



# Temperature sensitivity of soil respiration declines with climate warming in subalpine and alpine grassland soils

Khatab Abdalla · Larissa Schierling · Yue Sun · Max A. Schuchardt · Anke Jentsch · Thomas Deola · Peter Wolff · Ralf Kiese · Eva Lehndorff · Johanna Pausch · Nele Meyer

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**Abstract** Warming as a climate change phenomenon affects soil organic matter dynamics, especially in high elevation ecosystems. However, our understanding of the controls of soil organic matter mineralization and dynamics remains limited, particularly in alpine (above treeline) and subalpine (below treeline) grassland ecosystems. Here, we investigated how downslope (warming) and upslope (cooling) translocations, in a 5-years reciprocal transplanting experiment, affects soil respiration and its temperature sensitivity (Q10), soil aggregation, and soil organic

matter carbon (C) and nitrogen (N) composition (C/N ratio). Downslope translocation of the alpine (2440 m a.s.l.) and subalpine (1850 m a.s.l.) to the lowland site (350 m a.s.l.) resulted in a temperature change during the growing seasons of +4.4K and +3.3K, respectively. Warming of alpine soils (+4.4K) reduced soil organic carbon (SOC) content by 32%, which was accompanied by a significant decrease of soil macroaggregates. Macroaggregate breakdown induced an increased respiration quotient ( $q\text{CO}_2$ ) by 27% following warming of alpine soils. The increase in  $q\text{CO}_2$  respiration was associated with a significant decrease (from  $2.84 \pm 0.05$  to  $2.46 \pm 0.05$ ) in Q10, and a change in soil organic matter composition (lower C/N

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K. Abdalla (✉) · L. Schierling · Y. Sun · J. Pausch  
Chair of Agroecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany  
e-mail: Khatab.Abdalla@Uni-Bayreuth.de

K. Abdalla  
National Center for Research, Environment, Natural Resources and Desertification Research Institute, Khartoum, Sudan

Y. Sun  
Soil and Ecosystem Ecology Lab, The University of Manchester, Manchester, UK

M. A. Schuchardt · A. Jentsch · T. Deola · P. Wolff  
Chair of Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany

R. Kiese  
Institute for Meteorology and Climate Research, Atmospheric Environmental Research (IMK-IFU, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

E. Lehndorff  
Chair of Soil Ecology, Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany

N. Meyer  
Institute of Physical Geography, Goethe-University Frankfurt, Frankfurt, Germany

ratios). Cooling did not show the opposite patterns to warming, implying that other mechanisms, such as plant and microbial community shifts and adaptation, were involved. This study highlights the important role of SOC degradability in regulating the temperature response of soil organic matter mineralization. To predict the adverse effect of warming on soil CO<sub>2</sub> release and, consequently, its negative feedback on climate change, a comprehensive understanding of the mechanisms of C storage and turnover is needed, especially at high elevations in the Alps that are particularly affected by rising temperatures.

**Keywords** Grasslands · Soil aggregates · Soil organic matter · Climate change

## Introduction

The current increase of atmospheric greenhouse gas emissions induces a rapid increase in temperature, with cooler regions at high elevations in particular being exposed to faster warming than at low elevations (Pepin et al. 2022). Warmer temperatures may stimulate the loss of soil organic matter via accelerated decomposition resulting in a positive feedback on atmospheric CO<sub>2</sub> concentration (Ofiti et al. 2021). It is well-known that soils in colder climatic conditions have higher soil carbon (C) stocks than soils under warmer conditions. This C is mostly stored in the topsoil and is thus vulnerable to changes in climatic conditions (Yost and Hartemink 2019; Bai and Cotrufo 2022). To better understand the mechanisms by which especially vulnerable soil organic matter-rich soils in high elevation will respond to future temperature increase, a comprehensive understanding of the effect of warming on soil organic C (SOC) stocks and CO<sub>2</sub> fluxes is required.

Among other mechanisms, physical stabilization of C in soil aggregates plays a key role by limiting accessibility of soil microbes to the organic matter occluded within aggregates, which facilitates C accumulation and storage over time (Lützow et al. 2006). The SOC stability within aggregates increases with decreasing aggregate size, which in turn influences soil organic matter decomposition and thus CO<sub>2</sub> release to the atmosphere (Wang et al. 2015; Ozlu and Arriaga 2021). However, the role of different aggregate size classes (i.e., macroaggregates,

microaggregates and silt/clay-sized fractions) for SOC stability and its response to abiotic and biotic factors is still a matter of debate. There is a consensus that macroaggregates are less stable and contain more labile C than microaggregates and the silt/clay-sized fraction (Wiesmeier et al. 2012; Totsche et al. 2018). Therefore, the disintegration of larger soil aggregates results in increased soil organic matter mineralization, whereas smaller aggregates (i.e., microaggregates and silt/clay-sized fractions) may be associated with slower C turnover (Six et al. 2004; Wang et al. 2015). Despite the fact that soil organic matter in macroaggregates is more susceptible to decomposition, they are crucial for overall soil C sequestration, as they provide potential for the occlusion of newly formed microaggregates (Six et al. 2000; Totsche et al. 2018). However, warming may reduce aggregate stability by increasing the decomposition of soil organic matter as a binding agent, causing macroaggregate disruption, altering the distribution of SOC among aggregate size classes, and compromising the overall soil physical stability (Conant et al. 2011; Zhou et al. 2023; Garcia-Franco et al. 2024).

To study soil organic matter decomposition under warming, many previous studies measured temperature sensitivity of soil respiration, expressed as Q<sub>10</sub>, i.e., the factor by which soil respiration increases per 10°C rise in temperature (Conen et al. 2006; Muñoz et al. 2016; Qin et al. 2019). The Carbon Quality Temperature (CQT) hypothesis claims that the Q<sub>10</sub> of soil organic matter decomposition correlates negatively to C quality, meaning that fresh and labile soil organic matter would be less sensitive to warming (Bosatta and Ågren 1999; Davidson and Janssens 2006). In contrast, older and more stable organic matter would be more sensitive to warming because of its complex and stable molecular structure, which requires more activation energy to decompose compared to labile organic compounds (Davidson and Janssens 2006). In contrast, Conen et al. (2006) found no differences in temperature sensitivity between young and old soil organic matter, which suggests equal sensitivity for both C pools under warming (6 days of incubation). Since the resistance of soil organic matter to decomposition mostly depends on the accessibility of soil microbes to the physically protected C, it is important to link the Q<sub>10</sub> of soil organic matter to soil aggregate stability in warming experiments to simultaneously shed light on the labile and resistant C turnover, as

presented in the CQT-hypothesis (Davidson and Janssens 2006; Li et al. 2017).

