.01)	1.13	0.08
Footslope	Btg1	20	50	24.0	43.0	33.0	CL	4.32 (0.02)	0.54	0.08
Footslope	Btg2	50	70	15.3	42.6	42.1	SiC	4.04 (0.02)	0.54	0.09
Footslope	BCg	70	+	21.1	38.2	40.7	C	4.09 (0.02)	0.50	0.09
Toeslope	LFH	8	0	-	-	-	-	4.28 (0.03)	49.93	1.37
Toeslope	Ae	0	9	41.3	52.4	6.3	SiL	4.11 (0.01)	0.73	0.07
Toeslope	Bt	9	21	14.7	68.8	16.5	SiL	4.22 (0.02)	0.81	0.10
Toeslope	Btg	21	45	10.4	44.4	45.3	SiC	4.15 (0.01)	1.12	0.12
Toeslope	BCg	45	+	6.6	43.8	49.6	SiC	4.05 (0.02)	0.93	0.10
Depression Area	LFH	13	0	-	-	-	-	4.42 (0.02)	46.63	1.22
Depression Area	Ah	0	7	11.0	52.7	36.3	SiCL	6.15 (0.03)	4.10	0.25
Depression Area	Bg	7	17	28.1	33.8	38.1	CL	6.83 (0.03)	0.91	0.10
Depression Area	BCg	17	+	10.3	42.4	47.3	SiC	6.78 (0.02)	0.47	0.08

Table A-5.3 Forest floor morphological descriptions

Position	Rep.	Horizon descriptions and thickness			
-	-	Thickness (cm)	L	F	H
Summit	1	7.8	Lv 1cm: Broadleaf 95%; Needles 5%	Fa 3cm: Matted leaves. White Fungi abundant. Faunal droppings present. Fa 3.5cm: More decomposed leaves and roots with black aggregates. Increase in root density, darker colour	Hf 0.4 cm: Fine aggregates Few roots. Well mixed with charcoal
Summit	2	8.3	Lv 0.5 cm: Broadleaf 95%; Needles and grass 5%	fa 1cm: Shredded and matted leaves with abundant white hyphae, small faunal droppings present. Fm 1cm: increase in faunal droppings. Fr 5.5 cm: Sharp drop in hyphae, and an increase in fungi.	Hf 0.2cm: thin humic layer fine granules and greasy. Irregular boundary. Some charcoal intermixed/
Summit	3	8.3	Lv 1cm: Broadleaf 100%	Fm 3 cm: Shredded and matted leaves with abundant white hyphae and some faunal activity. Fr 4cm: Large increase in root density; abundant white hyphae. Some small droppings found.	Hf 0.3cm: Fine granules in an irregular boundary. Overtop of dark brown/black char layer
Summit	4	5.4	Lv 1cm: Broadleaf 100%	Fa 0.5 cm: Some droppings present- material predominately loose and friable leaves. Frm 4.5 cm: Large increase in root density, some fungi were common.	Hf 0.2cmL Fine granules. Fine and irregular boundary.
Shoulder	1	6.0	Broadleaf 100%	Fa 1.5 cm: Shredded and matted leaves with common droppings and white hyphae. Fm 3.5 cm: Increase in root density, and abundant hyphae.	Hf 0.1 cm: Fine granules at interface.
Shoulder	2	7.5	Lv 1.5cm: Broadleaf 75%; grass 10%; CWD 15%	Fa 2cmL Shredded and matted leaves, low density, with droppings and white hyphae. Frm/Fa 3.7cm: Increase in root density and faunal droppings, but a decrease in fungi.	Hf 0.3 cm: Fine granules, dark brown colour.
Shoulder	3	7.8	Lv 0.7cm: broadleaf 90%; grass 10%	Fm 3cm: Shredded and matted leaves among a network of abundant white fungi. Frm 3cm: Dense root network with fungi throughout, some faunal droppings present.	Hf 0.1cm: Fine granular, intermixed with charcoal. Fine irregular boundaries.
Upper Backslope	1	7.2	Lv 1cm: Broadleaf 80%; Grass	Fm 1cm: Shredded and matted beige leaves. White hyphae abundant. Frm 5 cm: Dense fabric like root network among shredded leaves. White hyphae	Hf 0.2cm: Fine irregular boundary, withy pockets of well decomposed H, but

