Experimental evidence of litter quality and soil moisture rather than temperature as the key driver of litter decomposition along a high-latitude elevational gradient

Eleanor R. Walker[1], Haydn J.D. Thomas[1], Isla H. Myers-Smith[1*]

1. School of GeoSciences, University of Edinburgh, Edinburgh, UK

* Corresponding author: Isla H. Myers-Smith, isla.myers-smith@ed.ac.uk,
ORCID: 0000-0002-8417-6112

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Abstract

High-latitude soils contain up to 60% of the world's carbon stocks, but are vulnerable to carbon loss as climate change alters temperature and precipitation, litter quality, and soil biota. Tundra soils are thought to be particularly sensitive to warming due to accelerated permafrost thaw, but quantifying the response of decomposition to changing soil moisture remains a challenge. Understanding the interaction between temperature, soil moisture and decomposition rates is therefore critical to predicting how the global carbon cycle will be influenced by climate change. We combined an elevational gradient with a moisture and temperature manipulation experiment to investigate differences in decomposition (mass loss) across a diverse range of soil moisture conditions along an elevational gradient from the boreal forest to alpine tundra. We used two standardised substrates of contrasting quality: green and rooibos tea, using the Tea Bag Index to isolate the effect of litter quality. We found that litter quality was the primary control on decomposition, highlighting the importance of litter inputs on rates of decomposition. Contrary to expectations, we observed an increase in litter mass loss with elevation, corresponding with higher soil moisture at higher elevations. In the moisture manipulation experiment, we also found greater litter mass loss in watered treatments for recalcitrant litter, but greater decomposition in warmed treatments for labile litter. Across both experiments, the effect of soil moisture was greater than the effect of soil temperature on litter mass loss. Overall, our findings suggest that decomposition is highly sensitive to litter quality, and that the direct impact of warming on decomposition at high latitudes will be mediated by soil moisture availability, informing predictions of the fate of high-latitude soil carbon under changing climatic conditions.

Introduction

Ecosystem functions such as decomposition are influenced by climate change across the planet and thus could alter the global carbon cycle (Bardgett et al., 2013; Chapin et al., 2009; Davidson & Janssens, 2006; Djukic et al., 2018). The influence of climate change on decomposition could be particularly dramatic at high latitudes (Wieder et al., 2019), which are warming at up to four times the rate of the world as a whole (Rantanen et al., 2022), and have already experienced a temperature increase of more than 2°C over the past 50 years (Meredith et al., 2019). Warming temperatures are predicted to cause a 30-70% decline in permafrost extent by the end of the 21st century, increasing active layer depth and altering patterns of soil moisture (Xue et al., 2016). Precipitation is also predicted to increase by up to 28% by the end of the 21st century, though with considerable uncertainty in projections (McCrystall et al., 2021; Meredith et al., 2019). Shifts in climatic and environmental conditions will also have wide and diverse consequences for tundra vegetation (Elmendorf et al., 2012; Myers-Smith et al., 2011), altering both the composition and traits of tundra plant communities, and could create large-scale feedbacks to the global climate system via carbon cycling and decomposition feedbacks (Mekonnen et al., 2021; Pearson et al., 2013). Thus, understanding the drivers of decomposition at high latitudes is critical for the improvement of models projecting carbon cycle responses to climate change (Wullschleger et al., 2014).

Decomposition is predominantly controlled by temperature, soil moisture, substrate quality and soil biota, all of which are predicted to be altered by climate change (Aerts, 2006; Joly et al., 2023). At global scales, temperature and moisture explain 50 to 70% of variation in decomposition (Davidson & Janssens, 2006; Keuskamp et al., 2013). Within the tundra biome, temperature is commonly considered to be the major control over decomposition (Aerts, 2006; Hobbie, 1996), with litter quality and decomposer community more influential at smaller spatial scales (Bradford et al., 2014; Christiansen et al., 2017). However, decomposition is not only limited by cold temperatures, but also by the xeric or saturated nature of soils (Davidson & Janssens, 2006; Hicks Pries et al., 2013; Sierra et al., 2015; Zona et al., 2023), which can be highly variable over space and time (Engstrom et al., 2005). Decomposition is thus highly likely to be altered by both shifts in temperature and moisture availability.

Decomposition is a central component of annual carbon fluxes to the atmosphere (Bond-Lamberty & Thomson, 2010). High-latitude ecosystems are particularly important in the global carbon cycle, with Arctic and boreal regions storing 20 to 60% of global soil carbon stocks (Hugelius et al., 2013). Decomposition at high latitudes is particularly sensitive to rising temperatures due to strong temperature limitation and the crossing of critical thresholds such as the freezing point of water (Sierra et al., 2015). High latitudes are thus predicted to be highly susceptible to carbon losses over the coming century (Crowther et al., 2016; van Gestel et al., 2018; Wieder et al., 2019). Future changes to decomposition will therefore likely have large repercussions for the global carbon cycle, with the potential formation of a positive feedback to climate change (Aerts, 2006; Bardgett et al., 2013; Crowther et al., 2016; Davidson & Janssens, 2006; van Gestel et al., 2018; Wieder et al., 2019).

Soil moisture is known to be an important control on decomposition in the tundra (Moyano et al., 2012; Sierra et al., 2015). For example, passive warming experiments that reduce surface soil moisture have exhibited lower levels of litter decomposition (Björnsdóttir et al., 2021; Rinnan et al., 2008; Sjögersten & Wookey, 2004). Soil moisture will likely increase in some regions as precipitation increases at high latitudes (McCrystall et al., 2021), or warming enhances permafrost thaw (Sierra et al., 2015). However, increased drainage and evapotranspiration could cause drying of tundra soils (Hicks Pries et al., 2013). The influence of soil moisture on decomposition is currently not consistently quantified across biogeochemical models (Sierra et al., 2015), which variously assume linear, saturating or optimal relationships between temperature and soil moisture (Sierra et al., 2015). Moreover, incubation experiments are commonly conducted in laboratory settings (Moyano et al., 2012) and few studies employ field-based observations. As such, interactions between temperature and soil moisture on litter decomposition rates remain unclear, resulting in counterintuitive results such as increasing decomposition with altitude (Withington & Sanford, 2007). High levels of observed variability in decomposition rates over space and time also make large scale predictions difficult (Chapin III et al., 1988; Zhang et al., 2008). Thus, there great uncertainty remains surrounding the interactive relationships between temperature and soil moisture as controls on decomposition.

Litter quality is a major factor determining decomposition rates across high-latitude ecosystems (Cleveland et al., 2014; Cornwell et al., 2008; Fierer et al., 2005; Murphy et al., 1998), and can exert strong within-site controls over decomposition across the tundra biome (Aerts, 2006). Shrub increases in tundra ecosystems, due to improved recruitment and growing conditions, could lead to a shift from graminoid to shrub dominance (Elmendorf et al., 2012; García Criado et al., 2020; Myers-Smith et al., 2011). This vegetation change alters community-level plant functional traits (Bjorkman et al., 2018), which could influence the quantity and chemistry of litter inputs, thus impacting rates of decomposition (Cornelissen et al., 2007; Myers-Smith et al., 2019). For example, an increase in shrub abundance could increase the proportion of recalcitrant stem and leaf litter inputs, promoting carbon storage in litter and potentially forming a negative feedback to the carbon cycle (Cornelissen et al., 2007). Furthermore, litter quality also influences the temperature sensitivity of decomposition, and thus the impact of warming, with recalcitrant litter more sensitive to changes in temperature and moisture than labile litters (Conant et al., 2008; Craine et al., 2010; Davidson & Janssens, 2006; Fierer et al., 2005; Suseela et al., 2013). Concurrent experimental research in Iceland has suggested that the influence of warming on decomposition may occur through longer term warming-induced changes in the composition of plant communities (Björnsdóttir et al., 2021). As such, there is substantial uncertainty regarding the magnitude that climate-induced litter change could have on litter decomposition, the timescales over which these changes could take place, and the subsequent impacts on carbon cycling and storage.

The magnitude and direction of change in carbon stores at high latitudes remains unclear due to large variability in model predictions (Sierra et al., 2015) and the relative importance of different controls on decomposition (Aerts, 2006; Joly et al., 2023). To address these unknowns, we investigate how litter decomposition varies along a natural gradient in elevation, temperature and soil moisture. We combine this elevational gradient with an experimental manipulation of temperature and soil moisture. To ensure consistency across experiments, and allow comparison with other sites, we use the Tea Bag Index (Djukic et al., 2018; Keuskamp et al., 2013; Sarneel et al., 2020), which uses recalcitrant and labile common substrates of green and rooibos tea respectively. Specifically, we asked the following research questions: 1) How does decomposition (mass loss) relate to variation in temperature, soil moisture and the interaction between these controls?, and 2) What effect does litter quality have on mass loss? We hypothesised that litter mass loss will decrease with elevation and increase with soil temperature and soil moisture across the natural elevational gradient, and across all experimental manipulation plots. We further hypothesised that litter quality, followed by soil temperature will have the greatest effect on mass loss. Findings provide important insights into the sensitivity of decomposition to temperature and soil moisture, allowing for improved prediction of the fate of soil carbon under changing climatic conditions.

Methods

1. Study region

Field sites were located along a gradient from the boreal forest to alpine tundra in the Kluane Lake region, 220 km northwest of Whitehorse in the southwest of the Yukon Territory, Canada (61.28° N, 138.75° W). This subarctic region has a mean summer temperature of 8 – 16°C along the latitudinal gradient from 794 m to 1926 m and average winter temperatures reaching -21°C. Temperatures in this region have warmed by approximately 2°C over the past 50 years and are projected to increase by 2 – 2.5°C over the next 50 years (Streicker, 2016). Mean annual precipitation is approximately 330 mm and is thought to have increased by approximately 6% over the past 50 years, though with notable variability (Streicker, 2016). Projections also suggest that annual precipitation will increase by 10 – 20% over the next half century in this region (Streicker, 2016).

