Title: Long-term climate regime modulates the impact of short-term climate variability on decomposition in alpine grassland soils.

Short title: Modulation of decomposition by long-term climate

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Manuscript highlights:

- Decomposition increases with temperature and decreases with increased precipitation
- Stabilization of labile fraction of litter varies among long-term climate regimes
- Long-term climate modulates decomposition through environmental characteristics

Abstract

Decomposition of plant litter is an important process in the terrestrial carbon cycle and makes up ~70% of the global carbon flux from soils to the atmosphere. Climate change is expected to have significant direct and indirect effects on litter decomposition processes at various time-scales. Using tea bag index (TBI), we investigated the impact on decomposition of short-term direct effects of temperature and precipitation by comparing temporal variability over years, versus long-term climate impacts that incorporate indirect effects mediated through environmental changes by comparing sites along climatic gradients. We measured the initial decomposition rate (*k*) and stabilization factor (*S*; amount of labile litter stabilizing) across a climate grid combining three levels of summer temperature (6.5-10.5°C) with four levels of annual precipitation (600-2700mm) in three summers with varying temperature and precipitation. Several (a)biotic factors were measured to characterize environmental differences between sites. Increased temperatures enhanced *k*, whereas increased precipitation decreased *k* across years and climatic regimes. In contrast, *S* showed diverse responses to annual changes in temperature and precipitation between climate regimes. Stabilization of labile litter fractions increased with temperature only in boreal and sub-alpine sites, while it

decreased with increasing precipitation only in sub-alpine and alpine sites. Environmental factors such as soil pH, soil C:N, litter C:N and plant diversity that are associated with long-term climate variation modulate the response of k and S. This highlights the importance of long-term climate in shaping the environmental conditions that influences the response of decomposition processes to climate change.

Introduction

Litter decomposition contributes about 70% to the global CO_2 flux from soils and is estimated to be in the range of 68 – 77 x 10^{15} gC yr^{-1} (Raich and Schlesinger, 1992; Raich and Potter, 1995). On a global scale, litter decomposition is regulated by a combination of geographic, climatic and litter quality variables (Zhang and others, 2008). Climate affects decomposition processes directly and at short time-scales through temperature and water availability as biological processes are highly sensitive to these factors. On longer time scales climate also affects decomposition indirectly, for example, by affecting the litter quality via plant community composition and structure, or by affecting decomposer and detritivore community composition (Aerts, 2006). Climate change is expected to have substantial effects on both direct and indirect controls of decomposition processes, and the associated CO_2 release could have a positive feedback on global warming (Davidson and Janssens, 2006; Crowther and others, 2016). It is therefore important to determine both direct and indirect effects of climate change on soil carbon dynamics to quantify more accurately the role of soil under future projections of climate change (Classen and others, 2015). In this study, we investigate the direct effects of climate change by studying the response of decomposition processes to short-term inter annual climate variation (hereafter: short-term climate), while indirect effects are studied through the use of spatial climate gradients that represent long-term climate (hereafter: long-term climate) which is an important state factor shaping ecosystem structure and functioning (Chapin and others, 2011). We use a climate grid in southern Norway, that combines three levels of summer temperature, *i.e.* the mean of the four warmest months June-September, representing different biogeographic zones (alpine ≈ 6.5°C, sub-alpine ≈ 8.5°C, boreal ≈ 10.5°C) with four levels of mean annual precipitation (1 ≈ 600 mm, 2 ≈1200 mm, 3 ≈ 2000 mm, 4 ≈ 2700 mm) while avoiding correlation between climatic factors (Meineri and others, 2013; Klanderud and others, 2015). This study design allows us to disentangle the short-term (direct) and long-term (indirect) impacts of climate on litter decomposition in alpine grasslands in three consecutive growing seasons with contrasting climates.

Climate change scenarios predict greater increases in surface temperature and enhanced precipitation for northern high-latitudes (IPCC, 2013). Because biological processes in these regions are generally temperature limited, litter decomposition is expected to increase (Hobbie and others, 2002; Robinson, 2002). The effect of global warming on decomposition in these regions is often studied by artificial warming experiments. This type of intra-site experiment studies the short-term direct effects of warming on decomposition but disregards the long-term indirect effects of climate that shape the local environment through edaphic factors and plant and decomposer communities. In addition, these experiments can be troubled by artifacts such as soil drying, and they often ignore the role of and projected changes in precipitation (Aerts, 2006). Field approaches that make use of extant climatic gradients – space-for-time approaches – can be performed at broad spatial scales, spanning entire or multiple continents (Berg and others, 1993; Cornelissen and others, 2007; Portillo-Estrada and others, 2016), or at a local scale, spanning a single gradient (e.g. Murphy and others, 1998; Salinas and others, 2011). Such gradient studies have the advantage of being able to incorporate indirect, long-term effects of climate. However, in most cases, covariation occurs between temperature and precipitation across the gradient, making it difficult to separate the effect of these climatic factors on decomposition. Temporal variability in climate between years is another way to study the direct effects of climate on decomposition (McCulley and others, 2005). The combination of climatic gradients together with annual climate variability is an opportunity to study both the short-term direct and the long-term indirect effects of climate on decomposition.

The majority of litter decomposition studies use native leaf material, which makes them very realistic, but this approach also has a drawback. Litter can decompose faster when it is placed under the plants from which the litter originated (“home”) than at locations with different plant species (“foreign”) (Ayres and others, 2009; Veen and others, 2015). This phenomenon is called “home-field advantage” (Gholz and others, 2000), and can bias results in studies using one local litter across sites with different species. Recently, Keuskamp and others (2013) developed the TeaBag Index (TBI) as a standardized method to negate litter quality and litter trait effects from environmental drivers of decomposition processes by removing this litter bias. This method uses two types of tea with contrasting decomposability as standard litter substrate in order to characterize two parameters of the decomposition process. The decomposition rate constant (k) is a measure of the speed of initial litter decomposition and the stabilization factor (S) is a measure of the proportion of the labile fraction of litter that will finally stabilize and become recalcitrant and transform into soil organic matter (SOM). Decomposition of native litter and the standard tea litter shows similar responses to changes in temperature and precipitation, indicating that the TBI is a suitable approach for assessing the role of environmental variables on litter decomposition (Didion and others, 2016).

In this study, we used the TBI to investigate the short-term (inter-annual variability) and long-term (environmental conditions shaped by differences in climate between sites) effects of climate on litter decomposition in mountain grasslands in southern Norway. We used a climate grid that consists of sites positioned along natural temperature and precipitation gradients explicitly selected to disentangle effects of temperature and precipitation. To investigate the response of decomposition processes to short-term climate variability we adopted the TBI approach in three consecutive summers that varied in temperature and precipitation. At each site, we measured a number of biotic and abiotic variables to determine how long-term differences in climate have shaped the local environment at the different sites. The combination of the climate grid and annual climate variability provided the opportunity to compare the impact of short-term variation in climate compared with long-term effects of regional climate gradients on decomposition processes.

Specifically we aimed to (1) determine how decomposition processes are affected by short-term variation in temperature and precipitation, (2) evaluate whether these responses are consistent across regional climate gradients and (3) assess to what degree short-term and long-term impacts of climate affect decomposition processes.

We expected decomposition to increase in sites and in growing seasons with higher temperatures and precipitation, because mountain ecosystems are known to be limited by temperature and productivity generally increases with precipitation. In addition, we expected the reaction to be strongest in sites where the other factor was not limiting, so that variation in precipitation (between sites and years) would cause larger differences in decomposition in the warmest locations than in cold locations where decomposition is limited by temperature. Vice versa, variation in temperature should cause larger differences in decomposition in the wettest location than in low-rainfall sites, where moisture limitation is more likely.