At high elevations of alpine (e.g., above 2000 m a.s.l.) and subalpine grasslands (e.g. below 2000 m a.s.l.), many empirical and modelling studies focused on the soil organic matter storage and turnover along elevation gradients (Garcia-Pausas et al. 2007; Leifeld et al. 2009; Budge et al. 2010, 2011; Garcia-Franco et al. 2021). A study on forest soils in the German Alps, for instance, reported a significant reduction (14%) in topsoil C using repeated measurements of SOC (1976–2010 and 1987–2011), which was explained by the loss of the labile C caused mainly by warming (Prietz et al. 2016). While these studies provide a profound knowledge of soil organic matter turnover along the elevation gradients with plant communities adapted to the respective soil conditions, temperature and precipitation, little is known about the response of high elevation plant-soil systems when exposed to warmer conditions (Berauer et al. 2019; Schuchardt et al. 2021, 2023a, b; Alongi et al. 2022; Niu et al. 2023). Reciprocal transplanting studies from cooler higher to warmer lower elevations or vice versa offer an opportunity to investigate soil organic matter decomposition, its temperature sensitivity and linkage to C stored in various aggregate size classes (Scowcroft et al. 2000; Link et al. 2003; Bond-Lamberty et al. 2016). While reciprocal transplanting experiments have the advantage that intact plant-soil cores can be investigated under changing climatic conditions, it was still not applied adequately to disentangle the complex mechanisms such as  $Q_{10}$  and soil aggregation regulating soil organic matter dynamics in response to warming and cooling, particularly for the alpine and subalpine grassland systems. Only a few studies, which used reciprocal transplants covering both warming and cooling to study the changes in SOC. For example, Norine et al. (2023) found a tendency towards a decrease in topsoil SOC with a high resistance of the remaining soil organic matter to temperature change after three years of transplanting alpine grassland soils to a subalpine site (warming of +3 C) in the French Alps. Therefore, understanding soil organic matter dynamics in relation to soil aggregate stability and temperature sensitivity using a field-simulated warming and cooling approach (reciprocal translocations) is important to assess the vulnerability of mountain grassland ecosystems to climate change.

The present study attempts to evaluate the effects of soil warming and cooling of mountain grassland soils (subalpine and alpine) on soil respiration and its temperature sensitivity ( $Q_{10}$ ) in order to understand future changes in soil organic matter triggered by warming. Entire plant-soil turfs were translocated reciprocally between lowland (350 m a.s.l.), subalpine (1850 m a.s.l.) and alpine (2440 m a.s.l.) sites (for details see Berauer et al. 2019), and soil was sampled five years thereafter. We hypothesized that (i) warming changes the soil organic matter composition towards a larger contribution of more degraded organic matter. As indicators of soil organic matter dynamics, including stability and degradation stage, we measure the  $qCO_2$ , the C/N ratio, and soil aggregation, to reflect both the decomposition process and physical stabilization. Furthermore, following the CQT-hypothesis, we expect that (ii) the increase of more stable C induced by warming will increase  $Q_{10}$ , resulting in SOC losses. Finally, (iii) long-term cooling is expected to generate contrary trends to warming, such as lower C stability and consequently lower  $Q_{10}$ .

## Material and methods

### Study sites

The study comprised three grassland sites: lowland grasslands, located in Bayreuth, Germany (49°55'16"N; 11°34'55"E, at 350 m a.s.l.), subalpine grassland in Stubai, Austria (47°07'44"N; 11°18'19"E, 1850 m a.s.l.) and alpine grassland at Furka, Switzerland (46°34'36"N; 08°25'17"E, 2440 m a.s.l.). The mean annual temperature and precipitation at the three grasslands were 8.2 °C and 724 mm in Bayreuth site; 3.0 °C and 1097 mm for Stubai; and -0.5 °C and 1600 mm for Furka (Berauer et al. 2019; Schuchardt et al. 2023b). The initial soil at the study sites has an acidic soil reaction (pH=5.23, 5.4 and 4.46 for the lowland, subalpine and alpine sites, respectively) with a soil texture that is sandy loam (10.4 and 67.2% for clay and sand, respectively) at the lowland site, sandy clay (13.3 and 50.2% for clay and sand, respectively) at the subalpine site and loam (10 and 60% for clay and sand, respectively) at the alpine site (Alongi et al. 2022). The lowland and subalpine grasslands are semi-natural, while the grasslands

at high elevation alpine are natural pastures above the treeline. These sites vary in the dominant species, such as, *Arrhenatheretum elatioris* in lowland grassland, *Trisetum flavescens* in subalpine and *Caricetum curvulae* in the alpine grassland (Berauer et al. 2019; Wilfahrt et al. 2021).

### Experimental setup and soil sampling

In early spring 2016, soil–plant mesocosms from the alpine and subalpine sites were translocated downslope to the lowland site (warming); oppositely, mesocosms from the lowland site were translocated upslope to the subalpine and alpine sites (cooling) to investigate potential changes in soil properties following long-term warming and cooling conditions (Fig. S1). The plant soil mesocosms were taken in PVC cylinders with a 30 cm diameter using a jackhammer from the upper 40 cm depth for the Bayreuth site and from the upper 25 cm from alpine and subalpine because of the shallow soil depth (Berauer et al. 2019; Schuchardt et al. 2023a). After excavation, the mesocosms were translocated to the recipient sites. In the lowland and alpine sites, the mesocosms were placed in raised beds, due to the higher groundwater level at the lowland site and to avoid strong disturbances of soils at the alpine. In the subalpine site, the mesocosms were inserted into the ground level within the recipient meadow plant canopy to avoid lateral frost impact on the excavated plant–soil turf. In addition, within each site, sets of mesocosms were translocated as control soils at all sites to compare changes in the translocated soils to the control of the same site. For continuing water flow, and to mimic the natural soil conditions the bottoms of the mesocosms were left open.

