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Availability of labile carbon controls the temperature-dependent response of soil organic matter decomposition in alpine soils

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Abstract. Soil organic matter (SOM) decomposition in alpine environments is influenced by multiple factors including temperature and substrate quality. As climate change will have an impact on both factors, it is essential to improve our knowledge, how, e.g., warming will modify carbon cycling in these environments to better prepare soil management for future conditions, even in alpine regions. This study investigates how warming and organic inputs affect SOM decomposition in alpine forest and pasture soils through a one-year laboratory incubation experiment. Soils were exposed to three temperatures (12.5°C, 16.5°C and 20.5°C), with and without the addition of fresh grass litter. While higher temperatures accelerated decomposition, the availability of fresh organic matter played a more decisive role, especially in the lignin-rich forest soil. Without fresh litter, SOM decomposition was limited, suggesting that substrate availability in combination with temperature increase plays a greater role in microbial activity than temperature alone. The forest soil exhibited greater carbon loss than the pasture soil, most likely due to microbial communities that are adapted to lignin decomposition. These results suggest that rising temperatures combined with changes in vegetation and organic inputs could enhance SOM decomposition and potentially transform the alpine soils from carbon sinks to sources.

1 Introduction

Soils represent one of the largest terrestrial reservoir of organic carbon (C) containing an estimated 2000 to 2700 Pg C (Batjes, 2016; Jackson et al., 2017). Soil systems are pivotal components of the global carbon cycle, acting both as significant sources and sinks of carbon dioxide (CO_2) by storing large amounts of organic carbon or releasing it through decomposition processes (Schmidt et al., 2011). The decomposition of soil organic matter (SOM) is an important factor that controls carbon fluxes to the atmosphere, directly impacting atmospheric CO_2 levels and influencing climate change (Conant et al., 2011; Crowther et al., 2016). This balance between carbon storage and release is particularly sensitive to temperature, with recent studies showing that rising temperatures can shift soils from being net carbon sinks to significant carbon sources (Crowther et al., 2016). Rising temperatures are expected to accelerate microbial activity, leading to faster SOM decomposition and increased carbon release from soils (Davidson and Janssens, 2006). This process not only reduces the capacity of soils to act as carbon sinks but also amplifies climate change by creating a positive feedback loop (Davidson and Janssens, 2006; Conant et al., 2011). Long-term warming experiments indicate that the decomposition of labile carbon pools occurs rapidly under elevated temperatures, and sustained warming can destabilize more complex and stable carbon pools, which were previously thought to be more resistant

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to microbial breakdown (Melillo et al., 2017; Hicks Pries et al., 2017; Ofiti et al., 2023; Zosso et al., 2023). This suggests that soil carbon stocks are highly vulnerable to warming, with significant implications for global carbon budgets.

Particularly alpine regions, which store substantial stocks of soil organic carbon (SOC), are discussed to be vulnerable to warming. These high-altitude ecosystems are characterized by unique conditions, including low temperatures, short growing seasons, and slow SOM decomposition rates, which historically have promoted the accumulation of organic carbon in soils (Zierl and Bugmann, 2007; Hiltbrunner et al., 2013). These regions are characterized by a suite of vegetation types ranging from lower-elevation forests to shrublands, grasslands, and pastures (Grabherr et al., 2010). In comparison to other ecosystems, alpine soils are more sensitive to climatic changes (Hock et al., 2019) due to their reliance on seasonal snow cover, limited vegetation inputs, and the predominance of organic matter with chemical structures that require specific microbial or enzymatic pathways for decomposition (Marschner et al., 2008; Djukic et al., 2010; Schmidt et al., 2011), e.g. the complex polymer lignin (Bahri et al., 2008). These characteristics not only make alpine soils significant carbon reservoirs, but also increase their vulnerability to warming-induced carbon losses.

Climate change is occurring more rapidly in alpine regions than in many other parts of the world, leading to significant environmental transformations (Beniston, 2003; Rogora et al., 2018). Rising temperatures (Hock et al., 2019), declining snow cover (Klein et al., 2016), extended growing periods (Rogora et al., 2018), and upward shifts in the tree line (Gehrig-Fasel et al., 2007) are altering vegetation composition and ecosystem dynamics (Hagedorn et al., 2019). Forest encroachment into alpine grasslands drives changes in SOM inputs and soil properties, affecting both the build-up and decomposition of organic matter (Hagedorn et al., 2019). As warming extends the short growing season during which microbial activity occurs, the decomposition of SOM accelerates, leading to greater CO_2 emissions from alpine soils (Hiltbrunner et al., 2013). Labile SOM fractions decompose rapidly under warmer conditions, while the decomposition of more chemically complex SOM components, such as lignin, may depend on shifts in microbial community composition and the availability of labile carbon substrates to fuel enzymatic activity (Fissore et al., 2013; Walker et al., 2018).

In this study, we investigate how increased temperatures influence the breakdown of fresh litter inputs and native SOM in alpine forest and pasture soils. Using a one-year laboratory incubation experiment under controlled conditions, we simulate projected climate warming scenarios to assess temperature-driven changes in SOM dynamics for soils derived from alpine grassland and coniferous forest sites. By examining the interplay between soils that developed under different vegetation types and temperature, this research aims to provide critical insights into the vulnerability of alpine soils to warming and their broader implications for global carbon cycling and climate change mitigation strategies. The primary research questions and hypotheses are thus as follows:

1. How does decomposition differ in alpine soils developed under pasture and coniferous forest vegetation when exposed to increasing temperature?
2. What is the influence of litter input on SOM decomposition in forest and pasture soils under varying temperature?
3. How do interactions between litter input and temperature affect the stability and decomposition of organic carbon in alpine soils developed under pasture and coniferous forests?

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We hypothesise an increased decomposition of SOM with increasing temperatures for both alpine forest and pasture soils, (Nottingham et al., 2020; Soong et al., 2021) with a potentially more pronounced stimulation in the soil developed under alpine pasture due to the potentially higher microbial activity and higher availability of more easily decomposable SOM compared to the soil developed under forest (Dirnböck et al., 2003; Hiltbrunner et al., 2013; Canedoli et al., 2020). In contrast, the coniferous forest soil, characterized by a fungal-dominated decomposition and the presence of harder decomposable SOM such as lignin, will show a slower but steady increase in SOM decomposition with warming (Ortiz et al., 2016), leading to gradual but persistent carbon release over time.

Litter input in the form of grass will enhance the decomposition of SOM (priming effect) by providing fresh, easily decomposable SOC stimulating microbial activity (Kuzyakov et al., 2000), especially in these alpine soils (Guo et al., 2022). In the forest soil, this might promote enhanced decomposition of also older, harder decomposable SOM such as lignin (Ibanez et al., 2021). In contrast, the alpine pasture soil might show a weaker increase of decomposition due to reduced C-limitation (Li et al., 2018).

Finally, we hypothesise that the interaction between litter input and temperature will lead to an overall decline in SOC stability in these alpine soils, as increasing temperatures enhances the mineralisation of SOM (Prietzel et al., 2016). We expect that this effect is more pronounced in the forest soil we examine, as the combination of warming and litter input could destabilize older carbon pools with harder decomposable SOM such as lignin and thus lead to a sustained C loss over time (Tian et al., 2016; Blanco et al., 2023).

2 Materials and methods

2.1 Study site and sample preparation

Soil material was collected on a south-facing slope above the village of Jaun, Canton of Fribourg, Switzerland [7°15'54 E; 46°37'17 N] from a pasture and an adjacent forest site. The two sites are located at altitudes between 1500 and 1550 m a.s.l. Mean air temperature reaches from 0.6 °C in winter to 12.5 °C in summer with mean annual precipitation of 1250 mm with maximal precipitation in summer (Hiltbrunner et al., 2013). According to the World Reference for Soil Resources (WRB) (IUSS Working Group WRB, 2015), soils were classified as Leptic Eutric Cambisol Clayic on a calcareous bedrock with clay-dominated texture for both the pasture site (60 % clay, 30 % silt, 8 % sand) as well as the forest site (50 % clay, 35 % silt, 12 % sand (Speckert et al., 2023)). The soils are acidic with a pH only slightly differing between the two sites with pH 5.08 for the pasture and pH 4.83 for the forest soil. The pasture site has been grazed by cattle during the summer months (May-September) (Hiltbrunner et al., 2013). The plant community consists mainly of herbaceous species with dominant occurrences of ribgrass (*Plantago lanceolata* L.) and reed fescue (*Festuca arundinacea* Schreb.). The forest site is dominated by Norway spruce (*Picea abies* L.) with tree ages of at least 130 years (Speckert et al., 2023). Mineral soil samples were collected July 2020 on an area of ca. 1 m^2 at a depth of 5-10 cm after removal of organic layers (forests) and surface mineral soil with high root frequencies. Overall, one composite sample (ca. 30 kg) of soil was collected for each of both sites. All replicate 50 g incubation subsamples

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derive from these two composites. Soils were sieved for <2mm and visible root remains were removed by tweezers. Thereafter, soils were homogenized by manual mixing with a hand shovel.

2.2 Incubation setup

To investigate differences in organic matter decomposition between soils that developed under different vegetation cover, forest and pasture soil samples were incubated in closed jars in temperature-controlled incubators (Panasonic MIR-554-PE). The influence of elevated temperature on the decomposition of organic material was targeted and therefore, soils were incubated under three different temperatures. The lowest temperature of 12.5 °C ($T_{12.5}$), acting as the control temperature, corresponds to the 2015 – 2020 average air temperature of the growing season between May and September of the sampling site (weather station Jaun-Forchen by WSL-SLF (2021)). This temperature was chosen as low temperature in this experiment and not the mean annual air temperature as the predominant decomposition of SOM is taking place during the warmer summer season and slows down during the winter season (Yao et al., 2011; Žifčáková et al., 2016), where the temperature at the sampling site is close to freezing (Hiltbrunner et al., 2013). The two treatments with increased temperatures of 16.5 °C (+4 °C, $T_{16.5}$) and 20.5 °C (+8 °C, $T_{20.5}$) correspond to the expected temperature increases in the European Alps predicted for the years 2080-2099 with emission scenario RCP8.5 (Hock et al., 2019). The incubation follows mainly the approach described in Abiven and Andreoli (2011). For each temperature treatment, 48 samples (24 forest soil, 24 pasture soil), each weighing 50 g, were placed in 2-l glass jars. At the beginning, 20 ml of water were added, corresponding to the field capacity of the soils, and vials containing 20 ml water were placed in the jars aside the soil to ensure increase of humidity in the air space of the jars and avoid drying of the soil (see setup in Figure A1). A pre-incubation of the samples for 18 days was conducted to stabilize and test the activity of the microbial community. After pre-incubation, 1.25 g of dried ca. 1-2 cm long cut leaf tissues from perennial ryegrass (*Lolium perenne*) grown in a ^{13}C enriched atmosphere (Studer et al., 2017) was added to 17 forest samples and 17 pasture samples for each temperature treatment. The carbon added to the soil by the litter addition was approximately equal to the carbon already present in the soil samples, resulting in a fresh to old carbon ratio of 1:1. The incubation ran for the period of 360 days. At different times throughout the incubation, a subset of the incubated soil samples was destructively sampled. An overview of the sampling scheme can be found in Fig. A2. During destructive sampling, samples were placed in plastic bags and immediately transferred to a freezer (-28°C). The incubated soil samples were freeze-dried to a constant weight and milled in a horizontal ball mill (MM400, Retsch, Germany).

2.3 Carbon and nitrogen analysis

To asses total carbon and nitrogen concentrations (TC, TN) of each sample, as well as stable carbon isotope composition ($\delta^{13}C$), 5 mg of the soil material were weighed into tin capsules and measured using an elemental analyzer coupled to an isotope ratio mass spectrometer (EA-IRMS; Flash 2000-HT Plus, linked by Conflo IV to Delta V Plus isotope ratio mass spectrometer, Thermo Fisher Scientific, Germany). The concentrations of carbon and nitrogen and the stable isotope composition were calibrated using a soil reference material (Haplic Chernozem, Harsum, Germany; University of Zurich 2023) as laboratory

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internal standards and IAEA-600 caffeine as certified standard. At least two analytical replicates were measured for each sample.

2.4 Lignin Analysis

The soil material was subjected to alkaline CuO oxidation procedure by Hedges and Ertel (1982) to break down the lignin polymer into its different monomers. An adapted version of the microwave digestion by Goñi and Montgomery (2000) was used (Heim and Schmidt, 2007). Approximately 600 mg of soil material was oxidized with 500 mg of CuO powder, 50 mg of ammonium iron-(II)-sulfate and 20 ml 2M NaOH in N_2 flushed microwave tubes at 150 °C for 90 minutes and subsequent cooling down. To each sample, an internal standard of 500 μl of cinnamic acid and ethylvanillin mix (each with a concentration of 1 g l^{-1}) was added. Solids were removed by centrifuging for 4 minutes at 3000 rpm and following decanting. The supernatant was adjusted to pH 2.10 with 32% HCl. The samples were subsequently collected on preconditioned (ethyl acetate, methanol, water) DSC-18 SPE columns and eluted with 5 x 500 μl ethyl acetate. Residual water was removed with Na_2SO_4 and the samples were dried under N_2 and then redissolved with 400 μl of internal standard solution (1 g l^{-1} anisic acid in ethyl acetate). Quantification of individual lignin monomers was performed after derivatization of 70 μl sample with 70 μl BSTFA/TCMS 99:1 derivatization reagent for 20 minutes at 60 °C. The analysis was performed by gas chromatography-flame ionization detection (GC-FID; 7890B GC System, Agilent, USA). A DB-5MS column (Agilent, USA; length 50 m, internal diameter 200 μm, film thickness 0.33 μm) was used with the following temperature program: Start at 80 °C, hold for 5 min, ramp to 110 °C with +2 °C min^{-1}, ramp to 170 °C with +0.5 °C min^{-1}, ramp to 320 °C with +15 °C min^{-1}, hold 10 min. Injection was done using a multimode inlet running in splitless mode (temperature program: start at 90 °C, hold for 0.5 min, ramp to 400 °C with +850 °C min^{-1}, hold 2 min). Compound identification was done by measurement under the same chromatographic conditions as explained above but analysed by gas chromatography mass spectrometry (GC-MS, 6890N GC System, 5973N MS System, Agilent, USA and by comparison to known standards and Wiley/NIST spectral libraries. Losses due to sample preparation were corrected using the cinnamic acid and vanillic acid internal standards (Heim and Schmidt, 2007).

