Microclimate explains little variation in year-round decomposition across an Arctic tundra landscape

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Abstract

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Keywords

Arctic tundra, carbon cycling, litter decomposition, microclimate, soil moisture, soil temperature, stratified random sampling, structural equation modelling, Tea Bag Index

Introduction

Feedbacks from high-latitude carbon cycling are pivotal for global climate change (Schuur et al. 2015, 2022). Not only is the Arctic experiencing rates of warming at three to four times the global average (AMAP 2021, Rantanen et al. 2022), tundra soils also store around half of terrestrial organic carbon (Tarnocai et al. 2009). Decomposition of leaf litter represents a key ecosystem process in this context, as it mediates the transition from living plant biomass to soil organic matter, thereby representing the primary carbon input to Arctic soils. Generally, it is assumed that decomposition rates in the Arctic will increase with warming (Aerts 2006, Xue et al. 2016), depending on moisture availability (Hicks Pries et al. 2013). However, as tundra ecosystems are characterised by high spatial heterogeneity in abiotic and biotic conditions, precise predictions of tundra soil carbon dynamics require a detailed understanding of how this variation in fine-scale soil temperature and moisture, hereafter termed 'soil microclimate', translates into litter decomposition dynamics (Bradford et al. 2016).

Local energy fluxes and hence soil abiotic conditions controlling decomposition rates are determined by tundra terrain features, vegetation and soil (Aalto et al. 2018, von Oppen et al. 2022; Figure 1). During the growing-season, topographical features, such as higher elevation, reduced sunlight exposure, or terrain depressions (Opedal et al. 2015, Aalto et al. 2018), and dense shrub cover (Blok et al. 2010, Myers-Smith and Hik 2013, Kemppinen et al. 2021, von Oppen et al. 2022) can cause lower soil temperatures that slow down litter decomposition rates by reducing decomposer activity. Similarly, terrain depressions or very fine soil texture can lead to extremely moist soil conditions that retard decay processes locally (Bryant et al. 1998, Robinson 2002, Christiansen et al. 2017, Sarneel et al. 2020, Venn and Thomas 2021). In contrast, tall shrubs might enhance decomposition rates (Blok et al. 2016) as they trap additional snow and create warmer soils through snow insulation during winter (Kropp et al. 2021). Generally, microclimatic variation has been shown to drive soil enzyme and microbial activity, as well as composition (Zak and Kling 2006, Wallenstein et al. 2009, Feng et al. 2020, Rijkers et al. 2023), thus causing variation in soil organic carbon stocks across tundra landscapes (Kemppinen et al. 2021). However, how the combined effects of terrain, vegetation and soil characteristics on soil microclimate affect *in situ* tundra decomposition rates remains uncertain.



Figure 1:

We hypothesise that direct and indirect effects of topography, vegetation and soil characteristics control litter decomposition in the Arctic tundra. Solid boxes indicate variables with field data. We did not collect data on soil organisms or microbial communities, but instead rely on strong established links between vegetation, soil, and microclimate with soil organisms and, ultimately, decomposition.

Plant functional traits as well as soil characteristics directly influence soil organisms, particularly microbes, and hence affect local decomposition rates and carbon cycling (Cornwell et al. 2008, Eskelinen et al. 2009, Sundqvist et al. 2011, Freschet et al. 2012). Decomposability of leaf litter, associated with traits such as leaf dry matter content (LDMC) or leaf carbon:nitrogen ratio (leaf C/N; e.g., Freschet et al. 2012), can differ widely between plant functional types (Cornelissen et al. 2007). Thus, traits of the local plant community can directly influence soil microbial communities and decomposition rates (Strickland et al. 2009, Keiser et al. 2011, DeMarco et al. 2014, Veen et al. 2015). Soil pH and nutrient concentrations also structure microbial communities in the ground and can therefore be expected to affect decomposition (Figure 1; Fierer

and Jackson 2006, Eskelinen et al. 2009). However, we do not yet understand to what extent these vegetation and soil characteristics influence decomposition rates directly, relative to the indirect influences of terrain and vegetation via their impact on microclimate. Disentangling these relationships is required for predicting future decomposition rates in changing tundra environments.