2. Litter substrate

We used the Tea Bag Index protocol, which employs standardised litter substrates, to assess variation in decomposition (Djukic et al., 2018; Keuskamp et al., 2013; Sarneel et al., 2020). This method uses a labile and recalcitrant litter using green and rooibos teabags that are obtained from a common source (Lipton, Unilever). Tea types provide contrasting measures of litter quality, with green tea exhibiting a lower carbon: nitrogen ration and a higher proportion of labile compounds than rooibos tea.

We set up all tea (litter) bag field incubations using a standardised procedure. We measured the initial weight of each bag, subtracting the mesh weight to obtain the mass of the tea. We buried one bag of each tea pairwise for each replicate to ensure that both bags were subject to the same conditions. We buried tea at a depth of 8 cm to ensure that the tea was influenced by soil conditions. Once recovered after 52 days of incubation, we dried the tea at 70°C for 48 hours in an oven, and then weighed the teabags, carefully removing soil and debris from the outside of the bag, to calculate the final mass.

We calculated mass loss as final mass divided by initial mass. We also calculated the stabilisation factor (*S*) and decomposition rate constant (*k*) of tea using a two-pool decomposition model, following methods set out in (Keuskamp et al., 2013). *S* represents the proportion of potentially decomposable material remaining once decomposition has stabilised, and is calculated using only green tea, which is assumed to stabilise within three months of burial (see Figure S1):

$$S = 1 - \left(\frac{a_g}{H_g}\right)$$

where a_g is the decomposable fraction (mass loss) of green tea and H_g is the hydrolysable fraction of green tea.

k represents the rate at which decomposable compounds are lost during decomposition, and is calculated using only rooibos tea, which is assumed not to have stabilised during the incubation period covered by this analysis.

$$\mathrm{k} = \ln\left(\frac{\mathrm{a_r}}{\mathrm{M_{t(r)}} - \mathrm{a_r}}\right) \mathrm{x}\ \frac{1}{\mathrm{t}}$$

where M is equal to the mass of rooibos tea at time point t and a_r is the decomposable fraction of rooibos tea. a_r is calculated from the hydrolysable fraction of rooibos tea (H_r) and stabilisation factor (S), whereby

$$a_r = H_r\ (1 - S)$$

This approach assumes that S consistent across tea types, and that loss of the recalcitrant pool is negligible during the study period.

3. Experimental set-up

Natural elevational gradient

In order to test how decomposition varied over a natural gradient in soil temperature and moisture, we established an elevational transect from 794 m above sea level to 1926 m above sea level (Figure 1). Clear vegetation zones were present within the transect, with boreal forest up to 1250 m, tall shrub tundra up to 1550 m, and alpine tundra above 1900 m. We established eleven sites along the transect, at every 125 m elevation from 794 m to 1926 m above sea level. At every site, we established a 60 x 30 cm ambient treatment plot and buried four tea bag replicates of each tea type pairwise directly into the ground (88 tea bags in total). We also established three additional treatments plots at every three sites (1: 794 m, 4: 1175 m, 7: 1551 m, 10: 1926 m) along the elevational transect to test the interaction between short term manipulation of temperature and moisture and long-term patterns across a natural gradient (see supplementary information).

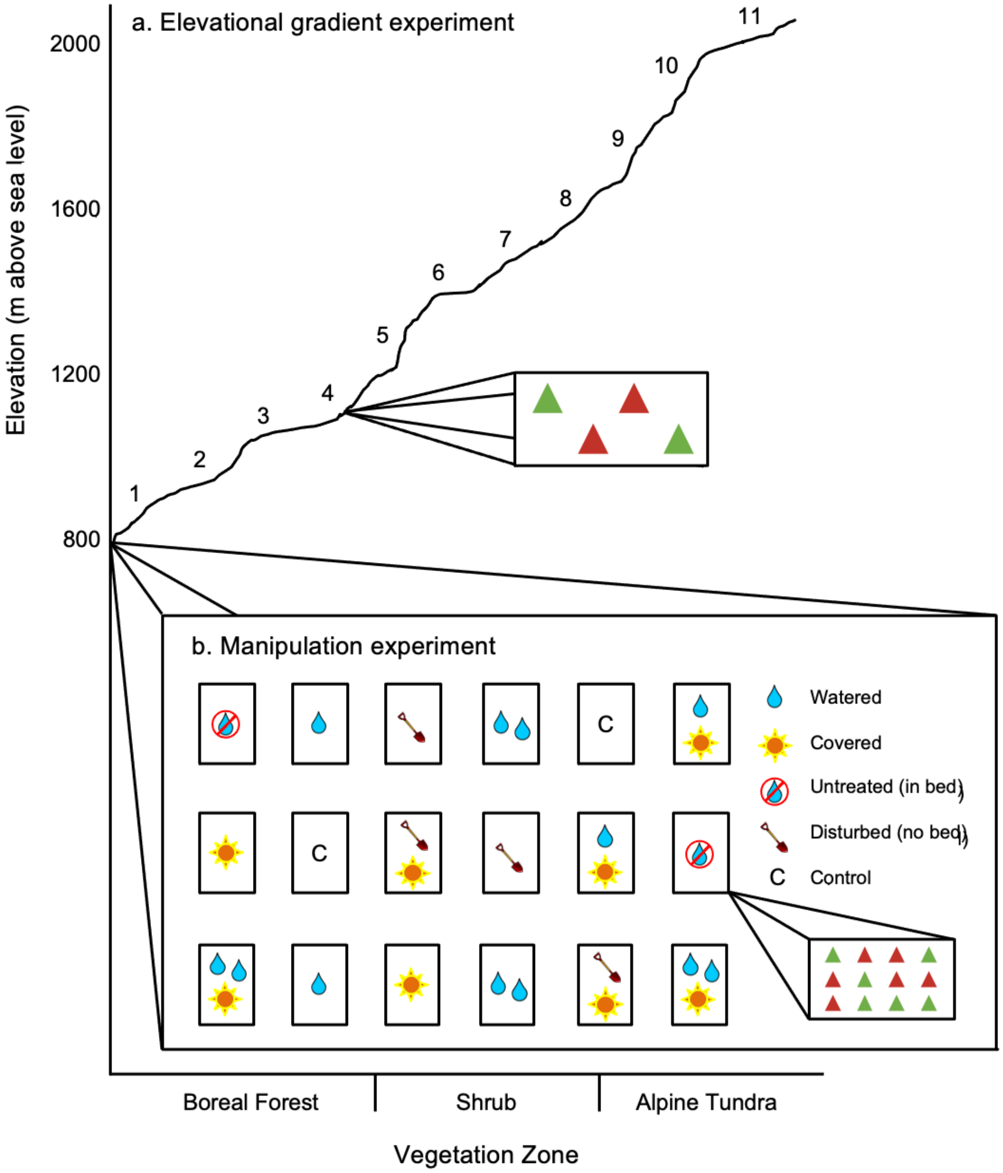

Figure 1. Experimental set-up for (a) elevational gradient experiment and (b) temperature and moisture manipulation experiment. Elevational gradient: we established eleven sites along a 1200 m elevational gradient, at every 125 m elevation from 800 m to 1925 m, with a final site at 2000 m above sea level. At every site, we established a 60 x 30cm ambient treatment plot and buried four tea bag replicates of each tea type pairwise directly into the ground. Manipulation experiment: we established 18 experimental beds in which we manipulated temperature and soil moisture over

the growing season. Treatment plots aimed to maximise the diversity of moisture and temperature conditions. We buried six tea bag replicates of each tea type pairwise per plot.

Single-site manipulation experiment

In order to test how decomposition varied across experimentally manipulated differences in soil temperature and moisture within a single site, we established a manipulation experiment in the subarctic boreal forest zone adjacent to Kluane Lake. The experiment site was located at 780 m a.s.l, approximately two kilometres from the lowest elevational gradient site, in an open area adjacent to white spruce (*Picea glauca*) forest. Vegetation within the site was largely uniform and consisted primarily of grasses, forb species with some willow shrubs, soils consisted of silty organic soils, and the topography was flat across the site.

We established 18 experimental beds in which we manipulated temperature and soil moisture over the growing season. Treatment plots aimed to maximise the diversity of moisture and temperature conditions (Table 1). We buried six tea bag replicates of each tea type pairwise per plot (216 tea bags in total). Tea bag incubations were established in late June and recovered in mid-August (52-day incubation period), such that the data collected were representative of the growing season. The location of each treatment within the experimental area was determined at random to reduce potential bias that might arise from microclimatic variation within the site.

Table 1. Treatments within the soil moisture manipulation experiment. Treatments with drainage holes had 12 x 1 cm^2 holes drilled into their base. Saturated treatments had no drainage holes to maximise water retention. Covered treatments had clear plastic covers to exclude precipitation and increase temperatures. Covers had six 5 cm by 15 cm holes drilled into the side to allow for air flow. Treatments subject to moisture manipulation were watered twice per week.

