



Landscape-scale patterns of soil organic carbon mineralization: Spatial, temporal, and vertical variability

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Abstract.

The mineralization of soil organic carbon (SOC) through microbial respiration is controlled by a complex interplay of environmental conditions, stabilization mechanisms, and substrate availability. SOC mineralization varies with land use, soil depth, and environmental conditions, but how these factors interact across entire soil profiles and throughout the year remains insufficiently understood. We investigated spatial, seasonal, and vertical patterns of SOC mineralization in coniferous forest, meadow, and cropland soils across a 20 × 20 km landscape in the Fichtelgebirge Mountains, Bavaria, Germany. Soil samples were collected 120 times within one year from depths down to 1 m and sliced into 10 cm increments. On the day of sampling, samples were incubated for multiple hours at field temperature and moisture to estimate mineralization under in situ conditions. Additional standardized laboratory incubations (10 days, 22°C and 50 % WHC) were used to determine potential SOC-specific mineralization as an indicator of SOC stability.

Potential SOC-specific mineralization did not consistently decrease with depth. Instead, it was higher in the deepest subsoil (70–100 cm) than in the topsoil (0–30 cm) and upper subsoil (30–70 cm) in coniferous forest and cropland, indicating that subsoil SOC is not necessarily more stable than topsoil SOC. Under in situ field conditions, mineralization rates were significantly higher in meadow soils than in cropland and coniferous forest soils across all depth intervals, demonstrating that land use influences SOC mineralization throughout the upper meter of the soil profile. Despite pronounced seasonal variation in soil temperature and moisture, no clear seasonal pattern in SOC mineralization emerged, potentially reflecting contrasting constraints imposed by temperature and water availability. Mineralization rates under field conditions of temperature and moisture declined with depth in cropland but remained comparatively stable with depth in meadow and coniferous forest soils, despite decreasing SOC stocks.

Our findings highlight that SOC stocks alone do not adequately explain patterns of mineralization and the resulting CO₂ release across space, time, and depth and that the relationships between SOC stability, land use, soil depth, and environmental conditions are complex. Accounting for these interactions is important for improving assessments of soil carbon dynamics across landscapes and for understanding the potential vulnerability of subsoil carbon to mineralization.



25 1 Introduction

The aerobic mineralization of soil organic carbon (SOC) to CO₂, i.e. heterotrophic CO₂ production, represents an important pathway of soil carbon cycling, linking soil organic carbon (SOC) stocks to soil CO₂ efflux and atmospheric CO₂ release. Due to the large quantity of SOC stored in the soil, even small shifts in SOC stocks can significantly affect atmospheric CO₂ concentrations and climate feedbacks (Yan and Kumar, 2021). Recent studies show the vulnerability of SOC to climate- and environmental changes and highlight rising heterotrophic CO₂ production rates (Bond-Lamberty et al., 2018) and decreasing SOC stocks (Crowther et al., 2016) in recent decades. Yet, predictions of climate change feedbacks and the development of management strategies to sequester additional SOC for climate change mitigation (i.e. 4 per mil initiative (Minasny et al., 2017)) require detailed knowledge on spatio-temporal patterns of SOC mineralization and their controlling factors across a landscape. Gathering such knowledge is complicated by the fact that absolute (i.e. amount of produced CO₂) and SOC-specific (i.e. amount of produced CO₂ per unit SOC) mineralization rates are highly variable in space (Tang and Baldocchi, 2005), depth (Fang and Moncrieff, 2005; Davidson et al., 2006a), and time (Tang and Baldocchi, 2005; Davidson et al., 2006a). This variability results from spatio-temporal variations of its controlling factors: SOC stocks (Meyer et al., 2018b; Cleveland et al., 2007), temperature (Lloyd and Taylor, 1994), soil moisture (Cook and Orchard, 2008), and physical, physicochemical and biochemical stabilization mechanisms (Von Lützow et al., 2008; Six et al., 2002), which are driving SOC mineralization via complex and non-linear interactions. Without knowledge on spatio-temporal SOC mineralization patterns, however, a quantification of the current state and predictions on the vulnerability to changing conditions remain speculative and limited to point measurements.

Especially the subsoil (30-70 cm) and deep subsoil (70-100 cm) received little attention in this context. Only few studies (Hirano, 2005; Davidson et al., 2006a) focus on the contribution of the subsoil to soil CO₂ efflux although it may account for 50% of the total SOC stock (Jobbágy and Jackson, 2000). Also, many subsoil studies are based on incubation experiments at altered (i.e. often optimal) conditions of temperature and moisture (Lomander et al., 1998; Fierer et al., 2003; Meyer et al., 2018a). Yet, such experiments may under- or overestimate the contribution of subsoil to CO₂ efflux because incubation temperatures and moisture conditions may differ substantially from those experienced by subsoils under field conditions. For many times of the year, the subsoil might be characterized by more favorable conditions for SOC mineralization than the topsoil (e.g., higher temperatures in winter, higher soil moisture in dry summer), thereby even contributing more to soil CO₂ efflux than the topsoil (Hirano, 2005; Davidson et al., 2006a). An assessment of SOC mineralization rates under actual temperature and moisture conditions would be needed to assess the stability of SOC in topsoil and subsoil and to unravel the respective contribution to soil CO₂ efflux.

