https://doi.org/10.5194/egusphere-2025-5429
Preprint. Discussion started: 13 November 2025

Vulnerability of carbon in subalpine soils in the face of warmer temperatures

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Abstract. Alpine and subalpine soils are significant reservoirs of labile carbon (C) and are highly sensitive to warming, yet the mechanistic interactions between temperature and organic inputs are poorly understood. A one-year laboratory incubation was conducted with mineral surface soils from a subalpine pasture and an adjacent coniferous forest site. Soil samples were incubated in closed jars at three different temperatures: Current growing season temperature (12.5 °C), and two increased temperature treatments (16.5 °C and 20.5 °C). To assess decomposition differences between litter and native soil organic matter (SOM), ^{13}C-labelled plant litter was added to a subset of the jars. CO_2 production, δ^{13}C partitioning, and phospholipid fatty acid (PLFA) profiles were used to quantify soil organic matter (SOM) and litter decomposition, and to assess microbial dynamics. Warming increased total CO_2 respiration by 15 – 37 % in pasture and 12 – 33 % in forest soils, with strongest stimulation in litter-amended soils. Positive priming of native soil organic matter (SOM) peaked within one week (up to +77 % over controls) and declined to near zero after one month. Cumulative litter-induced respiration (LIR) was highest at 16.5 °C (+6–10 % vs. 12.5 °C) in both soils, coinciding with maximum microbial biomass; 20.5 °C reduced microbial biomass by up to 25 % and accelerated ^{13}C label loss. The response of pasture soils was more rapid and pronounced compared to forest soils, which exhibited slower, more sustained responses. PLFA profiles revealed warming-induced declines in Gram$^+$ and Gram$^-$ bacteria and increased cyclopropyl markers at high temperature. These findings show that even moderate warming can accelerate C loss from subalpine soils, with vegetation history and microbial traits modulating both rate and timing of decomposition.

1 Introduction

Soil organic matter (SOM) is a major component of the global carbon (C) cycle, containing more C than the atmosphere and terrestrial plant C pool combined (Schmidt et al., 2011; Friedlingstein et al., 2025). Due to generally cold temperatures and short growing seasons, soils in alpine regions tend to accumulate thick organic layers and store high stocks of C (Budge et al., 2011; Bonfanti et al., 2025). These low temperatures slow down microbial decomposition, causing SOM to accumulate in a labile, easily decomposable form (Djukic et al., 2010). As a result, alpine and subalpine SOM is particularly sensitive to

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warming (Gobiet et al., 2014). A modest rise in soil temperature could greatly enhance microbial activity and thus CO_2 release from SOM, potentially creating a positive climate feedback (García-Palacios et al., 2021; Soong et al., 2021; Chen et al., 2024). Currently, mountain regions are warming faster than lowlands (Rogora et al., 2018; Hock et al., 2019), snow cover is declining (Klein et al., 2016), the growing season is prolonged (Rogora et al., 2018) and vegetation shifts occur due to upward shifts of the treeline and abandonment of pastures in alpine and subalpine areas (Gehrig-Fasel et al., 2007; Hagedorn et al., 2019). As a result, the fate of SOM in alpine soils under ongoing climate change is a critical open question.

Large areas in alpine and subalpine regions are covered by grasslands (Zehnder et al., 2020), either naturally due to cold temperatures at high elevations above the treeline or due to human management (Schwörer et al., 2015). Recent changes leading to shifts in vegetation are driven by warming temperatures as well as the abandonment of mountain pastures (Gehrig-Fasel et al., 2007). The most evident change is an increase of shrub encroachment and afforestation of former pasture landscape, but also on naturally existing grasslands at the treeline, which is rising due to warmer climate (Hagedorn et al., 2019; Zehnder et al., 2020). These vegetation shifts in alpine regions alter quality and quantity of C inputs into soils and SOC stocks (Gehrig-Fasel et al., 2007; Hagedorn et al., 2019). The up-slope movement of shrubs and trees introduce more woody tissues and generally thicker organic layers, altering SOM composition (Speckert et al., 2023). This also strongly influences soil microbial communities, as often significant shifts on bacterial and fungal populations can be observed following afforestation (Gunina et al., 2017b). Resulting changes are variable, and the implications for SOM stability and the sensitivity to warming are still unclear. Differences in microbial community composition between vegetation types can affect decomposition speed, with pasture soils often hosting more copiotrophic microorganisms adapted to fast cycling of labile C, and forest soils containing more microorganisms specialized in degrading complex organic matter (Solly et al., 2014; Kramer and Gleixner, 2008; Zhang et al., 2016; Lu et al., 2017). These contrasts are consistent with stronger warming-induced SOC losses reported in forests relative to grasslands (Poeplau et al., 2020). We therefore use the comparison between a subalpine pasture and a forest soil from the same site to capture how climatically driven shift from pasture to forest alters soil organic matter dynamics and carbon input quality in alpine systems.

Rising temperatures increase microbial decomposition of SOM by accelerating microbial and enzymatic processes (Fanin et al., 2022). According to the classical theory, a temperature rise of 10 °C can increase respiration by two to three times, although this temperature sensitivity is in reality often dampened by substrate quality or other environmental constraints (Davidson and Janssens, 2006; García-Palacios et al., 2021). In decomposition studies under field or lab conditions, warming often causes a strong initial pulse of rapid decomposition, followed by a decrease of the respiration rate as the labile C pools become depleted or microbial carbon use efficiency (CUE) declines (Davidson and Janssens, 2006; Melillo et al., 2017). Field studies often show a smaller increase compared to laboratory incubation studies under optimized conditions (Hanson et al., 2020; Soong et al., 2021). In alpine and subalpine soils, where low baseline temperatures, short growing seasons, and snow cover strongly influence biological activity, even modest warming can disproportionately stimulate decomposition and extend the period of microbial activity, while aggregate destabilization may further expose protected carbon to mineralization (Streit et al., 2014; Donhauser and Frey, 2018; Abdalla et al., 2024). Overall, rising temperature is likely to accelerate SOM mineralization and efflux of CO_2, leading to a positive C–climate feedback (García-Palacios et al., 2021; Chen et al., 2024). Nevertheless, the

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long-term net effect of warming on C stocks is uncertain, because increased plant growth and C input can partially offset the enhanced SOM decomposition (Chen et al., 2024; Bai et al., 2025). The temperature optimum for microbial processes can vary depending on substrate type, and the sensitivity of different SOC fractions is likely dependent on their quality. Chemically more complex SOM such as lignin may exhibit greater sensitivity compared to more labile compounds (Fierer et al., 2005; Wang et al., 2018), although some recent studies also found equal vulnerabilities of easily decomposable and more complex substances (Ofiti et al., 2021, 2022, 2023; Zosso et al., 2023). Extreme warming may further reduce efficiency due to increased maintenance costs and thermal stress on sensitive microbial taxa (Domeignoz-Horta et al., 2020; Nottingham et al., 2022; Dang et al., 2024; Zhu et al., 2023). In alpine and subalpine ecosystems, such compensatory effects may be weaker because plant productivity is more limited and microbial acclimation can be slower, leading to an enhanced vulnerability of soil carbon stocks under climate warming (Qi et al., 2021; Bonfanti et al., 2025).

The response of microbial communities in soils to warming is crucial for SOM stability. Warming alters microbial community composition, reduces biomass, and favors thermotolerant species (Melillo et al., 2017; Zosso et al., 2021; Fanin et al., 2022; Ofiti et al., 2024; Schindlbacher et al., 2011; Nottingham et al., 2022; Domeignoz-Horta et al., 2020), thereby lowering CUE and increasing the fraction of C released as CO_2. A potential mechanism contributing to these responses is the priming effect: fresh organic C entering the soil can increase the overall activity of soil microorganisms and thus enable them to also decompose native SOM for nutrients and energy (Kuzyakov et al., 2000). Elevated temperature can increase the strength of positive priming, leading to higher respiration also from older SOC (Tao et al., 2024). Recent work in high-elevation and high-latitude soils has highlighted the ecological relevance of these processes: warming not only increases microbial biomass turnover but also promotes the decomposition of previously more stable SOM pools, leading to measurable reductions in soil C stocks on annual to multi-annual timescales (Chen et al., 2024; Tao et al., 2024). However, it still remains uncertain how microbial feedbacks change over time and how microbial communities potentially acclimate to temperature increases and changes in substrate availability and quality.

Long-term experimental data on how temperature and plant-derived C inputs jointly influence soil C dynamics remain scarce (Classen et al., 2015), especially in alpine regions. Recent reviews emphasize that soil microorganisms drive alpine C cycling feedback to climate, but details remain uncertain (Chen et al., 2024; Bai et al., 2025). Thus, there is a clear need to link temperature regimes, vegetation-type, and substrate dynamics in subalpine soils, and to trace C flow through the soil–microorganism system. Moreover, the combined effects of warming and fresh litter inputs on both short-term decomposition pulses and long-term C stabilization remain poorly quantified in these systems (Tao et al., 2024). To significantly improve our understanding of the vulnerability of SOC in subalpine soils, we conducted a one-year incubation experiment, addressing the following research questions:

1. How do subalpine soils that developed under pasture and forest respond differently to warming and fresh litter inputs?
2. How does temperature affect soil CO_2 respiration following fresh litter input?
3. How do functional soil microbial communities respond over time to warming and litter input, and how do these responses relate to changes in carbon mineralization?