Treatment	**Description**	**Bed**	**Drainage**	**Watering**	**Cover**
Ambient	Tea buried directly in soil	No	NA	None	No
Disturbed	Tea buried within 60 cm x 30 cm soil core placed directly back into ground	No	NA	None	No
Cover only	Tea buried directly in soil. 60 cm x 30 cm clear plastic cover placed over plot	No	NA	None	Yes
Bed only	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed.	Yes	Yes	No	No
Bed and cover	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed. 60 cm x 30 cm clear plastic cover placed over plot.	Yes	Yes	None	Yes
Light watering	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed. Plot watered twice per week.	Yes	Yes	1.14 L	No
Light watering, cover	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed. Plot watered twice per week. 60 cm x 30 cm clear plastic cover placed over plot.	Yes	Yes	1.14 L	Yes
Saturated	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed. Plot watered twice per week.	Yes	No	2.27 L	No
Saturated, cover	Tea buried within 60 cm x 30 cm soil core placed inside plastic bed. Plot watered twice per week. 60 cm x 30 cm clear plastic cover placed over plot.	Yes	No	2.27 L	Yes

Environmental variables

We recorded soil temperature and soil moisture for both experiments and observations along the elevational transect. Soil temperature was recorded every hour using digital iButtons (DS1921G Thermochron iButtons, Maxim, San Jose, CA, US). We used average temperature at the plot-level to examine relationships between mass loss and soil temperature. Volumetric water content (VWC) of soils was measured at the start, during, and at the end of experiments using a

HydroSense II soil moisture meter, with three readings taken per plot per time period (Campbell Scientific, Leicestershire, UK). We used plot means to examine relationships between mass loss and moisture.

4. Statistical analysis

All data analysis was performed using R statistical software, version 1.0.136 (R Core Team, 2017). All data and code are archived in the following GitHub repository: https://github.com/ShrubHub/TeaElevationHub

Elevational gradient

We fitted linear mixed models with fixed slopes and random intercepts (due to non-convergence in random slope models) to test how mass loss, soil temperature, soil moisture, *k* and *S* changed with elevation. To test how decomposition varied with temperature and moisture, we fitted fixed slope linear mixed models with temperature and moisture as fixed effects with an interaction with each tea type, and with site as a random effect. As we found no significant interactions between temperature and moisture, we did not include the interaction effect in subsequent model. We also tested the relative effects of temperature and moisture on decomposition by mean centring and variance scaling variables.

Manipulation experiment

We tested differences in treatment effects on soil moisture, soil temperature and mass loss using linear mixed effect models with treatment as a fixed effect and plot as a random effect. To test for the effect of disturbance when setting up the experiment, we compared mass loss of tea in ambient treatments to the mass loss of tea in the disturbed treatments using an unpaired t-test. To test how decomposition varied with temperature and moisture, we fitted fixed slope linear mixed models with temperature and moisture as fixed effects with an interaction with each tea type, and with treatment as a random effect. As we found no significant interactions between temperature and moisture we did not include an interaction effect in the model.

Litter quality

We tested differences in mass loss between tea types using unpaired t-tests for the elevational gradient and the manipulation experiment, and for both experiments combined. We compared the effect size of tea type within linear models by mean centring and variance scaling environmental variables.

Results

Treatment effects

Mean soil temperature varied from 4.1°C to 10.7°C across the natural elevational gradient experiment, and from 14.0°C to 16.8°C across the single-site manipulation experiment. Soil moisture varied from 5.6% to 45.9% across the natural elevational gradient experiment, and from 1.8% to 52.6% across the single-site manipulation experiment.

We found a significant increase in soil moisture with elevation (LMM, elevation estimate = 2.53e-02 ± 6.70e-03, $P < 0.01$; Figure 2a), with lowest soil moisture in the boreal forest and highest soil moisture in the alpine tundra. In contrast, we found a non-significant decline in soil temperature with elevation (LMM, elevation estimate = -1.91e-03 ± 2.17e-03, $P = 0.41$; Figure 2b). Air temperature decreased by approximately 0.3°C per 100m altitude over the elevational gradient (Figure S2). There was a negative relationship between soil temperature and moisture across the elevational gradient (Figure S3).

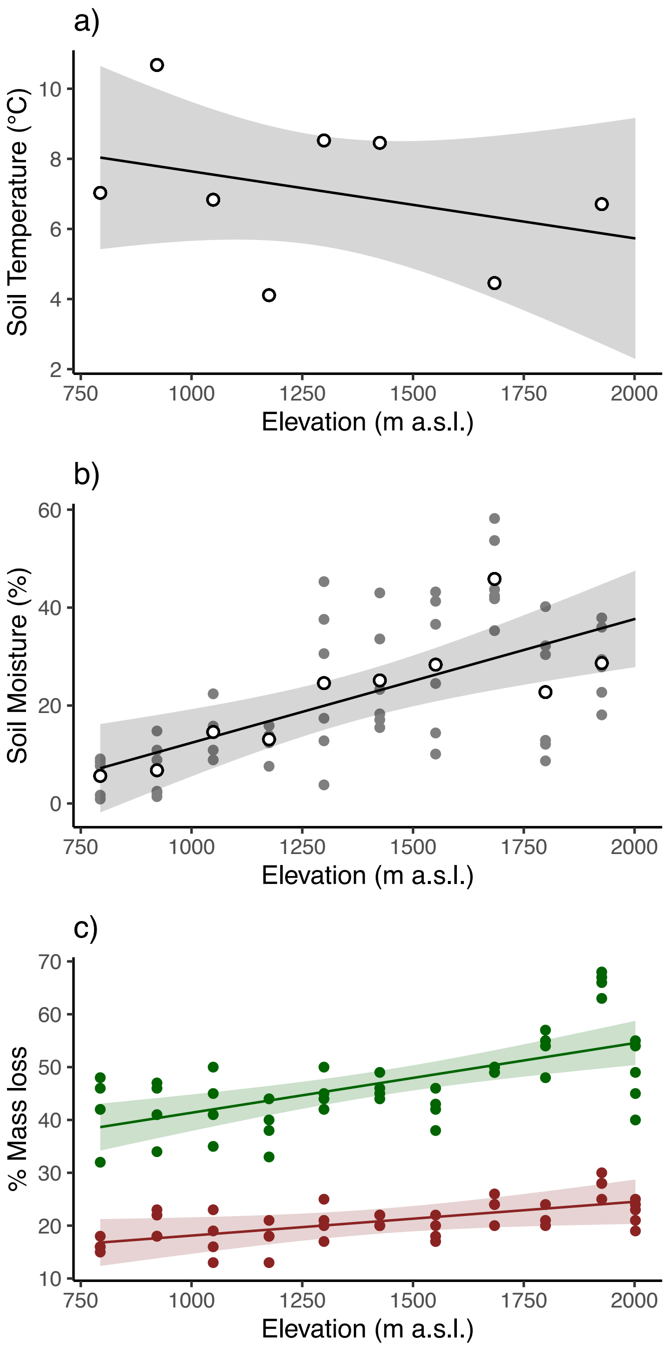

Figure 2. Soil temperature decreased, but soil moisture and mass loss of green and rooibos tea increased with elevation across the elevational gradient. Relationships between a) elevation and soil temperature and b) elevation and soil moisture. Relationships between c) elevation and mass loss. Grey points indicate raw data (soil moisture – moisture probe measurements, soil temperature - daily mean temperatures), white points indicate site means. Lines indicate model fit

and shaded areas 95% confidence intervals. Point colours indicate the two different tea types (green = green tea, red = rooibos tea). All relationships are significant.

Experimental watering treatments significantly increased soil moisture, while covered treatments significantly decreased soil moisture and increased soil temperature (Table S2, Figure S4). We found no significant difference between disturbed and undisturbed ambient treatments (paired t-test, $P = 0.34$), so disregarded the effect of disturbance on mass loss from further analysis. Treatment type alone had no significant effect on mass loss across both tea types, though mass loss significantly increased in the 'light water, covered' treatment (Table S2, Figure S4). Soil moisture and soil temperature were negatively correlated across all treatments (Figure S3). Warming and increased moisture treatments had inconsistent influences on mass loss in an experiment across the elevational gradient (Figure S5).

Mass loss - elevational gradient

We found that mass loss increased with elevation over the elevational gradient experiment (green tea: LMM, elevation estimate = 1.32e-02 ± 3.01e-03, $P < 0.01$; rooibos tea: elevation estimate = 6.40e-03 ± 2.19e-03, $P < 0.01$; Figure 2c). We found a marginally significant positive relationship between mass loss and soil moisture across the elevational gradient for both tea types (Table 2, Figure 3a), aligning with increases in both mass loss and soil moisture with elevation. In contrast, we found no relationship between mass loss and soil temperature for both tea types (Table 2, Figure 3b). Soil moisture had a 2.3 – 3.2 times greater effect on mass loss than soil temperature across the elevational gradient (Table S1). We found positive but non-significant relationships between moisture, temperature and decomposition rate (k) (higher moisture and temperature values associated with faster mass loss; Table S4, Figure 4a-b). We found negative but non-significant relationships between moisture, temperature and stabilisation factor (S) (higher moisture and temperature values associated with less mass remaining at stabilisation; Figure 4c-d).