Materials & Methods

Site description

The study was conducted in a climate grid consisting of 12 calcareous grassland sites spread across natural temperature and precipitation gradients, spanning almost 1000 m in elevation and 175 km in geographical distance. The sites of this grid were selected based on interpolated climate data from the normal period 1961-1990 with a resolution of 100 m (Tveito and others, 2005; Norwegian Meteorological Institute, 2010). It combines three levels of summer temperature, *i.e.* the mean of the four warmest months June–September, representing different biogeographic zones (alpine ≈ 6.5°C, sub-alpine ≈ 8.5°C, boreal ≈ 10.5°C) with four levels of mean annual precipitation (1 ≈ 600 mm, 2 ≈1200 mm, 3 ≈ 2000 mm, 4 ≈ 2700 mm; Figure 1). All sites are semi-natural grasslands on shallow slopes (5-20°) associated with calcareous bedrock and plant communities within the plant sociological association *Potentillo-Festucetum ovinae* (Fremstad, 1997) and other factors were kept as similar as possible; including aspect and land use (for more details see (Meineri and others, 2013; Klanderud and others, 2015); and also see Table S1). The sites are fenced during the snow-free season to prevent ungulate grazers from damaging the experimental set-up.

Climate data

The Norwegian Meteorological Institute (NMI) provided mean daily interpolated data on air temperature and precipitation at a resolution of 100 m for each site for the whole study period 2014-2016 (Norwegian Meteorological Institute, 2016). At each site, we measured soil temperature at 5 cm below ground with MT2-05 temperature sensors (Delta-T Devices, Cambridge, UK). Due to temperature sensor malfunction of climate stations at some sites, we do not have continuous soil temperature measurements at site level for each of the incubation periods. In 2014, iButton temperature loggers (DS1922L, Maxim Integrated, San Jose, CA, USA) were buried at five locations in each site at a depth of 8 cm. Temperature data from the different sources were compared to each other both visually and by pairwise Pearson correlation for the incubation periods of the tea bags (± 3 months in summer, see method section on litter decomposition measurements) at the different sites (Figure S1). Because the temperature data of NMI for incubation periods corresponded well with both buried iButton and climate stations at all the sites, $R^2 > 0.93$ and $R^2 > 0.83$ respectively, we decided to use air temperature data from NMI in the analyses. Mean temperature and total precipitation were calculated based on data from NMI for the incubation periods of tea bags for each site and year (Table S2).

Environmental variables representing long-term climate

Long-term climate plays an important role in shaping ecosystem structure by influencing the development of soil and determining the types and diversity of plants and organisms that can occur (Chapin and others, 2011). This climatically-driven variability in the biotic and abiotic environment could affect decomposition (*i.e.*, indirect effect of climate). To characterize these differences, we measured a number of biotic and abiotic characteristics at each site.

Soil properties

At each site, five composite soil samples were collected by combining three core rings (5 cm diameter). Soil pH of these samples was measured after mixing 30 g of sieved fresh soil with 30 ml deionized water. Additional soil samples from the surface layer (0–10 cm) were collected with a soil corer (25 mm diameter) from four locations at each site. These samples were oven dried at 30°C for 2–3 days and roots were carefully removed. Dried samples were ground thoroughly and passed through a 1 mm sieve. Subsequently, a 25 g subsample was milled at a frequency of 30 s^{-1} for 2–3 min with a mixer mill (MM200, Retsch Gmbh, Haan, Germany). Total soil C and N content was measured using a Vario MICRO cube elemental analyzer (Elementar Analysesystem GmbH, Germany). Soil mineral N availability was determined in summer 2010 with ion exchange resin bags (IERBs) (Fariñas, 2011). At each site, 10 IERBs were buried at 5 cm depth at the beginning of the growing season and collected at the end of August. The NH_4^+ and NO_3^- were extracted from the resin bags with NaCl and measured colorimetrically with a SmartChem autoanalyzer. Total availability of N was calculated from the sum of NH_4^+ and NO_3^- concentrations standardized by the number of days the IERBs had been deployed in the different sites (Giblin and others, 1994). Two extremely high values for available nitrogen (1059.67 and 487.78 mg g^{-1} N) at ALP3 were considered outliers and excluded from the analysis.

Vegetation characteristics

Plant diversity was quantified for each site by recording all vascular plant species in five vegetation plots (25 x 25 cm) and estimating the percentage of cover by eye at peak growing season in 2015 and 2016. The Shannon diversity index of the individual plots was calculated for each individual plot in the separate years and averaged to get a mean diversity index per site.

Carbon (C) and nitrogen (N) concentrations of living aboveground vegetation were determined from pooled samples based on three circular plots of 5 cm diameter harvested from five locations within each site at peak growing season in 2011 (Fariñas, 2011). The samples were dried (24h at 70°C), ground in a Wiley Mill (Thomas Scientific, Swedesboro, U.S.A) and analyzed using a Costech ECS 4010 elemental analyzer (Costech Analytical, Valencia, CA).

Litter quality for each site was determined from dead leaves that easily detached from live graminoids representative of the vegetation community collected along a transect within the fenced experimental site. The litter was collected in August/September 2013 for alpine sites and after snowmelt in May/June 2014 for sub-alpine and boreal sites, as litter could not be collected in the autumn because snowfall started earlier than the die-off of graminoids.

As we assume that very little decomposition occurs during winter we expect the litter collected after snowmelt to be representative of the litter quality entering the soil in summer at these sites. The litter was washed in deionized water to clean it of any soil particles, air dried at room temperature for at least seven days and subsequently stored in a well-ventilated room until processing. For each site two litter samples of 10 g were ground in a cyclone mill (TWISTER, Retsch GmbH, Haan, Germany). For each sample, two 5 mg subsamples were analyzed for C and N using a Vario MICRO cube elemental analyzer.

Litter decomposition measurements

Decomposition parameters were quantified for all 12 sites using the Teabag Index (TBI) (Keuskamp et al. 2013) for the summers of 2014, 2015 and 2016. For each site and year, air-dried, weighed Lipton green tea and Lipton rooibos tea–bags with a nylon mesh were buried directly after snowmelt and collected after an *in situ* incubation period of 60-98 days, depending on the duration of the snow–free season (see Table S3). At each site, 10 replicates of each tea were buried pair-wise, 8 cm below ground and with at least 10 cm between the two tea types. For two sites, the number of replicate tea bag pairs was higher in 2015 (12 replicates in ALP3 and 16 replicates at ALP2). After collection, adhering soil particles and roots were removed and the tea–bags were dried (48h at 60°C) and weighed. Three additional tea–bags of each type of tea were not buried but handled and dried the same way as the experimental tea–bags to allow correction for weight loss during transport and drying.

The TBI uses two types –green tea and rooibos tea– with contrasting decomposability, *i.e.* different labile and recalcitrant fractions, to determine two parameters of the decomposition process: decomposition rate k and stabilization factor S. Some of the labile compounds of litter stabilize and become recalcitrant in late stages of the decomposition process depending on environmental factors. The retardation of decomposition may be so strong that decomposition reaches a limit value where total mass loss of litter virtually stops and at which point it becomes soil organic matter (SOM) (Berg and Meentemeyer, 2002). Green tea decomposes quickly in comparison to rooibos tea and reaches its decomposition limit, while rooibos tea is still in its early stages of decomposition where labile material is still being decomposed. The difference between these litter types allows for an estimation of the decomposable fraction from green tea (a_g) and the decomposition rate constant k from rooibos tea at a single point in time.

The TBI assumes that during short field incubations, the weight loss of the recalcitrant fraction is negligible. Consequently, the decomposition curve can be modeled using a standard decay curve:

$W(t) = ae^{-kt} + (1 - a)$ eqn. 1

where W is the fraction of labile material remaining after time interval t, a is the labile fraction that decreases with decomposition rate k, and $1 - a$ is the recalcitrant fraction of the litter for which we assume that the decomposition rate is negligible (i.e. e^{-kt} is close to 1).

The TBI also assumes that incubation periods of about 90 days are long enough for green tea to reach the second phase of decomposition, where the remaining material will only decompose over very long time scales. This is represented by the deviation of the actual decomposed fraction a from the hydrolysable (i.e. chemically labile) fraction H and can be interpreted as the inhibiting effect of environmental conditions on the decomposition of the labile fraction, i.e. the stabilization factor (S). One can calculate the fraction of the labile component of green tea that did not decompose, but stabilized:

$S = 1 - \frac{a_g}{H_g}$ eqn.2

were a_g is the fraction of green tea remaining and $H_g = 0.842$ is the hydrolysable fraction of green tea (Keuskamp and others, 2013). Assuming that for the labile fraction of rooibos tea, the same proportion will be stabilized, one can predict how much material of rooibos tea (a_r) will remain in the second phase:

$a_r = H_r(1 - \mathrm{S})$ eqn.3

By substituting a_r in equation 1, and using the weight loss observed in rooibos tea, one can obtain the initial decomposition rate of the labile fraction of tea.

