Decomposition rate and stabilization across six tundra vegetation types exposed to >20 years of warming

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HIGHLIGHTS

- Warming with open top chambers decreased initial decomposition rate but not stabilization during decomposition in tundras.
- Soil moisture, temperature and metal concentrations explained differences in the tea bag index between vegetation types.
- In dry locations, initial decomposition rate and stabilization were not affected by soil temperature.
- In wetter locations, initial decomposition rate decreased and stabilization increased with increasing soil temperature.
- Increased soil metal concentrations impeded decomposition, which may affect decomposition irrespective of climate change.

GRAPHICAL ABSTRACT
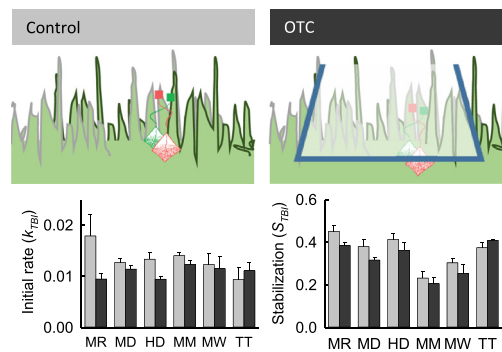
ABSTRACT

Aims: Litter decomposition is an important driver of soil carbon and nutrient cycling in nutrient-limited Arctic ecosystems. However, climate change is expected to induce changes that directly or indirectly affect decomposition. We examined the direct effects of long-term warming relative to differences in soil abiotic properties associated with vegetation type on litter decomposition across six subarctic vegetation types.
Methods: In six vegetation types, rooibos and green tea bags were buried for 70–75 days at 8 cm depth inside warmed (by open-top chambers) and control plots that had been in place for 20–25 years. Standardized initial decomposition rate and stabilization of the labile material fraction of tea (into less decomposable material) were calculated from tea mass losses. Soil moisture and temperature were measured bi-weekly during summer and plant-available nutrients were measured with resin probes.
Results: Initial decomposition rate was decreased by the warming treatment. Stabilization was less affected by warming and determined by vegetation type and soil moisture. Soil metal concentrations impeded both initial decomposition rate and stabilization.

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Conclusions: While a warmer Arctic climate will likely have direct effects on initial litter decomposition rates in tundra, stabilization of organic matter was more affected by vegetation type and soil parameters and less prone to be affected by direct effects of warming.

1. Introduction

Almost half of the terrestrial carbon resource is bound in high latitude tundra soils (Tarnocai et al., 2009). If climate change enhances decomposition of this 1672 Pg. carbon, this could significantly change nutrient cycling (Hobbie, 1996) and release considerable amounts of greenhouse gases into the atmosphere (Lu et al., 2013; Melillo et al., 2017; Tarnocai et al., 2009). This positive feedback mechanism could further enhance global warming and stimulate more decomposition. There are still large uncertainties around soil carbon cycling under global warming, and the discussion is partly hampered by limited knowledge on interactions between direct effects of warming and other abiotic drivers of decomposition (Keuskamp et al., 2013; van Gestel et al., 2018). Next to climatic factors, soil chemistry which varies between vegetation types and with topography, is one of the important factors for soil carbon processes like decomposition. Since global warming is more pronounced in Arctic regions (IPCC, 2013), and since decomposition greatly depends on temperature and soil chemistry (Hobbie, 1996; Lu et al., 2013), it is crucial to improve our understanding of how climate warming affects carbon cycling and litter decomposition across the Arctic.

Warming enhances decomposition directly via stimulation of metabolic activity and growth of almost all decomposers (Lu et al., 2013; Melillo et al., 2017). Changes in temperature may rapidly affect decomposer activity, while other environmental responses to temperature changes such as plant community composition, litter quantity and quality and soil quality may lag behind (Alatalo et al., 2017a; Bjorkman et al., 2018; Sarneel and Veen, 2017). Since soil quality is so important for decomposition, the relative importance of the direct effects of warming and other soil parameters is currently an important topic of discussion. Their interaction may determine the potential carbon release from soils under warming (Blok et al., 2018; Djukic et al., 2018; Sarneel and Veen, 2017). It is well established that plant communities can affect decomposition via differences in productivity, community composition (both soil organisms and plants), and litter and soil quality (Alatalo et al., 2017a; Althuizen et al., 2018; Cornelissen et al., 2007; Cornwell et al., 2008; Lu et al., 2013). Hence, due to climate driven vegetation changes, warming effects may not be linear along a temperature gradient. In addition, they may be conditional on, other environmental conditions such as soil moisture or vegetation type (Aerts, 2006; Bradford et al., 2017). For instance, it is frequently reported that warming treatments only increase litter decomposition if there is sufficient soil moisture (Aerts, 2006; Christiansen et al., 2017). Next to moisture and temperature, other soil characteristics (nutrient concentrations, pH, and microbial community composition), frequently associated with vegetation composition, affect decomposition rates (Berg, 2018; Hobbie et al., 2012). These latter factors however, are also largely driven by climate-independent factors such as topography. Apart from the well-studied role of soil moisture, the interaction between warming and vegetation type and its associated soil abiotic factors have often been overlooked in previous studies, especially in the Arctic.