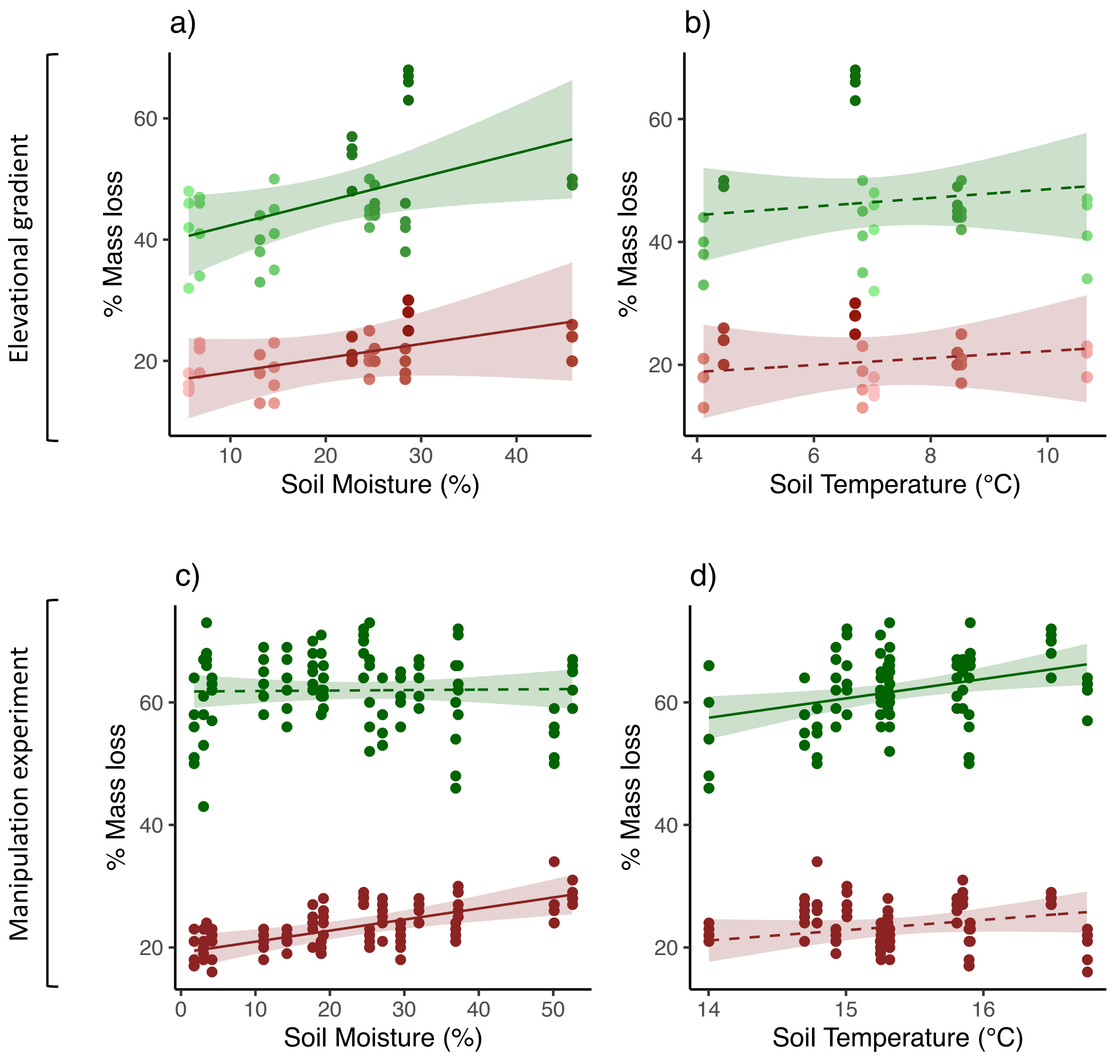

Figure 3. Soil moisture relationships with mass loss were stronger than for soil temperature across the elevational gradient. Mass loss increased with soil moisture for rooibos tea and temperature for green tea in the manipulation experiment. Relationships between a) soil moisture and mass loss, and b) soil temperature and mass loss across the elevational gradient. Relationships between c) mass loss and soil moisture, d) mass loss and soil temperature for the manipulation experiment. Point colour indicates tea type (green = green tea, red = rooibos tea), and shading indicates elevation (light = low elevation, dark = high elevation). Lines indicate linear mixed model

fit and shaded area the 95% confidence intervals. Solid lines indicate significant relationships; dashed lines indicate non-significant relationships (p = 0.05).

Table 2. Effect size and significance of environmental variables on mass loss based on linear mixed effects models for plots along the elevational gradient and all plots within the temperature and moisture manipulation experiment. Soil moisture and soil temperature effects are presented in original units; for relative effect sizes see Table S1. Significant models are highlighted in bold (. = *P* < 0.1, * = *P* < 0.05, ** = *P* <0.01, *** = *P* < 0.001).

Dataset	Tea type	Environmental variable	Effect size	Significance (*P)*
Elevational gradient	Green	**Soil moisture**	**0.40 ± 0.18**	**0.07 (.)**
		Soil temperature	0.70 ± 1.08	0.54
	Rooibos	**Soil moisture**	**0.23 ± 0.10**	**0.09 (.)**
		Soil temperature	0.57 ± 0.59	0.82
Manipulation experiment	Green	Soil moisture	0.01 ± 0.05	0.88
		Soil temperature	**3.17 ± 1.56**	**0.01 (*)**
	Rooibos	**Soil moisture**	**0.18 ± 0.04**	**< 0.001 (***)**
		Soil temperature	1.68 ± 0.91	0.11

Mass loss - manipulation experiment

We found a significant positive relationship between soil temperature and mass loss for the more labile green tea, but not for the more recalcitrant rooibos tea (Table 2, Figure 3c). Conversely, we found a significant positive relationship between soil moisture and mass loss for rooibos tea, but not for green tea (Figure 3d). Overall, soil moisture had a stronger effect on mass loss than soil temperature (Table S1). In line with these results, we found a significant positive relationship between soil moisture and *k* (LMM, moisture estimate = 1.97e-04 ± 4.46e-05, *P* < 0.001; estimated from rooibos tea, Figure 4e-f), and a negative but non-significant relationship between soil temperature and *S* (LMM, temperature estimate = -3.76e-02 ± 1.95e-02, *P* = 0.08; estimated from green tea; Table S4, Figure 4g-h).

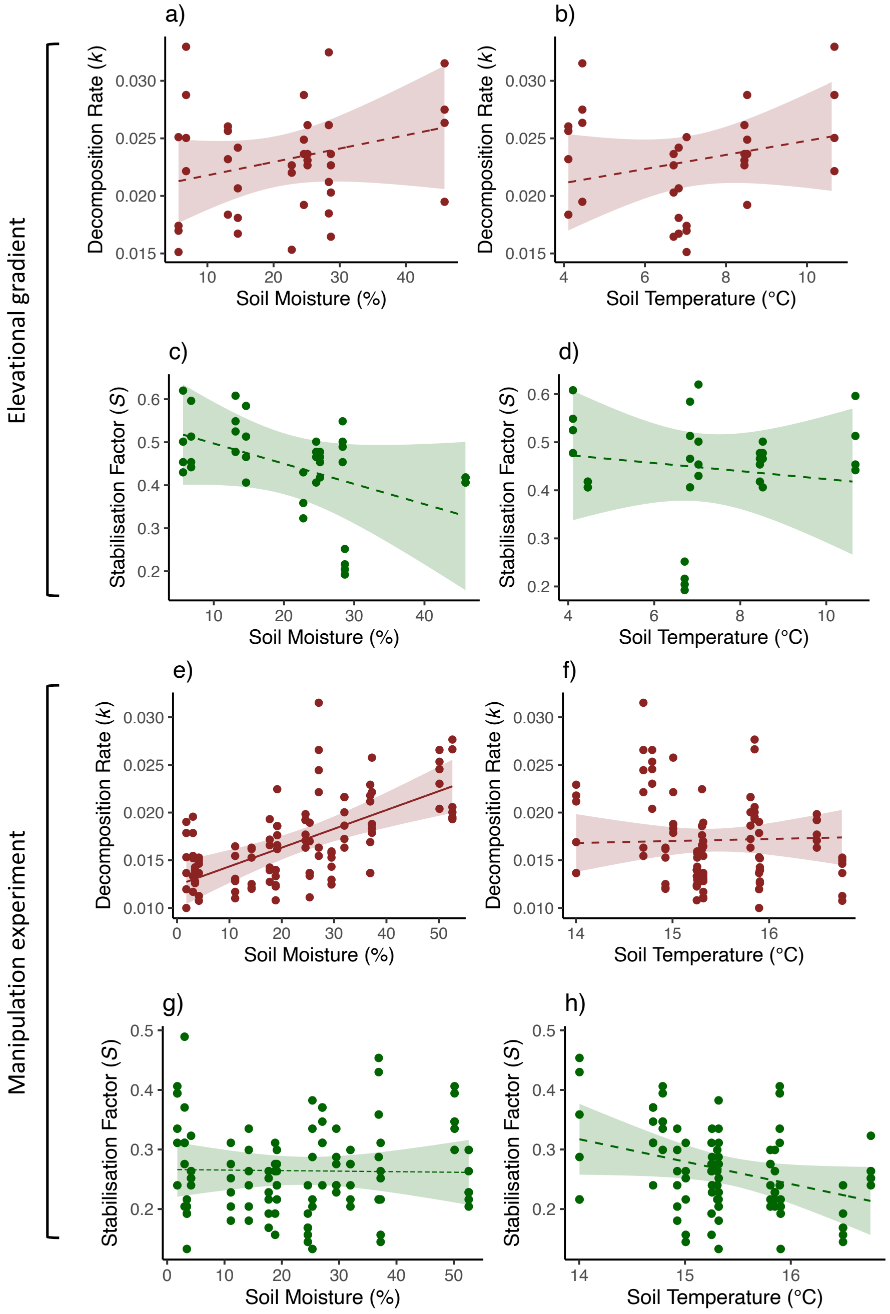

Figure 4. Decomposition rate (*k*) increased with soil moisture but not with soil temperature, while the stabilisation factor demonstrated non-significant decreases with both soil temperature and soil

moisture. Relationships between a) decomposition rate and soil moisture, b) decomposition rate and soil temperature, c) stabilisation factor and soil moisture, d) stabilisation factor and soil temperature for the elevational gradient experiment, and between e) decomposition rate and soil moisture, f) decomposition rate and soil temperature, g) stabilisation factor and soil moisture, h) stabilisation factor and soil temperature for the manipulation experiment. Lines indicate model fit and shaded area the 95% confidence intervals. Solid lines indicate significant relationships; dashed lines indicate non-significant relationships ($p = 0.05$).