From the 736 tea–bags buried,25 were not retrieved (12 green tea, 13 rooibos tea) and 24 were badly damaged (10 green tea, 14 rooibos tea) and were therefore excluded from analysis. To reduce the number of data points lost because of damaged tea bags, we calculated the mean *S* per site for each year and used these mean values to predict a_r for the calculation of *k*. After this, we had 21 missing values for *S* and 23 for *k*.

Data analysis

To determine the effect of short-term annual climate variability on the decomposition parameters *k* and *S* we constructed a mixed effects model, where we included year as a fixed factor and site as a random factor, using lmer in the R package lme4 (Bates and others, 2011). To assess the effect of temporal and spatial climate variability on *k* and *S*, we used variance decomposition to quantify how much of the total variation in *k* and *S* is explained by year and site, respectively. To determine the effect of temperature and precipitation on *k* and *S*, we used linear regression on the complete dataset and for the separate temperature and precipitation levels. Environmental variables (pH, available nitrogen, soil C:N, plant C:N, litter C:N, plant diversity) were analyzed for differences between temperature- and precipitation levels using two-way ANOVA, and for significant results ($P < 0.05$) pairwise T-tests were performed to compare the different temperature- or precipitation levels to each other ($P < 0.05$). Collinearity between environmental variables was evaluated using Pearson's correlations. We used multiple linear regression models to assess the relationship between *k* and *S* and the climatic and environmental predictor variables (temperature, precipitation, temperature level, precipitation level, pH, available nitrogen, plant C:N, soil C:N, litter C:N, plant diversity). Average values for *k* and *S* were calculated for each site in each year prior to model construction. Models selection followed a backward selection procedure using the R package: drop1 (Chambers J. M. and J., 1992). Based on Akaike's information criterion (AIC) scores, we only selected models of greater complexity when inclusion of an additional model parameter reduced AIC by more than 2 (Burnham and Anderson, 2002). Variance decomposition was used to determine how much of the variation in *k* and *S* was explained by each variable in the various models. All data analyses were performed in R version 3.4.0 (R Core Team, 2017).

Results

Annual climate variability

Summer climate during the incubation period of the tea–bags, which commenced shortly after snowmelt at each site, varied between the three growing seasons of this study (Figure 2a-f, Table S2). The year 2014 was relatively warm and dry, 2015 was a relatively cold, and 2016 had more precipitation. In 2014, temperature was on average 3.11°C and 1.84°C warmer across the grid compared to 2015 and 2016, respectively. Temperature decreased across biogeographic zones, boreal > sub-alpine > alpine and this was consistent across the various years (Figure 2a-c,Table S2). Total amount of precipitation was on average 39% and 33% higher in 2016 compared to 2014 and 2015, respectively, although not all sites received more precipitation and the magnitude of the precipitation difference varied between sites (Figure 2b, Table S2). Observed precipitation showed some inconsistencies relative to the original set-up of climatic levels within the climate grid (based on climate data of NMI over 30-year normal period).

Environmental characteristics of sites

Soil pH was higher in sites with a colder alpine climate and sites at the high end of the precipitation gradient ($F_{2,48} = 61.29$, $P < 0.001$ and $F_{3,48} = 5.25$, $P < 0.01$ respectively) and showed a positive correlation with both soil available N and soil C:N ratio (Pearson's $\rho = 0.56$, $P < 0.001$ and $\rho = 0.64$, $P < 0.001$ respectively). Soil C:N also increased along the temperature and precipitation gradients of the grid, being significantly higher in alpine sites and sites with high precipitation ($F_{2,48} =6.47$, $P < 0.05$ and $F_{3,48} = 18.45$, $P < 0.001$

respectively). Plant C:N and litter C:N were higher at sites on the high end of the precipitation gradient ($F_{3,48}$ = 15.45, $P < 0.001$ and $F_{3,24}$ = 137.66, $P < 0.001$ respectively). Plant diversity increased towards colder sites, with plant diversity being significantly higher in alpine sites than in boreal and subalpine sites ($F_{2,48}$ = 21.87, $P < 0.001$; Table 1).

Short-term and long-term climate controls on litter decomposition processes

There was a clear difference between decomposition of the two tea types after incubation time, as relative mass remaining ranged from 0.19 – 0.59 (g g^{-1}) for green tea and 0.62 – 0.88 (g g^{-1}) for rooibos tea. The highest values for relative mass remaining of green tea corresponded with the shortest incubation times (60 days, n=8). This shows that our data are generally within the range of Keuskamp and others (2013) and that the assumptions made by the TBI can be applied to our dataset, as rooibos tea remained in the first phase of decomposition and green tea has generally entered the second phase of decomposition.

There was no overall relationship between *k* and temperature when data from all sites across the three incubation periods were combined into one regression model (Figure 3a). However, short-term annual variation in climate had a significantly so effect on *k* ($\chi^2(2)$ = 33.47, $P < 0.001$). On average, *k* was 12.1% and 15.6% higher for 2014, a warm and relatively dry year, than for 2015 and 2016, respectively (Figure S2a). This temporal pattern is illustrated within each of the temperature levels within the grid, where *k* consistently increased with temperature, although not significantly in the alpine (alpine: $R^2 = 0.003$, $P = 0.07$, sub-alpine: $R^2 = 0.05$, $P < 0.05$, boreal: $R^2 = 0.08$, $P < 0.01$; Figure 3a, Table S4). Furthermore, *k* decreased with increasing precipitation (Figure 3b, Table S4), both for the complete dataset ($R^2 = 0.07$, $P < 0.001$) and within each temperature level of the climate grid (alpine: $R^2 = 0.12$, $P < 0.001$, sub-alpine: $R^2 = 0.13$, $P < 0.001$, boreal: $R^2 = 0.07$, $P < 0.01$). The precipitation gradients within the grid had no distinguishable effect on decomposition rate either in relation to annual temperature variability or annual precipitation variability (Table S4).

Short-term annual climate variability only explained 22% of the variance in mean *k*, while long-term climate variability (temperature- and precipitation gradients) explained 44% (Table 2). A model combining both long-term and short-term annual climate variability improved the proportion of variance explained to 72%. The variance explained by long-term climate variability can be mediated by a number of local environmental characteristics of the sites, namely: pH, soil C:N and plant diversity. While none of the environmental factors showed any significant relation with *k* across the grid or along climatic gradients except for a decrease in *k* with increasing plant diversity within the sub-alpine sites ($R^2 = 0.32$, $P < 0.05$), the selected model contained a number of environmental variables. This model explained 66% of the variation in *k* and included the predictors temperature (1.3% explained variation), precipitation (20.3%), plant diversity (22.3%), pH (14.3%) and soil C:N (7.7%) and showed no bias towards any climatic level (Figure S3a).

Short-term annual variation in climate had a significant effect on *S* ($\chi^2(2) = 28.62$, $P < 0.001$). On average, *S* was 8.3% and 17.1% higher for 2014, a warm and relatively dry year, compared to 2015 and 2016, respectively (Figure S2b). Stabilization factor *S* was negatively related to temperature for the complete dataset ($R^2=0.03$, $P < 0.001$) as it decreased along the temperature gradient within the grid (Figure 3c). However, within the different temperature levels of the grid *S* increased in warmer years (Figure 3c and Table S4), although not significantly for alpine sites (alpine: $R^2 = 0.001$, $P = 0.6$, sub-alpine: $R^2 = 0.07$, $P < 0.01$, boreal: $R^2 = 0.15$, $P < 0.001$). Increased precipitation had a negative effect on *S* for the complete dataset ($R^2 = 0.15$, $P < 0.001$), which was consistent within the different temperature levels of the grid except for boreal sites (alpine: $R^2 = 0.44$, $P < 0.001$, sub-alpine: $R^2 = 0.08$, $P < 0.01$, boreal: $R^2 = 0.02$, $P = 0.13$; Figure 3d). Increased temperature had a stronger effect on

S in sites at higher temperature levels of the grid, while the effect of increased precipitation weakened towards warmer sites (Figure3cd, Table S4). Within the precipitation levels of the grid, temperature did not have a significant effect on *S*, while increased summer precipitation significantly affected *S* across all precipitation levels, except for precipitation level 2 (Table S4). The precipitation gradients within the grid had no distinguishable effect on the stabilization factor in relation to annual temperature variability, but showed a consistent pattern with increased summer precipitation, except for precipitation level 2 (Table S4).