To measure compound-specific stable carbon ($\delta^{13}C$) isotope composition, samples were analyzed in triplicate using a gas chromatograph (TRACE 1310, Thermo Scientific, Germany) coupled to a Delta V Plus isotope ratio mass spectrometer via GC-Isolink II and ConFlo IV (Thermo Fisher Scientific, Germany). The shift in the isotopic composition introduced by adding trimethylsilyl carbon during derivatozation was corrected using the mass balance equation by Dignac et al. (2005) (Equation (1)):

$$\delta_{UD} = \frac{n_D}{n_{UD}}\delta_D - \frac{n_{BSTFA}}{n_{UD}}\delta_{BSTFA} \quad (1)$$

where δ_{UD} represents the isotopic ratio of the underivatized phenol, n_D is the number of C atoms in the derivatized phenol, n_{UD} the number of C atoms in the underivatized phenol, δ_D is the isotopic ratio of the derivatized phenol (measured on GC-IRMS), n_{BSTFA} is the number of C atoms added from BSTFA (depending on the phenol) and δ_{BSTFA} is the isotopic ratio of BSTFA (measured with GC-IRMS and compared to underivatized standards).

Natural abundance isotope ratios in samples without litter addition are expressed as δ ^{13}C relative to the international Vienna

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Pee Dee Belemnite (VPDB). In labelled samples with litter addition, the enrichment is expressed in units of atom % excess (APE):

$$APE = (atom\%)_{L^+} - (atom\%)_{L^-} \quad (2)$$

with $(atom\%)_{L^+}$ as the concentration of ^{13}C of the labelled samples and $(atom\%)_{L^-}$ as the concentration of ^{13}C of the samples without litter addition (Slater et al., 2001). For $(atom\%)_{L^-}$, two different averaged values were used for forest and pasture soil, respectively.

2.5 Statistics

All statistical analyses were performed using R software version 4.4.1 (R Core Team, 2024). Prior to analysis, all data were tested for normality and homogeneity of variances using the Shapiro-Wilk test and Levene's test, respectively. Where necessary, data were log-transformed to meet assumptions of parametric tests.

To assess the effects of litter addition (with vs. without), vegetation type (forest vs. pasture), temperature (control vs. elevated), and incubation time (short-term vs. long-term) on SOM decomposition, a four-way analysis of variance (ANOVA) was conducted. This model allowed us to test for both main effects and interaction effects between factors. When significant interaction terms were detected, post-hoc pairwise comparisons were conducted using Tukey's Honest Significant Difference (HSD) test to further explore specific differences between treatment combinations.

To evaluate the temporal dynamics of SOM decomposition, repeated measurements of ANOVA were applied to examine changes over the different incubation time points, considering litter presence, vegetation type, and temperature as between-subject factors.

All statistical tests were two-tailed, with a significance level set at α = 0.05. Results are presented as means ± standard error of the mean (SEM), unless otherwise indicated.

3 Results

3.1 Total organic carbon concentrations

At the beginning of the incubation experiment, total organic carbon (TOC) concentrations of forest soil samples without litter addition (L^-) averaged at 43.8 ± 1.6 mg g^{-1} across all temperature treatments (Fig. 1(a)). Initial TOC was slightly higher for pasture L^- soils (45.5 ± 1.1 mg g^{-1}). We observed a decrease for forest L^- soils during the incubation period of 360 days (-6.7 ± 2.4 %, p = 0.012), which was almost twice as high as for the pasture L^- soils (-3.3 ± 1.6 %, p = 0.053). Until the end of the incubation experiment, there was no difference in the temporal trend between different temperature treatments for forest and pasture L^- soils (p = 0.39; p = 0.52). Litter addition (L^+) initially increased TOC of forest (+21.5 ± 1.2 %, p < 0.001) and pasture (+26.9 ± 2.0 %, p < 0.001) soils (Fig. 1(b)). The average decrease of TOC of forest L^+ and pasture L^+ soils was significantly stronger in comparison with the respective L^- soils. Forest L^+ soils showed an almost twofold decrease compared to forest L^- soils (-11.8 ± 1.1 %) during the incubation period. For the L^+ pasture soils, the decrease was almost sixfold compared to the

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pasture L^- soils (-17.4 ± 1.9 %). Generally, we observed for both, forest and pasture L^+ soils, decreasing TOC with increasing temperature. Differences between different temperature treatments, however, were only significant at certain points during the incubation period (see *p*-values in Table A4).

3.2 Total organic carbon isotope composition

Forest L^- soils ($\delta^{13}C$ -25.8 ± 0.02 ‰) were slightly less depleted in ^{13}C (Fig. 1(g)) compared to pasture L^- soils ($\delta^{13}C$ -26.6 ± 0.01 ‰, $p < 0.001$). No change in $\delta^{13}C$ was detected in forest L^- soils during the incubation period. For pasture L^- soils, we observed a slight decrease of $\delta^{13}C$ ($p = 0.01$), mainly due to slightly increased values for $T_{12.5}$ after 14 and 28 days. No temperature effect was visible in L^- soils for both, forest and pasture soil samples (see Table A5). Litter addition (Fig. 1(h)) increased initial ^{13}C for both soils to a similar degree (forest: +0.56 ± 0.03 %, $p < 0.001$; pasture: +0.58 ± 0.03 %, $p < 0.001$). In L^+ soils, significant decreases in atomic % excess (APE) ^{13}C were observed during the incubation period for all treatments (see Table A1). A much stronger decrease was noted during the first 28 days of the experiment, which was less pronounced for the remainder of the incubation period (Table A2).

The influence of temperature on the decomposition rates varied between forest and pasture. Forest soil samples exhibited a relatively constant ratio between short (28 d) - and long-term (360 d) decomposition rates across different temperatures. In contrast, in the pasture soil we could detect a slight increase in this ratio with temperature.

L^+ soils showed a clear trend with temperature, with both pasture and forest having a stronger decrease of APE^{13}C at higher temperatures ($p < 0.001$). This trend was visible at most time points during the incubation, especially between $T_{12.5}$ and the increased temperatures (see Table A5).

3.3 Nitrogen concentrations

Initial total nitrogen (TN, Fig. 1(c)) concentrations were on average lower in the forest L^- soil than in the pasture L^- soil (3.4 ± 0.1 mg g^{-1}, 4.7 ± 0.1 mg g^{-1}, respectively). TN did not change in L^- soils during the incubation. Litter addition increased initial TN for forest and pasture soil, which was more pronounced for forest soil than for pasture soil samples (+15.6 ± 1.8 %, $p < 0.001$; +10.7 ± 1.9 %, $p < 0.001$). In L^+ soils (Fig. 1(d)), an increase was observable from day 0 to day 56 for the $T_{12.5}$ treatment, from day 0-28 for $T_{16.5}$ treatment and for day 0-14 for $T_{20.5}$ treatment. Thereafter, TN dropped until the end of the experiment or stayed almost constant after they first dropped ($T_{20.5}$ pasture). We saw mostly differences between $T_{16.5}$ and $T_{20.5}$ in the beginning of the incubation and at a later stage between $T_{12.5}$ and the elevated temperature treatments (see Table A6).

3.4 Carbon to nitrogen ratios

We observed significantly higher initial carbon to nitrogen ratios (C/N, Fig. 1(e)) in forest L^- soils compared to pasture L^- soils (12.8 ± 0.1, 9.6 ± 0.05, $p < 0.001$). During the whole incubation experiment, this difference remained similar. The C/N ratio decreased significantly during the incubation period for forest L^- (-5.3 ± 1.0 %, $p = 0.002$) and pasture L^- soils (-3.6 ± 0.6 %, $p < 0.001$). There were only differences between different temperatures (Table A7) after 28 days in pasture L^- soils between

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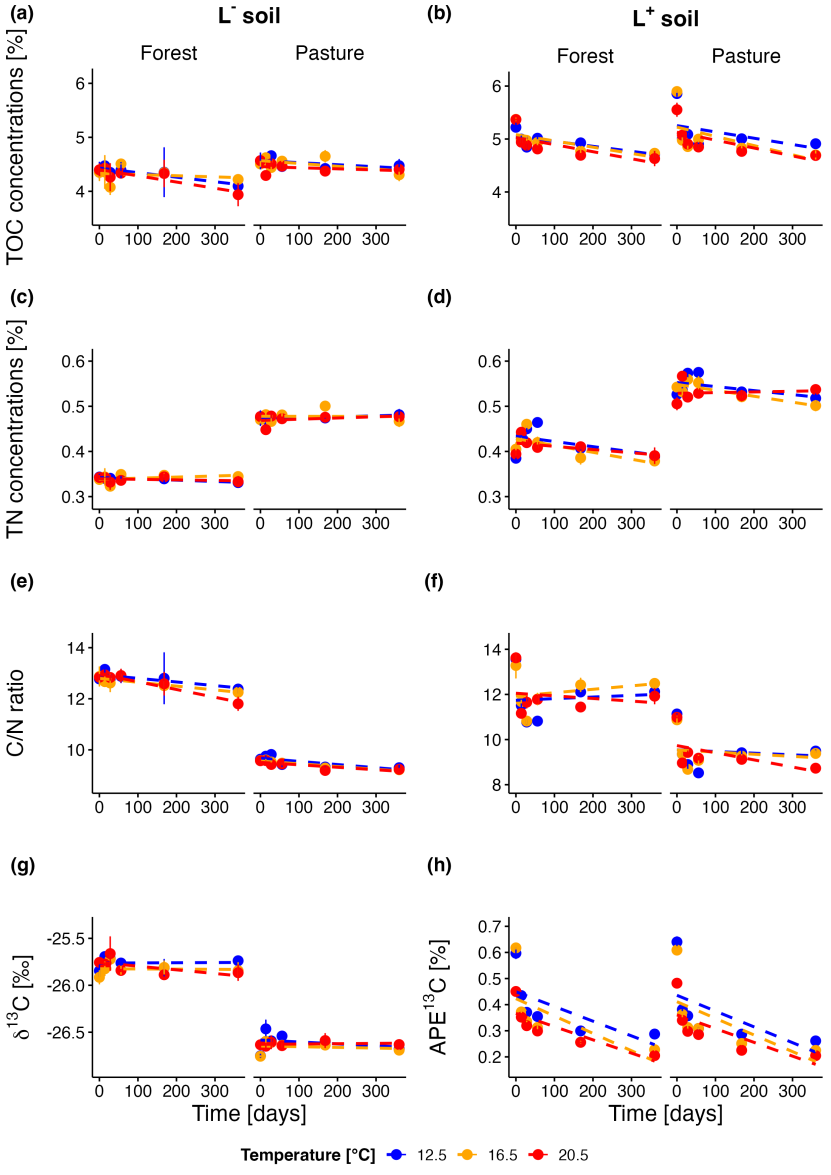

Figure 1. TOC concentrations over the incubation period for forest and pasture soils without (L^-; (a)) and with litter addition (L^+; (b)); TN concentrations over the incubation period for forest and pasture soils without (L^-; (c)) and with litter addition (L^+; (d)); C/N ratio evolution over the incubation period for forest and pasture soils without (L^-; (e)) and with litter addition ((L^+; (f)); Natural abundance δ ^{13}C over the incubation period for forest and pasture soils without litter addition ((L^-; (g)); Atomic % excess of δ ^{13}C over the incubation period for forest and pasture soils with litter addition. (L^+; (h))

$T_{12.5}$ and $T_{16.5}$ (p = 0.002), and $T_{12.5}$ and $T_{20.5}$ (p = 0.006). Litter addition (Fig. 1(f)) led to an initial increase of the C/N ratio for both forest and pasture L^+ soils, with a more pronounced increase for the latter (+5.1 ± 1.4 %, p = 0.01; +14.6 ± 0.8 %, p

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< 0.001). During the incubation period, the C/N ratio decrease was more pronounced in L^+ than L^- soils, with forest L^+ soils showing a lower decrease than pasture L^+ soils (-9.7 ± 1.5 %, $p < 0.001$; -16.3 ± 0.0 %, $p < 0.001$). While the decrease of the C/N ratio in L^- soils was almost consistent over the entire incubation period, it showed a different pattern in L^+ soils. We observed a strong decrease during the first 28 days followed by a much less pronounced decrease or even slight increase of the C/N ratio until the end of the incubation period. Throughout most of the incubation period in both forest and pasture soils, a significant temperature trend was observed, with higher temperatures associated with lower C/N ratios (Table A7).

3.5 Phenol concentrations

Total phenol concentrations averaged over all temperatures were higher in forest L^- compared to pasture L^- soils with initial concentrations of 1509.5 ± 95.1 $\mu g\ g^{-1}$ and 1260.9 ± 63.4 $\mu g\ g^{-1}$ (Fig. 2). In L^+ soil, we observed higher phenol concentrations for both forest and pasture soils (1760.4 ± 56.0 $\mu g\ g^{-1}$, 1465.4 ± 43.4 $\mu g\ g^{-1}$, respectively, Fig. 3). During the incubation period, phenol concentrations decreased significantly in all treatments. We observed a stronger decrease for forest L^+ and L^- soils (-31.1 ± 1.5 %, $p = 0.009$; -21.7 ± 1.7 %, $p = 0.097$) compared to pasture L^+ and L^- soils (-24.1 ± 1.2 %, $p < 0.001$; -15.0 ± 0.9 %, $p = 0.25$). To test the influence of temperature on phenol concentrations, we compared the concentration decrease with different temperatures of different phenol groups: Vanillyl (vanillin, vanillic acid, acetovanillone), syringyl (syringaldehyde, syringic acid, acetosyringone), cinnamyl (coumaric acid, ferulic acid), and p-hydroxyl (salicylaldehyde, salicylic acid, piceol) phenols. For the individual groups, we could detect significant decreases over time for vanillyl (forest L^-, $p = 0.040$), syringil (forest L^-, $p = 0.016$; pasture L^+, $p = 0.005$), cinnamyl (all treatments, $p < 0.001$) and p-hydroxyl (forest L^-, $p = 0.006$; forest L^+, $p = 0.009$; pasture L^-, $p = 0.045$) phenol concentrations. We could not detect significant differences between different temperature treatments for total phenol concentrations. For the individual phenol groups, only cinnamyl phenols in pasture L^+ soils showed a significant temperature dependency ($p = 0.005$) with differences between $T_{12.5}$ and $T_{16.5}$, and $T_{12.5}$ and $T_{20.5}$ ($p = 0.010$, $p = 0.011$).

