

**Effects of temperature and land-use change on soil organic  
matter dynamics in a permafrost-affected ecosystem**

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*“Hier oben Landwirtschaft zu betreiben ist eigentlich Wahnsinn“*

Jens W., Farmer

# Zusammenfassung

Subarktische Ökosysteme gehören zu den am stärksten vom Klimawandel betroffenen Region der Erde. Im Zuge der Erderwärmung lässt sich eine Verlagerung der landwirtschaftlichen Zentren in Richtung der Pole beobachten, die zu einer Ausbreitung der Landwirtschaft hinein in subarktische Waldregionen führt. Da Landwirtschaft in Regionen nördlich von 60°N bislang nur eine untergeordnete Rolle spielte, existieren kaum Studien, die den Effekt des Landnutzungswandel von Wald zu Acker und Wald zu Grünland auf den Bodenkohlenstoff systematisch erfasst haben. Ziel der Dissertation war es, die Auswirkungen des Landnutzungswandels von borealem Wald zu Acker und Grünland auf die Vorräte und die Zusammensetzung der organischen Bodensubstanz zu quantifizieren. Den Kern der Dissertation bilden drei Studien, die im kanadischen Yukon Territory durchgeführt wurden. Zunächst wurde der Effekt von Bodenerwärmung auf die Vorräte und Fraktionen der organischen Bodensubstanz quantifiziert, in dem eine geothermale Quelle als Langzeit-Erwärmungsexperiment genutzt wurde. Im Rahmen der zweiten Studie wurden an 18 Standorten sowohl Waldböden, als auch benachbarte landwirtschaftlich genutzte Flächen in Hinblick auf die organische Bodensubstanz beprobt. Im Zuge dessen wurden Flächen mit und ohne Permafrost und Farmen unterschiedlichen Alters ausgewählt, um den Einfluss des Permafrostes auf die Kohlenstoffdynamik zu berücksichtigen und um mögliche Einflüsse der Nutzungsdauer zu quantifizieren. Ziel der dritten Studie war es, den Effekt der Landnutzungsänderung auf die Bodentemperatur und den Streuabbau zu messen. Hierfür wurden an denselben Standorten wie in der zweiten Studie Teebeutel und Temperatursensoren im Oberboden (10 cm) und im Unterboden (50 cm) vergraben und nach zwei Jahren geborgen. Die vorliegende Arbeit hat insgesamt gezeigt, dass Entwaldung für die Etablierung landwirtschaftlicher Flächen zur Erwärmung und somit zum Verlust des oberflächennahen Permafrostes führt, was wiederum große Verluste des Bodenkohlenstoffes nach sich zieht. Ferner fanden sich Hinweise darauf, dass Verluste des Bodenkohlenstoffes durch die Beschränkung der Entwaldung auf permafrostfreie Flächen und durch angepasst Entwaldungstechniken minimiert werden können.

## Schlagworte

Boden, Permafrost, Landnutzungswandel, Erwärmung, Klimawandel, Streuabbau, Kohlenstoff



# Abstract

Subarctic ecosystems are among the regions on earth that experience the strongest impact by climate change. As a result of global warming, agricultural centers are shifting poleward into previously non-viable regions of subarctic forests. These subarctic ecosystems are among those predicted to be most strongly impacted by rising global temperatures. Additionally, because agriculture north of 60 degrees latitude has been historically limited, there are few studies which systematically examine the effect of converting subarctic forests for cropland or grassland use on soil carbon. The aim of this thesis was to quantify the effects of land-use change from boreal forest to cropland and grassland on the stocks and composition soil organic carbon. Therefore, three studies were conducted in the Canadian Yukon Territory. First, the effect of soil warming on stocks and fractions of the soil organic matter was quantified by using proximity to a geothermal spring in a subarctic ecosystem as a long-term warming experiment. In the second study, 18 sites covering forest soils as well as adjacent agricultural land were sampled to assess differences in soil organic matter. Included were sites with and without permafrost as well as farms of different age, selected to quantify the influence of permafrost and duration of agricultural use on soil carbon dynamics. The aim of the third study was to measure the effect of land-use change on soil temperature and litter decomposition. Tea bags and temperature sensors were buried in the topsoil (10 cm) and in the subsoil (50 cm) at the same sites as used for the second study and retrieved after two years. This work has shown that deforestation for the purpose of agriculture leads to soil warming and therefore to the loss of near-surface permafrost. Consequently, a large loss of soil organic carbon was observed. Furthermore, the results indicated that the loss of soil organic carbon could be minimised if deforestation is restricted to permafrost-free soils and if the deforestation technique is adapted to minimal disturbance of the topsoil.

## Keywords

soil, permafrost, land-use change, warming, climate change, litter decomposition, carbon

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# 1. Introduction

## 1.1. Soil carbon and the role of permafrost in high latitude ecosystems

Increasing greenhouse gas (GHG) emissions has led to global warming of  $0.87 \pm 0.12^\circ\text{C}$ , with an even stronger increase in temperature over the land surface alone by  $1.53 \pm 0.15^\circ\text{C}$ , compared to the pre-industrial era between 1850 and 1900 (IPCC 2019). Furthermore, current modeling scenarios of future GHG-emissions show an expected increase in global mean temperatures between  $1.5$  and  $4.2^\circ\text{C}$  by 2100, compared to the pre-industrial era (Hébert *et al.* 2021). GHGs such as carbon dioxide ( $\text{CO}_2$ ), methane ( $\text{CH}_4$ ), or nitrous oxide ( $\text{N}_2\text{O}$ ) are anthropogenically produced by a vast range of activities such as the burning of fossil fuels, agriculture, forestry, or other land-use related processes (IPCC 2019). While the atmosphere contains approximately 875 Pg of carbon (C), marine ecosystems, including surface sediments, store around 39 453 Pg C; terrestrial ecosystems, including vegetation, soils and permafrost store around 3 550 Pg C; rivers, lakes and coast store 10 – 45 Pg C; and fossil C reserves such as gas, oil and coal store around 905 Pg C, summing to a global carbon stock of 44 793 – 44 828 Pg C (Friedlingstein *et al.* 2022). Globally, most terrestrial C is stored in subarctic regions with permanently frozen soils. The soils of the northern permafrost zone store around  $1035 \pm 150$  Pg C within the uppermost 3 metres (Schuur *et al.* 2015), which corresponds to only 2.3 % of the global C stocks but is 1.2-fold the atmospheric C pool.

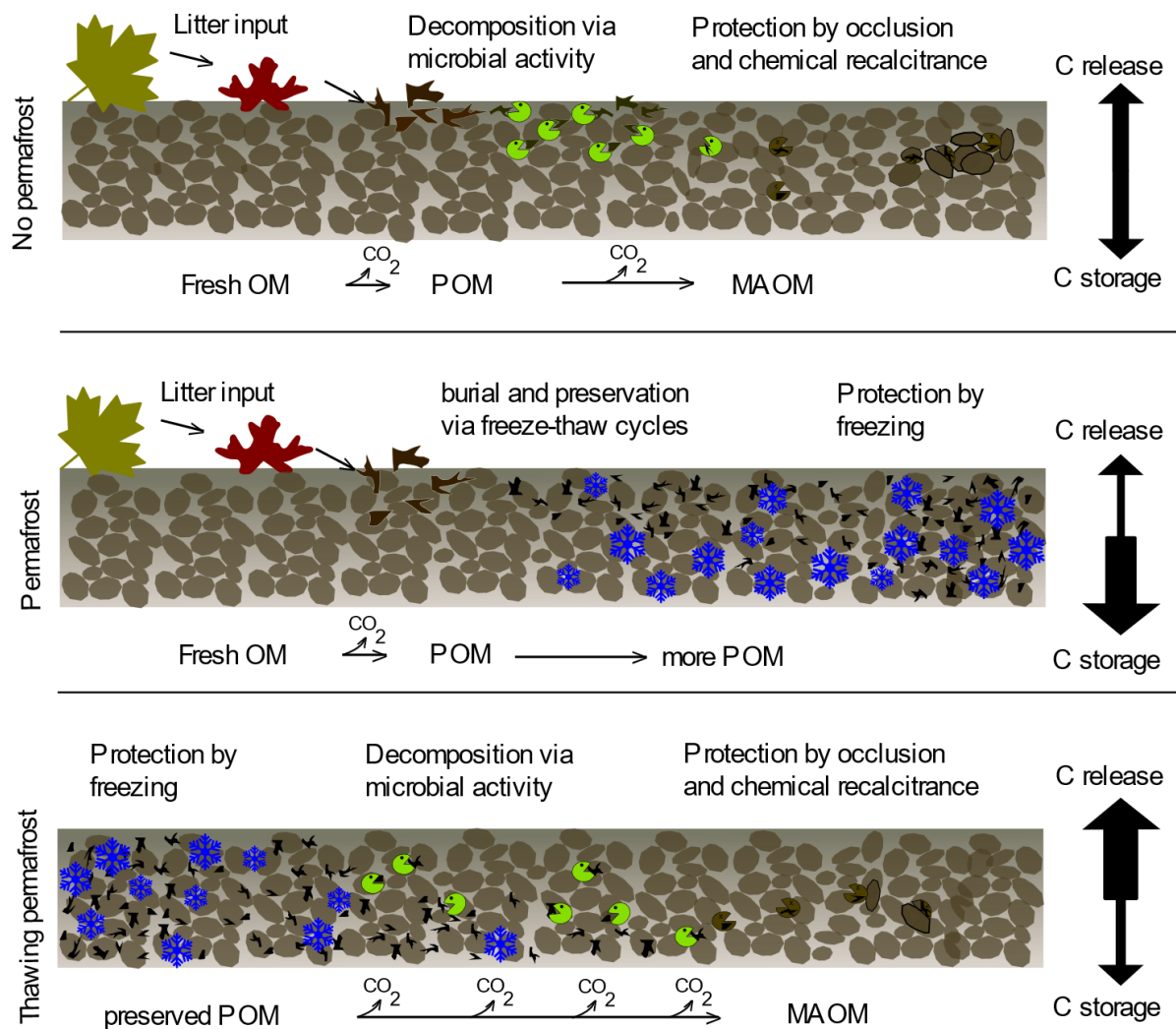
Permafrost is defined as soil or sediment (both terrestrial or coastal) with a temperature not exceeding  $0^\circ\text{C}$  for at least two consecutive years, with a subsurface frozen layer, and an active overlying layer (Biskaborn *et al.* 2019). The presence of an active layer enables microbial activity, plant growth, and mass transfer via cryoturbation (the transfer of material via expansion and contraction of the soil upon freeze and thaw) and is, therefore, essential for the functionality of high-latitude ecosystems. Annual freeze-thaw cycles of the active layer provide water to plants, while the underlying frozen permafrost table hinders the leaching of nutrients (Yang *et al.* 2010). On a regional scale, permafrost can be characterised based on its spatial distribution. If a given

area of land is entirely (91 – 100%) underlain by frozen ground, it is considered continuous permafrost, while areas with less permafrost cover are defined on a continuous scale as discontinuous (51 – 90%), sporadic (10 – 50%) or isolated (< 10%) permafrost (Anisimov *et al.* 2010).

Soil organic matter (SOM) is a heterogeneous mixture of various organic compounds, originating from all kinds of plant and animal remains. Via bioturbation, SOM is transported from the surface deeper into the soil, where it is processed by microorganisms (Blume *et al.* 2009). During microbial processing, also known as mineralization, fresh SOM is broken down into smaller compounds and partly respired as CO<sub>2</sub> (aerobic conditions) or CH<sub>4</sub> (anaerobic conditions). Moreover, SOM may be stabilized against further mineralization by various mechanisms such as selective preservation of chemically recalcitrant organic compounds, occlusion within soil aggregates, or interactions with mineral surfaces (Lützow *et al.* 2006). To characterize the manifold organic compounds and their distinct mineralization rates within the soil, the concept of fractions was introduced and has been intensively discussed and refined over the last decades (Lützow *et al.* 2007). While there is a vast range of SOM fractionation methods (Poeplau *et al.* 2018) with different, but often overlapping, definitions, there is an emerging consensus (Lavalley *et al.* 2020, Cotrufo *et al.* 2019, Liu *et al.* 2022) of using two, mechanistically distinct, fractions. The particulate organic matter (POM) fraction, is more labile, fresh, and relatively unprocessed whereas the mineral-associated organic matter (MAOM) fraction is more stable, highly processed, and long-lasting. Nevertheless, depending on the research question, e.g., in modelling approaches or when results should be compared to other studies, it might be useful to use more than two fractions to gain a more differentiated understanding of SOM processing in the soil (Zimmermann *et al.* 2007).

Low temperatures in permafrost soils, poor drainage, and burial of SOM via cryoturbation hamper the decomposition of SOM, which therefore accumulates far beyond levels possible at lower latitudes and remains in the soil for centuries to millennia (Dutta *et al.* 2006; Davidson & Janssens 2006). At latitudes north of 60°, SOM in the uppermost metre has a mean age between 8 000 and

10 000 years, while SOM in more southern, warmer regions has a mean age between 1 000 and 6 000 years (Shi *et al.* 2020). Upon thawing, permafrost soils are drained and therefore aeriated, exposing the SOM to increased microbial activity, which consequently increases decomposition and the release of GHG (Schuur *et al.* 2015). The release of GHG from permafrost thaw depends on the quality of SOM, which in turn depends on the climatic conditions under which it was initially formed (Knoblauch *et al.* 2013). As decomposition is slow in permafrost soils and fresh litter inputs are quickly incorporated in deeper soil layers via cryoturbation (Figure 1.1), a large proportion of stored SOM consists of weakly processed and rather labile POM (Mueller *et al.* 2015). In contrast to permafrost soils, non-permafrost soils contain less SOC but a more diverse mixture of fractions with varying susceptibility to mineralization, such as mineral-bound SOC, SOC occluded in stable aggregates, or dissolved OC (DOC).



**Figure 1.1: Conceptual difference in organic matter (OM) cycling in soils with and without permafrost. Fresh OM is quickly degraded to particulate organic matter (POM) consisting of plant residues. POM in soils without permafrost is quickly decomposed by microbes. Via respiration, carbon is emitted to the atmosphere as CO<sub>2</sub> and a smaller fraction is protected by attachment to mineral surfaces and occlusion within aggregates. In permafrost soils, POM is accumulated over the years, as low temperatures hamper microbial activity and OM is buried, and protected by freezing.**

## 1.2. Nordic agriculture in a changing climate

Nordic agriculture, here defined as agriculture in the subarctic region north of 60°N, is traditionally small of scale, producing mostly food for local consumption and only a small proportion is sold nationwide or exported (Poeplau *et al.* 2019). As Poeplau *et al.* 2019 showed in an extensive farmers questionnaire, there are big differences in subarctic agriculture between Europe and North America in terms of historic development, recent agricultural practices, and challenges for farmers. Agriculture was not practiced in subarctic North America until European settlers expanded their colonies northwards, forcibly introducing agriculture to the local First

Nations (Joseph 2018). The Canadian Yukon Territory, also referred to as “the Yukon”, is a subarctic region in North America which has experienced an enormous increase in small scale farms that produce food for local consumption (Government of Yukon 2018). The natural conditions in the Yukon pose challenges to agriculture that hamper the development of agricultural industry on a larger scale. In particular, short vegetation periods, cold and dry climate (Table 1.1) and permafrost counteract the long days with lots of sunlight during the vegetation period and lower risk of insect pests compared to warmer regions (Stevenson *et al.* 2014).

It has long been stated that due to climate change, high-latitude regions will experience increasing yields as climatic conditions become more favourable for agriculture (Rosenzweig & Parry 1994) and recent studies expect an overall shift of agricultural centres towards the poles (Tchebakova *et al.* 2011, Franke *et al.* 2022). Further, recent climate change models showed a systematic change to warmer and wetter conditions with an extended growing season in subarctic Canada (Table 1.1). Warmer temperatures accelerate permafrost thaw, which opens new opportunities for farmers at the edge of the discontinuous permafrost, as new soils can be used for growing food. A growing population in northern regions such as the Yukon (Statistics Canada 2016), combined with rising demand for locally produced food (Government of Yukon 2018) may put additional pressure on soils and ecosystems in the Subarctic.

**Table 1.1: Observed and projected mean temperature [°C], mean annual precipitation [mm], number of frost days and length of the frost-free season [number of days per years] at the main settlements in the Yukon. Data from climateatlas.ca, 2022**

	Annual mean temperature		Mean annual precipitation		Frost days		Frost-free season	
	1976-2005	2021-2050	1976-2005	2021-2050	1976-2005	2021-2050	1976-2005	2021-2050
Whitehorse	-2.7	-0.5	310	339	252.8	227.9	71.4	99.1
Dawson	-5.5	-3.1	355	396	250.1	232.7	62.8	82.5
Mayo	-3.5	-1.2	339	379	236.3	216.9	95.3	116.2
Haines Junction	-2.1	0.1	326	352	248.2	222.3	74.5	104.5



### 1.3. Deforestation and soil organic carbon

Research about the effects of land-use change on soil organic carbon (SOC) and the manifold feedback loops between climate, agriculture, and soils has been carried out globally across various climatic zones. In an extensive meta-analysis of 385 studies, Don *et al.* (2011) reported that land-use change from primary forest to cropland in the tropics resulted in SOC losses of around  $25.2 \pm 3.3\%$  or  $20.1 \pm 5.2 \text{ Mg C ha}^{-1}$  and land-use change from primary forest to grassland resulted in  $12.1 \pm 2.3\%$  or  $12.6 \pm 3.0 \text{ Mg C ha}^{-1}$ . For the temperate zone, Poeplau *et al.* (2011) reported a long-term (100 years) SOC loss of  $32.2 \pm 19.9\%$ , compiling data from eight studies within a total data set of 95 studies spanning various types of land-use change. Globally, deforestation for cropland establishment is accompanied by significant SOC losses due to the deprivation of fresh litter input via harvesting. Moreover, converting native forest to grassland may increase SOC stocks, as OM input via roots is enhanced and soil erosion is reduced to the permanent vegetation cover (Guo & Gifford 2002). Reviews by Poeplau *et al.* 2011 (temperate zone) and Lal 2002 (tropics and subtropics) summarize these land-use change dynamics, but empirical evidence for the effect of deforestation for agriculture is scarce in the Subarctic since agriculture has been of minor importance in these regions.

The clearing of subarctic forests removes the insulating vegetation, thereby increasing temperature fluctuations (Frenne *et al.* 2021). Increasing the soil temperature enhances the microbial activity, leading to increased respiration and, consequently, to increased decomposition of SOM (Gregorich *et al.* 2017). At the same time, agricultural practices such as fertilising or establishing grasslands with dense vegetation cover and root systems foster net primary production, potentially increasing SOM inputs to the soil via enhanced root growth and litter inputs (Bolinder *et al.* 2007). A case study in Alaska reported that the conversion of forest for agricultural use led to soil warming of up to  $5^{\circ}\text{C}$ , and a commensurate increase in soil respiration of 25% (Grünzweig *et al.* 2003). Furthermore, Grünzweig *et al.* (2004) reported losses of SOC upon land-use change from boreal forest to agriculture that followed a time-dependent pattern with strong losses within the first two decades after forest clearing followed by increases within the

next decades until SOC stocks were equal or higher after 60 years of grassland management. According to Grünzweig *et al.* (2004), the occurrence of permafrost is an important driver for the degree of SOC loss, as the proportion of labile SOC fractions and the preservation of SOC depend highly on permafrost occurrence. The occurrence of permafrost has been observed to control both the time and magnitude of SOC loss upon deforestation, with a reported loss of 31 Mg ha<sup>-1</sup> within six years after deforestation on permafrost soils and 11 Mg ha<sup>-1</sup> within several decades on soils without permafrost (Grünzweig *et al.* 2015).

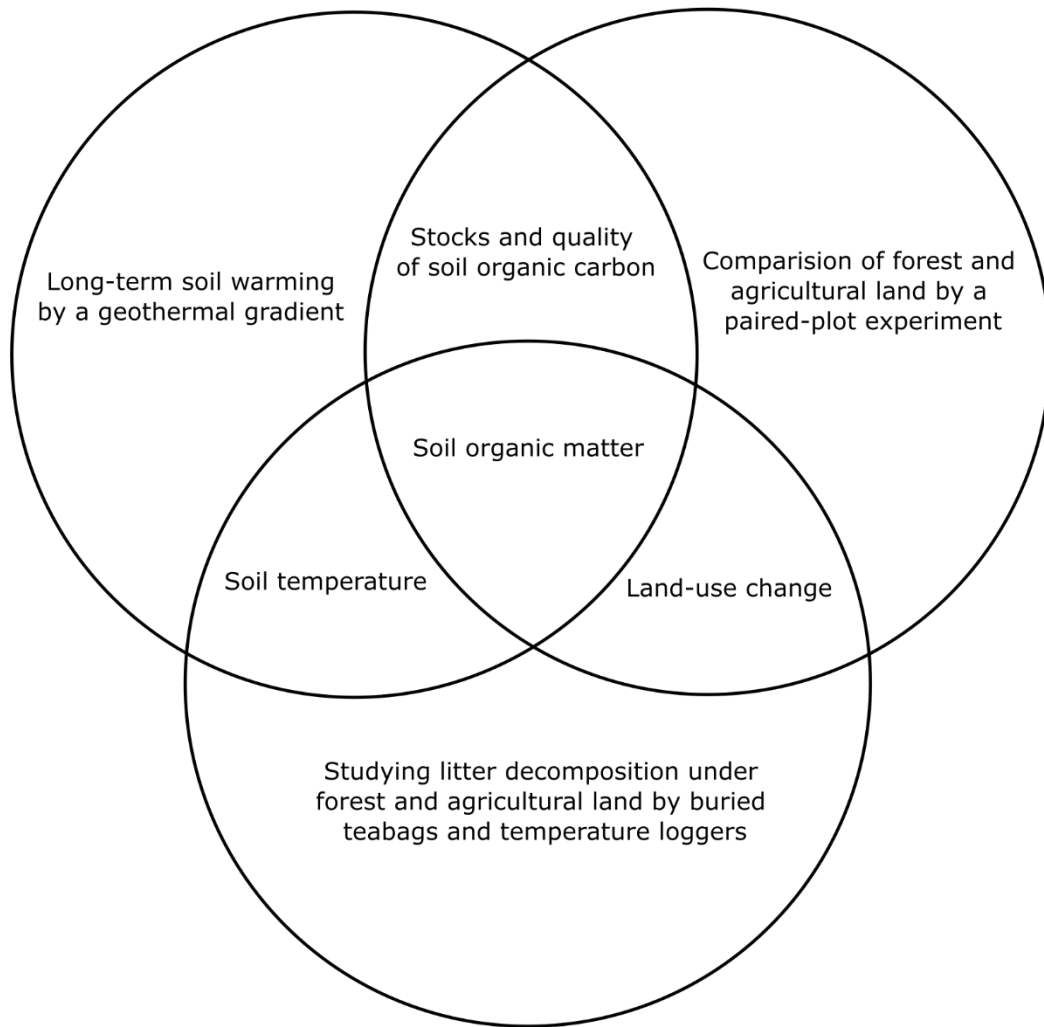
#### 1.4. Aims and objectives

The intensive work of Grünzweig *et al.* (2003, 2004, 2015) in Alaska showed that deforestation for agriculture has impacted SOC stocks and suggested that permafrost occurrence is a major driver of SOC losses. However, detailed data on management effects, SOC fractions, and microclimatic variables are still missing and limit the current knowledge about possible feedbacks between land-use change and SOC to rough estimations. Despite the relatively large number of studies from regions worldwide, there is still only limited knowledge about the effects of temperature and land-use change on SOM dynamics in permafrost-affected ecosystems since agriculture in permafrost-affected ecosystems is still of minor, but recently growing, importance for the global food production. The objective of this thesis was to gain a deep understanding of how establishing agriculture on deforested subarctic soils affects the SOC quantity and quality. To meet this objective, the following questions were addressed:

- 1) How does land-use change from forest to agriculture affect SOC stocks and fractions?
- 2) Is there an influence of permafrost on SOC dynamics following land-use change?
- 3) What is the effect of land-use change on soil microclimate and how do soil temperature changes affect SOC dynamics?

Three studies have been conducted in the Yukon, Canada, to assess the research questions. This subarctic region provides ideal conditions to observe the establishment of agricultural systems

for two primary reasons: first, the Yukon covers the entire transition zone between continuous permafrost through sporadic to permafrost-free, and second, farms in the Yukon cover a wide range of farming systems found in subarctic regions all over the world. The studies conducted for this thesis are connected by a common methodology and a common set of study sites, each addressing different aspects of the thesis objectives (Figure 1.2). The first study (Chapter 2) was conducted to isolate the effect of warming on soils from other, interfering factors such as land cover or soil properties. A geothermal gradient was used to study the long-term effect of soil warming on SOC stocks and fractions as well as on the short-term litter decomposition. The second study (Chapter 3) focussed on the role of permafrost in expanding agricultural systems. By comparing farms that were established on permafrost soils with farms that were established on permafrost-free soils it was possible to examine the importance of permafrost for SOC storage in mineral soils. Furthermore, the inclusion of two different land-use types (cropland and grassland) and various farm-ages between 10 and 115 years allowed assessment of the effect of management intensity on SOC stocks and fractions. The third study (Chapter 4) assessed the effect of land-use change on soil temperature and litter decomposition. By using standardized litter material and soil temperature loggers, it was possible to compare litter decomposition dynamics under different microclimatic conditions and to quantify the effect of land cover on soil temperature regimes.



**Figure 1.2: Conceptual diagram of the relations between the studies carried out in order to assess the interactions between climate change, land-use change and soil organic matter**

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## 2. Long-term geothermal warming reduced stocks of carbon but not nitrogen in a subarctic forest soil

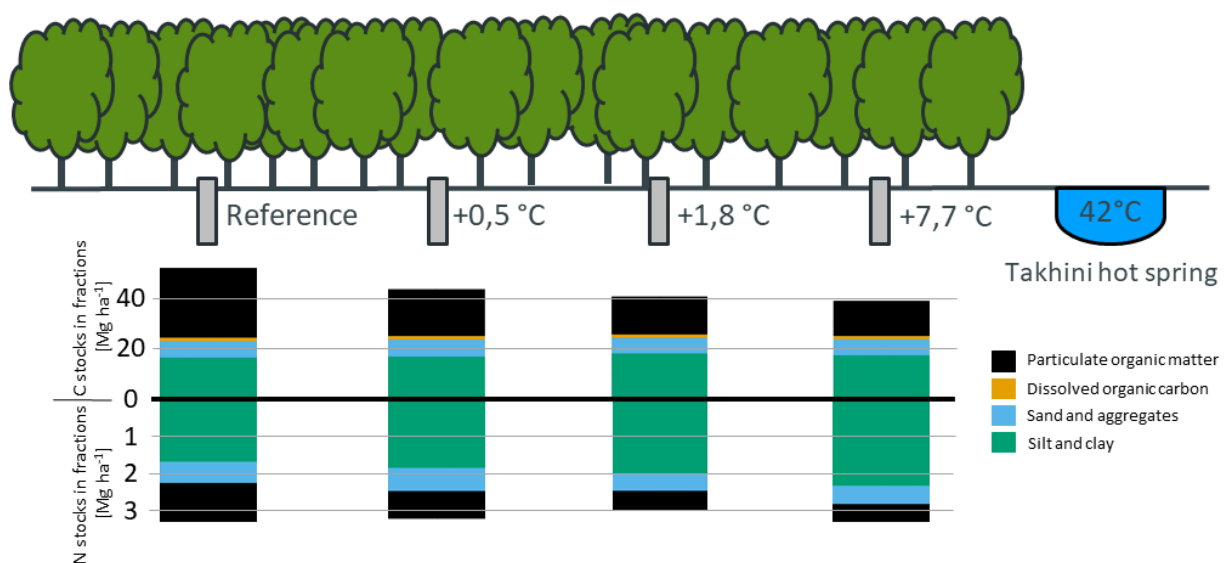
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**Graphical abstract 1: Long-term geothermal warming reduced stocks of carbon but not nitrogen in a subarctic forest soil**

## 2.0. Abstract

Global warming is accelerating the decomposition of soil organic matter (SOM). When predicting the net SOM dynamics in response to warming, there are considerable uncertainties owing to experimental limitations. Long-term *in-situ* whole-profile soil warming studies are particularly rare. This study used a long-term, naturally occurring geothermal gradient in Yukon, Canada, to investigate warming effects on SOM in a forest ecosystem. Soils were sampled along this thermosequence which exhibited warming of up to 7.7 °C; samples were collected to a depth of 80 cm and analysed for soil organic carbon (SOC) and nitrogen (N) content, and estimates made of SOC stock and fractions. Potential litter decomposition rates as a function of soil temperature and depth were observed for a 1-year period using buried teabags and temperature loggers.

The SOC in the topsoil (0-20 cm) and subsoil (20-80 cm) responded similarly to warming. A negative relationship was found between soil temperature and whole-profile SOC stocks, with a total loss of 27 % between the warmest and reference plots, and a relative loss of 3 % °C<sup>-1</sup>. SOC losses were restricted to the particulate organic matter (POM) and dissolved organic carbon (DOC) fractions with net whole-profile depletions. Losses in POM-C accounted for the largest share of the total SOC losses.

In contrast to SOC, N was not lost from the soil as a result of warming, but was redistributed with a relatively large accumulation in the silt and clay fraction (+40 %). This suggests an immobilization of N by microbes building up in mineral-associated organic matter.

These results confirm that soil warming accelerates SOC turnover throughout the profile and C is lost in both the topsoil and subsoil. Since N stocks remained constant with warming, SOM stoichiometry changed considerably and this in turn could affect C cycling through changes in microbial metabolism.

## 2.1. Introduction

Climate change and the associated rise in temperatures leads to warming of soils (Heimann and Reichstein 2008). Microbial activity, and thus decomposition of soil organic matter (SOM), is stimulated by warming and is likely to turn soils into a net source of carbon dioxide (CO<sub>2</sub>), inducing a climate-carbon cycle feedback loop (Heimann and Reichstein 2008). The largest temperature increases are expected in high latitudes (IPCC 2013, IPCC 2019), where soils store the most (FAO and ITPS 2017) and oldest SOM (Shi et al. 2020). Therefore, boreal biomes are considered to be of major importance for the global C cycle and play an important role in climate change feedbacks (Carey et al. 2016). The effect of rising air temperatures and other global change drivers on ecosystems has been extensively studied in the last four decades (Song et al. 2019). However, predictions about the responses of SOM to warming are difficult and uncertain, due to a lack of long-term field warming experiments, investigating whole-soil profile interactions between soil warming and the C and nitrogen (N) cycles. Most *in-situ* warming studies have a time span of less than a decade, and usually of just 1-3 years (Eliasson et al. 2005, Hicks Pries et al. 2017, Ineson et al. 1998, Li et al. 2018, Luo et al. 2001, Nottingham et al. 2020). Furthermore, also laboratory incubation experiments have short time spans of observations (Aaltonen et al. 2019, Conen et al. 2006, Dutta et al. 2006, Karhu et al. 2010), while climate change is a slow, gradual process with many interactions between ecosystem components that require longer observations. Depending on warming intensity and the soil parameters being investigated, abrupt soil warming can lead to overshoot reactions or relatively fast equilibration (Walker et al., 2020). Melillo et al. (2017) reported strong temporal trends in SOC losses over 26 years of soil warming with different stages of SOC loss and build-up, resulting in a non-linear relationship between warming duration and SOC loss. Short-term experiments might thus risk overestimating warming effects when linearly extrapolated to longer timescales (Crowther 2016); they certainly fail to predict how strongly, depending on warming intensity, ecosystem processes will change before a new steady state might be reached (Walker et al. 2020). However, understanding the new baseline of specific

parameters after long-term warming is crucial for an overall quantitative understanding of warming effects on ecosystem processes.

Even though subsoil (usually defined as the soil below the A-horizon or the soil below the main rooting zone) stores around 50% of total SOC stocks (Hicks Pries et al. 2017, Koarashi et al. 2012, Rumpel and Kögel-Knabner 2011, Wordell-Dietrich et al. 2017), most warming experiments have focused on the topsoil. Few studies have evaluated whole-profile warming (e.g. Nottingham et al. 2020: 120 cm, Hicks Pries et al. 2017: 100 cm). In subsoils, the abiotic conditions, the availability of fresh substrates, SOM composition and the size and structure of the microbial community are very different from those in topsoils (Fierer et al. 2003, Rumpel and Kögel-Knabner 2011). It is therefore reasonable to expect that the response of subsoils to warming would be different than that of topsoils.

The fate of N under long-term warming has not been thoroughly characterized in studies evaluating the response of SOM to warming. When SOM is decomposed and C is largely respired back to the atmosphere as CO<sub>2</sub>, the mineralized N becomes available for microbes and plants and this, in turn, could enhance ecosystem productivity (Melillo et al. 2002, Rustad et al. 2001). However, N could also be lost via leaching or directly immobilized by microbes. Not much is currently known about the net effect of soil warming on total N stocks in the soil. This deserves further study so that potential interactions between C and N cycles can be identified and a more comprehensive understanding about whole-ecosystem responses to warming can be developed.

Geothermal areas can help to fill these knowledge gaps because in these areas the whole soil profile has been warmed for long periods of time. When soils are unaffected chemically by geothermal waters, the resultant soil warming may be considered a cost-effective long-term manipulation (O’Gorman et al. 2014). O’Gorman et al. (2014) highlighted the importance of temperature gradients for an in-depth understanding of warming responses including identification of potential tipping points. Another opportunity of geothermal warming is that temperature gradients across the landscape can be identified with different degrees or intensities

of warming developed as part of an experimental set-up. In this study, it was possible to take advantage of geothermal soil warming at the Takhini hot springs, located in a subarctic deciduous forest near Whitehorse, Yukon in Canada. It is not known how long the soils have been warmed by the spring, but the spring has been commercially used as a recreational area since around 1907 and we can therefore assume that at least 100 years of warming has occurred. One of the few examples of a comparable site is the ForHot experimental site in Hveragerdir, Iceland (Sigurdsson et al. 2016), where soil has been warmed since an earthquake in 2008 in one valley and for more than 50 years in a neighbouring valley (Walker et al. 2020).