Short-term annual climate variability only explained 33% of the variation in *S*, while long-term climate (temperature- and precipitation gradients) explained more than half (54%) of the variation (Table 2). Combining climate gradients and short-term annual climate variability in one model improved the percentage of variance explained to 78%. Litter C:N was the only significant environmental variable and improved the model by reducing complexity as it substituted the precipitation gradient (Table 2). Stabilization tends to increase with higher litter C:N across the grid, however not significantly. Although litter C:N ratio does not have a significant relationship with *S*, the selected model that incorporated litter C:N as a predictor explained the variation in *S* quite well and shows no bias towards any climatic levels (Figure S3b). The best model for *S* explained 65% of the variation and included temperature (7%), precipitation (20.2%) and their interaction (10.1%), temperature levels (19.6%) and litter C:N (8.3%).

Discussion

The selected models explained the variation in decomposition rate and stabilization factor relatively well – 72% and 65% of the variation, respectively, and included factors representing short-term annual variability in climate as well as factors representing long-term effects of climate. Long-term climate, represented by the climatic gradients within the grid or environmental factors reflecting long-term climate regimes, explained a large part of the variation in both litter decomposition rate and in litter stabilization: 44% and 28%, respectively. Short-term annual variation in summer precipitation was another major driver and explained about 20% of the variation for both litter decomposition and litter stabilization, while short-term annual variation in summer temperature only had a minor influence on decomposition processes.

We observed an increase in decomposition rate of the labile fraction with increased summer temperature within each temperature level in the climate grid. The enhanced decomposition with increased temperatures is in accordance with our expectations, and is in line with results from experimental warming studies in cold biomes (Aerts, 2006) and a study using the TBI along an elevational gradient (Didion and others, 2016). However, factors related to long-term climate differences between sites appear to be such strong modulators that this temperature effect was not visible across the grid (Figure 3a, Table S4). The selected model for *k* supports the proposition that long-term climate shapes environmental conditions that modulate *k*, most likely through differences in soil pH, soil C:N and plant diversity that together explained almost 45% of the variation in decomposition rate. Soil pH and plant diversity varied significantly along the temperature gradient, and soil C:N varied significantly along both temperature and precipitation gradients. Soil pH, soil C:N and plant diversity have been shown to influence soil microbial community composition both directly and indirectly (Zak and others, 2003; Rousk and others, 2010; Wan and others, 2015). We speculate that differences in decomposition rate across the grid could be partly traced back to differences in microbial community composition between sites. In our study sites, soil pH is a strong determinant of microbial community composition between alpine and sub-alpine sites (Guittar and others, unpublished results), which matches the differences observed between climatic regimes.

In a year of increased precipitation, initial decomposition rates of the labile fraction slowed down across the whole grid and was consistent within each temperature level (Figure 3b). Although the direction of the change is in contrast with our expectations, this shows that short-term variation in precipitation affects decomposition in the same way across sites in different climatic regimes. This implies that temperature-limited sites have the same sensitivity to short-term variation in precipitation as warmer sites. In other regional and global cross-biome studies (using a one-phase model) decomposition rate is usually positively correlated with mean annual precipitation (Epstein and others, 2002; Zhang and others, 2008; Portillo-Estrada and others, 2016), although a few studies that use a two phased TBI decomposition model show a decrease in decomposition with increased mean annual precipitation or increasing soil moisture (Didion and others, 2016; Sarneel and Veen, 2017). Besides differences in model assumptions, a possible explanation for the negative effect of precipitation on decomposition rate could be that, in our relatively moist study region, high amounts of precipitation induce oxygen limitation to microbial communities and therefore limit decomposition rates (Schuur, 2001), but not the degree to which material is broken down. Soil respiration, which reflects decomposition, has also been found to be very low under conditions with very high soil moisture content (Suh and others, 2009).

We found that stabilization of labile material is also modulated by long-term climate, as S decreases along the temperature gradient within the grid (Figure 3c, Table S4). This is in accordance with another study that found the size of the recalcitrant fraction of standard plant material to increase with elevation (Coûteaux and others, 2002). However, within each temperature level of the grid, and in particular in the boreal and sub-alpine sites, we found that short-term temperature variation has the opposite effect on stabilization as S increased with higher summer temperatures (Figure 3c, Table S4). This indicates that long-term climate is an important modulator for stabilization of labile material through shaping environmental conditions, but that short-term increases in temperature can have a significant and opposite effect on this stabilization. Increased temperatures could lead to smaller amounts of labile litter being stabilized and turned into SOM in the long-term, even if short-term results indicate the opposite.

Higher amounts of precipitation showed varied effects on litter stabilization along the temperature gradient within the grid, but were relatively consistent along the precipitation gradient (Table S4). In contrast to our expectations, the colder sites were more sensitive to short-term variation in precipitation compared to the warmer (boreal) sites. In alpine and sub-alpine sites, increased precipitation decreased stabilization and SOM production while in boreal sites it had no effect (Figure 3d, Table S4). This again shows that tne long-term climate regime played an important role in modulating stabilization. The temperature gradient explained about 20% of the variation in *S*, but this variation could not be attributed to any of the measured environmental characteristics. The only environmental variable that was included in the model that best explained *S* was litter C:N, but this explained only a relatively minor proportion of the variation (8.3%). Organic matter can be stabilized in various ways: by physical stabilization through micro-aggregation, chemical stabilization through intimate association with silt and clay particles and biochemically through formation of recalcitrant SOM compounds (Six and others, 2002). It is therefore possible that other environmental factors, such as soil structure or soil clay and silt content, could explain the difference in stabilization to changes in summer precipitation along the temperature gradient.

Overall, there was a very clear difference between the effects of short-term variation in climate (i.e., between growing season) and long-term effects of the different climate regimes characterizing the different sites (i.e., climatic gradients). We expected decomposition processes in cold locations to be most sensitive to temperature, and decomposition processes in warm locations to be more sensitive to precipitation. Instead, we see that *k* and *S* showed a stronger response to short-term variation in temperature in warmer sites and that short-term variation in precipitation had a greater effect on *S* in colder sites. The decomposition rate of the labile fraction was enhanced by increased summer temperatures within each temperature level, though across the grid this relationship with temperature was not found. On the other hand, high precipitation had a consistent inhibiting effect on decomposition as it lowered the decomposition rate across the grid and within each temperature level. On the other hand, more stabilization of labile material occurred with increased annual temperatures within most temperature levels, while a decrease in stabilization was found across the different long-term climatic regimes. Further, stabilization of labile material was more sensitive to short-term variation in precipitation in colder sites compared to warmer (boreal) sites. Increased temperatures would thus stimulate decomposition, but at the same time, would also lead to more stabilization and transformation to SOM, while increased precipitation limits decomposition but also decreases stabilization of litter and transformation to SOM. These results imply that, over the short-term, increases in temperature and precipitation could offset one another in terms of effects on decomposition processes, as climate change is expected to both increase temperature and precipitation in northern ecosystems. However, short-term effects within a particular climatic regime are not necessarily predictive of the long-term outcome after the ecosystem has adapted to a new climate.