We hypothesize the following:

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1. Total soil respiration and litter-induced respiration will increase with temperature, with higher peaks and faster declines at warmer temperatures due to rapid depletion of labile carbon. Forest and pasture soils will respond differently due to similar total SOC but contrasting substrate quality and microbial community composition, with forest soils containing more woody-derived organic matter and pasture soils being adapted to steady labile C inputs.

2. Litter addition will stimulate soil respiration and cause positive priming of native SOM, with stronger priming at higher temperatures.

3. Forest soil will show greater CO_2 respiration and stronger priming under warming and litter addition than pasture soil, due to differences in substrate quality and microbial community composition, while pasture soil will respond more rapidly but with smaller overall increases.

2 Materials and methods

2.1 Field site and soil sampling

The soil material for the incubation experiment was sampled in July 2020 at a field site close to the village of Jaun, Canton of Fribourg, Switzerland, on a south-facing slope at an altitude between 1500 and 1550 m a.s.l. and for two different vegetation covers, a coniferous forest site and a pasture site (Püntener et al., 2025). The forest site consists mainly of Norway spruce (*Picea abies* L.) with a stand age of at least 130 years, whereas the pasture site is dominated by herbaceous species, mainly ribgrass (*Plantago lanceolata* L.) and reed fescues (*Festuca arundinacea* Schreb.) (Speckert et al., 2023). Annual mean precipitation amounts to 1250 mm and mean air temperatures reach from 0.6 °C in winter to 11.4 °C in summer (Hiltbrunner et al., 2013). The soils were classified as Leptic Eutric Cambisol Clayic (IUSS Working Group WRB, 2015) and developed on a calcareous material (Speckert et al., 2023). The soils are acidic, with only a slight difference in pH between the two sites: pH 5.08 in the pasture soil and pH 4.83 in the forest soil (Püntener et al., 2025). During sampling, the organic layer was removed in the forest and high root frequency mineral soil in pasture. The mineral soil was sampled on an area of approximately 1 m^2 at a depth of 5 – 10 cm. In total, approximately 30 kg of soil material were collected at each of the two sites. The material was sieved <2 mm, roots were removed, followed by manual homogenization (Püntener et al., 2025).

2.2 Incubation Setup

The incubation setup is described in detail in Püntener et al. (2025). Briefly, the two soils were incubated at three different temperatures, with the 2015 – 2020 average growing season temperature from mid May to mid September of 12.5 °C as lowest temperature treatment and two increased temperature treatments of 16.5 °C and 20.5 °C. These increased temperature treatments correspond to the expected temperature rise with a high emission scenario (RCP8.5) in alpine regions by the end of the century (Hock et al., 2019). To trace the decomposition of fresh litter, ^{13}C-labelled (δ^{13}C 2255 ± 248 ‰Vienna Pee Dee Belemnite (V-PDB)) aboveground plant litter from perennial ryegrass (*Lolium perenne*) were added to a subset of the samples.

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The incubation was conducted for 360 days, with six destructive samplings and more regular measurement of respired CO_2 during the incubation period (see sampling scheme in Supplement Table S1).

2.3 Soil respiration: CO_2 concentration and C isotope composition

To trace CO_2 respired from the soil, a 20 ml sodium hydroxide trap (1 M NaOH) was placed into each incubation jar. The traps were replaced frequently to prevent saturation. The concentration of respired CO_2 was estimated using the method by Wollum and Gomez (1970) by measuring the electrical conductivity of the NaOH solution using a conductivity meter (LF 320 Conductivity Meter, WTW, Germany). To correct for temperature, individual temperature measurements were taken for each sample. The measured $NaHCO_3$ in the NaOH traps was converted to CO_2 using the calibration by Abiven and Andreoli (2011):

$$[\mathrm{CO_{2;NaOH}}] = -0.168 \times \mathrm{EC_{NaOH;sample}} + 28.639, \quad (1)$$

with $\mathrm{EC_{NaOH,\,sample}}$ as the measured conductivity within the NaOH traps (in mS cm^{-1}, corrected to a temperature of 25 °C. From this, total respired CO_2-C (CO_2-C_{total}; in mg) was calculated using:

$$\mathrm{CO_2\text{-}C_{total}} = [\mathrm{CO_{2;NaOH}}] \times v_{\mathrm{NaOH}} \times 0.2729, \quad (2)$$

with the volume of the NaOH trap v_{NaOH} (in ml) and considering the mass fraction of C (Abiven and Andreoli, 2011; Schiedung et al., 2023).

To measure $\delta^{13}C$ of the respired CO_2-C, 2.5 ml of each NaOH trap were mixed with 5 ml of 1 M $SrCl_2$ solution to obtain a precipitate of $SrCO_3$ (Schiedung et al., 2023). Each sample was centrifuged (1000 g; 5 min), the supernatant was decanted and the precipitate dried at 50 °C.

After dissolving the precipitate with phosphoric acid on a gas bench (GB), the C isotope composition of the respired CO_2 was measured using isotope ratio mass spectrometry (IRMS, Delta V Plus, Thermo Fisher Scientific, Germany). Each sample was measured 10 times.

All natural abundance isotope ratios are expressed as $\delta^{13}C$ relative to the Vienna Pee Dee Belemnite (vs. V-PDB) standard. The labelled samples with litter addition are presented as units of atom % excess (APE), calculated as:

$$APE = (atom\%)_{L^+} - (atom\%)_{L^-} \quad (3)$$

where $(atom\%)_{L^+}$ corresponds to the concentration of ^{13}C of the labelled samples and $(atom\%)_{L^-}$ to the ^{13}C concentration of the control samples with no litter (Slater et al., 2001).

Priming effect, defined as the change in native SOC mineralization induced by litter addition, was calculated using a two-step isotopic partitioning approach (Kuzyakov et al., 2000). For each sampling day and treatment, the fraction of respired CO_2 derived from the labelled litter ($f_{\mathrm{substrate}}$) was calculated from the difference in atom % ^{13}C (AP) between samples with litter addition (L^+) and control (L^-) treatments without litter addition, normalized to the ^{13}C enrichment of the litter:

$$f_{\mathrm{substrate}} = \frac{\mathrm{AP}_{L^+} - \mathrm{AP}_{L^-}}{\mathrm{AP}_{\mathrm{litter}} - \mathrm{AP}_{L^-}}$$

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Native SOC-derived respiration in litter-amended samples ($C_{\mathrm{soil\_lbl}}$) was then obtained by:

$$C_{\mathrm{soil\_lbl}} = R_{\mathrm{total}} \times (1 - f_{\mathrm{substrate}})$$

where R_{total} is the total respiration rate (g C–CO_2 kg^{-1} soil). The priming effect was determined as:

$$\mathrm{PE} = C_{\mathrm{soil\_lbl}} - R_{\mathrm{ctrl}}$$

where R_{ctrl} is the native SOC-derived respiration in the corresponding sample without litter addition. Positive values of PE indicate stimulation of SOC mineralization (positive priming), whereas negative values indicate suppression.

To detect increases in respiration from litter addition, the litter-induced respiration (LIR) was calculated as the difference between L^+ and L^- respiration.

2.4 PLFA analysis

The PLFA analysis was performed using the method described by Frostegård et al. (1991), following the Zosso and Wiesenberg (2021) adaptations of the protocols by Waldrop and Firestone (2006), and Gunina et al. (2017a). For each sample, 4 g of freeze-dried, milled soil material were used for a first extraction for 2 h with 4 ml of extraction solution (1:2:0.8 of chloroform ($CHCl_3$): methanol (MeOH): citric acid buffer (pH 4)) per g soil. An internal standard (50 μg 1,2-dinonadecanoyl-sn-glycero-3-phosphocholine; PC19:0; Avanti Polar Lipids, USA) was added for quantification. After centrifuging for 10 min at 800 g, the supernatant was transferred to separation funnels. The extraction was repeated three times with 10 ml of the solvent mixture during each round. After phase separation, the organic phase was eluted and reduced to 100 μl using a multivapor (Multivapor P-6, Büchi Labortechnik AG, Switzerland). The individual fractions were separated using a column with activated silica gel (Silica 60, Honeywell Fluka, USA; activated at 110 °C overnight). The neutral fraction was eluted with 5 × 1 ml $CHCl_3$, the glycolipid fraction with 4 × 5 ml acetone, and the phospholipid fraction with 4 × 5 ml MeOH. After reduction to 100 μl, remaining water was removed using a column filled with anhydrous Na_2SO_4. The method by Wiesenberg and Gocke (2017) was used for methylation. Briefly, 5 μg of $D_{39}C_{20}$ acid were added as a control standard, followed by dissolving in 300 μl dichloromethane (CH_2Cl_2). As methylation reagent, 500 μl of a BF_3-MeOH solution (10 % v/v, Sigma Aldrich, Inc., USA) were added to each sample. The samples were heated at 60 °C for 15 min on a heating block. After the samples reached room temperature, 500 μL of ultra-purified water was added. The samples were centrifuged, and the organic phase was transferred onto anhydrous Na_2SO_4, filtered, and the filtrate collected in an autosampler vial. CH_2Cl_2 was added another 5 – 8 times to the methylation solution until the organic phase was colorless.