Here, we address this knowledge gap by adapting the Tea Bag Index (TBI; (Keuskamp et al. 2013) protocol for a network of stratified randomly placed microclimate monitoring plots. We buried pairs of standard tea bags with litter of contrasting quality along gradients of topography, vegetation productivity and water availability across an Arctic tundra landscape at Qeqertarsuaq (Disko Island), Western Greenland (Figure 2), with the following research questions in mind: (1) How important is micro-environmental variation in determining variation in decomposition rates across a tundra landscape?; (2) Does the relative importance of environmental drivers of mass loss differ between labile (Green Tea) and recalcitrant (Rooibos Tea) litter?; and (3) Within the hypothesised system of topography, vegetation, soil and decomposition (Figure 1), are direct (traits) or indirect (microclimate) effects of variation in vegetation more influential for determining decomposition?

Our study improves our understanding of the factors driving variation in litter decomposition across a tundra landscape and will help to inform predictions of future decomposition and carbon cycling dynamics in the changing Arctic.

Material and methods

Study area and plot layout

The study was performed across the eastern and western slopes of the Blæsedalen valley outside the town of Qeqertarsuaq, Disko Island, Western Greenland. The landscape features a heterogeneous topography, basaltic soils, and dwarf shrub-dominated tundra vegetation of variable density. We selected a total of 90 locations stratified randomly, aiming to cover gradients of elevation, vegetation productivity and water availability, across an area of 15 km² (von Oppen et al. 2022; Figure 2a). At plot establishment, we buried a soil temperature logger (HOBO MX-2201, Onset Corp., Bourne, MA, USA) in 6 cm depth at 10 cm into true South direction from the plot centre. Additionally, we placed a TMS-4 microclimate logger (TOMST, Prague, Czech Republic; Wild et al. 2019) at 10 cm into true North direction from the plot centre, which recorded topsoil moisture content (Figure 2b). We established the plots between 26 June and 01 July 2019 and retrieved tea bags and soil temperature loggers between 19 and 27 August 2020, with the length of incubation period varying by a maximum of 12 days across plots.

Figure 2:

Study design and environmental variation. a) Study area on Disko Island, Western Greenland. White circles indicate plot locations and numbers show elevation strata used for stratified random plot placement (separated by black contours). b) Positioning of loggers (TMS-T4: black dot; HOBO: black diamond) and teabags (triangles) within sample plots. Arrangement of tea types was randomised between plots. c) Variation of topographic (brown), vegetation/soil (green) and microclimate (blue) variables across sample plots. Horizontal jittering of points indicates the density of the value distribution. Grey points in the background for the gridded topographic variables show values for 1000 randomly sampled points within the study area (representing the full environmental variation in the region).

Topography, vegetation and soil variables

We recorded position and elevation at the centre of each plot location using a Trimble R8s dGNSS system (Trimble Inc., Sunnyvale, California, U.S.). We also measured local slope direction and inclination across a

4 m-diameter circle using a handheld inclinometer, from which we calculated local solar radiation as mean Solar Radiation Index (SRI; Keating et al. 2007) across the study period. In addition, we used the ArcticDEM (digital elevation model) at 2 m resolution (version 3.0; Porter et al. 2018) to extract (i) Topographic Position Index (TPI; Weiss 2001) within a 30 m radius, and (ii) Topographic Wetness Index (TWI; Beven and Kirkby 1979), following recommendations by Kopecký et al. (2021), through the SAGA GIS (Conrad et al. 2015) TPI and TWI modules, respectively, for our plot locations.