SOM is highly complex and this complexity should be accounted for when trying to predict its dynamics (Lavallee et al. 2019). This is often done by separating multiple components of contrasting behavior by various fractionation approaches (Lützow et al. 2007). In recent years, physical fractionation methods, and in particular, the separation of size and/or density fractions, have been widely used (Lavallee et al. 2019, Poeplau et al. 2018). This is in line with the current understanding of the major pathways of SOM stabilization (Dynarski et al. 2020), with reduced accessibility of SOM by mineral association as a key mechanism (Dungait et al. 2012, Kögel-Knabner et al. 2008). However, few warming studies have evaluated the response of different SOM fractions to in situ warming (Lavallee et al. 2019). This hampers the in-depth understanding needed for accurate prediction of SOM cycling and transformation in response to global changes that are occurring (Conant et al. 2011). The temperature sensitivity of different SOM fractions has long been a matter of debate, owing to a wide range of different experimental approaches and definitions of temperature sensitivity (Conant et al. 2011, Conen et al. 2006, Karhu et al. 2010, Knorr et al. 2005). Apart from evaluating changes in SOM quality, fractionation can also be used to indicate soil structural changes or reveal prevailing destabilization mechanisms. For example, in the Icelandic geothermal warming experiment mentioned earlier, Poeplau et al. (2016, 2020) detected the depletion of stable aggregates associated with loss of SOM and concluded that either loss of SOM decreased aggregate stability or weakening of aggregate binding mechanisms led to the destabilization of SOM.

Our aim in this study was to use a natural thermosequence in a subarctic deciduous forest to quantify the effect of long-term whole-profile soil warming on SOC and total soil N stocks and fractions, as well as potential litter decomposition. The latter was used as a proxy to test the hypothesis that SOM losses in the topsoil and subsoil are driven mainly by the warming-induced acceleration of microbial activity.

## 2.2. Material and methods

### 2.2.1. Study site

The Takhini hot springs (60°52'43.9"N, 135°21'30.7"W, <http://takhinihotpools.com/>) are located near the Takhini river in south-western Yukon Territory, west of Whitehorse in the discontinuous permafrost region (Smith et al. 2004). The study area is located on the margins of the Whitehorse Trough, a Mesozoic marine basin with sediments and volcanic rocks of Jurassic to Triassic age, locally overlain by glacial and periglacial deposits. At the Takhini hot springs, water is heated by natural decay of plutonic rocks (Langevin et al. 2019) at a depth of several hundred metres and reaches the surface through geological faults (Fraser et al. 2018). This water is captured in a commercial pool with a temperature of 42°C, heating the surrounding soil at a depth of 50 cm from annual temperatures of -4.8°C in winter and 3.7°C in summer (Smith et al. 1998) up to temperatures consistently above freezing. Before the spring's commercial exploitation as a recreational area around 100 years ago, the area was used by the Ta'an Kwäch'än First Nation. There is no scientific work about the exact age of the spring or about the duration of soil warming. We know from old documents such as early photographs and newspapers that the spring was already in use by 1907 and must have delivered hot water to the surface beforehand ([http://www.explorenorth.com/library/history/takhini\\_hotsprings.html](http://www.explorenorth.com/library/history/takhini_hotsprings.html)). Therefore, we assume that soil warming has occurred for more than hundred years. There is no evidence to suggest that any geothermal water affected the area where the plots were located. At the four plots, the soils had similar soil properties (see Table S1.1). The geothermal water is rich in calcium and iron, leading to visible precipitates whenever the water comes to the surface. To avoid a chemical influence of the geothermal water on the soils, the plots were established at the back of the spring,

where no water directly reaches the surface. The soil pH was similar at all of the plots, which indicated that the soils were not chemically affected by the geothermal water and warming.

The research area is located in an Aspen forest (*Populus tremuloides*, MICHX) on Orthic Eutric Brunisols (Canadian Soil Classification; Mougeot 1997) that developed from glaciolacustrine deposits and till (Bond et al. 2005), originating from the late Pleistocene Cordilleran Ice Sheet (Duk-Rodkin 1999). The soil at the experimental site has a loamy to silty-loamy texture (average of 20% sand, 63% silt and 17% clay) and a neutral to alkaline  $\text{pH}_{\text{H}_2\text{O}}$  of between 6.7 and 8.8 (Table S1.1). Carbonates are present below a depth of approximately 50 cm.

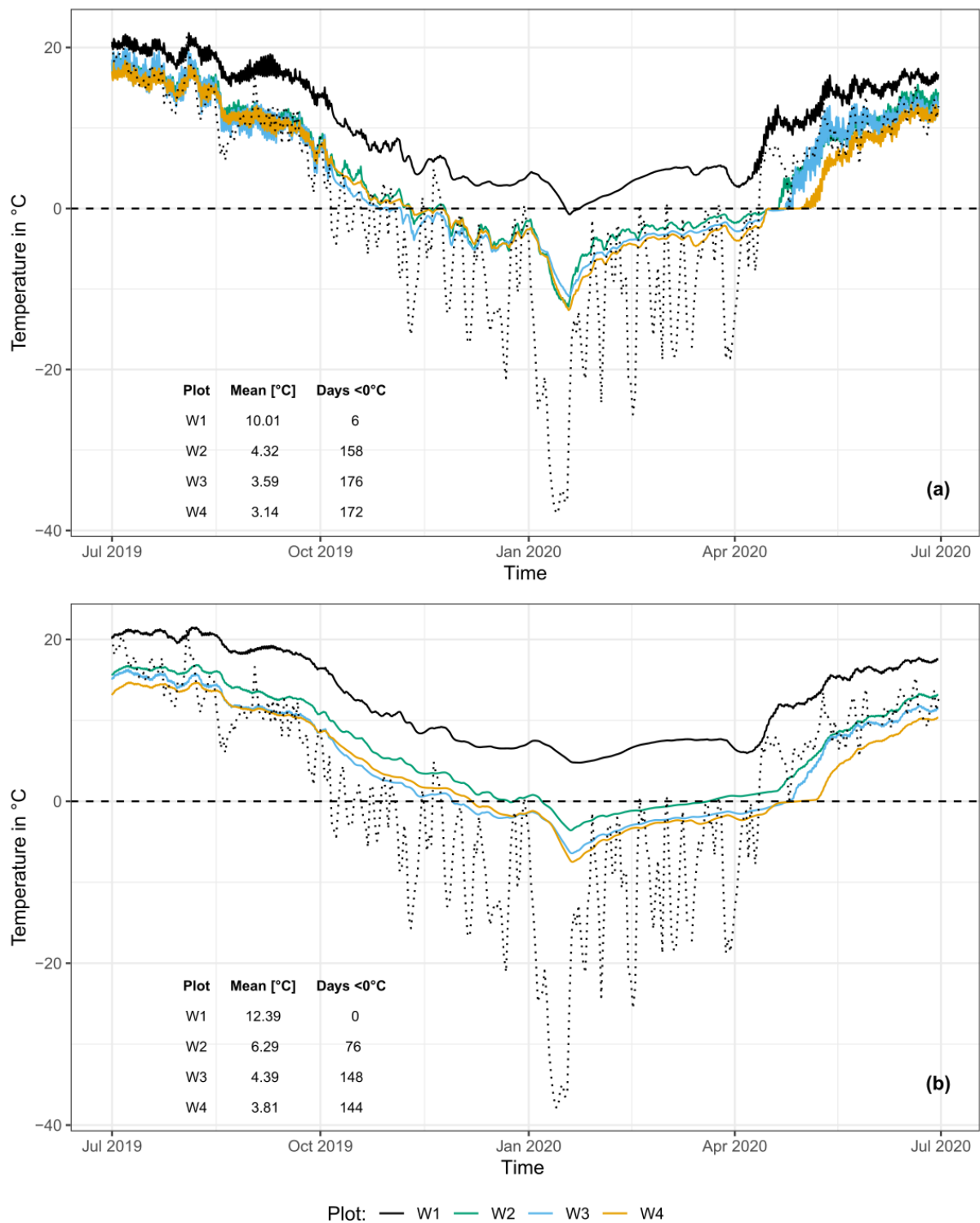
The research site has an annual precipitation of 267 mm and an annual mean temperature of  $-1.6^\circ\text{C}$  according to Canadian Climate Normals (Environment Climate Change Canada 2020) using data from 1981 to 2010.

### **2.2.2. Plot selection and soil temperature measurement**

Sampling plots were selected by measuring the current soil temperature, which decreased with a distance from the hot spring. The four sampling plots (W1, W2, W3, and W4, with W1 closest and W4 furthest away from the spring), each represented a specific warming intensity, were selected on the basis of relatively undisturbed forest patches on flat terrain. To ensure this, sampling plots had to be small ( $3 \times 3 \text{ m}^2$ ) due to the infrastructure around the spring. Overall, the resulting thermosequence was of small spatial dimension with very close coordinates: W4 =  $60.879159^\circ\text{N} / -135.361128^\circ\text{E}$ , W3 =  $60.879011^\circ\text{N} / -135.360853^\circ\text{E}$ , W2 =  $60.879118^\circ\text{N} / -135.359916^\circ\text{E}$ , W1 =  $60.878867^\circ\text{N} / -135.360272^\circ\text{E}$ . The plots were located within 60 m of the spring. At each plot, temperature loggers (Tinytag Plus 2 TGP 4017, Gemini Data Loggers Ltd) were buried at 10 and 50 cm soil depths to log the temperature with a resolution of 2 h for 1 year (July 2019 – July 2020). After 1 year of logging, the temperature loggers provided a detailed picture of the soil temperature pattern throughout the year. Figure 2.1 shows that the plot closest to the hot spring (W1) was continuously warmer than the reference plot (W4), with a maximum temperature difference of  $8.6^\circ\text{C}$  at 50 cm depth. As temperature data were obtained for two depths, reference is made to the

mean of both depths and the warming intensity compared with the reference plot (W4), which is 7.7°C (W1), 1.8°C (W2) and 0.5°C (W3). At the warmest plot (W1), the temperature dropped below 0°C only in exceptional cases (6 days in January), while all other plots remained frozen for at least part of the winter (Figure 2.1). While plots W2, W3 and W4 had similar, often overlapping temperature curves at 10 cm depth, the temperature at 50 cm was clearly different among the plots, indicating a greater influence of the geothermal heat source deeper in the soil.





**Figure 2.1:** Soil temperature over a 1 -year period at depths of (a) 10 cm and (b) 50 cm for all four plots (W1-W4), with the dashed line indicating the freezing point and the dotted line indicating air temperature recorded at the closest weather station in Whitehorse (air temperature data provided by the Computer Research Institute of Montréal, 2020).

### 2.2.3. Sampling and field measurements

A transect of the four established plots was sampled in July 2019. The litter layer was sampled using a metal cylinder of 12.5 cm diameter (8 cm height) prior to soil coring. The thickness of the

litter layer did not exceed 4 cm. A slide hammer-driven soil corer with an auger of 7 cm diameter and 20 cm length was used for soil sampling at four random locations in each plot. The soil cores were divided into five depth increments (0-10, 10-20, 20-40, 40-60 and 60-80 cm). The separate sampling of all depth increments with the 20-cm auger precluded the deformation of soil cores (compaction/stretching) and thus ensured correct volume-based sampling. In two replicates of one plot (W4), the 60-80 cm depth increment could not be sampled due to the high gravel content.

To determine the potential litter decomposition rate, teabags with green tea ("Bio Grüner Tee", Paulsen Tee, Fockbeck, Germany, Charge No. 187896FC) were used (Keuskamp et al. 2013, modified). The teabags were buried at depths of 10 and 50 cm in the centre of each plot (three bags per depth and plot, resulting in 24 teabags) to study warming effects on potential litter decomposition as a proxy for microbial activity. The teabags were tagged and weighed before burying. After 1 year, the teabags were recovered, cleaned, dried at 60 C, and weighed again to determine tea mass loss. Six of the 24 teabags could not be recovered.

#### **2.2.4. Sample preparation and analyses**

The freshly sampled soil was air-dried, weighed, sieved through a 2-mm sieve and weighed again to calculate the fine soil mass and stone content (Equation 1). An aliquot sample of the sieved soil was then shipped to Germany, where all further parameters were measured. The water content of each air-dried sample was determined to correct the fine soil mass estimate by subjecting an aliquot to 105°C oven-drying and calculating the weight-difference between air- and oven-dried samples.

For the measurement of pH and texture, the four field replicates of each plot and depth were pooled into one sample per depth increment, resulting in five samples per plot. The pH of each pooled sample was measured in water with a soil:water ratio of 1:5 (10 g soil and 50 g water) after 1-h shaking (ISO 10390, 2005; Table S1.1). Soil texture was determined for the samples from the second depth increment (10-20 cm) according to DIN ISO 11277:2002-08, which is based on sieving and sedimentation of suspended fine particles (Köhn 1929).

Milled aliquots of each sample were used for analysis of SOC, total inorganic carbon and total N analysis by dry combustion with an elemental analyser (LECO TruMac). Samples with a  $\text{pH}_{\text{H}_2\text{O}} > 6.2$  were combusted in a muffle furnace prior to dry combustion to determine total inorganic carbon. Milled aliquots of the litter samples were analysed for SOC and N.

#### **2.2.5. Fractionation**

SOM fractions were isolated in all 78 samples according to the method of Zimmermann et al. (2007) which had been slightly modified by Poeplau et al. (2018). Briefly, 30 g of the bulk soil were dispersed with an ultrasonic probe at 22 J and then wet-sieved with 2.2 L deionized water through a 63- $\mu\text{m}$  sieve (the threshold between silt and sand in the German Soil Classification; Ad-hoc-Arbeitsgruppe Boden 2005). The fine fraction was then centrifuged and the supernatant fluid was filtered (0.45  $\mu\text{m}$ ) and analysed for water-extractable carbon (here referred to as DOC). DOC was measured with a Dimatoc 2000 (Dimatec GmbH, Essen). The remaining silt and clay fraction (S+C) was dried until the weight was constant at 50°C, weighed and analysed for C content. From the S+C-fraction, 1 g was used to determine the resistant soil organic carbon (rSOC) and resistant soil nitrogen (rSN) using oxidation with 6 % sodiumhypochlorite (NaOCl). In this step, the 1 g sample was stored in a 50-ml centrifuge tube and filled to 45 ml with NaOCl. After shaking, the tubes were left open for 16 h to ensure maximum oxidation and prevent the tubes from bursting due to gas produced by the ongoing oxidation process. Afterwards, the tubes were centrifuged, decanted, washed twice with deionized water and refilled with NaOCl. After three repetitions, the washed sample was dried at 50°C and the remaining material was analysed for C and N content.

The coarse fraction from the wet sieving was dried at 50°C and then weighed. Afterwards, this fraction was mixed with a sodium polytungstate solution adjusted to a density of 1.8  $\text{g}/\text{cm}^3$ . After mixing and centrifuging, the particulate organic matter (POM) floating on the heavy solution was decanted, washed with deionized water, dried again at 50°C, weighed, milled and analysed for C and N contents. The same procedure was applied for the heavy sand and aggregate fraction (S+A).

This fractionation method leads to a small loss of both sample mass and carbon, and the recovery (sum of all isolated fractions) was measured to be 97% for the initial bulk soil mass and 90% for the initial bulk soil carbon. Due to high carbonate content between 40 and 80 cm, the rSOC fraction could not be accurately evaluated and was not considered at these depths. As the rSOC fraction consisted of less than 1 g, it was not possible to distinguish inorganic C and SOC. The fractionation method developed by Zimmermann et al. (2007) has been applied in other comparable geothermal warming studies (Poeplau et al. 2016 and 2020). Furthermore, in a large-scale method comparison with 20 different fractionation methods, this method was found to be among the most successful in isolating pools of distinct turnover rates (Poeplau et al. 2018). The method not only allows for the isolation of POM and mineral-associated OM, which are used in other fractionation methods, but also provides information about soil structure from the S+A fraction, and about desorption and leaching processes by the DOC fraction.

#### 2.2.6. SOC stock calculation and mass correction

Considerable variability in the rock fragment fraction was observed across the plots (Table S1.1). To avoid a bias in SOC stock estimates caused by the high proportion of rock fragments in the soil samples and assuming that this variation was not temperature-driven, SOC stocks were calculated as  $SOCstock_i$  using the following equations (M2 in Poeplau et al. 2017):

$$BD_{fine\ soil} = \frac{mass_{sample} - mass_{rock\ fragments}}{volume_{sample} - \frac{mass_{rock\ fragments}}{\rho_{rock\ fragments}}} \quad (\text{Eq. 1})$$

$$SOCstock_i = SOCcon_{fine\ soil} * BD_{fine\ soil} * depth_i \quad (\text{Eq. 2})$$

where  $mass_{sample}$  is the total mass of the sample,  $mass_{rock\ fragments}$  is the total mass of the rock fragments (> 2 mm),  $volume_{sample}$  is the volume of the sample,  $\rho_{rock\ fragments}$  is the density of the rock fragments (assumed to be 2.6 g cm<sup>3</sup>),  $SOCcon_{fine\ soil}$  is the SOC content of the fine soil and  $depth_i$  is the sampling depth of the corresponding increment.

As a change in treatments is often accompanied by changes in horizon thickness and bulk density, a mass correction of the measured SOC concentration is needed (Ellert und Bettany 1995). The

correction of SOC stocks for bulk density was performed according to Poeplau et al. (2011), where the soil mass of the lightest core (0-80 cm) is used as the reference soil mass, and soil and C masses in the other cores are adjusted relative to it. In this case, the mean of the four cores from the reference plot (W4) was used. Mass corrections along the whole profile affect each depth increment and lead to a change in the depth of these increments. This makes it difficult to compare SOC stocks of specific depth increments. To avoid overcorrection, we calculated the mass correction in a first step only for the two uppermost depth increments (0-10 and 10-20 cm), which are herein referred to as topsoil, and in a second step for all five depth increments, which are referred to as subsoil. To obtain mass-corrected subsoil SOC stocks, we subtracted the corrected topsoil SOC stocks from the corrected whole-profile SOC stocks. Therefore, our use of terms “topsoil” and “subsoil” does not refer to pedogenic or diagnostic horizons and topsoil is representative of the SOM-rich rooting zone of the investigated soil.

### **2.2.7. Statistical analysis**

All statistical analyses were conducted using R version 3.6.1 (R Core Team 2019) with the packages readxl (Wickham and Bryan 2019), openxlsx (Schauberger and Walker 2020), ggplot2 (Wickham 2016), ggpubr (Kassambra 2020), dplyr (Wickham et al. 2020), plyr (Wickham 2011), reshape2 (Wickham 2007), gridExtra (Auguie 2017) and vegan (Oksanen et al. 2019). In order to test the sensitivity of SOC and N stocks, contents and SOC fractions to soil warming, linear and logarithmic regression models were applied for each depth and variable, from which the best fit (best  $R^2$ ) was chosen (Supplement Tables S.1.3 – S1.6). Furthermore, Spearman’s correlation coefficient was calculated to test for rank correlation between soil temperature and average stocks of C and N.

To test for differences in SOC and N fraction composition between the plots, an analysis of similarity (ANOSIM) was performed with the vegan-package (Oksanen et al. 2019). The calculated R values give the measure of dissimilarity between all four groups, with corresponding  $p$ -values to account for statistical significance ( $p < 0.05$ ). This means that ANOSIM could be used to analyse a change in the distribution of fractions between plots.

Furthermore, the ratio of the SOC and N contents between the warmed plots and the reference plot was calculated as the response ratio (RR) to quantify the accumulation or depletion in response to warming:

$$RR = \frac{X_{warm}}{X_{ref}} \quad (\text{Eq. 3})$$

where RR is the response ratio,  $X_{ref}$  is the content of SOC or N in the reference plot and  $X_{warm}$  is the content of SOC or N in the warmed plot.

The decomposition of the green tea as a function of soil temperature was best described by the following model:

$$Y = n + \log(x) * m \quad (\text{Eq. 4})$$

where  $Y$  is the decomposition within 1 year;  $x$  is the mean annual soil temperature; and  $n$  and  $m$  are the fitted parameters of the model function.

The temperature data were processed with a Hampel filter using a moving window of eight measurements and the twofold median absolute deviation (Pearson et al. 2016). The Hampel filter corrects for outliers in the data, such as temperature changes of several degrees between 2 h, while keeping the natural intraday variations in the data. For comparisons with air temperature, the data of daily mean air temperatures from Whitehorse were used (Computer Research Institute of Montréal, 2020).

## 2.3. Results

### 2.3.1. Bulk soil C and N

In all plots, SOC and N contents were highly variable (Figure 2.2a, b). As expected, SOC contents were highest in the reference plot and lowest in the warmest plot (Figure 2.2a). In all plots, SOC decreased exponentially with depth. Consistent with SOC contents, the whole-profile SOC stocks were also highest in the reference plot (Figure 2.3a). The warmest plot, W1 (+7.7°C), contained on average 14.32 Mg ha<sup>-1</sup> (27%) less SOC in the whole profile (0-80 cm) than the reference plot. Assuming a linear loss of SOC over the temperature range between the warmest plot and the reference plot, this is equivalent to a loss in SOC of 1.86 Mg ha<sup>-1</sup> or 3% per °C warming. In the 0-20 cm topsoil layer, the difference in SOC stock between the warmest plot and the reference was 4.79 Mg ha<sup>-1</sup> (which represents a loss of 16%), while the subsoil lost 9.53 Mg ha<sup>-1</sup> (34%; see Table S1.2 and Figure 2.3a). The C:N ratio (Figure 2.2c) was strongly related to temperature and decreased with increasing temperature; this effect was strongest in the subsoil. N stocks (Figure 2.3b) remained constant with warming, indicating that no N was lost from the soil due to warming. Litter C and N stocks remained unaffected by warming (Table S1.2, Figure 2.3a, b). Moreover, no statistically significant effects of warming were detected on bulk soil C and N contents and stocks, due to high within-plot variability. However, significant ( $p < 0.05$ ) correlations, using the Spearman's rank test, were found between temperature and average subsoil SOC stocks (Rho = -0.62,  $p = 0.01$ ) and whole profile SOC stocks (Rho = -0.52,  $p = 0.04$ ), where no significant correlation was observed for the topsoil SOC (Rho = -0.23,  $p = 0.39$ ). Soil N was not significantly correlated with temperature.

A response ratio (RR) < 1 indicates a loss in SOC or N content in the warmed plot relative to the reference plot, whereas a RR > 1 indicates that SOC or N had accumulated in the warmed plot. Since RR is based on contents (g kg<sup>-1</sup>), it is independent from any correction of soil mass. Across plots, the RR (Table 2.1) values decreased with warming but did not change with depth indicating that changes in SOC contents were related to warming but not to depth in the soil profile. In contrast to the SOC, the RRs of soil N contents did not decrease with warming, but it appears that

there was a slight relocation of N to deeper soil layers because the RR values indicated a loss in the uppermost layer with a concomitant gain in deeper layers.

**Table 2.1: Response ratio (RR) of C and N contents between the reference and the three warmed plots for each depth increment.**

	C			N		
	+0.5 °C	+1.8 °C	+7.7 °C	+0.5 °C	+1.8 °C	+7.7 °C
0 - 10 cm	0.52	0.63	0.55	0.65	0.77	0.64
10 - 20 cm	0.74	1.22	0.95	0.85	1.16	1.08
20 - 40 cm	0.94	0.91	0.81	1.06	1.09	1.20
40 - 60 cm	0.87	0.73	0.57	1.02	0.99	1.03
60 - 80 cm	0.98	0.78	0.73	1.15	0.97	1.07

**Table 2.2: Results of the ANOSIM for the relative composition of the soil organic matter (SOM) fractions in C and N for each depth increment.**

Depth	Relative distribution of C		Relative distribution of N	
	R	p	R	p
0 - 10 cm	0.75*	0.035	0.75*	0.03
10 - 20 cm	-0.052	0.643	0.083	0.291
20 - 40 cm	0.635*	0.023	1*	0.001
40 - 60 cm	0.594	0.05	0.542*	0.037
60 - 80 cm	1*	0.033	1*	0.027

\*significant differences between the warming plots with  $p < 0.05$

### 2.3.2. SOM fractions

The sum of C in all fractions tended to decrease with increasing soil temperature in three out of four depth increments (Figure 2.4a), but regression analysis indicated that no significant trends were found. A significant effect of warming was found for the stocks of POM at 20-40 and 40-60 cm layers (negative) and for rSOC at 40-60 cm, as well as for the C concentrations at 20-40 cm



(POM and rSOC) and 40-60 cm (POM, S+C, DOC). A detailed description of these results is provided in Tables S1.3 and S1.4. Carbon stored in POM decreased with warming across all depths, except for 10-20 cm, where it remained constant (Figure 2.4a). The other fractions showed minor responses, except for the S+C fraction. Carbon stored in the S+C fraction showed an inconsistent response to warming, with an increase at 60 – 80 cm, a decrease at 40 – 60 cm but was unchanged at other depths. The relative contribution of C in the different fractions (Figure 2.4b) revealed a more consistent pattern. With warming, POM showed again the strongest response of all fractions. In contrast, the proportion of the S+C fraction tended to increase with warming in all plots. No clear difference between the response of the oxidation-resistant rSOC fraction and the oxidizable S+C fraction was observed.

Across all fractions and depth increments, the response to warming was greatest in the POM fraction. Over the entire 80 cm soil profile, POM-C accounted for about half of the bulk SOC stock in the reference plot, and its share became significantly smaller with every warming step (Figure 2.3c). In contrast, the stocks of the other fractions remained almost constant throughout all warming steps. As depicted in Figure 2.3c, the loss of POM was driving total SOC loss. Over the whole soil profile, POM was depleted by 13.94 Mg ha<sup>-1</sup>, while the other fractions contributed much less, with less than 1 Mg ha<sup>-1</sup> for each fraction. After POM, the DOC fraction had the greatest proportional loss with 0.24 Mg ha<sup>-1</sup>, which equals 15% of the DOC in the reference plot.

Nitrogen stocks were not reduced by warming, as shown in Figure 2.3b and the constant RR values across plots (Table 2.1). The results of the ANOSIM (Table 2.2) and the distribution of N between the fractions (Figure 2.5) show a significant shift of 0.55 Mg ha<sup>-1</sup> N from POM to the S+C fraction and an overall accumulation of N in the S+C fraction of 0.64 Mg ha<sup>-1</sup>, representing a 40% increase in N in the S+C fraction (Figure 2.3d). As a result of changes in SOC and no concomitant changes in N, the C:N ratio became narrower with warming (Figure 2.2c); this change was consistent across depth increments but was most pronounced in the subsoil. Finally, for N stocks (Figure 2.3b and 2.5a), a slight distribution shift from topsoil to subsoil with warming was observed. In the reference plot, 45% of soil N (1.46 ± 0.17 Mg ha<sup>-1</sup>) was stored in the topsoil and 55% (1.77 ±

0.16 Mg ha<sup>-1</sup>) in the subsoil. Whereas in the warmest plot, 41% of N (1.34 ± 0.23 Mg ha<sup>-1</sup>) was stored in the topsoil and 59% (1.91 ± 0.08 Mg ha<sup>-1</sup>) in the subsoil.

The ANOSIM (Table 2.2) revealed that there was a significant change in the distribution of SOC and total N among the five fractions, suggesting there were distinct responses to warming. At least for N, which did not change in absolute amounts, this indicates that it was transferred between fractions.

### 2.3.3. Litter Decomposition

The teabag experiment indicated that temperature had a significant effect on litter decomposition rates (Figure 2.6). Overall, the tea litter at 50 cm depth was less decomposed and observations were more variable than at 10 cm. The intercept of the regression equation shows that decomposition is generally lower at 50 cm than at 10 cm (54.5 at 50 cm and 38.1 at 10 cm), whereas the slope coefficients indicate a similar response to warming at both depths (12.65 at 50 cm and 12.38 at 10 cm). The difference in R<sup>2</sup> between 50 cm and 10 cm indicates that observations at 50 cm depth had a higher uncertainty than observations at 10 cm depth. The *p*-values of the regressions were 0.002 at 50 cm and <0.001 at 10 cm.

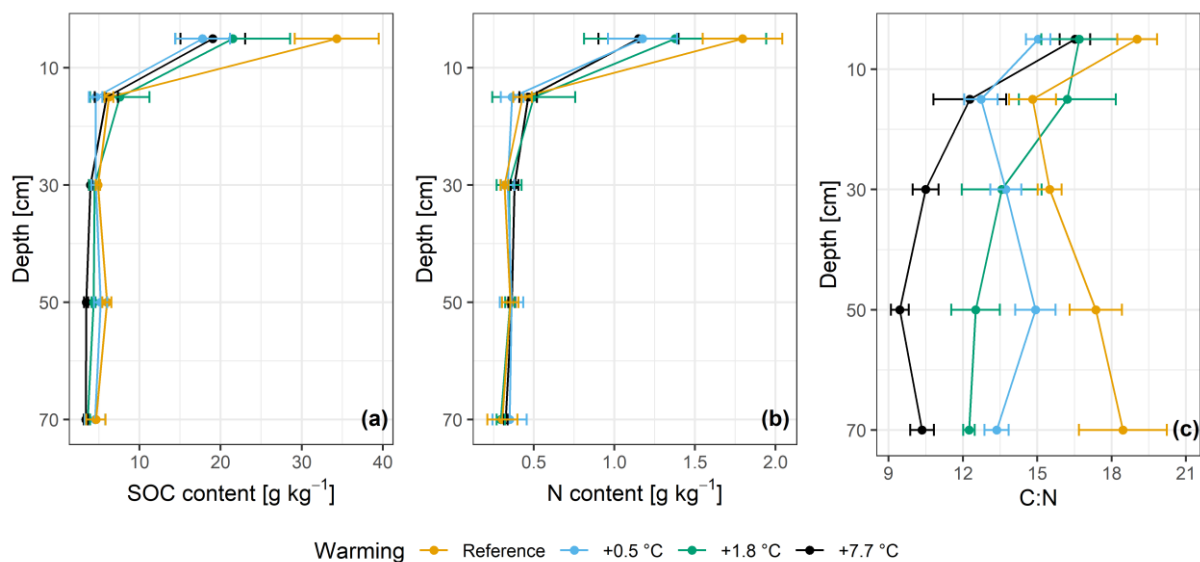
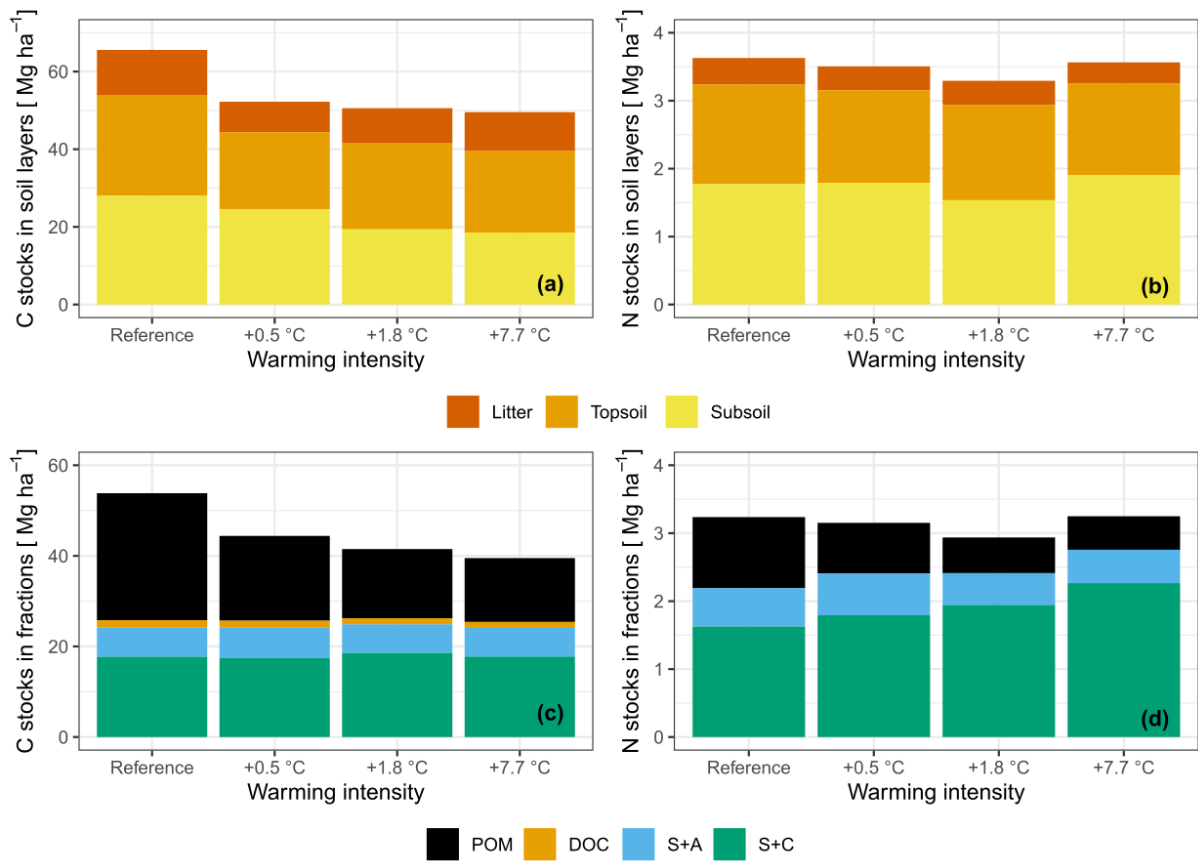
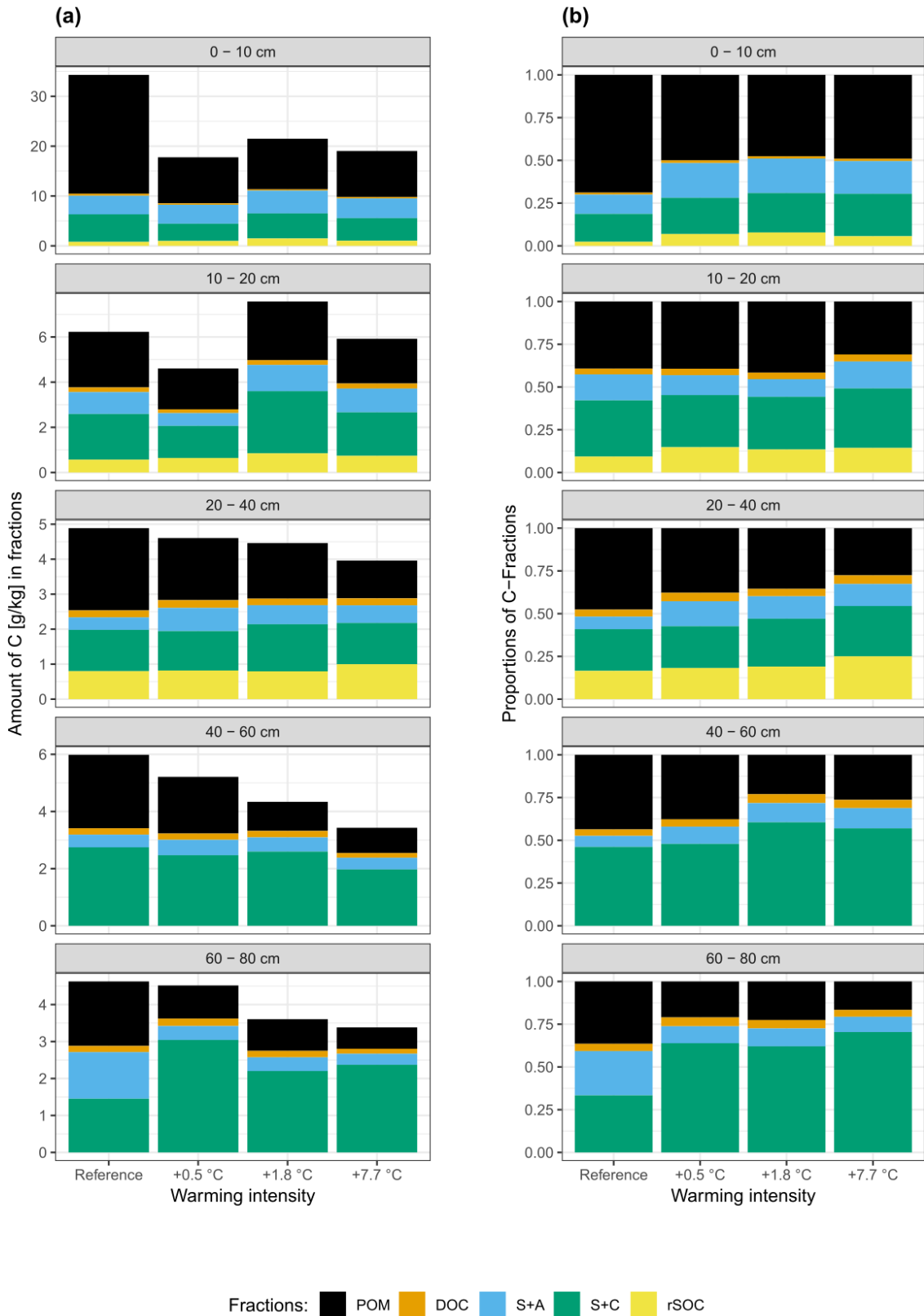