Quantification was carried out using a gas chromatograph with a flame ionization detector (GC-FID, Agilent 7890 B, Agilent Technologies, Inc., USA, equipped with 50 m × 0.2 mm × 0.32 μm Agilent J&W DB-5MS column) with a multi-mode inlet (MMI). The GC temperature program was as follows: Start at 50 °C for 4 min, increase to 150 °C with a rate of 10 °C min^{-1}, followed by an incremental increase (2 °C min^{-1} to 160 °C, 0.5 °C min^{-1} to 170 °C, 0.2 °C min^{-1} to 190 °C, 2 °C min^{-1} to 210 °C) to a maximum temperature of 320 °C that was held for 15 min (Zosso and Wiesenberg, 2021). Compound peaks were matched against a suite of 24 fatty acid standards (Larodan; Sigma-Aldrich; Avanti Polar Lipids) and additionally confirmed by

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running samples on a GC (Agilent 6890 N, Agilent Technologies, Inc., USA, equipped with the same column as the GC-FID) coupled to a mass spectrometer (MS, Agilent 5973 N, Agilent Technologies, Inc., USA). The spectra were also compared to Wiley/NIST mass spectra libraries.

The PLFAs were grouped as in Zosso and Wiesenberg (2021) according to Willers et al. (2015) to differentiate the functionally different parts of the microbial communities: fungi ($C_{18:2\omega\,6,9}$), Gram negative bacteria (Gram$^-$; $C_{16:1\omega5c}$, $C_{16:1\omega7c}$, $C_{16:1\omega9c}$, $C_{18:1\omega5c}$, $C_{18:1\omega11c}$), Gram positive bacteria (Gram$^+$; $iC_{14:0}$, $aC_{14:0}$, $iC_{15:0}$, $aC_{15:0}$, $iC_{16:0}$, $aC_{16:0}$, $aC_{17:0}$), actinobacteria ($10MeC_{16:0}$, $10MeC_{18:0}$), and cyclopropyl bacteria ($cyC_{17:0}$, $cyC_{19:0}$). Microbial abundance was calculated using the sum of these diagnostic PLFA markers and the non-diagnostic saturated PLFAs ($C_{14:0}$, $C_{15:0}$, $C_{16:0}$, $C_{17:0}$, $C_{18:0}$), which are general bacterial markers (Zosso and Wiesenberg, 2021). The total concentrations of PLFAs were calculated in relation to the internal standard.

Carbon isotope composition of the PLFAs was analyzed using a GC (TRACE 1310, Thermo Fisher Scientific, Germany) which is coupled to an isotope ratio MS (Delta V Plus IRMS, Thermo Fisher Scientific, Germany) via GC-Isolink II and ConFlo IV (Thermo Fisher Scientific, Germany). For compound-specific isotope analysis of phospholipid-derived fatty acids (PLFAs), the isotopic effect of adding methyl groups during BF_3-MeOH methylation was corrected using a mass balance approach adapted from Dignac et al. (2005) (Equation 4):

$$\delta_{UD} = \frac{n_D}{n_{UD}}\,\delta_D - \frac{n_{\mathrm{MeOH}}}{n_{UD}}\,\delta_{\mathrm{MeOH}} \tag{4}$$

In this equation, δ_{UD} denotes the carbon isotopic ratio of the original, underivatized PLFA; n_D is the total number of carbon atoms in the methylated PLFA (FAME); n_{UD} is the number of carbon atoms in the underivatized fatty acid; δ_D is the isotopic ratio of the methylated PLFA measured by GC-IRMS; n_{MeOH} represents the number of carbon atoms introduced from the methanol reagent during derivatization (one carbon per methyl group); and δ_{MeOH} is the carbon isotopic ratio of the methanol reagent, measured via GC-IRMS relative to underivatized reference compounds.

Consistent with the reporting of the C isotope composition of the respired CO_2, $\delta^{13}C$ values of samples without litter addition are expressed relative to the V-PDB standard, whereas samples with ^{13}C-labelled litter are reported as atom % excess (APE).

Only PLFA biomarkers representing the functional groups actinobacteria, general bacteria, Gram$^+$ bacteria, and Gram$^-$ bacteria are reported here, as clear and quantifiable peaks were obtained only for these compounds.

2.5 Statistics

All statistical analyses were conducted in RStudio (version 2025.05.0+496, using R version 4.4.1, R Core Team (2025)). Respiration and isotope data were tested for normality (Shapiro-Wilk) and log-transformed. For visualization and descriptive summaries, we calculated treatment-wise means and standard deviations (SD) of respiration rates, cumulative respiration and C isotope composition. To assess the treatment effects over the incubation time, raw respiration values were analyzed using linear mixed-effects models (LMMs) with the `lmer()` function from the *lme4* package. Temperature, vegetation type (forest vs. pasture), litter addition (L^+ vs. L^-), and sampling day were included as fixed effects. Sample number was treated as a random intercept to account for the repeated measurements of the same incubation jars during the incubation. For pairwise

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post-hoc comparisons, we calculated marginal means (EMMs) using the *emmeans* package. Differences between temperature levels, vegetation types, and litter treatments were tested using a Tukey-adjusted pairwise comparison.

3 Results

3.1 Respiration

Cumulative respiration increased with increased temperatures $T_{16.5}$ and $T_{20.5}$ compared to control temperature $T_{12.5}$ (both $p < 0.001$) for both, L^- (Fig. 1a) and L^+ soil samples (Fig. 1b). Litter addition significantly increased the respiration rate ($p < 0.001$), with the strongest responses observed under elevated temperature. Slightly higher respiration rates were measured for forest samples compared to pasture samples in both, L^- and L^+ soils, especially at higher temperatures. However, the difference between the two vegetation types was not significant ($p = 0.45$). The respiration trajectories between L^- and L^+ measurements differed ($p < 0.001$). In L^+ treatments, early respiration (within the first 30 days) accounted for 83–90% of total cumulative respiration across all temperatures and vegetation types. In contrast, L- treatments showed substantially lower early respiration, with averages ranging from 58% to 74%, indicating a more gradual release of CO_2 over time.

The initial increase of the litter-induced respiration (LIR, Fig. 2(a)) with a maximum on day 8 exhibited a clear increase with increasing temperature (on day 3 and day 8, all $p < 0.0001$). Additionally, the respiration was between 4-23% higher in the pasture soil compared to the forest soil (day 8, all $p < 0.0001$). After the initial peak, LIR decreased drastically and faster with higher temperature, and faster for pasture than for forest samples (day 10: $p < 0.0001$ for temperature and land use). For the remaining incubation duration, LIR remained at a low rate, however with small increases at days 91 and 231 for all treatments. In forest $T_{12.5}$, LIR dropped by more than 67% from day 8 to day 10 ($p < 0.0001$), followed by a partial rebound of 36% by day 14. Smaller secondary peaks of >30% also occurred in forest $T_{20.5}$ (e.g., between day 91 and 112, $p < 0.05$). A deviation was observable from day 70 with the highest respiration for pasture $T_{16.5}$, which became even more pronounced on day 91 ($p < 0.04$) and remained highest until day 197. This increased respiration was also reflected in the cumulative LIR, which was highest for pasture $T_{16.5}$ (Fig. 2b), being 9.6% higher relative to $T_{12.5}$ compared to only 6.2% higher LIR at $T_{20.5}$. For the overall incubation period, higher cumulative LIR was observed for pasture samples compared to forest samples ($p < 0.0001$). Identical as for pasture soil, cumulative LIR in the forest soil was higher for samples with $T_{16.5}$ (9.3 % higher than $T_{12.5}$), followed by $T_{20.5}$ (5.2% higher than $T_{12.5}$).

3.2 δ^{13}C Respiration

The C isotope composition of the respired CO_2 of the L^- soils only showed small temporal fluctuations over the whole incubation period (Fig. 3(a)). At the beginning of the incubation, we observed a shift towards increasing δ^{13}C values in both, forest and pasture soils, followed by a shift to more negative values with minima around days 56 to 70, which were more pronounced in forest soil than in pasture soil. From there, δ^{13}C increased until day 197, followed by a decrease and values becoming more negative towards the end of the incubation experiment. In warmed samples, the shifts occurred slightly faster ($p = 0.002$) com-