In the present study, 54 mesocosms (3 sites  $\times$  9 replicates  $\times$  2 variants (on-site control and translocated) were sampled in late 2020. As the plant–soil turfs were transported in early spring of 2016 (before the growing season), the altered growing seasons were 2016, 2017, 2018, 2019 and 2020 (5 years). The downslope translocations caused a temperature increase of +3.3K for the subalpine (9.87 °C) and +4.4K for the alpine (8.8 °C) translocated to the lowland site (13.2 °C) during growing season, respectively. The upslope translocations resulted in opposite temperature changes, – 3.3K for the lowland–subalpine translocation and – 4.4K for the lowland–alpine

translocation (Schuchardt et al. 2023b). The temperature change is higher (i.e., +5.2K and +8.7K) when the mean annual temperature is considered: 8.2 °C, 3 °C and –0.5 °C, for the lowland, subalpine and alpine sites, respectively. A composite sample from the upper 10 cm of each monolith was collected for the analysis. Two subsamples (500 g each) were sieved separately. The first one was sieved to 2 mm and stored at 4 °C until further microbiological and chemical analysis and the second one was sieved to 8 mm and reserved for aggregate analysis.

### Soil carbon and nitrogen

The total soil carbon (C) and nitrogen (N) were analysed in bulk soil samples and aggregate fractions using an Elemental Analyser (EA3100, EuroVector, Tecnologico di Pavia, Italy). The total soil C was considered equivalent to the soil organic C (SOC) due to the lack of reaction following HCl (1 M) additions to the soil.

### Aggregate size classes

The soil was fractionated using wet sieving (Elliott 1986; Six et al. 2000) for five replicates (instead of nine) per study site. In brief, moist soil was sieved through a 8000  $\mu$ m sieve. Subsequently, an amount of moist soil equivalent to 70 g of air-dried soil was weighed, and submerged in deionized water for five minutes. The mixture of the soil and water was poured on top of a 250  $\mu$ m sieve, placed inside a dish pan filled up-to 10 cm with deionized water. The wet sieving was done by moving the sieve up and down manually for 2 min. The material that remained on the top of the 250  $\mu$ m sieve was collected by backwashing the material inside a pre-weighted drying-pan. The above procedure was repeated using a 63  $\mu$ m sieve for the material that passed through the 250  $\mu$ m sieve to yield three size classes of soil: macroaggregate size (>250  $\mu$ m), microaggregate size (63  $\mu$ m–250  $\mu$ m), and silt/clay-sized fraction (<63  $\mu$ m). The recovery rate, which was calculated by the sum of the weight of the fractions to the initial soils was about 99–100%. The mean weight diameter (MWD) as a proxy for soil aggregate stability was calculated according to Eq. (1) (Kemper and Rosenau 1986).

$$MWD = \sum_{i=1}^n X_i W_i \quad (1)$$

where  $X_i$  is the mean diameter for each fraction size,  $W_i$  is the proportional weight of the fraction from the total dry weight of soil, and  $n$  is the number of aggregate classes.

### Soil respiration

For the soil respiration measurements, an amount of field moist soil corresponding to 40 g of dry soil was weighed into plastic vessels and rewetted with deionized water to achieve a water holding capacity of 50%. Thereafter, the soils were slightly compressed to a bulk density of 1.0 g cm<sup>-3</sup> to create standardized conditions. For the CO<sub>2</sub> measurements, the respirometer Respicond V was used, allowing simultaneous incubation of 96 samples, connected to a conductometer via a multiplexer. When CO<sub>2</sub> is released from the soils, it is trapped in potassium hydroxide (KOH) (Nordgren 1988). The trapped CO<sub>2</sub> reacts with KOH, forms carbonate ions, and decreases the electric conductivity, which is continuously (every hour) measured by platinum electrodes. The change in conductivity is converted to CO<sub>2</sub> evolution rates based on Eq. (2) (Nordgren 1988; Smirnova et al. 2014).

$$CO_2 = Ax \frac{C_{t0} - C_{t1}}{C_{t0}} \quad (2)$$

where  $C(t_0)$ , is the conductance at time zero ( $t_0$ ),  $C(t_1)$  is the conductance at time 1, and  $A$  was determined constant calculated as  $A = CO_2$  if  $C(t_1) = 0$ .

In total, 81 samples plus 9 blanks were measured. This method was used to quantify CO<sub>2</sub> efflux for temperature sensitivity (Q10) and basal and substrate-induced respiration as described below.

### Temperature sensitivity (Q10)

For temperature sensitivity of soil respiration (Q10) determination, the soils were pre-incubated for 5 days at 15 °C. The incubation was started by setting the temperature of the water bath to 7 °C, 10 °C, 15 °C, 20 °C, 25 °C and backwards every 24 h. The relationship between temperature and soil respiration was fitted over the total temperature range of 7–25 °C using an exponential equation (Eq. 3). Finally, the

Q10-values were calculated by inserting parameter  $b$  in Eq. (4) (Meyer et al., 2017):

$$SR_T = ax \exp^{bxt} \quad (3)$$

where  $SR_T$  is the soil respiration at a given temperature ( $T$ ),  $a$  and  $b$  are the fitted parameters.

$$Q10 = \exp^{10xt} \quad (4)$$

### Basal respiration and substrate induced respiration

After completion of Q10 determination, the temperature of the water bath was set to 22 °C and soil basal respiration was measured for 48 h. The subsequent determination of microbial biomass C (MBC) was based on the substrate-induced respiration (SIR) after glucose addition (Anderson and Domsch 1978; Nordgren 1992). Briefly, 320 mg glucose was added to 40 g of soil and incubated for 5 days at 22 °C. The MBC was calculated according to Anderson and Domsch (1978) as in Eq. 5:

$$MBC [\mu g g^{-1} soil] = CO_2 [\mu l CO_2 g^{-1} soil h^{-1}] \times 40.04 + 0.37 \quad (5)$$

where CO<sub>2</sub> is CO<sub>2</sub> release at 22 °C.