Mass loss of both tea types was significantly higher in the moisture manipulation experiment compared to the elevational gradient (green tea: 47.00 ± 8.31% vs 61.87 ± 6.12%, Welch two sample t-test: $t = 10.84$, $P < 0.001$. Rooibos tea: 23.34 ± 3.51% vs 20.75 ± 3.86% Welch two sample t-test: $t = 3.86$, $P < 0.001$).

Litter quality

We found that tea type best explained variation in mass loss across both experiments (Figure 5). Tea type consistently had the strongest effect on mass loss compared to environmental variables across all models (elevational gradient: green tea estimate = 26.10 ± 1.10, $P < 0.001$; manipulation experiment: 38.71 ± 0.56, $P < 0.001$). Mass loss was also greater for green tea than rooibos tea across all elevational gradient plots (Welch two sample t-test: $t = 29.61$, $P < 0.001$), with an average mass loss of 47.00 ± 8.31%, compared to 20.75 ± 3.86% for rooibos tea (Figure 5a), across all experimental manipulation plots (Welch two sample t-test: $t = 56.77$, $P < 0.001$; green tea mean mass loss = 61.87 ± 6.12%, rooibos mean mass loss = 23.34 ± 3.51%; Figure 5b), and across both experiments combined (Welch two sample t-test: $t = 41.79$, $P = <0.001$, green tea mean mass loss = 57.64 ± 9.57%, rooibos mean mass loss = 22.62 ± 3.79 %; Figure 5c).

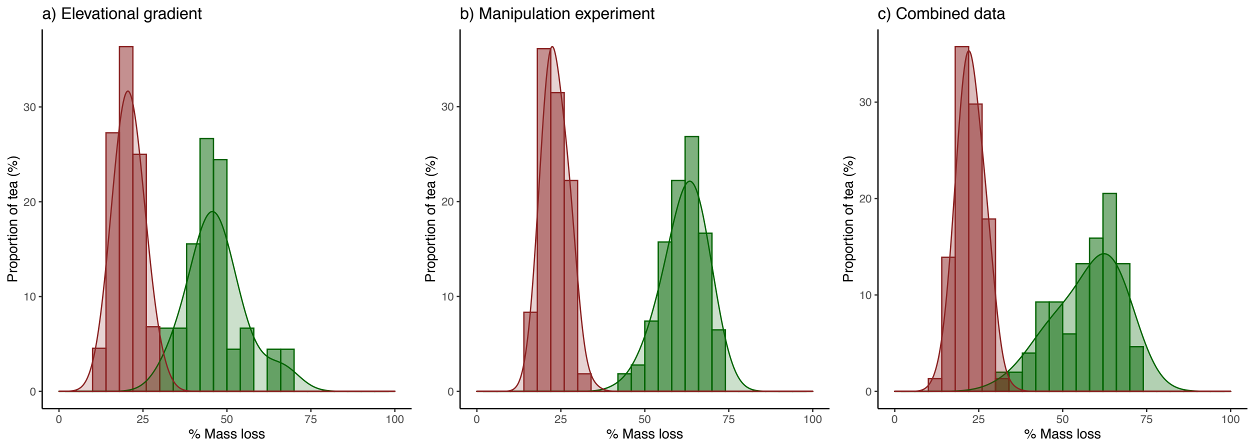

Figure 5. Green tea had greater mass loss than rooibos tea across the elevational gradient and in the moisture manipulation experiment. Distribution of mass loss for each tea type for a) the elevational gradient b) the manipulation experiment. Colours represent tea types (green = green tea, red = rooibos tea). Histograms are fitted with a smoothed density curve.

Discussion

Soil moisture, rather that temperature, best explained variation in decomposition

In this study, we found that litter decomposition increased with elevation along an elevational gradient from the boreal forest to alpine tundra (Figure 2). Moisture had similar or greater effect on decomposition compared to soil temperature across the elevational gradient and experiments (Figures 3 and 4). This surprising finding is contrary to our expectation that mass loss would decrease with elevation due to lower temperatures, and contrasts with several previous studies (Speed et al., 2015; Sveinbjörnsson et al., 1995; Withington & Sanford, 2007). We suggest that this finding is driven by differences in soil moisture. Soil moisture exhibited a positive relationship with mass loss along the natural elevational gradient (Figure 4), led to greater mass loss of the more recalcitrant litter type in the single-site manipulation experiment (Figure S4), and a had a similar or greater effect on mass loss in combined temperature-moisture models. Results were inconsistent with experimental manipulations across the elevational gradient (Figure S5). Our results highlight that soil moisture in addition to soil temperature is an important and potentially spatially variable control on litter decomposition rates.

Our results, though surprising, are consistent with other studies of decomposition in tundra ecosystems. A similar experimental study found that both temperature and soil moisture controlled rates of decomposition in Swedish tundra, with decomposition rate decreasing and stabilisation increasing with increasing soil temperature in wetter locations (Sarneel et al., 2020). Although temperature is often considered more important than moisture as a control over decomposition rates (Hobbie, 1996; Sierra et al., 2015), low moisture levels have been shown to constrain enzyme activity (Hicks Pries et al., 2013; Murphy et al., 1998) and reduce the activity of soil detritivores (Thakur et al., 2018). Our results suggest that moisture levels did not surpass the threshold at which decomposition decreases due to anoxia, with soil volumetric water content not exceeding 50% in either the elevational gradient or moisture manipulation. Taken together our results suggest that below a certain level of soil moisture, the importance of moisture may outweigh that of temperature in high-latitude soils (Aerts, 2006; Hicks Pries et al., 2013; Sarneel et al., 2020). These findings highlight the importance of interactions between temperature and moisture (Davidson & Janssens, 2006), and suggest that decomposition may only increase with warming at high latitudes if there is sufficient soil moisture.

We found that mass loss was better explained by elevation than by soil temperature or soil moisture (Figures 2 – 4). These finding highlights the importance of environmental gradients on decomposition rates and factors that covary with elevation, such as vegetation cover and microbial community (García-Palacios et al., 2013; Sjögersten & Wookey, 2004; Xue et al., 2016). Although microbial diversity in this study is unlikely to vary substantially across the 10 km study transect (Fierer et al., 2011), changes to microbial communities or soil properties with elevation and changing plant communities could account for some of the observed differences in decomposition

(García-Palacios et al., 2013). The high variability of soil moisture and soil temperature within our study emphasises the importance of microclimatic and topographic effects on decomposition (Bradford et al., 2014; Cahoon et al., 2012; Y. Chen et al., 2018). An observed increase in soil moisture with elevation may have resulted from input from snow melt at higher sites, evidenced by low soil moisture in treatments that prevented through-flow of water (see supplementary information, Figure S5).

Litter quality was the strongest determinant of decomposition

Despite differences in decomposition over the elevational gradient and between experimental treatments, litter quality was the primary determinant of decomposition across our study (Figure 5). Our findings support a range of site-specific results indicating that the effect of litter quality on decomposition outweighs that of climatic variation in high-latitude ecosystems (Baptist et al., 2010; Blok et al., 2016; Cleveland et al., 2014; Cornelissen et al., 2007; Hobbie, 1996), and strongly suggest that litter quality is the most important driver of litter decomposition in the tundra biome (Fierer et al., 2005; Sundqvist et al., 2011; Thomas et al., in revision) and beyond to other global biomes (Djukic et al., 2018; Joly et al., 2023).

A long-term shift in the composition of tundra plant communities and their functional traits could alter biotic and abiotic controls over decomposition and nutrient cycling (Bjorkman et al., 2018; Christiansen et al., 2018; Cornelissen et al., 2007; De Deyn et al., 2008; Hobbie, 1996; Myers-Smith et al., 2019; Shaver et al., 2006). Across the tundra biome, plant communities are shifting from graminoid or forb to shrub dominance (Elmendorf et al., 2012; García Criado et al., 2020; Myers-Smith et al., 2011). For example, dendroecological evidence indicates an upslope advancement of willow species at this field site (Myers-Smith & Hik, 2017). Given that shrub litter decomposes three to eight times more slowly than graminoid litter, partly due to the higher volumes of recalcitrant wood (Cornelissen et al., 2007; Shaver et al., 2006), a shift from graminoid to shrub dominance in tundra ecosystems could lead to greater storage of carbon and nitrogen in litter pools (Cornelissen et al., 2007; Mekonnen et al., 2021; Weintraub & Schimel, 2005) or to losses of carbon due to below-ground processes (Parker et al., 2021). Alternatively, increasing shrub abundance could be offset by changes in abundance of other functional groups (e.g., moss; Elmendorf et al., 2012), or shifts in traits within functional groups (Bjorkman et al., 2018).

Vegetation change also alters local conditions, for example albedo (Bonfils et al., 2012; Sturm, 2005; Williamson et al., 2016) and surface microclimate (Aguirre et al., 2021; Cahoon et al., 2012; Y. Chen et al., 2018; Kemppinen et al., 2021; Myers-Smith & Hik, 2013; Sturm et al., 2001). Due to these altered local conditions, decomposition could vary among different vegetation types (Aguirre et al., 2021; Christiansen et al., 2018; McLaren et al., 2017; Parker et al., 2021) or with vegetation change resulting from warming (Björnsdóttir et al., 2021). However, recent studies highlight the lack of evidence for microclimate variation in temperature as a control on decomposition in tundra (Gallois et al., 2022) and temperate forest ecosystems (Joly et al., 2023). Reducing uncertainty surrounding the magnitude and timing of feedbacks between vegetation change, decomposition and nutrient cycling remains a major challenge (Mekonnen et al., 2021).