Litter decomposition is often divided into two conceptual phases. During the initial phase, all labile fractions (sugars, etc.) are decomposed at relatively fast rates. In the second phase, decomposition rates are almost negligible and more recalcitrant material fractions remains intact, which is referred to as a stabilization or limit value (Berg, 2018; Keuskamp et al., 2013). Both phases have been shown to be affected by environmental conditions such as nutrient addition, flooding, pH, or species composition (Althuizen et al., 2018; Barel et al., 2019; Berg, 2018; Hobbie et al., 2012; Riggs et al., 2015; Sarneel and Veen, 2017). Although the concept of the two phases is well established (Berg and Meentemeyer, 2002), it is only recently that studies have started to look at both decomposition phases (e.g. Keuskamp et al., 2013). These studies have often been conducted along elevational gradients and have confirmed complex interactions between temperature and soil moisture on decomposition (Althuizen et al., 2018; Mueller et al., 2018; Petraglia et al., 2019; Sarneel and Veen, 2017) and show a remarkably strong influence of vegetation type (Althuizen et al., 2018; Barel et al., 2019; Petraglia et al., 2019). It is, however, debated how this effect of plant community composition on decomposition rate and stabilization relates to or interacts with abiotic conditions such as temperature and moisture (Althuizen et al., 2018; Barel et al., 2019; Petraglia et al., 2019). Further exploration of mechanisms underlying these patterns would thus benefit from a more direct evaluation of warming alone across vegetation types.

Warming experiments with open-top chambers (OTC), heating cables, or lamps are an effective way of studying the interactions between warming and environmental conditions (Aerts, 1997; Blok et al., 2018; Bokhorst et al., 2013). Passive warming methods (OTC) have been show to increase soil and air temperatures by about 0.8 °C, depending on the mean photosynthetic active radiation (PAR) received by the location (Bokhorst et al., 2013; Elmendorf et al., 2012). Since mean annual air temperatures in Arctic regions have increased by ~0.4 to 0.8 °C per decade in the past half-century (Biskaborn et al., 2019; Chapin et al., 2000; McBean et al., 2009) and climate predictions estimate an increase of 1.4–3.5 °C by the mid-21st century (IPCC, 2013), the warming effect in such experiments is of a relevant magnitude.

To study the effect of warming on decomposition across tundra soils, we measured initial decomposition rates and stabilization under long-term warmed and ambient conditions in six contrasting subarctic vegetation types. We used long-term warming studies, as previous studies have shown that directly after initiating experimental warming treatments, decomposition and thereby soil respiration strongly increases (Melillo et al., 2017; Romero-Olivares et al., 2017) likely due to faster respiration of labile carbon sources. After the first decade, differences in soil respiration between warmed and ambient plots become smaller because changes in litter production and soil microbial community composition cause stabilizing feedbacks (Melillo et al., 2017). Given that our OTCs were installed in the early 1990s, it is reasonable to assume that the results of our study represent conditions of an adapted soil system. We employed the standardized tea bag index (Keuskamp et al., 2013), which uses rooibos tea and green tea to determine how environmental parameters affect both initial decomposition rate and stabilization. By correlating initial decomposition rate and stabilization to soil abiotic conditions (nutrients, metals, minerals, pH, soil moisture, soil temperature), we aim to unravel how environmental variables that differ between vegetation types determine decomposition in a warming Arctic.

Our starting hypothesis was that warming increases the initial decomposition rate and decreases stabilization across vegetation types. Second, we hypothesized that there would be a difference between vegetation types, that can be explained by differences in soil moisture,

temperature, soil chemistry and pH. Vegetation types with higher soil moisture and pH are expected to have higher decomposition rates and lower stabilization. Therefore, we hypothesize that natural environmental differences in temperature between vegetation types match the changes in initial decomposition rate and stabilization by direct warming (within vegetation type).