The calculated MBC was used for the metabolic quotient (qCO<sub>2</sub>) calculation (qCO<sub>2</sub> = basal CO<sub>2</sub> / MBC) as indicator for C stability as it represents the amount of C release per unit of microbial biomass (Deng et al. 2016).

### Statistical analysis

Normal distribution of the data was determined using the Shapiro–Wilk test ( $P \leq 0.05$ ). In a few cases (i.e. pH and Q10) where the data were not normally distributed, the non-parametric Mann–Whitney U test was performed. For the downslope translocation (warming), where the subalpine and alpine soils were translocated to the lowland site, the data was statistically analysed using the t-test separately, where the translocated soils were compared to the control soils. However, in the upslope translocation (cooling), where lowland soil was translocated to subalpine and alpine sites, a one-way analysis of variance was used to compare the translocated soil against the control. Statistical differences of the means of all data were tested to a significance level  $P \leq 0.05$ . The data was



statistically analysed using SigmaPlot (SigmaPlot for Windows Version 14.5). Correlations between the measured parameters at each site were analysed with the Pearson correlation coefficient ( $p < 0.05$ ).

## Results

### Change in soil pH, C quality indicators and Q10 in response to warming

Warming (downslope translocation) of alpine soil to the lowland site (+4.4K) significantly decreased soil pH, SOC, N and MBC (Table 1). Among these variables, SOC and MBC were the most affected variables, where warming caused a 32% and 56% lower SOC and MBC, respectively. However, this was not the case for the translocation of subalpine soil to the lowland site (+3.3K), where no effect on SOC, TN and MBC was observed (Table 1). Warming of the subalpine soil significantly increased soil pH (Table 1).

Warming of both alpine and subalpine soils affected soil C quality indicators with strongest effects observed in the translocated alpine site (Fig. 1). Warming of alpine soil decreased soil C/N ratio from  $15.2 \pm 0.66$  to  $12.8 \pm 0.27$  compared to the control, but no effect was observed for the relatively lower C/N ratio (e.g., C/N ratio =  $9.2 \pm 0.22$ ) of the translocated subalpine soil (Fig. 1a). However,  $qCO_2$  for both warming sites showed an opposite trend to the C/N ratio, which was only significant for the alpine soil (Fig. 1b). The translocated alpine soil (+4.4K) showed a 27% higher  $qCO_2$  associated with a significant decrease of soil basal respiration than the control (Fig. 1b and Fig. S2). Oppositely, the Q10 for both translocated soils

decreased significantly by 20% and 16% for subalpine and alpine soil, respectively.

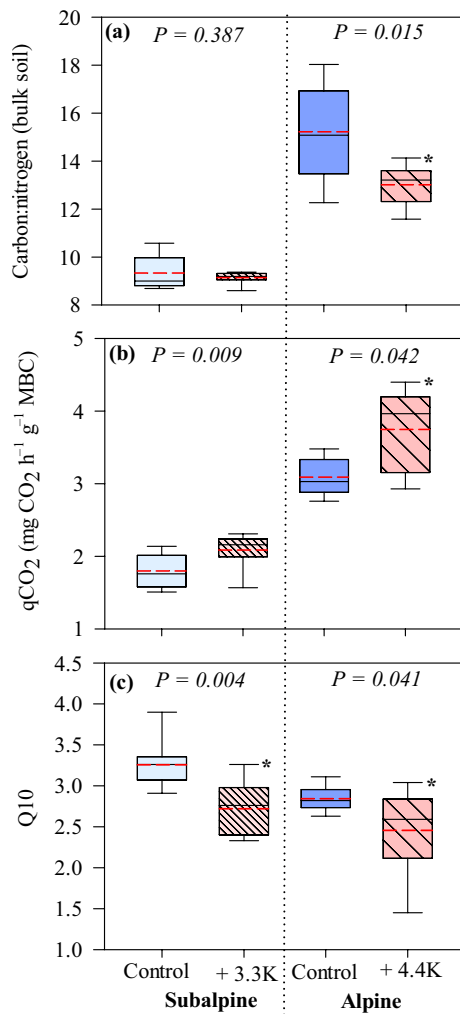
### Changes in soil aggregates and their associated SOC and TN in response to warming

The overall aggregate size class distribution and SOC and TN within soil size fractions varied between the translocated and the control soils in all sites (Fig. 2). The size distribution was strongly dominated by macroaggregate size in both soils, followed by microaggregate size and the silt/clay-sized fraction (Fig. 2a). Warming decreased the proportion of macroaggregate size by 33% for subalpine and by 40% for alpine soils. In contrast, the proportion of silt/clay-sized fractions and especially of microaggregate size increased with warming. Similar to the soil size distribution the SOC and N associated with the size fractions decreased with warming in the macroaggregate size and increased in microaggregate size and silt/clay-sized fractions (Fig. 2b, c). Compared to the control, warming caused a reduction in SOC content associated with the macroaggregate fraction by 25% for the subalpine and by 29% for the alpine soil (Fig. 2b). However, the SOC and N associated with the microaggregates and silt/clay-sized fractions increased in both soils with warming, with a larger increase observed in alpine soil (Fig. 2b and c). A significant increase in C/N ratio with increasing temperature was only observed in the silt/clay-sized fraction in subalpine soil, where the C/N ratio doubled from  $4.2 \pm 0.07$  in the control to  $8.1 \pm 0.09$  in the translocated soil (Fig. 2d).