During the 2019 growing season, we visually quantified the proportional cover of shrubs, graminoids, forbs, bryophytes and lichens within a circle of 50 cm radius around the plot centre (Figure 2b) and subsequently summed their cover values into a single vegetation cover variable. Values for vegetation cover could surpass 100~% in case of multiple vegetation layers. In addition, we sampled functional traits for a subset of the most dominant species in the 60 plots on the eastern slope. As dominant species we considered those with >5% cover in one or more of the first 18 plots surveyed across low, mid and high elevation levels, plus additional locally abundant species with >5% cover in any given plot. For each species within each plot, we selected up to three (if available) healthy individuals closest to the plot centre and within the plot radius. For these individuals, we measured both vegetative and maximum plant height as the vertical distance from the ground to the tallest vegetative plant part or tallest plant part irrespective of tissue type. Furthermore, we sampled up to three leaves, or a small branch for small-leaved dwarf shrubs, from each individual for leaf trait assessment (n = 522 samples). We then determined the leaves' fresh weight and scanned them for leaf area calculation through ImageJ (Schindelin et al. 2012), before drying leaves at 70 °C for 48 hours. Using the leaves' dry weight, we calculated Specific Leaf Area (SLA) as dry weight per area, and Leaf Dry Matter Content as leaf dry weight divided by fresh weight. Due to limited resources, we could only determine chemical traits for a subset of 300 samples, with one random sample per species, elevation band and approximate water availability category (see sampling design in von Oppen et al. 2022). Dry soil and leaf samples were milled. We then used 5 to 20 mg per sample, depending upon organic matter content, to measure total C and N as well as isotopic ratios of C (13C/12C) and N (15N/14N). These analyses were carried out using an elemental analyzer by Dumas combustion at 1020 °C (Flash 2000, Thermo Scientific, Bremen, Germany) coupled to a Thermo Delta V Advantage IRMS in continuous flow.

We imputed community-level trait moments for the remaining 30 plots using hierarchical nonparametric bootstrapping through the *traitstrap* package (Maitner et al. 2021) incorporating the plots' moisture and productivity classes as determined during stratified plot placement. We subsequently performed a principal component analysis (PCA) from which we extracted plot scores along the first and second main axis of trait variation, which were related to leaf economics (PC1) and plant size (PC2), respectively (Figure S1). These axes aligned well with previous findings for global (Díaz et al. 2016) and tundra plant functional trait space (Thomas et al. 2020).

We took soil samples 10 cm north ("central") as well as at 50 and 150 cm distance into all intercardinal directions from the plot centre using a metal corer with 6 cm diameter and 3 cm depth. Samples were only taken if there was enough soil to fill at least 50 % of corer volume. Samples were oven-dried at 45 °C to constant mass and sieved to obtain gravel (> 2 mm diameter) and soil (< 2 mm) fractions. If less than 40 g of dry soil were available for a central sample, we selected one of the outer samples with sufficient material ($n_{50 \text{ cm}} = 30$, $n_{150 \text{ cm}} = 16$). If that was not the case for any of the nine samples, we pooled soil across samples, recording the contribution from each location (n = 22). Subsamples of 10 g were used to determine contents of several macro- (carbon, nitrogen, phosphorus) and micronutrients (Ca, K, Mg, Na), as well as soil pH and cation exchange capacity. Particle size fractions were determined from the remaining 30 g of soil (see Table S1 for a list of instruments used for soil analyses). We then performed a principal component analysis including all soil variables and, for each plot, extracted the scores for the first and second axis of variation. The two axes mainly corresponded to nutrient content, and soil pH and texture (higher silt, lower sand content), respectively (Figure S2).

Soil temperature and moisture data

We set soil temperature loggers to record soil temperature at 15-minute intervals throughout the tea bag incubation period. After visual assessment of temperature and moisture curves, we removed measurements from known periods of disturbance (field observations) during the 2019 growing season (± 1 day). These occurred for example if animals had removed loggers from the ground (n = 5). We also excluded records entirely if temperature loggers had been removed from the ground between 2019 and 2020 (n = 5). For each plot, we eventually calculated temperature sums (growing-degree days above 0 °C, GDD₀) across the incubation period.

Soil moisture loggers recorded at 10-minute intervals over the 2019 growing season (27 June – 07 August). We removed values from known periods of logger disturbance (n = 2) and where extremely low moisture signals indicated insufficient contact of the probe with the soil matrix during the measurement period (n = 2). We calibrated soil moisture using soil type-specific calibration curves provided by the manufacturer, assigning soil types to plots based on minimum Euclidean distances for particle size fractions. As we obtained a few negative moisture values for some plots due to imperfect calibration, we scaled soil moisture values to the range of individual measurements. We then calculated mean soil moisture across the 2019 growing season for each plot.