3.6 Phenol isotope composition

In forest L^- soils, the $\delta^{13}C$ values were significantly higher in all vanillyl phenols ($p < 0.01$), as well as in the syringyl phenols syringaldehyde ($p = 0.002$) and syringic acid ($p = 0.04$), compared to pasture L^- soils (Fig. 4). Throughout the entire incubation period, we observed a decrease of $\delta^{13}C$ values in forest L^- soils for vanillic acid and acetosyringone ($p = 0.04$, $p = 0.04$). In pasture L^- soils, $\delta^{13}C$ decreased in vanillin ($p < 0.001$) and, surprisingly, showed a slight increase in piceol ($p = 0.01$). No temperature trend was visible for any of the phenols. Litter addition led to a significant increase of ^{13}C in both forest and pasture soil for all phenols (all $p < 0.001$).

Over the entire incubation period, atomic % excess (APE) of ^{13}C decreased for all phenols in forest L^+ soils, except for vanillic acid, which showed no decline (Fig. 5). In pasture L^+ soils, we could detect a significant decrease in APE from start to end for all phenols except for piceol ($p = 0.29$) and vanillic acid ($p = 0.78$). In forest L^+ soils, a stronger decrease in APE with higher temperature was observed for vanillin ($T_{12.5}$ - $T_{20.5}$, $p = 0.01$), syringaldehyde ($T_{12.5}$ - $T_{20.5}$, $T_{16.5}$ - $T_{20.5}$; $p < 0.001$, $p = 0.02$), salicylic acid ($T_{12.5}$ - $T_{16.5}$, $T_{12.5}$ - $T_{20.5}$; $p = 0.02$, $p = 0.003$), coumaric acid (all temperatures, $p = 0.005$, $p < 0.001$, $p = 0.04$)

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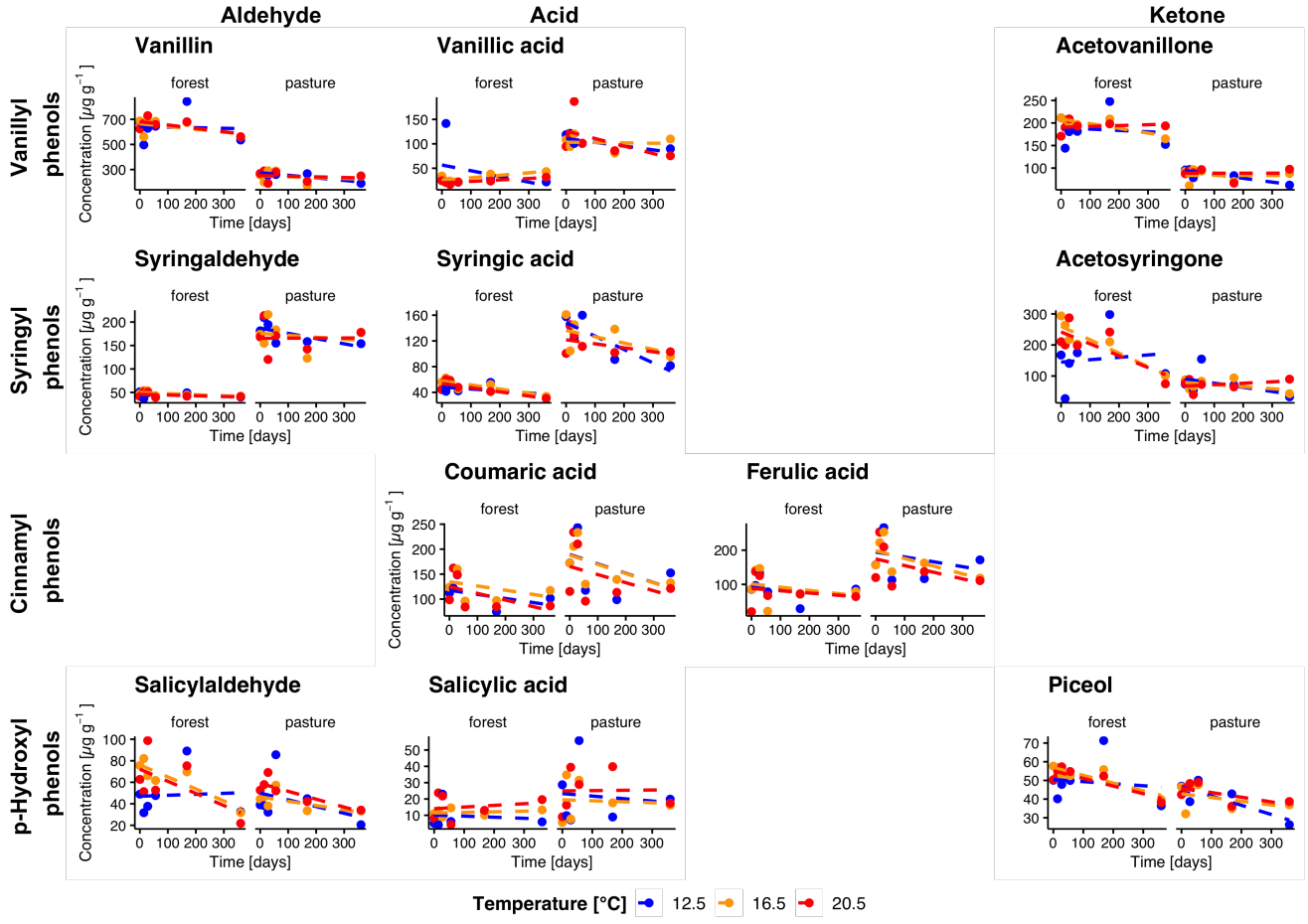

Figure 2. Temporal changes in individual phenol concentrations during incubation for forest and pasture soil samples without litter addition (L^-). Phenols are grouped horizontally into vanillyl, syringyl, cinnamyl, and p-hydroxyl compounds and vertically by functional class as aldehydes, acids, and ketones. Each point corresponds to the mean of the extracted samples (n = min. 3).

and ferulic acid ($T_{12.5}$ - $T_{20.5}$, $p = 0.005$). In pasture L^+ soils, similar phenols showed a temperature dependency: Vanillin ($T_{12.5}$ - $T_{16.5}$, $T_{12.5}$ - $T_{20.5}$; $p = 0.03$, $p = 0.004$), syringaldehyde ($T_{12.5}$ - $T_{16.5}$, $T_{12.5}$ - $T_{20.5}$; $p = 0.003$, $p < 0.001$), coumaric acid ($T_{12.5}$ - $T_{16.5}$, $T_{12.5}$ - $T_{20.5}$; $p < 0.001$, $p < 0.001$).

4 Discussion

4.1 Decomposition of soil organic matter without litter addition at control temperature

The forest and pasture soil samples without litter addition maintained at an incubation temperature of 12.5 °C provide a baseline to compare the decomposition of OM under different conditions. These conditions represent the current average growing

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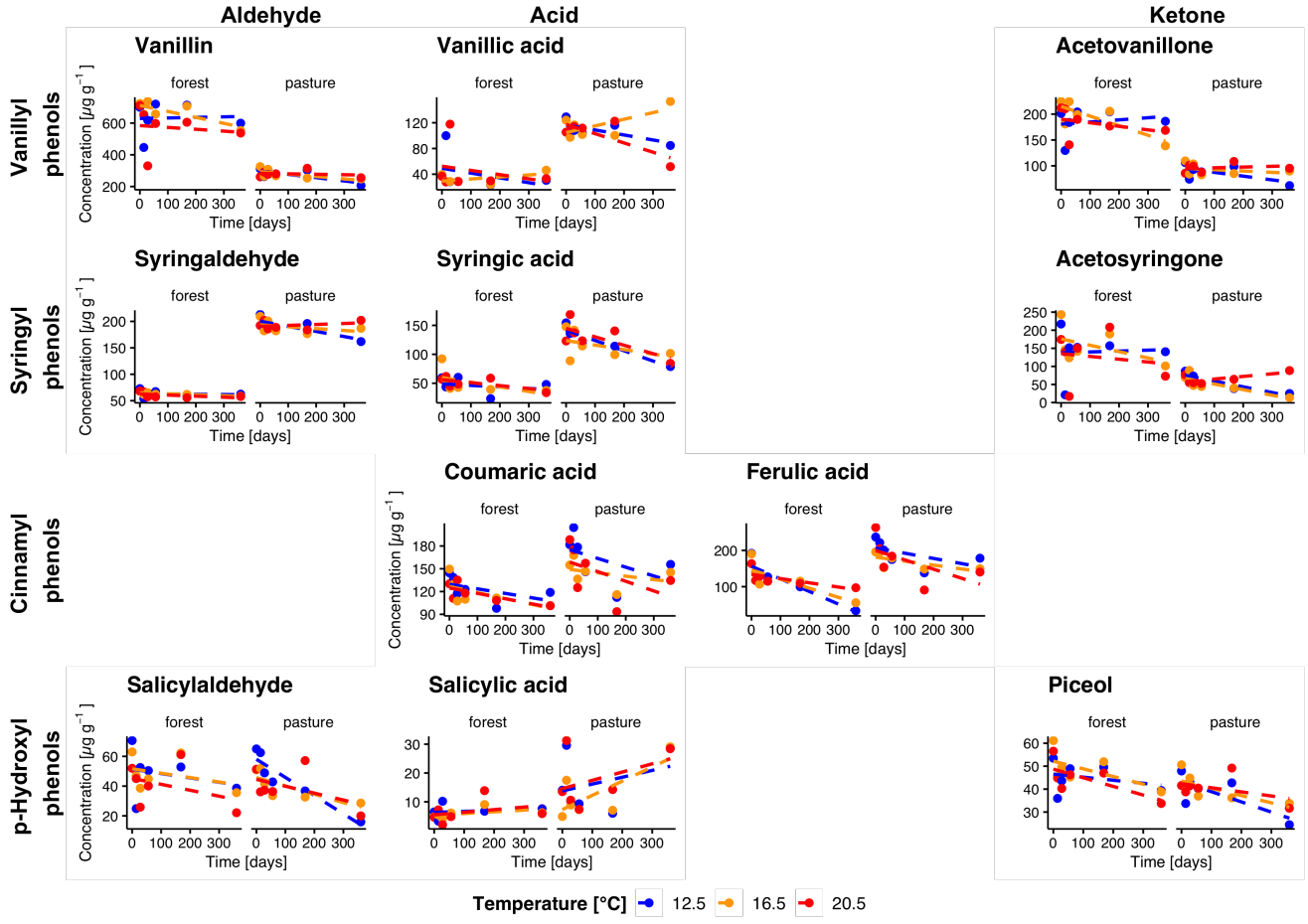

Figure 3. Temporal changes in individual phenol concentrations during incubation for forest and pasture soil samples with litter addition (L^+). Phenols are grouped horizontally into vanillyl, syringyl, cinnamyl, and p-hydroxyl compounds and vertically by functional class as aldehydes, acids, and ketones. Each point corresponds to the mean of the extracted samples for each treatment group (n = 4 for sampling at 14 days, n = 3 for other samplings).

season temperature at the study site, a subalpine site in the Swiss Alps (Hiltbrunner et al., 2013; Speckert et al., 2023), providing insights into the inherent differences between the two soils under controlled conditions. Our findings indicate that the pasture soil exhibited slightly higher initial total organic carbon (TOC) concentrations compared to the forest soil. TOC concentrations in both soils align with previous findings from the same site (Hiltbrunner et al., 2013; Speckert et al., 2023) and
265 are comparable to those reported for other comparable alpine regions in Switzerland (Hoffmann et al., 2014). The difference between forest and pasture soils is attributable to the nature of OM inputs characteristic of the respective ecosystems. Pasture soils receive regular inputs of both above- and belowground biomass inputs, as well as periodic manure deposition from grazing animals (Conant et al., 2011; Don et al., 2007). These inputs are rich in labile, easily degradable compounds such as sugars