			5%; CWD 15%	common throughout.	surrounded by hyphae to roots, dark brown/black in colour.
Upper Backslope	2	5.7	Lv 1.5 cm: Broadleaf litter 100%	Fm 3.1cm: Matted leaves among a dense white hyphae network. Droppings and CWD were also found. Fr 1cm: Dense network of root fabric. Dark brown colour.	Hf 0.1cm: Fine aggregates at interface, with pieces of charcoal intermixed.
Upper Backslope	3	5.3	Lv 1cm: Broadleaf 90% Grass 10%	Fm 1cm: leaves in various stages of decomposition. White and yellow fungal hyphae common throughout with some roots. Frm 3.2cm: Dense network of roots and white/yellow hyphae. Some recognisable leaf tissue.	Hf 0.1cm: Fine and irregular at pieces at the interface, charcoal pieces intermixed.
Lower Backslope	1	7.0	Lv 1.6 cm: Broadleaf 20%; CWD 20%; moss 20%; grass 40%	Fa/Fz 2.1cm: Very well decomposed leaf litter, with abundant fungi and droppings. Fr/Fz 2.3 cm: Root like fabric and an increase in density, lots of fungi present, colour lighter than above F horizon.	Hfw 1cm: Fine granules with very low density-intermixed with charcoal, and some CWD present.
Lower Backslope	2	6.7	Lv 1.1 cm: Broadleaf 95%; Needles 5%	Fm 2cm: Very dry leaves, mostly intact, but covered in white and yellow hyphae. Fm/Fa 3.4 cm: Increase in density, more matted (but not shredded(leaves covered with hyphae, some droppings present.	Hf 0.2 cm: Very irregular boundaries, fine granular at base, material intermixed with charcoal.
Lower Backslope	3	5.9	Lv 1.5 cm: Broadleaf 70%; Grass 20%; CWD 10%	Fm 1.3cm: Shredded and matted leaves with some white hyphae. Some faunal droppings present. Frm 3cm: Dense root fabric, some CWD and white hyphae.	Hf 0.1cm: Fine and irregular granules at interface
Footslope	1	9.0	Lv 1.6 cm: Broadleaf 90%; needles 10%.	Fm 1.7 cm: Dark brown colour, matted leaves among hyphae network, needles also common. Fm/Fz 2cm: Shredded leaves increase in fungi density. Frm 2cm: Increase in root density, horizon was fabric like, plant litter was more decomposed. Also an increase in white fungi.	Hf 1.7 cm: Dark brown to black, with fine loose granules throughout the horizon. Few roots and no fungi. More common droppings. Charcoal intermixed.