2. Methods

2.1. Location

We selected six contrasting plant communities in the Latnjajaure valley in northernmost Sweden (68°21′N 18°29′E, Fig. 1), which has a subarctic-alpine climate with a mean annual temperature between −1 and − 3 °C and mean annual precipitation of 600–900 mm. The valley is located at an elevation of ~1000 m a.s.l. and harbors strong ecotones from dry, nutrient-poor, and acidic to wet and base-rich conditions (Table 1). We selected the following vegetation types: Wet Meadow (MW), Rich Meadow (MR) Mesic Meadow (MM), Dry meadow (MD), Dry heath (HD) and Tussock Tundra (TT). In the wet meadow, *Ranunculus nivalis* prevailed, in the rich meadow, the vegetation was characterized by a species-rich mixture of forbs and graminoids, whereas in mesic meadow, *Carex* species dominated. Dry meadow was characterized by the abundant occurrence of *Dryas octapetala*, dry heath was dominated by *Cassiope* sp. and Tussock Tundra by *Eriophorum* sp. The selected OTCs are previously reported to induce phenological changes such as longer growing and flowering periods (Molau, 1997; Stenström and Jonsdottir, 1997). In response to warming inside the OTC, species shifts occurred including decreased lichen and bryophyte diversity and cover (Alatalo et al., 2019; Alatalo et al., 2017b; Molau and Alatalo, 1998), and increased *Vaccinium* sp. cover (Molau, 2010). Warming has further induced some changes in soil
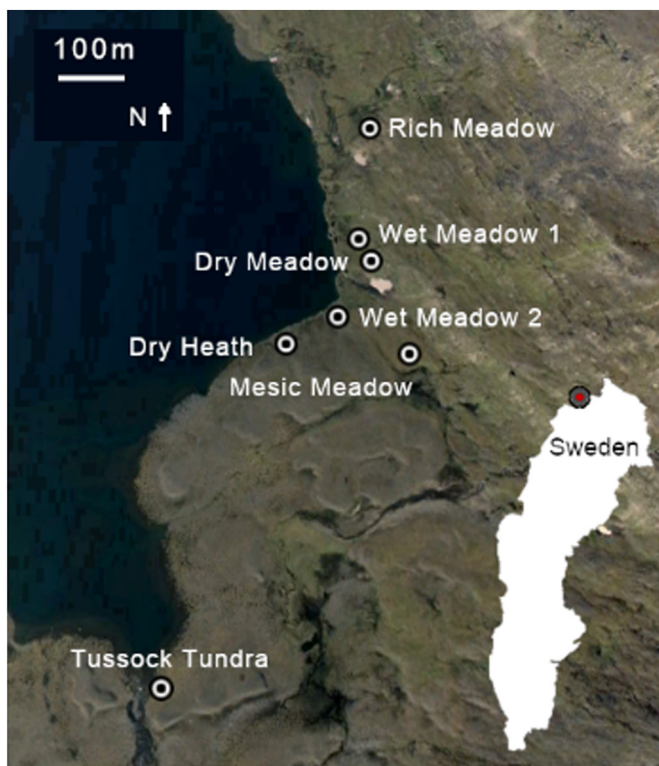

Fig. 1. Overview of the six different vegetation types studied in the Latnjajaure valley with a map of Sweden showing the location of the valley (red dot; 68°21′N 18°29′E). The Wet Meadow vegetation type was divided over two sub-locations but are treated as one vegetation type.

chemistry of the mineral soil layer (increased C:N ratio) in this valley (Alatalo et al., 2017a). See Appendix Table A1 for detailed vegetation descriptions, previously used location names and detailed previous results.

2.2. Experimental set-up

At the time of the study, warming experiments had been running for 21 years in MM and MR and 23 years in the other vegetation types. OTC warming plots (1 m²) were installed in each vegetation type using permanent hexagonal open-top chambers, using the standard International Tundra Experiment (ITEX) design (Marion et al., 1997; Molau and Mølgaard, 1996). Control plots (1 m²) were established in the relative vicinity of each warmed plot. The number of replicates for each treatment differed among vegetation types, depending on the availability of open-top chambers (Table 1), while the same number of OTC and control plots were placed within each vegetation type. Care was taken to ensure that all OTCs and controls within one vegetation type had comparable plant composition at the start of the experiment. Since other abiotic factors important for this study were not considered during plot selection, we treat the replicates as non-paired in accordance with previous studies (Alatalo et al., 2017a).

2.3. Decomposition measurements

Pairs of rooibos and green tea bags were buried on 16–18 June 2016 following the standardized tea bag index method for decomposition (Keuskamp et al., 2013). Each tea bag was weighed before the start of the experiment. One rooibos tea bag and one green tea bag were buried at 8 cm depth in each of the warmed and ambient control plots in each vegetation type. After an incubation period of 70–75 days, all bags were harvested, cleaned without water, and dried (48 h at 70 °C), after which the mass of the remaining tea was determined.

2.4. Environmental characteristics

We measured soil temperature (at 5 cm depth) using a handheld soil thermometer (±0.1 °C precision) and soil moisture (top 6 cm) with a Delta ML2x Theta probe (Delta-T Devices Ltd., Cambridge, U.K.). Soil temperature and moisture were measured bi-weekly during the growing season of 2017 and 2018. Since the experiment in rich meadow and five of the ten replicates in the mesic meadow was discontinued after 2016, temperature and moisture could not be measured in those plots. We found strong correlations between temperature measurements in 2017 and 2018 (Linear regression: $F_{1, 46} = 59.25$, $P < 0.001$, $R^2 = 0.56$) as well as for soil moisture ($F_{1, 46} = 917.7$, $P < 0.001$, $R^2 = 0.95$). This indicates that there are consistent temperature and moisture differences between plots over the two years. Because the mean summer temperature in 2016 (daily summer mean 6.4 ± 0.4 S.E. °C) did not deviate too much from 2017 (6.0 ± 0.4 °C) and 2018 (7.6 ± 0.6 °C) nor from the long term mean (6.9 ± 0.2 °C), we used the mean soil temperature of 2017 and 2018 as a proxy for the temperatures and temperature gradients between our vegetation types during our study year (Appendix Fig. B1).

We used Plant Root Simulator (PRS®) probes (Western Ag Innovations Inc., Saskatoon, SK Canada) to estimate plant-available nutrient supply rate for all soil ions simultaneously. The probes consist of a plastic casing containing a 55 mm × 16 mm ion exchange resin membrane (two-sided area of 176 cm²), which is intended to mimic the action of a plant root, acting as an 'infinite' sink of labile nutrients until membrane saturation after ~10 days. The probes were inserted 1–6 cm vertically into the uppermost soil layer between 16 and 30 June 2016. Directly after harvesting, the probes were cleaned of soil in the laboratory according to the manufacturer's instructions and shipped to Western AG, Canada, in insulated containers for analysis. The PRS(tm)-probe supply rates ($\mu g\ 10\ cm^{-2}$) were determined for total nitrogen (N), N

Table 1
Overview of the soil characteristics of the plant communities in the control plots where n = number of replicate plots per treatment per vegetation type. The mean ($\pm$ S.E.) concentrations (μg 10 cm^{-2}) are provided with the highest value of each element in bold, and the lowest value underlined.