Conclusions

We studied the short-term, direct (*i.e.*, annual variation in temperature and precipitation) and long-term, indirect (*i.e.*, climatic regime of different sites) effects of climate on two phases of the decomposition process; decomposition rate (*k*) and stabilization factor (*S*) using the

Teabag Index (TBI) in three consecutive growing seasons in a climate grid combining both temperature and precipitation gradients. We found that the response of the initial decomposition rate of labile litter to annual increases in temperature is rather consistent within climate regimes but not across different climate regimes, while annual increases in precipitation had a consistent negative effect both within and across climatic regimes. Stabilization of the labile litter fraction increased with higher annual temperatures within climatic regimes, while stabilization decreased from sites experiencing colder climate regimes to warmer climate regimes. In addition, stabilization was more sensitive to short-term variation in precipitation in sites with colder climatic regimes compared to warmer sites. Short-term effects of temperature and precipitation within a particular climatic regime showed discrepancy with long-term climate and will therefore not necessarily reflect changes due to climate change on the long-term. Environmental characteristics of the sites related to long-term climate (e.g. soil properties and plant diversity) played a significant role in regulating decomposition processes. This supports the statement that multiple factors regulate litter decomposition but that they change in predominance as the values of regulatory factors also change (Bradford and others, 2016). Our findings highlight the importance of long-term climate in shaping environmental conditions that influence the response of decomposition processes to climate change.

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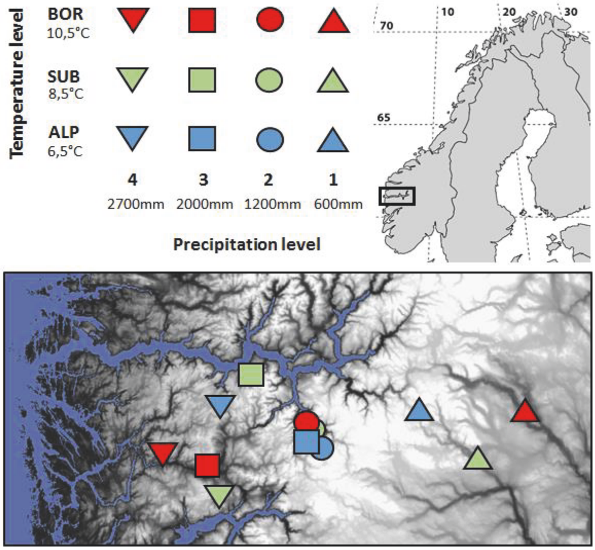


Figure 1. Location of the study sites along the temperature and precipitation gradients in southern Norway. The summer temperature range, alpine ≈ 6.5°C, sub-alpine ≈ 8.5°C and boreal ≈ 10.5°C, is indicated by the different colors. The levels of annual precipitation, 1 ≈ 600 mm, 2 ≈ 1200 mm, 3 ≈ 2000 mm and 4 ≈ 2700 mm, are indicated with the different shapes, 1 (▲), 2 (●), 3 (■) and 4 (▼). Color-coding and symbols presented in this figure will be consistent throughout the manuscript.

Table 1. Mean ± S.D. of environmental variables for the alpine, sub-alpine and boreal sites along precipitation gradients (low [1] to high [4]) in southern Norway. For information on the significances of differences in environmental variables between temperature- and precipitation levels, see text.

	Site	**Soil pH**	**Available N (mg g^{-1} m^{-2} day^{-1})**	**Soil C:N**	**Plant C:N**	**Litter C:N**	**Plant diversity (Shannon's H)**
Boreal	BOR1	5.2±0.1	114.5±44.4	11.6±0.5	23.9±2.2	37.7±1.4	2.39±0.16
	BOR2	5.2±0.1	108.8±23.1	11.8±0.7	27.6±1.6	30.3±1.0	2.00±0.36
	BOR3	5.2±0.1	68.1±20.0	13.0±1.4	27.6±3.7	42.4±1.1	2.17±0.30
	BOR4	5.3±0.1	58.7±19.3	13.4±0.3	28.5±4.3	41.8±2.0	1.50±0.28
Sub-alpine	SUB1	5.5±0.1	116.3±57.0	13.1±1.6	19.4±0.8	36.7±0.8	2.01±0.1
	SUB2	5.1±0.1	77.7±15.6	11.6±0.3	28.5±3.3	34.6±1.0	2.21±0.22
	SUB3	5.6±0.3	150.1±92.8	14.6±1.1	31.2±5.4	47.9±1.4	2.20±0.38
	SUB4	5.7±0.2	162.1±95.3	14.0±0.9	27.8±2.2	53.9±2.2	2.86±0.15
Alpine	ALP1	5.7±0.2	181.6±161.0	12.8±0.8	24.6±3.3	25.2±0.4	2.57±0.30
	ALP2	6.0±0.1	175.7±84.8	12.9±0.6	21.9±2.4	42.1±1.5	2.53±0.43
	ALP3	6.1±0.2	140.1±94.3	13.5±1.3	31.7±3.9	49.3±2.2	2.50±0.33
	ALP4	6.0±0.4	70.7±16.2	14.8±1.6	27.5±1.3	31.8±0.2	2.51±0.19

Table 2. Multiple regression models relating site averaged decomposition rate *k* (n = 36) and stabilization factor *S* (n = 36) to climatic and environmental variables. Climatic and environmental variables included in the models represent: temperature level (TL), precipitation level (PL), mean air temperature (t), total precipitation (p), pH, soil C:N ratio (Soil C:N), Litter C:N ratio (Litter C:N) and plant diversity (Pdiv). Significance of models are shown, with */**/*** indicating $p < 0.05$, $p < 0.01$ and $p < 0.001$ respectively.

Decomposition proxy	Model	Adj R^2	AIC	Var. expl. (%)
Decomposition rate *k*	t + p	0.17*	-465.82	22%
	TL x PL	0.18	-459.67	44%
	t + p + TL x PL	0.55**	-480.59	72%
	t + p + pH + Pdiv + Soil C:N	0.60***	-489.83	66%
Stabilisation factor *S*	t + p	0.27**	-209.35	33%
	TL x PL	0.33*	-206.75	54%
	t x p + TL x PL	0.63***	-226.45	78%
	t x p + TL + Litter C:N	0.58***	-226.69	65%