Footslope	2	9.2	Lv 1.3 cm: Broadleaf 95%; needles 5%	Fa 3.3cm: Shredded and matted leaves with faunal hyphae common throughout. High faunal activity with a lot of droppings. Fa/Faw 3 cm: Leaves were shredded to a higher degree and much less recognisable, more H-like. Lots of CWD and white hyphae abundant.	Hf 1.6 cm: Fine granules, brown in colour, sharp drop in root density, and consistence of horizon. Charcoal intermixed.
Footslope	3	8.9	Lv 1.5cm: Needles 40%; Broadleaf 60%.	Fm/Fa 2 cm: Loose leaf and needle litter at initial stages of decomposition: where leaves were shredded and matted. White and yellow hyphae were abundant, faunal droppings were present in localized areas. Fr/Fa 3.3 cm: Very well decomposed material but with an increase in root and white hyphae density. Droppings abundant.	Hfw: 2.1 very well decomposed fine granules and woody bits.
Toeslope	1	8.8	S 1cm: Moss 80%; Broadleaf 15%; Needles 5%	Fsm 3.8cm: Shredded and matted moss, needles, and leaves, small faunal droppings abundant, Roots and hyphae common. Fsm 4cm: Increase in droppings and CWD, some H-aggregates in material, Some charcoal intermixed.	NA
Toeslope	2	7.8	S 0.8 cm: Moss 90% CWD 5%; Needles 5%	Fsz 3.0cm: Loose and friable. Decomposed moss tissue with abundant needles and faunal droppings. Some localized fungi, and CWD. Fsz 4.0 cm: Shredded/decomposed to a higher extent. Increased density and more matted, faunal droppings abundant, but an increase in white hyphae	NA
Toeslope	3	8.1	S 1cm: Moss 90%; Needles 10%	Fsz 2cm: Decomposed moss tissue with common faunal droppings, loose and friable, and some localized hyphae. Fsm 4.1: White fungi more abundant, most tissue was decomposed to a higher degree. CWD common throughout, and some droppings present. Fs 1cm: Moss decomposed to a higher degree, darker colour. Charcoal intermixed at interface.	NA
Depression Area	1	17.5	S 1.5cm: Moss 100%	Fsz 9 cm: Needles intermixed with moss tissue, roots abundant throughout, but not matted. Faunal droppings abundant. Fs 6cm: Increase in density, dark brown colour. Decrease in faunal activity, some CWD and some un-decomposed needles.	Hh 1cm: Smeared when rubbed, dark brown/black in colour, amorphous structure. Some charcoal intermixed

Depression Area	2	9.9	S 0.9cm: Moss 90% Needle 10%	Fsm 4cm: Decomposed moss tissue, grey and fluffy fungi, common throughout profile. Needles very abundant, as were leaves and CWD. Frmw/Fsmw 5cm: decomposed moss tissue, white fungi common, lots of un-decomposed needles, and localized faunal droppings were common.	NA
Depression Area	3	11.9	S 1cm: Moss 80%; Needles 20%	Fsa 6cm: Moss and needles in loser layer, dominated by white hyphae. Faunal droppings were common. Fsz 3cm: Dominated by moss tissue, almost red in colour, lots of CWD and droppings. Fs 1.9cm: Well decomposed, colour leached and black./ Lots of leaf and needle tissue, and CWD. Charcoal intermixed at base.	NA

Appendix A-6 Chapter 3 statistics summary

Table A-6.1: Results of Permutational ANOVA testing for differences in forest floor C:N among each topographic position.

Variable	Degrees of freedom	F-value	p-value
Forest floor C:N	6	36.96	<0.0001

Table A-6.2: Results of Tukey's Honestly significant difference (HSD) test, comparing mean C:N ratios of forest floors from each topographic position.

	Summit	Shoulder	Upper backslope	Lower backslope	Footslope	Toeslope
Shoulder	0.5759	-	-	-	-	-
Upper backslope	0.1281	1.0000	-	-	-	-
Lower backslope	0.1155	1.0000	1.0000	-	-	-
Footslope	0.0628	1.0000	1.0000	1.0000	-	-
Toeslope	0.8914	1.0000	1.0000	1.0000	1.0000	-
Depression area	0.9594	1.0000	0.0000	0.0000	0.0000	1.0000

Table A-6.3: Results of Permutational ANOVA testing for differences in active carbon pools among each topographic position.

Variable	Degrees of freedom	F-value	p-value
Active Carbon	6	105.9	<0.0001

Table A-6.4: Results of Tukey's Honestly significant difference (HSD) test, comparing the mean active carbon pools of forest floors from each topographic position.

	Summit	Shoulder	Upper backslope	Lower backslope	Footslope	Toeslope
Shoulder	0.9156					
Upper backslope	0.9083	1.0000				
Lower backslope	0.9612	0.4357	0.4240			
Footslope	0.0002	0.0013	0.0014	0.0000		
Toeslope	0.0000	0.0000	0.0000	0.0000	0.0000	
Depression area	1.0000	0.9030	0.8951	0.9681	0.0001	0.0000