	Dry meadow	Mesic meadow	Rich meadow	Wet meadow	Tussock tundra	Dry heath
n	5	10	5	5	5	4
Iron	2.492 ± 1.00	2.935 ± 0.47	1.166 ± 0.09	13.96 ± 6.51	**703.3 ± 552**	4.418 ± 0.84
Copper	0.172 ± 0.05	0.269 ± 0.10	0.018 ± 0.01	0.812 ± 0.46	**4.246 ± 1.95**	0.135 ± 0.05
Manganese	0.470 ± 0.09	1.381 ± 0.43	0.940 ± 0.41	2.832 ± 1.11	**12.78 ± 2.72**	2.663 ± 0.56
Zinc	0.364 ± 0.05	0.785 ± 0.22	1.202 ± 0.50	1.692 ± 0.70	**5.730 ± 1.52**	1.273 ± 0.24
Phosphorus	1.242 ± 0.74	0.495 ± 0.14	2.848 ± 1.00	0.430 ± 0.13	**27.95 ± 21.0**	1.213 ± 1.10
Aluminum	14.16 ± 3.71	11.74 ± 1.73	11.32 ± 1.55	14.78 ± 3.42	**22.27 ± 1.98**	11.44 ± 1.86
Nitrogen	2.028 ± 0.40	1.622 ± 0.24	2.104 ± 0.62	**8.328 ± 4.92**	2.084 ± 0.88	4.565 ± 2.01
Calcium	**2624 ± 155**	2314 ± 149	1334 ± 122	2162 ± 117	207.5 ± 31.5	137.7 ± 27.2
Magnesium	**334.5 ± 18.1**	271.2 ± 12.5	286.7 ± 16.2	270.1 ± 14.7	112.6 ± 20.2	108.0 ± 32.7
Potassium	35.17 ± 10.9	45.50 ± 16.1	160.6 ± 11.5	24.01 ± 6.49	**348.9 ± 92.7**	143.7 ± 31.8
Sulfur	434.9 ± 193	**1221 ± 193**	46.90 ± 8.68	1018 ± 313	212.5 ± 159	22.03 ± 1.19

bound in NO^{3-} and in NH^{4+}, total phosphorus (P), boron (B) and sulfur (S), and several base cations, specifically, calcium (Ca), magnesium (Mg), potassium (K), and metals like iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), lead (Pb), aluminum (Al), and cadmium (Cd). The PRS probes only measure mobile elements and thereby provide relative measures of plant-available nutrient content in the soil (Qian and Schoenau, 2002).

In addition we measured soil pH by taking soil cores from the top 5 cm of each plot in July 2019, to complement the data. Soil samples where sieved through a 2 mm mesh then mixed with deionized water (1:10 mass ratio) for 30 min on a reciprocating shaker (140 rpm). pH was measured ($\pm$0.005 precision) after letting the soil material settle overnight. pH values agreed well with values obtained in 2013 by Alatalo et al. (2017a) in the same valley.

3. Calculation

We used the Tea Bag Index which quantifies decomposition mainly by microbial activity as the mesh size of the bag material (0.25 mm) does not allow for larger organisms to enter. Using the mass loss of the tea bags combined with the hydrolysable fraction of rooibos tea and green tea, obtained from Keuskamp et al. (2013), we calculated the Tea Bag Index (TBI) consisting of the initial decomposition rate (k_{TBI}) and stabilization (S_{TBI}) of the labile fraction of the tea, assuming a two-phase decomposition model with fast initial decomposition rate and negligible decomposition rate during the second phase when only recalcitrant material remains:

$$M(t) = ae^{-kt} + (1-a) \tag{1}$$

where $M(t)$ is the mass proportion of the substrate after incubation time t in days, a is the decomposed labile fraction of the litter, 1-a is the remaining fraction, and k is the decomposition rate of the labile material fraction. After 2–3 months of incubation, green tea is in the second phase of decomposition and the remaining mass thus allows the decomposed fraction of green tea (a_g) to be calculated as:

$$a_g = 1 - \frac{M(t)}{M_g(0)} \tag{2}$$

where $M_g(0)$ is the starting mass of green tea.

The fraction of the labile material that is not decomposed by microorganisms, but stabilized (S_{TBI}), was then calculated using the hydrolysable fraction of green tea (H_g):

$$S_{TBI} = 1 - \frac{a_g}{H_g} \tag{3}$$

Assuming that S_{TBI} is equal for rooibos and green tea, and using the hydrolysable fraction of rooibos tea (H_r), the decomposed fraction of rooibos tea (a_r) was calculated as:

$$a_r = H_r(1 - S_{TBI}) \tag{4}$$

The a_r value obtained was entered into Eq. (1) to derive k_{TBI}.