**Table 1** Changes in means  $\pm$  SE (n=9) soil pH, soil organic carbon (SOC), total nitrogen (TN) and microbial biomass carbon (MBC) following the warming translocation (downslope) of subalpine (+3.3K) and alpine soil (+4.4K) to lowland site

Parameters	Subalpine to lowland		T-test		Alpine to lowland		T-test	
	Control	+3.3K	T-value	P-value	Control	+4.4K	T-value	P-value
pH	$5.40 \pm 0.10$	$5.76 \pm 0.10^*$	-2.483	0.025	$4.46 \pm 0.02$	$4.29 \pm 0.08^*$	2.041	0.050
SOC (g C kg <sup>-1</sup> soil)	$50.31 \pm 2.23$	$47.86 \pm 1.88$	0.793	0.440	$93.60 \pm 9.50$	$63.83 \pm 3.14^*$	2.624	0.029
TN (g N kg <sup>-1</sup> soil)	$5.38 \pm 0.16$	$5.24 \pm 0.22$	0.472	0.643	$6.21 \pm 0.43$	$4.92 \pm 0.29^*$	2.421	0.036
MBC (mg C g <sup>-1</sup> soil)	$1.85 \pm 0.08$	$1.84 \pm 0.13$	0.041	0.968	$2.22 \pm 0.16$	$0.98 \pm 0.09^*$	6.561	<0.001

Mean soil parameters followed by an asterisk (\*) indicate a significant difference between the translocated soil and the control of the same soil ( $P \leq 0.05$ ; n=9)



**Fig. 1** **a** C/N of the bulk soil, **b** metabolic microbial quotient ( $q\text{CO}_2$ ) and **c** temperature sensitivity of soil respiration (Q10) for warming translocations (downslope) of subalpine (+3.3K) and alpine (+4.4K) soils to lowland site. The short-dashed red line represents the mean value and an asterisk (\*) indicates a significant difference between the mean of the translocated soil and the control of the same soil ( $P \leq 0.05$ ;  $n=9$ )

#### Change in soil pH and C quality indicators in response to cooling

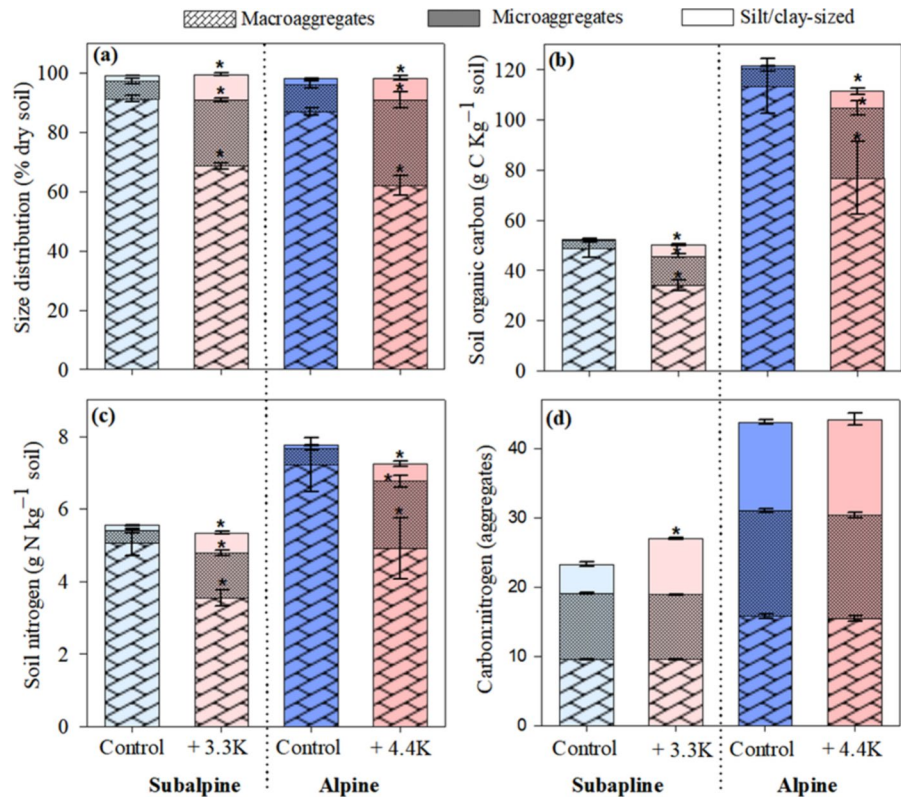
Cooling (upslope translocation) of lowland soil to the subalpine (−3.3K) and alpine site (−4.4K) caused a significant decrease in soil pH, SOC, TN and MBC (Table 2). A significant reduction of basal respiration was only observed in the case of the upslope translocation to the subalpine (Fig. S3). Compared to the control, the soil under colder

conditions became more acidic over the time of 5 years. Similarly, SOC decreased, yet only significantly for soil translocated from the lowland to the subalpine grassland. Furthermore, cooling of lowland to the subalpine site caused a decrease in TN by 21% and in MBC by 60%. However, MBC was reduced by 29% when lowland soil was transferred even to cooler conditions at the alpine site. However, the soil C/N ratio, as a main soil organic matter quality indicator, was lowest in the lowland control and increased with decreasing temperature; however, this was only significant for soils translocated to the alpine site (Fig. 3a). The soil  $q\text{CO}_2$  increased by 5% following the cooling of lowland soil to the subalpine and by 22% following the cooling of lowland soil to the alpine sites (Fig. 3b), again only significant for the alpine soil. Against our expectation, the upslope translocation of lowland soil to the subalpine and alpine sites had no significant effect on Q10 (Fig. 3c).

#### Changes in soil aggregates and its associated SOC and TN in response to cooling

The soil size distribution, and SOC and TN of the aggregate size fractions in response to cooling showed less variation compared to warming treatments (Fig. 4). Compared to lowland soil as a control, cooling decreased macroaggregate size fractions and increased the proportion of microaggregate size and silt/clay-sized fraction in subalpine soils, but the opposite trends were observed in alpine soils (Fig. 4). Significant variation was only observed in the proportion of the silt/clay-sized fraction between the control lowland soil and the soil translocated to the subalpine site. While the SOC within the macroaggregate size fractions increased significantly (by 11%) following the upslope translocation to the alpine site, the SOC associated with the microaggregate size fraction decreased by 48% (Fig. 4b). Furthermore, the upslope translocation decreased the TN content of the microaggregate size fraction by 29% in the soil translocated to the subalpine and up to 50% in the soil translocated to the alpine site (Fig. 4c). The upslope translocation of the lowland soil to the alpine site increased the C/N ratio of silt/clay-sized fraction (Fig. 4d).