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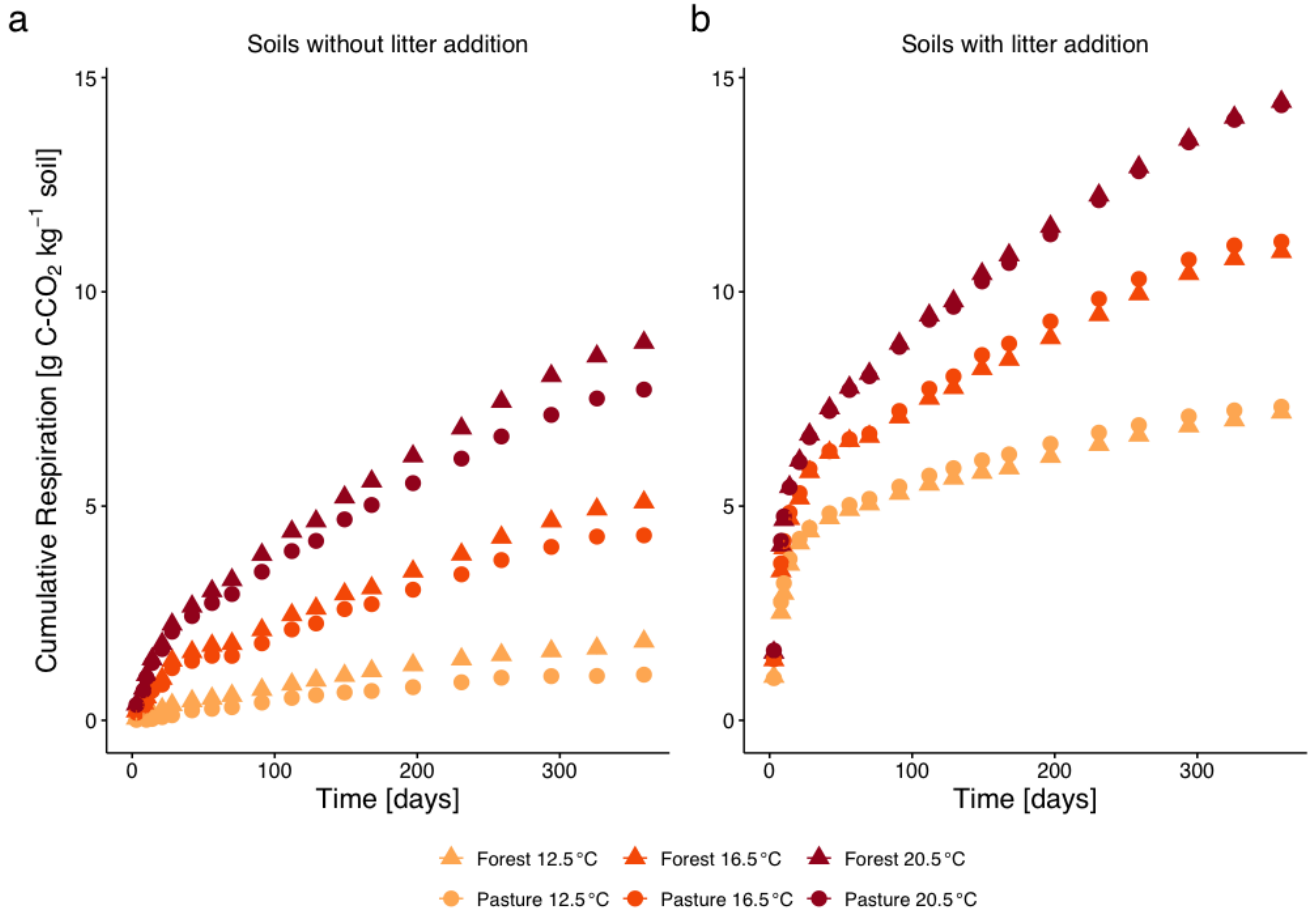

Figure 1. Cumulative CO_2-C respiration (mean ± SE, errors smaller than symbols and thus not visible) from subalpine forest and pasture soils without litter addition (a) and with ^{13}C-labelled aboveground *L. perenne* litter addition (b) over 360 days of incubation at three temperatures (12.5 °C, 16.5 °C, 20.5 °C). Different colours represent the different incubation temperatures, different symbols the two different land cover types.

pared to $T_{12.5}$ samples. δ^{13}C dynamics did not differ between forest and pasture soil.

Litter addition significantly increased ^{13}C concentration ($p < 0.0001$) in both forest and pasture soils, indicated by the high atom percent excess of ^{13}C (APE ^{13}C) at the beginning of the incubation. (Fig. 3(b)). At day 3, APE ^{13}C reached about +3.00% in forest soils and +2.85% in pasture soils, corresponding to relative increases of +275% and +261% over control samples. The ^{13}C excess decreased rapidly within the first two weeks of incubation. For the remaining incubation period, APE ^{13}C only decreased slowly, with some fluctuations throughout. Warming significantly modulated this decrease ($p = 0.02$), with a stronger decrease in the beginning and a consequential lower excess throughout the incubation period. No significant difference was detectable between forest and pasture soil.

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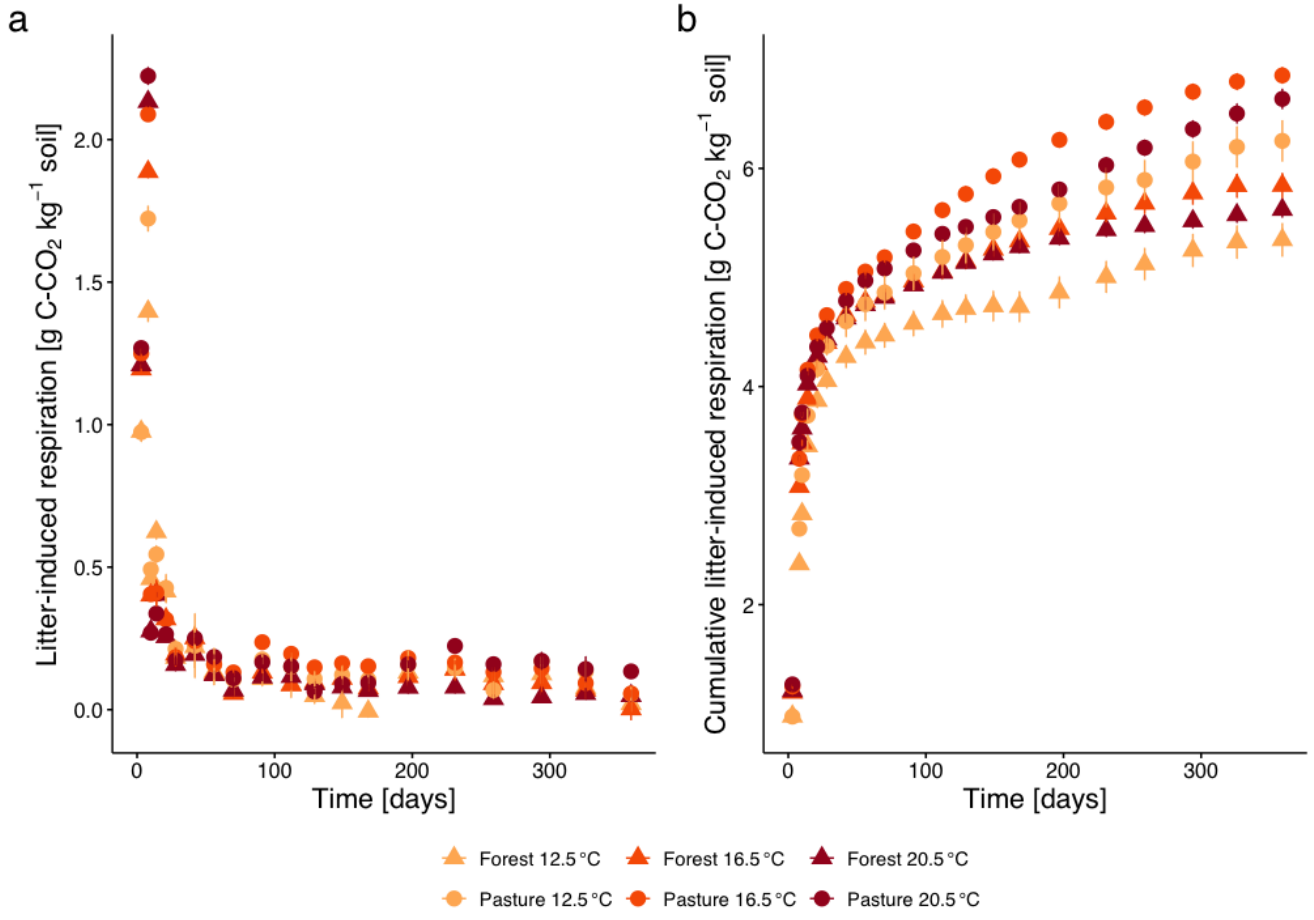

Figure 2. (a) Litter-induced respiration (LIR; mean ± SE), calculated as the difference between respiration of soils with and without *L. perenne* litter addition, for subalpine forest and pasture soils over the incubation period at three temperatures (12.5 °C, 16.5 °C, 20.5 °C). Different colours represent the different incubation temperatures, different symbols the two different land cover types. (b) Cumulative LIR (mean ± SE) over 360 days.