In this study, we first calculated the mean S_{TBI} per vegetation type and treatment combination and used this mean to calculate the values for k_{TBI} in each replicate. This enabled us to calculate k_{TBI} in cases where the green tea bag was lost or destroyed ($n = 3$).Six rooibos teabags were lost or destroyed (6.6% of a total of 136 bags).

Differences in k_{TBI} and S_{TBI}, soil temperature, moisture and pH between warmed and ambient plots in the different vegetation types were tested using two-way ANOVA. Whenever ANOVAs revealed significant effects of a treatment factor we used Tukey's post hoc test. We used ln-transformed K_{TBI} and pH values to conform to the assumptions on normally distributed data for ANOVA. To further explore abiotic environmental conditions that could drive differences among vegetation types, we first performed factor analysis on soil chemistry parameters and then ran a stepwise regression analysis including those factors and other measured soil parameters. This approach was necessary since the resin stick method is a quite coarse method, suitable only for detecting general trends. To have a consistent dataset, the factor analysis was performed on all plots for which also soil moisture, temperature and pH measurements were also available. Further, nitrogen (N) bound in NO$_3^-$ and in NH$_4^+$, as well as B, Pb, and Cd were excluded from the analysis, as >75% of the values for each element were below the detection limit. Total N and Cu were included even though 48% and 51% respectively of their values were below the detection limit, due to their ecological relevance and because differences were consistent among vegetation types. We transformed the data by taking a natural logarithm of values to which 0.1 was added to improve the distribution of the data. We extracted two factors using a Bartlett regression model and a varimax rotation using the nFactors package (Raiche and Magis, 2015). The number of factors was determined by visual assessment of the scree plot. Using two-way ANOVA as before, we tested for effects of warming treatment and vegetation type on abiotic environmental parameters (Factors 1 and 2), pH, soil moisture and temperature. To explore potential driving factors for k_{TBI} and S_{TBI} across vegetation types, we ran stepwise linear regression models that included the environmental factors, pH, soil moisture and soil temperature as main factors. We only included the interaction between temperature and moisture due to the limited replication in our dataset. The best model was selected using the Akaike Information Criterion (AIC) in the MASS package (Ripley et al., 2018). All analyses were performed in R 3.6.1 (R Core Team, 2019)

4. Results

4.1. Environmental characteristics

Overall, the warming treatments resulted in the strongest temperature increase for soils of drier vegetation types (+0.76 and +0.72 °C for Dry Meadow and Dry Heath, respectively). Intermediate increases were observed in Tussock Tundra (+0.41 °C) and in the remaining meadow vegetation types the warming treatment barely changed soil temperature (0.16 °C in MM and 0.04 °C in MW). Over the growing season, the OTC effect on soil temperatures ranged from −1.37 to +2.57 °C (Appendix Fig. B1). Summer mean soil temperature was consistently +0.34 ± 0.13 °C warmer inside the open-top chambers across the five vegetation types but did not differ significantly from the soil temperature in the controls (Fig. 2a). There was a clear difference in soil temperature among vegetation types. Mesic Meadow vegetation was the coldest and (Dry and Wet) Meadow vegetation was the warmest (Fig. 2a, Table 1). Soils inside the warmed plots were significantly drier than control plots ($F_{1,38} = 11.400$, $P = 0.002$). Dry Heath had the lowest soil moisture, while Wet and Mesic meadow had the highest soil moisture (Fig. 2b). Soil pH was not affected by warming treatment
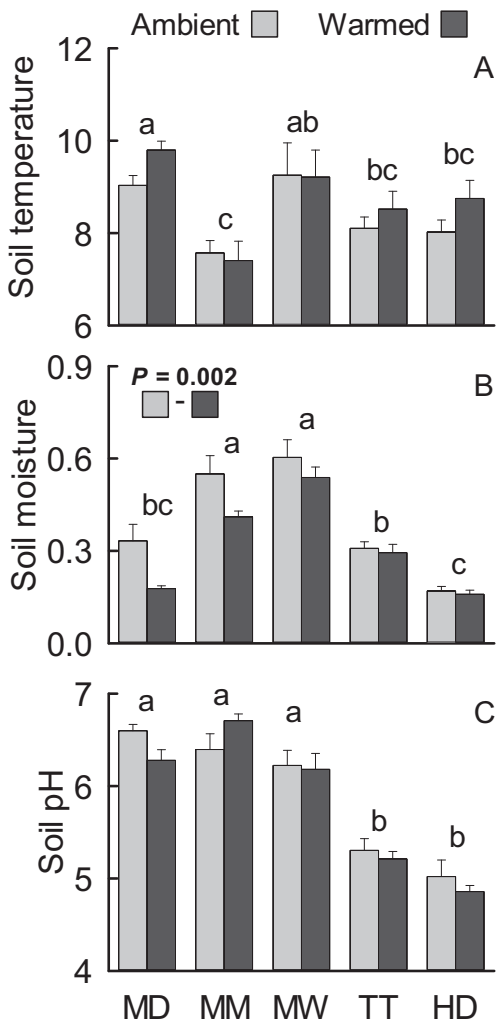
($F_{1,38} = 0.572$, $P = 0.454$), but differed significantly between vegetation types ($F_{4,38} = 62.02$, $P < 0.001$; Fig. 2c). Dry heath had the lowest soil pH (4.94 ± 0.09 S.E.), followed by Tussock Tundra (5.26 ± 0.07 S.E.) and mesic meadow had the highest pH (6.55 ± 0.07 S.E.). None of the measured soil chemical parameters differed significantly between treatments (Appendix Table B1).