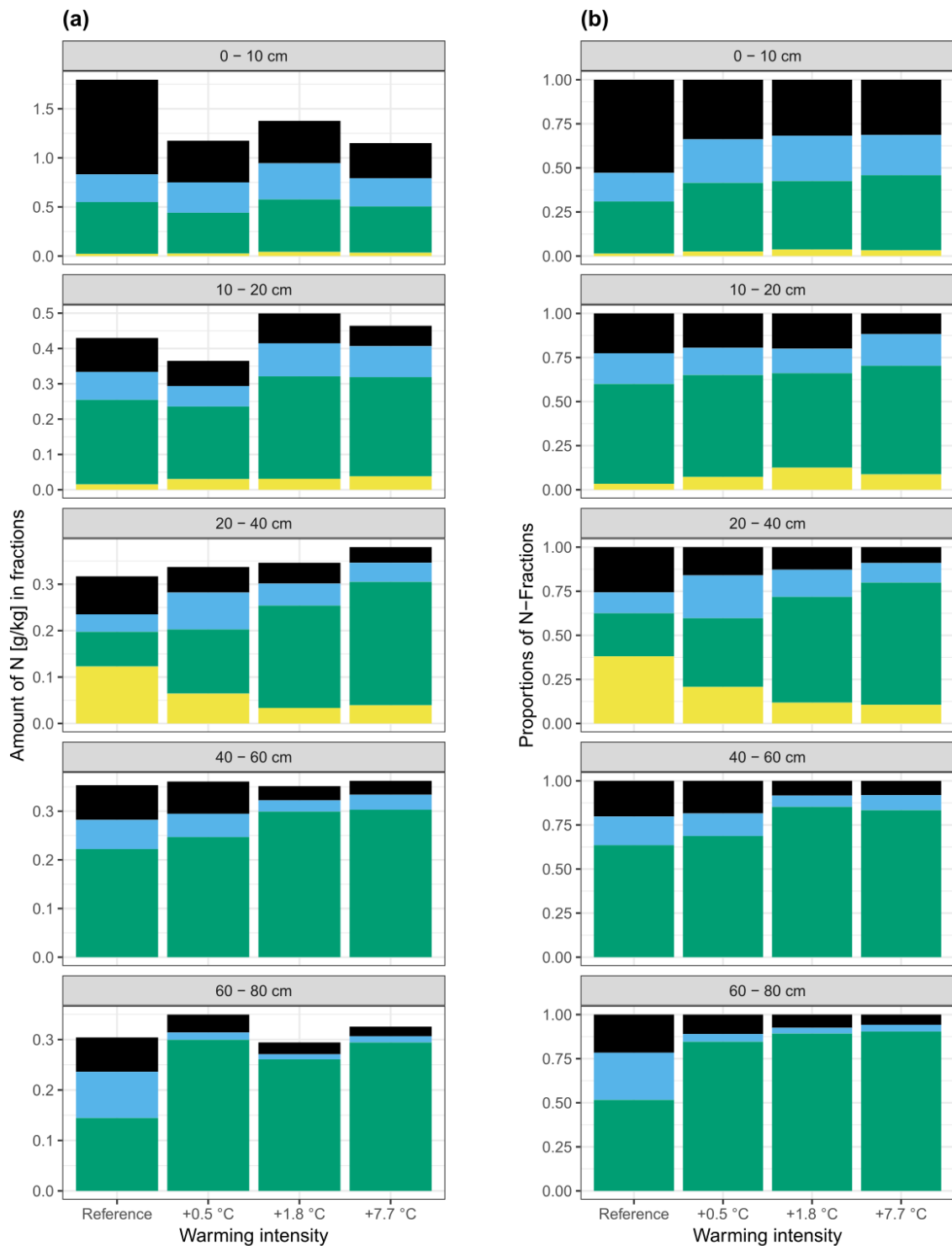
Figure 2.2: Depth profiles with mean (points) and standard error (horizontal bars) of (a) soil organic carbon (SOC) content, (b) nitrogen (N) and (c) C:N ratio



**Figure 2.3: (a) Contribution of litter layer, topsoil (0 – 20 cm) and subsoil (20 – 80 cm) C to total C stocks. (b) Contribution of litter layer, topsoil and subsoil N to total N stocks. All displayed stocks are corrected to the reference soil mass of topsoil and subsoil. (c) Contribution of the C fractions (DOC, dissolved organic matter; POM, particulate organic matter; S+A, sand and stable aggregates; S+C, silt and clay) to the total C stocks. (d) Contribution of the N fractions (POM, S+A and S+C) to total N stocks.**



**Figure 2.4: Bar plots of amount of C (a) and proportional share of C (b) in particulate organic matter (POM), dissolved organic carbon (DOC), sand and stable aggregates (S+A), silt and clay (S+C) and resistant organic carbon (rSOC) in relation to soil warming**



**Figure 2.5: Bar plots of amount of N (a) and proportional share of N (b) in particulate organic matter (POM), sand and stable aggregates (S+A), silt and clay (S+C) and the resistant organic carbon fraction (rSN) in relation to soil warming.**

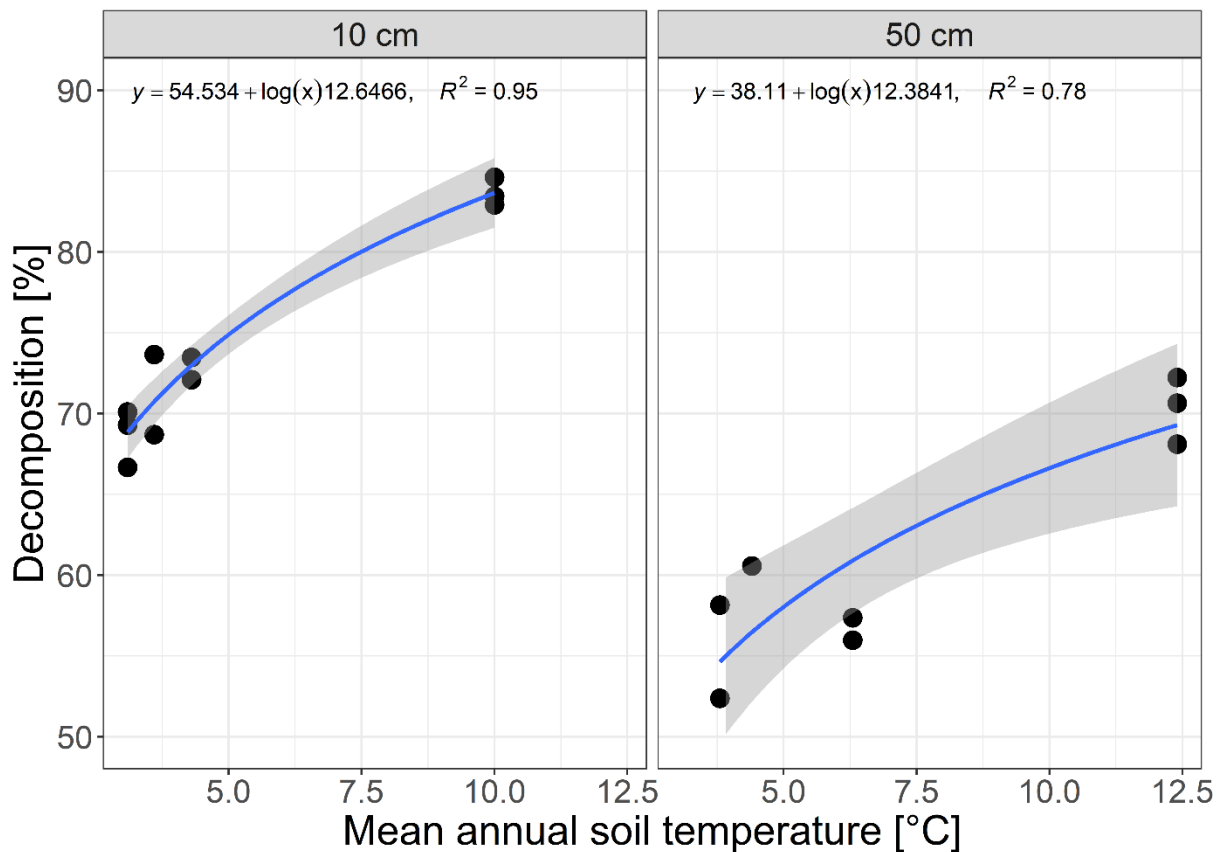


Figure 2.6: Decomposition of litter (green tea) at 10 and 50 cm depths after being buried for 1 year.

## 2.4. Discussion

### 2.4.1. Response of bulk SOM

Bulk SOC stocks showed a long-term loss of approximately  $1.86 \text{ Mg ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$ , or 27%, with a maximum warming intensity of  $7.7^{\circ}\text{C}$ . This total loss was considerably lower than the predictions of Crowther et al. (2016), who reported losses of up to  $30 \text{ Mg ha}^{-1}$  under conservative climate change scenarios by 2050. These losses were the result of linear extrapolation of data from mostly short-term warming experiments. But this approach may overestimate what actually occurs over the long term (van Gestel et al. 2018, Walker et al. 2020). Studies with a relatively long time span of observation (e.g. Poeplau et al. 2020, Melillo et al. 2002, Melillo et al. 2017) reported results that are consistent with our findings. Melillo et al. (2017) observed a long-term pattern of rapid SOC loss at the start of soil warming but reaching a new equilibrium between SOC mineralization

and build-up later in the experiment. They reported that the largest loss of bulk SOC occurred within the first 10 years after the onset of heating. It has been suggested that continued heating might lead to a decrease in microbial biomass and changes in microbial growth and turnover without losing more SOC (Walker et al. 2018). Thus, the assumption that short-term warming responses can be extrapolated to longer time periods (Crowther et al. 2016) might not be valid (Walker et al. 2020). Our results are consistent with the observations of Melillo et al. (2017), because even after more than 100 years of warming, the SOC losses we observed were not greater than those observed in other studies. Furthermore, Poeplau et al. (2020) observed SOC losses between 3.6% and 4.5% °C<sup>-1</sup> in topsoil and subsoil after 10 years of warming, which is slightly higher than our observed whole-profile loss of 3% °C<sup>-1</sup> after at least 100 years of warming. If these two subarctic forest ecosystems are comparable, then the results from the two studies would provide evidence that a new equilibrium is rapidly reached after several years of warming. But direct evidence for such response to warming is still limited. Knowledge of the temporal dynamics of SOC immediately after the onset of warming is necessary to correctly interpret the findings of in situ warming experiments.

The results of our study suggest that SOC throughout the soil profile was reduced by warming. Even if the loss in the subsoil was overestimated by calculations to correct for comparable soil masses, the results of this study indicate that subsoil SOC was strongly reduced by warming. This is because firstly, the C fractions showed a strong change in their relative shares in the deepest soil horizon, which cannot be explained by correction for soil mass. Secondly, the RR values of SOC contents, which are independent of soil mass correction, indicate there was a warming-induced response in both topsoil and subsoil C. The SOC losses we observed in the subsoil highlight why whole-profile studies are important for determining the overall climate C cycle feedback (Crowther et al. 2016, Hicks Pries et al. 2017, Liebmann et al. 2020).

The narrowing C:N ratio revealed that a change in chemical composition of SOM occurred with warming. This can be interpreted as a shift from more fresh plant-derived OM with a wide C:N ratio (Ferlian et al. 2017), to a stronger microbial influence on OM, which usually results in a

narrower C:N ratio (Hassink 1994). Such a shift in SOM quality towards more microbial-derived compounds after whole-profile soil warming was recently also observed by Ofiti et al. (2021), who used molecular biomarkers to characterize the changes in SOM quality after warming. This interpretation is supported by the relative gains of the mineral fractions, since much of the C stabilized in those fractions probably consist of microbial residues (Hassink 1994, Ludwig et al. 2015). The increasing differences of the C:N ratio with depth and warming across plots could indicate that less fresh plant-derived organic matter reaches the subsoil in the warmer plots, which would also be in line with the findings of Ofiti et al. (2021). This may be due to: (i) greater evaporation at the surface of warmer soils and thus less leaching of fresh DOC from the topsoil; (ii) lower root growth into deeper soil layers, due to greater availability of N in the topsoil in warmer plots; or (iii) changes in turnover of fresh OM. To understand these processes in detail, a closer look at soil water content, root abundance and net primary production would be necessary. It is noteworthy that the soil N stock was not affected by warming; this indicates that increased decomposition of organic matter did not lead to N loss from the soil. This in turn suggests more efficient cycling of N in warmer soils. Our hypothesis regarding SOM losses in both topsoil and subsoil due to warming-induced acceleration of decomposition was confirmed, but only for C, because bulk N stocks were unaltered with warming.

The lack of any loss in N stocks as result of soil warming in this study contradict the findings of Li et al. (2018), who observed considerable losses of N after soil warming by 5°C. But their study was conducted in a subtropical ecosystem with a monsoon climate, so the question arises as to whether more N leaching would occur in warmer and wetter conditions than in the continental subarctic ecosystem studied here. Our findings are consistent with those of Melillo et al. (2002), who observed increased N mineralization after warming by 5°C for 10 years, but with no leaching or gaseous loss of N. Less leaching of N and more N in the soil profile could have fostered greater net primary productivity, which might have compensated for C losses, for example, by increased root-derived C input. Indeed, in the warmest plot (W1), more herbaceous ground vegetation was observed than in the reference plot, which is indicative of a change in ecosystem productivity. This



would however stand in contrast to the observation of increased silt and clay-associated N and reduced POM-N, which makes it more likely that microbes were more competitive for the increased available N than plants.

#### **2.4.2. Response of different soil organic matter fractions**

We found a response to long-term warming by the different SOM fractions to be in the following order: POM > bulk soil > DOC > S+A > SC-rSOC > rSOC. We ascribe the differences among the fractions to differences in accessibility (location in the soil matrix) and chemical composition of the various SOM fractions. This is in agreement with previous studies in a naturally warmed subarctic spruce forest (Poeplau et al. 2020) and matches the observed responses to land use change (Poeplau and Don 2013). The fact that detected SOC losses can be almost entirely assigned to losses in the POM fraction confirms that this unprotected pool of SOM is highly vulnerable to environmental change (Del Galdo et al. 2003, Lajtha et al. 2014). The amount of mineral-associated SOC (i.e., that in the S+A, S+C and rSOC fractions) was the same in all soils along the warming gradient. This is in contrast to the findings reported in a similar geothermal warming experiment in Iceland, where SOC in the S+A fraction, as well as aggregates, declined strongly with warming; in this study the silt and clay-associated SOC was lost at a similar rate as bulk SOC (Poeplau et al. 2020, 2016). However, this does not imply that those fractions were not affected by warming in the present study. It is noteworthy that we observed a strong accumulation of N in the S+C fraction because while POM lost 0.55 Mg N ha<sup>-1</sup> (-52%) and S+A lost 0.07 Mg N ha<sup>-1</sup> (-12.5%), S+C was enriched by 0.8 Mg ha<sup>-1</sup> (+60%) in soils along the warming gradient. The microbial turnover pathway is suggested to be a main pathway of SOC stabilization and formation of mineral-associated organic matter (Cotrufo et al. 2019, Sokol et al. 2019). It is also likely that, in addition to increased turnover of POM and N availability, microbial growth and turnover were enhanced (Walker et al. 2018). This may have finally led to an increased flux of microbial-derived organic matter to the S+C fraction, potentially compensating for losses or reduced inputs of plant-derived organic matter. In a recent review, Angst et al. (2021) found a positive correlation of the amino sugar content in mineral-associated organic matter and mean annual temperature, which

might support this accumulation. An alternative mechanism for the accumulation of N in S+C could be adsorption of ammonium, particularly to clay minerals following increased N mineralization (Nieder et al. 2011). Few studies have focussed on the impact of warming on N processes in soil. Ineson et al. (1998) found no significant effect of heating on N leaching in a mountainous ecosystem under a tundra climate. They concluded that any warming-induced increase of decomposition is compensated by an increased plant uptake of N. Rustad et al. (2001) summarized the results of studies on N mineralization after soil warming and found that warmer temperatures increased N mineralization, with subsequent microbial uptake and immobilization of the mineralized N. They concluded that these processes would eventually increase plant productivity and cause a shift of N between different pools, which is consistent with our results.

### **2.4.3. Potential litter decomposition**

The teabag experiment allowed us to directly quantify temperature effects on potential litter decomposition and thus microbial activity. Mass loss of the teabags was accurately described by a logarithmic model. The temperature-dependent pattern of litter decomposition was very similar at 10 and 50 cm depths, as shown by the regression model, while the teabags at 50 cm showed lower mass losses than teabags at 10 cm. Other whole-profile studies (Hicks Pries et al. 2017, Nottingham et al. 2020) also observed that subsoils have a similar temperature sensitivity than topsoils, supporting our findings.

The lower mass loss at 50 cm depth indicates that microbial communities in the subsoil responded similar to warming as those in the topsoil, but were less abundant and/or less active, possibly because of lower substrate availability. The results of this short-term (1 year) incubation experiment with green tea as a relatively labile substrate revealed a similar response to that of the total, whole-profile SOC stock after centuries of warming. The mass loss of green tea in the warmest plot was 15% higher than in the reference plot, and total SOC was reduced by approximately 25% in the most extreme warming intensity as compared with the reference. The similarity of these values indicates that long-term SOC losses were most likely driven by increased microbial activity and that potential shifts in organic matter inputs did not compensate much of

these respiratory losses. However, this might also be related to the experimental limitation of this study, namely that only the soil, not the whole ecosystem, was warmed, which could have additional effects on the aboveground part of the ecosystem. We conclude that the temperature effect on mass loss of tea adds support to our hypothesis that SOM losses are driven by warming-induced acceleration of microbial activity.

#### **2.4.4. Implications for SOC dynamics under climate change and further research**

With regard to understanding climate change effects on ecosystem C fluxes, an experimental shortcoming of this and similar studies is that only the soil, and not the aboveground part of the ecosystem, was warmed. The response of net primary productivity to warming and CO<sub>2</sub> fertilization, especially in combination with potentially increased N availability, might compensate for the C losses from the soil (Song et al. 2019) to some extent. This was not the case in our study, since relative SOC losses appear to be consistent with potential litter decomposition rates as shown by mass losses in tea litter. Furthermore, this study also highlights the experimental difficulties in detecting warming effects. While the warming effects on SOM stocks and fractions were consistent across the warming gradient, hardly any statistically significant differences were detected, even at a warming intensity of 7.7°C, due to high intra-plot variability. This implies that large sample sizes and strong warming treatments are necessary in order to detect significant changes (Poeplau et al. 2016, Schöning et al. 2006). Nevertheless, the use of natural soil warming gradients presents a unique opportunity to study processes in an undisturbed natural setting. The Pacific Climate Impacts Consortium (PCIC) projects a rise in annual mean temperature of between 1.8 and 2.1°C (depending on the emission scenario) for the period 2021 – 2050 and of 2.9 – 4.2°C for the period 2051 – 2080, with the strongest warming during winter, resulting in a shorter frost period and less snow cover. Precipitation is expected to rise by 8% – 9% between 2021 and 2050, and by 18% – 20% between 2051 and 2080 (PCIC 2014). Using the observed C loss of 1.86 Mg ha<sup>-1</sup> °C<sup>-1</sup>, the projected rise in mean annual temperature in the study area could lead to a SOC loss of 3.3 – 3.9 Mg ha<sup>-1</sup> or 5.4 – 7.8 Mg ha<sup>-1</sup> respectively, depending on the emission scenario. The loss of SOC in the form of CO<sub>2</sub> contributes not only to

climate change, but also decreases overall soil quality and productivity (Larsbo et al. 2016). A possible structural change of the soil such as a greater decay of stable aggregates (Poepflau et al. 2020) might affect soil water flow and solute transport, which play an important role in soil respiration and plant growth, especially in semi-arid areas such as the Yukon Territory. The questions of structural changes in the soil should be studied in more detail in undisturbed soil columns. The recycling of N may change the SOM chemical composition, which in turn could affect microbial community composition and metabolism (Manzoni 2017, Takriti et al. 2018). Recently, Ofiti et al. 2021 also found that SOM in warmed soil was altered in its chemical composition and comprised more microbial-derived compounds. They related this to reduced plant-derived inputs and increased microbial decomposition of organic matter. We assume that this is similar at our study site. However, insights on warming-induced changes in plant inputs and organic matter quality will be necessary to fully understand the opposing trends in C and N stocks we observed. Nevertheless, the use of natural soil warming gradients presents a unique opportunity to study processes in an undisturbed natural setting and are therefore valuable for improving our understanding of ecosystem responses to warming.

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## 2.6. Data availability

All data used for this study, including an R-script to reproduce the presented results, can be found at <https://doi.org/10.5281/zenodo.4954979>

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### 3. Subarctic soil carbon losses after deforestation for agriculture depend on permafrost abundance

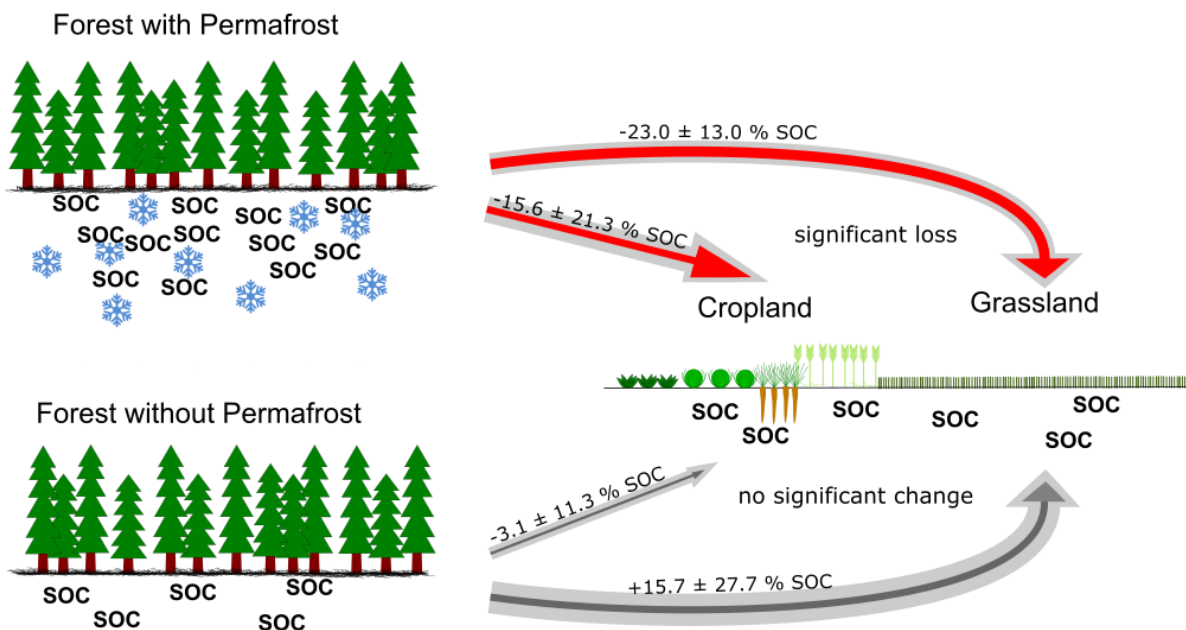
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Graphical abstract 2: Subarctic soil carbon losses after deforestation for agriculture depend on permafrost abundance



### 3.0. Abstract

The northern circumpolar permafrost region is experiencing considerable warming due to climate change, which is allowing agricultural production to expand into regions of discontinuous and continuous permafrost. The conversion of forests to arable land might further enhance permafrost thaw and affect soil organic carbon (SOC) that had previously been protected by frozen ground. The interactive effect of permafrost abundance and deforestation on SOC stocks has hardly been studied. In this study, soils were sampled on 18 farms across the Yukon on permafrost and non-permafrost soils to quantify the impact of land-use change from forest to cropland and grassland on SOC stocks. Furthermore, the soils were physically and chemically fractionated to assess the impact of land-use change on different functional pools of SOC. On average, permafrost-affected forest soils lost  $15.6 \pm 21.3\%$  of SOC when converted to cropland and  $23.0 \pm 13.0\%$  when converted to grassland. No permafrost was detected in the deforested soils, indicating that land-use change strongly enhanced warming and subsequent thawing. In contrast, the change in SOC at sites without permafrost was not significant but had a slight tendency to be positive. SOC stocks were generally lower at sites without permafrost under forest. Furthermore, land-use change increased mineral-associated SOC, while the fate of particulate organic matter (POM) after land-use change depended on permafrost occurrence. Permafrost soils showed significant POM losses after land-use change, while grassland sites without permafrost gained POM in the topsoil. The results showed that the fate of SOC after land-use change greatly depended on the abundance of permafrost in the pristine forest, which was driven by climatic conditions more than by soil properties. It can be concluded that in regions of discontinuous permafrost in particular, initial conditions in forest soils should be considered before deforestation to minimise its climate impact.

### 3.1. Introduction

With the increase in temperatures linked to climate change, agriculture is expected to shift poleward (Tchebakova et al. 2011, Franke et al. 2021). The cold and dry climate with a short vegetation period and widespread permanently frozen soils has hampered the development of a strong agricultural sector in the subarctic, leaving wide areas of subarctic forests so far untouched. However, especially in regions with sporadic to discontinuous permafrost, agricultural development might become more likely in the near future, although the environmental impacts of this are highly uncertain (Poeplau et al. 2019). Within the global carbon (C) cycle, soils of the northern permafrost region are very important due to the large amounts of preserved C they contain (Dutta et al. 2006, Tarnocai et al. 2009). The permafrost has protected soil organic matter from microbial breakdown since the last ice age (Dutta et al. 2006). Climate change is predicted to be most pronounced at high latitudes, where stronger warming than the global average is expected (Pepin et al. 2015), inevitably leading to the thawing of permafrost (Biskaborn et al. 2019) and a climate-carbon feedback (Davidson and Janssens 2006, Heimann and Reichstein 2008). Furthermore, deforestation promotes permafrost thaw by changing the microclimate because vegetation and the litter layer in natural forests act as insulating layers between the atmosphere and the soil. After deforestation, forced soil warming in summer can enhance permafrost thaw (Runyan et al. 2012). Therefore, land-use change from forest to agricultural land in the subarctic may accelerate the thawing of permafrost.

Globally, across ecosystems, conversion of forests to agricultural land leads to the depletion of soil organic carbon (SOC), with the highest losses per area in regions with high SOC stocks (Guo and Gifford 2002, Smith 2008). Moreover, conversion of forest to cropland has mostly been observed to decrease SOC stocks (Deng et al. 2016, Guo and Gifford 2002, Grünzweig et al. 2015, Poeplau et al. 2011), while conversion of forest to grassland has been observed to increase or not change SOC stocks (Deng et al. 2016, Guo and Gifford 2002). Specifically at high latitudes, there is some empirical evidence for SOC losses after conversion of forests to grassland (Grünzweig et al. 2004), which might be related to subsequent permafrost thaw. In regions of discontinuous permafrost,

only a certain proportion of the soil under native vegetation is affected by shallow permafrost. It has been suggested, that such initial conditions might strongly influence the direction and magnitude of SOC stock change after deforestation (Grünzweig et al. 2015). However, systematic and comprehensive studies on the interactive effect of permafrost abundance and land-use change on SOC stocks are lacking. Increased net primary productivity (NPP) following land-use change may enhance the input of C into the soil (Köchy et al. 2015), as microclimate changes after deforestation and the fertilisation of agricultural soils encourage plant growth. In contrast, permafrost loss as a consequence of a changed microclimate (Murton 2021) may reduce SOC stocks at greater levels than can be offset by increased NPP.

SOC is a complex matter, consisting of many compounds with different chemical and physical properties. It is crucial to understand how these compounds react to environmental changes because positive and negative feedbacks between SOC and environment can reinforce or buffer such changes (Lavalée et al. 2020). A wide range of studies have evaluated the impact of either land-use change (Guimarães et al. 2013, Poeplau and Don 2013, Wei et al. 2014) or permafrost-thaw (Schuur et al. 2015, Xu et al. 2009) on SOC stocks and fractions. However, little is known about the interactions between land-use change and permafrost loss since many studies on permafrost focus on pristine ecosystems, free of direct anthropogenic impacts. Permafrost soils store large proportions of SOC in various forms of particulate organic matter (POM) (Höfle et al. 2013, Xu et al. 2009). POM is plant-derived organic matter with a lower density and greater susceptibility to microbial breakdown than mineral-associated organic matter (Lützow et al. 2007). Due to the low temperatures and often wet and anoxic conditions in the soil, the labile POM is well protected against microbial breakdown, but is quickly decomposed once the soil has been thawed (Ping et al. 2015). Effects of land-use change on SOC can vary greatly between fractions. Poeplau and Don (2013) observed that POM is most sensitive to land-use change, compared with total SOC and other SOC fractions. Accordingly, mineral-associated SOC fractions, such as the fraction attached to silt and clay particles, appear to be less sensitive to land-use change than total SOC. It was therefore hypothesised that the remaining SOC under converted land consists of

relatively more silt- and clay-attached SOC, as POM is mostly removed by deforestation or quickly decomposed after the introduction of the new land use and loss of permafrost.

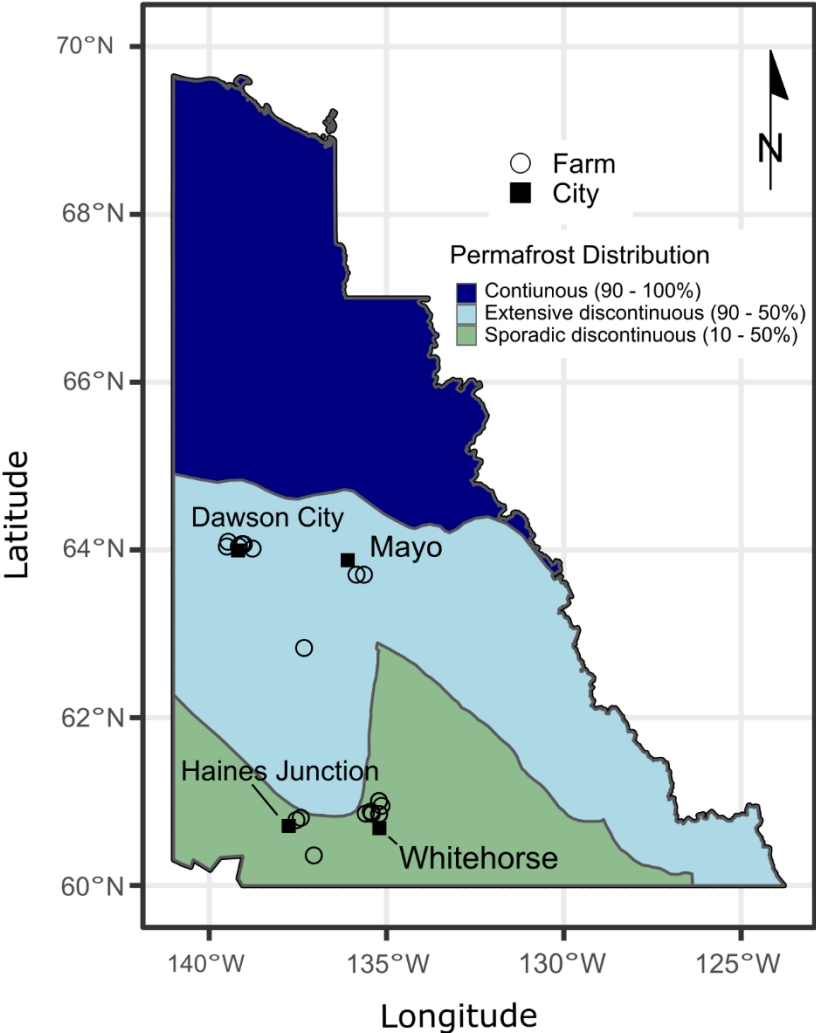
The aim of this study was to investigate the effect of deforestation on SOC stocks and fractions in the subarctic and how the presence of shallow permafrost drives SOC dynamics after land-use change. It is important to understand whether the abundance of permafrost plays a significant role in the response of SOC to land-use change in order to inform land-use strategies as well as earth system models. Based on the scarce available literature on permafrost agriculture, it was hypothesised that: i) land-use change leads to greater SOC losses in permafrost soils than in soils that are not affected by permafrost, ii) initial losses of SOC due to deforestation might be offset in the long run and iii) SOC under converted land consists of relatively more carbon stored in the fine mineral fraction than SOC under native forest.