3.3 Priming

Priming of native soil C (Fig. 4) increased in the first week of incubation for both forest and pasture with a peak on day 8 with stronger priming with higher temperature (forest: $T_{12.5}$ 0.84 ± 0.45 g C-CO_2 kg^{-1} soil d^{-1}, $T_{16.5}$ 1.35 ± 0.71 g C-CO_2 kg^{-1} soil d^{-1} and $T_{20.5}$ 1.42 ± 0.79 g C-CO_2 kg^{-1} soil d^{-1}; pasture: $T_{12.5}$ 1.15 ± 0.52 g C-CO_2 kg^{-1} soil d^{-1}, $T_{16.5}$ 1.44 ± 0.76 g C-CO_2 kg^{-1} soil d^{-1} and $T_{20.5}$ 1.66 ± 0.79 g C-CO_2 kg^{-1} soil d^{-1}). Subsequently, priming declined rapidly to near zero by day 28 and remained low thereafter. A small, but significant overall higher priming was measured in pasture versus forest soil (p =

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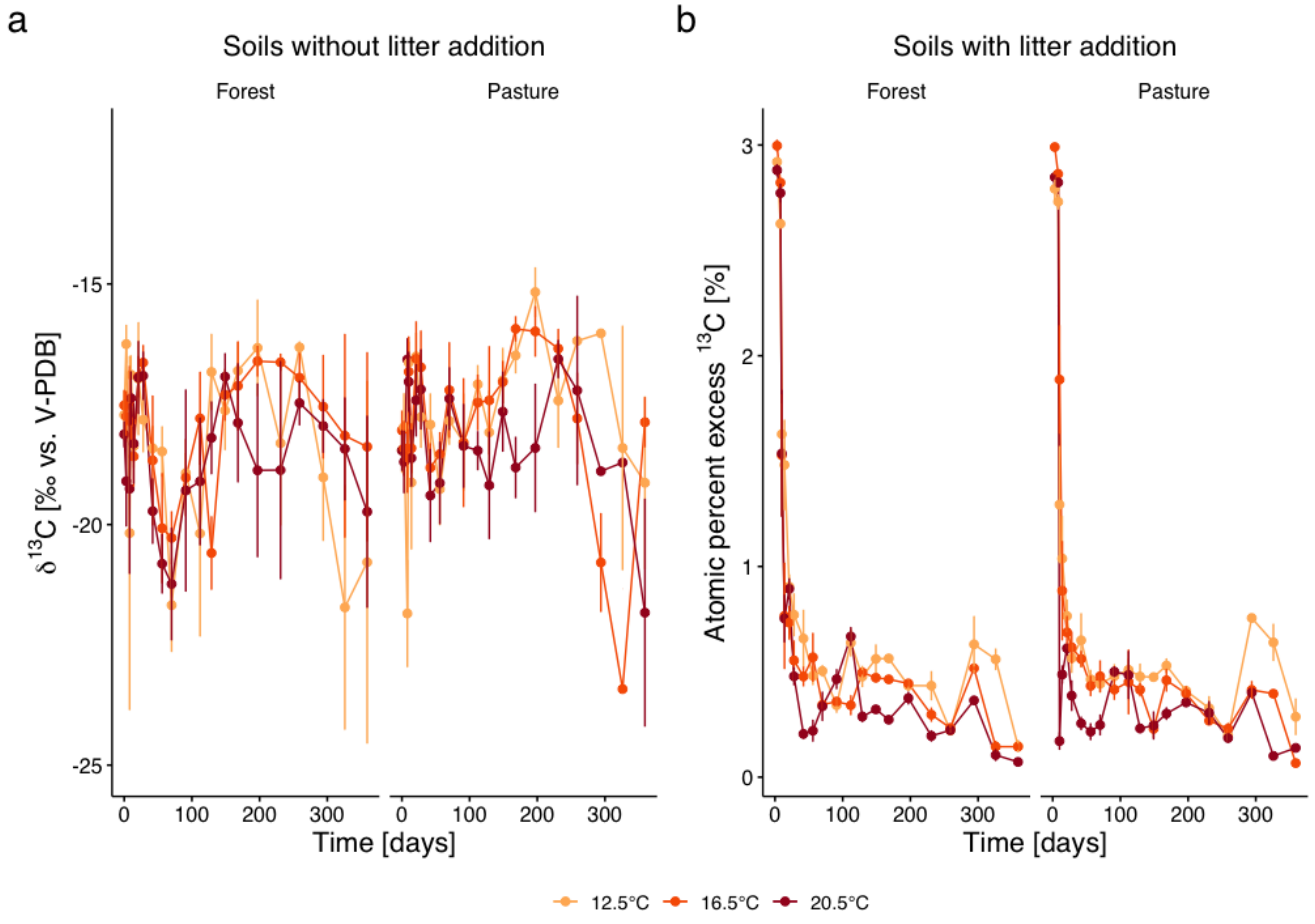

Figure 3. (a) $\delta^{13}C$ values (‰ vs. V-PDB; mean ± SD) of the respired CO_2 from subalpine forest and pasture soils without litter addition over the incubation period of 360 days under three incubation temperatures (12.5 °C, 16.5 °C, 20.5 °C). Different colours represent the different incubation temperatures, different symbols the two different land cover types. (b) Atom % excess (APE; mean ± SE) ^{13}C of respired CO_2 from soils with *L. perenne* litter addition over 360 days.

0.048). No significant overall differences in priming were detectable between different temperature treatments, but the warmed treatments exhibited a faster drop of high priming rates compared to $T_{12.5}$ between days 10 – 21 ($p < 0.01$).

3.4 Phospholipid fatty acids composition and compound-specific isotopes

In the beginning of the incubation experiment, phospholipid fatty acid (PLFA) concentrations in soils without litter addition (L^-) ranged between approximately 300 and 550 $\mu g\ g^{-1}$ dry soil. Across all treatments, total PLFA concentrations declined over time. PLFA concentrations in L^- samples (Fig. 5a, b) at $T_{20.5}$ were lower than those at $T_{12.5}$ and $T_{16.5}$, especially at later stages

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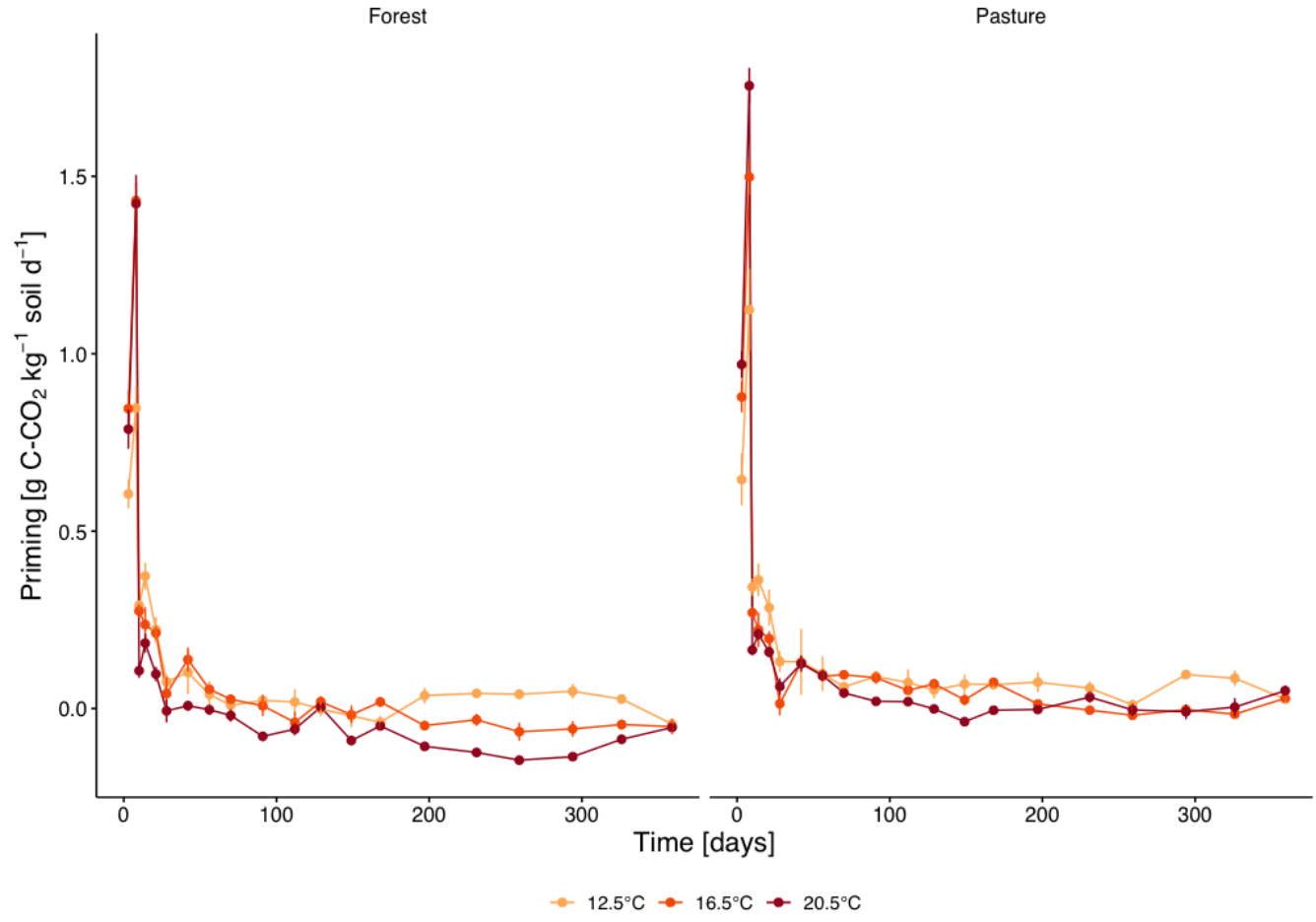

Figure 4. Priming of native soil organic carbon (mean ± SE) in subalpine forest and pasture soils at three incubation temperatures (12.5 °C, 16.5 °C, 20.5 °C) over 360 days. Different colours represent the different incubation temperatures.

of the experiment.

In forest L^- soil (Fig. 5a), $Gram^+$ and $Gram^-$ bacteria consistently accounted for up to 60% of total PLFA at all timepoints. Cyclopropyl and general bacteria proportions stayed relatively constant during the incubation, although with small increases of cyclopropyl bacteria at $T_{20.5}$ during the middle of the incubation period at days 56 and 168. Fungal PLFA concentrations remained low throughout the incubation, with values rarely exceeding 25 $\mu g\ g^{-1}$ and a slight increase at the beginning of the incubation (day 14 to 28).