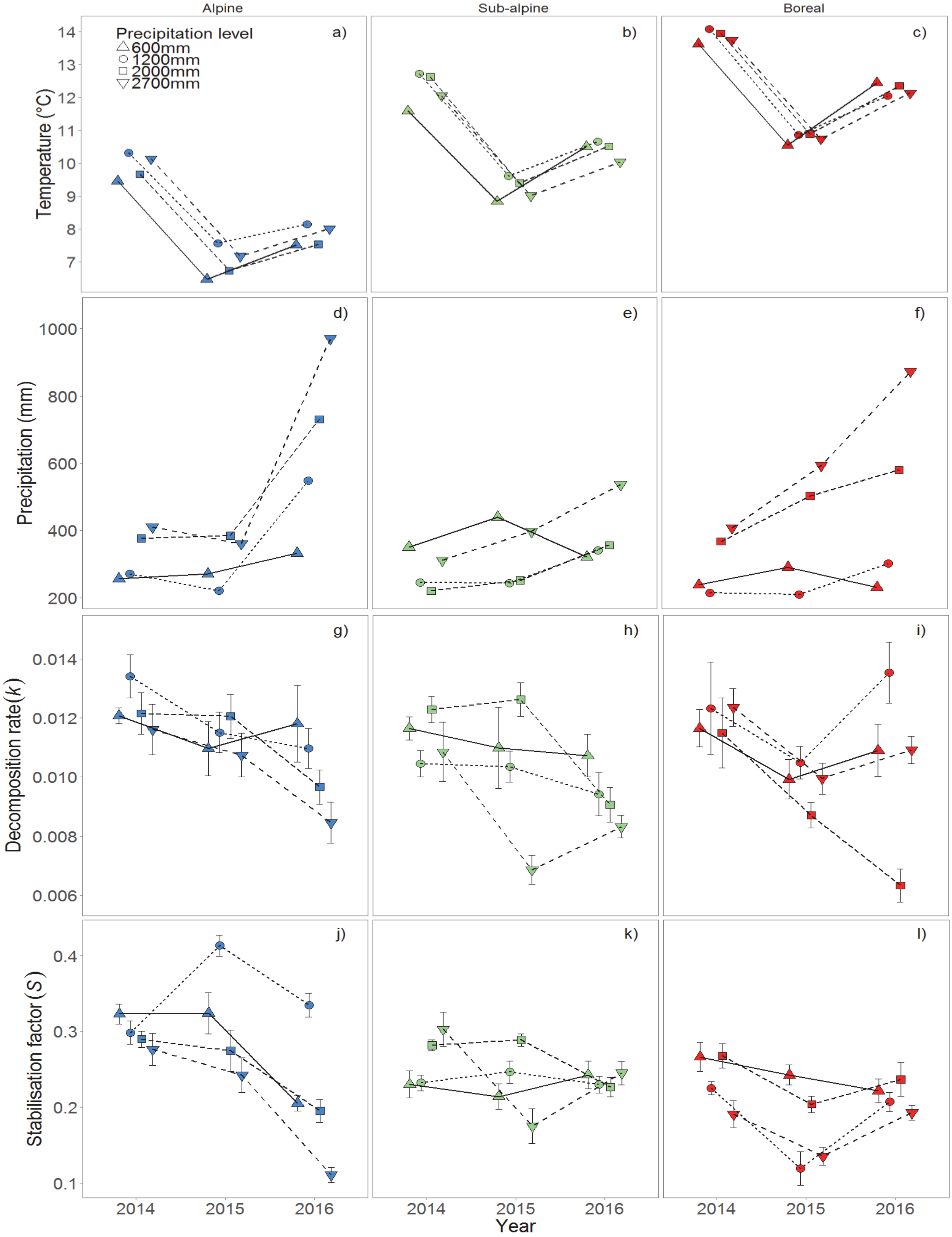


Figure 2. Mean temperature (a-c), total precipitation (d-f), mean *k* ± S.E. (g-h) and mean *S* ± S.E (j-k). for the different precipitation levels, 1 ≈ 600 mm (▲), 2 ≈ 1200 mm (●), 3 ≈ 2000 mm (■) and 4 ≈ 2700 mm (▼), within each temperature level, alpine ≈ 6.5°C (blue), sub-alpine ≈ 8.5°C (green) and boreal ≈ 10.5°C (red).

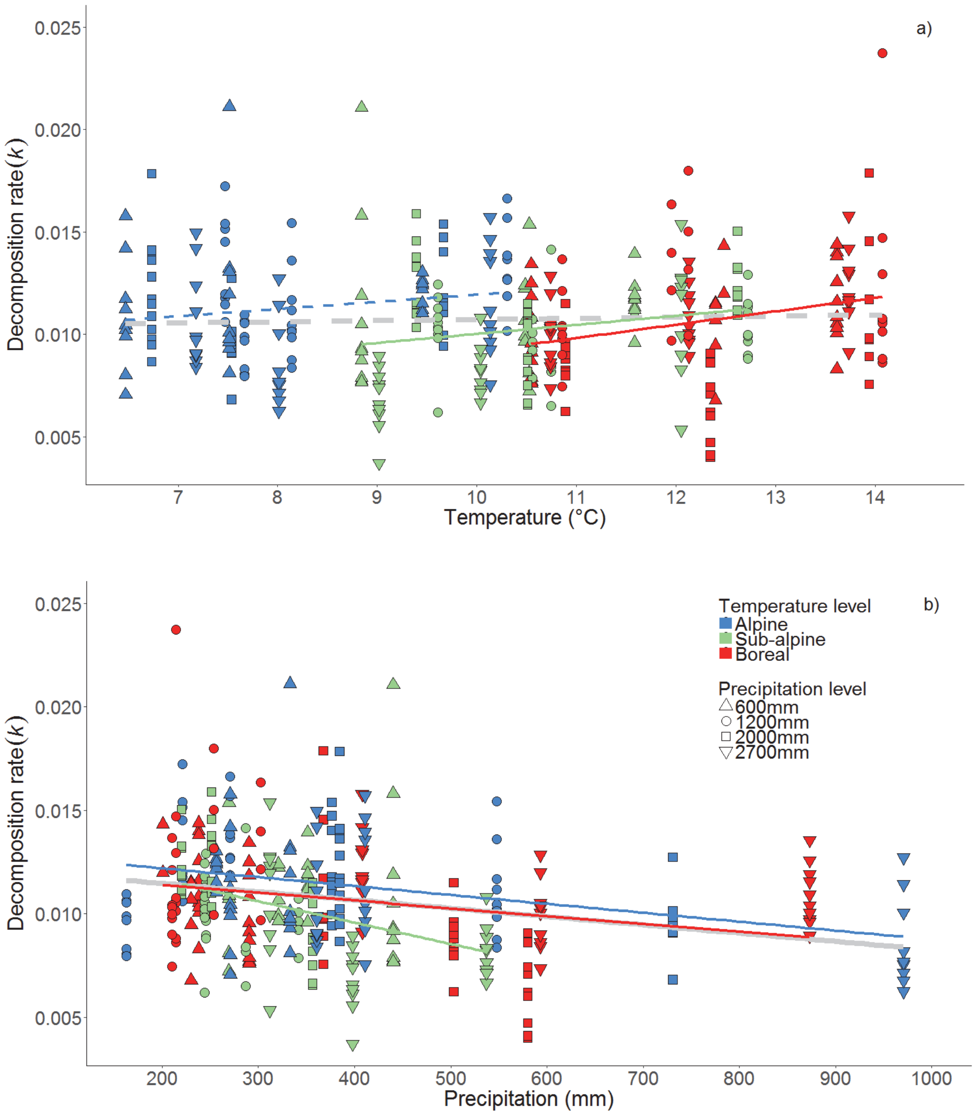
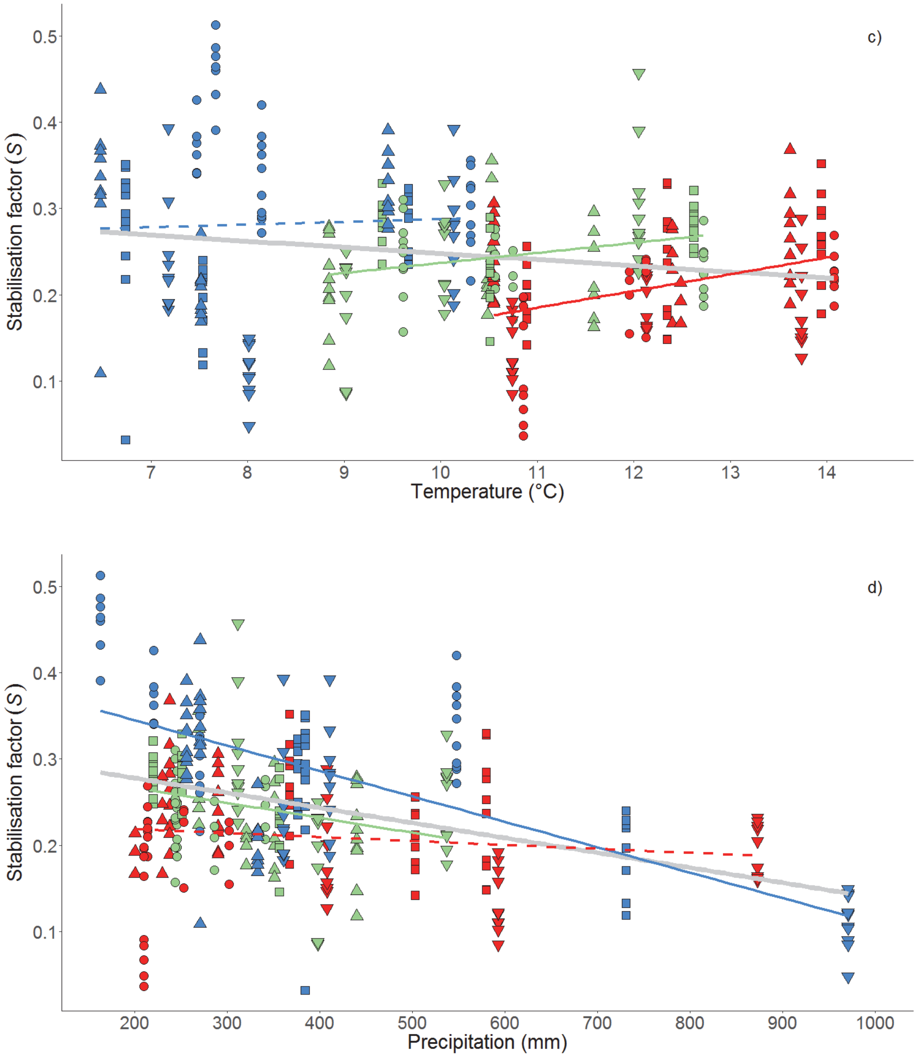