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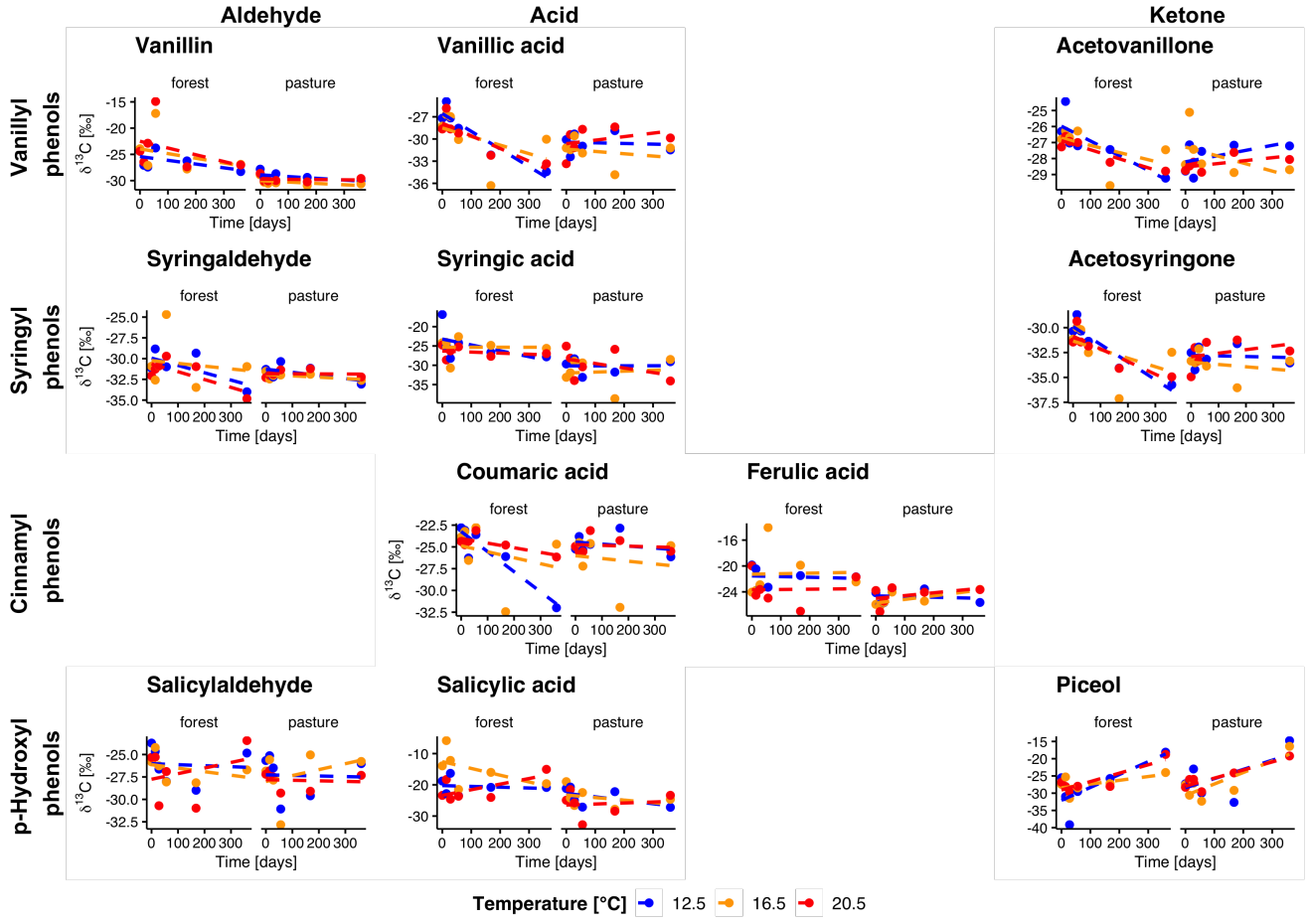

Figure 4. Evolution of natural abundance δ ^{13}C in individual phenols over the incubation period for forest and pasture soil without litter addition (L$^-$). Phenols are grouped horizontally into vanillyl, syringyl, cinnamyl, and p-hydroxyl compounds and vertically by functional class as aldehydes, acids, and ketones. Each point corresponds to the mean of the extracted samples (n = min. 3).

and proteins, leading to high TOC concentration (Rumpel, 2011). In contrast, the forest soils primarily receive litterfall composed of needles and woody debris, being rich in lignin and cellulose that accumulate in the litter layer and organic horizons (Speckert et al., 2023). These compounds are complex polymers that decompose more slowly than grass-derived OM due to their chemical structures (Prescott, 2010). These differences in OM inputs between pasture and forest soils are also reflected in the carbon-to-nitrogen (C/N) ratio of the soils, which we could confirm in our study. Forest soils typically have wider C/N ratios, resulting from lignin-rich inputs with high carbon content and lower nitrogen availability. Such wide C/N ratios can constrain microbial decomposition by limiting nitrogen required for growth and enzyme production (Melillo et al., 1982). Despite the higher initial TOC in the pasture soil, we observed a more pronounced decrease of TOC in the forest soil samples over the whole incubation period, being almost doubled compared to the decrease in the pasture soil. The stable carbon isotope

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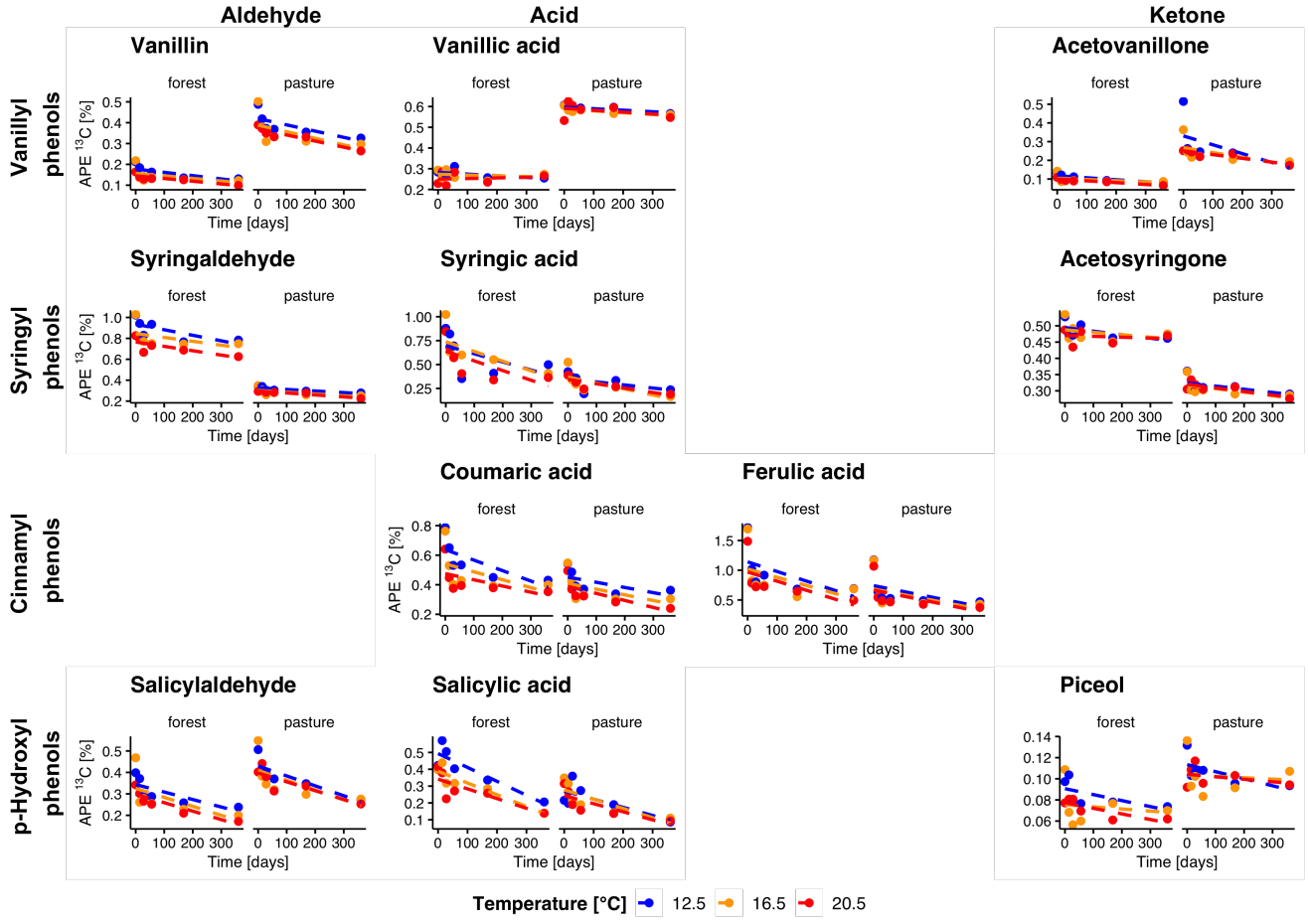

Figure 5. Evolution of natural abundance δ ^{13}C in individual phenols over the incubation period for forest and pasture soil with litter addition (L^+). Phenols are grouped horizontally into vanillyl, syringyl, cinnamyl, and p-hydroxyl compounds and vertically by functional class as aldehydes, acids, and ketones. Each point corresponds to the mean of the extracted samples for each treatment group (n = 4 for sampling at 14 days, n = 3 for other samplings).

(δ^{13}C) signature indicates a consistent decomposition source likely originating from lignin-rich material inherent to forest soils (Boutton et al., 1998). Our results imply that, without fresh organic inputs, the forest soil in this study lost a larger fraction of its stored carbon than the pasture soil did. If this pattern holds more generally, alpine forest soils could be more prone to old carbon losses in the absence of new litter inputs. During the incubation, a significant decrease in lignin-derived phenols such as vanillyl and syringyl monomers was observed in the forest soil samples. This argues for active lignin decomposition (Hall et al., 2020), contributing to the overall decline in TOC concentrations as seen in our data. The enhanced decomposition of phenolic compounds in forest compared with pasture soil can be attributed to the adaptation of their microbial communities to the different sources of plant-derived OM (Otto and Simpson, 2006). Forest soils harbour specialized decomposers,

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including lignin-degrading fungi like white-rot and brown-rot fungi, capable of breaking down complex aromatic structures (Thevenot et al., 2010). These microorganisms possess enzymes that facilitate the decomposition of lignin into simpler compounds (Janusz et al., 2017). Even when labile carbon is scarce, these specialized decomposers in forest soils can sustain their activity by metabolizing lignin-derived substrates (Wilhelm et al., 2019), efficiently accessing carbon in otherwise more complex SOM.

In our study, the absence of fresh, labile carbon inputs inhibits the microbial community in the pasture soil, leading to lower decomposition rates compared to the forest soil. The microbial communities in pasture soils are adapted to frequent inputs of easily degradable OM (Shi et al., 2023). They primarily consist of bacteria and fungi that rapidly utilize simple substrates but may exhibit reduced activity when such substrates are depleted (Paterson et al., 2007). Without fresh inputs, the microbial decomposition in pasture soils slows down, resulting in a smaller decline in both TOC and phenolic compounds during incubation. This reduced decomposition is accompanied by a slight decrease in δ^{13}C in the pasture soil, suggesting that, as labile carbon sources diminish, microbial communities increasingly turn to isotopically heavier, most likely older carbon sources that are generally more difficult to decompose (Dijkstra et al., 2006). This subtle isotope shift highlights the microorganisms' reduced efficiency when preferred, labile OM becomes unavailable, contrasting with the more steady decomposition of lignin-dominated material in the forest soil (Balesdent et al., 1987). This dependency on labile carbon inputs underscores the different substrate preferences and adaptation strategies between pasture and forest soil microbial communities.

4.2 Decomposition of grass leaf litter in forest and pasture soil

The addition of *Lolium perenne* leaf litter at 12.5°C introduces fresh organic material into soil at the beginning of the incubation period which was assumed to have a strong impact on soil carbon and nitrogen dynamics. Since the same litter is used for pasture and forest soil, the comparative analysis describes how different soil characteristics influence the decomposition under the same conditions for both soil types. Litter input increased, as expected, TOC and phenol concentrations in both, pasture and forest soil. The introduction of fresh grass leaf litter and thus presumably labile carbon fractions (Zhang et al., 2020) led to enhanced microbial activity, resulting in higher decomposition rates compared to control samples without litter addition. This input provided a readily accessible energy source, which not only stimulated the breakdown of the added litter but also facilitated the decomposition of more complex components of the SOM, such as lignin (Kögel-Knabner, 2002). This is confirmed by the increased decomposition of phenolic compounds observed in litter-amended soils compared to controls.

The stronger decrease in TOC in the pasture soil compared to the forest soil is likely due to the grass type of litter used. The soil microorganisms tend to decompose litter found at the site better than litter to which the microbial community is not adapted (Wallenstein et al., 2013; Paul, 2016). In our case, this means that the soil microbial community in the pasture is more adapted to the grass input compared to the one in the forest soil. Additionally, we added more labile carbon to the soils with the litter, which corresponds more to the conditions in the pasture.

If we look at the different phenol groups, we can also find an indication that the soil fauna in the forest soil is better adapted to the decomposition of more complex organic matter containing more lignin then the one in the pasture soil. In the more easily degradable lignin monomers of the cinnamyl group (Thevenot et al., 2010), we observed a similarly rapid decomposition

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in both soils after addition of the litter. In the somewhat less easily decomposable syringyl phenols, we determined a more pronounced decrease in the forest soil, while decomposition in the pasture is slower. In the most stable vanillin phenols, the decomposition is rather low for both soils, but still significant in the forest soil (Hedges and Parker, 1976; Hedges and Ertel, 1982; Thevenot et al., 2010).

The initial increase in TN concentrations following litter addition was more pronounced in forest soil than in pasture soil samples, likely due to the lower initial TN content in the forest soil and the higher TN of the added litter relative to the soil. However, TN did not change significantly during the incubation period in either soil type, suggesting that nitrogen was retained within the microbial biomass or cycled within the system (Schimel and Bennett, 2004). Additionally, as the soils are rather N-limited, microorganisms tend to retain most N within the system, resulting in a lower N mineralization (Mooshammer et al., 2014). Litter addition increased the C/N ratio in both soils, more so in pasture compared to forest. During incubation, the C/N ratio decreased significantly in both litter-amended soils, with a more pronounced decrease in pasture than in forest soil likely due to the already discussed differences in substrate susceptibility between the two soils. This indicates that carbon was lost at a faster rate than nitrogen, consistent with microbial decomposition of the added litter and possibly native SOM (Manzoni et al., 2008).

4.3 Influence of increasing temperature on the decomposition of organic matter

In soils without litter addition temperature did not significantly influence the rate of SOM decomposition based on TOC concentrations in either soil type. It is surprising that no temperature trend was observed in TOC for these soils, given the general expectation that temperature would influence SOM decomposition (Nottingham et al., 2020; Soong et al., 2021). Carbon isotope composition also remained constant, with no observable temperature trend in either forest or pasture soil. Similarly, decomposition rates of the different phenol groups showed no significant variation across temperature treatments.

In contrast, soils with litter addition exhibited a clear temperature-dependent decrease in TOC. This decrease has been seen in many long-term warming experiments, some even despite an increased plant-derived organic matter input (San Román et al., 2024). Although total phenol concentrations in litter-amended soils did not differ significantly between temperature treatments, certain phenol groups showed increased decomposition with rising temperatures, both in TOC concentrations and isotope signals. This effect is consistent with the increased decomposition of lignin phenols at higher temperatures, a process well-documented, where microbial activity and the temperature sensitivity of lignin-degrading enzymes enhance decomposition under elevated temperatures (Davidson and Janssens, 2006; Craine et al., 2010; Conant et al., 2011). Long-term warming experiments have also observed this increased decomposition of more complex organic matter, e.g. Tao et al. (2020), vandenEnden et al. (2021) and Zosso et al. (2023).