In pasture L^- soil (Fig. 5b), the microbial composition was also dominated by $Gram^+$ and $Gram^-$ bacteria, which declined steadily over time, with a stronger decrease for $T_{20.5}$ compared to the lower temperature treatments. The same trend was visible for the general bacteria group. The abundance of fungi was low (around 10–20 $\mu g\ g^{-1}$ on average), while actinobacteria were

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slightly higher (15–30 μg g^{-1}), but both groups remained relatively constant throughout the incubation period with only small fluctuations.

Litter addition (L^+) led to a strong increase in PLFA abundance at the beginning of the incubation period, exceeding 700 μg g^{-1} dry soil. Throughout the incubation period, these high values decreased to levels approaching or below those of L^- samples. Interestingly, highest total PLFA concentrations were most often found at $T_{16.5}$ across all timepoints.

Forest L^+ (Fig. 5c) had highest PLFA general bacteria group concentrations during early incubation, especially at $T_{12.5}$ and $T_{16.5}$. General bacteria, $Gram^+$, and $Gram^-$ bacteria concentrations declined strongly over time, with a stronger decrease under elevated temperature. Fungal PLFAs showed an increase in the beginning of the incubation experiment, with a rapid decrease after the first 28 days and they were almost absent by the end of the incubation experiment. Similar as to L^- soils, cyclopropyl bacteria exhibited an increase at days 56 and 168 under elevated temperatures.

Pasture L^+ (Fig. 5d) showed a similar pattern to the forest soil, with general bacteria as dominating microbial group and a fast decline of PLFA concentrations in the first 28 days, especially under elevated temperature. At intermediate timepoints (days 56 and 168) in the warmed treatments ($T_{16.5}$ and $T_{20.5}$), cyclopropyl bacteria increased stronger than in L^- soils, where this mid-incubation increase was less pronounced. In comparison to pasture L^-, $Gram^+$ and $Gram^-$ bacteria were less dominant and exhibited a stronger decrease with warming. Fungal PLFAs showed a short-lived increase between days 14 and 28, especially at $T_{12.5}$ and $T_{16.5}$, but declined quickly thereafter. Actinobacteria remained a minor group (typically 10–25 μg g^{-1}), but exhibited slight increases at days 56 and 168, especially under cooler temperatures ($T_{12.5}$ and $T_{16.5}$).

In L^- soils (Fig. 6a), weighted average $\delta^{13}C$ values of all microbial functional groups based on PLFA remained near natural abundance throughout the whole incubation period. The $\delta^{13}C$ values of the individual groups varied between -32 ‰ to -26 ‰, with general and $Gram^+$ bacteria showing values closer to -28 to -30 ‰, and $Gram^-$ bacteria occasionally reaching -26 ‰. The temporal variation was only minor but still visible for some groups, with fluctuations of up to ±2.5 ‰ observed at days 28, 56, and 168. The differences between the individual functional groups were small, with pasture soils being slightly more depleted in ^{13}C than forest soils, with a shift of ca. 1–22 ‰.

In L^+ soils (Fig. 6b), the PLFA biomarkers showed a clear incorporation of the ^{13}C labelled litter C. This was evident from strongly elevated $\delta^{13}C$ values (e.g., up to -10 ‰ in general bacteria at day 14) compared to natural abundance, which remained below -25 ‰. ^{13}C excess peaked at day 14. Only the general bacteria group exhibited the highest values at the beginning of the incubation period. Following the initial peak, the ^{13}C label decreased in all groups rapidly, but remained above natural abundance during the whole incubation period. For the other microbial functional groups ($Gram^+$ and $Gram^-$ bacteria, actinobacteria), ^{13}C incorporation was highest at day 14 or 28, but the peak was less pronounced than for general bacteria. Across all time points, a temperature effect was visible, with the highest ^{13}C excess values generally found at $T_{12.5}$, while values at $T_{16.5}$ and $T_{20.5}$ were more similar and clearly lower.

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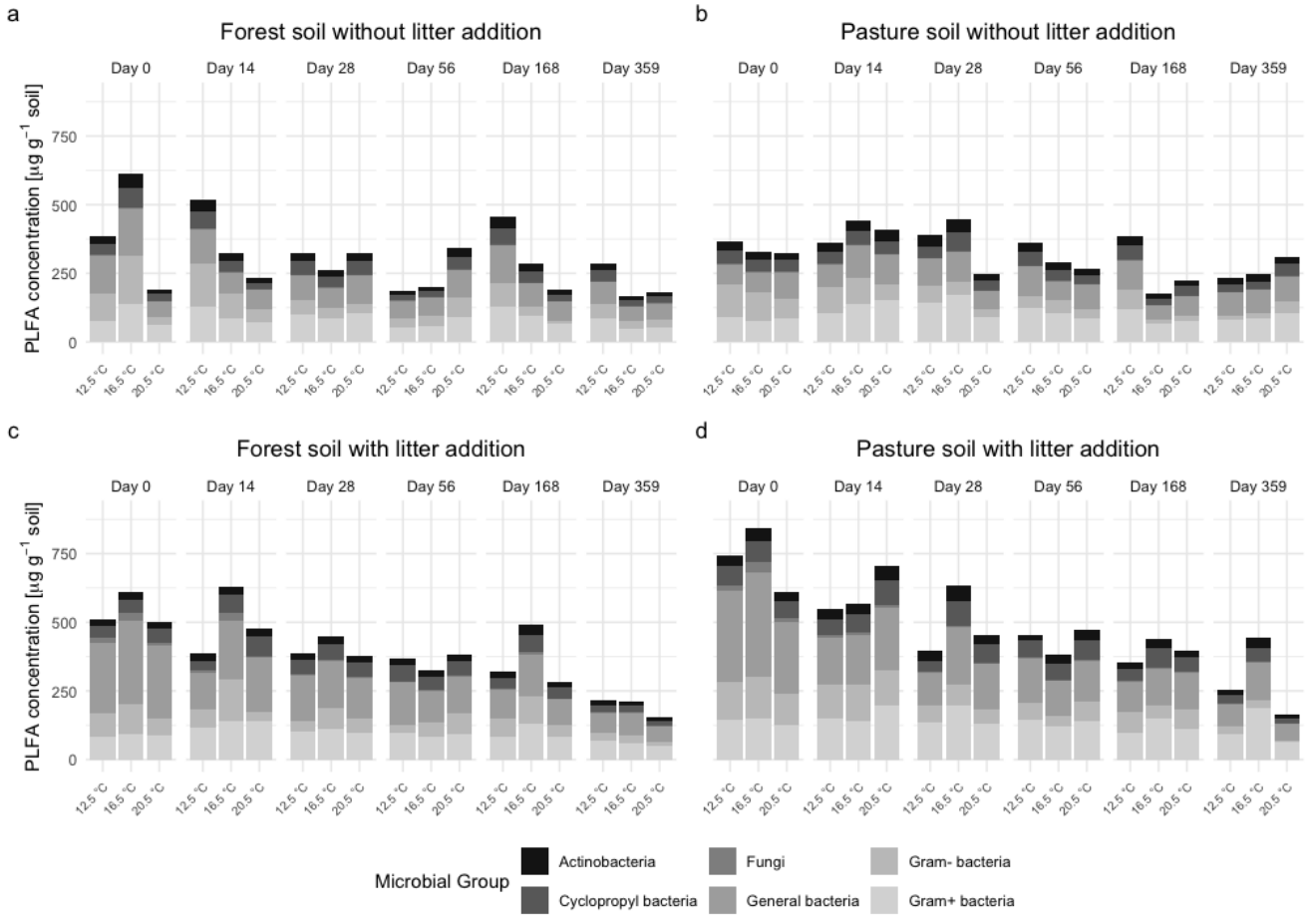

Figure 5. Total phospholipid fatty acid (PLFA) concentrations for functional microbial groups (general bacteria, Gram$^+$ bacteria, Gram$^-$ bacteria, fungi, actinobacteria, cyclopropyl bacteria) in (a) subalpine forest soil without litter addition, (b) subalpine pasture soil without litter addition, (c) subalpine forest soil with *L. perenne* litter addition, and (d) subalpine pasture soil with *L. perenne* litter addition. Soils were incubated for 360 days at three temperatures (12.5 °C, 16.5 °C, 20.5 °C).