## 3.2. Material and methods

### 3.2.1. Research area and farms

To test these hypotheses, the Yukon Territory in northwest Canada was chosen as a study area that is typical for land-use change in the subarctic. Yukon is located at the transition zone between continuous and discontinuous permafrost and is greatly affected by climate change (IPCC 2013). Due to the gold rush at the end of the 19<sup>th</sup> century, the Yukon has some exceptionally old farms at this latitude in North America, while a young agricultural sector is also expanding due to growing demand for locally produced food (Yukon Agriculture Branch 2020). Therefore, this area provides unique conditions for comparing land-use change on permafrost (here defined as soils that have detectable ice in the upper 80 cm of the soil profile during sampling in midsummer) and non-permafrost soils. The existence of both old (>100 years) and fairly new (<30 years) farms allows land-use change effects to be assessed in a quasi-chronosequential, paired-plot approach (Poeplau et al. 2011). Most farms in the Yukon are located along river banks, therefore there are few topographic or pedogenetic differences between the sampling points. In July of 2019, 18 farms located between the cities of Whitehorse and Dawson were selected for sampling (Figure 3.1). The

farms' age (i.e. time since the forest was cleared), management and size cover a broad range of Yukon's agricultural sector. Croplands were small fields with vegetables, greens and herbs grown for local markets. Grasslands were used as pasture for livestock grazing (cattle, horses) or meadows for hay production. The common practice for preparing the land for agriculture was to cut down trees, pile up stumps and roots, and burn it all. Irrigation and application of locally produced (on-farm and at nearby farms) organic fertiliser (compost and manure) were common practices at most sites, with mineral fertiliser applied in only a few cases. Croplands were tilled occasionally using a rototiller to a depth of between 10 and 30 cm (Table S2.1).



**Figure 3.1: Yukon Territory: Overview showing sample farms (circles), major cities (squares) and permafrost occurrence (colours) (modified from Heginbottom et al. 1995)**

On each farm, a paired plot design was established for sampling. Each pair of plots consisted of a forest as the reference and an adjacent cropland or grassland site or both. Forests were usually mixed wood forests of the boreal cordillera ecoregion with black (*Picea mariana*) and white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*) (Smith et al. 2004). The shares of individual species were not determined at each farm, but the dominating tree type has been recorded (Table S2.1). For plot selection, an auger-based pre-assessment of the soil was undertaken, following the advice of the farmers which area of the farms might be most suitable for comparative sampling. To ensure comparability between forest and agricultural land, the focus of the pre-assessment was on soil texture and visible properties. Furthermore, the plots were selected within a maximum distance between forest and agricultural land of about 500 m, and in many cases the forest was directly adjacent to the agricultural field, making distances between the plots <50 m. The third criterion for plot selection was a similar elevation and flat terrain at both forest and agricultural land to avoid effects of the relief, which could potentially lead to geomorphological related differences in SOC (Schiedung et al. 2022). At each plot, a slide hammer-driven soil corer with a diameter of 7 cm and a sample length of 20 cm was used to sample five soil cores to a maximum depth of 80 cm below the surface of the mineral soil (Figure 3.2). The soil cores were divided into five increments: 0-10 cm, 10-20 cm, 20-40 cm, 40-60 cm and 60-80 cm. Additionally, the litter layer of the forest floor was sampled using a metal ring 10 cm in diameter. In the centre of every forest plot, a soil profile was dug to a depth of 80 cm, or as deep as possible if the permafrost or bedrock was at a shallower depth. Despite the fact that digging a soil profile to 80 cm was not possible at every site, sampling with the soil corer could be done down to 80 cm at every site, except for NB, where the bedrock was hit at 50 cm. The permafrost depth at the date of sampling was determined visually (abundance of visible or tangible ice) in the soil pit. At 11 out of the 18 sites, permafrost was found in the soil cores of the forest, with an average active layer depth of 50 cm. Seven out of the 18 sites had no permafrost within the first 80 cm in the forest. The agricultural land plots generally had no permafrost within the uppermost 80 cm, which was a strong indicator that land-use change encouraged the

deepening of the active layer. Further indicators of permafrost loss upon land-use change, such as thermokarst, have been observed at one particular site. However, due to the relatively low ice content of the permafrost in this semiarid area, cryogenic soil or landscape features were scarce. At sites with permafrost, six grassland and nine cropland plots were sampled. At sites without permafrost, a total of six grassland and four cropland plots were sampled. A detailed overview with general site parameters can be found in Table 3.1. Management information regarding clearing, tilling, fertilisation, irrigation and crop rotation (Table S2.1) was assessed by means of a short questionnaire, which was completed by 14 of the 18 farmers.

**Table 3.1: General site parameters of the sampled sites: land use, latitude, longitude, elevation, mean annual precipitation, mean annual temperature, years since land-use change, texture and pH (H<sub>2</sub>O). Mean annual precipitation, mean annual temperature and cumulative degree days were obtained from Climate Data Canada (2021)**

Site	Land use	Latitude [°N]	Longitude [°E]	Elevation [m.a.s.l.]	Mean annual precipitation [mm]	Mean annual temperature [°C]	Cumulative degree days > 0°C	Years since LUC (in 2019)	Texture: sand/silt/clay [g/kg]	pH <sub>H<sub>2</sub>O</sub>
Sites with permafrost										
DR	Grassland	64.01164	-138.766494	427	354	-3.2	1887	34	Forest: 442/467/91 Grassland: 453/464/84	5.45 6.93
DW	Grassland	60.784162	-137.534659	637	343	-0.7	1804	9	Forest: 68/642/290 Grassland: 49/573/379	7.94 8.17
KK	Cropland	64.036097	-139.492003	347	363	-3.5	1870	119	Forest: 125/776/99 Cropland: 233/684/83	7.68 7.75
KL	Cropland	64.064224	-139.067374	378	361	-3.4	1879	21	Forest: 418/491/91 Cropland: 338/555/107	6.04 6.24
MA	Grassland	60.364461	-137.045507	680	433	-0.3	1700	60	Forest: 171/623/206 Grassland: 145/646/209	6.24 6.90
MG		60.952879	-135.143858	628	308	+0.1	1996	32	Forest: 289/535/176 Cropland: 198/621/181	8.53 8.89



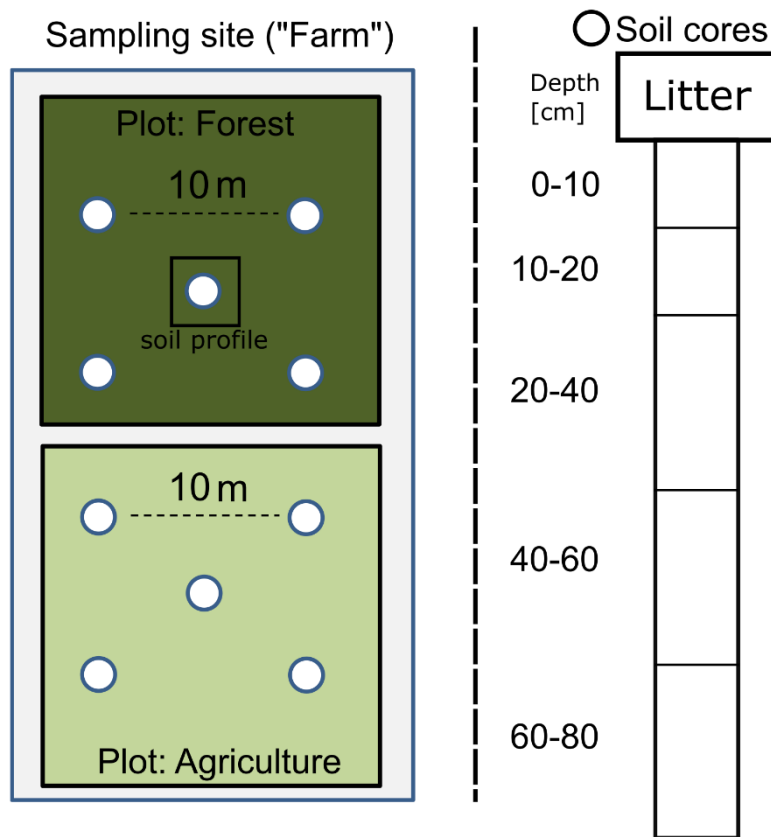
	Cropland and grassland								Grassland: 166/606/228	8.24
PC	Cropland and grassland	62.828496	-137.323740	461	337	-3.0	1807	Both 118	Forest: 44/782/174	7.70
									Cropland: 414/484/72	8.31
									Grassland: 62/793/145	8.59
RC	Cropland	60.811823	-	673	340	-0.5	1841	3	Forest: 69/546/385	7.52
			137.4105572						Cropland: 251/515/234	7.96
RF	Two croplands, different ages	60.855739	-135.209860	663	314	+0.2	1985	Old plot: 49 Young plot: 4	Forest: 431/513/56	7.15
									Old Cropland: 212/701/87	7.99
									Young Cropland: 364/574/62	7.71
SI	Cropland	64.092483	-139.458949	317	362	-3.5	1874	117	Forest: 43/816/141	8.07
									Cropland: 520/398/82	8.30
TH	Cropland and grassland	64.036959	-139.154052	361	361	-3.4	1879	Both 100	Forest: 557/346/97	6.81
									Cropland: 65/723/212	5.79
									Grassland: 320/573/107	7.19
Sites without permafrost										
CD		60.860362	-135.592933	646	315	-0.1	1909	43	Forest: 406/369/225	8.19

	Cropland								Cropland: 163/642/195	7.19
	and								Grassland: 174/598/228	8.77
	grassland									
EF	Grassland	60.833628	-135.438689	701	315	0.0	1949	26	Forest: 86/618/296	8.43
									Grassland: 81/702/217	8.44
EG	Grassland	60.859964	-135.411148	638	315	0.0	1949	23	Forest:	8.01
									465/486/49	
									Grassland:	8.32
									263/645/92	
GV	Cropland	61.009636	-	741	307	-0.2	1938	Both 26	Forest: 89/832/79	7.41
	and		1335.212049						Cropland: 97/807/96	7.70
	grassland								Grassland: 88/826/86	7.84
LR	Cropland	61.061670	-135.178039	635	307	-0.2	1938	10	Forest: 102/301/597	7.53
									Cropland: 109/313/578	7.90
NB	Grassland,	63.701581	-135.844904	599	367	-2.1	1978	38	Forest: 143/747/110	5.54
	only								Grassland: 105/728/167	6.59
	topsoil									
VE		64.062466	-139.016306	387	361	-3.4	1879	Cropland: 119	Forest: 473/418/109	6.22
								Grassland: 100	Cropland: 57/705/238	5.94

Cropland  
and  
grassland

---

Grassland: 100/672/228 6.11



**Figure 3.2: Sampling scheme. Five soil cores were sampled in each plot. The soil core consisted of five depth increments. The litter layer was also sampled with a metal ring (10 cm diameter)**

### 3.2.2. Laboratory analyses

#### 3.2.2.1. Sample preparation

Directly after sampling, soil was air-dried, weighed, sieved to  $\leq 2$  mm and weighed again to calculate the fine soil mass, stone and root content, and bulk density from the mass proportions and core volume. An aliquot of fine soil was dried at 105°C to correct for residual water content in the samples. All subsequent analyses were performed on the  $\leq 2$  mm sieved fine soil samples. Aliquots of the five field replicates of each plot and depth (n=1077) were pooled to a mixed sample (n=216). Carbon (C) and nitrogen (N) content were analysed in all samples (individual field replicates and mixed samples), while all the other analyses were performed on the mixed samples only.

### **3.2.2.2. Fractionation**

Fractionation was performed on mixed samples from the depth of 10-20 cm (referred to as topsoil) and from 40-60 cm (referred to as subsoil). The second depth increment was selected rather than the first increment due to the acknowledged difficulties in determining the exact border between litter layer and mineral soil in the forest soils. Soil carbon fractions were isolated according to the method of Zimmermann et al. (2007), modified by Poeplau et al. (2018). In brief, 30 g of the bulk soil was dispersed with an ultrasonic probe at 22 J and then wet-sieved with 2.2 l deionised water through a 63  $\mu\text{m}$  sieve in order to separate the coarse POM and sand and aggregate fractions (S+A) from the fine mineral fraction. After sieving, the fine fraction was centrifuged and the supernatant fluid was filtered through a 0.45  $\mu\text{m}$  filter and analysed for water-extractable carbon (here defined as DOC). The remaining silt and clay fraction (S+C) was dried until weight constancy at 50°C, and analysed for C and N content. From the S+C fraction, a 1 g aliquot was used to determine resistant soil organic carbon (rSOC) with a 6% sodium hypochlorite solution (NaOCl). In this step, the 1 g sample was stored in a 50 ml centrifuge tube that was filled to 45 ml with NaOCl. After shaking, the tubes were left open for 16 hours to ensure optimal oxidation and prevent the tubes from bursting due to gas produced by the ongoing oxidation process. Afterwards, the tubes were centrifuged, decanted, washed twice with deionised water and refilled with NaOCl. After three repetitions, the washed sample was dried at 50°C until weight constancy and the remaining material was analysed for C and N content.

The POM and S+A fraction was dried until weight constancy at 50°C. This fraction was then mixed with a sodium polytungstate solution, which was adjusted to a density of 1.8 g/cm<sup>3</sup>. After mixing and centrifuging, the POM floating on the sodium polytungstate was decanted, washed with deionised water, and dried again until weight constancy at 50°C. These samples were subsequently milled and analysed for C and N content. The same washing procedure was applied for the heavy, sinking fraction, which was considered to be the S+A fraction consisting of sand and stable aggregates.

### **3.2.2.3. Main soil parameters**

The C and N content was measured with an elemental analyser (LECO TruMac CN, St. Joseph, MI, USA). Dissolved organic carbon (DOC, one of the investigated fractions described below) was measured with a Dimatoc 2000 (Dimatec GmbH, Essen, Germany). To distinguish between total organic carbon (TOC) and total inorganic carbon (TIC), samples with  $\text{pH}_{\text{H}_2\text{O}} > 6.2$  were heated in a muffle furnace at  $440^\circ\text{C}$  prior to elemental analyses.

The pH was determined in accordance with ISO 10390: an aliquot of 10 g soil was used to measure pH in  $\text{H}_2\text{O}$  at a soil:water ratio of 1:5. The sample was shaken in a horizontal shaker for one hour and then measured with a potentiometric pH meter.

Soil texture was determined for the samples from the second depth increment (10-20 cm) according to DIN ISO 11277:2002-08, which is based on a combination of sieving and sedimentation of suspended particles according to Köhn (1929). The second depth increment was chosen in order to ensure comparability of the soil texture data with the results of the fractionation and to avoid a potential influence of the measurement by forest litter on top of the first depth increment.

Furthermore, soil phosphorus (P) was extracted from all the mixed samples from the first depth increment (0-10 cm) with the Olsen-P method (Olsen et al. 1954), and analysed via inductively coupled plasma optical emission spectroscopy (ICP-OES). The first depth increment was chosen in order to quantify the potential impacts of fertiliser application at the agricultural plots.

### **3.2.2.4. Calculation of soil organic carbon stocks**

Cumulative SOC stocks of each soil core (0-80 cm) were calculated using Eq. 1, with the total organic carbon content ( $\text{TOC}_i$  [g/kg]), the dry mass of the fine soil ( $\text{Mass}_i$  [g]), the volume of the soil core ( $\text{Volume}_i$  [ $\text{cm}^3$ ]) and the thickness ( $\text{Thickness}_i$  [cm]) of every depth increment  $i$ .

$$\text{SOC} [\text{Mg ha}^{-1}] = \sum_1^i \left( \frac{\text{TOC}_i}{1000} * \left( \frac{\text{Mass}_i}{\text{Volume}_i} * 100 * \text{Thickness}_i \right) \right) \quad \text{Eq. 1}$$

Changes in bulk density after land-use change made it necessary to apply a mass correction, as discussed in various studies (Ellert and Bettany 1995, Wendt and Hauser 2013, Rovira et al. 2015). The individual cropland and grassland soil cores were mass corrected with the mean of the forest soil cores (mineral soil, without the litter layer), as described in Rovira et al. (2015). First, the cumulative mineral fine soil (*MFS*) of the soil cores was calculated as described in Eq. 2 and then organic matter, as derived from the TOC and the van Bemmelen factor, was subtracted from the total fine soil (*FS* [ $\text{Mg ha}^{-1}$ ]).

$$MFS [\text{Mg ha}^{-1}] = \sum_1^i FS_i * (1 - (1.724 * TOC_i)) \quad \text{Eq. 2}$$

The reference *MFS* for every site was then calculated as the mean *MFS* of the five forest soil cores. Afterwards, *MFS* of the cropland and grassland plots was adjusted to the reference *MFS*, and SOC stocks were calculated on the basis of a linear relationship between *MFS* and SOC stocks. Changes in SOC stocks were assessed by calculating the absolute difference (in  $\text{Mg ha}^{-1}$ ) and the relative difference (Eq. 3) between agricultural land and forest, where  $SOC_{\text{new}}$  is the SOC stock of the cropland or grassland plot and  $SOC_{\text{forest}}$  is the SOC stock of the adjacent forest plot. Afterwards, litter C stocks were added to the SOC stocks of the mineral soil.

$$\Delta SOC [\%] = \frac{SOC_{\text{new}} - SOC_{\text{forest}}}{SOC_{\text{forest}}} * 100 \quad \text{Eq. 3}$$

In the exceptional cases of data gaps in bulk density, i.e. when not all five soil cores could be sampled entirely, the mean bulk density value of the remaining four soil cores were used for the missing soil sample. At the DW site it was not possible to sample the deepest depth increment with the correct bulk density in all five soil cores. There, a pedo-transfer function based on the carbon content and bulk density of the overlying depth increment was used to estimate the bulk density of the deepest depth increment.

### **3.2.2.5. Statistics**

In order to identify patterns in the dataset and between the different variables, an analysis of the most important correlations in the dataset was performed. The dataset consisted of variables with

different scale levels and non-linear relationships, therefore the conditions (continuous scales in linear relationship) for a Pearson product correlation were not fulfilled and Spearman's rank correlation was used instead.

To calculate the influence of permafrost, time since land-use change and type of land-use change on SOC, the dataset was split into groups with type of change ("forest to cropland" or "forest to grassland") and occurrence of permafrost ("yes" or "no"). To test the hypothesis that SOC stocks of the plots with new land use are significantly different from SOC stocks of the corresponding forest plot, two linear mixed-effects models were fitted using SOC stock as the dependent variable, land use and permafrost (one model for the cropland/forest pairs and one model for the grassland/forest pairs) as fixed effects, and the specific sites as random effects. After checking the assumptions for linear mixed-effects models (homoscedasticity, normality of the residuals and linearity of the dataset), log transformation of the SOC stocks was necessary to meet all the criteria. After performing the linear mixed-effects models, ANOVA and estimated marginal means with Tukey adjustment were used to obtain pairwise comparisons of all groups of the linear mixed-effects model (confidence level = 0.95).

The influence of time since land-use change on changes in SOC stocks was assessed using regression analysis. Based on the Akaike information criterion (AIC), a linear function or a second-degree polynomial was used. The regression was applied to cropland and grassland together, since the sample size of each group would have been too small for a meaningful regression. In the model,  $\Delta$ SOC was the dependent variable, time since conversion from forest served as the explanatory variable and permafrost occurrence was used as the grouping variable.

To assess the influence of land-use change and permafrost occurrence on SOC fractions, the dataset was split into four groups (cropland and grassland sites with and without permafrost) and tested for significant differences between forest and the new land use. For relative shares of the fractions (all fractions normalised to 100%) as well as absolute values (g C per kg soil), a Wilcoxon



rank sum test was used since the assumptions for parametric tests were not fulfilled and the subsets had only small sample sites.

All statistical analyses were conducted using R version 4.0.4 (R Core Team 2021) with the packages dplyr (Wickham et al. 2020), emmeans (Lenth 2021), ggplot2 (Wickham 2016), ggpubr (Kassambra 2020), ggthemes (Arnold 2021), lme4 (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). The level of significance for all statistical analyses was selected as  $\alpha = 0.05$ .

### 3.3. Results

#### 3.3.1. SOC stocks

Both cropland and grassland had significantly smaller SOC stocks than the adjacent forest when permafrost was present at 0-80 cm depth. When permafrost-affected forest soils were converted to croplands, the average losses were  $15.6 \pm 21.3\%$  or  $23.7 \pm 42.2 \text{ Mg ha}^{-1}$ . When converted to grasslands, the average losses amounted to  $23.0 \pm 13.0\%$  or  $40.9 \pm 23.0 \text{ Mg ha}^{-1}$ . Sites without permafrost in the forest plots showed no statistically significant change in SOC stocks upon conversion, with  $-3.1 \pm 11.3\%$  or  $2.4 \pm 14.0 \text{ Mg ha}^{-1}$  after conversion to cropland and  $15.7 \pm 27.7\%$  or  $15.0 \pm 20.6 \text{ Mg ha}^{-1}$  after conversion to grassland (Figure 3.3). Table 3.2 summarises the SOC stocks of the four observed land-use change classes: sites with permafrost had significantly higher mean SOC stocks in both forest and agricultural land than sites without permafrost. Overall, soils lost  $30.6 \pm 35.8 \text{ Mg ha}^{-1}$  ( $18.6 \pm 18.3\%$ ) SOC at sites with permafrost and gained  $10.0 \pm 18.5 \text{ Mg C ha}^{-1}$  ( $8.2 \pm 23.7\%$ ) at sites without permafrost after land-use change, with the latter not being statistically significant. Reductions of SOC stocks were mostly, but not exclusively, connected to reductions of the carbon content in the uppermost 30 cm of the mineral soil (Figure S3.2).

#### 3.3.2. Soil organic matter fractions

In order to assess the influence of land-use change and permafrost on SOC fractions, the dataset was split into four groups: 1) change to cropland at sites without permafrost, 2) change to cropland at sites with permafrost, 3) change to grassland at sites without permafrost, and 4) change to grassland at sites with permafrost. Each group contained the SOC fractions of the forest

samples and the samples of the new land use. Comparisons were made within each group between forest and new land use. The fractionation showed that land-use change had the strongest effects on POM and S+C. The proportional share of these fractions changed significantly with land-use change: at sites with permafrost, POM was significantly lower in cropland and grassland soils than in forest soils, while S+C increased significantly (Figure 3.4). However, except for permafrost-affected croplands, only fractions of the topsoil changed significantly. In absolute terms (Figure 3.5, Table S2.2), the topsoil of the agricultural plots (cropland and grassland) had more SOC stored in the S+C fractions than the forest, irrespective of permafrost occurrence. Topsoil POM of the permafrost-affected sites showed a strong dependency on the occurrence of permafrost in the forest, with large losses in both cropland and grassland. Due to high variability and relatively small sample sizes, statistically significant differences were only observed in grassland soils with and without permafrost and in cropland soils without permafrost. Overall, the share of rSOC and DOC was small in both absolute content and relative share of total SOC. Furthermore, due to inorganic carbon in some subsoils, it was not possible to determine reliable rSOC values at all sites, hence rSOC is not reported in the subsoil fractions.

### **3.3.3. Temporal dynamic and additional drivers of SOC change**

The temporal dynamic of differences in SOC stocks between forest and agricultural land was best described (i.e.  $p < 0.05$  and best AIC) by a second-order polynomial fit, but only in the case of relative changes at sites with permafrost (Figure 3.6). For sites without permafrost, as well as for absolute changes, no significance was found in any regression, hence no regression line is displayed. The fit showed that there was a large loss of SOC shortly after land-use change and a tendency for subsequent SOC replenishment. At sites without permafrost, agricultural land tended to have larger SOC stocks than the forest after 100 years. SOC losses at young sites without permafrost were small compared with sites with permafrost. In general, temporal trends were less clear than expected, which might be due to a relatively small sample size along the time axis and a lack of sites aged between 50 and 100 years.

Spearman's correlation coefficient (Figure 3.7) revealed distinct patterns in the dataset and delivered a broad overview of the most important site variables. SOC stocks of the forest soils were significantly correlated with geographical variables (longitude, latitude mean annual precipitation, mean annual temperature, frost days and cumulative degree days). There was no correlation between forest SOC stocks and the general soil parameters (soil texture, pH, Olsen-P), except for C:N ratio. The content of the C fractions (Fraction forest) correlated significantly negatively with the C fractions of the agricultural land ( $\Delta$ Fraction). The depth of permafrost was significantly correlated with the thickness of the A-horizon in the forest as well as with the C-stock of the litter layer. Overall, the correlation matrix suggested that climatic drivers were more important for SOC than soil properties.

**Table 3.2: Summary of SOC stocks (mineral soil and litter layer) and forest litter C stock under the different permafrost occurrences and land uses. Values are reported as mean  $\pm$  standard deviation**

Permafrost in forest	New land use	Forest mineral soil SOC stock [Mg ha <sup>-1</sup> ]	Forest litter C stock [Mg ha <sup>-1</sup> ]	Total SOC stock in forest [Mg ha <sup>-1</sup> ]	Total SOC stock in new land use [Mg ha <sup>-1</sup> ]	Farms sampled
No	Cropland	118.4 $\pm$ 79.6	13.3 $\pm$ 4.1	131.7 $\pm$ 80.9	134.1 $\pm$ 94.8	4
	Grassland	85.4 $\pm$ 70.8	13.6 $\pm$ 4.8	98.5 $\pm$ 70.2	113.5 $\pm$ 81.7	6
Yes	Cropland	144.1 $\pm$ 78.1	21.1 $\pm$ 8.0	163.8 $\pm$ 79.4	140.1 $\pm$ 78.6	9
	Grassland	171.9 $\pm$ 54.2	25.5 $\pm$ 8.6	194.2 $\pm$ 59.9	153.3 $\pm$ 67.9	6

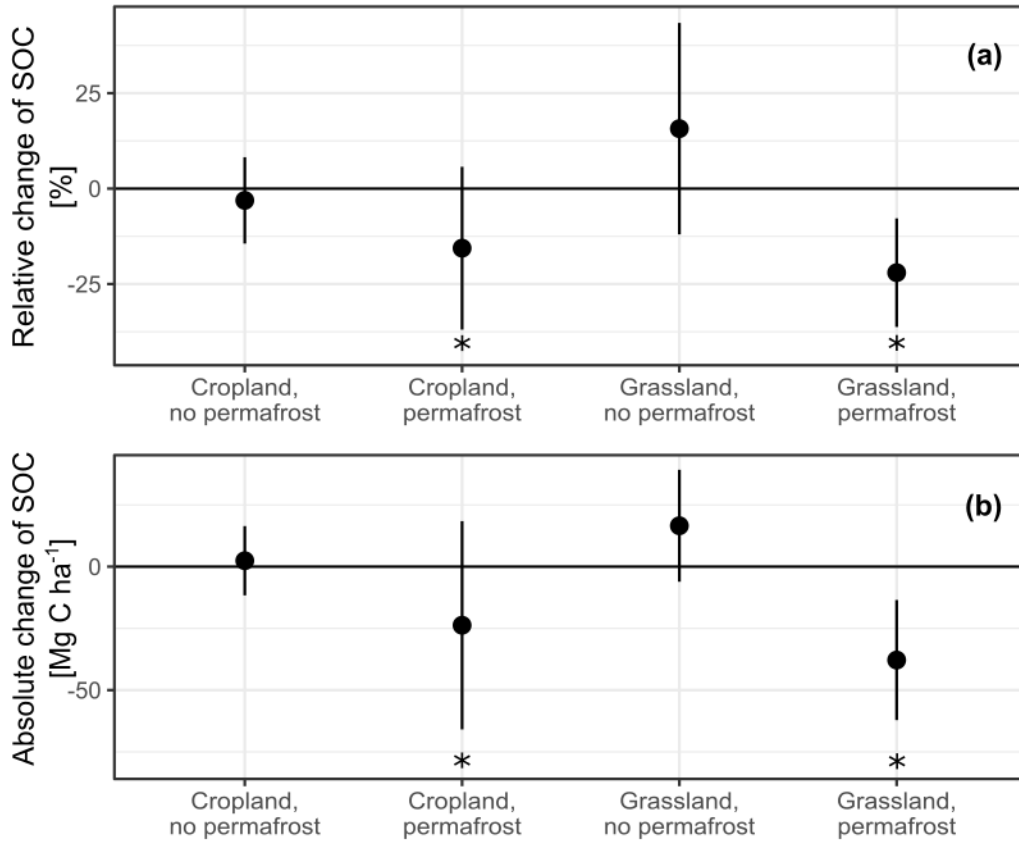
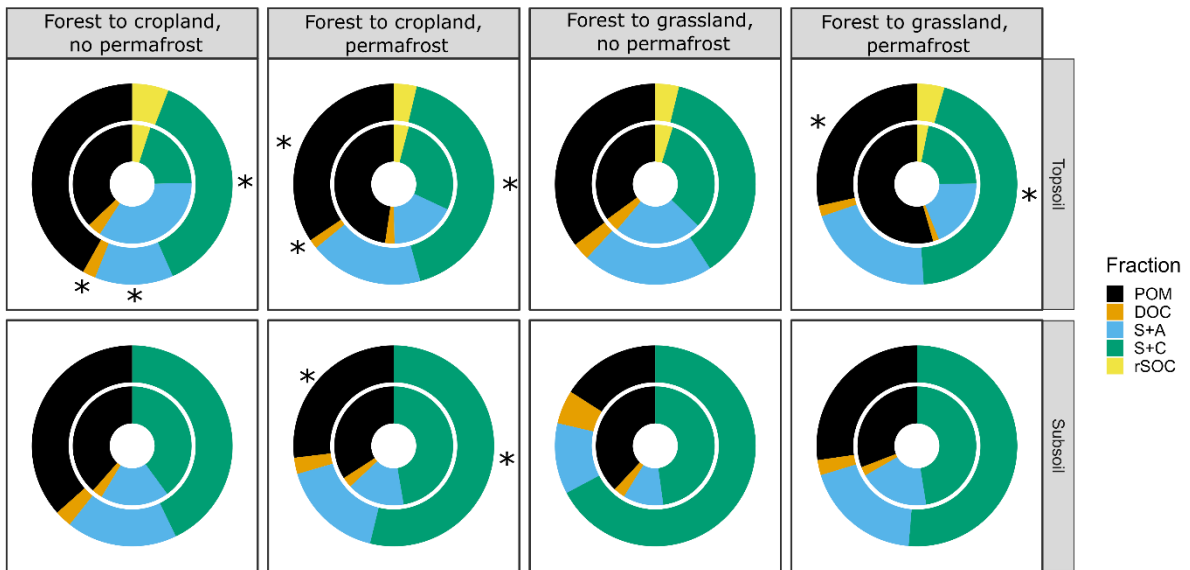


Figure 3.3: (a) Relative [%] and (b) absolute [Mg ha<sup>-1</sup>] changes in soil organic carbon (SOC) stocks under cropland and grassland, compared with forest with and without permafrost. Points indicate the mean change and error bars indicate the standard deviation of the change in SOC stocks. \* indicates whether the SOC stocks of the given land use class are significantly different ( $p < 0.05$ ) from the corresponding forest plots (zero line).