The temperature trend is visible for more phenols in the forest soil samples than in pasture soil. This is likely another indicator for the initial presence of different soil microbial communities adapted to different input sources. Forest soils often harbour a more diverse microbial community than grassland soils, which might contribute to a greater sensitivity in the decomposition of lignin in the forest soil than in the pasture soil (de Boer et al., 2005).

A temperature increase as in our study would typically be expected to enhance microbial activity (D'Alò et al., 2021), leading

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to an increased decomposition of SOM (Davidson and Janssens, 2006; Conant et al., 2011). The fact that we did not observe this increase in soils without litter addition is likely due to the limited availability of more easily decomposable carbon for decomposition. Several studies have shown that microbial communities in soils with a high availability of easy degradable carbon input react stronger to temperature increases compared to those in soils that are depleted in labile carbon (Fissore et al., 2013; Eberwein et al., 2015). Without fresh litter, soil microorganisms might be limited by the availability of fresh C, constraining the ability to respond to the temperature increases (Bradford et al., 2017), thus limiting microbial growth and enzyme production (Allison et al., 2010).

Similar as for the higher decomposition of TOC in pasture soil samples with litter addition, the earlier appearance of temperature trends in pasture L+ soils compared to forest L+ soils may be influenced by the type of litter used. Microbial communities in the pasture soil, already adapted to grass-derived litter, may more readily respond to temperature increases due to familiarity with the substrate (Vanhala et al., 2008). This adaptation allows them to allocate resources efficiently towards enzyme production and metabolic processes that are enhanced at higher temperatures.

4.4 Early-phase vs. late-phase decomposition

The observed differences between short-term and long-term decomposition during the incubation experiment highlight the dynamic nature of SOM turnover and the factors influencing it. In the initial phase of decomposition, spanning the first 28 days, there is a rapid decline in total organic carbon (TOC), phenol concentrations, and changes in $\delta^{13}C$ across all treatments (see Table A2). This rapid phase is driven by the swift microbial utilization of readily available, labile C sources, such as simple sugars provided by the fresh litter addition in soils with litter addition or residual plant inputs in the soils without litter addition (Prescott and Vesterdal, 2021). Elevated temperatures amplify these processes by enhancing microbial metabolic rates and enzyme activities, leading to accelerated decomposition of these easily degradable substrates (Davidson and Janssens, 2006).

In the later phase of the incubation experiment, the rate of carbon loss diminishes significantly. Microorganisms in the soils deplete the easily accessible substrates and likely shift to metabolizing more complex compounds like lignin-derived phenols, which are inherently more resistant to microbial breakdown (Kögel-Knabner, 2002). This transition results in a slower overall decomposition rate and reduced temperature sensitivity, as the decomposition of complex organic molecules depends more on specialized enzymes and microbial community adaptations than on temperature alone (Thevenot et al., 2010; Conant et al., 2011).

The differences between forest and pasture soil become more pronounced during the long-term decomposition phase. Forest soils, containing lignin-rich organic matter originating from woody debris and leaf litter, harbour microbial communities that are adapted to degrade complex aromatic compounds (Baldrian, 2017). These communities may sustain decomposition rates more effectively over extended periods, even when labile substrates are scarce. In contrast, pasture soils receive typically more frequent inputs of labile OM such as root exudates, more aboveground litter and changing sources of OM during the growing season because of changing vegetation (Billings, 2006). Therefore, these soils may experience a sharper decline in microbial activity once these substrates are exhausted. If their microbial communities are less capable to decompose more complex compounds, this can lead to a more significant slowdown in long-term decomposition (Fontaine et al., 2007). The study of Feng

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and Simpson (2008) also highlights the importance of microbial adaptations, showing that the temperature sensitivity of lignin decomposition is modulated by the microbial access to these substrates, particularly in soils where lignin is in a more degraded state.

The influence of temperature on decomposition diminishes over time as the availability of fresh, labile carbon decreases. In the short term, higher temperatures significantly enhance microbial activity, leading to rapid decomposition of not only labile carbon sources, but also more complex compounds. However, as the more labile substrates become depleted, microbial activity slows down, and the decomposition shifts to more complex polymeric organic matter such as lignin (Manzoni, 2017). This slower decomposition process is less sensitive to temperature increases, as it relies more on the presence and activity of specialized microorganisms and enzymes, which are constrained by the availability of energy from labile substrates rather than by general microbial metabolic rates (Knorr et al., 2005; Davidson and Janssens, 2006; Fontaine et al., 2007). Without a continuous energy source from labile carbon, the metabolic response to temperature becomes less pronounced, as microbial populations transition to more specialized, slower-growing organisms capable of degrading more complex substrates (Fontaine et al., 2007). Moreover, the physical and chemical protection of more complex SOM within soil aggregates and interactions with minerals often shields these compounds from microbial access (Schmidt et al., 2011; Lehmann and Kleber, 2015). This protective mechanism further reduces the sensitivity of more complex SOM to temperature increases, as noted by Schmidt et al. (2011). Therefore, while elevated temperatures can enhance microbial metabolism and enzyme activity, the lack of readily available energy from labile substrates remains the primary limiting factor for the long-term decomposition of more complex OM.

Our findings align with this interpretation, as we observed a significant decrease in temperature sensitivity over time, especially in soils where labile carbon had been depleted. Even under elevated temperature conditions, the decomposition of more complex SOM did not increase proportionally, indicating that carbon availability was the dominant factor regulating microbial activity and enzyme production, rather than temperature alone.

4.5 Decomposition of SOM in future alpine ecosystems

Our results provide evidence that the two alpine pasture and forest soils host functionally different microbial communities. This has also been shown in other studies, with more bacteria-dominated alpine grassland soils and forest soils with a higher abundance of fungal microorganisms (Djukic et al., 2010). These different communities react differently to the influence of rising temperatures and changes in the input of litter. Vegetation changes such as afforestation or shrub encroachment, as they occur in many alpine areas, can therefore have a strong influence on the carbon cycle. Additionally, the projected strong temperature increase in alpine region in the next decades will have an especially large influence on soil carbon cycling. Our findings implicate a likely increase in decomposition of SOM in alpine regions. The question arises as to how these temperatures affect the growth of the vegetation and thus the plant derived OM input in these soils. With an earlier onset of snow melt due to climate change (Rogora et al., 2018), the time window in which SOM can be decomposed on a large scale is also increasing (Magnani et al., 2017). Alpine coniferous forests have the largest amount of litter fall in late summer and autumn (Pausas, 1997). A large proportion of the easily degradable carbon contained therein is presumably decomposed

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within a few weeks, as our results suggest: We observed a phase of strong C loss within the first month of incubation across treatments, which would correspond to the fast decomposition of simple substrates soon after litterfall. In addition, an increase in temperature seems to lead to earlier senescence of litter and thus a longer decomposition phase before the onset of snow cover (Ernakovich et al., 2014; Möhl et al., 2022). At the beginning of spring with the onset of snow melt, the SOM therefore consists largely of rather complex compounds. If we consider this from the perspective of our results, in which we observed a still considerable decomposition of SOM in the forest soil without fresh litter, an increased decomposition of SOM in the course of a year can be expected. With additional input of fresh litter, the increased temperatures will also lead to a further increase in the decomposition of SOM, not only of simple compounds but also of more complex polymers such as lignin. Even though a one-year laboratory experiment allows only limited conclusions, our results seem to support the hypothesis of increased SOM decomposition in alpine regions with increasing temperatures, as has already been found in many other studies in alpine regions for both grassland (Chen et al., 2024) as well as forest ecosystems (Albrich et al., 2023). NPP generally increases with rising temperatures (Rustad et al., 2001), especially in alpine regions (Wang et al., 2023), which could lead to an increased input of litter into the soil. However, this would also increase the availability of fresh organic material and thus stimulate the decomposition, as we have seen in our experiment. Therefore, while many alpine soils are still sinks of C, they could therefore potentially develop into sources of C into the atmosphere as temperature rises.

5 Conclusions

Our study emphasises that substrate quality, in particular the availability of labile carbon, is the most important driver of SOM decomposition in the examined alpine forest and pasture soils, outweighing the influence of temperature alone. While temperature increases decomposition, this effect is only enhanced in the presence of labile carbon, especially originating from fresh litter. Contrary to our initial hypothesis, the alpine forest soil (with its lignin-rich material) showed higher carbon loss without litter presumably due to specialised microbial communities, while the pasture soil without labile carbon input exhibited only limited decomposition. The addition of grass litter greatly accelerated decomposition in both investigated soils, confirming our hypothesis that fresh input acts as a priming agent. Decomposition occurs in the short term due to the decomposition of more labile carbon, but slows down in the long term as complex substrates such as lignin dominate. Our findings imply that if alpine ecosystems experience warming along with shifts in vegetation that increase labile litter inputs, SOM decomposition could accelerate substantially. This scenario could potentially reduce the soil C sink strength of similar high elevation soils and in the worst case turning a C sink into a source. Accounting for carbon availability in climate modelling is essential for a better prediction of soil carbon dynamics under future climate scenarios.

Author contributions. DP: Conceptualization, Data Curation, Formal Analysis, Investigation, Visualization, Writing – Original Draft. TCS: Conceptualization, Investigation, Writing – Review & Editing. YAB: Methodology, Resources, Writing – Review & Editing. GLBW: Conceptualization, Funding Acquisition, Investigation, Methodology, Project Administration, Resources, Supervision, Writing – Review & Editing.

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

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Figure A1. Incubation setup: A 2-l glass jar containing a Petri dish filled with 50 g of soil material, a brown vial containing NaOH solution to trap the respired CO^2 and a smaller clear vial containing water to keep a constant humidity within the jar.

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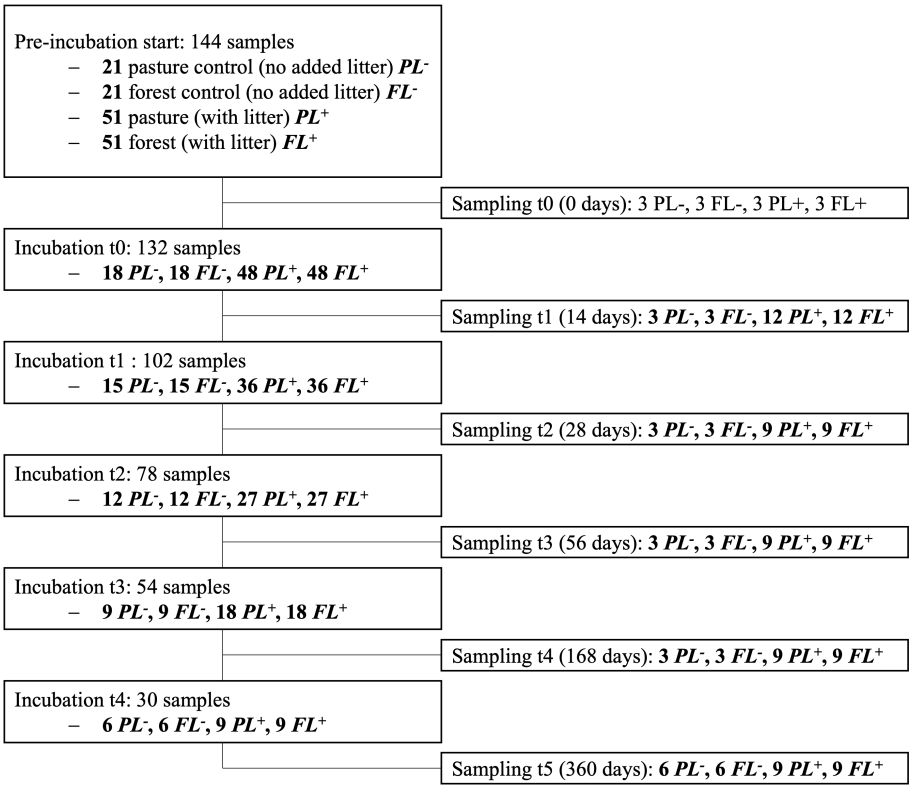

Figure A2. Incubation flowchart illustrating sample progression over time. The left side represents the number of samples remaining in incubation, while the right side denotes the sampling time points (0, 14, 28, 56, 168, and 360 days) and the number of samples collected from each treatment group. **P** refers to pasture, **F** to forest, $\mathbf{L}^-$ to samples without litter, and $\mathbf{L}^+$ to samples with litter.

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Table A1. Overview of incubation experiment parameters and measured soil properties. The table includes sample number, replicate, incubation temperature, vegetation type (P = Pasture, F = Forest), sample type (L– = no litter, L+ = with litter addition), and incubation duration. Measured parameters include total organic carbon (TOC) and total nitrogen (TN) concentrations, the carbon-to-nitrogen (C/N) ratio, and $\delta^{13}C$ values (‰ vs. VPDB).

Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
133	A	12.5	P	L+	0	5.80	0.52	11.11	526.94
133	B	12.5	P	L+	0	5.92	0.53	11.15	565.02
134	A	16.5	P	L+	0	5.92	0.55	10.70	532.11
134	B	16.5	P	L+	0	5.87	0.53	11.05	503.86
135	A	20.5	P	L+	0	5.69	0.52	10.94	411.33
135	B	20.5	P	L+	0	5.42	0.49	11.03	397.92
136	A	12.5	F	L+	0	5.14	0.38	13.55	488.41
136	B	12.5	F	L+	0	5.31	0.39	13.58	528.03
137	A	16.5	F	L+	0	5.40	0.39	13.86	532.11
137	B	16.5	F	L+	0	5.34	0.42	12.71	520.85
138	A	20.5	F	L+	0	5.35	0.39	13.86	370.78
138	B	20.5	F	L+	0	5.39	0.40	13.38	383.55
139	A	12.5	P	L-	0	4.41	0.46	9.66	-26.77
139	B	12.5	P	L-	0	4.72	0.49	9.61	-26.73
140	A	16.5	P	L-	0	4.45	0.46	9.64	-26.77
140	B	16.5	P	L-	0	4.56	0.48	9.53	-26.75
141	A	20.5	P	L-	0	4.57	0.47	9.75	-26.66
141	B	20.5	P	L-	0	4.57	0.49	9.40	-26.60
142	A	12.5	F	L-	0	4.55	0.35	12.97	-25.78
142	B	12.5	F	L-	0	4.23	0.34	12.58	-25.91
143	A	16.5	F	L-	0	4.19	0.34	12.48	-25.84
143	B	16.5	F	L-	0	4.51	0.34	13.26	-25.99
144	A	20.5	F	L-	0	4.28	0.34	12.72	-25.75
144	B	20.5	F	L-	0	4.52	0.35	12.97	-25.77
1	A	12.5	P	L+	14	4.74	0.51	9.34	293.04
1	B	12.5	P	L+	14	4.83	0.53	9.14	325.39
2	A	12.5	P	L+	14	5.02	0.53	9.39	311.21
2	B	12.5	P	L+	14	5.08	0.56	9.06	297.56
3	A	12.5	P	L+	14	5.13	0.52	9.80	325.25

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
3	B	12.5	P	L+	14	5.06	0.54	9.35	332.62
4	A	12.5	P	L+	14	5.01	0.53	9.47	302.97
4	B	12.5	P	L+	14	5.23	0.56	9.30	328.49
5	A	16.5	P	L+	14	5.05	0.51	9.99	290.06
5	B	16.5	P	L+	14	5.24	0.56	9.40	311.00
6	A	16.5	P	L+	14	4.89	0.53	9.18	327.51
6	B	16.5	P	L+	14	4.78	0.51	9.33	306.28
7	A	16.5	P	L+	14	5.18	0.56	9.28	327.06
7	B	16.5	P	L+	14	4.71	0.51	9.24	295.07
8	A	16.5	P	L+	14	5.05	0.55	9.17	251.67
8	B	16.5	P	L+	14	4.93	0.53	9.28	270.66
9	A	20.5	P	L+	14	5.02	0.52	9.69	286.34
9	B	20.5	P	L+	14	5.28	0.57	9.24	302.53
10	A	20.5	P	L+	14	5.07	0.58	8.71	294.63
10	B	20.5	P	L+	14	5.18	0.59	8.78	264.14
11	A	20.5	P	L+	14	5.00	0.57	8.82	283.08
11	B	20.5	P	L+	14	4.98	0.57	8.67	282.83
12	A	20.5	P	L+	14	4.91	0.56	8.77	250.63
12	B	20.5	P	L+	14	5.15	0.57	9.02	255.79
49	A	12.5	P	L-	14	4.58	0.47	9.72	-26.37
49	B	12.5	P	L-	14	4.61	0.47	9.78	-26.56
55	A	16.5	P	L-	14	4.58	0.47	9.64	-26.65
55	B	16.5	P	L-	14	4.67	0.49	9.57	-26.54
61	A	20.5	P	L-	14	4.34	0.45	9.57	-26.69
61	B	20.5	P	L-	14	4.25	0.44	9.59	-26.61
67	A	12.5	F	L+	14	4.94	0.42	11.90	376.39
67	B	12.5	F	L+	14	5.32	0.47	11.26	382.63
68	A	12.5	F	L+	14	5.11	0.44	11.57	352.30
68	B	12.5	F	L+	14	4.89	0.44	11.15	339.61
69	A	12.5	F	L+	14	5.11	0.43	11.79	368.44
69	B	12.5	F	L+	14	4.91	0.44	11.19	370.35
70	A	12.5	F	L+	14	5.00	0.42	11.83	351.05
70	B	12.5	F	L+	14	4.71	0.41	11.39	363.57
71	A	16.5	F	L+	14	4.72	0.40	11.73	298.25

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
71	B	16.5	F	L+	14	5.01	0.42	11.81	307.45
72	A	16.5	F	L+	14	5.09	0.43	11.78	301.26
72	B	16.5	F	L+	14	5.06	0.43	11.82	321.63
73	A	16.5	F	L+	14	5.11	0.43	11.97	295.59
73	B	16.5	F	L+	14	5.06	0.45	11.36	318.60
74	A	16.5	F	L+	14	4.88	0.43	11.34	304.14
74	B	16.5	F	L+	14	4.87	0.42	11.65	309.18
75	A	20.5	F	L+	14	4.64	0.42	11.13	274.22
75	B	20.5	F	L+	14	5.12	0.44	11.60	265.65
76	A	20.5	F	L+	14	5.43	0.47	11.59	317.33
76	B	20.5	F	L+	14	4.98	0.44	11.20	310.71
77	A	20.5	F	L+	14	4.91	0.44	11.14	276.67
77	B	20.5	F	L+	14	4.67	0.42	10.99	279.66
78	A	20.5	F	L+	14	4.90	0.44	11.05	291.93
78	B	20.5	F	L+	14	4.89	0.46	10.61	297.70
115	A	12.5	F	L-	14	4.41	0.34	13.02	-25.70
115	B	12.5	F	L-	14	4.54	0.34	13.28	-25.69
121	A	16.5	F	L-	14	4.67	0.36	12.87	-25.90
121	B	16.5	F	L-	14	4.05	0.32	12.47	-25.75
127	A	20.5	F	L-	14	4.42	0.34	12.95	-25.76
127	B	20.5	F	L-	14	4.43	0.34	12.92	-25.79
13	A	12.5	P	L+	28	4.94	0.58	8.59	329.44
13	B	12.5	P	L+	28	5.25	0.61	8.65	298.57
14	A	12.5	P	L+	28	5.04	0.59	8.48	283.27
14	B	12.5	P	L+	28	4.98	0.58	8.62	282.29
15	A	12.5	P	L+	28	5.12	0.54	9.55	278.72
15	B	12.5	P	L+	28	5.20	0.55	9.47	285.28
17	A	16.5	P	L+	28	4.84	0.55	8.75	220.36
17	B	16.5	P	L+	28	4.99	0.58	8.64	230.86
18	A	16.5	P	L+	28	4.72	0.55	8.62	253.13
18	B	16.5	P	L+	28	4.80	0.56	8.64	263.44
19	A	16.5	P	L+	28	4.98	0.57	8.72	271.27
19	B	16.5	P	L+	28	4.81	0.55	8.71	277.40
21	A	20.5	P	L+	28	4.90	0.51	9.51	265.85

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
21	B	20.5	P	L+	28	4.96	0.55	9.03	247.11
22	A	20.5	P	L+	28	4.77	0.51	9.43	210.26
22	B	20.5	P	L+	28	4.99	0.52	9.63	212.31
23	A	20.5	P	L+	28	4.90	0.52	9.44	248.89
23	B	20.5	P	L+	28	4.93	0.52	9.55	253.74
50	A	12.5	P	L-	28	4.75	0.48	9.84	-26.62
50	B	12.5	P	L-	28	4.57	0.47	9.80	-26.56
56	A	16.5	P	L-	28	4.52	0.48	9.51	-26.55
56	B	16.5	P	L-	28	4.36	0.46	9.54	-26.67
62	A	20.5	P	L-	28	4.57	0.48	9.45	-26.53
62	B	20.5	P	L-	28	4.45	0.47	9.41	-26.68
79	A	12.5	F	L+	28	4.80	0.45	10.60	307.62
79	B	12.5	F	L+	28	4.80	0.44	10.95	311.78
80	A	12.5	F	L+	28	4.61	0.43	10.71	298.02
80	B	12.5	F	L+	28	5.00	0.48	10.37	319.32
81	A	12.5	F	L+	28	4.98	0.45	11.05	288.54
81	B	12.5	F	L+	28	4.90	0.45	10.98	308.89
83	A	16.5	F	L+	28	5.08	0.50	10.16	273.48
83	B	16.5	F	L+	28	4.96	0.45	11.05	271.37
84	A	16.5	F	L+	28	4.96	0.46	10.77	280.88
84	B	16.5	F	L+	28	5.00	0.46	10.93	275.73
85	A	16.5	F	L+	28	4.80	0.44	10.80	278.34
85	B	16.5	F	L+	28	5.04	0.45	11.21	265.79
87	A	20.5	F	L+	28	5.21	0.41	12.69	246.40
87	B	20.5	F	L+	28	4.72	0.40	11.90	274.25
88	A	20.5	F	L+	28	5.07	0.42	11.99	269.54
88	B	20.5	F	L+	28	4.78	0.44	10.77	269.69
89	A	20.5	F	L+	28	4.77	0.42	11.42	242.51
89	B	20.5	F	L+	28	4.74	0.42	11.16	256.93
116	A	12.5	F	L-	28	4.45	0.35	12.65	-25.72
116	B	12.5	F	L-	28	4.25	0.33	12.90	-25.71
122	A	16.5	F	L-	28	3.93	0.32	12.26	-25.77
122	B	16.5	F	L-	28	4.22	0.33	12.97	-25.67
128	A	20.5	F	L-	28	4.00	0.32	12.71	-25.48

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
128	B	20.5	F	L-	28	4.52	0.35	12.96	-25.85
16	A	12.5	P	L+	56	4.88	0.58	8.39	248.72
16	B	12.5	P	L+	56	4.87	0.57	8.55	255.01
20	A	16.5	P	L+	56	4.85	0.58	8.40	244.72
20	B	16.5	P	L+	56	5.14	0.55	9.39	250.12
24	A	20.5	P	L+	56	4.78	0.54	8.82	231.68
24	B	20.5	P	L+	56	4.94	0.54	9.14	239.64
25	A	12.5	P	L+	56	4.69	0.54	8.62	229.94
25	B	12.5	P	L+	56	5.11	0.60	8.53	257.47
26	A	12.5	P	L+	56	4.83	0.56	8.63	255.43
26	B	12.5	P	L+	56	5.01	0.60	8.41	251.91
29	A	16.5	P	L+	56	5.14	0.61	8.43	262.85
29	B	16.5	P	L+	56	5.13	0.52	9.91	258.37
30	A	16.5	P	L+	56	4.86	0.52	9.27	242.75
30	B	16.5	P	L+	56	4.86	0.53	9.09	239.44
33	A	20.5	P	L+	56	4.73	0.50	9.54	234.68
33	B	20.5	P	L+	56	4.86	0.52	9.33	239.29
34	A	20.5	P	L+	56	4.71	0.52	9.00	211.55
34	B	20.5	P	L+	56	5.07	0.55	9.22	215.71
51	A	12.5	P	L-	56	4.50	0.47	9.51	-26.58
51	B	12.5	P	L-	56	4.42	0.47	9.34	-26.50
57	A	16.5	P	L-	56	4.58	0.48	9.46	-26.61
57	B	16.5	P	L-	56	4.54	0.48	9.51	-26.66
63	A	20.5	P	L-	56	4.52	0.47	9.52	-26.68
63	B	20.5	P	L-	56	4.42	0.47	9.38	-26.61
82	A	12.5	F	L+	56	5.01	0.46	10.93	275.77
82	B	12.5	F	L+	56	5.09	0.50	10.23	283.44
86	A	16.5	F	L+	56	5.00	0.48	10.49	245.42
86	B	16.5	F	L+	56	5.01	0.41	12.20	250.33
90	A	20.5	F	L+	56	4.81	0.41	11.74	232.21
90	B	20.5	F	L+	56	5.06	0.41	12.22	251.38
91	A	12.5	F	L+	56	4.90	0.43	11.46	297.77
91	B	12.5	F	L+	56	4.85	0.46	10.60	319.55
92	A	12.5	F	L+	56	5.25	0.48	10.96	283.06

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
92	B	12.5	F	L+	56	4.99	0.46	10.73	288.41
95	A	16.5	F	L+	56	5.13	0.42	12.16	242.70
95	B	16.5	F	L+	56	4.72	0.39	12.23	278.69
96	A	16.5	F	L+	56	4.79	0.40	12.01	264.48
96	B	16.5	F	L+	56	4.96	0.42	11.68	241.90
99	A	20.5	F	L+	56	4.69	0.39	12.12	239.80
99	B	20.5	F	L+	56	4.66	0.43	10.77	245.28
100	A	20.5	F	L+	56	4.68	0.40	11.75	241.98
100	B	20.5	F	L+	56	4.98	0.41	12.07	239.86
117	A	12.5	F	L-	56	4.24	0.34	12.61	-25.80
117	B	12.5	F	L-	56	4.54	0.35	13.14	-25.72
123	A	16.5	F	L-	56	4.50	0.35	12.84	-25.89
123	B	16.5	F	L-	56	4.52	0.35	12.98	-25.79
129	A	20.5	F	L-	56	4.29	0.34	12.64	-25.86
129	B	20.5	F	L-	56	4.38	0.33	13.17	-25.83
27	A	12.5	P	L+	168	5.20	0.53	9.75	227.38
27	B	12.5	P	L+	168	5.06	0.52	9.82	233.21
28	A	12.5	P	L+	168	4.77	0.52	9.24	227.65
28	B	12.5	P	L+	168	4.78	0.53	8.97	237.95
31	A	16.5	P	L+	168	4.82	0.52	9.34	212.12
31	B	16.5	P	L+	168	4.95	0.52	9.61	214.25
32	A	16.5	P	L+	168	4.94	0.53	9.29	181.40
32	B	16.5	P	L+	168	4.77	0.52	9.25	189.36
35	A	20.5	P	L+	168	4.98	0.57	8.74	189.08
35	B	20.5	P	L+	168	4.73	0.55	8.59	197.79
36	A	20.5	P	L+	168	4.83	0.52	9.38	189.69
36	B	20.5	P	L+	168	4.80	0.50	9.69	196.10
37	A	12.5	P	L+	168	5.17	0.53	9.78	231.85
37	B	12.5	P	L+	168	5.04	0.56	8.93	223.01
41	A	16.5	P	L+	168	4.71	0.52	9.04	196.60
41	B	16.5	P	L+	168	4.77	0.53	9.08	195.10
45	A	20.5	P	L+	168	4.62	0.49	9.38	137.43
45	B	20.5	P	L+	168	4.63	0.52	8.96	138.61
52	A	12.5	P	L-	168	4.42	0.47	9.34	-26.63