4 Discussion

4.1 Elevated temperature stimulates subalpine soil organic matter decomposition

Our one-year incubation experiment demonstrated that higher temperature accelerated the decomposition of organic matter in the subalpine soils investigated here, which is in line with other studies identifying temperature as an important regulator of C turnover in soils (Davidson and Janssens, 2006; Nottingham et al., 2019). Total cumulative CO_2 emissions were significantly higher at higher temperatures compared to the current growing season temperature of 12.5 °C, indicating a stronger microbial

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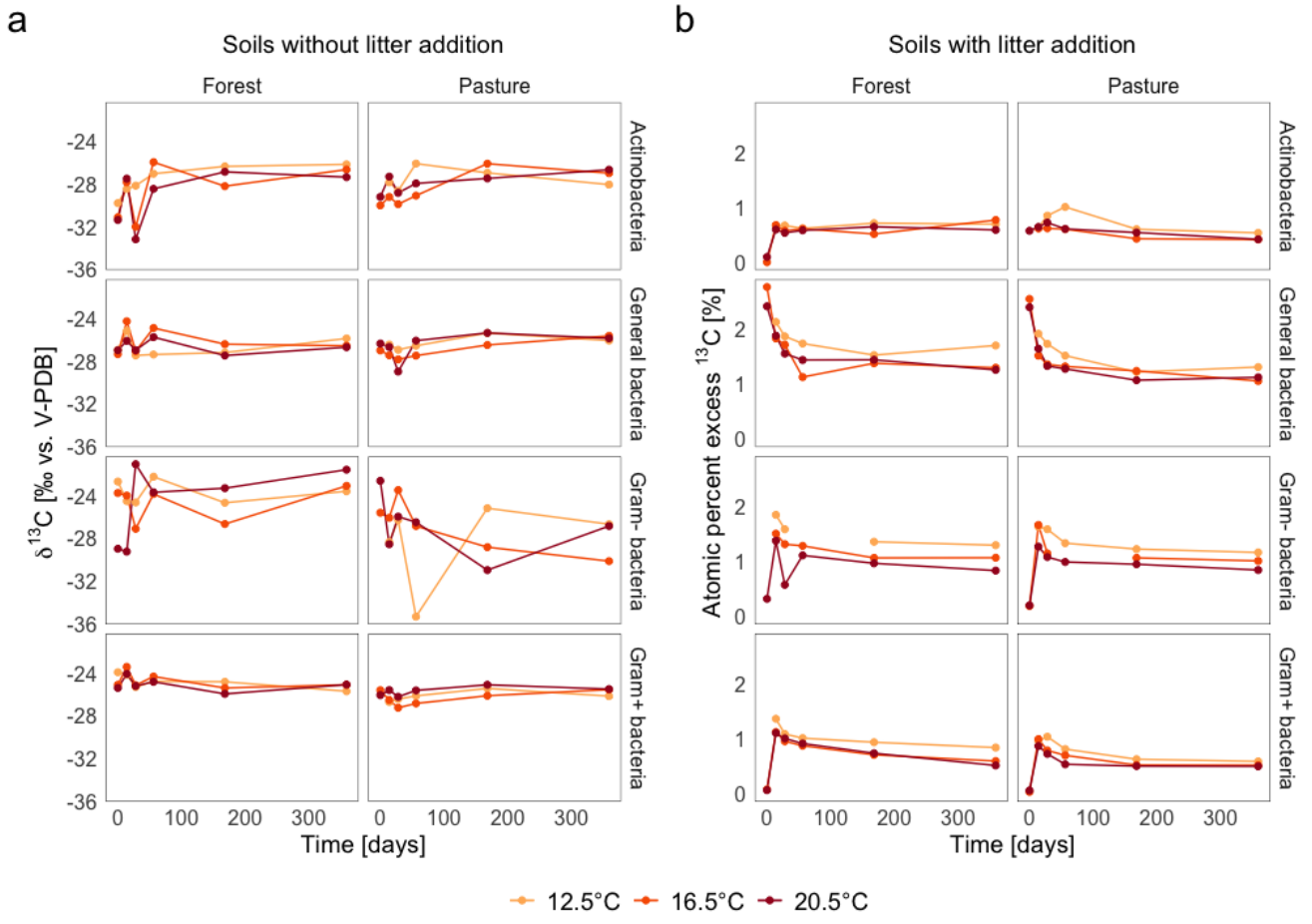

Figure 6. Weighted mean $\delta^{13}C$ values (‰ V-PDB for soils without litter addition; atom % excess for soils with litter addition) of PLFA biomarkers representing functional microbial groups in (a) soils without litter addition and (b) soils with litter addition over 360 days at three incubation temperatures.

breakdown of both, native SOM and the added litter under increased temperature. These findings confirm our hypothesis and align with the positive relationship between temperature and SOM mineralization rates (Crowther et al., 2016; Chen et al., 2024). Higher temperatures increase microbial metabolic rates (Xu et al., 2023) and enzyme activities (Chen et al., 2018), which leads to increased decomposition of SOM and thus an increased release of CO_2 from the soils. This observed
320 increase argues for a positive soil carbon-feedback, especially in these high-altitude soils that are rich in SOC. Already the lower temperature increase of +4 °C increased total CO_2 efflux up to 50% compared to control temperature, a finding that is consistent to those of several field studies (Hanson et al., 2020; Soong et al., 2021; Chen et al., 2024), where a temperature increase led to an increased heterotrophic respiration of 26-37% compared to our 50-100% increase under optimal conditions

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for higher temperature. This temperature driven increase of CO_2 flux emphasizes the vulnerability of alpine and subalpine soil SOC stocks to even modest warming expected with climate change (Crowther et al., 2016; Wang et al., 2022).

The warming effects were more pronounced in the L+ soils for both, forest and pasture. While Bastida et al. (2019) revealed in a global data analysis that fresh labile C inputs can stimulate microbial activity and modulate the priming responses, our results extend this pattern to subalpine soils. This aligns with experiments in alpine regions showing that warming elevates microbial activity and substrate use and that greater fresh inputs intensify warming-induced soil C losses in alpine ecosystems (Streit et al., 2014; Walker et al., 2022; Ye et al., 2022). This was also visible in the incubated soils for total SOM and the less decomposable lignin monomers, where decomposition was only higher with higher temperatures in the presence of litter (Püntener et al., 2025). One reason for this might be positive priming (Kuzyakov, 2010). Addition of labile C in the form of the litter accelerated the decomposition of native SOM. The metabolic cost of warming is therefore offset by this improved and increased energy supply (Wild et al., 2016). This higher decomposition of native SOM, which consists of older, less easily decomposable organic compounds, aligns with studies reporting that these pools can be particularly responsive to increased temperatures (Craine et al., 2010; Frey et al., 2013), especially with a high abundance of labile carbon (Püntener et al., 2025).

4.2 Contrasting decomposition dynamics between pasture and forest soils

During the first week of incubation, litter-induced respiration (LIR) showed marked differences in peak timing and magnitude between the soils. The pasture soil responded more rapidly to the litter input than the forest soil. Litter-induced respiration peaked during the first week of the incubation for both soils, but were significantly higher in pasture soils. The decrease after the first peak was faster in pasture than forest soils, which was also identical to the $\delta^{13}C$ decrease, reflecting a rapid mineralization of the added plant litter. In L^- soils, the $\delta^{13}C$ signal of respired CO_2 followed a similar overall pattern in both soils, with values becoming less negative at the start of the incubation and later shifting back toward more negative values. The initial shift occurred only slightly earlier in the pasture (around day 3–10) than in the forest soil (around day 10), however the shift back to more negative values happened earlier in pasture soil after around 20 days, whereas in the forest, the minimum of that shift was only reached after around 80 days. Consistently, PLFA-derived microbial biomass peaked earlier and stronger in the pasture soils, whereas forest biomass peaked later and less strongly. These differences in the early stage of the incubation period are likely due to differences in microbial community composition. The pasture site supposedly experienced greater daily temperature shifts and a higher concentration of readily available C input from grass litter and root exudates (Peplau et al., 2023). These systems often harbor greater proportions of fast-growing, copiotrophic microorganisms than, e.g., forest soils (Solly et al., 2014; Liu et al., 2023). In our data, this is supported by the larger concentration of $Gram^-$ in pasture soils, which are known to mainly process more labile C sources (Creamer et al., 2016; Zheng et al., 2021). In the pasture soil, the $\delta^{13}C$ value of the respired CO_2 also exhibited fluctuations earlier in the incubation period, indicating a rapid shift in substrate use from one C source to another, a pattern consistent with studies showing that grassland microbial communities can rapidly adjust their metabolism to changes in available substrates (Creamer et al., 2016; Liu et al., 2023; Wang et al., 2023). This faster response has also been observed in alpine grasslands where microbial communities are dominated by fast-growing taxa (Budge et al., 2011; Donhauser et al., 2020). The forest site, in contrast to the pasture soil, is characterised by a microbial community

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that is more adapted to the litter input from spruce containing more polyphenols and lignin, which are harder to decompose than grass litter in the pasture soil (Solly et al., 2014; Ortiz et al., 2016). For our soils, this difference in the microbial community is documented by the larger concentration of $Gram^+$ bacteria and fungi in the forest soil compared to the pasture soil. Certain members of these functional microbial groups (e.g. firmicutes) are known to process preferentially less decomposable organic compounds (Kramer and Gleixner, 2008; Zhang et al., 2016; Lu et al., 2017). In the forest soil, the $\delta^{13}C$ trends shifted more slowly, which may reflect a more buffered system with microbial communities adapted to the continuous but lower-quality litter inputs from spruce needles (e.g., high in lignin) (Kramer and Gleixner, 2008; Hiltbrunner et al., 2013; Lu et al., 2017). Such microbial communities may require more time to switch to alternative carbon sources, leading to a delayed response of the isotopic signal, as reported for forest soils with more complex SOM pools and microbial communities specialized in decomposing this type of OM (Schindlbacher et al., 2011; Ortiz et al., 2016; Gunina et al., 2017b). In our experiment, the presence of *Lolium perenne* litter in both soils acted as a high quality substrate and leveled out possible substrate differences. Nevertheless, the pasture soil might have had a slight advantage, being adapted to grass litter inputs and therefore rapidly decomposing the added ryegrass, whereas the forest microbial community was initially less efficient in decomposing the less familiar substrate.