**Fig. 2** **a** Aggregates size distribution, **b** soil organic carbon content, **c** soil nitrogen content, and **d** carbon to nitrogen ratio, associated with aggregates fractions following warming translocations (downslope) to the lowland site from subalpine (+3.3K) and alpine (+4.4K). An asterisk (\*) indicates a significant difference between the mean of the translocated soil and the control of the same aggregate size and soil ( $P \leq 0.05$ ;  $n = 5$ )



**Table 2** Changes in means  $\pm$  SE ( $n=9$ ) soil pH, soil organic carbon (SOC), soil total nitrogen (TN) content and microbial biomass carbon (MBC) following the cooling translocation (upslope) from lowland site to subalpine (-3.3K) and alpine (-4.4K)

Parameters	Lowland site			One way ANOVA	
	Control	Subalpine (-3.3K)	Alpine (-4.4K)	F- value	P- value
pH	5.23 $\pm$ 0.08	4.62 $\pm$ 0.10*	4.89 $\pm$ 0.04*	14.82	<0.001
SOC (g C kg <sup>-1</sup> soil)	27.60 $\pm$ 1.37	22.15 $\pm$ 0.50*	24.05 $\pm$ 0.78*	7.44	0.003
TN (g N kg <sup>-1</sup> soil)	2.13 $\pm$ 0.11	1.68 $\pm$ 0.06*	1.73 $\pm$ 0.04*	8.73	0.001
MBC (mg C g <sup>-1</sup> soil)	0.84 $\pm$ 0.09	0.34 $\pm$ 0.03*	0.60 $\pm$ 0.04*	15.87	<0.001

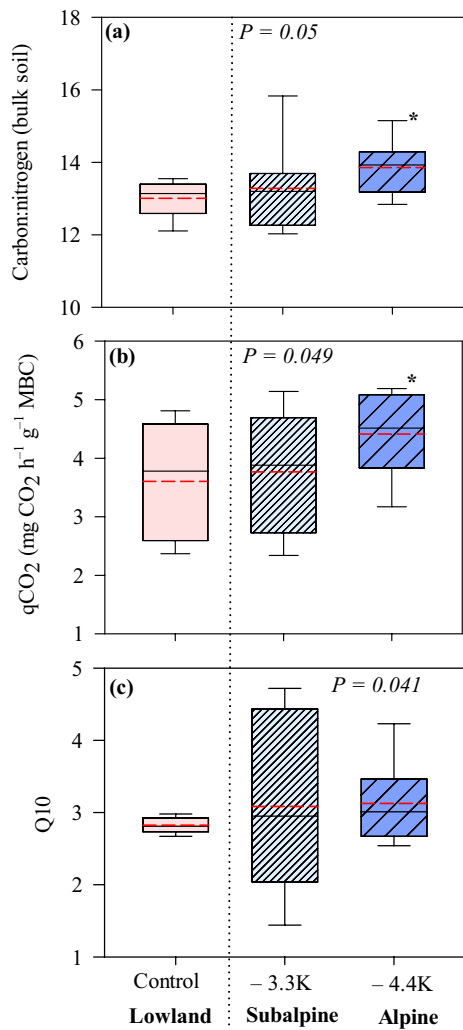
Mean soil parameters followed by an asterisk (\*) indicate a significant difference between the translocated soil and the control of the same soil ( $P \leq 0.05$ ;  $n=9$ )

## Discussion

The microbial metabolic quotient ( $qCO_2$ ), as an indicator for the C source mineralization efficiency of the microbial community (the lower the  $qCO_2$  the higher the efficiency) is closely related to the C/N ratio of the soil (Martínez-García et al. 2018). In previous studies, a low  $qCO_2$  and wide C/N ratio indicated that soil organic matter is comparatively

stable and, for stoichiometric reasons, not easily available as it contains little nutrients (Spohn 2015; Brust 2019). According to the carbon-quality temperature (CQT) hypothesis, less easily degradable soil organic matter requires high activation energy associated with greater temperature sensitivity (Q10) of soil respiration (Davidson and Janssens 2006; Conant et al. 2008). In line with the CQT hypothesis, our results showed that warming of





**Fig. 3** **a** C/N of the bulk soil, **b** metabolic microbial quotient ( $q\text{CO}_2$ ) and **c** temperature sensitivity of soil respiration (Q10) for cooling translocations (upslope) of lowland site to subalpine ( $-3.3\text{K}$ ) and alpine ( $-4.4\text{K}$ ). The short-dashed red line represents the mean value and an asterisk (\*) indicates a significant difference between the mean of the translocated soil and the control of the same soil ( $P \leq 0.05$ ;  $n = 9$ )

the subalpine and alpine grassland soils reduced SOC (Table 1) and Q10, and increased  $q\text{CO}_2$  (Fig. 1), which might be explained by macroaggregate breakdown (Fig. 2), exposing the formerly occluded C to the soil decomposers (Rillig et al. 2002; Poepflau et al. 2020; Tamura and Suseela 2021).