Figure 3. Decomposition rate *k* in relation to temperature (a) and precipitation (b), and stabilization factor *S* in relation to temperature (c) and precipitation (d). Colors correspond to temperature level; alpine ≈ 6.5°C (blue), sub-alpine ≈ 8.5°C (green) and boreal ≈ 10.5°C (red). Different symbols correspond to precipitation level 1 ≈ 600 mm (▲), 2 ≈ 1200 mm (●), 3 ≈ 2000 mm (■) and 4 ≈ 2700 mm (▼). Colored lines indicate relation between *k* or *S* and the climatic variable for the particular temperature levels, while grey lines show the relationship between *k* or *S* and the climatic variable across the entire grid. Solid lines indicate significant relationships while dashed lines indicate non-significant relationships.


c)
Stabilisation factor (S)
0.1
0.2
0.3
0.4
0.5
7
8
9
10
11
12
13
14
Temperature (°C)
d)
Stabilisation factor (S)
0.1
0.2
0.3
0.4
0.5
200
300
400
500
600
700
800
900
1000
Precipitation (mm)

Supplementary data

Supplementary table 1. Geographic and climatic information of the 12 field sites. The table includes site codes, biogeographic zones and sections, site names, longitudes and latitudes in decimal degrees, elevation in metres above sea level, precipitation in millimeters per year and growing season temperature measured as the mean air temperature of the four warmest months (June-September) for the period 1961-1990.

Site	Biogeogr. zones	Longitude (°E)	Latitude (°N)	Elevation (m. a. s. l)	Precipitation (mm)	Temperature (°C)
ALP1	Alpine	8.12343	61.0243	1208	596	6.17
ALP2	Alpine	7.27596	60.8231	1097	1321	6.45
ALP3	Alpine	7.17561	60.8328	1213	1925	5.87
ALP4	Alpine	6.41504	60.9335	1088	2725	6.58
SUB1	Sub-alpine	8.70466	60.8203	815	789	9.14
SUB2	Sub-alpine	7.17666	60.8760	700	1356	9.17
SUB3	Sub-alpine	6.63028	61.0866	769	1848	8.77
SUB4	Sub-alpine	6.51468	60.5445	797	3029	8.67
BOR1	North-Boreal	9.07876	61.0355	589	600	10.30
BOR2	North-Boreal	7.16982	60.8803	474	1161	10.55
BOR3	North-Boreal	6.33738	60.6652	431	2044	10.60
BOR4	North-Boreal	5.96487	60.6901	346	2923	10.78

Supplementary Table 2. Mean air temperature (°C) and maximal total precipitation (mm) during incubation period of tea bags (± 3 months in summer season) for the various years, and average air temperature (°C) and total precipitation (mm) across the whole climate grid during incubation periods for the various years.

Site		**2014**		**2015**		**2016**	
		Temperature	Precipitation	Temperature	Precipitation	Temperature	Precipitation
boreal	BOR1	13.62	238.0	10.54	290.4	12.44	230.2
	BOR2	14.08	214.4	10.86	210.1	12.04	302.2
	BOR3	13.94	367.5	10.89	503.0	12.35	579.9
	BOR4	13.74	407.9	10.74	593.0	12.13	872.9
sub-	SUB1	11.59	351.1	8.84	440.2	10.51	320.9
	SUB2	12.72	245.6	9.61	244.1	10.65	341.4
	SUB3	12.62	220.2	9.39	251.3	10.51	356.4
	SUB4	12.05	311.8	9.02	397.9	10.04	537.2
alpine	ALP1	9.45	256.3	6.47	270.8	7.51	333.0
	ALP2	10.31	270.3	7.57	220.8	8.14	547.9
	ALP3	9.66	376.4	6.73	384.3	7.54	730.7
	ALP4	10.13	410.7	7.18	360.8	8.01	970.6
	Average	11.99 ± 1.67^{a}	305.6 ± 71.0^{A}	8.88 ± 1.59^{b}	338.3 ± 120.5^{AB}	10.15 ± 1.84^{b}	502.6 ± 239.3^{B}

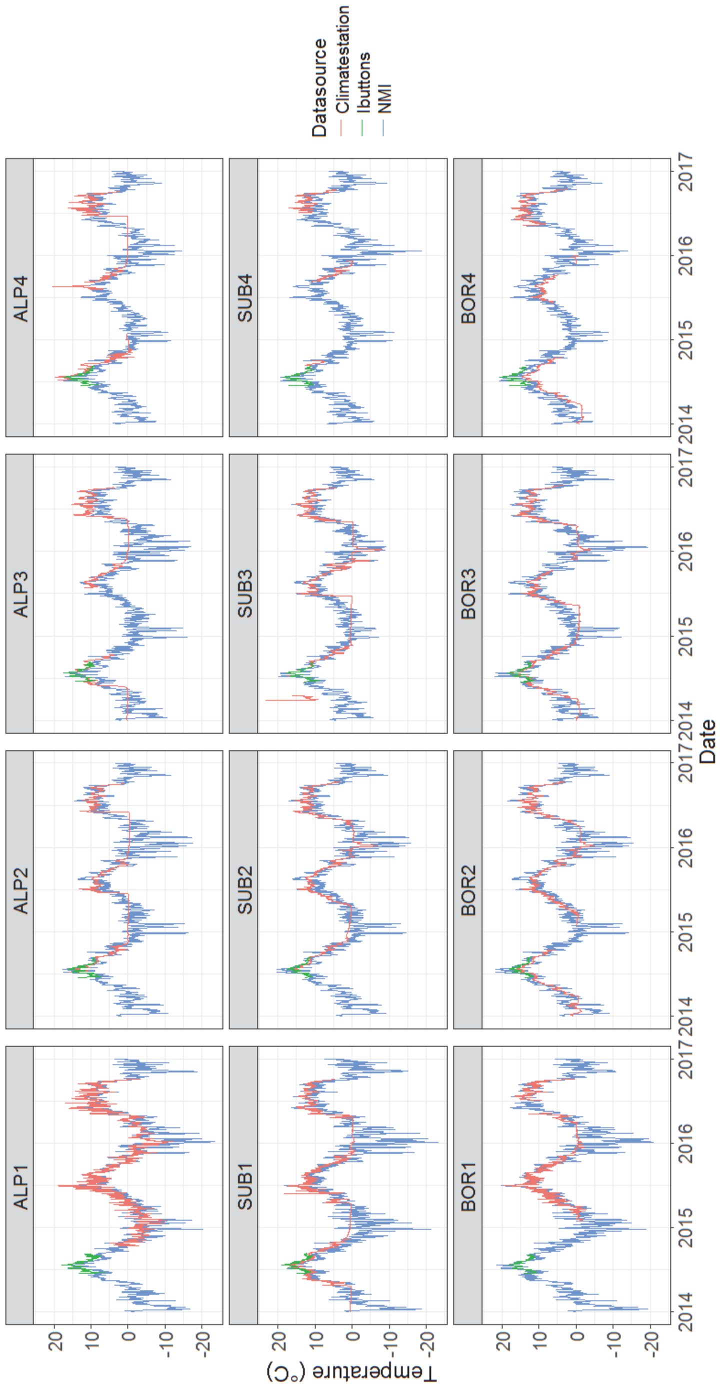
$^{a,b/A,B}$ Different letters identify difference in mean temperature (small letters) or total precipitation (capitol letters) between years according to Tukey's honestly significant difference (HSD) post hoc test, (p<0.05).

Supplementary table 3. Burial and collection dates of the tea bags for the different years.