\* difference between forest and new land use statistically significant with  $p < 0.05$

Figure 3.4: Relative share of particulate organic matter (POM), dissolved organic carbon (DOC), sand and stable aggregates (S+A), silt and clay (S+C) and recalcitrant soil organic carbon (rSOC) in forests (inner circle) and

new land use (outer circle) at 10-20 cm (topsoil, upper row) and 40-60 cm (subsoil, lower row), differentiated by permafrost occurrence and land use (columns)

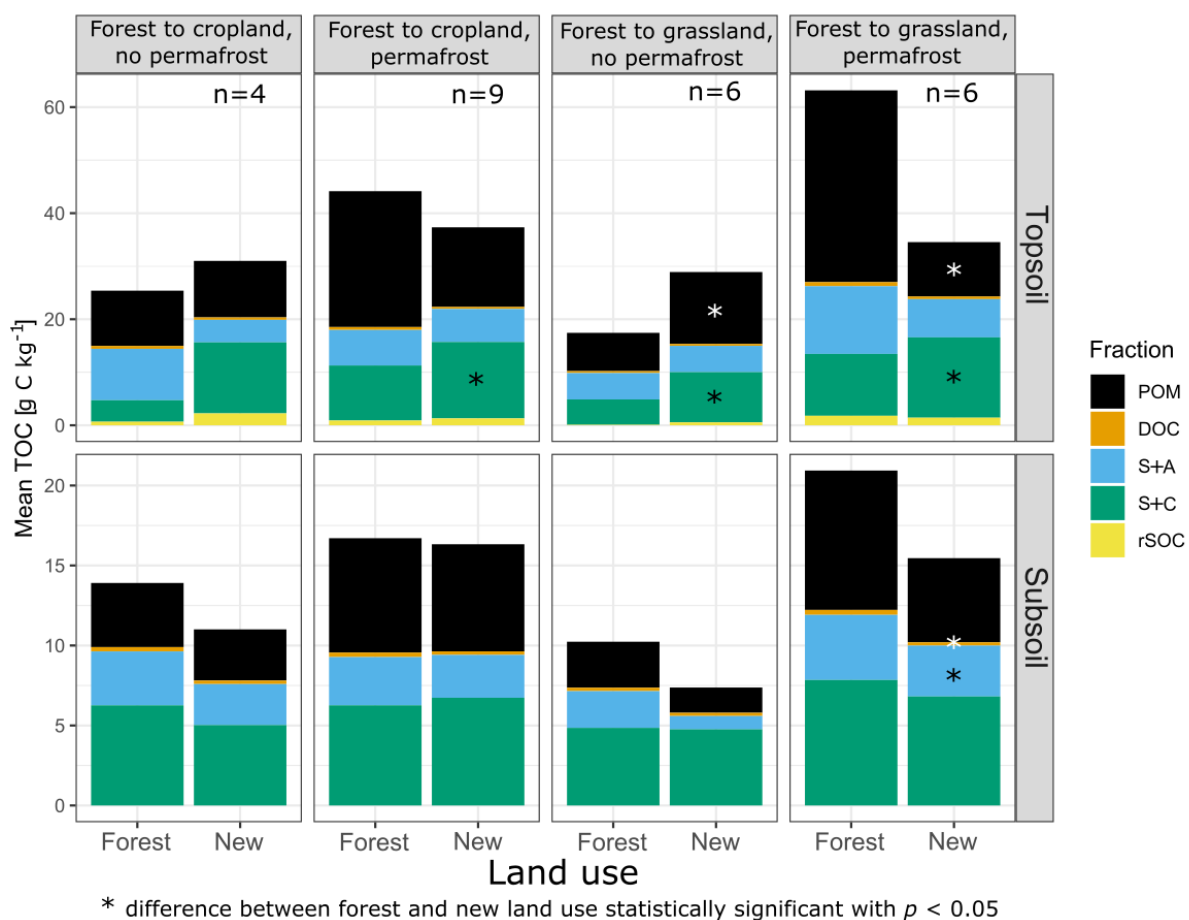
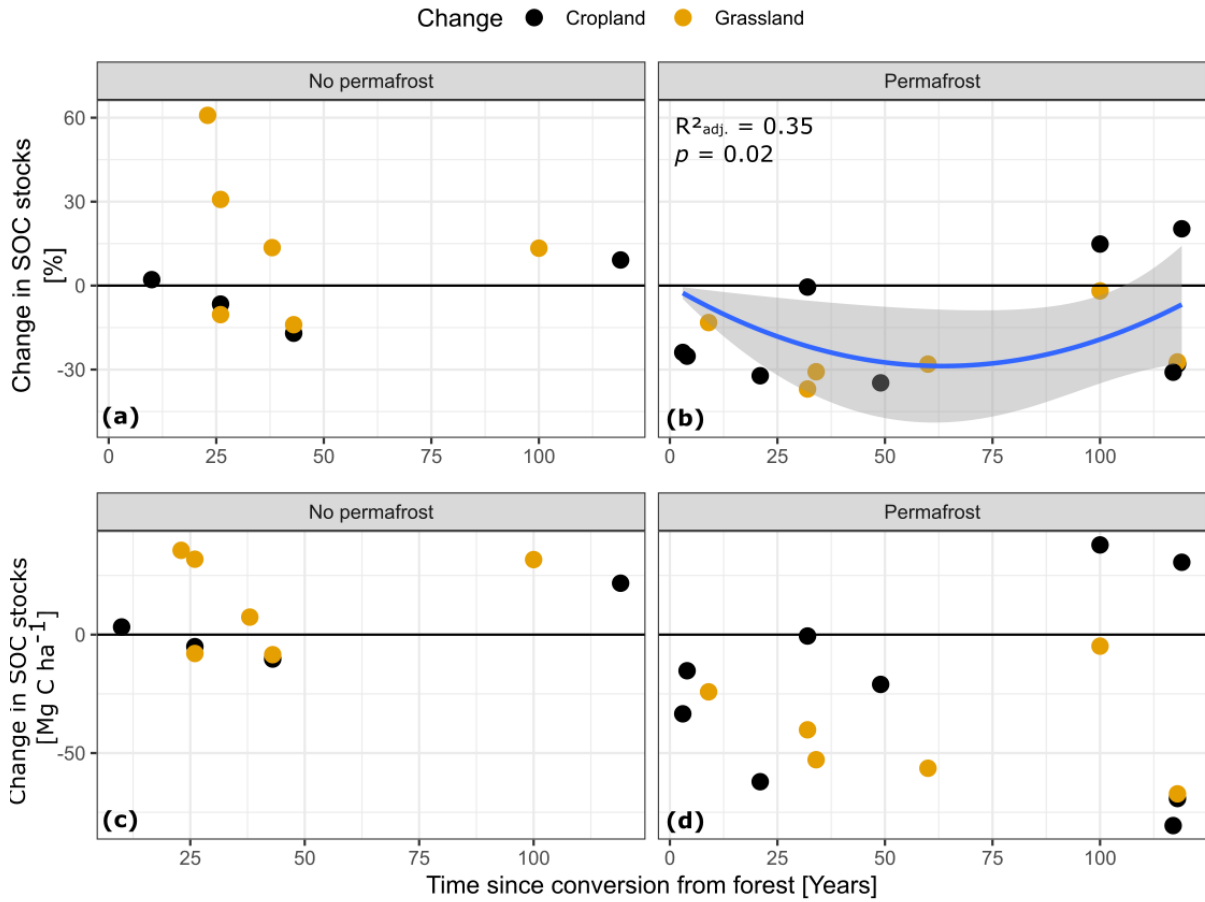
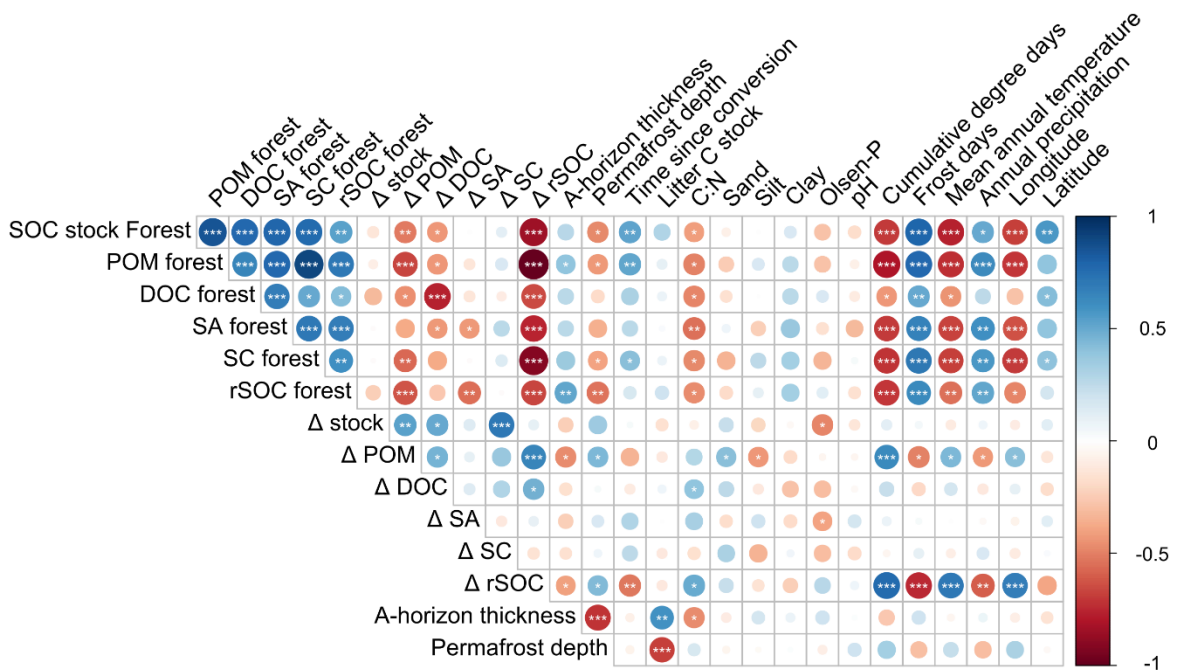


Figure 3.5: Comparison of mean total organic carbon (TOC) content of particulate organic matter (POM), dissolved organic carbon (DOC), sand and stable aggregates (S+A), silt and clay (S+C) and recalcitrant soil organic carbon (rSOC) at 10-20 cm (topsoil, upper row) and 40-60 cm (subsoil, lower row), differentiated by permafrost occurrence and land use (columns). Significant differences between forest and new land use are indicated by \*, with  $p < 0.05$



**Figure 3.6: Time-dependent change in total soil organic carbon (SOC) stocks, with relative (a+b) and absolute changes (c+d) at sites without (a+c) and with (b+d) permafrost. The solid blue line indicates the only significant model fit and the grey area indicates the standard deviation of the fit.**



**Figure 3.7: Correlograms of the Spearman's correlation coefficient. Colours represent the correlation coefficient, statistical significance is indicated by asterisks, with \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ) and \*\*\* ( $p < 0.001$ )**

## 3.4. Discussion

### 3.4.1. SOC stocks and permafrost

It was hypothesised that land-use change leads to larger SOC losses from permafrost-affected soils than from non-permafrost soils. This was strongly supported by the data obtained in this study, as an average SOC loss of  $30.6 \pm 35.8 \text{ Mg ha}^{-1}$  ( $18.6 \pm 18.3\%$ ) was identified at sites with permafrost. For sites without permafrost, no statistically significant changes in SOC were detected. From the difference between sites with and without permafrost, it was concluded that abiotic site conditions were of major importance for the magnitude and direction of SOC dynamics after deforestation.

These results are in line with Grünzweig et al. (2015), who also found dramatic SOC losses (69%) after conversion of forests to agriculture on permafrost soils in Alaska, while forests without permafrost showed lower SOC losses upon conversion. Greater losses from sites with permafrost can be attributed to the rapid thaw of permafrost that previously protected SOM from decomposition (Grünzweig et al. 2015). When removing the insulating forest vegetation and litter layer, the microclimate of a site, and thus also the soil temperature and moisture regime, is greatly changed (Shur and Jorgenson 2007). In fact, during the sampling campaign, no signs of frost were detected in the 0-80 cm soil profiles in any of the agricultural fields sampled, while the permafrost-affected forests had an average active layer depth of 50 cm. The fact, that the conversion from permafrost-affected forests to grassland resulted in higher SOC losses than the conversion to cropland is most likely explicable by the differences in hydrology of the sites. Forest sites with the highest carbon stocks, thickest A-horizons and the shallowest permafrost were also the wettest and thus also those that were least suitable for cropping. Permafrost-affected forests that became grasslands had an average SOC stock of  $194 \pm 60 \text{ Mg C ha}^{-1}$ , while permafrost affected forest soils that were converted to croplands had an average  $164 \pm 79 \text{ Mg C ha}^{-1}$ . Soil hydrology plays a major role in permafrost regions, since permafrost acts as a barrier for infiltrating water (Klinge et al. 2021). In fact, individual farmers reported that after clear cutting, soils are usually left to drain for some years before they can be cultivated. This has also been reported for soils in the Fairbanks

Area of Alaska in the mid of the last century (Pewe 1954). Furthermore, much of the SOC losses were observed to occur in the topsoil, which is not permanently frozen (Figure S3.2). This might additionally indicate that it is indeed largely a drainage effect that causes SOC losses after conversion to agricultural land and the associated deepening of the active layer. At the same time, irrigation can also cause permafrost thaw as infiltrating water in summer may lead to an amplified heat transport from the ground surface to the permafrost (Lopez et al. 2010). Conversely, SOM in permafrost-free soils is more vulnerable to decomposition than SOM in permafrost soils, and permafrost-free soils are therefore generally lower in SOC (Zimov et al. 2006). When these soils are irrigated and fertilised, plant growth is encouraged, leading to increased biomass production and C inputs to the soil and thus potentially also higher SOC stocks after conversion (Grünzweig et al. 2004). It should however be noted, that carbon stocks in agricultural soils are also fed by external carbon inputs (Table S2.1), which should have partly compensated or even overcompensated losses after deforestation. Most farmers applied compost, animal manure and similar organic fertilizers to their fields, which were partly derived from external sources such as imported animal fodder. Unfortunately, even after a detailed farmers questionnaire, the data was not good enough to make reliable estimates on the contribution of external organic fertilizers on the overall SOC stock difference between forest and agricultural soils. Maillard and Angers (2014) reported in a global meta-analysis that around  $12 \pm 4\%$  of manure-C is retained as SOC, when applied regularly. As a very rough estimate, we calculated the potential manure effect of 100 chickens as a realistic, yet high, number for Yukon farms: Fresh chicken manure contains around 20% C (Singh et al. 2018) and a chicken produces around 25 kg manure per year (Tanczuk et al. 2019). This would result in 2.5 Mg manure farm<sup>-1</sup> year<sup>-1</sup> and 0.5 Mg manure-C farm<sup>-1</sup> year<sup>-1</sup>. If 12 % of this C is retained in the soil, 0.06 Mg C would be added to the farm's soil. This is a negligible amount of carbon when compared to the land use change effects of up to -80.6 Mg C ha<sup>-1</sup>(site "SI"). We thus assume that fertilization practices did not add a significant bias to the comparison of permafrost and non-permafrost affected soils, even if organic fertilization would have fully relied on external sources. Moreover, SOC gains after deforestation should also not be interpreted as net carbon sinks, since losses from forest biomass are not accounted for in this study.



At sites without permafrost, no statistically significant difference in SOC change was found between the conversion to cropland and grassland, although grasslands tended to gain more SOC at sites without permafrost. The pattern of grasslands gaining SOC, which was found at sites without permafrost, was also observed by Deng et al. (2016) in a global meta-analysis. Conversion of forest to grassland increased SOC stocks by 11.53 Mg ha<sup>-1</sup>, while conversion of forest to cropland decreased SOC stocks. In a meta-analysis focusing on Canadian soils without permafrost, VandenBygaart et al. (2003) also found large losses (24%) in SOC when native land was converted to agricultural land. Moreover, VandenBygaart et al. (2010) compared various long-term cropping experiments across Canada and found a significant increase in SOC when annual cropland was converted into perennial grassland, which is in line with the trend observed in the present study of increasing SOC under grassland at sites without permafrost. VandenBygaart et al. (2003) identified management and land-use change as important drivers of SOC dynamics, but also emphasised the interactive effects of climate variables and management. In dry conditions in western Canada, SOC storage could be increased by switching from conventional agriculture to conservation agriculture, but that was not found to be the case in the more humid eastern part of Canada. This indicates that climatic conditions need to be considered in order to predict the magnitude and direction of SOC change after alterations to land use or management. In the present study, management of the agricultural land at sites with and without permafrost was similar, so changes in microclimate may have played a major role in the magnitude of the changes, supported strongly by the correlation between SOC stocks and climate variables.

### **3.4.2. Long-term trends in SOC changes**

Differences between agricultural land and associated forest were compared on the basis of time since conversion. Clear evidence was found that sites with permafrost lost large amounts of SOC in the first years after clearing. At sites with permafrost, old farms (> 50 years) had smaller losses than young farms or even more SOC in cropland than in the forest. This result has to be interpreted with care as, despite being statistically significant, this trend of SOC accumulation was driven by two cropland sites (KK and TH). These sites had a very high small-scale variability in the SOC

content (Figure S3.1), which might not be explained by land-use change but by their location on the banks of the Yukon and Klondike rivers. The differences in soil texture (Table 3.1) between forest and cropland, especially at TH, support this interpretation. As visualised by the large confidence interval (Figure 3.6b), it is thus highly uncertain whether initial SOC losses from former permafrost soils can be offset by appropriate agricultural management. However, the long-term replenishment of SOC, i.e. smaller losses at old farms at sites with permafrost, fits well with the observations of Grünzweig et al. (2004) who explained this pattern of short-term loss and long-term gain by quick decomposition of rather labile forest-derived organic matter after clearing, followed by slower breakdown of more stable organic matter and simultaneously subsequent higher input of fresh crop-derived organic matter. At some of the sites without permafrost, a short-term increase in SOC was found, which may be explained by the incorporation of forest litter into the mineral soil when the forest was cleared (Table S2.1, sites EF, EG, LR and NB). This effect has also been reported in other studies (Karhu et al. 2011, Grünzweig et al. 2004, Dean et al. 2017).

It was also hypothesised that forest soils with initially low SOC stocks accumulate SOC over decades when turned into agricultural land, leading to the same level or even higher SOC stocks in agricultural land compared with forest. However, at sites without permafrost, no statistically significant evidence for a time dependency of SOC changes was found, hence this hypothesis must be rejected. At six sites, equal or increased SOC stocks were found in the agricultural land compared with forest, but these sites covered a wide range of SOC stocks (Figure S3.1) and were not limited to those sites low in forest SOC. Moreover, it remains unclear how SOC at young farms will develop in the next few decades.

At sites with permafrost, it was possible to sample farms of various ages, well distributed over time back to the days of the gold rush. However, farms that were 43 to 100 years old without permafrost could not be sampled, which may explain the absence of statistical evidence for this hypothesis. Furthermore, observations of around 100 years may be considered long term for a study about the effect of agriculture on SOC, but could still be short term in relation to organic

matter turnover in subarctic regions. Even though the IPCC assumes 20 years of linear carbon sequestration for ecosystems to reach a new equilibrium after land-use change (IPCC 2003), other authors have estimated different times to reach equilibrium. Depending on the type of land-use change, Poeplau et al. (2011) used exponential, polynomial and linear functions to calculate the time to reach a new equilibrium after land-use change. According to Poeplau et al. (2011), it takes between 23 years (land-use change from forest to cropland) and over 200 years (land-use change from grassland to forest) to reach a new steady state in temperate soils. Moreover, Karhu et al. (2011) also concluded that longer time spans than the IPCC default value are necessary to observe land-use change effects on SOC in the boreal region.

### **3.4.3. Changes in SOC fractions**

It was hypothesised that the remaining SOC under agricultural land consists of relatively more carbon of the fine mineral fraction than under native forest, as POM is partly removed by clearing and quickly decomposed after the start of the new land use (Chen et al. 2019, Grünzweig et al. 2015, Poeplau and Don 2013). Significant changes in SOC fractions were found, mostly at sites with permafrost. At these sites, POM-C was significantly reduced, while the S+C fraction had more C in agricultural land than in the forest. Therefore this hypothesis was well supported for sites with permafrost. The S+A fraction, as an intermediately labile fraction (Zimmermann et al. 2007), was reduced in agricultural land independently of permafrost, again supporting the hypothesis of this study. Despite all statistical evidence, results from SOC fractionation should be considered as an indicative characterization of the soil organic matter composition and not as mass balance.

The POM fraction was observed to increase after land-use change to grassland at sites without permafrost and to decrease at sites with permafrost, underlining the sensitivity of the POM fraction to permafrost thaw. The observed decrease in POM in the topsoil after permafrost thaw was also in line with the results of Mueller et al. (2015). In permafrost soils in Alaska, Mueller et al. (2015) reported that most SOC was stored within the active layer and that the largest part (around 73%) of SOC within the uppermost metre consisted of POM, which is mostly composed of easily degradable carbohydrates. Since the active layer depth at the sites with permafrost in the

present study decreased rapidly after land-use change, the labile POM fraction was exposed to decomposition, leading to large losses of SOC. Losses of POM-C after deforestation have also been observed in other studies (Balesdent et al. 1998, Del Galdo et al. 2003, Karhu et al. 2011) and are in line with the results of the present study. The observed accumulation of mineral-associated carbon, here represented by the S+C fraction, pointed to greater stabilisation of SOC during agricultural land use. This could potentially suggest a shift from plant-derived compounds to more microbial-derived ones (Angst et al. 2020), which are acknowledged to be a dominant fraction of mineral-associated organic matter (Ludwig et al. 2015, Buckeridge 2020). Indeed, Schroeder et al. (in prep.) found higher microbial carbon-use efficiencies (i.e. more biomass production per total carbon uptake) in croplands and grasslands than in forest soils (the same soils as used in the present study), which might indicate an increased importance of this in-vivo pathway of SOM stabilisation (Sokol 2019, Liang 2017).

#### **3.4.4. Implications for future subarctic agriculture**

The shift of agricultural regions will inevitably lead to the conversion of subarctic forest to agricultural land. Climate change and a growing demand for locally produced food in the north are encouraging the establishment of food production systems even in largely untouched areas, putting pressure on vulnerable subarctic forests. As shown in this study, subarctic agriculture can have strong negative impacts on SOC, potentially accelerating the positive feedback loop of warming and loss of SOC (Heimann and Reichstein 2008). However, the present study also highlighted that the impacts of agriculture on SOC can be minimised or even offset when the potential new agricultural land is limited to areas without permafrost and if short-term losses of SOC can be minimised. However, the focus of this study was on SOC, and did not quantify losses of other ecosystem C pools due to land-use change. In a synthesis, Kurz et al. (2013) calculated that boreal forests of Canada store around 40 Mg C ha<sup>-1</sup> (21% of ecosystem C) in aboveground biomass, 10 Mg C ha<sup>-1</sup> (6% of ecosystem C) in belowground biomass, i.e. living roots, and around 20 Mg C ha<sup>-1</sup> (11% of ecosystem C) as deadwood, which is not included in the litter layer. Considering that these amounts of C (38% of ecosystem C) are certainly removed by deforestation, the small gains

in SOC at sites without permafrost are negligible. This study revealed that, in terms of SOC storage, the abundance of permafrost within the upper first metre of forest soil should be carefully considered when establishing agriculture in pristine subarctic ecosystems. Furthermore, the focus of this study was on permafrost at a depth that is relevant for agriculture, but no account was taken of deeper permafrost. Therefore, sites that were classified as having no permafrost may have permanently frozen layers that could thaw due to land-use change. Short-term losses can potentially be avoided by adapted management and deforestation techniques that conserve as much of the litter layer as possible. Sustainable land management has been studied extensively in pedo-climatic regions with a distinct agricultural sector, but is understudied in the cold and dry subarctic where agriculture currently plays a minor role. In temperate climates, no till is acknowledged to have no significant effect on whole-profile SOC stocks (Chenu et al. 2019), but there is evidence that cropland soils in cold and dry regions may benefit from no till (VandenBygaart et al. 2010). In this study, no direct effect of tillage depth on SOC was identified, but since most farmers till only irregularly, the database may be insufficient for any evidence of tillage or other management effects. Promising concepts for more sustainable clearing, such as chipping and spreading or mulching and subsoiling of deforestation residues (roots, stumps, deadwood and litter layer) instead of burning or the introduction of silvopasture (Lim et al. 2018) or agroforestry (Tsuji et al. 2019) instead of clear-cutting, may help to reduce the negative impacts of agriculture on subarctic SOC.

### 3.5. Acknowledgements

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### 3.6. Data availability statement

All data and the R-script used for this study is freely available at [10.5281/zenodo.6460208](https://zenodo.org/record/6460208)

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#### 4. Deforestation for agriculture leads to soil warming and enhanced litter decomposition in subarctic soils

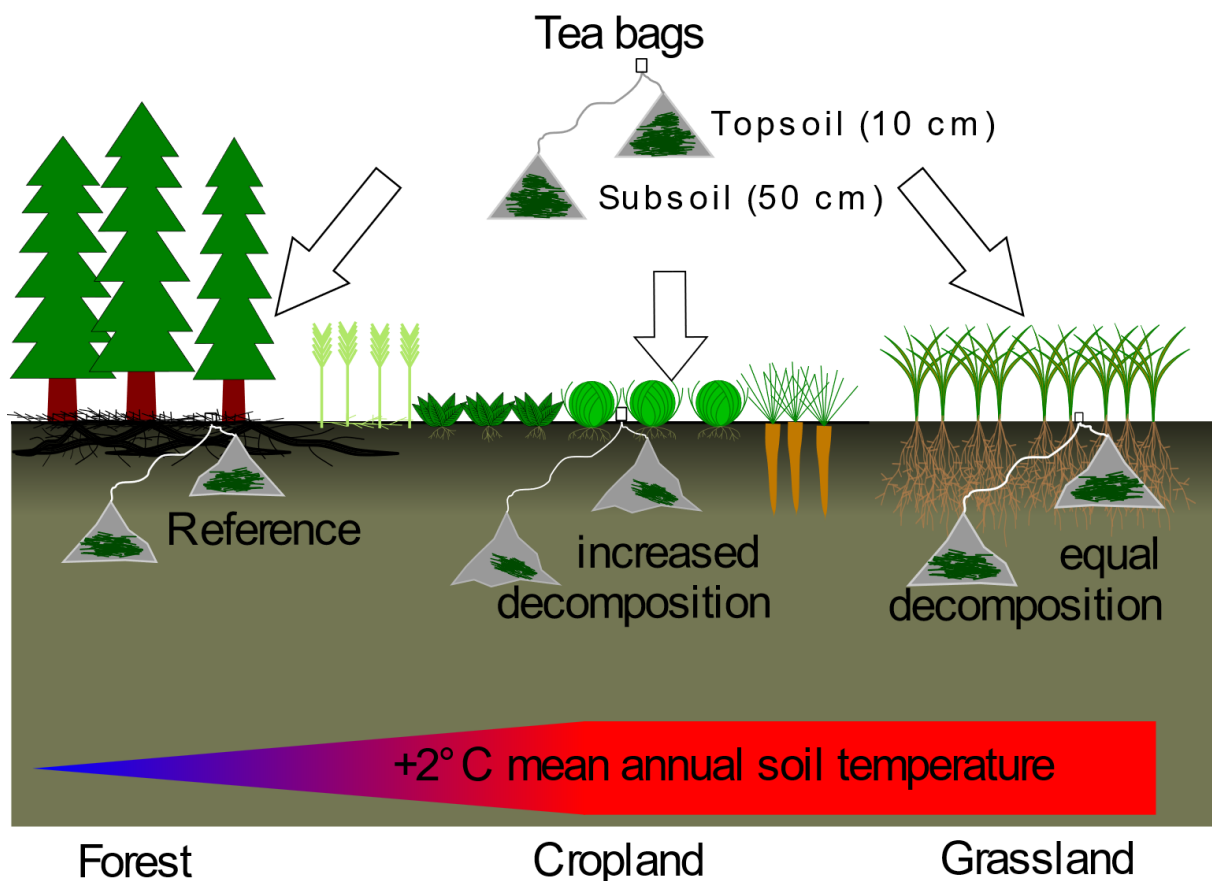
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Graphical abstract 3: Deforestation for agriculture leads to soil warming and enhanced litter decomposition in subarctic soils

#### 4.0. Abstract

The climate-change induced poleward shift of agriculture could lead to enforced deforestation of subarctic forest. Deforestation alters the microclimate and, thus, soil temperature, which is an important driver of decomposition. The consequences of land-use change on soil temperature and decomposition in temperature-limited ecosystems is not well understood. In this study, we buried litter bags together with soil temperature loggers at two depths (10 and 50 cm) in native subarctic forest soils and adjacent agricultural land in the Yukon Territory, Canada. A total of 37 plots was established on a wide range of different soils and resampled after two years to quantify the land-use effect on soil temperature and decomposition of fresh organic matter. Average soil temperature over the whole soil profile was  $2.1 \pm 1.0^\circ\text{C}$  and  $2.0 \pm 0.8^\circ\text{C}$  higher in cropland and grassland soils compared to forest soils. Cumulative degree days (the annual sum of daily mean temperatures  $> 0^\circ\text{C}$ ) increased significantly by  $773 \pm 243$  (cropland) and  $670 \pm 285$  (grassland). Litter decomposition was enhanced by  $2.0 \pm 10.4\%$  and  $7.5 \pm 8.6\%$  in cropland topsoil and subsoil, compared to forest soils, but no significant difference in decomposition was found between grassland and forest soils. Increased litter decomposition may not be attributed to increased temperature alone, but also to management effects, such as irrigation of croplands. The results suggest that deforestation-driven temperature changes exceed the soil temperature increase already observed in Canada due to climate change. Deforestation thus amplifies the climate-carbon feedback by increasing soil warming and organic matter decomposition.



## 4.1. Introduction

The poleward shift of agriculture due to climate change (Franke et al. 2022) will alter the land cover of vast areas in subarctic regions. As the global mean temperature rises, permafrost soils of the boreal forest region thaw (Biskaborn et al. 2019) and agriculture in high latitudes expands to regions that had previously been less suitable for agriculture (Tchebakova et al. 2011). Climate change warms the Subarctic more strongly than the global average (IPCC 2013). So, subarctic soils are especially prone to SOC loss. Subarctic soils store large amounts of soil organic carbon (SOC) (Hugelius et al. 2014) that are easily decomposable (Mueller et al. 2015). Moreover, the conversion of pristine subarctic forests to agricultural land has been reported to cause large losses of SOC (Grünzweig et al. 2004, Karhu et al. 2011, Peplau et al. 2022), which in turn fosters climate change. The mechanisms behind deforestation-induced loss of SOC may be manifold and are not understood in detail. This hampers process-based modelling to extrapolate land-use change effects in space and time.

Besides alterations in species composition and net primary productivity, the replacement of forests by open landscapes has a strong impact on the microclimate, particularly on the temperature regime. Due to missing canopy upon deforestation, the ground is exposed to more direct sunlight and air flow is favoured, leading to more variable near-surface temperatures in open landscapes compared to closed forests (Frenne et al. 2021). The more rapid intra-day temperature changes of the near-surface air have unclear implications for soil temperature. As Lembrechts et al. (2022) showed, there is an offset between air and soil temperature, which depends on the climatic conditions, and soils are around 3.6°C warmer than the air in boreal forests. Surface air temperature may decrease (Lee et al. 2011), but, regardless of the intensity and direction of air temperature changes, little is known about the effects of land-use change on soil temperature. This applies particularly in the context of subarctic agriculture, since the removal of pristine vegetation and management techniques may have opposing effects on soil temperature. Consequently, potential feedbacks between land-use change, soil temperature and soil organic matter decomposition are also unclear.

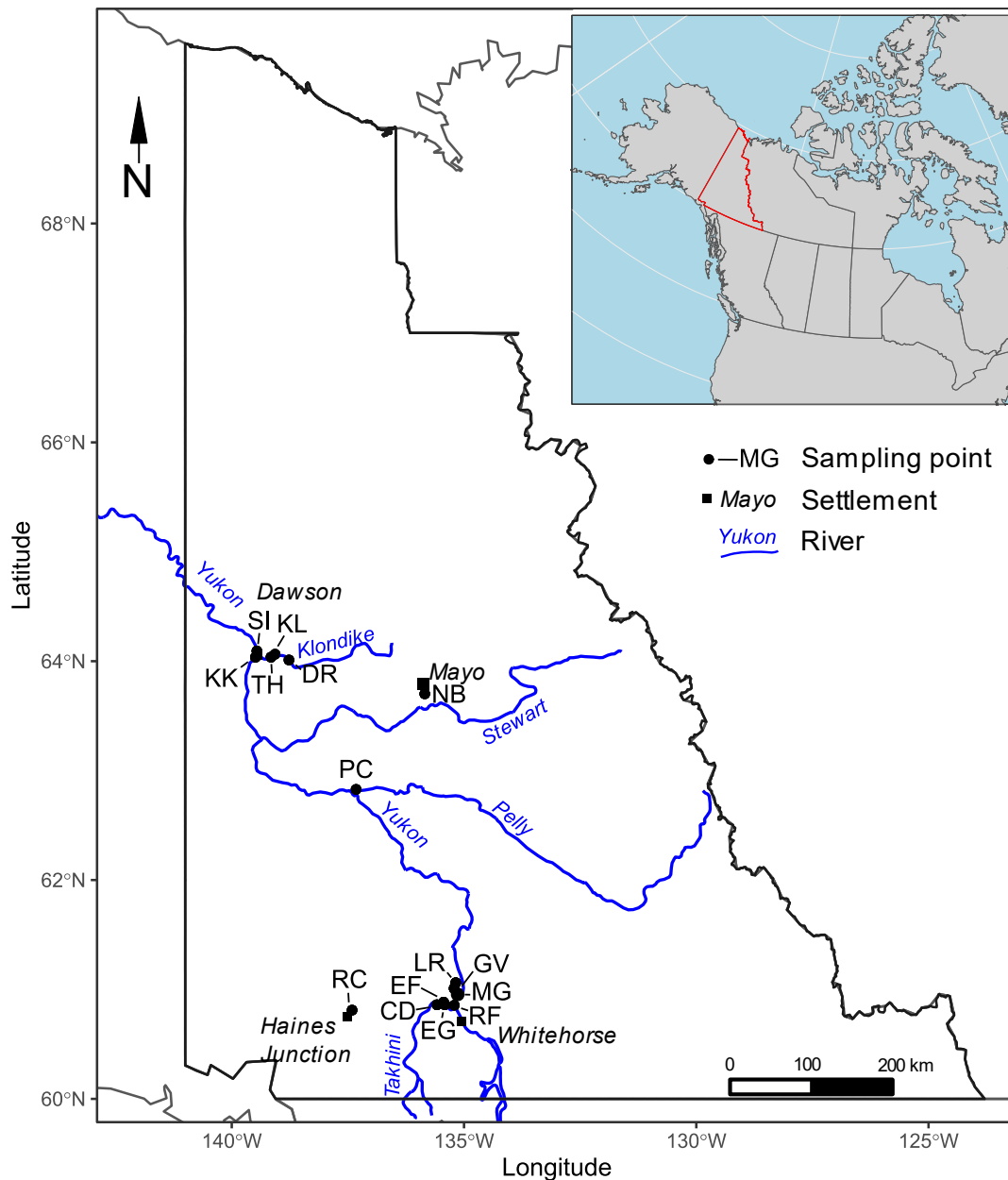
Temperature is the most important driver for the decomposition of fresh organic matter (Gregorich et al. 2017), along with moisture (Petraglia et al. 2019) and substrate quality (Fierer et al. 2005). There has been extensive research about the mechanisms behind the effects of soil warming on organic matter decomposition: at first hand, depolymerization of complex organic structures, microbial enzyme production, sorption processes and aggregate turnover are key for temperature-induced changes in soil organic matter decomposition (Conant et al. 2011). The effect of warming on soil organic matter cycling is indirectly influenced by various site properties, such as evapotranspiration, mineralogy or plant litter chemistry (Davidson et al. 2000) and is, therefore, regionally highly variable (Carey et al. 2016). In subarctic forests, losses of SOC due to accelerated decomposition exceed the warming-induced gain in SOC due to enhanced net primary productivity (Karhu et al. 2010), as the large share of labile SOC is quickly decomposed upon warming (Peplau et al. 2021). Despite a different composition of SOC in grasslands than in forests (Grünzweig et al. 2004), it has been shown that subarctic grasslands are also highly prone to SOC loss upon warming (Poeplau et al. 2017).