Burial and processing of tea bags, calculation of decomposition metrics

To measure decomposition dynamics, we used commercially available Green Tea and Rooibos Tea (EAN 8714100770542 and 8711327514348; Lipton, Unilever Inc.), on the basis of the TBI protocol (Keuskamp et al. 2013). The TBI has been used previously in numerous locations across the Arctic tundra (Sarneel et al. 2020, Gallois et al. 2022, Björnsdóttir et al. 2022, Thomas et al. 2023). The method should therefore be well suited to investigate the effects of multiple landscape-scale environmental gradients on litter decomposition.

We labelled and dried tea bags at 70 °C for 48 hours before recording the initial dry weight of each individual bag. During plot establishment, we buried tea bags at 2 cm depth and 10 cm distance into intercardinal directions from loggers (i.e., NW and NE of microclimate loggers and SW and SE of temperature loggers; Figure 2b), in order NW - NE - SW - SE irrespective of tea type to randomise positioning, corresponding to two replicates per type per plot and a total of 360 tea bags. Exact position and/or depth could vary slightly in response to local soil conditions. We retrieved tea bags after approx. 14 months (416 to 428 days). Due to occasional damage or disturbance by animals, we collected 285 intact bags (81 %). The number of plots with at least one intact sample was 83 for Green Tea, 79 for Rooibos Tea, and 79 for both Green Tea and Rooibos Tea. We dried the bags at 70 °C for 72 hours and placed them in ziplock bags with silica gel for transport and storage. Starting in August 2021, we dried tea bags again at 60 °C for 24 hours to remove any moisture potentially drawn during the storage period. We then determined post-burial dry weight and subtracted the average weight of 10 empty bags from all weights to obtain initial and remaining weight as well as mass loss of tea for each sample. Finally, we calculated relative mass loss for Green Tea and Rooibos Tea for each sample, and mean values per plot.

The TBI (Keuskamp et al. 2013; see therein for all parameters and equations in this subsection) describes litter decomposition dynamics according to a two-phase model - fast decomposition during the initial phase and slow decomposition during the second phase. Green Tea as a labile substrate is characterised by a high hydrolysable fraction ($H_g = 0.842$). Green Tea therefore has a relatively short first phase of decomposition, which enables estimation of how quickly a labile substrate stabilises in a given environment. The stabilisation factor S quantifies this amount of undecomposed labile litter, with high values of S indicating less favourable conditions for decomposition. It is calculated as:

$$S = 1 - a_a \cdot H_a^{-1}$$

with a_q as relative mass loss of Green Tea. Second, Rooibos Tea as a more recalcitrant material has a lower

hydrolysable fraction ($H_r = 0.552$) and its first phase of decomposition therefore stretches over a longer time period. However, assuming that S is constant for both substrate types, the theoretically decomposable fraction of Rooibos Tea (a_r) can be calculated as:

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

This can then be used to calculate the decomposition rate constantk, which describes how fast this gradual decay process occurred for the decomposable litter fraction:

$$k = ln(\frac{a_r}{M_r - (1 - a_r)}) \cdot \frac{1}{t}$$

Here, M_r is the relative remaining mass of Rooibos Tea, and the length of the incubation period in days. High values of ktherefore indicate rapid turnover of litter.

Tundra-wide decomposition data

To put decomposition rates from our study area into context, we obtained data on mass loss, k and S from the TundraTea initiative, which encompasses coordinated studies applying the TBI protocol across Arctic and alpine tundra regions (Thomas et al. 2023). We only included data from year-round incubations in untreated plots comparable to our study, and from regions with at least three unique plots to ensure variation in environmental conditions. This resulted in a total of 191 plots from 11 regions (1318 individual tea bags; Table S2).

Statistical analyses

From the 79 plots with complete decomposition response values, we removed: one extreme outlier with 2.4 times the next largest value for k, one plot which had no trait values due to sparse vegetation cover, and six plots with erroneous or missing microclimate measurements (resulting n = 71).