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
52	B	12.5	P	L-	168	4.43	0.48	9.32	-26.57
58	A	16.5	P	L-	168	4.76	0.51	9.31	-26.63
58	B	16.5	P	L-	168	4.53	0.49	9.26	-26.64
64	A	20.5	P	L-	168	4.45	0.48	9.32	-26.67
64	B	20.5	P	L-	168	4.30	0.47	9.06	-26.51
93	A	12.5	F	L+	168	4.73	0.40	11.74	229.32
93	B	12.5	F	L+	168	5.06	0.41	12.23	245.17
94	A	12.5	F	L+	168	5.04	0.40	12.49	250.33
94	B	12.5	F	L+	168	5.10	0.43	11.94	230.15
97	A	16.5	F	L+	168	4.70	0.35	13.44	184.39
97	B	16.5	F	L+	168	4.43	0.33	13.36	198.99
98	A	16.5	F	L+	168	4.98	0.42	11.96	203.78
98	B	16.5	F	L+	168	4.74	0.40	11.93	217.10
101	A	20.5	F	L+	168	4.56	0.39	11.63	206.16
101	B	20.5	F	L+	168	4.76	0.40	11.76	191.10
102	A	20.5	F	L+	168	4.59	0.41	11.14	201.42
102	B	20.5	F	L+	168	4.68	0.43	11.02	206.49
103	A	12.5	F	L+	168	4.89	0.40	12.30	252.46
103	B	12.5	F	L+	168	4.75	0.40	11.96	244.41
107	A	16.5	F	L+	168	5.05	0.42	12.14	206.37
107	B	16.5	F	L+	168	4.72	0.40	11.70	210.03
111	A	20.5	F	L+	168	4.72	0.40	11.88	208.87
111	B	20.5	F	L+	168	4.84	0.43	11.23	203.52
118	A	12.5	F	L-	168	4.81	0.35	13.82	-25.91
118	B	12.5	F	L-	168	3.89	0.33	11.79	-25.72
124	A	16.5	F	L-	168	4.47	0.35	12.70	-25.88
124	B	16.5	F	L-	168	4.22	0.34	12.33	-25.74
130	A	20.5	F	L-	168	4.08	0.34	12.13	-25.88
130	B	20.5	F	L-	168	4.58	0.35	13.05	-25.89
38	A	12.5	P	L+	360	4.88	0.50	9.68	207.84
38	B	12.5	P	L+	360	4.81	0.50	9.59	203.36
39	A	12.5	P	L+	360	5.07	0.53	9.55	213.46
39	B	12.5	P	L+	360	5.19	0.56	9.22	195.88
40	A	12.5	P	L+	360	4.65	0.49	9.40	202.20

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
40	B	12.5	P	L+	360	4.87	0.51	9.49	218.98
42	A	16.5	P	L+	360	4.69	0.49	9.52	179.50
42	B	16.5	P	L+	360	4.64	0.49	9.41	171.13
43	A	16.5	P	L+	360	5.01	0.53	9.42	169.92
43	B	16.5	P	L+	360	4.69	0.54	8.70	170.92
44	A	16.5	P	L+	360	4.81	0.50	9.66	192.64
44	B	16.5	P	L+	360	4.37	0.46	9.59	162.46
46	A	20.5	P	L+	360	4.71	0.54	8.80	142.88
46	B	20.5	P	L+	360	4.72	0.55	8.52	139.64
47	A	20.5	P	L+	360	4.67	0.52	8.96	148.37
47	B	20.5	P	L+	360	4.61	0.53	8.61	149.10
48	A	20.5	P	L+	360	4.59	0.53	8.71	173.34
48	B	20.5	P	L+	360	4.84	0.55	8.77	185.34
53	A	12.5	P	L-	360	4.58	0.48	9.53	-26.70
53	B	12.5	P	L-	360	4.25	0.45	9.39	-26.69
54	A	12.5	P	L-	360	4.77	0.51	9.27	-26.68
54	B	12.5	P	L-	360	4.30	0.48	9.01	-26.64
59	A	16.5	P	L-	360	4.10	0.44	9.23	-26.72
59	B	16.5	P	L-	360	4.37	0.47	9.21	-26.67
60	A	16.5	P	L-	360	4.61	0.50	9.22	-26.71
60	B	16.5	P	L-	360	4.14	0.45	9.22	-26.66
65	A	20.5	P	L-	360	4.48	0.48	9.40	-26.67
65	B	20.5	P	L-	360	4.29	0.47	9.17	-26.69
66	A	20.5	P	L-	360	4.40	0.48	9.25	-26.48
66	B	20.5	P	L-	360	4.45	0.49	9.13	-26.68
104	A	12.5	F	L+	360	4.62	0.38	12.22	233.09
104	B	12.5	F	L+	360	4.53	0.37	12.08	232.51
105	A	12.5	F	L+	360	4.61	0.39	11.97	233.23
105	B	12.5	F	L+	360	4.73	0.38	12.38	254.17
106	A	12.5	F	L+	360	5.06	0.41	12.35	225.30
106	B	12.5	F	L+	360	4.69	0.40	11.74	209.30
108	A	16.5	F	L+	360	4.43	0.38	11.80	168.50
108	B	16.5	F	L+	360	4.90	0.39	12.58	187.77
109	A	16.5	F	L+	360	4.97	0.39	12.73	167.07

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Sample number	Replicate	Temperature [°C]	Vegetation	Type	Incubation duration [d]	TOC concentration [%]	TN concentration [%]	C/N ratio	$\delta^{13}C$ [‰ vs. VPDB]
109	B	16.5	F	L+	360	4.85	0.39	12.42	166.48
110	A	16.5	F	L+	360	4.62	0.36	12.91	187.33
110	B	16.5	F	L+	360	4.61	0.37	12.50	189.20
112	A	20.5	F	L+	360	4.39	0.42	10.46	160.01
112	B	20.5	F	L+	360	5.11	0.45	11.35	151.03
113	A	20.5	F	L+	360	4.67	0.39	12.12	155.10
113	B	20.5	F	L+	360	4.99	0.41	12.21	157.37
114	A	20.5	F	L+	360	4.36	0.35	12.63	163.92
114	B	20.5	F	L+	360	4.26	0.33	12.77	157.20
119	A	12.5	F	L-	360	4.24	0.34	12.49	-25.69
119	B	12.5	F	L-	360	3.90	0.32	12.03	-25.70
120	A	12.5	F	L-	360	4.04	0.33	12.20	-25.75
120	B	12.5	F	L-	360	4.21	0.33	12.81	-25.80
125	A	16.5	F	L-	360	4.26	0.33	12.73	-26.08
125	B	16.5	F	L-	360	4.36	0.35	12.30	-25.72
126	A	16.5	F	L-	360	4.24	0.35	11.98	-25.91
126	B	16.5	F	L-	360	4.02	0.34	12.00	-25.68
131	A	20.5	F	L-	360	4.19	0.35	11.93	-25.88
131	B	20.5	F	L-	360	3.94	0.34	11.49	-25.80
132	A	20.5	F	L-	360	3.34	0.30	11.27	-25.69
132	B	20.5	F	L-	360	4.28	0.34	12.52	-26.10

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Table A2. Decomposition constants of APE for L^+ soils and the different incubation conditions. The table presents the decomposition constant (k) and its standard error (SE) for two incubation durations (early phase 0–28 days and 0–360 days), expressed in per day and per year units.

Temperature	**Vegetation**	k **(0–28 days)** $[d^{-1}]$	**SE** k **(0–28 days)** $[d^{-1}]$	k **(0–360 days)** $[d^{-1}]$	**SE** k **(0–360 days)** $[d^{-1}]$	k **(0–360 days)** $[d^{-1}]$	**SE** k **(0–360 days)** $[d^{-1}]$
12.5	Forest	4.2×10^{-3}	1.4×10^{-5}	1.4×10^{-6}	6.5×10^{-9}	4.9×10^{-4}	2.4×10^{-6}
12.5	Pasture	5.1×10^{-3}	3.1×10^{-5}	1.6×10^{-6}	4.5×10^{-9}	5.8×10^{-4}	1.6×10^{-6}
16.5	Forest	5.1×10^{-3}	0.9×10^{-5}	1.7×10^{-6}	6.7×10^{-9}	6.2×10^{-4}	2.4×10^{-6}
16.5	Pasture	6.2×10^{-3}	4.6×10^{-5}	1.8×10^{-6}	6.6×10^{-9}	6.6×10^{-4}	2.4×10^{-6}
20.5	Forest	5.5×10^{-3}	2.4×10^{-5}	1.8×10^{-6}	2.8×10^{-9}	6.7×10^{-4}	1.0×10^{-6}
20.5	Pasture	6.6×10^{-3}	5.0×10^{-5}	1.9×10^{-6}	12.6×10^{-9}	7.0×10^{-4}	4.6×10^{-6}

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Table A3. Lignin phenol concentrations in soil samples under different incubation conditions. The table includes sample number, incubation temperature (Temp.), vegetation type (Veg.; P = pasture, F = forest), sample type (L- = no litter, L+ = with litter addition), and incubation duration (Inc. Dur.), along with measured concentrations of individual lignin-derived phenols. The abbreviations for the phenols used here are the following: V = Vanillin, VAc = Vanillic acid, AV = Acetovanillone, SyAl = Syringaldehyde, SyAc = Syringic acid, AS = Acetosyringone, CAc = Coumaric acid, FAc = Ferulic acid, SaAl = Salicylaldehyde, SaAc = Salicylic acid, P = Piceol.

Sample Nr.	Temp. [°C]	Veg.	Type	Inc. Dur. [d]	V [μg g^{-1}]	VAc [μg g^{-1}]	AV [μg g^{-1}]	SAl [μg g^{-1}]	SyAc [μg g^{-1}]	AS [μg g^{-1}]	CAc [μg g^{-1}]	FAc [μg g^{-1}]	SaAl [μg g^{-1}]	SaAc [μg g^{-1}]	P [μg g^{-1}]
258B21TS1	12.5	P	L+	14	233.8	114.0	65.3	176.9	120.9	74.9	206.4	225.1	71.9	39.5	5.2
258B21TS2	12.5	P	L+	14	285.9	95.6	87.8	208.4	138.2	89.0	180.4	190.1	51.1	13.2	2.6
258B21TS3	12.5	P	L+	14	255.0	100.2	73.0	197.9	138.2	78.8	213.7	232.7	52.0	16.8	4.4
258B21TS4	12.5	P	L+	14	275.1	123.1	70.8	168.7	147.0	65.9	217.0	237.3	75.1	49.0	19.0
258B21TS5	16.5	P	L+	14	265.1	97.3	84.1	182.2	88.8	88.8	167.7	194.4	51.8	17.5	38.9
258B21TS9	20.5	P	L+	14	291.1	109.2	101.0	202.1	168.8	55.0	175.1	205.0	36.1	31.3	38.8
258B21TS13	12.5	P	L+	28	289.8	108.0	93.0	195.5	137.1	73.3	178.5	200.9	48.9	10.1	43.0
258B21TS16	12.5	P	L+	56	279.6	104.5	88.4	186.8	118.4	51.3	146.0	175.0	42.8	9.3	40.3
258B21TS17	16.5	P	L+	28	308.7	116.6	103.7	200.8	141.7	47.2	136.5	152.3	41.7	8.9	44.9
258B21TS20	16.5	P	L+	56	267.9	101.8	82.6	182.2	114.5	44.4	146.6	179.0	33.6	7.3	37.0
258B21TS21	20.5	P	L+	28	276.8	114.1	99.4	185.8	137.2	54.7	125.2	153.9	37.2	10.6	41.4
258B21TS24	20.5	P	L+	56	280.1	111.7	87.6	188.8	123.4	52.6	157.3	184.2	36.3	7.4	40.5
258B21TS27	12.5	P	L+	168	303.8	116.1	98.9	196.0	114.1	38.5	112.3	138.0	36.7	6.0	42.7
258B21TS31	16.5	P	L+	168	253.4	100.3	85.0	176.7	99.4	40.2	115.9	148.6	32.6	7.1	36.2
258B21TS35	20.5	P	L+	168	315.2	122.4	108.5	183.9	140.4	64.4	82.5	90.8	57.1	14.3	49.2
258B21TS38	12.5	P	L+	360	206.0	84.7	61.8	161.8	78.8	25.0	155.7	178.5	15.9	28.5	24.5
258B21TS42	16.5	P	L+	360	248.1	153.1	89.9	186.9	101.5	13.4	145.3	149.5	28.6	29.1	33.8
258B21TS46	20.5	P	L+	360	255.7	51.8	95.3	202.1	84.4	88.4	134.6	140.4	20.0	28.4	31.7
258B21TS49	12.5	P	L-	14	280.2	121.4	96.7	209.2	144.0	72.3	234.1	253.6	38.3	9.8	43.9
258B21TS50	12.5	P	L-	28	255.3	100.8	78.8	194.5	125.2	54.6	243.3	266.3	32.2	7.2	38.6
258B21TS51	12.5	P	L-	56	260.2	100.7	95.9	155.0	160.0	154.6	117.7	113.1	85.6	55.8	50.1
258B21TS52	12.5	P	L-	168	267.0	85.1	83.2	158.2	91.1	70.8	98.8	116.7	44.7	9.0	42.8
258B21TS53	12.5	P	L-	360	156.0	85.9	53.1	131.6	78.8	35.7	148.7	169.1	21.6	25.1	23.6
258B21TS54	12.5	P	L-	360	223.7	94.0	71.5	176.1	84.3	29.9	156.1	174.2	19.4	14.7	28.9
258B21TS55	16.5	P	L-	14	229.7	96.9	67.6	171.5	128.9	124.1	256.3	279.6	97.1	90.1	37.8
258B21TS56	16.5	P	L-	56	288.8	101.3	93.2	183.5	111.9	83.2	129.9	136.9	57.3	31.5	47.7
258B21TS57	16.5	P	L-	28	290.3	120.2	96.4	216.1	145.2	65.6	233.4	253.3	38.1	7.7	46.4