The objectives of this study were 1) to quantify changes in soil temperature when subarctic forest is converted into agricultural land (i.e. grassland and cropland), 2) to elucidate the influence of various soil properties on such temperature changes and 3) to compare the decomposition of fresh organic matter in forest and agricultural soils. It was hypothesized that the removal of insulating vegetation by deforestation is shifting the soil temperature regime from relatively moderate temperatures in forest soils to more extreme temperatures in agricultural soils with warmer summer and colder winter temperatures in agricultural soils than in forest soils. Furthermore, it was hypothesized that warmer summer temperatures encourage the decomposition of soil organic matter in agricultural soils compared to forest soils.

## 4.2. Material and Methods

### 4.2.1. Research area

A paired-plot litter decomposition experiment was set up in the Yukon Territory in Northwest Canada, at the southern edge of the northern circumpolar permafrost region. The experiment compared litter decomposition and soil temperature in forest and agricultural land (cropland / market garden, summarized as cropland and / or grassland). Since the Klondike gold rush at the end of the 19<sup>th</sup> century, the Yukon has an established agricultural sector with farms that are suitable for studying the effects of land-use change from forest to grassland and forest to cropland in the Subarctic. Farms were considered to be suitable for studying the effects of land-use change from forest to grassland or cropland when they (1) originated from forest, (2) were located on mineral soils and (3) had a remaining native forest nearby. Furthermore, both forest and agricultural land needed to be located on flat terrain with comparable soil properties. This was checked in an auger-based pre-assessment in consultation with the farmers. In total, 15 farms were included in this study and they provided 21 pairs of forest and cropland (n = 12) or forest and grassland (n = 9) (Figure 4.1).



**Figure 4.1:** Map of the sampling locations and major rivers and settlements of the Yukon. Top right: The Yukon's location (red) within North America (grey).

#### 4.2.2. Litter decomposition experiment

In order to investigate the effects of land-use change on soil temperature regime and litter decomposition, tea bags and temperature loggers were buried at the chosen farms in summer 2019. Tea bags with green tea ('Bio Grüner Tee', Paulsen Tee, Fockbeck, Germany, Charge No. 187896FC) as a standard litter material were weighed, tagged and buried at depths of 10 and 50 cm from the soil surface (n=3 per depth), based on the methodology of Keuskamp et al. (2013). Temperature loggers (Tinytag Plus 2 TGP 4017, Gemini Data Loggers Ltd) were buried at the same

depths (n=1 per depth) and set up to record the soil temperature every two hours. The tea bags were buried at spots considered as representative of the given plots by placing them approximately 30 cm apart from each other around the temperature loggers. After two years, the tea bags and temperature loggers were dug out in September 2021. The tea bags were cleaned of roots and soil, dried at 60 °C, opened in order to manually pick out fine roots that grew into the tea bag and weighed again to determine mass loss as a proxy for decomposition. The tea bags from very clayey sites were additionally washed prior to opening to remove clay particles from the tea bag material.

In total, 209 out of 216 tea bags and all 72 temperature loggers were recovered. After downloading the data from the loggers, measurements were checked for plausibility (no abrupt changes that would exceed normal hourly fluctuations) and completeness (no missing data) before further processing.

#### **4.2.3. Soil parameters**

In addition to the burial of tea bags and temperature loggers, soil samples were taken from every plot to characterize the soils of the sites investigated. The sampling was done in summer 2019, at the same time of the burial of the tea bags. Details about the soil sampling and laboratory analyses can be found in Peplau et al. (2022). Soil was sampled from depth increments of 0-10 cm and 40-60 cm matching the depth of the buried sensors and tea bags. Five field replicates of every depth increment were pooled to a mixed sample and analyzed for organic and inorganic carbon (C) and total N content,  $\text{pH}_{\text{H}_2\text{O}}$  (ISO 10390), plant available phosphorus (Olsen et al. 1954), SOC fractions (Zimmermann et al. 2007) and texture (Köhn 1929). The soils in the research area were Cambisols and Cryosols (Jones et al. 2009) with pH values between 5.5 and 8.9 (mean: 7.4) and clay contents between 49 and 578 g kg<sup>-1</sup> (mean: 178 g kg<sup>-1</sup>). Soil parameters and values of SOC stocks were obtained from an earlier study at the same sites (Peplau et al. 2022). In this earlier study, soils were sampled from 0-80 cm, with depth increments of 0-10 cm, 10-20 cm, 20-40 cm, 40-60 cm and 60-80 cm. The organic C was measured with an elemental analyser (LECO TruMac CN). To

distinguish between organic C and inorganic C, samples with pH > 6.2 were heated in a muffle furnace at 440°C before the measurement.

#### **4.2.4. Statistics**

The descriptive variables of annual mean temperature, minimum temperature, maximum temperature, temperature amplitude, number of frost days (i.e. days with a mean temperature lower than 0°C) and cumulative degree days (temperature sum of days with a mean temperature above 0°C) were calculated from the original two-year temperature dataset. The number of frost days and cumulative degree days were divided by 2 to obtain the average of both years.

To test for significant differences in litter decomposition and soil temperature parameters between forest, cropland and grassland, linear mixed-effects models were used with land-use type as fixed effect and site and depth as random effects, allowing for random intercept. Homoscedasticity, normality of the residuals and linearity of the dataset were given and no transformation of the data was necessary. Since cropland and grassland soils did not have the identical reference forests, separate models were used for cropland/forest and grassland/forest pairs. After performing the linear mixed-effects models, estimated marginal means were used to obtain pairwise comparisons of all groups of the linear mixed-effects model (confidence level = 0.95).

In order to identify variables that are driving the decomposition of the buried tea bags, the Pearson's correlation coefficient was calculated separately for the complete dataset and for every land-use type and depth.

All statistical analyses were conducted using R version 4.0.4 (R Core Team 2021) with the packages readxl (Wickham & Bryan 2019), tidyverse (Wickham et al. 2019), dplyr (Wickham et al. 2020), purrr (Henry and Wickham 2020), ggplot2 (Wickham 2016), ggpubr (Kassambra 2020), ggthemes (Arnold 2021), ggpmisc (Aphalo 2021), corrplot (Wei and Simko 2021), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), multcomp (Hothorn et al. 2008), multcompView (Graves et al. 2019) and emmeans (Lenth 2021). The level of significance for all statistical analyses

was selected as  $\alpha = 0.05$ . All data used for this study is openly available at DOI 10.5281/zenodo.7219753

## 4.3. Results

### 4.3.1. Soil temperature as affected by land use

Forest soils were cooler and had smaller intra-day variations in temperature than cropland and grassland soils (Figure 4.2). During winter, the soil temperature of all land uses did not exceed 0°C and showed very little short-term variations within a couple of days. With the beginning of spring in April, soil temperature at 10 cm depth increased sharply to above 0°C and short-term variations in temperature became larger. At 50 cm, the spring soil temperature increase was visible, but less pronounced than at 10 cm. The sharp increase in soil temperature to above 0°C was visible at all sites at the same time, independent of how low the soil temperature was beforehand. On average, grasslands soils were  $2.2 \pm 0.9^\circ\text{C}$  and  $1.8 \pm 0.5^\circ\text{C}$  warmer than forest soils at 10 and 50 cm and cropland soils were  $2.1 \pm 1.1^\circ\text{C}$  and  $2.0 \pm 0.9^\circ\text{C}$  warmer than forest soils at 10 and 50 cm (Figure 4.3), which was significant with  $p < 0.05$ . Moreover, significantly larger cumulative degree days indicated warmer soils under agricultural use than under forest. Cumulative degree days at 10 and 50 cm were elevated by  $606 \pm 222$  and  $733 \pm 338$  in grassland soils and by  $768 \pm 262$  and  $779 \pm 237$  in cropland soils. This roughly corresponds to a doubling of cumulative degree days upon land-use change. Detailed information about the soil temperature at every site, land-use type and depth can be found in Table S3.1.

Significant differences between forest and grassland at both depth increments were found in mean temperature, minimum temperature, maximum temperature, total amplitude and cumulative degree days, but not in the number of frost days (Table 4.1). The comparison between forest and cropland resulted in significant differences at 10 and 50 cm for mean temperature, maximum temperature, total amplitude, cumulative degree days and frost days. In contrast to grasslands, croplands had no different minimum temperature, but fewer frost days than forests.

Temperature differences between forest and grassland were smaller in soils with high clay content, while there was no such correlation observed in cropland soils (Figure 4.4).

#### **4.3.2. Litter mass loss**

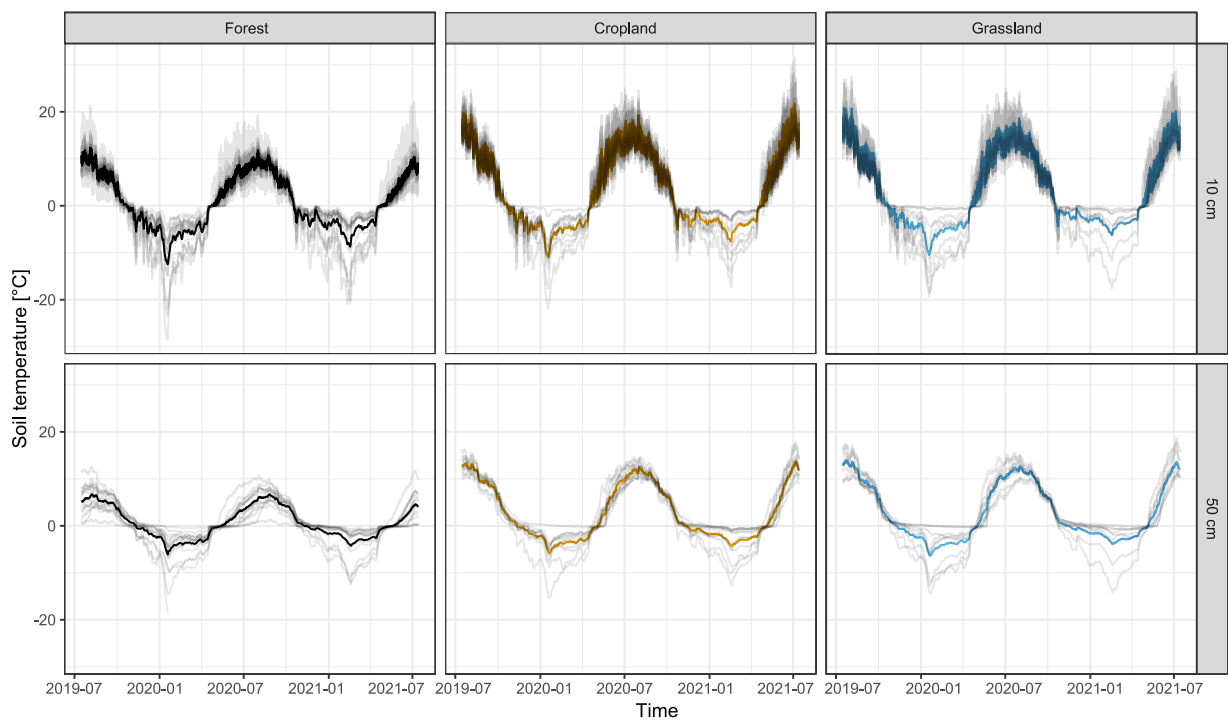
We observed significant differences in litter mass loss between cropland and forest soils, but not between grassland and forest soils (Figure 4.5). In forest-cropland pairs, the mean proportional loss of added litter was lower in forest soils ( $70 \pm 7\%$  and  $52 \pm 4\%$  at 10 and 50 cm) than in cropland soils ( $73 \pm 8\%$  and  $61 \pm 8\%$  at 10 and 50 cm). In forest-grassland pairs, mean decomposition of added litter in forest soils was  $70 \pm 4\%$  and  $60 \pm 12\%$  at 10 and 50 cm, while it was  $67 \pm 7\%$  and  $53 \pm 18\%$  in grassland soils at 10 and 50 cm. Detailed information about mass loss at every site, land use and depth can be found in Table S3.1.

#### **4.3.3. Soil properties and microclimate explaining tea mass loss**

The correlation between litter mass loss and soil temperature, site characteristics and soil properties strongly differed between agricultural land and forest. In forest topsoils, only minimum temperature was significantly negatively correlated with mass loss of tea, while mass loss in subsoils was significantly correlated with minimum temperature, number of frost days and total temperature amplitude (Figure 4.6). In cropland soils, significant correlations were only observed in topsoils. In contrast to forest soils, mass loss in cropland soil was positively correlated with minimum temperature. Furthermore, there was a significant negative correlation between mass loss and silt content. In grassland soils, tea mass loss was only correlated with temperature parameters (mean temperature, maximum temperature, amplitude, number of frost days and cumulative degree days). In contrast to croplands, there was no significant correlation between decomposition and SOC fractions in grassland soils. Across all land-use types and depths, mass loss correlated significantly with soil temperature parameters, except for mean temperature and number of frost days. Weaker, yet significant, correlations were observed between mass loss and soil organic matter (C and N content as well as SOC fractions). This was not observed when separating the sample set into the different land-use types and depths, except for forest subsoils (soil organic matter parameters) and grassland subsoils (temperature parameters). Besides



elevated mean and maximum temperature, which may be biased by single extreme values, cumulated degree days also increased in cropland and grassland soils, compared to forest soils. This increase had a highly significant effect on litter decomposition (Figure 4.7) ( $p < 0.001$ ). Furthermore, there was a good correlation between SOC stocks and mean soil temperature in forest soils with higher SOC stocks in colder soils, something that was not observed in agricultural land (Figure 4.8).



**Figure 4.2: Soil temperature profile in Forest, Cropland and Grassland at 10 and 50 cm. Grey lines show the temperature of the individual sites; coloured lines indicate average temperatures.**

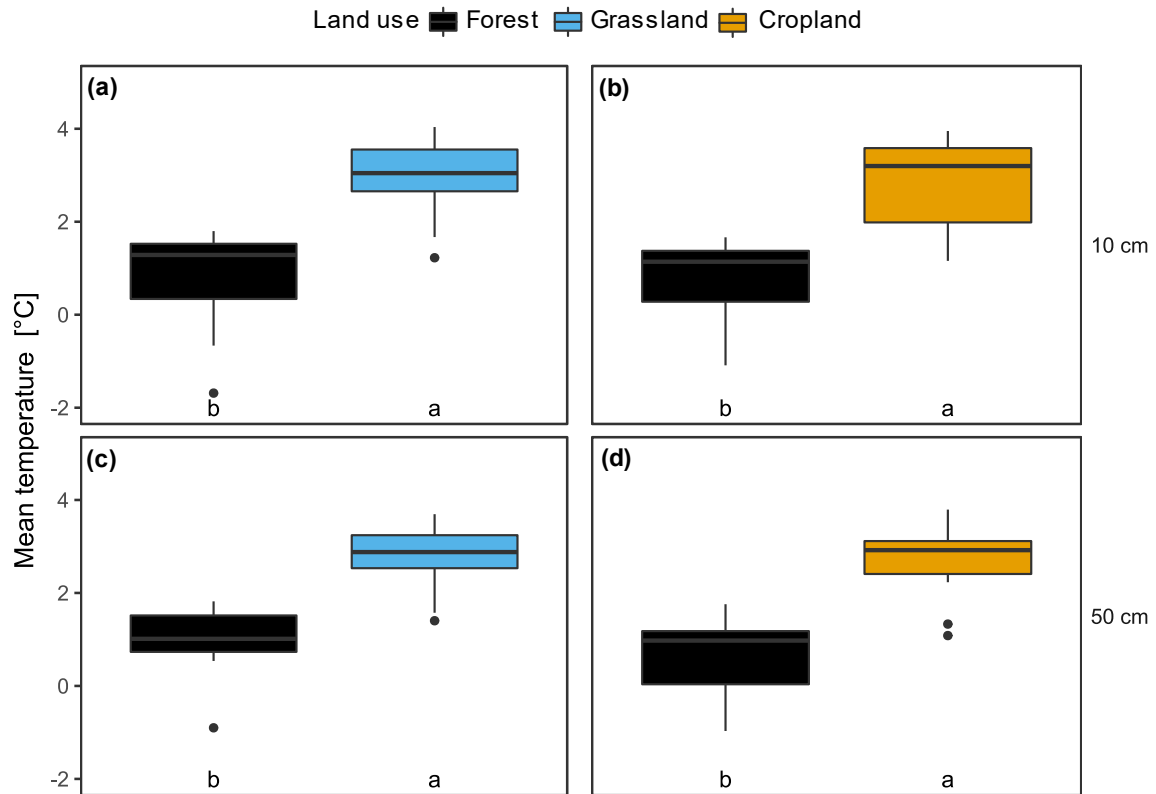


Figure 4.3: Tukey-style boxplot of the mean temperature in grassland/forest pairs ( $n = 9$ ) (a+c) and cropland/forest pairs ( $n = 12$ ) (b+c) at 10 (a+b) and 50 cm (c+d) depth. Different letters at the bottom of each panel indicate statistically significant differences in mean temperature based on estimated marginal means at a level of significance of  $\alpha = 0.95$  ( $p < 0.05$ ).

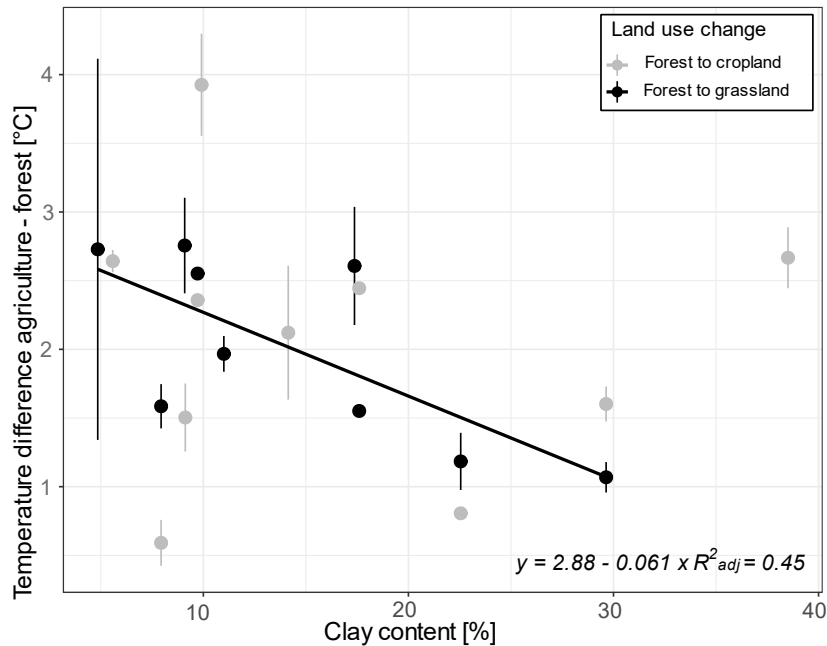


Figure 4.4: Relationship between clay content [%] and soil temperature difference between agricultural land and forest. Points indicate mean values between 10 and 50 cm depth; vertical lines indicate standard deviation of the mean temperature between 10 and 50 cm. The thick line (black) and the formula show the linear regression of the correlation for the conversion from forest to grassland ( $p < 0.05$ ).

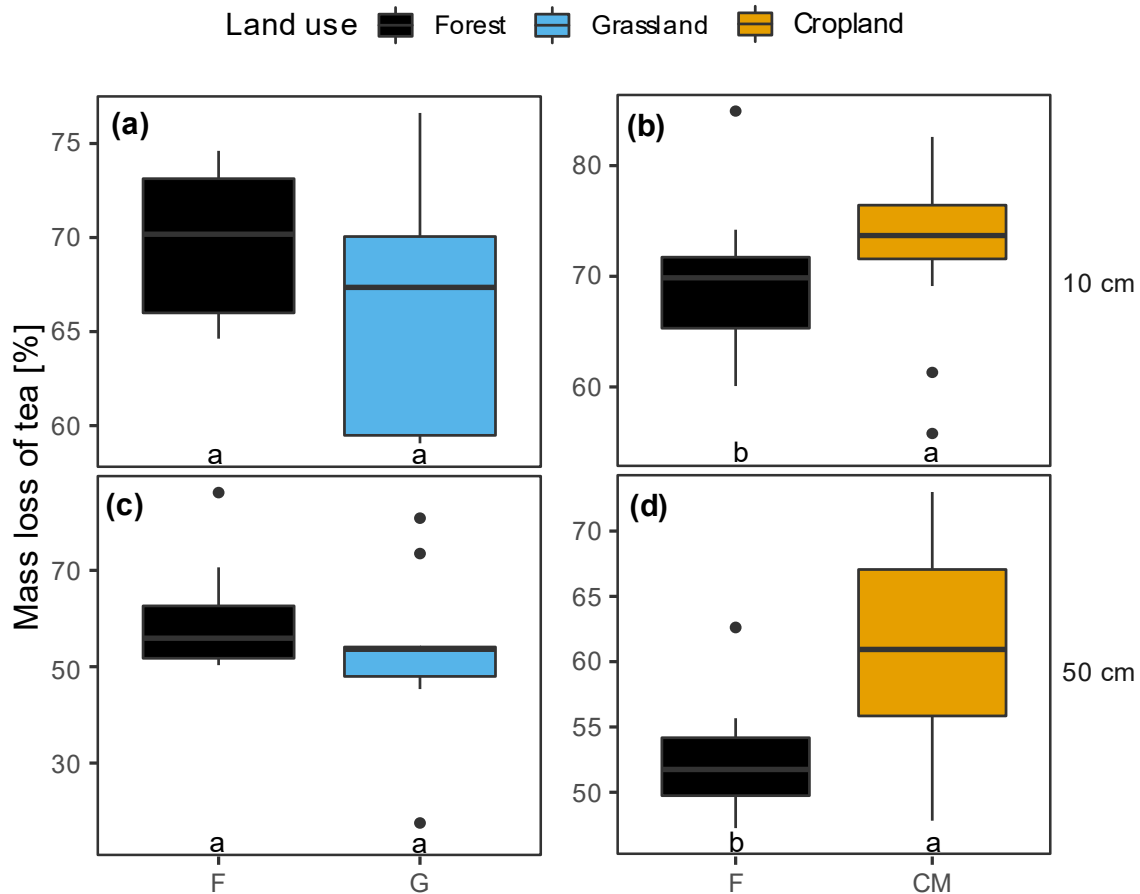


Figure 4.5: Tukey-style boxplot, comparing mean decomposition of the buried tea bags in grassland/forest pairs ( $n = 9$ ) (a+c) and cropland/forest pairs ( $n = 12$ ) (b+d) at 10 (a+b) and 50 cm (c+d) depth. Different letters at the bottom of each panel indicate statistically significant differences in mass loss based on estimated marginal means at a level of significance of  $\alpha = 0.95$  ( $p < 0.05$ ).

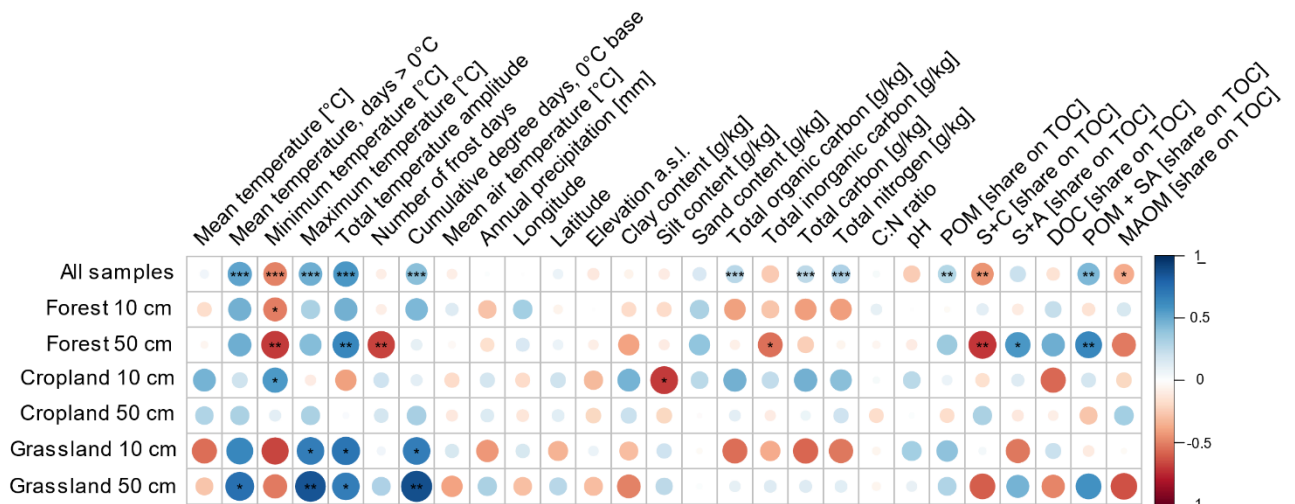


Figure 4.6: Correlogram of the Pearson's correlation coefficient, showing the correlation of mean litter decomposition and the most important soil temperature parameters, site characteristics and soil properties. The size and colour of the points represent the direction and the value of the correlation coefficient. Asterisks indicate statistical significance with \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$ .

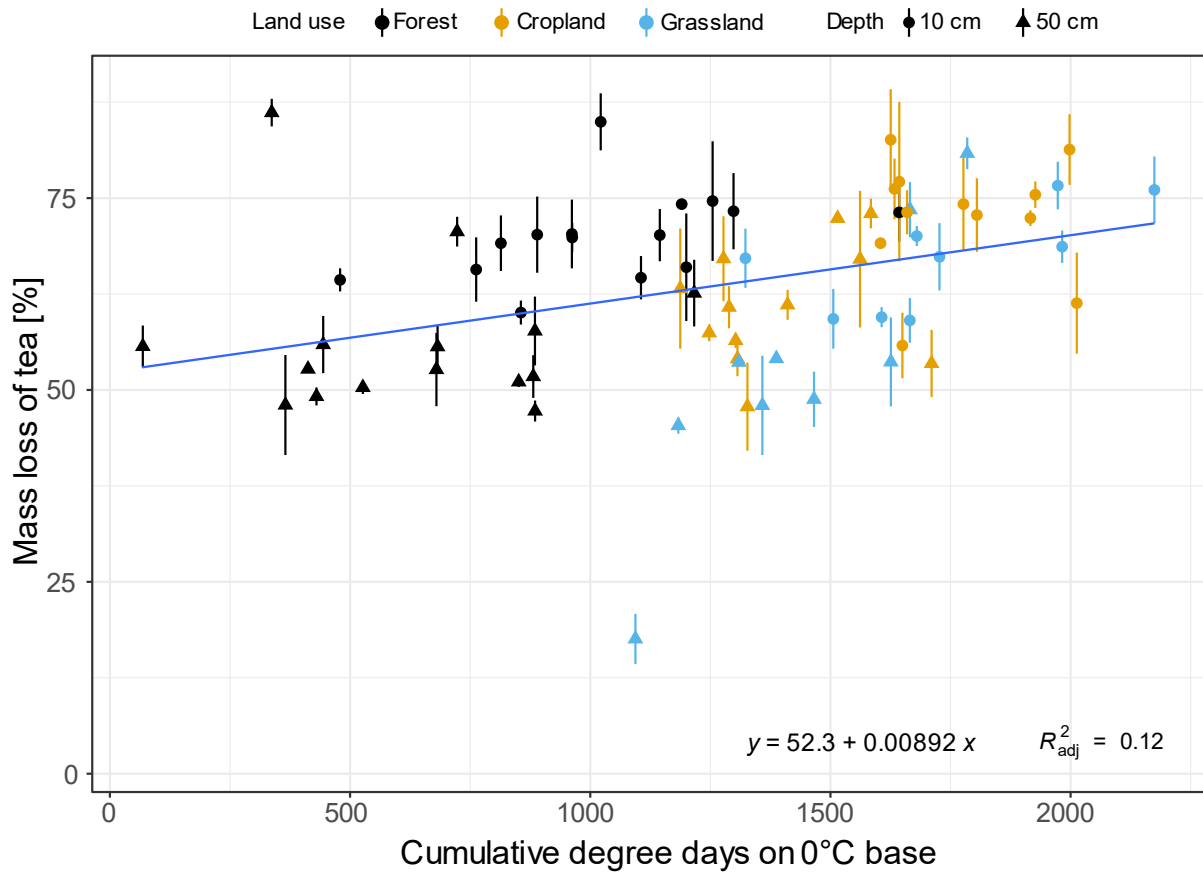


Figure 4.7: Point range and regression line ( $p < 0.05$ ) of tea decomposition over cumulative degree days at 10 cm depth (circles) and 50 cm depth (triangles). Shapes indicate mean values; vertical lines indicate standard deviation of the decomposition. The regression line was fitted using all datapoints.

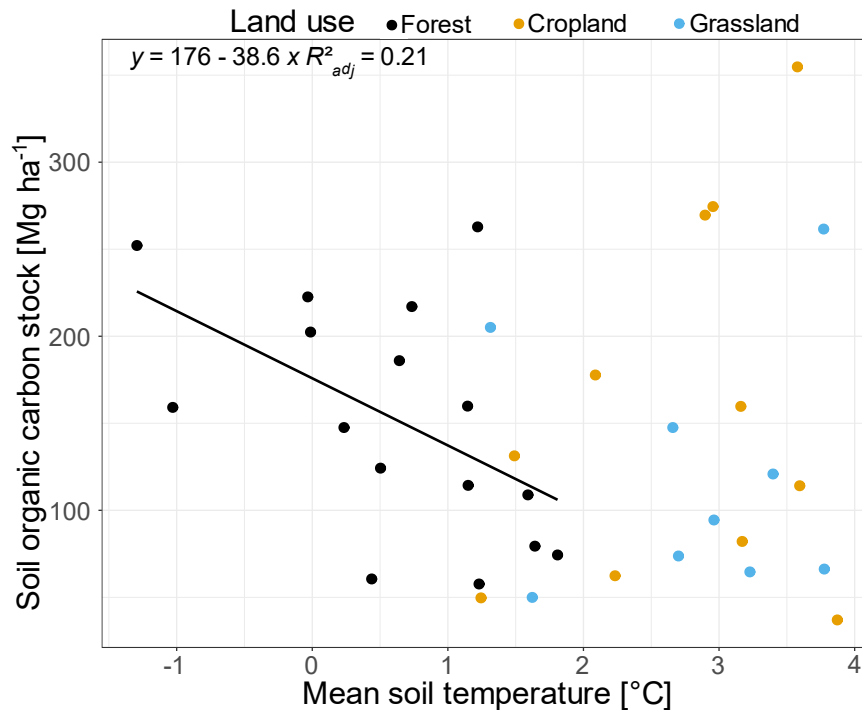


Figure 4.8: Soil organic carbon (SOC) stocks between 0-80 cm depth [ $\text{Mg/ha}$ ] and mean soil temperature [ $^{\circ}\text{C}$ ] of forest, grassland and cropland soils with a significant ( $p < 0.05$ ) correlation (solid line) between SOC stocks and soil temperature in forest soils. Mean temperature was calculated from soil temperatures at 10 and 50 cm.

**Table 4.1: Mean, minimum and maximum temperature, temperature amplitude, number of frost days and cumulative degree days on 0°C base in forest, grassland and cropland soils. Values are means with standard deviation. Asterisks indicate significant difference ( $p < 0.05$ ) between agricultural land and forest.**

Land use change	Land use	Depth [cm]	Mean temperature [°C]	Minimum temperature [°C]	Maximum temperature [°C]	Total amplitude [°C]	Frost days	Cumulative degree days	
Forest to grassland	Forest	10	0.7 ± 1.2	-14.3 ± 8.3	14.1 ± 3.8	28.4 ± 11.3	188.9 ± 9.1	1131.6 ± 268.3	
		50	1.0 ± 0.8	-7.5 ± 6.1	8.4 ± 2.2	15.9 ± 7.8	168.2 ± 51.3	697.4 ± 288.8	
	Grassland	10	<b>2.9 ± 0.9*</b>	<b>-10.9 ± 6.7*</b>	<b>22.5 ± 4.6*</b>	<b>33.4 ± 10.5*</b>	189.8 ± 6.4	<b>1737.6 ± 264.0*</b>	
		50	<b>2.7 ± 0.8*</b>	<b>-7.0 ± 5.5*</b>	<b>14.6 ± 2.6*</b>	<b>21.6 ± 7.5*</b>	154.9 ± 31.3	<b>1430.5 ± 228.1*</b>	
	Forest to cropland	Forest	10	0.8 ± 0.8	-12.1 ± 5.1	12.9 ± 3.6	24.9 ± 8.3	195.4 ± 12.5	1011.2 ± 290.1
			50	0.6 ± 0.8	-6.2 ± 3.8	7.2 ± 2.8	13.4 ± 6.2	197.4 ± 23.5	636.3 ± 317.7
Cropland		10	<b>2.9 ± 0.9*</b>	-12.0 ± 4.4	<b>23.6 ± 4.3*</b>	<b>35.6 ± 7.3*</b>	<b>187.8 ± 6.4*</b>	<b>1771.0 ± 156.0*</b>	
		50	<b>2.7 ± 0.8*</b>	-6.4 ± 3.7	<b>14.5 ± 1.7*</b>	<b>20.9 ± 4.7*</b>	<b>168.7 ± 18.7*</b>	<b>1393.3 ± 162.0*</b>	

## 4.4. Discussion

### 4.4.1. Land-use change alters soil temperature in subarctic soils

The higher temperatures, cumulative degree days and greater amplitude that we measured in grassland and cropland soils supported our hypothesis that deforestation is shifting the soil temperature regimes from a moderate temperature amplitude, with relatively low summer temperatures in forest soils, to more extreme amplitudes in agricultural soils, with particularly

warm summer temperatures. The observed soil warming upon deforestation is in line with results from earlier studies, reporting temperature increases of 2.0°C in the tropics (Jiménez et al. 2007), between 2.5 and 3.3°C in the temperate zone (Morecroft et al. 1998) and up to 5.0°C, during summer, in boreal Alaska (Grünzweig et al. 2003). Similar to our results, forest soils in all of the three studies mentioned were on average cooler in summer compared to agricultural land, which is due to shading by the forest canopy. During summer, we observed that forest soils were on average 4.0°C cooler in topsoil and subsoil than croplands and 3.8 and 4.2°C cooler than grasslands, which is slightly less than observed by Grünzweig et al. (2003). Also, cumulative degree days increased between 600 and 800, which is almost a doubling of cumulative degree days upon land-use change. This is a similar increase as reported by Grünzweig et al. (2003), which was between 500 and 650 annually. As shown in a modelling study for all of Canada, warmer winter soil temperatures can be related to thicker snow cover in deforested land compared to forest (Zhang et al. 2005). Snow cover, along with vegetation, is the most important factor determining soil temperature patterns (Qian et al. 2011, Zhang et al. 2005). Warmer winter soil temperatures in agricultural land compared to forest as a consequence of thicker snow cover on open land than on forests were also reported by Grünzweig et al. (2003). Agricultural soils of the Yukon were equally cold (cropland) and slightly warmer (grassland) than the forest soils during winter. This emphasizes the importance of vegetation for the soil temperature. Snow cover on bare soil might insulate the soil in a similar way to natural forest vegetation, but the combination of dense grasses and overlaying snow cover adds an additional insulation effect.