We used Structural Equation Modelling (SEM) to analyse the effects of variation in topography, vegetation and soil, and microclimate on decomposition dynamics. We chose SEM as the method is well suited to test our hypothesised system of direct and indirect processes influencing tundra soil decomposition, while also allowing us to account for any potential latent relationships not specified by us (Grace et al. 2015). According to our hypothesis (Figure 1), we fitted eleven sub-models (Table S3) describing the local impacts (i) of topography (elevation, solar radiation, topographic position and wetness) on vegetation (vascular plant cover and community-level leaf economic and size trait composition) as well as soil (nutrients and texture); (ii) of topography, vegetation and soil on microclimate (year-round GDD_0 and growing-season soil water content); and (iii) of plant community traits, soil and microclimate on each of the decomposition response variables, i.e. mass loss of either tea type, as well as on decomposition rate k and stabilisation factor S. We then combined the sub-models into a single multiple linear regression model within the SEM, using the piecewiseSEM package (Lefcheck 2016) in R. We inspected residual distributions for all sub-models to ensure assumptions about homoscedasticity were met. We also calculated pairwise linear relationships between decomposition response and explanatory variables within sub-models for comparison (i.e., not incorporating any covariates, residual variation from other models, or effect size standardisation; Table S4). These individual relationships were consistent with SEM results in terms of magnitude and direction of relationships as well as significance level (Tables S3, S4), hence we describe and discuss only SEM results in the following, as they better represent our initial hypothesis.

All data management and analyses were performed in R v4.1.1 (R Core Team 2021).

Results

Our study plots covered a range of topographic, vegetation and microclimatic conditions (Figure 2c). Plots were distributed between 53 m and 773 m a.s.l. and experienced solar radiation values between 0.81 SRI and 0.96 SRI. Relative positioning of plots in the landscape varied as well, with TPI ranging from -3.9 to 1.9 and TWI ranging from 4.3 to 10.6. Vegetation contexts varied widely, from almost barren plots (minimum 5 % cover) to densely vegetated plots with overlapping vegetation layers (maximum 168 % cover), also reflected in plant communities' variable leaf economic and size traits (Figure S1). Similarly, plots covered a range of soil conditions regarding nutrient content and texture (Figure S2). Finally, microclimate differed largely across plots, with accumulated soil temperatures over the incubation period ranging from 593 to 2200 GDD₀, and scaled mean growing-season volumetric soil moisture ranging between 2.8 and 68.9 % (Figure 2c).

Median mass loss in Green Tea and Rooibos Tea across sample plots was 60.3 % (95 % confidence interval: 51.1 - 71.9 %) and 24.8 % (18.6 - 31.4 %), respectively, over the approx. 14 months of incubation (Figure 3a,S3). Median decomposition rate k was 0.002 (0.0015 - 0.0040) and median stabilisation factor S was 0.284 (0.141 - 0.393; Figure 3b). These values were generally comparable to other studies from across the tundra biome (Figure 3), with relatively low values for k reflecting a slightly longer incubation time than those observed by other studies (Table S2).



Figure 3:

Tea mass loss and decomposition metrics were comparable to other sites across the tundra. Points and whiskers represent site-specific medians and 95 % quantiles, respectively, of a) relative mass loss in the two litter types and b) decomposition rate constant k and stabilisation factor S. White diamonds and coloured whiskers show values for this study, while grey dots and whiskers show values from 11 other sites across the tundra (Table S2; Thomas et al. 2023). Note that axes are truncated at the lower end.

We found that the micro-environmental predictors explained little variation in tea mass loss and decomposition metrics (Figure 4). While we observed some differences in the importance of environmental predictors for decomposition between the two tea types, the overall predictive power was low (Figure 4a). Specifically, Green Tea mass loss was lower in warmer soils (p < 0.01) and was typically greater with higher soil moisture, though the relationship was not significant (p = 0.15). Green Tea mass loss did not vary significantly with community leaf traits or soil characteristics (Figure 4a). None of the environmental factors predicted variation in Rooibos Tea mass loss (Figure 4a) and we observed no particular spatial patterns in mass loss for either litter type (Figure S4).



Figure 4:

Tea mass loss and decomposition metrics showed little variation in response to environmental factors. Points represent plot-level averages of a) relative mass loss in the two litter types, b) decomposition rate constant k, and c)stabilisation factor S. Trend lines and ribbons show mean and 95% confidence intervals of predicted linear relationships, respectively. Slope, intercept and p-values were extracted from individual sub-models within the Structural Equation Model (see Figure 5).