Based on clusters of variables that were strongly correlated with each other, the factor analysis extracted two environmental gradients that together explained 57% of the total variance (Table 2). Factor 1 clustered the variables that together represent the abundance of metals and is therefore highly correlated to variables like copper, iron and zinc. Factor 2 clustered variables that together represent the availability of base cations or base saturation, which may be associated with weathering.

Both factors differed between vegetation types (Factor 1, $F_{1, 38} = 28.22$, $P < 0.001$, Factor 2, $F_{1, 38} = 44.07$, $P < 0.001$). Tussock tundra and wet meadow were associated with metal-rich soils while the remaining vegetation types were metal poor. Further, dry heath and tussock tundra were associated with base-poor soils while other vegetation types had a higher base saturation. There was no significant warming effects on either factor (Factor 1, $F_{1, 38} = 0.080$, $P = 0.779$; Factor 2, $F_{1, 38} = 2.224$, $P = 0.144$). See Appendix Fig. B2 and Table B2 for statistics and graphs.

Simple correlations showed that Factor 1 negatively correlated to soil pH (Pearson $r = -0.297$, $P = 0.041$) while Factor 2 positively correlated to soil moisture and pH (respectively, $r = 0.640$, $P < 0.001$ and $r = 0.835$, $P < 0.001$). Adding soil pH, soil moisture and temperature to the factor analysis did not change the general patterns (Appendix Table B3). The same variables grouped with each other, and soil moisture and temperature made minor contributions to the already existing variables. Adding soil moisture and temperature to the factor analysis would therefore not allow us to test their direct effects on decomposition, as they would be integrated with other factors. This was especially problematic for temperature that was poorly represented by any factor.

4.2. Decomposition

Across all six vegetation types, experimental warming significantly decreased initial decomposition rate, k_{TBI} ($F_{1, 48} = 4.140$, $P = 0.047$; Fig. 3) and tended to decrease stabilization, S_{TBI} ($F_{1,53} = 3.214$, $P = 0.079$; Fig. 3). Vegetation type did not affect k_{TBI} ($F_{5,48} = 1.258$, $P = 0.297$), but S_{TBI} differed significantly among vegetation types ($F_{5,53} = 15.69$, $P < 0.01$; Fig. 3). Both k_{TBI} and S_{TBI} decreased in warmed compared to control plots in all vegetation types except Tussock tundra where warming increased k_{TBI} and S_{TBI}. However, there was no significant interactive effect between vegetation type and treatment for either k_{TBI} or S_{TBI} (k_{TBI}; $F_{5, 48} = 1.752$, $P = 0.141$ and S_{TBI}; $F_{1,53} = 0.705$, $P = 0.622$).

Fig. 2. Mean summer temperature (a) moisture (b) and pH (c) in five vegetation types. MD = dry meadow MM = mesic meadow MW = wet meadow TT = tussock tundra HD = dry heath. Rich meadow (MR) is not included due to removal of these OTC after 2016, while measurements of temperature and moisture were done in 2017 and 2018, and pH in 2019. *P*-values indicate differences between warmed and ambient treatments and significant differences among vegetation types are indicated by different letters above the bars. Error bars are S.E. *n* = 4, except for dry heath, where *n* = 4.

Table 2
Pearson correlation coefficients of the soil variables in control plots and experimentally warmed plots (20–25 years of warming) across six tundra vegetation types to the two factors extracted with factor analysis (*n* = 48, ten control and OTC plots were excluded due to missing values). Only correlation coefficients higher than 0.4 are shown (except for Nitrogen where the highest value is shown) and correlations stronger than (−) 0.7 are in bold.

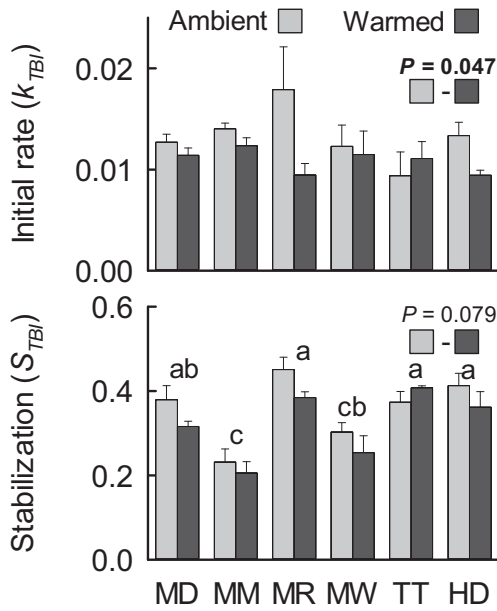| Environmental variable	Factor 1 (metals)	Factor 2 (base saturation)
Iron	**0.96**	
Copper	**0.88**	
Manganese	0.72	−0.46
Zinc	0.65	
Phosphorus	0.46	
Aluminum	0.41	
Nitrogen	−0.12	
Calcium		**0.96**
Magnesium		**0.86**
Potassium	0.43	−0.69
Sulfur		0.65
Cumulative variance	0.30	0.57

Fig. 3. Effects of long-term experimental warming on initial decomposition rate (k_{TBI}) and stabilization (S_{TBI}) across six tundra vegetation types. Legend codes as in Fig. 2. *P*-values are indicated for the difference between warmed and ambient treatments and significant differences among vegetation types are indicated by different letters above the bars. Error bars are S.E. $n = 4$, except for mesic meadow ($n = 10$) and dry heath ($n = 4$).