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Sample Nr.	Temp. [°C]	Veg.	Type	Inc. Dur. [d]	V [µg g^{-1}]	VAc [µg g^{-1}]	AV [µg g^{-1}]	SAl [µg g^{-1}]	SyAc [µg g^{-1}]	AS [µg g^{-1}]	CAc [µg g^{-1}]	FAc [µg g^{-1}]	SaAl [µg g^{-1}]	SaAc [µg g^{-1}]	P [µg g^{-1}]
258B21TS58	16.5	P	L-	168	172.3	81.3	70.4	122.7	138.2	94.1	139.3	162.5	33.5	17.6	34.9
258B21TS59	16.5	P	L-	360	223.8	90.2	74.7	168.9	86.6	34.1	151.7	161.8	19.4	10.8	29.2
258B21TS60	16.5	P	L-	360	269.8	129.5	101.6	187.7	104.5	52.3	113.5	75.0	47.3	21.5	44.6
258B21TS61	20.5	P	L-	14	289.0	117.0	93.9	213.6	145.3	89.2	234.2	252.4	57.8	16.2	45.8
258B21TS62	20.5	P	L-	28	190.3	186.7	89.9	76.9	129.3	40.1	210.4	209.5	69.1	39.4	48.3
258B21TS63	20.5	P	L-	56	279.4	101.3	96.6	170.9	111.3	72.7	95.9	94.8	52.0	28.9	48.9
258B21TS64	20.5	P	L-	168	205.5	85.9	66.7	142.3	101.9	64.9	113.5	137.3	42.1	0.2	36.2
258B21TS65	20.5	P	L-	360	205.0	106.1	81.9	157.6	99.2	49.3	126.7	127.3	26.8	12.4	32.9
258B21TS66	20.5	P	L-	360	294.4	45.1	113.1	197.8	107.0	130.5	115.7	94.6	41.4	22.5	44.5
258B21TS67	12.5	F	L+	14	666.9	231.3	177.9	68.4	45.9	26.5	140.7	128.0	61.3	8.1	21.2
258B21TS71	16.5	F	L+	14	656.2	28.8	180.9	61.8	55.4	146.0	129.5	136.3	47.1	5.4	45.5
258B21TS75	20.5	F	L+	14	651.8	28.0	210.3	66.8	61.8	140.0	111.0	117.1	45.0	7.2	44.9
258B21TS79	12.5	F	L+	28	617.6	28.3	183.9	59.5	42.2	151.5	117.3	128.6	52.5	10.2	43.6
258B21TS82	12.5	F	L+	56	719.6	29.1	204.2	67.2	60.2	152.5	122.8	126.9	50.4	5.9	48.9
258B21TS83	16.5	F	L+	28	736.6	28.7	224.3	65.2	41.1	123.7	107.5	107.0	38.6	4.1	49.6
258B21TS86	16.5	F	L+	56	656.8	29.1	199.1	62.2	42.7	141.9	109.8	115.0	44.8	6.1	45.3
258B21TS87	20.5	F	L+	28	698.9	233.8	220.2	67.6	68.9	244.3	109.8	108.4	185.7	130.8	58.4
258B21TS90	20.5	F	L+	56	597.6	28.5	189.7	57.2	48.5	150.2	117.9	115.1	40.1	4.9	46.3
258B21TS93	12.5	F	L+	168	713.3	23.3	204.5	60.2	23.4	157.0	97.9	99.7	52.9	6.7	49.6
258B21TS97	16.5	F	L+	168	707.2	24.1	205.6	62.0	39.3	189.5	111.5	115.3	62.3	9.0	51.9
258B21TS101	20.5	F	L+	168	605.4	29.8	176.9	55.6	58.8	208.4	108.2	109.0	61.2	13.9	47.0
258B21TS104	12.5	F	L+	360	599.2	30.5	186.1	62.4	47.9	140.5	118.9	33.7	38.6	7.6	39.4
258B21TS108	16.5	F	L+	360	552.7	46.3	138.6	58.7	37.5	101.0	101.6	55.6	35.6	6.2	38.8
258B21TS112	20.5	F	L+	360	537.1	33.2	168.6	57.9	33.7	72.9	101.3	97.1	22.1	5.9	33.7
258B21TS115	12.5	F	L-	14	638.5	9.6	176.0	47.0	66.9	359.7	185.0	134.7	156.2	112.9	50.4
258B21TS116	12.5	F	L-	28	629.0	20.5	180.8	49.0	54.5	140.8	148.5	133.5	37.7	22.9	47.8
258B21TS117	12.5	F	L-	56	645.1	21.5	181.4	42.8	42.4	174.8	95.7	78.3	47.7	6.2	50.0
258B21TS118	12.5	F	L-	168	842.5	28.8	247.8	49.2	55.5	298.2	74.8	29.0	89.1	12.4	71.3
258B21TS119	12.5	F	L-	360	303.8	116.1	98.9	196.0	114.1	38.5	112.3	138.0	36.7	6.0	42.7
258B21TS120	12.5	F	L-	360	513.1	25.4	135.1	39.8	25.2	105.5	96.6	82.6	33.2	6.6	35.7
258B21TS121	16.5	F	L-	14	561.1	22.8	207.6	54.0	62.4	264.2	161.7	141.6	82.1	12.8	56.9
258B21TS122	16.5	F	L-	28	682.3	24.0	199.7	53.5	58.2	217.2	160.0	146.7	66.1	9.0	52.7
258B21TS123	16.5	F	L-	56	684.0	22.5	196.6	42.9	45.5	202.9	95.8	21.5	61.7	14.5	52.5

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Sample Nr.	Temp. [°C]	Veg.	Type	Inc. Dur. [d]	V [µg g^{-1}]	VAc [µg g^{-1}]	AV [µg g^{-1}]	SAl [µg g^{-1}]	SyAc [µg g^{-1}]	AS [µg g^{-1}]	CAc [µg g^{-1}]	FAc [µg g^{-1}]	SaAl [µg g^{-1}]	SaAc [µg g^{-1}]	P [µg g^{-1}]
258B21TS124	16.5	F	L-	168	673.7	38.0	208.8	44.5	52.2	209.9	97.1	73.6	69.7	10.1	55.8
258B21TS125	16.5	F	L-	360	463.3	34.9	134.4	36.2	31.4	86.0	111.4	76.0	22.7	18.7	33.7
258B21TS126	16.5	F	L-	360	657.9	51.5	195.4	48.4	36.0	116.6	123.0	82.3	40.8	7.9	45.7
258B21TS127	20.5	F	L-	14	667.7	136.0	190.1	51.4	60.0	64.0	162.2	137.2	51.3	23.7	52.5
258B21TS128	20.5	F	L-	28	729.1	16.8	209.0	50.9	58.7	287.2	149.1	125.5	98.8	21.8	57.3
258B21TS129	20.5	F	L-	56	658.5	21.7	193.1	39.5	48.0	198.1	84.3	67.4	52.6	4.4	54.8
258B21TS130	20.5	F	L-	168	680.6	23.9	198.0	41.9	41.4	241.6	84.9	71.6	75.3	13.0	52.3
258B21TS131	20.5	F	L-	360	572.3	35.7	181.8	42.1	32.3	88.0	100.2	73.8	25.6	20.5	38.3
258B21TS132	20.5	F	L-	360	551.8	28.1	205.4	40.1	28.8	61.7	72.7	54.8	17.9	18.7	37.8
258B21TS133	12.5	P	L+	0	312.8	129.1	106.3	213.1	154.4	86.8	181.7	236.8	65.0	14.0	47.9
258B21TS134	16.5	P	L+	0	325.8	124.0	109.5	209.5	147.7	69.2	154.9	195.8	51.0	4.9	50.6
258B21TS135	20.5	P	L+	0	261.2	105.3	85.7	192.3	123.1	76.8	188.3	263.1	51.4	13.5	41.6
258B21TS136	12.5	F	L+	0	699.4	37.4	201.3	72.8	59.4	217.1	144.6	192.1	70.6	6.5	53.5
258B21TS137	16.5	F	L+	0	723.6	39.4	224.5	67.9	92.2	243.5	149.6	190.3	63.0	4.8	61.2
258B21TS138	20.5	F	L+	0	711.2	36.7	211.9	68.2	56.8	174.5	130.2	163.6	52.0	4.7	56.5
258B21TS139	12.5	P	L-	0	268.6	118.7	95.8	181.3	157.7	73.9	172.4	157.2	39.0	28.7	46.9
258B21TS140	16.5	P	L-	0	257.9	108.5	92.6	173.9	161.1	87.7	172.1	156.5	44.3	5.6	46.5
258B21TS141	20.5	P	L-	0	267.9	94.6	87.4	168.2	100.5	77.4	115.4	120.0	52.6	9.1	42.4
258B21TS142	12.5	F	L-	0	680.7	32.4	211.4	51.4	44.7	167.6	112.3	85.4	48.9	5.1	50.1
258B21TS143	16.5	F	L-	0	686.8	34.1	211.4	46.7	56.1	293.6	123.8	86.4	75.6	11.1	57.6
258B21TS144	20.5	F	L-	0	624.5	24.5	170.7	41.3	44.1	210.4	98.6	20.2	62.7	8.1	50.3

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Table A4. Statistical significance (*p*-values) of total organic carbon (TOC) differences between temperature treatments on individual days during the incubation period. Values represent pairwise comparisons of two temperatures, with significant differences ($p < 0.05$) highlighted.

Total organic carbon			
Pasture L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.78	0.98	0.47
14	0.66	0.06	**0.03**
28	0.22	0.33	0.56
56	0.21	0.93	0.29
168	0.30	0.64	0.20
360	0.36	0.62	0.47
Forest L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.88	0.97	0.83
14	0.78	0.60	0.86
28	0.27	0.79	0.61
56	0.58	0.77	0.14
168	0.99	0.97	0.96
360	0.30	0.52	0.28
Pasture L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.37	0.16	0.64
14	0.97	**0.02**	**0.02**
28	0.33	**0.04**	**<0.01**
56	0.07	**<0.01**	0.73
168	0.46	0.26	0.48
360	0.52	**<0.01**	**<0.01**
Forest L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.30	0.32	0.94
14	0.77	0.60	0.74
28	0.11	0.74	0.36
56	0.37	**0.05**	0.23
168	0.20	**0.02**	0.46
360	0.84	0.65	0.57

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Table A5. Statistical significance (*p*-values) of total organic carbon (TOC) isotope composition (δ ^{13}C) differences between temperature treatments on individual days during the incubation period. Values represent pairwise comparisons of two temperatures, with significant differences (p <0.05) highlighted.

TOC isotopic composition d13C			
Pasture L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.87	0.09	0.12
14	0.39	0.29	0.52
28	0.83	0.88	0.99
56	0.19	0.18	0.93
168	0.43	0.91	0.65
360	0.53	0.43	0.33
Forest L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.56	0.40	0.28
14	0.34	0.13	0.63
28	0.91	0.82	0.80
56	0.34	0.26	0.97
168	0.98	0.56	0.48
360	0.33	0.24	0.87
Pasture L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.37	0.06	**0.04**
14	0.14	**<0.01**	0.11
28	**<0.01**	**<0.01**	0.35
56	0.99	**<0.01**	**<0.01**
168	**<0.01**	**<0.01**	0.11
360	**<0.01**	**<0.01**	0.07
Forest L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.52	0.07	**<0.01**
14	**<0.01**	**<0.01**	**0.03**
28	**<0.01**	**<0.01**	**0.04**
56	**<0.01**	**<0.01**	0.11
168	**<0.01**	**<0.01**	0.92
360	**<0.01**	**<0.01**	**<0.02**

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Table A6. Statistical significance (*p*-values) of total nitrogen (TN) differences between temperature treatments on individual days during the incubation period. Values represent pairwise comparisons of two temperatures, with significant differences (p <0.05) highlighted.

Total nitrogen			
Pasture L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.88	0.87	0.63
14	0.36	0.13	0.06
28	0.58	0.74	0.39
56	0.26	0.77	0.19
168	0.25	0.50	0.26
360	0.47	0.77	0.51
Forest L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.58	0.92	0.58
14	0.88	0.39	0.95
28	0.35	0.72	0.69
56	0.30	0.48	0.15
168	0.55	0.75	0.74
360	0.10	0.88	0.45
Pasture L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.36	0.37	0.19
14	0.72	**<0.01**	**<0.01**
28	0.29	**<0.01**	**<0.01**
56	0.21	**<0.01**	0.2
168	0.20	0.58	0.85
360	0.34	0.14	**0.03**
Forest L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.39	0.47	0.61
14	0.30	0.39	**0.04**
28	0.38	**0.01**	**<0.01**
56	**0.02**	**<0.01**	0.48
168	0.22	0.67	0.17
360	0.25	0.91	0.56

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Table A7. Statistical significance (p-values) of carbon to nitrogen ratio differences between temperature treatments on individual days during the incubation period. Values represent pairwise comparisons of two temperatures, with significant differences ($p < 0.05$) highlighted.

Carbon to nitrogen ratio			
Pasture L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.50	0.79	0.97
14	0.09	0.10	0.65
28	**0.01**	**<0.01**	0.08
56	0.64	0.83	0.76
168	0.32	0.49	0.60
360	0.52	0.63	0.80
Forest L-	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.85	0.80	0.95
14	0.21	0.34	0.41
28	0.73	0.78	0.65
56	0.92	0.94	0.99
168	0.82	0.87	0.90
360	0.62	0.14	0.23
Pasture L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.37	0.16	0.64
14	0.97	**0.02**	**0.02**
28	0.33	**0.04**	**<0.01**
56	0.07	**<0.01**	0.73
168	0.46	0.26	0.48
360	0.52	**<0.01**	**<0.01**
Forest L+	Temperatures		
Incubation duration [d]	12.5 °C to 16.5 °C	12.5 °C to 20.5 °C	16.5 °C to 20.5 °C
0	0.71	0.85	0.66
14	0.22	**0.04**	**<0.01**
28	0.82	**0.02**	**0.03**
56	**0.02**	**<0.01**	0.97
168	0.38	**<0.01**	**0.03**
360	0.08	0.61	0.19