Environmental variation explained only a small amount of variation in our observed decomposition rate constant (k) and stabilisation rate (S). However, we observed a slightly higher explanatory power for microclimate (indirect vegetation/soil influence) compared to plant trait or soil-related explanatory variables (direct vegetation/soil influence; Figures 4b,c). Warmer plots had higher S (p < 0.01) and slightly (non-significant) higher k (p = 0.08), and S was slightly lower in moist soils (p = 0.15). However, neither leaf traits nor soil characteristics explained variation in decomposition metrics (Figures 4b,c). Also, no spatial patterns were visible for either decomposition variable (Figure S4).

Overall, our hypothesised system of topography, vegetation and soils, and microclimate explained little variation in decomposition, reflected in a low overall model fit of the SEM (Fisher's C = 769.5, df = 106, p< 0.001; Table S3). Explanatory power was highest for leaf economic traits ($R^2 = 0.45$) and soil parameters (pH / texture: $R^2 = 0.28$; nutrients: $R^2 = 0.27$; GDD₀: $R^2 = 0.38$) but low for decomposition variables (Green Tea mass loss: $R^2 = 0.16$; Rooibos Tea mass loss: $R^2 = 0.05$; $k: R^2 = 0.08$; $S: R^2 = 0.16$; Figure 5). Moreover, SEM relationships between variables besides decomposition only partly reflected our expectations (Figures 1,5). Elevation and solar radiation were the most influential topographic predictors. Higher elevation significantly predicted lower vegetation cover, more acquisitive leaf traits, lower soil nutrient content, and lower soil temperatures (all p < 0.001), as well as higher silt and lower sand content in the soil (p < 0.05). Higher solar radiation was related to higher soil moisture (p < 0.01, with solar radiation being highly negatively correlated with slope (Pearson's r = -0.93), as well as to cooler soils, smaller plants, and more acquisitive leaf traits (all p < 0.05). In addition, higher TWI predicted higher soil pH and higher silt rather than sand content (p < 0.01) and higher soil nutrient concentration (p < 0.05). TPI did not predict any variation in vegetation, soil or microclimate variables (Figure 5). Only one of the tested relationships between vegetation and microclimate was significant, as higher vegetation cover predicted lower soil temperatures (p < 0.001). Soil texture did not predict any variation in soil moisture (Figure 5).



Figure 5:

Results of the structural equation model analysing links between topography, vegetation, soil, and microclimate on decomposition. Individual relationships were tested using multiple linear regression. Purple arrows indicate negative, orange arrows positive, and grey dotted arrows non-significant links. Thicker lines correspond to stronger identified links (larger effect sizes). R^2 values represent model fit for individual sub-models. Relationships between vegetation, soil and microclimate predictors and decomposition responses were tested for each decomposition response variable individually, indicated by the dashed boxes, but GDD₀only significantly predicted variation in stabilisation factors (see also Figure 4). See Table S3 for full model output and Table S4 for comparison with individual pairwise relationships of decomposition responses with their explanatory variables.

Discussion

Our structural equation modelling of the variation in decomposition rates across the tundra landscape in Western Greenland indicated that: (1) micro-environmental factors play a minor role in explaining variation in decomposition at the landscape scale; (2) environmental predictors differ little in their importance for mass loss of Green Tea (soil temperature and moisture) and Rooibos Tea (no significant predictors); and (3) only some indirect effects of vegetation on decomposition through microclimate were significant, while there was no evidence for direct (trait) related effects. However, the overall explanatory power of our SEM was low and the overall fit was non-significant. This suggests that other factors than the topographical, vegetation, soil and microclimate variables included here control the mechanisms behind decomposition across our studied tundra landscape, such as decomposer communities or annual and seasonal variation in micro-environmental conditions (see detailed discussion below). Overall, our results highlight the need for further research to advance our understanding of decomposition processes and carbon cycling in the changing Arctic. Below, we discuss the findings in relation to our research questions and derive some general recommendations for future decomposition studies in the tundra.