Across all vegetation types, the best model selected in our stepwise regression ($F_{2,36} = 2.69$, $P = 0.06$, $R^2 = 0.18$) showed that k_{TBI} was negatively related to Factor 1 ($\alpha = -0.072 \pm 0.048$, $P = 0.146$), positively related to mean summer temperature ($\beta = 0.085 \pm 0.107$, $P = 0.429$) and soil moisture ($\beta = 3.425 \pm 2.025$, $P = 0.091$), and was impacted by the interaction of moisture and temperature ($\alpha = -0.377 \pm 0.232$, $P = 0.114$),. The best model for S_{TBI} ($F_{4,42} = 7.86$, $P < 0.001$, $R^2 = 0.43$) included a strong significant negative effect of soil moisture ($\beta = -1.320 \pm 0.460$, $P = 0.006$) and temperature ($\beta = -0.047 \pm 0.024$, $P = 0.062$), and positive effect of Factor 1 (metals; $\beta = 0.018 \pm 0.011$, $P = 0.101$) and the interaction between soil moisture and temperature ($\beta = 0.118 \pm 0.053$, $P = 0.030$). The interaction for both k_{TBI} and S_{TBI} was characterized by a lower responsiveness to soil moisture in warmer environments compared to colder environments (Fig. 4). Under cold temperatures (<8.5 °C), k_{TBI} increased while S_{TBI} decreased in wetter plots, whereas no or weaker trends were observed under warmer temperatures.

5. Discussion

We found that the microbially driven initial decomposition rate (k_{TBI}) across six vegetation types in the Arctic was decreased by the direct effects of experimental warming. Stabilization (S_{TBI}) of litter material during the second phase of microbially driven decomposition also decreased upon experimental warming, but significant differences were found between vegetation type, which could be correlated to differences in soil moisture and its interaction with temperature. Interestingly, metal concentrations, notably Fe and Cu, were negatively related to k_{TBI}, and positively related to S_{TBI} indicating overall suppression of the decomposition process.

Overall, our results confirm that warming affects decomposition across vegetation types, but our hypothesis was only partly supported. The soil temperature differences observed in this study indicated that the OTCs were capable of warming soils in the same order of magnitude as Molau and Alatalo (1998) observed for air temperatures in the rich meadow and dry heath. We further observed that warming effects were smaller in vegetation types with higher soil moisture (wet and mesic meadow), which may suggest some buffering effect of soil

moisture on temperature. However, the effect of the warming treatment on k_{TBI} and S_{TBI} was not restricted to the vegetation types where the warming treatment increased soil temperature (Fig. 2). With the stepwise regression we could show that especially under wetter conditions, temperature mattered for both decomposition parameters whereas at drier locations, where soil moisture is likely limiting decomposition, k_{TBI} and S_{TBI} were less affected by temperature. This agrees well with the assumption that decomposition is first constrained by soil moisture and secondary by temperature (Prescott, 2010). The patterns obtained with our correlative approach in the stepwise regression, however, match the effects of the OTC treatment quite well. In contrast to our hypothesis that warming would generally enhance decomposition, we observed opposite reactions to warming for the two decomposition parameters. Whereas the reaction of K_{TBI} to warming reflects reduced decomposition, the reaction of S_{TBI} to warming indicates enhanced decomposition. This shows a certain degree of decoupling of the two phases in the decomposition process, which aligns with observations in other studies (Sarneel and Veen, 2017), but remains poorly understood.

Our study underlines the overall importance of both soil temperature and soil moisture for decomposition (Aerts, 2006; Christiansen et al., 2017; Moore et al., 1999). Our results also indicate that the interactive effect of temperature and soil moisture may be less straightforward when considering a two phased decomposition model than previously thought. In contrast with our starting hypothesis and
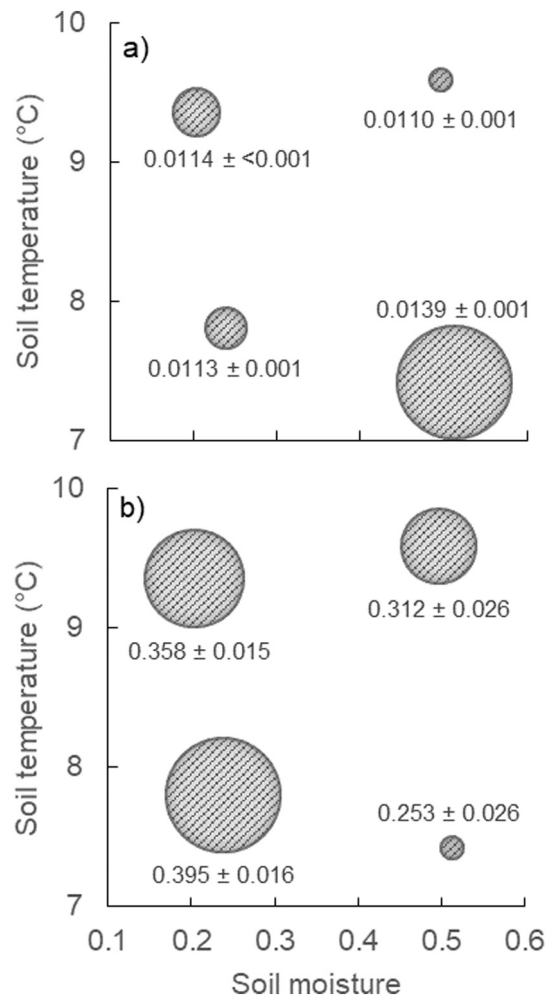