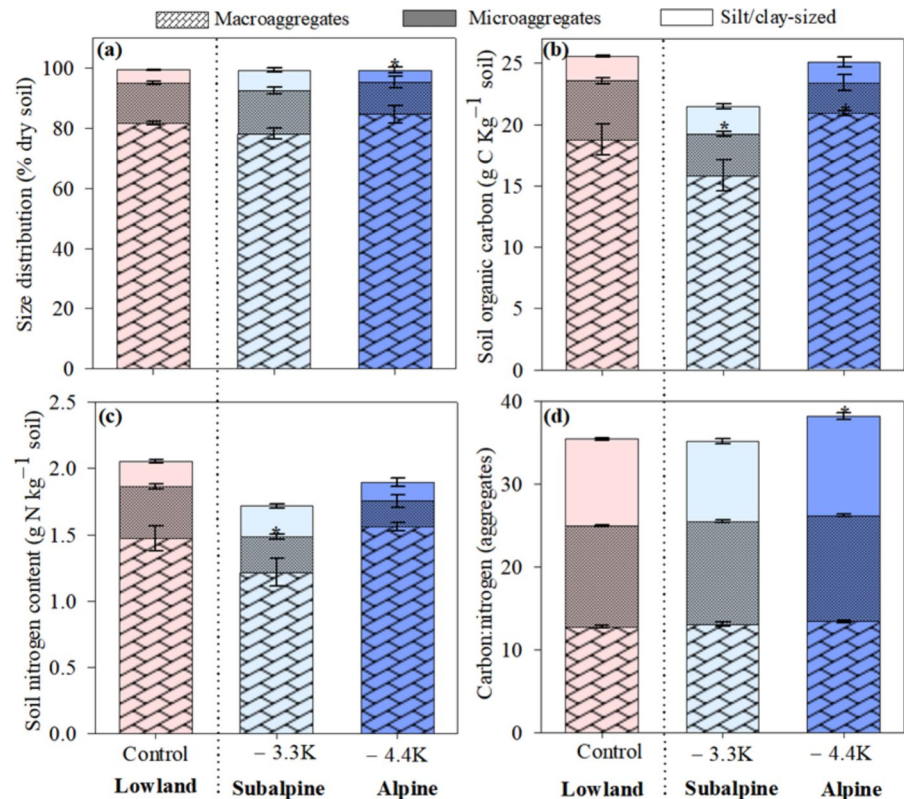
### Soil organic matter degradability increases with warming

Five years of warming of alpine and subalpine soils affected the stability of soil organic matter. The  $q\text{CO}_2$  increased with warming in both alpine and subalpine soils (Fig. 1b). Also other studies supported that long-term warming (e.g., 14 years,  $+4^\circ\text{C}$ ) increases microbial biomass-specific growth (by 25%) and microbial turnover (by 14%), with a decrease in MBC of forest soils from the Northern Limestone Alps, Austria (Tian et al. 2023). We assume that the  $q\text{CO}_2$  increased with warming as SOC becomes more easily available to microorganisms.

Besides, the  $q\text{CO}_2$  serves as proxy for soil organic matter stability (Martins et al. 2011; Błońska et al. 2018), while the C/N ratio of soil organic matter has widely been used as an indicator for the degree of organic matter decomposition. During microbial decomposition, C is lost as  $\text{CO}_2$ , while a large portion of N is retained in soils resulting in a gradually decreasing C/N ratio. This decrease in C/N of the soil organic matter, therefore, implies a higher degree of soil organic matter decomposition (Jiang et al. 2017; Xia et al. 2021).

In the present study, the C/N ratio of the alpine soil was highest, likely due to lower decomposition rates at colder temperatures. The C/N ratio of the soil organic matter decreased significantly with warming from  $15.2 \pm 0.66$  to  $12.8 \pm 0.27$  (Fig. 1a), suggesting that warming accelerated the degradation of soil organic matter. The accelerated decomposition of soil organic matter following warming can also be supported by the significant decrease in soil pH of the translocated alpine soils (Table 1). During the decomposition of organic matter, microbes produce various organic acids (such as acetic acid, citric acid and humic acids), which release hydrogen ions ( $\text{H}^+$ ) into the soil, thereby lowering the pH (Zhang et al. 2020). However, this was not the case for the translocation of subalpine soils (i.e., subalpine to lowland;  $+3.3\text{K}$ ), where the C/N ratio was  $<10$ , only a tendency towards decreasing C/N ratios occurred (Fig. 1a), and the soil pH increased significantly (Table 1). Therefore, the different responses observed for alpine and subalpine soils are likely to be due not only to the different warming rates, but also to different initial soil C/N ratios. Also, distinct soil properties, plant and microbial communities of the alpine and subalpine

**Fig. 4** Aggregates size distribution **a** soil organic carbon content **b** soil nitrogen content **c** and carbon to nitrogen ratio **d** associated with aggregates translocations (upslope) of lowland site soil to subalpine (− 3.3K) and alpine (− 4.4K). An asterisk (\*) indicates a significant difference between the mean of the translocated soil and the control of the same aggregate size ( $P \leq 0.05$ ;  $n = 5$ )



soil could contribute to this finding (Donhauser and Frey 2018; Tian et al. 2023).

The physical stabilization of soil organic matter within aggregates is a crucial mechanism involved in C sequestration by protecting soil organic matter from decomposers, thereby increasing its residence times in soils (Six et al. 1998; Burgeon et al. 2021). In the present study, the macroaggregate size fraction decreased significantly with warming (Fig. 2a). This resulted in a relative increase in the microaggregate size fraction and silt/clay size particles. Hence, warming resulted in an increase of the smaller aggregate size fraction by 28% for alpine and by 24% for subalpine soils (Fig. S4). Recently, also Zhou et al. (2023) found that 15 years of warming resulted in increased proportion of non-aggregated silt/clay-sized fractions. Several studies propose that soil organic matter mineralization is faster in the macroaggregate compared to the microaggregate fraction (Rabbi et al. 2014; Bischoff et al. 2017; Kan et al. 2020), mainly because soil microorganisms have limited access to the soil organic matter within microaggregates (Six et al. 2002; Davidson and Janssens 2006). Yet,

macroaggregates provide additional stabilization of microaggregates occluded therein. We did not analyze macroaggregate-occluded microaggregates in this study. However, as a large degree of macroaggregation usually goes along with an increasing number of occluded microaggregates (Totsche et al. 2018), we conclude that the breakdown of macroaggregates which represents more than 80% in our soil (Fig. 2a) causes a decrease in physical stability with warming. Together, with the narrower C/N ratio and the increased  $qCO_2$ , our results point to an increasing soil organic matter degradation with warming, supporting our first hypothesis that warming increases the degradation of soil organic matter.