Weak links between microclimate, plant traits, and decomposition at the landscape scale could be explained by absence of other known controls not accounted for in our analysis Despite considerable variation in both environmental conditions (Figure 2c) and decomposition (Figure 3) across our study plots, the observed relationships between environmental conditions and decomposition were weak (Figure 4). This suggests that the topographical, vegetation, soil, and microclimate predictors we measured did not capture all ecologically relevant conditions and processes that control decomposition dynamics within this tundra landscape. For instance, we did not explicitly measure differences in decomposer communities and/or temporal activity. Comparable SEM studies from both tundra (Robinson et al. 2022) and other environments (e.g., Tresch et al. 2019, Xiao et al. 2019) identified decomposer community composition and activity as a key control on decomposition (but see Joly et al. 2023), and vegetation patterns along elevational gradients might not always reflect differences in microbial communities (Bryant et al. 2008, Fierer et al. 2011). Furthermore, soil organic matter content has been shown to drive abundances of soil microbial groups as well as decomposition rates in subarctic Iceland (Robinson et al. 2022). Also, longerterm soil moisture measurements might more accurately capture the variability in soil moisture conditions experienced by decomposers than our short (one growing season) time-series and hence could hold more power for predicting decomposition rates (Blok et al. 2010, Christiansen et al. 2017). Similarly, as environmental conditions in the Arctic tundra vary considerably between growing season and winter, complementing burial periods (e.g., growing season vs. winter vs. year-round) would help to disentangle potential seasonal differences in the controlling factors of Arctic decomposition dynamics, as well as differences in early vs. late-stage decomposition (Keuskamp et al. 2013, García-Palacios et al. 2016, Canessa et al. 2021). We suggest that future studies account for these additional factors to model tundra plant litter decomposition more accurately.

Little difference in importance of environmental variables among contrasting tea types

Although relative mass loss was higher in Green Tea than in Rooibos Tea (Figure S3), relationships of mass loss with plant traits, soil characteristics, and microclimate differed little between tea types (Figure 4a). This indicates that, overall, variation in environmental conditions did not selectively stimulate primary decomposer groups that prefer either labile or recalcitrant litter. Higher mass loss in Green Tea compared to Rooibos Tea reflected differences in substrate quality, as for instance nitrogen content and water-soluble fraction in Green Tea are two to three times higher than in Rooibos Tea, respectively (Keuskamp et al. 2013). This result corroborates the importance of litter identity in the light of tundra vegetation changes and increasingly recalcitrant litter (Cornelissen et al. 2007, Myers-Smith et al. 2011, Thomas et al. 2023). Yet, largely constant mass loss across environmental gradients suggests that both bacterial (main decomposers of labile litter) and fungal communities (main decomposers of recalcitrant litter) varied little among plots (Yang et al. 2021). The only relationships that differed slightly between tea types were those associated with microclimatic variables. For instance, we observed lower mass loss at warmer and drier conditions for Green Tea, but not for Rooibos Tea (Figure 4a). These differences could reflect the effect of warming-induced evaporation. which can reduce decomposer activity at suboptimal moisture conditions (Christiansen et al. 2017). Overall, our findings suggest that vegetation changes and reduced litter quality might be more important for future tundra decomposition than immediate microclimatic changes related to warming (Cornelissen et al. 2007, Cornwell et al. 2008, Thomas et al. 2023). However, more targeted sampling of decomposer communities could help to disentangle these relationships.

Direct vs. indirect controls of decomposition

How future warming and associated vegetation changes will impact decomposition rates in the tundra will also depend on the balance of microbial community priming by plant traits (Veen et al. 2015) and increases in decomposer activity with warming (Rijkers et al. 2023). The weak relationships between environmental controls and decomposition responses observed in our study suggest that neither the direct (traits) nor indirect (microclimatic) vegetation effects that we measured were particularly important for decomposition in our study system. Microclimate was associated with weak trends in Green Tea mass loss and stabilisation rates, while we did not find any link between plant community or soil traits and decomposition. These findings could point to a higher importance of abiotic conditions, for instance induced by shrub shading (Blok et al. 2010, Myers-Smith and Hik 2013), snow accumulation (Sturm et al. 2001) or bryophyte cooling (Blok et al. 2011), compared to substrate quality effects for controlling decomposers. This is also in line with earlier predictions that climate represents the dominant control on litter decomposition in harsh environments (Coûteaux et al. 1995). While our study was limited to certain predictors and gradients, follow-up studies explicitly stratifying across these microenvironmental factors might help elucidate this further.