The litter substrates used in this experiment are not native to study sites, and were selected for their ease of use and consistency among sites and across global experiments (Djukic et al., 2018; Keuskamp et al., 2013). However, decomposition rates of the two litter types are comparable with local tundra species (Figure S6), with annual mass loss of rooibos tea corresponding closely to native evergreen shrubs (e.g., *Rhododendron groenlandica*), and green tea corresponding to native graminoid species (e.g., *Festuca rubra*). There is some evidence for a ‘home-field advantage’ for litter decomposition, whereby native litter decomposes faster than non-native litter due to adaptation of the soil microbial community (Perez et al., 2013). Although the litter substrates used here are non-native, local adaptation towards particular litter traits could still result in produce a similar ‘home advantage’ effect. However, we did not find any evidence for this type of effect as we did not see an increase in mass loss within the shrub tundra zone, which corresponds most closely in litter traits to the two tea species. In contrast, there is also some evidence that non-native litters are colonised faster by decomposers and show greater mass loss (Pioli et al., 2020), thus the ‘home advantage’ effect may not be important.

We found that the two litter types responded differently to environmental drivers. Mass loss of recalcitrant litter (rooibos tea), but not labile litter (green tea), increased with soil moisture in experimental treatments. In contrast, mass loss of labile litter, but not recalcitrant litter, increased with temperature within experiments (Table 2, Figure 4), and demonstrated much greater differences in mass loss between the colder elevational gradient and the warmer moisture manipulation site located in the boreal forest. The point at which decomposition stabilised (*S*) was also more strongly related to temperature, while the decomposition rate (*k*) was more strongly related to soil moisture. These relationships are in line with findings that *k* and *S* were not strongly correlated over multiple sites (Keuskamp et al., 2013). The incubation position within the soil profile also influences the relationships between the stabilisation factor and the decomposition rate (Fanin et al., 2020). Thus, *k* and *S* are likely affected by different environmental variables and/or different decomposition processes. For example, the labile litter fraction could be controlled by the growth rate and metabolic rates of microbes (Moorhead et al., 2014), or water solubility (Day et al., 2018).

Our findings underline that the sensitivity of litter decomposition to environmental change is dependent upon initial litter characteristics. All litters will not respond to change equally (Conant et al., 2008; Craine et al., 2010; Davidson & Janssens, 2006; Djukic et al., 2018; Fanin et al., 2020; Fierer et al., 2005; Joly et al., 2023; McLaren et al., 2017; Suseela et al., 2013). The influence of vegetation change on decomposition remains unquantified due to uncertainty in projections of litter inputs and quality with warming (Björnsdóttir et al., 2021; Cornelissen et al., 2007) and uncertainty in the environmental conditions created by vegetation change (Christiansen et al., 2018; Keuper et al., 2020; McLaren et al., 2017; Parker et al., 2021). Thus, the sensitivity of litter decomposition to climate change remains a key uncertainty in our understanding of future carbon cycling and storage (X. Chen & Chen, 2018; Mekonnen et al., 2021).

The interpretation of our results are constrained by a number of caveats. We used homogenous plant litter following the Tea Bag Index protocol (Keuskamp et al., 2013), rather than local plant litters. In addition, we used above-ground plant litters in a soil decomposition experiment, which will influence the extrapolation of our results to local plant species and root litter decomposition (Aguirre et al., 2021). Our study was conducted during the growing season (June – August) and cannot represent year-round factors influencing decomposition, or long-term decomposition dynamics. Although the majority of decomposition occurs during the growing season (Bokhorst et al., 2011, 2013), such long-term perspectives will be critical to understanding carbon and nutrient cycling over longer timescales. Future decomposition research should focus on understanding both the abiotic and biotic controls on decomposition across variation in microclimate, litter inputs with vegetation change and over different timescales to shed further light on how decomposition will respond to climate change in rapidly warming tundra ecosystems (Gallois et al., 2022; Mekonnen et al., 2021).

Conclusion

Our results suggest that in a warming climate, levels of decomposition will only increase if there is sufficient soil moisture (Hicks Pries et al., 2013; Sierra et al., 2015), though further observational and experimental work is needed to test whether these findings are consistent over longer time scales and across sites. Our findings of differences in mass loss between substrates of contrasting quality reinforce the importance of litter quality as a controlling factor over rates of decomposition

(Björnsdóttir et al., 2021; Cleveland et al., 2014; Fanin et al., 2020; Fierer et al., 2005; García-Palacios et al., 2013; Joly et al., 2023; Lynch et al., 2018; Murphy et al., 1998). Vegetation change in high-latitude regions could alter rates of decomposition through the modification of organic matter input, which could outweigh the impacts of climate warming and soil wetting or drying (Björnsdóttir et al., 2021; Cornelissen et al., 2007; Fanin et al., 2020; Hobbie, 1996; Joly et al., 2023; Lynch et al., 2018; Mekonnen et al., 2021; Parker et al., 2018, 2021; Sundqvist et al., 2011). Our findings highlight the complexity and interactions among climate, environmental and biological controls on decomposition in high-latitude ecosystems across scales (Baptist et al., 2010; Björnsdóttir et al., 2021; Blok et al., 2016; Gallois et al., 2022; Hicks Pries et al., 2013; Sarneel et al., 2020; Sjögersten & Wookey, 2004; Thomas et al., in revision). Our findings, when combined with decomposition studies for sites across the tundra biome, will address uncertainties associated with predicting future carbon stocks and fluxes at high latitudes (Bardgett et al., 2013; Cahoon et al., 2012; Chapin et al., 2009; Crowther et al., 2016; Davidson & Janssens, 2006; McGuire et al., 2009; Mekonnen et al., 2021; van Gestel et al., 2018; Xue et al., 2016; Zona et al., 2023).

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Author contributions

EW, HT and IM-S conceived the study. EW and HT set up field experiments and conducted laboratory analysis. EW conducted the statistical analysis. EW and HT wrote the manuscript with input from IM-S.

Code and data repository

The code and data used for this study are available here:

https://github.com/ShrubHub/TeaElevationHub

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Supplementary Information

Supplementary Experiment: Multisite manipulation experiment

In order to test the interaction between short-term manipulation of temperature and moisture and long-term patterns across a natural elevational gradient, we also established three additional treatments plots at every three sites (1: 794 m, 4: 1175 m, 7: 1551 m, 10: 1926 m) along the elevational transect. These experimental plots comprised a control plot (see main text) and three experimental treatments:

1) The moisture treatment used a 60 x 30 cm plastic bed buried to approximately 20cm depth to retain precipitation, but restrict through-flow. Intact soil and vegetation cores were placed within each bed.
2) The temperature treatment used a 60 x 30 cm clear plastic cover to create greenhouse heating and exclude precipitation.
3) The combined treatment used both the bed and cover treatments (see also main text, Table 1).

In every treatment plot, we buried four tea bag replicates of each tea type pairwise (96 tea bags in total). Treatments were passive and remained unmanipulated after set up, and did not appear to affect plant growth or lead to plant mortality.

We tested differences among treatments using a random slope and intercept model with elevation and tea type as fixed effects and site and plot as nested random effects. To test how decomposition varied with temperature and moisture, we fitted a fixed slope model for each tea type using data from all plots, with site and day of measurement (temperature only) as random effects.

Experimental treatments plots along the elevational gradient had a significant effect on soil moisture (LMM, temperature treatment = 1.78 ±3.08, P = 0.58; moisture treatment = -2.67 ± 3.08, P < 0.41; combined treatments = -10.85 ± 3.08, P < 0.01) and on soil temperature (LMM, temperature treatment = 2.30 ± 0.55, P < 0.01; moisture treatment = 2.79 ± 0.55, P < 0.001, combined treatments = 3.93 ± 0.55, P < 0.001) across the elevational gradient. However, experimental treatments plots along the elevational gradient only had a significant effect on mass loss for green tea (Figure S6, Table S3). Mass loss was positively related to soil moisture within experimental treatments and across experimental sites, and positively related to temperature for green tea but not rooibos tea (Figure S6).

Supplementary Tables

Table S1. Relative effect size and significance of environmental variables versus mass loss based on linear mixed effects models for the elevational gradient and manipulation experiment. Soil moisture and soil temperature were mean centred and variance scaled. Significant models are highlighted in bold (. = P < 0.1).

	Tea type	Environmental variable	Relative effect size	Significance (P)
Elevational gradient	Green	Soil moisture	4.58 ± 2.03	0.07 (.)
		Soil temperature	1.43 ± 2.21	0.54
	Rooibos	Soil moisture	2.69 ± 1.11	0.09 (.)
		Soil temperature	1.16 ± 1.21	0.82
Manipulation experiment	Green	Soil moisture	0.12 ± 0.78	0.88
		Soil temperature	2.13 ± 0.78	0.01 (*)
	Rooibos	Soil moisture	2.70 ± 0.61	< 0.001 (***)
		Soil temperature	1.13 ± 0.61	0.11

Table S2. Effect of moisture manipulation treatments versus soil moisture, soil temperature, and mass loss of tea. Effect sizes indicate difference from ambient plots. Significant treatments are highlighted in bold (. = P <0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Treatment	**Soil Moisture**	**Soil Temperature**	**Mass Loss (all)**	**Mass Loss (Green)**	**Mass Loss (Rooibos)**
Disturbed	-9.25	0.43	1.54	3.83	-0.75
Cover only	-28.15 (***)	1.66 (*)	-1.63	-1.08	-2.17
Bed only	-27.88 (***)	1.24	1.33	2.92	-0.25
Bed and cover	-16.15 (*)	0.62	4.73	2.17	-1.00
Light water	-8.02	0.34	1.83	0.25	3.41 (*)
Light water, covered	-10.00 (*)	1.83 (*)	5.97 (.)	7.92	4.01 (*)
Saturated	20.25 (***)	0.66	2.83	-0.33	6.00 (**)
Saturated, covered	3.48	0.75	4.88	4.67	5.08 (**)

Table S3. Effect of elevational gradient treatments versus soil moisture, soil temperature, and mass loss of tea. Effect sizes indicate difference from ambient plots. Significant treatments are highlighted in bold (. = P <0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Treatment	**Soil Moisture**	**Soil Temperature**	**Mass Loss (Green)**	**Mass Loss (Rooibos)**
Temperature	1.78	2.30 (**)	0.18	0.81
Moisture	-2.67	2.79 (***)	2.50	1.88
Combined	-10.85 (***)	3.93 (***)	-4.45 (*)	-2.81

Table S4. Relative effect size and significance of environmental variables on stabilisation factor and decomposition rate for the elevational gradient and moisture manipulation experiment. Significant relationships are highlighted in bold (. = P <0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001).