The temperature difference between forest and agricultural land appeared to be influenced not only by insulation of the soil by vegetation or snow but by inherent soil thermal properties, which are regulated by soil texture. Clayey grassland sites had smaller temperature differences upon deforestation than sandy sites. This can be related to the differences in the thermal properties of air, water and different minerals with clayey sites having the lowest and sandy sites having the highest thermal conductivity (Dong et al. 2015). Overall, clayey soils have a larger pore volume and are, therefore, more buffered thermally than sandy soils, if the pore space is not water filled

but contains a lot of air. Under wet conditions, heat exchange between the soil and the atmosphere is increased and soils cool down more strongly than under dry conditions. In cropland soils, no relationship between soil texture and temperature was supported statistically. Since croplands in the Yukon are irrigated regularly, the thermal insulation of the soils might be reduced at all cropland sites, independent of soil texture, which was not the case in unirrigated grassland sites. Moreover, the effects of soil properties on the soil temperature regime might be masked by differences in vegetation.

As we have shown, land-use change has a soil warming effect of around 2.1°C. Due to climate change, Canadian soils warmed by 0.6°C during the 20<sup>th</sup> century, with regional differences between -2 and +5°C, underlining the great importance of spatially distributed soil temperature measurements (Zhang et al. 2005). Climate change related alterations in the temperature of Canadian soils have been observed to be greatest in spring (0.26 – 0.30°C per decade since the 1950s), while winter soil temperatures have not changed significantly (Qiang et al. 2011). In contrast, air temperatures in Canada have increased most strongly in winter (2.3°C between 1950 and 2010) and less so in spring (1.7°C between 1950 and 2010). The annual mean air temperature increased by 1.5°C between 1950 and 2010 or 0.25°C per decade (Vincent et al. 2012), which is slightly less than the increase in soil temperature within the same time. Our results imply that land-use change from pristine forest to agriculture exceeds the effect of climate change on soil temperature and is particularly strong during summer, when biological activity is highest in subarctic ecosystems. Common models of SOC turnover are fed by air temperature instead of soil temperature (Balesdent et al. 2018, Kaczynski et al. 2017, Crowther et al. 2016). Thus, one of the most important drivers of microbial activity and SOC mineralization, that is temperature, is assumed to be independent of the vegetation cover. The present study highlights that this might be a severe shortcoming in such models, which often fail to capture land-use change effects (Boysen et al. 2021, Gottschalk et al. 2010).

#### **4.4.2. Litter decomposition and its implications for SOC dynamics in subarctic soils**

It was hypothesized that warmer summer temperatures foster the decomposition of fresh soil organic matter in agricultural soils compared to forest soils. Indeed, there was a greater mass loss of tea in cropland soils than in forest soils. Particularly in subsoils, mass loss was around 8.7% higher in croplands than in forests, while it was 2.9% in topsoil, which might be related to the fact that the temperature effect was more masked by agricultural management in the topsoil. However, the hypothesis must be rejected for grassland soils, since there was no significant difference in litter decomposition between forest and grassland soils, despite warmer soil temperatures in grasslands than in forests. This might suggest that not only did the deforestation induce soil warming but also agricultural management controlled litter decomposition. In a global study, Djukic et al. (2018) reported that precipitation is the most important climatic factor for litter decomposition and temperature appeared to be less important. However, their study was conducted only during summer, where water availability, and not temperature, was the limiting factor. Our results suggest that, in temperature-limited regions, the temperature may play an important role in litter decomposition, as shown by the relationship between cumulative degree days and litter mass loss. However, missing evidence for this relationship in grassland/forest pairs might underline the importance of water availability as a prerequisite for decomposition. Soil moisture was not quantified in this study, but we can assume that croplands had higher soil moisture than grasslands, as croplands are irrigated regularly due to the dry climate in the research area (on average, 262 mm annual precipitation (Environment Climate Change Canada 2020)) and grasslands remain rainfed. However, litter decomposition might be underestimated in grassland plots, since there were more fine roots potentially growing into the tea bags, which might not have been removed entirely before weighing.

Various studies have reported losses of SOC after land-use change (Grünzweig et al. 2003, Grünzweig et al. 2004, Guo and Gifford 2002, Wei et al. 2014, Poeplau 2011). A certain proportion of these losses can be assigned to deforestation-induced removal of the uppermost soil layers, including litter and parts of the topsoil (Grünzweig et al. 2003). C input quantity (Luo et al. 2017)



and quality (Cotrufo et al. 2019) as well as frequent soil disturbances and changes in aggregate stability (Six et al. 2000) can add to the land-use change driven alterations in SOC stocks. Here, we were able to show that microclimatic changes and their effect on litter decomposition are another relevant driver of SOC stock change after deforestation. Under natural conditions, as represented by the forest sites, SOC stocks were related to mean soil temperature to some extent. The coldest forest soils stored significantly more SOC than the warmest forest soils, with a linear decrease in SOC of  $38.6 \pm 17.2 \text{ Mg C ha}^{-1} \text{ per } ^\circ\text{C}$  ( $p < 0.05$ ) warming (Figure 4.8). This slope is one order of magnitude higher than values observed in warming experiments (Peplau et al. 2021:  $1.9 \text{ Mg C ha}^{-1} \text{ per } ^\circ\text{C}$ , Verbrigghe et al. 2022:  $2.8 \text{ Mg C ha}^{-1} \text{ per } ^\circ\text{C}$ ). This might indicate that the observed range in forest SOC stocks cannot solely be explained by a direct temperature effect. Instead, it has been observed that the coldest sites, which were also characterized by shallow permafrost (detectable ground ice in summer within the upper 50 cm), were rather wet sites with thick, C-rich A horizons. Farmers reported that the waterlogging ceased after deforestation, i.e. with the deepening of the permafrost layer (Peplau et al. 2022). Despite a high general variability in SOC stocks across forest sites, our data suggests that, in the presence of permafrost, warming might have a much more severe effect than in non-permafrost soils. This is because water infiltration is hampered by underlying ice layers and soils remain wetter during summer than sites without permafrost. The linear relationship between soil temperature and SOC stocks was not apparent in agricultural soils, although SOC stocks were reduced significantly in cropland soils (Peplau et al. 2022). The decoupling of SOC stocks from soil temperature in agricultural soils shows that the natural, climate-driven balance between C input, mineralization and C storage is heavily disturbed by agricultural activity. Depending on agricultural practices (i.e. cultivated crops, soil management, irrigation), the amount and quality of C input varies greatly from natural habitats and also between sites. This makes the quantification of land-use change induced alterations of C mineralization more complicated. Given that land-use change will increase soil temperatures in subarctic soils, the future spread of agriculture on permafrost soils may therefore additionally accelerate the climate-carbon feedback, causing more SOC loss than already caused by climate change and the warming of pristine forests. The observed different effects of land-use change on

soil temperature and decomposition in croplands and grasslands indicate that changes in the soil water regime might be essential for prospective land-use carbon feedbacks. Since warmed soils have a deeper (or entirely thawed) active layer, soils naturally dry upon warming due to drainage effects (Andresen et al. 2020).

#### 4.5. Conclusion

The aim of this study was to quantify the effect of land-use change from subarctic forest to agricultural land on soil temperature and decomposition of fresh soil organic matter. Using tea as a standardized litter material which is easy to compare under varying site properties allowed us to couple soil temperature as influenced by land-use type with litter decomposition in diverse soils under subarctic agriculture. Overall, the effect of land-use change on soil temperature exceeded the effect of past climate change and thus strongly enhances the climate-carbon feedback. Deforestation resulted in soil warming, but the consequences for litter decomposition depended on the subsequent management. Cropland soils, which are more often disturbed by field operations and irrigation, had a greater decomposition of fresh organic matter than forests. This was not the case in grasslands, even though they exhibited a greater difference in soil temperature. Therefore, future climate mitigation strategies and modelling efforts need to consider the effect of land cover on soil temperature changes, additional to air temperature changes.

#### 4.6. Data availability

All data used for this study is openly available at DOI [10.5281/zenodo.7219753](https://doi.org/10.5281/zenodo.7219753)

#### 4.7. Author contribution

C.P. and J.S. designed the tea bag and temperature experiments and were responsible for the field setup. J.S. and T.P. finalized the experiments. T.P. was responsible for writing the original draft, including figures and statistical analysis, and all co-authors contributed by reviewing and editing. E.G. provided additional language editing.

#### 4.8. Competing interests

The authors declare that they have no conflicts of interest.

#### 4.9. Acknowledgements

We would like to thank all the farmers who participated in this study and allowed us to use their land for our experiments. We are also grateful to Yukon's First Nations who granted us permission to study their traditional land, without which this study would not have been possible. This study was part of the project 'Braking the Ice', funded by the German Research Foundation, grant number 401106790. Funding for E.G. was provided by the Science & Technology Branch of Agriculture & Agri-Food Canada (Project J-001756 'Biological Soil Carbon Stabilization').

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## 5. Synthesis

### 5.1. Contribution to current research

This thesis aimed to understand how the transition from pristine subarctic forests to agricultural systems affects the quality and quantity of SOC. There were substantial knowledge gaps regarding potential feedbacks between land-use change, SOC and climate warming in subarctic regions, which have been addressed in three studies.

First, it was possible to use a geothermal spring to establish a thermosequence by sampling soils at different distances from the spring, with different soil temperatures (Peplau *et al.* 2021). The Takhini hot springs provided the rare opportunity to observe naturally warmed mineral soils instead of peatlands. As it turned out during the sampling campaign 2021, most hot springs in the Yukon are surrounded by wetlands with organic soils, which would not be comparable to the results of studies on mineral soils. The first study of this thesis (Peplau *et al.* 2021) has shown that the use of geothermal warming has some methodological advantages over the established application of laboratory incubation or artificial soil warming. However, this study also highlighted some major concerns, which is why geothermal warming is best used in combination with some of the well-established methods for studying soil warming (Figure 5.1).

The second study of this thesis added meaningful information to the sparse body of data regarding the effects of deforestation for agricultural purposes in subarctic ecosystems (Peplau *et al.* 2022). The systematic sampling design of the study facilitated the quantification of various soil- and site-parameters' influence on SOC dynamics. Permafrost occurrence (Grünzweig *et al.* 2015), age of the agricultural plots (Deng *et al.* 2016), management (VandenBygaart *et al.* 2003) and soil properties (Fu *et al.* 2022) have been proposed as relevant for SOC dynamics upon land-use change, but no systematic case study accounting for all of these parameters had yet been carried out.

In addition to sampling for the second study (Peplau *et al.* 2022), the setup for another experiment was prepared during the field campaign in 2019, which was presented in Chapter 4 (Peplau *et al.*

in review). Tea bags are standardized, easily obtained and more affordable when compared to other litter bags. Thus, studies interested in OM decomposition across different ecosystems have often been carried out using teabags as fresh OM analogues (Djukic *et al.* 2018). Detailed recording of soil temperature helps to characterize the microclimatic differences of soil under different vegetation and while there have been many studies that include differences in air temperature or soil temperature between different land-use types, there are no studies that directly assess the effect of land-use change on soil temperature and litter decomposition (Mahmood *et al.* 2014; Lembrechts *et al.* 2022). This lack of data hampers the precise quantification of temperature effects on the C-cycle in earth system models. Although Peplau *et al.* (in review) is missing some data regarding soil moisture, and there were sometimes difficulties in distinguishing between root and tea OM, the study provides meaningful methodological insights and comparison data for future studies.”

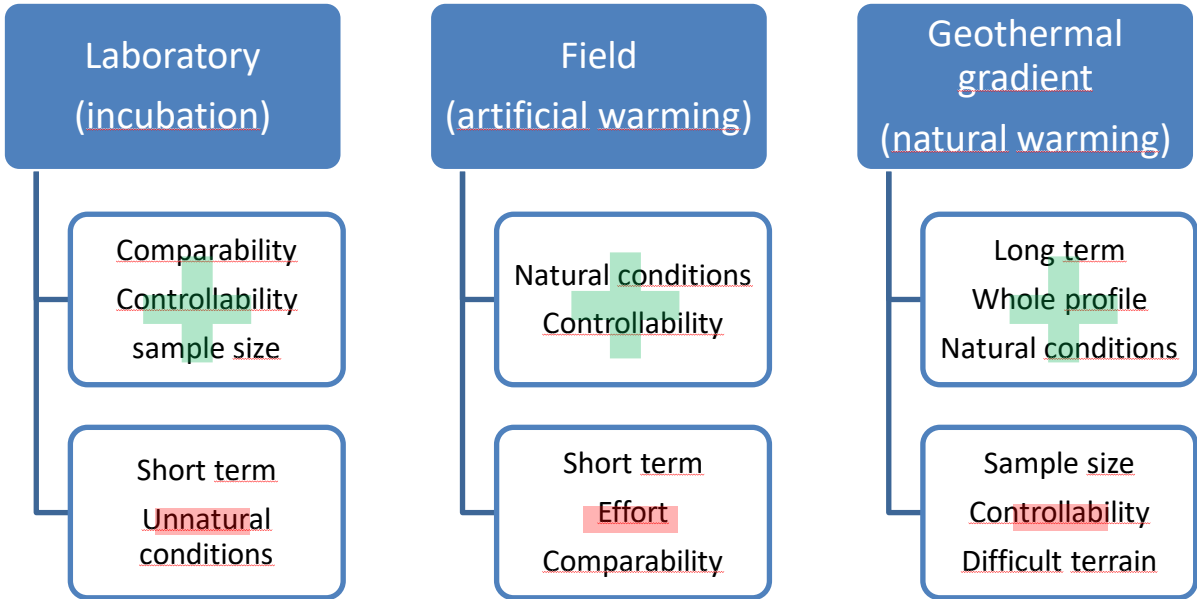


Figure 5.1: Comparison of the advantages and shortcomings of laboratory, artificial field, and geothermal warming experiments

## 5.2. Answering the research questions

### 5.2.1. How does land-use change from forest to agriculture affects SOC stocks and fractions?

Subarctic forests typically store large amounts of SOC (FAO & ITPS 2018), the majority of which is weakly decomposed, plant-derived, POM (Mueller *et al.* 2015; Peplau *et al.* 2022). Forest clearing for the purpose of agriculture in subarctic regions is typically carried out by cutting down the trees and then piling up roots and remaining trunks by pushing of the first few centimetres of soil with a bulldozer. The piles of forest debris are then burned and resulting ash is then spread across the new field. Farmers then wait for up to five years to allow for potential permafrost to thaw and the soil to drain (Peplau *et al.* 2022). This practice initially leads to great losses of SOC, as the forests' topsoil contains the majority of SOC (Hossain *et al.* 2007). However, it has been shown in Peplau *et al.* (2022) that agricultural soils of the Yukon often contain more mineral associated carbon than the forest soils. This accumulation indicates an increase in SOC stabilization, which is usually associated with a shift from plant-derived OM to microbial-derived OM (Angst *et al.* 2021). This result is also in line with observations of Schroeder *et al.* (2022a; 2022b), which reported an increase in microbial carbon use efficiency in the Yukon's soils upon land-use change.

### 5.2.2. Is there an influence of permafrost on SOC dynamics upon land use change?

The presence of permafrost is crucial for SOC dynamics, as it preserves large amounts of labile SOC (Peplau *et al.* 2022). The methodology of this thesis systematically compared land-use change effects at sites with and without permafrost, thereby highlighting the differences in SOC stocks between sites with and without permafrost and quantifying the changes of SOC stocks upon the establishment of agricultural land. Farms established at sites without permafrost had similar SOC stocks to adjacent forests but there was an enormous SOC loss at sites with permafrost (Peplau *et al.* 2022). Grasslands, meanwhile, not only lost SOC when compared to the global average (Deng *et al.* 2016), but additionally lost SOC to a greater degree than croplands originating from permafrost forests. As litter decomposition was not increased in grassland soils (Peplau *et al.* in

review), the loss of SOC in grassland soil originating from permafrost cannot be explained by quick decomposition of freshly exposed labile POM alone. It is possible the greater drainage depth of thawed permafrost soils increases leaching of soluble compounds (Frey & Smith 2005) or that increased aggregate decay upon warming (Poeplau *et al.* 2016) exposes additional labile SOM, while there might be considerable differences in C-inputs among the different land-use categories. As discussed in chapters 3 and 4 of this thesis (Peplau *et al.* 2022; in review), water availability may, additionally, play an important role by explaining such differences. However, when compared to forests, both the discrepancy observed in SOC losses in grasslands and differences in stable litter decomposition, require further investigation including the quantification of C-inputs and soil hydrology.

It has been proposed in the literature (Grünzweig *et al.* 2015, Dean *et al.* 2017) that the change in SOC stocks depends on the time since conversion, with rapid short-term losses of SOC and gradual regain of SOC afterwards. This could not be entirely confirmed for agricultural systems in the Yukon, despite sampling farms with a broad range of durations under cultivation (Peplau *et al.* 2022). While, statistically, time since conversion had an influence on SOC stocks in sites with permafrost, results must be interpreted with care as the sample size was small and significance could be driven by individual farms. Furthermore, statistical significance was detected in relative, but not absolute, changes of SOC stocks (chapter 3, Peplau *et al.* 2022).

### **5.2.3. What is the effect of land-use change on soil microclimate and how do soil temperature changes affect SOC dynamics?**

Deforestation invariably leads to an increase in mean annual soil temperature in subarctic soils (chapter 4, Peplau *et al.* in review). Summer temperatures were especially elevated, while winter temperatures, although partially increased, remained well under the freezing point. Warmer summer temperatures led to an increase of the cumulative degree days, which is an important measure in plant-cultivation and indicates an extension of the vegetation period and potentially quicker crop development (Hamdi *et al.* 2012). Farmers might welcome the increase of cumulative degree days, because it encourages the development of the planted crops (Bonhomme 2000) but

it also has implications for the soil microbiome. Because fungal and bacterial growth have different temperature optima with bacteria having lower growth-rates at high temperatures than fungi and vice versa (Bárcenas-Moreno *et al.* 2009), it is likely that soil warming plays an important role for microbial community composition. Since Yukon soils had a greater microbial growth in agricultural land than in forests (Schroeder *et al.* 2022a; 2022b) these changes to community composition may result in changes to the carbon use efficiency, and consequently SOC storage dynamics, of subarctic agricultural soils.

The effect of deforestation on soil temperatures as well as on SOC stocks and fractions was studied at farms with different ages between 119 and 10 years. We determined that the effect of time since deforestation may be negligible (chapter 3, Peplau *et al.* 2022) and that litter decomposition was not affected by the age of the farms (chapter 4, Peplau *et al.* in review). However, the results of Peplau *et al.* 2021 (chapter 2) suggest that soil warming might have a long-term effect on litter decomposition. While the actual litter layer was not affected by soil warming, which might be due to unchanged air-temperatures along the thermosequence, the results of the tea bag experiment at the geothermal gradient (chapter 3, Peplau *et al.* 2021) showed that there was an increase in litter decomposition in warmed soils. Changes of C:N ratio in soils due to enhanced C mineralization and unchanged N content give a glimpse of future changes in SOC dynamics. It is likely that warming, either climate-change driven or land-use driven, will lead to overall SOC losses. However, results from subarctic soils suggest a shift in the remaining SOC towards more stable forms as a result of increased carbon use efficiency (Schroeder *et al.* 2022b) and accumulation of C in the mineral-associated fractions (Peplau *et al.* 2021, 2022).

### 5.3. Conclusions and outlook

This thesis serves as an intensive examination of the effects of temperature and land-use change on SOM dynamics in the Yukon. The three studies herein covered a broad range of factors that influence the stocks and quality of SOM stored in subarctic forest soils (Figure 5.2). Both land-use change and climate change will lead to a shift from POM-dominated SOM to more MAOM-dominated SOM, the consequence of which is a large overall loss of SOC. Deforestation in subarctic

regions enhances natural climate-warming effects, and places additional stress on an ecosystem which is inherently highly sensitive to environmental changes. The role of permafrost is particularly important, as much more SOC is released into the atmosphere from permafrost soils than from non-permafrost soils.

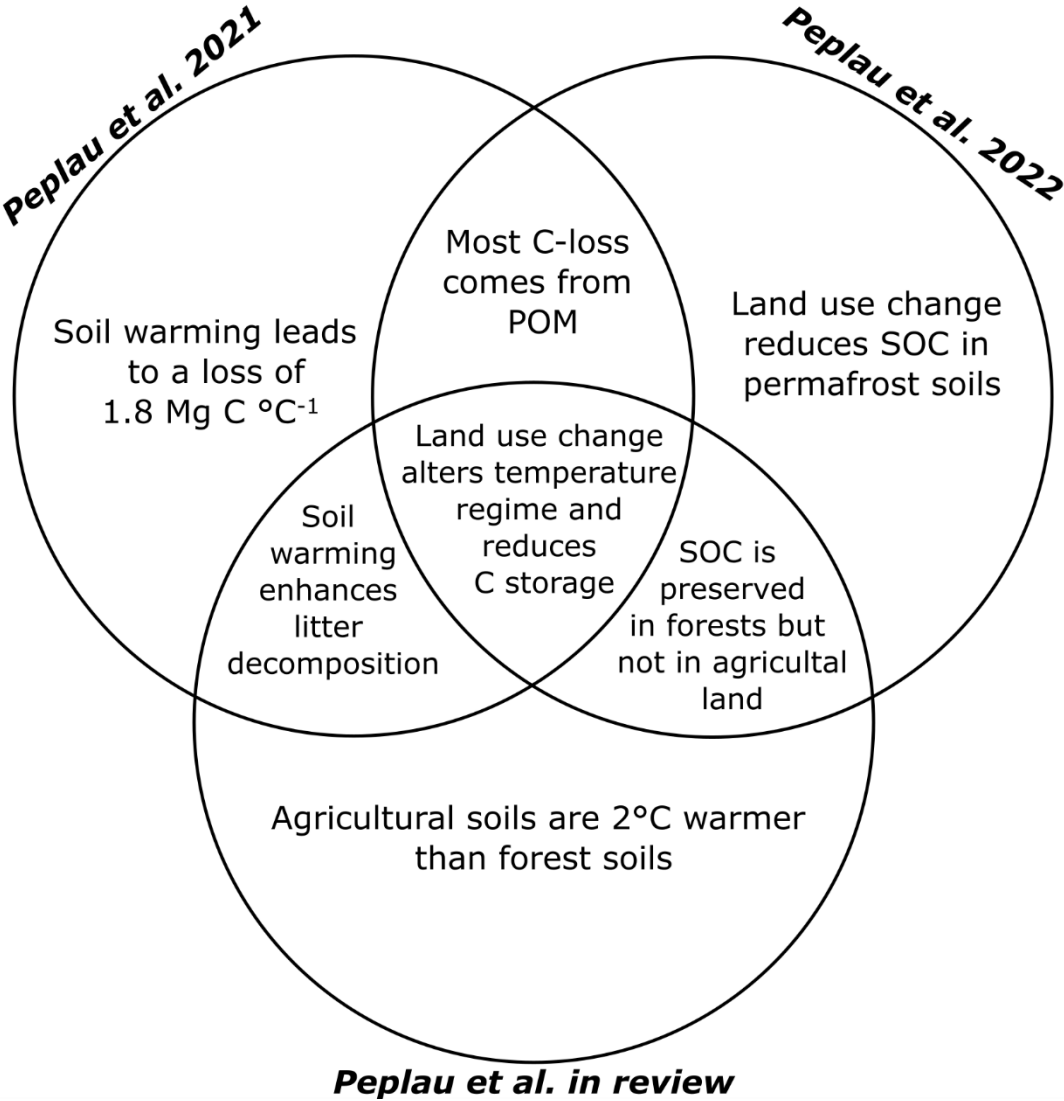
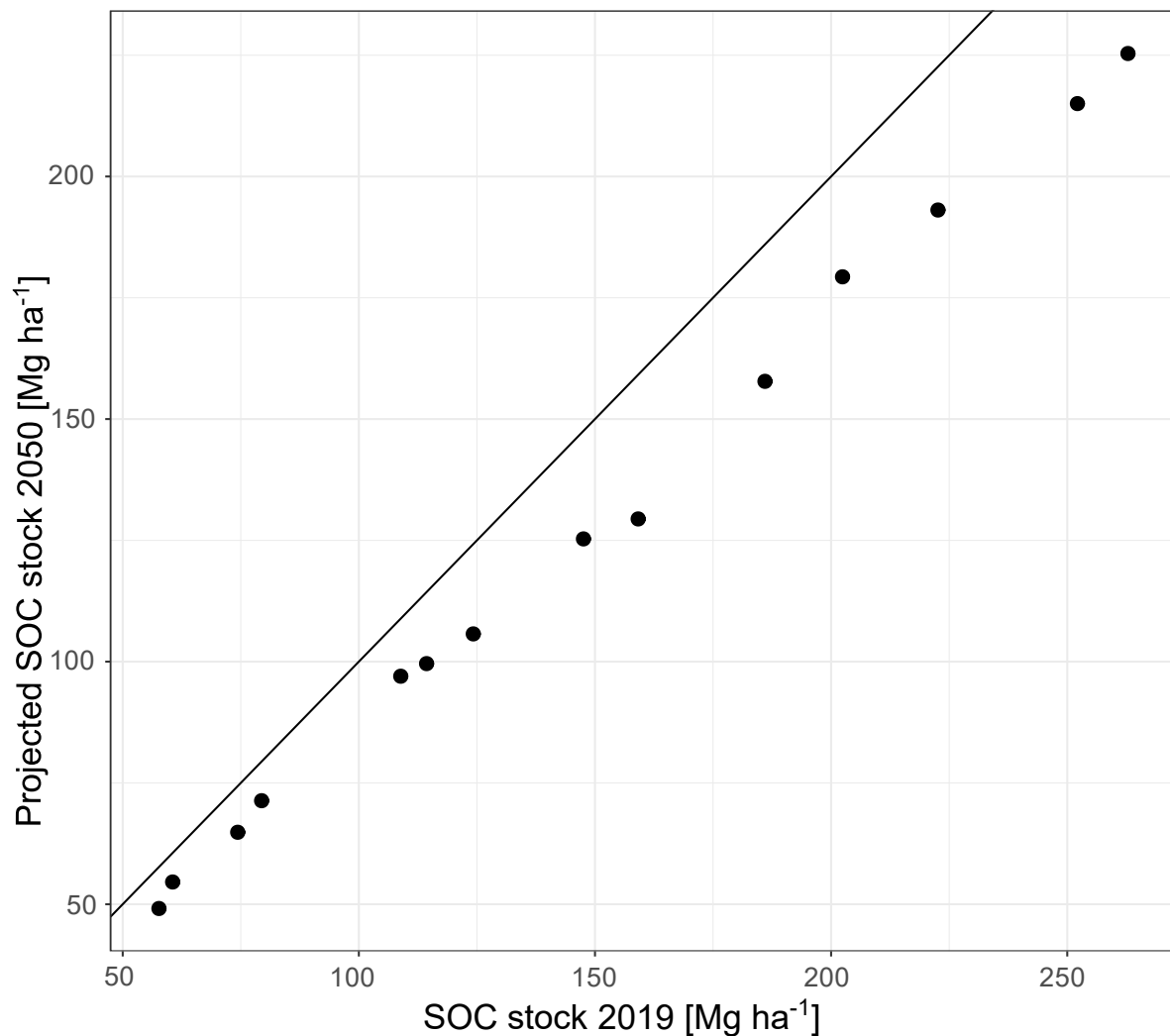


Figure 5.2: Conceptual diagram of the major conclusions from the three studies conducted for this thesis.

Climate change will likely warm the main centres of the Yukon by 2.2 to 2.4 °C by 2050 (Table 1.1). Along with warmer air temperature comes warmer soil temperature, which will accelerate SOC mineralization and intensify the feedback between warming and additional C-emissions. For every °C warming, 1.8 Mg C ha<sup>-1</sup> (or 3%) of the total SOC stock will be lost in the long run (chapter



2, Peplau *et al.* 2021). Additionally, converting natural ecosystems for agriculture warms soils by  $\sim 2^{\circ}\text{C}$ , and is additive to climate-induced warming (chapter 4, Peplau *et al.* in review). The result is a mean loss of  $20.3 \pm 10.9 \text{ Mg C ha}^{-1}$  with the largest losses from soils with high SOC stocks (Figure 5.3).



**Figure 5.3: Recent (2019) and predicted (2050) soil organic carbon (SOC) stocks in mineral soils of the Yukon. Points represent the sampled forest soils from Peplau *et al.* in review. The solid line depicts the 1:1 line of actual and predicted SOC stocks. Predictions are based on the assumption of  $2.3^{\circ}\text{C}$  climate change (climatedata.ca) and on the mean soil temperature difference between forest and agricultural land at each site (mean of measured soil temperature at 10 and 50 cm in cropland and/or grassland)**

This thesis revealed meaningful insights into the interrelations between climate change, northwards-expanding agriculture and the role of soils as an essential part of the global C-cycle. Earth system models may help to mitigate ongoing climate change and could support decision

making by predicting the consequences of climate change, deforestation and agricultural activities but great uncertainties remain because human impacts mask many natural processes. Irrigation and soil hydrological properties appear to be of major importance for crop production and SOC dynamics but the strength of this interaction remains unclear. Climate change-induced shifts in precipitation patterns, e.g. time and amount of rainfall or snow cover, may accelerate or slow down decomposition processes and change the requirement for irrigation. Meanwhile, warming induced increases of the depth of the active layer could similarly alter such effects. For a detailed assessment of the C cycle in Nordic agriculture it is also necessary to determine not only SOC dynamics but also ecosystem losses and inputs; for example, C losses via harvest and C inputs via application of organic fertilizer. Carbon inputs, which might be imported directly, as with compost or pellets from outside the farms, or indirectly in the form of forage, affect the overall C balance of the agricultural system by partially compensating for losses due to harvest (chapter 3, Peplau *et al.* 2022), but might also cause C losses in the regions from which the C is imported. Additionally, when the permanent vegetation cover of forests is removed, a greater temperature amplitude (chapter 4, Peplau *et al.* in review) may enhance physical weathering and the cultivation of crops is likely to foster or hamper biological activity. Consequently, microbial activity may be altered, which has the potential to affect the stability and dynamics of SOM (Schroeder *et al.* 2022b).

Expanding agricultural areas to untouched forest may be necessary to provide food-security for northern communities and, despite the decreases in SOC shown in this thesis, reduce the overall GHG emissions of feeding the peoples of the Yukon by reducing the CO<sub>2</sub> cost of fossil fuels necessary for delivery to these remote areas (Kissinger 2012). However, selecting the most suitable patch of land to establish cropland and grassland is crucial to obtain a sustainable production cycle. In order to minimise energy cost and reduce GHG emissions, permafrost-soils and especially remote areas should be avoided for establishment of new agricultural areas. If Nordic farmlands are proactively planned with this in mind, environmental impact can be limited while preserving pristine subarctic ecosystems.