Relationships between topography, vegetation, soil and microclimate

Our study sites covered a range of abiotic and biotic environmental conditions (Figure 2c), indicating that the stratified random sampling approach overall captured environmental gradients in the area. Yet, relationships between topographic, vegetation and soil variables and microclimate only partly reflected our expectations (Figure 5). As expected, soil temperature decreased with higher elevation and underneath higher vegetation cover, corroborating trends previously found in Fennoscandian tundra (Kemppinen et al. 2021). In contrast, solar radiation predicted trends opposite to expected relationships, particularly lower rather than higher soil temperature but higher rather than lower soil moisture, possibly due to its close association with slope values. Local topography as quantified by TPI did not explain variation in any vegetation or soil parameter, perhaps because variation in TPI was more constrained than in other variables (Figure 2c), thus not well representing differences in snow accumulation or wind exposure across the landscape. Also, neither TWI nor soil texture explained variation in growing-season soil moisture among plots. Here, our gradient most likely did not cover the entire spectrum of conditions present in the area, as very wet locations were not covered (Figure 2c), probably as a result of the dry summer in 2019 and of standing water areas being masked out during the stratification process. The example highlights the difficult issue of obtaining reliable soil moisture predictions in tundra ecosystems (Kemppinen et al. 2018). In addition, implicit uncertainty in gridded topographic variables might have added further noise to our dataset.

Towards improved stratified random studies of tundra decomposition

Although our findings were overall inconclusive with regard to quantifying controls of tundra decomposition dynamics, they point to potential avenues for improving Arctic decomposition studies.

Incubating locally sampled litter alongside standardised substrate, in addition to including community traits as explanatory variables, would be an essential step to contextualise decomposition patterns in standard litter and enable more precise conclusions on feedbacks of vegetation change on decomposition (Joly et al. 2023). In a laboratory experiment, Duddigan et al. (2020) found that both tea types generally follow patterns of natural leaf litter decomposition, and studies in specific alpine (Didion et al. 2016, von Oppen 2017) and Arctic (Thomas et al. 2023) sites have shown that the two tea types well represent mass loss in local litter. However, a comparative study is still missing for the Arctic tundra biome at large, resulting in uncertainty about the representativeness of mass loss rates inferred from standard substrate. More generally though, the informative value of standard-litter experiments can be limited if nutritional differences between local litter and standard substrate are not accounted for explicitly (Joly et al. 2023). Given the importance of tundra carbon cycling, a systematic assessment of the representativeness of standard decomposition protocols (e.g., TBI) will be essential for adequate quantification of litter decomposition in Arctic environments.

Many regions across the Arctic tundra biome are experiencing notable vegetation changes in response to warming or degrading permafrost (Heijmans et al. 2022). However, a lack of coordinated systematic investigations of tundra decomposition dynamics across tundra zones and habitat types, is impeding biome-wide predictions of tundra carbon dynamics (Bonan et al. 2013); but see Thomas et al. 2023). Large-scale replication of stratified-random sampling could fill this gap, enabling representative sampling of environmental gradients across and within sites, as well as evaluation of the relative importance of macro- vs. microclimate for tundra litter decomposition (Joly et al. 2023). Our findings underline the importance of considering variables representing the complete decomposition process, particularly decomposer organisms as well as both local and standard litter, and both fine- and more broad-scale environmental data. Ultimately, such coordinated studies could be of high value to inform predictions of the future carbon balance of tundra soils with projected vegetation and environmental changes (van Gestel et al. 2018).

Conclusion

We incubated two types of standard litter of contrasting quality (Green Tea and Rooibos Tea) over 14 months across an Arctic tundra landscape, covering several environmental gradients of topography, vegetation, soil and microclimate. Although we found significant links between topography, vegetation, soils and microclimate, the micro-environmental variation itself explained little variation in decomposition responses. This suggests that other factors not accounted for in our study, like long-term moisture availability, snow patterns, or other seasonal effects might control activity and community composition of decomposers. Nonetheless, our systematic approach could serve as guidance for coordinated studies of tundra decomposition dynamics, particularly across large extents. Further research should explicitly include local litter material, decomposer communities, and temporal variation to improve model fit and explanatory power, and to support better predictions of Arctic tundra litter decomposition and carbon cycling dynamics.

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