Fig. 4. Interaction between soil moisture and temperature on a) initial decomposition rate (K_{TBI}) and b) stabilization (S_{TBI}) across five vegetation types in the arctic tundra. Moisture and temperature classes are defined to result in equal sample sizes ($n = 12$). Numbers indicate group means of the respective classes and S.E.

previous studies on limit values and S_{TBI} (Althuizen et al., 2018; Berg, 2018; Fanin et al., 2019; Petraglia et al., 2019), we observed stronger responses of k_{TBI} and S_{TBI} to soil moisture at lower temperatures compared to responses at higher temperatures. The interaction between soil moisture and warming treatment observed in our study is also in contrast with Oberbauer et al. (2007) who found that warming-induced ecosystem respiration was greatest in drier locations. However, similar to our findings these authors observed considerable variability around the mean values. This could point towards a potentially important role for micro-site differences (such as in microbial communities), irrespective of temperature and moisture (Althuizen et al., 2018). The indications of more complicated and possibly conditional interactions between soil moisture and temperature for both k_{TBI} and S_{TBI} found in our study, as well as in tropical mountains (Becker and Kuzyakov, 2018) and river banks (Sarneel and Veen, 2017) calls for detailed studies explicitly addressing their interactive effects during both of these decomposition phases. Especially the three way relation between soil chemistry, vegetation type and changes in the microbial community may need further attention (Barel et al., 2019; Bradford et al., 2017).

Besides the effects of the climatic variables, we found that higher metal concentrations were related to slower litter decomposition and higher stabilization. This is in line with previous findings in decomposition studies on other litter materials (Berg, 2018), and likely related to metals interfering with microbial growth and activity (Bååth, 1989). Total P also positively correlated to Factor 1 (metals), likely because P binds to metal cations like iron and aluminum (Giesler et al., 2012; Vincent et al., 2014). This implies a slower decomposition at higher total P and iron and aluminum concentrations, likely resulting from high P sorption to metal cations while rendering P less available for soil microbes. It should be noted that P concentrations were relatively low (20% of the data was below the detection limit). Higher metal concentrations and potentially associated P limitation could overrule the potential stimulating effect that a relatively small P enrichment can have on decomposition. Such factors may underlie the counterintuitive interaction between soil moisture and temperature since our metal-rich vegetation types were either relatively dry or relatively warm and wet. The results from the stepwise regression showing that metal concentrations increase stabilization, is in line with, for instance, the absence of warming effects in metal rich Tussock Tundra. Here the high metal concentration may have overruled potential warming effects. This suggest that across the vegetation types, metal concentrations may play an important role in determining decomposition. Disentangling such conditional effects of different climate factors and soil chemistry is important in understanding drivers of decomposition, especially when extrapolating local effects to more regional gradients (Bradford et al., 2017).

With warming, shrubs tend to become more dominant in large parts of the tundra (Myers-Smith and Hik, 2018). Of our vegetation types, Rich Meadow, Dry Heath and Wet Meadow are relatively shrub-dominated. Interestingly, we measured a relatively high S_{TBI} in those vegetation types, which may form a negative feedback loop, with higher stabilization due to vegetation changes despite warming.

6. Conclusions and implications

The decreased stabilization in warmer environments, and differences between vegetation types could have important implications for future carbon storage in a warming Arctic. As hypothesized, differences in vegetation types affected the stabilization phase during decomposition, and our results reveal differences in metal concentrations as important drivers. It is only recently that studies have started to look at both decomposition phases unaffected by warming, and metal concentrations did not differ between warming treatments in our study. Because metal concentrations also have large effects on vegetation composition, they may increase the resilience of the system by stabilizing ecosystem processes like decomposition. Further, initial

decomposition rates were affected by the warming treatment and soil moisture in more complex ways than hypothesized, and our findings suggest a potential large role of soil moisture in driving decomposition patterns across vegetation types under warming. It is still unclear what changes during earlier decomposition phases (K_{TBI}) mean for ecosystem functioning and carbon emissions, but K_{TBI} may be associated with nutrient cycling rates, soil respiration, and decomposer community composition.

Credit authorship contribution statement

Judith M. Sarneel: Methodology, Formal analysis, Writing - original draft, Writing - review & editing.**Maja K. Sundqvist:**Writing - original draft, Writing - review & editing.**Ulf Molau:**Methodology, Writing - review & editing.**Mats P. Björkman:**Investigation, Writing - original draft, Writing - review & editing.**Juha M. Alatalo:**Methodology, Investigation, Writing - review & editing.

Declaration of competing interest

We state that we have no conflicts of interest to declare.

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Appendix A and B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.138304.

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