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# Supplementary Material

## Supplement A: Peplau et al. 2021

**Table S A 1: General soil parameters. Mean of four field replicates**

Warming	Texture (Sand/silt/clay)	Depth [cm]	pH	TIC [%]	Rock fragments [mass-%]	BD <sub>finesoil</sub>	C/N
+7.7 °C	14/63/21	0-10	7.52	0.10	3.92	0.93	16.52
		10-20	7.42	0.03	7.42	0.95	12.27
		20-40	7.79	0.05	0.63	1.18	10.49
		40-60	7.96	0.57	0.17	1.26	9.45
		60-80	8.08	1.29	0.34	1.22	10.35
+ 1.8	12/70/15	0-10	7.31	0.15	3.69	0.86	16.69
		10-20	7.51	0.09	1.96	1.14	16.21
		20-40	7.62	0.03	0.46	1.08	13.56
		40-60	8.12	0.55	0.41	1.36	12.51
		60-80	8.16	1.08	1.12	1.10	12.24
+ 0.5	25/59/16	0-10	7.99	0.08	4.67	0.95	15.03
		10-20	8.06	0.02	2.89	1.15	12.73
		20-40	8.22	0.02	11.34	1.01	13.73
		40-60	8.21	0.14	9.28	1.02	14.92
		60-80	8.37	0.93	8.33	1.14	13.36
Reference	29/58/13	0-10	6.69	0.04	5.22	0.57	19.03
		10-20	6.9	0.02	5.58	1.06	14.81
		20-40	7.42	0.02	5.07	1.18	15.50
		40-60	8.07	0.13	3.57	0.77	17.36

		60-80	8.82	0.59	2.85	0.79	18.55
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**Table S A 2: C and N stocks [Mg ha<sup>-1</sup>] in litter, topsoil and subsoil at the four plots. Mean values (n = 4) with standard error in brackets.**

	+7.7 °C		+1.8 °C		+0.5 °C		Reference	
	C	N	C	N	C	N	C	N
Litter	10.06 (2.0)	0.31 (0.04)	9.07 (0.16)	0.36 (0.04)	7.83 (1.07)	0.35 (0.05)	11.75 (2.15)	0.39 (0.07)
Topsoil (0 - 20 cm)	21.02 (3.43)	1.34 (0.23)	22.13 (6.87)	1.40 (0.50)	19.91 (3.43)	1.36 (0.23)	25.81 (3.03)	1.46 (0.17)
Subsoil (20 - 80 cm)	18.48 (0.64)	1.91 (0.09)	19.37 (1.33)	1.53 (0.13)	24.49 (3.94)	1.79 (0.33)	28.02 (1.86)	1.77 (0.16)

**Table S A 3: Results of the linear model for C stocks. \*significant with p<0.05**

Depth	Fraction	Transformatio n	Intercep t	Slope	R2	p
5	SOC stock	log	2.80	-0.01	0.01	0.67
5	POM	linear	10.19	-0.39	0.10	0.23
5	SA_C_stock	linear	2.83	0.08	0.02	0.60
5	SC_C_stock	linear	3.19	0.12	0.10	0.22
5	rSOC_stock	log	-0.36	0.04	0.06	0.35
5	DOC_C_stock	log	-1.51	-0.01	0.01	0.66
15	SOC_corr_Topsoil	log	1.49	-0.03	0.02	0.61
15	POM_C_stock	log	0.89	-0.07	0.29*	0.03
15	SA_C_stock	linear	0.85	-0.01	0.00	0.86
15	SC_C_stock	linear	2.06	-0.04	0.02	0.60



15	rSOC_stock	log	-0.35	-0.01	0.01	0.70
15	DOC_C_stock	linear	0.21	0.00	0.01	0.69
30	SOC_corr	linear	10.27	-0.15	0.06	0.36
30	POM_C_stock	log	1.43	-0.07	0.34*	0.02
30	SA_C_stock	log	0.03	0.02	0.04	0.47
30	SC_C_stock	log	0.90	0.01	0.01	0.67
30	rSOC_stock	linear	1.72	0.08	0.30*	0.03
30	DOC_C_stock	log	-0.84	0.01	0.02	0.61
50	SOC_corr	linear	9.57	-0.29	0.07	0.32
50	POM_C_stock	linear	3.49	-0.23	0.22	0.07
50	SA_C_stock	linear	0.95	-0.01	0.00	0.90
50	SC_C_stock	linear	4.72	-0.04	0.01	0.75
50	DOC_C_stock	linear	0.41	0.00	0.01	0.72
70	SOC_corr	linear	4.52	-0.47	0.12	0.19
70	POM_C_stock	linear	1.37	-0.18	0.17	0.12
70	SA_C_stock	linear	0.87	-0.11	0.14	0.15
70	SC_C_stock	linear	2.10	-0.16	0.05	0.41
70	DOC_C_stock	linear	0.18	-0.02	0.12	0.19

**Table S A 4: Results of the linear model for C content. \*significant with  $p < 0.05$**

Depth	Fraction	Transformation	Intercept	Slope	R2	p
5	SOC gkg	linear	25.62	-0.99	0.08	0.30
5	POM	linear	15.58	-0.98	0.14	0.16
5	SA_C_gkg	log	1.26	-0.02	0.01	0.76
5	SC_C_gkg	linear	4.69	-0.02	0.00	0.93
5	rSOC_gkg	log	-0.04	0.01	0.00	0.80

5	DOC_gkg	log	-1.19	-0.04	0.08	0.29
15	TOC_gkg	log	1.68	0.00	0.00	0.94
15	POM_C_gkg	log	0.77	-0.04	0.05	0.39
15	SA_C_gkg	linear	0.86	0.03	0.01	0.72
15	SC_C_gkg	log	0.51	0.01	0.01	0.79
15	rSOC_gkg	log	-0.46	0.02	0.03	0.53
15	DOC_gkg	log	-1.68	0.02	0.07	0.31
30	SOC_corr	linear	10.27	-0.15	0.06	0.36
30	POM_C_gkg	log	0.66	-0.08	0.44*	0.01
30	SA_C_gkg	log	-0.74	0.01	0.01	0.77
30	SC_C_gkg	log	0.13	0.00	0.00	0.98
30	rSOC_gkg	linear	0.79	0.03	0.33*	0.02
30	DOC_gkg	linear	0.20	0.00	0.01	0.75
50	SOC_corr	linear	9.57	-0.29	0.07	0.32
50	POM_C_gkg	linear	2.04	-0.17	0.44*	<0.001
50	SA_C_gkg	linear	0.50	-0.01	0.01	0.68
50	SC_C_gkg	log	0.97	-0.04	0.29*	0.03
50	DOC_gkg	log	-1.49	-0.04	0.32*	0.02
70	SOC_corr	linear	4.52	-0.47	0.12	0.19
70	POM_C_gkg	log	0.06	-0.10	0.23	0.06
70	SA_C_gkg	log	-0.54	-0.10	0.24	0.05
70	SC_C_gkg	log	0.62	0.04	0.05	0.38
70	DOC_gkg	linear	0.19	-0.01	0.16	0.12

**Table S A 5: Results of the linear model for N stocks. \*significant with p<0.05**

Depth	Fraction	Transformatio n	Intercept	Slope	R2	p
5	N stock	log	-0.02	-0.01	0.01	0.79
5	POM	linear	0.43	-0.02	0.14	0.15
5	SA_N_stock	linear	0.23	0.00	0.01	0.74
5	SC_N_stock	linear	0.34	0.01	0.08	0.30
5	rN_stock	linear	0.02	0.00	0.15	0.13
15	N_corr_Topsoi l	linear	0.39	-0.01	0.00	0.84
15	POM_N_stock	log	-2.41	-0.10	0.50*	<0.001
15	SA_N_stock	log	-2.81	0.00	0.00	0.96
15	SC_N_stock	linear	0.25	0.00	0.00	0.89
15	rN_stock	linear	0.03	0.00	0.04	0.49
30	N_corr	log	-0.38	0.03	0.18	0.11
30	POM_N_stock	log	-2.05	-0.07	0.24	0.06
30	SA_N_stock	log	-2.18	-0.04	0.08	0.29
30	SC_N_stock	linear	0.26	0.05	0.49*	<0.001
30	rN_stock	linear	0.18	-0.01	0.18	0.11
50	N_corr	log	-0.58	0.05	0.11	0.20
50	POM_N_stock	linear	0.11	-0.01	0.16	0.12
50	SA_N_stock	linear	0.09	0.00	0.04	0.48
50	SC_N_stock	linear	0.43	0.03	0.27*	0.04
70	N_Corr	linear	0.32	-0.03	0.07	0.34
70	POM_N_stock	linear	0.05	-0.01	0.17	0.12
70	SA_N_stock	linear	0.05	-0.01	0.13	0.17
70	SC_N_stock	linear	0.21	-0.01	0.02	0.58

**Table S A 6: Results of the linear model for N content. \*significant with p<0.05**

Depth	Fraction	Transformation	Intercept	Slope	R2	p
5	SOC_gkg	log	0.30	-0.04	0.05	0.39
5	POM	linear	0.66	-0.05	0.16	0.12
5	SA_N_gkg	log	-1.28	-0.03	0.02	0.63
5	SC_N_gkg	log	-0.79	0.00	0.00	0.89
5	rSN_gkg	linear	0.03	0.00	0.05	0.41
15	TN_gkg	log	-0.99	0.02	0.03	0.53
15	POM_N_gkg	log	-2.52	-0.07	0.16	0.12
15	SA_N_gkg	log	-2.92	0.03	0.02	0.62
15	SC_N_gkg	log	-1.59	0.03	0.04	0.47
15	rSN_gkg	linear	0.02	0.00	0.05	0.40
30	TN_gkg	log	-1.15	0.02	0.09	0.26
30	POM_N_gkg	log	-2.82	-0.08	0.30*	0.03
30	SA_N_gkg	log	-2.95	-0.05	0.10	0.23
30	SC_N_gkg	log	-2.25	0.13	0.42	0.01
30	rSN_gkg	linear	0.08	-0.01	0.22	0.07
50	TN_gkg	log	-1.08	0.01	0.01	0.72
50	POM_N_gkg	log	-2.90	-0.10	0.37*	0.01
50	SA_N_gkg	linear	0.05	0.00	0.07	0.33
50	SC_N_gkg	log	-1.45	0.04	0.15	0.14
70	TN_gkg	log	-1.30	0.02	0.03	0.56
70	POM_N_gkg	log	-3.31	-0.10	0.21	0.07
70	SA_N_gkg	linear	0.05	-0.01	0.14	0.16
70	SC_N_gkg	log	-1.69	0.07	0.14	0.15

Supplement B: Peplau et al. 2022

**Table S B 3: Site preparation and management at sampling sites**

Site	Clearing	Irrigation	Organic fertilisation	Mineral fertilisation	Crop types	Dominating tree types	Tilling depth
Sites with permafrost							
DR	No information	No information	No information	No information	No information	Broadleaf and coniferous, evenly mixed	No information
DW	No information	No information	No information	No information	No information	Coniferous	No information
KK	Bulldozer, removal of stems and roots	Yes	Wood ash from nearby heating plant, in exchange for own coarse roots and stumps	No	Vegetables in crop rotation (potatoes, green manure, leaf, brassica, root crops, cereals)	Coniferous	20 cm
KL	Chainsaw, sled dogs, burn brush	Yes	Plant-based compost, pelletised manure, occasionally composted manure	No	Annual vegetables (zucchini, potato), perennial fruits (strawberries), onions and trees	Coniferous	30 cm
MA	No information	No information	No information	No information	No information	Broadleaf	No information

MG	Bulldozer, burn piles	Yes	Composted poultry manure	No	Berries, vegetables (peas, carrots, potatoes, broccoli, cabbage)	Broadleaf and coniferous, evenly mixed	10 cm
PC	Bulldozer, burn piles	Yes	Manure from own animals	No	Vegetables/pasture	Coniferous	30 cm
RC	Bulldozer, burn piles, disking	No	Horse and steer manure	No	Oats	Coniferous	30 cm
RF	No information	No information	No information	No information	No information	Broadleaf and Coniferous, evenly mixed	No information
SI	Burnt brush	Yes	Organic pellet fertiliser, occasionally own compost	No	Vegetables	Broadleaf	30 cm
TH	Burning piles, chipping, pigs	Yes	Blood and bone meal	No	Vegetables (potatoes, brassicas, onions), greens	Coniferous	20 cm
Sites without permafrost							
CD	Bulldozer, burn piles, tillage	No	Cow manure by grazing cows	No	Pasture/grass	Broadleaf and coniferous, evenly mixed	20 cm after clearing, no-till

							seed drill afterwards
EF	Bulldozer, burn piles, grading	Yes	Compost, plant ferments	Various mineral fertilisers	Vegetables, poultry grazing, green manures	Broadleaf	20 cm
EG	Bulldozer, burn piles, disking	Yes	No	Pellet fertiliser, urea	Grasses, oats in some years	Coniferous	23 cm
GV	Cutting trees, tilling, pigs	Yes	Composted poultry manure	No	Vegetables (carrots, potatoes, lettuce, onions, parsley, dill)	Broadleaf and coniferous, evenly mixed	10 cm
LR	Bulldozer after wildfire, burn piles	Yes	Composted manure	No	Greens (arugula, spinach, kale, chard, lettuce), herbs (cilantro, dill, parsley), vegetables (cabbage, beets, carrots, potatoes, kohlrabi, rutabaga, fennel)	Coniferous	5 cm

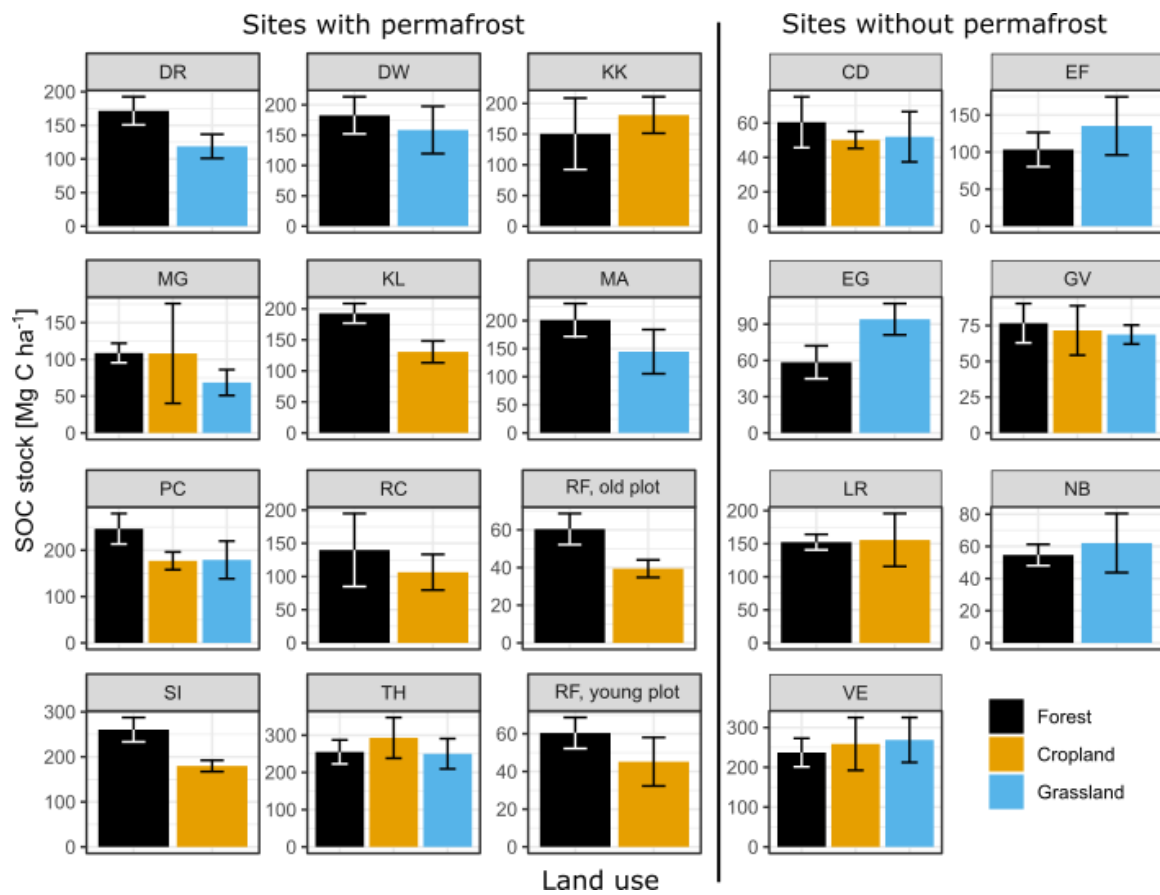
NB	Bulldozer, burn piles, liming	No	No information	No information	No information	Broadleaf and coniferous, evenly mixed	No information
VE	No information	No information	No information	No information	No information	Coniferous	No information

**Table S B 4: C content [g kg] per fraction and land use/permafrost class**

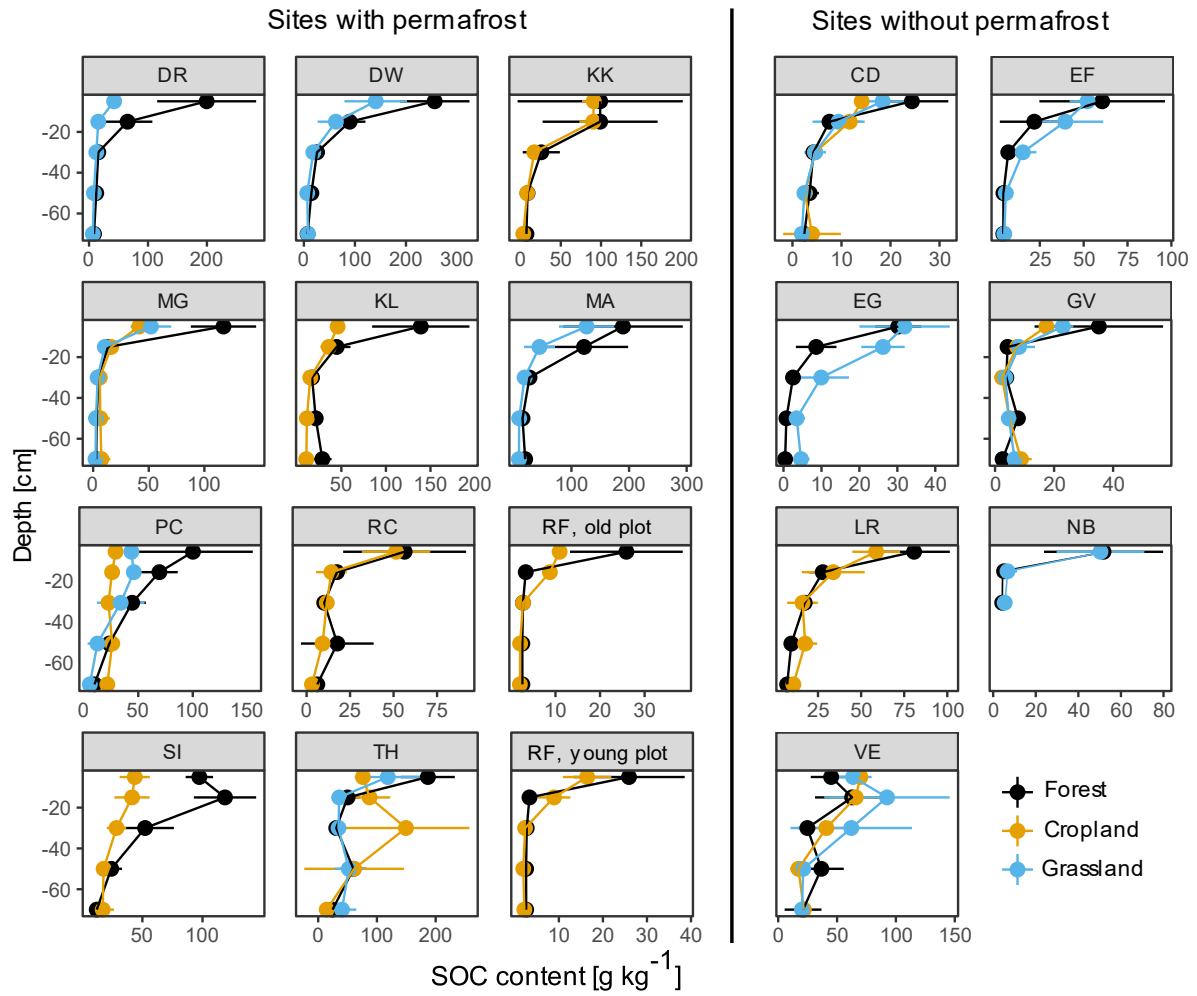
		Forest					New land use				
		POM	DOC	S+A	S+C	rSOC	POM	DOC	S+A	S+C	rSOC
Cropland, no permafrost	Tops	10.42 ±	0.55 ±	9.70 ±	4.05 ±	0.67 ±	10.66 ±	0.46 ±	4.25 ±	13.39 ±	2.24 ±
	oil	11.85	0.31	9.89	3.32	0.19	8.52	0.24	4.78	13.05	2.24
	Subsoil	4.01 ± 3.64	0.27 ±	3.37 ±	6.26 ±	NA	3.2 ± 2.78	0.22 ±	2.56 ±	5.03 ± 4.33	NA
Grassland, no permafrost	Tops	7.22 ±	0.36 ±	4.98 ±	4.79 ±	0.08 ±	13.56 ±	0.36 ±	4.96 ±	9.47 ± 7.92	0.55 ±
	oil	10.02	0.14	7.84	4.60	1.13	15.7	0.16	4.73		1.23
	Subsoil	2.87 ± 3.72	0.22 ±	2.30 ±	4.85 ±	NA	1.58 ±	0.20 ±	0.83 ±	4.76 ± 5.55	NA
Cropland, no permafrost	Tops	21.11 ±	0.62 ±	7.10 ±	9.01 ±	0.73 ±	10.85 ±	0.41 ±	6.58 ±	10.82 ±	1.13 ±
	oil	26.60	0.42	7.50	8.09	0.40	14.4	0.25	5.59	6.54	1.27



	Subsoil	7.15 ± 10.70	0.28 ± 0.15	3.01 ± 3.5	6.26 ± 4.46	NA	6.69 ± 11.61	0.22 ± 0.16	2.68 ± 2.53	6.73 ± 4.25	NA
Grassland, permafrost	Tops	36.16 ±	0.77 ±	12.77 ±	11.67 ±	1.79 ±	10.25 ±	0.51 ±	7.21 ±	15.15 ±	1.43 ±
	oil	21.63	0.45	9.77	7.39	1.10	6.99	0.23	4.36	9.14	0.97
	Subsoil	8.71 ± 12.91	0.31 ± 0.14	4.07 ± 3.69	7.85 ± 4.21	NA	5.26 ± 8.57	0.21 ± 0.10	3.18 ± 3.43	6.81 ± 6.74	NA



**Figure S B 1: Soil organic carbon (SOC) stocks to a depth of 80 cm (site NB: 40 cm) at each of the sampled farms. Bars indicate mean values, lines indicate standard deviation. n = 5 per land use plot. At farm “RF”, two cropland plots of different ages were compared with the same forest plot**



**Figure S B 2: Soil organic carbon (SOC) content [g/kg] from 0-80 cm (site NB: 40 cm) of all plots sorted by farms. Dots indicate mean values; horizontal lines indicate standard deviation. n = 5 per plot. At site RF, the same forest plot was used for comparison with two cropland plots of different age**





**Figure S B 3: Cropland at KK. Foto taken in fall 2021 (different sampling campaign, same site as 2019)**



**Figure S B 4: Grassland and cropland at GV**





Figure S B 5: Grassland at PC



**Figure S B 6: Cropland at RC**

Supplement C: Peplau et al. in review

**Table S C 5: Tea mass loss, annual mean temperature, temperature amplitude and cumulative degree days at every site, land-use type and depth. Land-use abbreviations: CM = Cropland / Market Garden, G = Grassland, F = Forest, y = younger, o = older (applies at sites with two CM plots)**

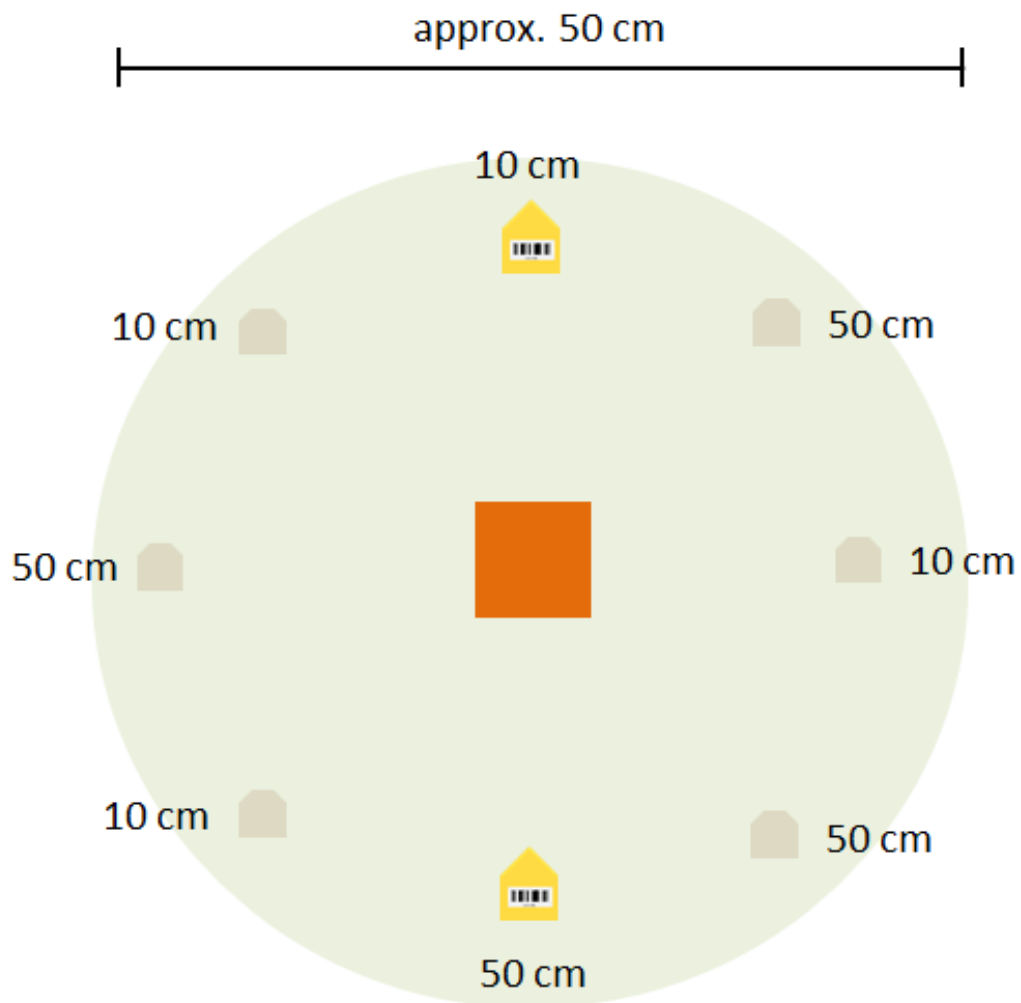
Site	Land-use	Depth [cm]	Tea bags recovered	Mean tea loss [%]	Annual mean temperature [°C]	Temperature amplitude	Cumulative degree days
CD	CM	10	3	61.3 ± 6.6	1.15	50.01	2013
		50	3	53.5 ± 4.4	1.33	32.80	1711
	F	10	3	73.1 ± 3.8	0.33	45.69	1643

		50	3	62.6 ± 4.3	0.53	27.11	1216
	G	10	3	68.7 ± 2.1	1.67	47.46	1982
		50	3	53.7 ± 5.8	1.57	30.49	1626
DR	F	10	3	65.7 ± 4.2	0.55	17.73	763
		50	3	55.9 ± 3.7	0.73	8.620	444
	G	10	3	67.4 ± 4.4	3.55	26.93	1727
		50	3	54.1 ± 0.4	3.24	17.43	1387
EF	CM	10	3	82.6 ± 6.6	3.35	29.08	1625
		50	3	67.1 ± 5.5	3.02	18.62	1277
	F	10	3	66.0 ± 7.0	1.66	27.84	1200
		50	3	51.1 ± 0.7	1.51	15.50	851
	G	10	3	59.1 ± 2.9	2.65	34.54	1665
		50	3	45.4 ± 1.1	2.66	16.99	1183
EG	F	10	2	73.3 ± 5.0	-0.66	44.42	1298
		50	3	86.1 ± 1.8	1.13	28.62	337
	G	10	2	76.6 ± 3.1	3.04	43.79	1973
		50	3	73.5 ± 3.6	2.87	31.48	1666
GV	CM	10	2	55.8 ± 4.3	1.99	41.48	1650
		50	3	47.8 ± 5.7	2.46	21.36	1327
	F	10	3	64.6 ± 2.8	1.52	24.80	1106
		50	3	51.7 ± 2.8	1.75	13.43	881
	G	10	3	70.1 ± 1.3	3.22	32.01	1680
		50	3	48.8 ± 3.6	3.22	19.42	1466
KK	CM	10	3	75.4 ± 1.7	3.09	34.56	1927
		50	2	73.0 ± 1.9	2.69	23.63	1584

	F	10	2	69.9 ± 1.9	-1.08	27.38	962
		50	2	55.6 ± 2.8	-0.96	19.14	682
KL	CM	10	3	76.2 ± 3.9	1.89	34.66	1633
		50	3	63.2 ± 7.8	1.08	23.66	1187
	F	10	3	64.3 ± 1.5	0.21	14.91	479
		50	3	55.7 ± 2.7	-0.24	3.788	69
LR	F	10	2	74.2 ± 0.4	1.13	28.12	1190
		50	3	47.3 ± 1.4	1.15	15.51	885
	CMo	10	3	77.1 ± 10.3	2.86	30.53	1643
		50	3	56.4 ± 1.0	3.04	15.92	1303
	CMy	10	3	81.3 ± 4.6	3.29	40.50	1998
		50	2	72.4 ± 0.1	3.02	20.14	1515
MG	CM	10	3	74.2 ± 6.1	3.76	31.49	1777
		50	2	61.1 ± 1.9	3.42	20.25	1411
	F	10	3	69.1 ± 3.6	1.28	18.52	814
		50	3	50.3 ± 0.9	1.01	10.50	527
	G	10	3	67.2 ± 3.9	2.86	25.12	1323
		50	2	17.6 ± 3.3	2.53	17.40	1094
NB	F	10	3	70.2 ± 3.4	1.79	22.13	1145
		50	3	57.7 ± 4.5	1.81	12.13	885
	G	10	2	59.3 ± 3.9	3.85	20.99	1506
		50	3	48.0 ± 6.5	3.69	14.53	1358
PC	F	10	2	74.6 ± 7.8	-1.68	36.93	1255
		50	3	70.6 ± 1.9	-0.90	20.10	723
	G	10	3	76.1 ± 4.4	1.22	47.31	2174



		50	3	$80.8 \pm 2.1$	1.40	31.95	1785
RC	CM	10	3	$72.8 \pm 4.8$	3.52	34.27	1805
		50	3	$60.8 \pm 2.7$	2.81	17.75	1289
	F	10	3	$60.1 \pm 1.6$	0.70	21.11	856
		50	3	$49.2 \pm 1.2$	0.30	10.55	430
RF	CM	10	3	$72.4 \pm 1.0$	3.95	45.11	1916
		50	3	$67.0 \pm 8.9$	3.79	22.91	1562
	F	10	3	$84.9 \pm 3.7$	1.25	27.07	1022
		50	3	$52.7 \pm 4.8$	1.20	14.16	680
SI	CM	10	3	$73.2 \pm 2.9$	1.94	30.85	1560
		50	3	$54.1 \pm 2.3$	2.23	18.30	1307
	F	10	3	$70.2 \pm 5.0$	0.16	21.65	890
		50	3	$48.0 \pm 6.5$	-0.23	10.85	365
TH	CM	10	2	$69.1 \pm 0.1$	3.83	24.74	1604
		50	3	$57.4 \pm 1.1$	3.32	14.81	1248
	F	10	3	$70.3 \pm 4.5$	1.46	17.28	962
		50	3	$52.7 \pm 0.4$	0.97	6.957	412
	G	10	3	$59.5 \pm 1.3$	4.03	22.28	1607
		50	3	$53.6 \pm 0.5$	3.50	14.42	1309



**Figure S C 6: Schematic sketch of the arrangement of the tea bags (grey hexagons) and temperature loggers (yellow pentagons). The equipment was placed circular around and attached to a metal plate (red)**

## Curriculum vitae

# Tino Andreas Peplau

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### Education

- Since August 2019 **PhD student (Dr. rer. nat.)**  
Leibniz University Hannover, Institute of Soil Science
- 2016 – 2018 **M. Sc. Geography: Resource Analysis and Resource Management**  
Georg-August-University Göttingen  
*Master thesis* *Interrelations between soil chemistry and larch succession after forest fires in northern Khangai-Mountains, Mongolia*
- 2012 – 2016 **B. Sc. Geographical Sciences**  
Freie Universität Berlin  
*Bachelor thesis* *Changes of the groundwater level in the Lietzengraben-catchment area*
- 2012 **Secondary school**  
Goethe-Oberschule, Berlin-Lichterfelde

### Professional experience

- Since August 2019 **Research Assistant**, Thünen Institute of Climate-Smart Agriculture  
*Project "Breaking the ice"*
- October 2018 – July 2019 **Research Assistant**, University of Göttingen, Department of Geography  
*Project "Sediments and paleo soils as archives of landscape development under increasing influence of human activities"*
- 2017 – 2018 **Student Assistant**, University of Göttingen, Department of Geography  
*Support Project "Analysis of geoecological control factors for the distribution of forests and discontinuous permafrost under the influence of wildfires, forest use and climate change in the forest-steppe of central Mongolia"*

## List of publications

Schroeder, J.; **Peplau, T.**; Pennekamp, F.; Gregorich, Edward; Tebbe, Christoph C.; Poeplau, C. (2022): Deforestation for agriculture increases microbial carbon use efficiency in subarctic soils. In *Biology and Fertility of Soils* DOI: <https://doi.org/10.1007/s00374-022-01669-2>

**Peplau, T.**; Schroeder, J.; Gregorich, E.; Poeplau, C. (2022): Subarctic soil carbon losses after deforestation for agriculture depend on permafrost abundance. In: *Global Change Biology*, DOI: 10.1111/gcb.16307

Schroeder, J.; **Peplau, T.**; Gregorich, E.; Tebbe, C.; Poeplau, C. (2022): Unexpected microbial metabolic responses to elevated temperatures and nitrogen addition in subarctic soils under different land uses. In: *Biogeochemistry*, DOI: 10.1007/s10533-022-00943-7

**Peplau, T.**; Schroeder, J.; Gregorich, E.; Poeplau, C. (2021): Long-term geothermal warming reduced stocks of carbon but not nitrogen in a subarctic forest soil. In: *Global Change Biology*, 27:5341-5355, DOI: 10.1111/gcb.15754

Schneider, F.; Klinge, M.; Brodthuhn, J.; **Peplau, T.**; Sauer, D. (2021): Hydrological soil properties control tree regrowth after forest disturbance in the forest-steppe of central Mongolia. In: *SOIL*, 7, 563-584, DOI: <https://doi.org/10.5194/soil-7-563-2021>