Temperature sensitivity (Q10) decreases with warming

Higher temperatures are known to increase soil organic matter mineralization rates, due to increased microbial activity (Davidson and Janssens 2006; Nyberg and Hovenden 2020). This was also the case in our five-year field translocation experiment, where

warming of the alpine soil (+4.4K) decreased SOC by 32%, suggesting high SOC losses under warmer conditions. The same trend was observed for the warming of the subalpine soil (+3.3K), but the reduction in SOC was not significant. The lack of a significant change in SOC in the subalpine soil compared to the alpine soil could be explained by the lower degree of warming. The alpine soils were exposed to colder temperatures than the subalpine soils, so that the mineralization of soil organic matter in the subalpine was limited by temperature for a comparatively longer period of the year. Therefore, in line with the Carbon Quality-Temperature (CQT) hypothesis, warmer temperatures induced a greater reduction in SOC compared to the lower temperature change.

The CQT-hypothesis deduces that more stable soil organic matter is more vulnerable to increasing temperatures compared to labile soil organic matter because of the high activation energy required by soil microbes to breakdown the more chemically complex C (Bosatta and Ågren 1999; Davidson and Janssens 2006). Many studies (Wang et al. 2015; Ding et al. 2016; Li et al. 2017; Meyer et al. 2018) reported that labile soil organic matter pool is less sensitive to warming than the more stable soil organic matter, thus supporting the CQT hypothesis. In line with the CQT-hypothesis, our results showed a decrease in Q10 under warming (Fig. 1c), associated with a decrease in soil organic matter stability as also indicated by  $q\text{CO}_2$  and less aggregate stability. Thus, our results show that warming will increase soil respiration and turnover of SOC but this effect is regulated by a negative feedback mechanism: warming decreases the temperature sensitivity of soil respiration, thereby lowering SOC losses. Future soil organic matter losses in the translocated soils will likely occur at lower rates.

Does cooling translocation induce the opposite effect of warming?

Against our third hypothesis, the effect of cooling translocation did not induce opposite trends to warming. These are surprising results, as warming and cooling are expected to induce contrasting effects on these parameters mainly because of their effect on microbial functions, organic C inputs by vegetation and soil organic matter quality (Qin et al. 2019; Li et al. 2020). It is important to note that cooling

showed a tendency in the opposite direction compared to warming for C/N ratio (Fig. 3a) and aggregate stability (Fig. S5), but not for  $q\text{CO}_2$  and Q10 (Fig. 3c and b). A possible explanation is that cooling slows down microbial processes in soil and organic matter cycling. The effect of warming, in contrast, might be detectable earlier due to increased soil organic matter turnover. Another reason might be the fact that the soil translocated upslope (cooling) had much lower SOC content and MBC (Table 2) compared to the alpine and subalpine soils (Table 1). This may have resulted in the observed negligible changes in some parameters (e.g., Q10) following cooling.

In general, the response of SOC dynamics to warming and cooling may not be a linear opposite process as the translocated soil microbes and plant species required time to adapt to the new environment. Therefore, our results suggest that longer experimental time (>5 years) may be required for more pronounced changes.

Intricate effects of the translocations on soil carbon dynamics

Overall, our results showed that SOC, TN, MBC and C/N ratio decreased with the translocation regardless of cooling or warming (Table 1 and 2; Fig. 1 and 2) indicating that translocated microbial and plant communities needed time to adapt to the new environmental conditions. This new environment differs not only in temperature but also in other weather factors, such as precipitation and humidity. Therefore, the role of plant adaptation and shift in response to the new environment differ in soil moisture and temperature and the consequent effects on the plant C allocation and microbial activities cannot be neglected in this context. This is especially true in our study sites, where a decrease in plant biomass and species richness was observed only one year after downslope translocation (Berauer et al. 2019) and loss or replacement of native species at a later stage (Schuchardt et al. 2023b). This means that downslope translocated plants and soil microbes immediately begin to adapt to the new environment. During the adaptation period, soils may lose SOC due to the mineralization of the native SOC until plants are able to cope with the new conditions and provide more substrate for soil microbes.

The lowland grassland site also experienced a severe heat wave and drought in 2017, with less

severe droughts in the following years, i.e., 2018 and 2020 (Bastos et al. 2020; Schuchardt et al. 2023b; Berauer et al. 2019). This led to the implementation of an additional irrigation treatment in the lowland site to alleviate water limitation. The irrigation treatment aimed to mimic a subalpine precipitation pattern and provide additional water to compensate for the reduced precipitation at the lowland site. Despite the supplementary irrigation, biomass production was reduced by an average 24% of the alpine and subalpine soils, which have been transported to the lowland site in 2017 (Berauer et al. 2019), and significant changes in species identity and strong colonization by novel species were observed (Schuchardt et al. 2023b). The decrease in biomass production implies a decrease in soil C input due to lower rhizodeposition, which may lead to lower SOC in downslope translocated alpine and supalpine grasslands. Conversely, the decrease in SOC due to cooling (ranging from 12 to 19% at much lower SOC contents) may also be associated with lower biomass production related to the adaptation to the cooler environment (Wingler and Hennessy 2016). Thus, in addition to warming and cooling effects, biomass production also controls SOC dynamics. However, our results may also be influenced by the lack of baseline SOC data, as the control at the lowland site may also have been affected by the climatic stressors and associated disturbance. Therefore, the lack of the initial soil data from the control and the translocated soils can be considered as a limiting factor to our study results. In addition, longer-term warming and cooling experiments are needed to improve our understanding of the potential plant-soil-microbial interactions that drive soil organic matter dynamics in response to abrupt environmental change.

## Conclusion

Five years of downslope translocation (warming) of plant-soil mesocosms from subalpine and alpine sites to a lowland site resulted in a significant reduction in SOC and a decrease in soil macroaggregates. Conversely, upslope translocation (cooling) did not produce the exact opposite effects as anticipated. This suggests that the response of SOC dynamics to temperature changes is likely influenced by the interactions among plant and microbial

communities, as well as edaphic properties. These findings provide strong evidence that increased climate warming has severe impacts on soil organic carbon and soil aggregation in high-elevation grassland ecosystems. Therefore, implementing appropriate management practices to enhance soil carbon sequestration is crucial to mitigate the escalating risks posed by climate change in these vulnerable ecosystems.

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**Data availability** The datasets generated during and/or analysed during the current study are not publicly available but can be obtained from the corresponding author upon request.

## Declarations

**Competing interests** The authors have no relevant financial or non-financial interests to disclose.

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