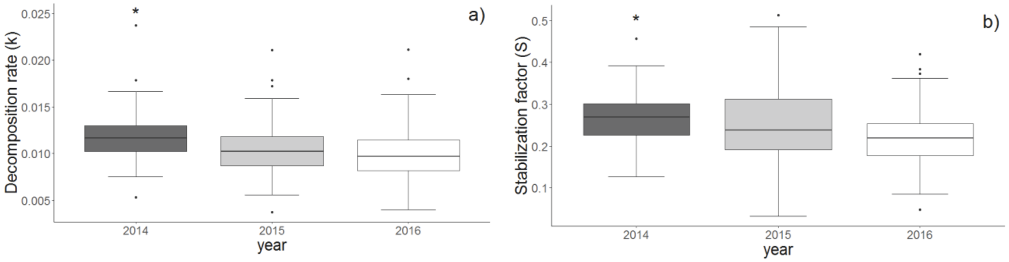
	2014		**2015**		**2016**	
Site	Burial	Collection	Burial	Collection	Burial	Collection
BOR1	19.06.2014	06.09.2014	10.07.2015	09.10.2015	18.05.2016/07.06.2016	24.08.2016
BOR2	17.06.2014	11.09.2014	11.07.2015	07.10.2015	19.05.2016/06.06.2016	24.08.2016
BOR3	16.06.2014	08.09.2014	16.07.2015	11.10.2015	23.05.2016	25.08.2016
BOR4	16.06.2014	08.09.2014	20.07.2015	12.10.2015	23.05.2016	25.08.2016
SUB1	19.06.2014	12.09.2014	09.07.2015	08.10.2015	18.05.2016/06.06.2016	24.08.2016
SUB2	17.06.2014	11.09.2014	11.07.2015	06.10.2015	19.05.2016/06.06.2016	24.08.2016
SUB3	17.06.2014	07.09.2014	15.07.2015	10.10.2015	24.05.2016	29.08.2016
SUB4	16.06.2014	08.09.2014	15.07.2015	11.10.2015	24.05.2016	3**0**.08.2016
ALP1	18.06.2014	12.09.2014	16.07.2015	08.10.2015	30.06.2016	05.10.2016
ALP2	18.06.2014	11.09.2014	21.07.2015/07.08.2015	06.10.2016	29.06.2016	04.10.2016
ALP3	18.06.2014	11.09.2014	13.07.2015	05.10.2015	29.06.2016	04.10.2016
ALP4	17.06.2014	08.09.2014	06.08.2015	10.10.2015	30.06.2016	03.10.2016

Supplementary table 4. Results of linear regression for decomposition characteristics *k* and *S* with annual variability in temperature and precipitation across the entire grid (ALL) and for separate climate levels in the grid.

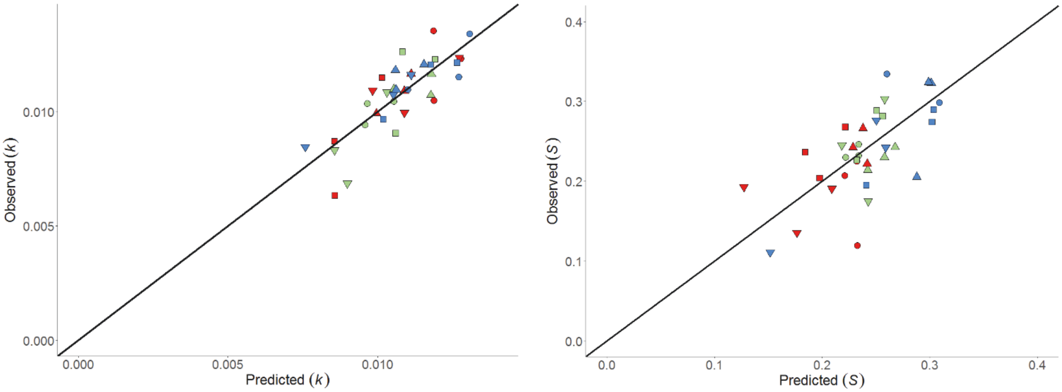
Variable	**Data**	**Formula**	**n**	**Multiple R^2**	**p**
k	Temperature:				
	ALL	$1.015\text{x}10^{-2} + 5.62\text{x}10^{-5}\ t$	345	0.002	0.42
	ALP	$0.0084 + 0.00035\ t$	119	0.003	0.07
	SUB	$0.0056 + 0.00044\ t$	115	0.05	<0.05
	BOR	$0.0026 + 0.00065\ t$	111	0.08	<0.01
	PL1	$1.113\text{x}10^{-2} – 3.33\text{x}10^{-6}\ t$	90	0	1
	PL2	$1.026\text{x}10^{-2} + 1.03\text{x}10^{-4}\ t$	89	0.006	0.47
	PL3	$1.\ 312\text{x}10^{-2} – 2.57\text{x}10^{-4}\ t$	86	0.04	0.06
	PL4	$0.052\text{x}10^{-2} + 4.67\text{x}10^{-4}\ t$	88	0.13	<0.001
	Precipitation:				
	ALL	$1.227\text{x}10^{-2} – 4.0\text{x}10^{-6}\ p$	345	0.07	<0.001
	ALP	$1.306\text{x}10^{-2} – 4.3\text{x}10^{-6}\ p$	119	0.12	<0.001
	SUB	$1.370\text{x}10^{-2} – 1.0\text{x}10^{-6}\ p$	115	0.13	<0.001
	BOR	$1.213\text{x}10^{-2} – 3.7\text{x}10^{-6}\ p$	111	0.07	<0.01
	PL1	$1.133\text{x}10^{-2} – 5.55\text{x}10^{-7}\ p$	82	0	0.9
	PL2	$1.148\text{x}10^{-2} – 5.99\text{x}10^{-7}\ p$	89	0	0.8
	PL3	$1.451\text{x}10^{-2} – 9.73\text{x}10^{-6}\ p$	86	0.25	<0.001
	PL4	$1.086\text{x}10^{-2} – 5.62\text{x}10^{-6}\ p$	88	0.02	0.2
S	Temperature:				
	ALL	$0.319 – 0.007\ t$	347	0.03	<0.001
	ALP	$0.256 + 0.003\ t$	121	0.001	=0.6
	SUB	$0.121 + 0.012\ t$	115	0.07	<0.01
	BOR	$-0.028 + 0.019\ t$	111	0.15	<0.001
	PL1	$0.302 – 4.9\text{x}10^{-4}\ p$	83	0.03	0.14
	PL2	$0.591 – 31\text{x}10^{-3}\ p$	88	0.42	<0.001
	PL3	$0.239 + 1.3\text{x}10^{-3}\ p$	90	0.002	0.65
	PL4	$0.145 + 6.0\text{x}10^{-3}\ p$	86	0.02	0.18
	Precipitation:				
	ALL	$0.312 – 1.7\text{x}10^{-4}\ p$	347	0.15	<0.001
	ALP	$0.404 – 2.9\text{x}10^{-4}\ p$	121	0.44	<0.001
	SUB	$0.301 – 1.7\text{x}10^{-4}\ p$	115	0.08	<0.01
	BOR	$0.228 – 4.6\text{x}10^{-5}\ p$	111	0.02	0.013
	PL1	$0.356 – 3.\ 4\text{x}10^{-4}\ p$	83	0.11	<0.01
	PL2	$0.248 + 0.8\text{x}10^{-4}\ p$	88	0.007	0.42
	PL3	$0.329 – 1.8\text{x}10^{-4}\ p$	90	0.21	<0.001
	PL4	$0.309 – 1.8\text{x}10^{-4}\ p$	86	0.27	<0.001



Supplementary figure 1. Temperature data from different sources; Temperature loggers from climate stations, Ibutton loggers buried with tea bags in 2014 and gridded data from NMI.



Supplementary figure 2ab. Decomposition rates k (a) and stabilization factor S (b) for the different years. The different years are indicated by the different colors, 2014, 2015 and 2016. Boxes show the first to third quartile range with median (thick horizontal line). Whiskers indicate the minimum and maximum values except where there are extreme values (filled dots), in which case they show 1.5 times the interquartile range. Significant differences between years ($p < 0.05$) are indicated with “*”.



Supplementary figure 3ab. Relation between observed and predicted for decomposition rate *k* (a) and for stabilization factor *S* (b), where the solid line indicates the 1:1 relationship. Colors correspond to temperature level; Alpine (blue), Sub-alpine (green) and Boreal (red). Different symbols correspond to precipitation level1 ≈ 600 mm (▲), 2 ≈ 1200 mm (●), 3 ≈ 2000 mm (■) and 4 ≈2700 mm.