Dataset	**Tea type**	**Environmental variable**	**Effect size**	**Significance (*P*)**
Elevational gradient	Stabilisation factor (S)	Soil moisture	-1.69e-03 ± 1.23e-03	0.19
		Soil temperature	3.60e-03 ± 6.45e-03	0.54
	Decomposition rate (*k*)	Soil moisture	6.05e-05 ± 5.07e-05	0.26
		Soil temperature	-8.62e-06 ± 2.80e-04	0.98
Manipulation experiment	Stabilisation factor (S)	Soil moisture	-9.17e-05 ± 8.74e-04	0.92
		Soil temperature	3.76e-02 ± 1.95e-02	0.08 (.)
	Decomposition rate (*k*)	**Soil moisture**	**1.97e-04 ± 4.46e-05**	**< 0.001 (***)**
		Soil temperature	2.12e-04 ± 9.92e-04	0.83

Supplementary Figures

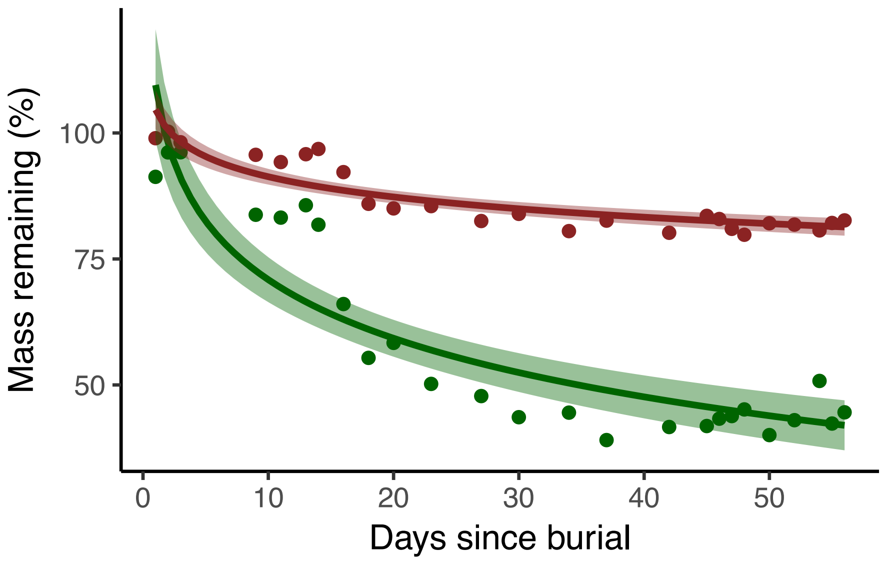


Figure S1. Mass loss over time during the incubation period of this study (52 days). Tea types are indicated by colours (green = green tea, red = rooibos tea). Lines are fitted to a single pool exponential decay model (formula = log(loss) ~ time, estimate (green) = -1.52e-02 ± 1.67e-03, P < 0.001, estimate (rooibos) = 3.74e-03 ± 4.03e-04, P < 0.001). Mass loss over time was established by removing two ambient tea bag replicates from the moisture manipulation study site every one or two days, and following mass loss protocols outlined in the main text. Mass loss was averaged over both replicates. Following (Keuskamp et al., 2013), green tea was found to stabilise during the study period, while rooibos tea continued to decay.

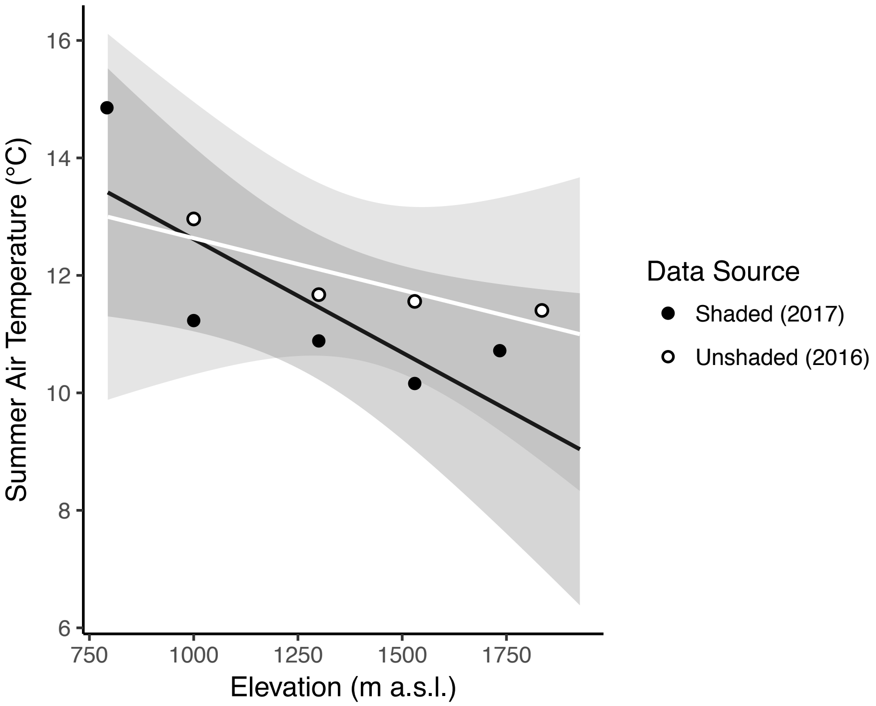


Figure S2. Decrease in mean summer surface air temperature (25 June – 12 August) with elevation across the elevational gradient. Air temperatures were measured as part of other experiments at the site over the same time period (Lembrechts et al., 2020), so dates do not align exactly with the tea incubation period. Air temperatures were measured using iButtons (DS1921G Thermochron iButtons, Maxim, San Jose, CA, US) placed at the ground surface. iButtons were unshaded in 2016 and shaded in 2017 with radiation shields. Point fill indicates sensor type (black = unshaded, white = shaded). Lines indicate linear mixed model fit and shaded area the 95% confidence intervals (LMM, shaded estimate =-0.004 ± 0.001, P = 0.04; unshaded estimate = -0.002 ± 0.002, P = 0.39).

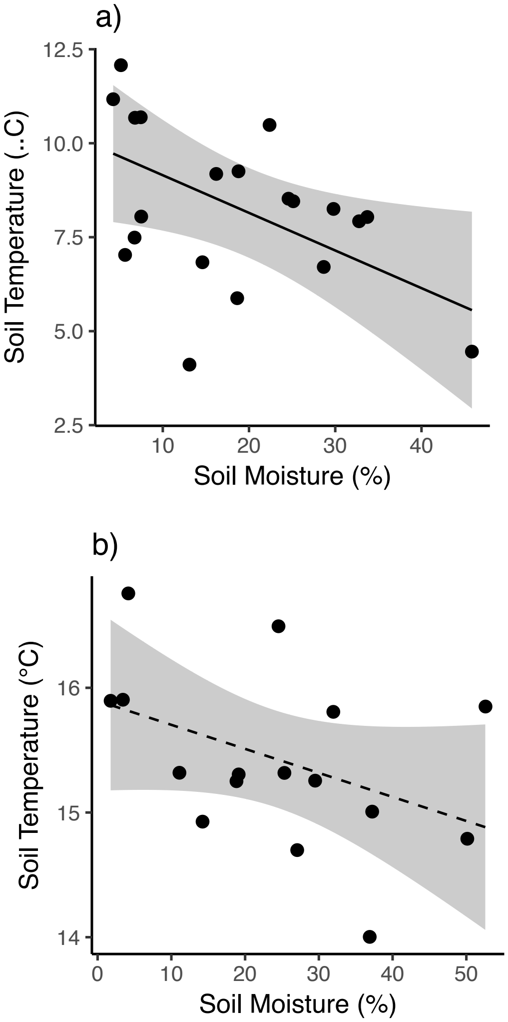


Figure S3. Relationship between plot-level soil moisture and soil temperature for a) elevational gradient plots, and b) moisture manipulation experiment plots. Lines indicate linear model fit and 95% confidence intervals (a: LMM; moisture estimate = -0.09 ± .0.04, $P < 0.05$; b: LM; moisture estimate = -0.09 ± 0.06, $P = 0.15$). The solid line indicates a significant relationship and the dashed line indicates a non-significant relationship.