The temporal pattern of native SOM decomposition can also further support the theory of the two different systems. The initial stimulation of native C mineralization was stronger in pasture than in forest soils but declined more rapidly. Such pronounced, short-lived responses are characteristic for a system that is dominated by a copiotrophic microbial community (Bastida et al., 2019; Wang et al., 2023).

Together, the findings of our experiment characterise the pasture soil as a dynamic, fast cycling system, in contrast to a more static, slow cycling system in the forest soil. This has important implications for C cycling in alpine and subalpine soils under the influence of climate change. Rising temperatures might lead to a faster loss of C from dynamic systems like pasture, while slower cycling systems like our forest soil might temporarily mitigate C losses (Verbrigghe et al., 2022; Peplau et al., 2023; Chen et al., 2024). However, this does not guarantee long-term stability of SOC in a warmer future, as we have seen in our L^- cumulative respiration rate, which was higher for the forest than for the pasture soil, indicating an additional strong decomposition in the absence of fresh litter. Additionally, a slow adaptation to higher temperature, as happens with climate change, will lead to shifts in microbial communities, reducing the soils' resistance to loss of SOC (Nottingham et al., 2019; Yuan et al., 2021).

4.3 Diverging temperature optima of total and litter-induced respiration

In contrast to the subsequent rise of total soil respiration with temperature, LIR peaked at the intermediate temperature of 16.5 °C. This apparent contradiction highlights distinct temperature sensitivities of microbial communities when decomposing native SOM versus the added litter. The LIR optimum was consistent across both soils from different vegetation covers and coincided with the highest PLFA concentrations, suggesting that the microorganisms that decompose the litter operate near their physiological optimum at this temperature (Kravchenko et al., 2019).

At highest temperature $T_{20.5}$, the lower microbial biomass, a faster loss of the ^{13}C label, and an increase in cyclopropyl PLFA

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point to thermal or nutrient stress (Willers et al., 2015; Zhu et al., 2023), rapid decomposition of more labile litter compounds, and likely a reduced CUE (Schindlbacher et al., 2011). At higher temperatures, microorganisms invest a greater proportion of the assimilated C into respiration rather than growth (Frey et al., 2013; Pold et al., 2020; Dang et al., 2024), leading to a faster decomposition of the litter and a lower accumulation of microbial biomass. This shift in C partitioning towards higher temperature likely shortened the duration of high litter decomposition rates at $T_{20.5}$.

Litter use dynamics and microbial physiology explain the divergence in thermal optima. Litter-derived OM consist to a large part of simple, more labile compounds that can be rapidly decomposed by fast-growing microbial taxa, especially $Gram^-$ bacteria (Creamer et al., 2016; Zheng et al., 2021). These microorganisms may have a narrower thermal tolerance range and a lower heat resistance than microbial groups involved in the decomposition of SOM, such as certain $Gram^+$ bacteria or fungi (Cui et al., 2022; Zhu et al., 2023). With the highest temperature $T_{20.5}$ likely exceeding their thermal optimum, the litter decomposing microorganisms may lose competitive advantage, resulting in a reduced LIR even though total soil respiration remains high due to SOM decomposition by more thermotolerant taxa.

Another influence is the thermal adaptation of microbial communities. Laboratory warming experiments have shown that microbial growth temperature optimum can increase after prolonged exposure to high temperatures, however these shifts are often accompanied by community changes towards more heat-adapted taxa (Donhauser et al., 2020). In our controlled incubation, the absence of such long-term adaptation processes may explain why LIR peaked below the highest temperature tested. In natural field settings, such adaptation could be slower or incomplete, particularly in alpine and subalpine soils with historically low temperatures.

These results imply that standard incubation temperatures of 20–25 °C may exceed the natural optima for litter decomposition in these subalpine soils, especially for those parts of the microbial community that are adapted to cooler conditions. Applying local temperature ranges in laboratory incubations would better reflect the *in-situ* microbial performance and capture realistic temperature responses. The observed difference between LIR and total respiration also underscores that litter-derived and SOM-derived CO_2 fluxes cannot be assumed to respond identically to warming; fresh inputs may have narrower, lower-temperature optima shaped by substrate traits and decomposer ecology (Moinet et al., 2018). Such differences in thermal optima among carbon pools should be considered when projecting soil carbon–climate feedbacks, as warming may shift the relative contribution of litter versus SOM to total CO_2 respiration.

4.4 Broader implications

Our findings provide new insights into the response of subalpine soils to climate warming and vegetation shifts and the resulting consequences for SOC stability and ecosystem functioning across alpine landscapes (Donhauser et al., 2020). The observed increase of total soil respiration under elevated temperature, combined with a substrate-specific decomposition response and land cover-dependent dynamics of the microbial community, suggest that subalpine and alpine soils are vulnerable to enhanced C losses under future climatic conditions .

The different temperature sensitivities between native SOM and litter decomposition in our incubation experiment are particularly relevant, as they imply that warming may alter the relative contribution of different C pools to microbial soil respiration.

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Particularly, a potential long-term depletion of native SOC stocks could be the result of a continued SOM mineralization at high temperatures (Davidson and Janssens, 2006; Nyberg and Hovenden, 2020). Previous studies have shown that warming can reduce microbial C retention (Frey et al., 2013; Domeignoz-Horta et al., 2020), thereby increasing the proportion of assimilated carbon lost as CO_2 rather than incorporated into the microbial biomass. These observed trends suggest that warming could shift alpine and subalpine soils toward increased C vulnerability, especially during seasons or in ecosystems where the availability of litter input is limited.

Changes in the vegetation composition such as treeline upward movement and shrub encroachment or afforestation, which are widespread in alpine regions, can lead to further changes in SOC dynamics (Dengzeng et al., 2022; Laorden-Camacho et al., 2025). The results of our incubation experiment highlight that forest and pasture soils have different decomposition dynamics, even under identical experimental conditions. Similar differences have been found in other alpine ecosystems, where shrub encroachment changed the microbial community composition and SOC dynamics (Dengzeng et al., 2022; Laorden-Camacho et al., 2025). This supports that changes in litter quality and microbial communities induced by changing vegetation can influence the turnover of SOM under warming.

Furthermore, our findings reveal that warming increased respiration in L^- soils, indicating enhanced microbial mineralization of native SOC in the absence of fresh litter inputs (Nyberg and Hovenden, 2020). This higher CO_2 efflux suggests that warming can accelerate the breakdown of SOM that would otherwise remain more stable under cooler conditions, potentially by increasing microbial activity and enzymatic degradation rates, and by reducing physical or chemical protection of organic matter (Ofiti et al., 2022; Zosso et al., 2023).

Combining all these dynamics, we can conclude that the subalpine pasture systems may respond to warming with large, transient CO_2 fluxes, whereas the forested soils may experience a slower, but more sustained SOM loss. These responses are not only shaped by temperature, but also by the composition of soil microbial communities induced by vegetation shifts and the availability and quality of litter input.

Afforestation, cessation of grazing of alpine pastures followed by shrub encroachment or shrub clearing can have a strong influence on soil C dynamics as our findings emphasized. These interventions must therefore be evaluated not only for their aboveground effects but also and likely even more for their influence on SOC dynamics. Warming-induced increases in SOM mineralization might negate any anticipated increase of SOC concentration due to changes in land-use and vegetation cover, specifically in such alpine soils that are comparatively enriched in SOC (Speckert et al., 2023).

5 Conclusions

Under future warming, alpine and subalpine soils are at risk of becoming significant sources of atmospheric carbon. Our findings of a one-year laboratory incubation experiment demonstrate that not only temperature but also vegetation type and microbial functioning critically shape soil carbon dynamics. The strong stimulation of CO_2 release with warming highlights the sensitivity of native SOM to even moderate temperature increases. Distinct decomposition patterns in pasture and forest soils show that microbial communities and their vegetation history influence how quickly and persistently soil carbon is lost.

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Importantly, the non-linear response of litter-induced respiration, with a peak at intermediate temperatures, suggests that microbial efficiency declines beyond certain thresholds, thus limiting their capacity to retain carbon under long-term warming. These mechanisms together point to a destabilization of alpine soil organic carbon stocks under projected climate scenarios. To anticipate long-term consequences, it will be essential to integrate microbial thermal responses and vegetation shifts into ecosystem models and monitoring efforts.

Author contributions. DP: conceptualization, data curation, formal analysis, investigation, visualization, supervision, writing – original draft, writing – review & editing. PZ: investigation, data curation, formal analysis. TCS: conceptualization, investigation, data curation, supervision. CLT: conceptualization, investigation, data curation, writing – review and editing. GLBW: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – review & editing.

Competing interests. The authors declare that they have no conflict of interest.

Acknowledgements. We thank Barbara Siegfried, Sonja Eisenring, and Nadja Hertel for their support during the laboratory work. This research was funded by the Swiss National Science Foundation (SNSF) under grant no. 188684, as part of the IQ-SASS project (Improved Quantitative Source Assessment of Organic Matter in Soils and Sediments using Molecular Markers and Inverse Modelling).

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