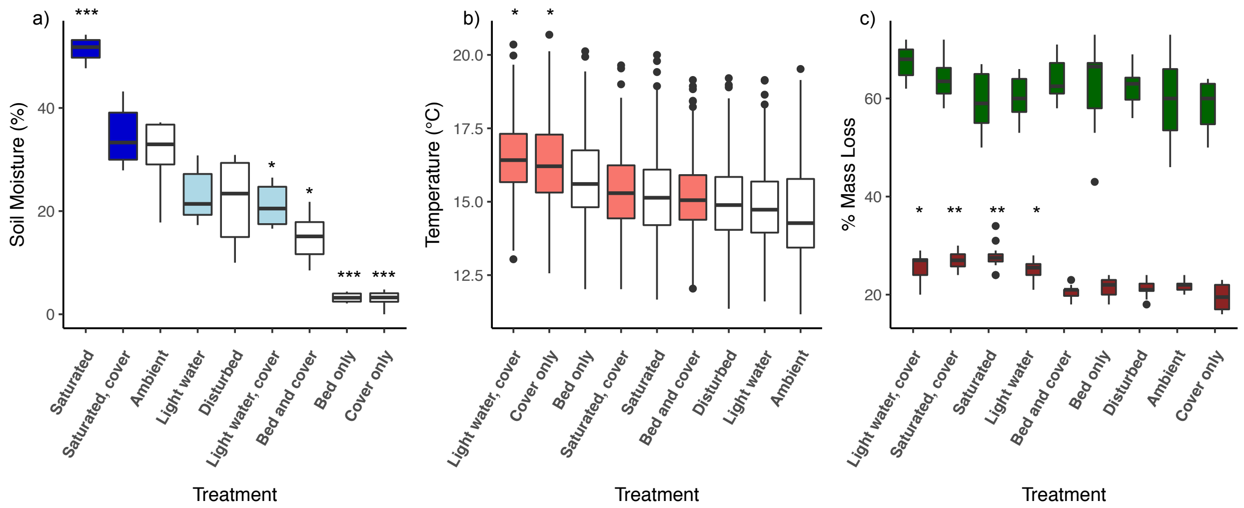
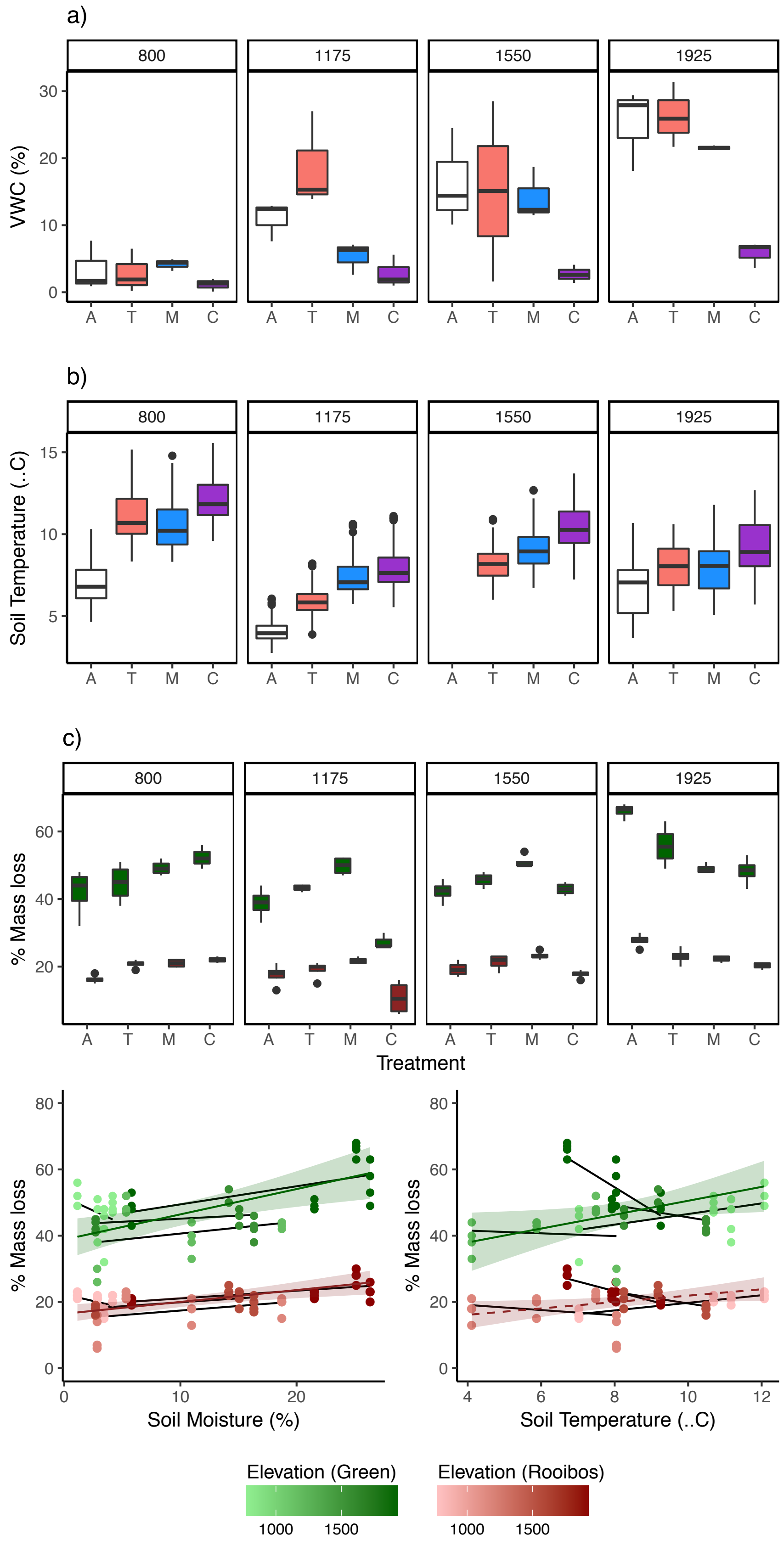


Figure S4. Experimental treatments significantly altered soil temperature, soil moisture and mass loss for rooibos tea, but not green tea. Differences in a) soil moisture, b) soil temperature, and c) mass loss among moisture manipulation experiment treatments. Colours indicate experimental treatment categories and tea type (a) dark blue = heavy watering, light blue = light watering; b) red = covered; c) dark red = rooibos tea, green = green tea). Treatments are sorted in descending order of response variable for each panel. Significance of models is indicated by symbols (. = P < 0.1, * = P < 0.05, ** = P < 0.01, *** = P < 0.001). Full model results are outlined in Table S1.


a)
800
1175
1550
1925
VWC (%)
0
10
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30
A T M C
b)
800
1175
1550
1925
Soil Temperature (..C)
5
10
15
A T M C
c)
800
1175
1550
1925
% Mass loss
20
40
60
A T M C
Treatment
% Mass loss
0
20
40
60
80
Soil Moisture (%)
0
10
20
Soil Temperature (..C)
4
6
8
10
12
Elevation (Green)
1000
1500
Elevation (Rooibos)
1000
1500

Figure S5. Combined treatments of warming and increased moisture lead to the greatest mass loss at the lowest, but not the highest elevations in an experiment across the elevational gradient. Differences in a) soil moisture, b) soil temperature and c) mass loss among elevational gradient treatments. Colours indicate experimental treatments and tea type (top two panels: A = ambient (white), T = temperature treatment (light red), M = moisture treatment (blue), C = combined temperature and moisture treatments (purple); bottom panel: dark red = rooibos tea, green = green tea). Effect sizes and significance of treatments are outlined in Table S1. The elevation of each plot (m a.s.l.) is indicated in the header of each box.

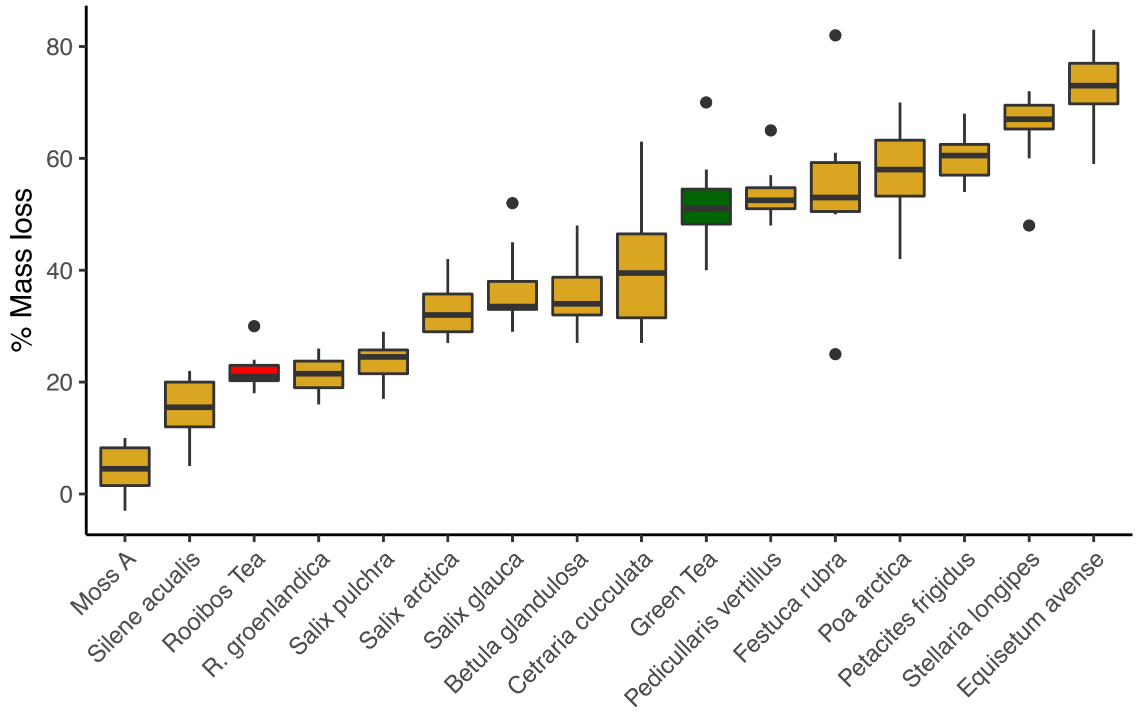

Figure S6. Annual mass loss of green and rooibos tea compared to annual mass loss of a range of representative tundra species. Tundra species were collected from two sites: the Kluane Range Mountains, Yukon, Canada (62° N) and Qikiqtaruk-Herschel Island, Yukon, Canada (70° N). All litter and tea were decomposed in a common litter bed at Kluane Lake following methods outlined in Cornelissen et al (2007). See (Thomas et al., in revision) for more information.