Besides temperature and moisture, also biochemical and physical stabilization mechanisms determine patterns of SOC mineralization rate (Von Lützow et al., 2008). Molecular characteristics like, for example, woody vegetation with high lignin concentrations lead to a higher primary recalcitrance to microbial mineralization than lignin-poorer plants such as grasses or



cereal crops in grassland and arable systems. This is commonly cited as one driver for the generally higher carbon contents of forest soils (Martens et al., 2004; Osono et al., 2014; Pisani et al., 2016). Furthermore, the biochemical composition and pathways of SOC inputs vary vertically within the soil profile. Whereas aboveground litter represents a major source of fresh C in the topsoil, subsoil C inputs occur predominantly through root-derived carbon and dissolved organic carbon (DOC). (Rumpel and Kögel-Knabner, 2011). Although fine roots, which dominate root-derived C inputs, often decompose as fast as aboveground litter (Silver and Miya, 2001), root-derived C is nevertheless preferentially stabilized in soil compared to litter-derived C (Rasse et al., 2005; Kätterer et al., 2011), likely because roots and their microbial breakdown products are deposited directly at mineral surfaces, particularly in deeper soil layers (Rasse et al., 2005; Jackson et al., 2017). Further, the association of SOC with mineral surfaces and its physical occlusion within soil aggregates can reduce its accessibility to microbial decomposers and thereby contribute to SOC persistence (Kleber et al., 2021; Sokol et al., 2022). Physio-chemical stabilization of SOC through aggregate formation and breakdown is influenced by external abiotic factors, including drying-wetting and freezing-thawing cycles, as well as mechanical disturbance such as tillage (Borken and Matzner, 2009; Matzner and Borken, 2008; Andruschkewitsch et al., 2013). Physical stabilization may be more pronounced in deeper soil layers, where more mineral surfaces are abundant relative to SOC content (Schrumpf et al., 2013). Due to these varying mechanisms, subsoil SOC is consequently assumed to be older and has been reported to be more stable than topsoil SOC (Rumpel et al., 2002; Shi et al., 2020; Schulze et al., 2009).

All the above mentioned mechanisms that control SOC mineralization are influenced by the land use type with different vegetation cover, soil management, and fertilization. Yao et al. (2019) found that in grasslands the abundance of recalcitrant SOC compounds (e.g. lignin) is higher than in agriculturally managed soils. They attribute this to the removal of plant litter from cultivated soil, leaving only the plants roots, containing more lignin and fewer lipids and carbohydrates. Another example is the disturbance of aggregates and the loss of moisture due to soil treatments like tillage. Devine et al. (2014) found a lower aggregate stability in the topsoil comparing conventional tillage to no tillage cropland. In addition to a reduced capacity to physically protect SOC from mineralization, tillage can decrease the soil water holding capacity and therefore alter microbial activity (Devine et al., 2014; Zibilske and Bradford, 2007). While these management methods mostly take place in the topsoil, studies have shown that land use can also affect the subsoil C pools and dynamics, e.g. DOC leaching (Rumpel and Kögel-Knabner, 2011; Sanderman and Amundson, 2008; Fang and Moncrieff, 2005). In forest soils, SOC mineralization is influenced by continuous litter and root-C inputs. In coniferous forests, relatively lignin-rich and high-C/N needle litter can slow mineralization and promote organic layer SOC accumulation, providing an important pool for subsequent mineralization (Kalbitz et al., 2006; Grüneberg et al., 2019).

To quantify and understand landscape SOC mineralization patterns there is a clear need to study SOC mineralization rates and their controlling factors in all dimensions: Space, depth, and time. While studies on the spatial (Meyer et al., 2018b), temporal (Suseela et al., 2012), spatio-temporal (Tang and Baldocchi, 2005), or vertical and temporal (Davidson et al., 2006a) variability of SOC mineralization have been conducted, they are often restricted to single land use types, and we are not aware of any studies combining spatio-temporal patterns with a vertical pattern. Further studies on spatio-temporal patterns of soil CO₂ efflux have been conducted, but these miss out the vertical dimension and, as also autotrophic CO₂ production



adds to soil CO₂ efflux, are not explicitly approaching SOC mineralization (Rayment and Jarvis, 2000; Reichstein et al., 2003; Rodeghiero and Cescatti, 2008; Warner et al., 2019; Baumberger et al., 2026). Quantifying heterotrophic SOC mineralization therefore requires separating root-derived CO₂ from total soil CO₂ release, for which component integration, i.e. measuring
95 soil and extracted roots separately, is the only approach applicable to depth-resolved samples from many plots (Hanson et al., 2000; Kuzyakov, 2006). Combined with immediate incubation under in situ temperature and moisture, it yields field-like heterotrophic mineralization rates across entire soil profiles that surface CO₂ efflux measurements cannot provide (Subke et al., 2006).

This study aims to quantify SOC mineralization across spatial, temporal, and vertical gradients in the Fichtelgebirge moun-
100 tains (Bavaria, Germany). For this purpose, field and laboratory measurements were conducted on coniferous forest, meadow, and cropland plots over one year, with 120 plots sampled in total (10 per season and land use type). Soil cores were collected to a depth of 1 m, sectioned into 10 cm increments, and incubated within a few hours of sampling under in situ soil temperature and moisture conditions to approximate field-like SOC mineralization rates. Potential SOC-specific mineralization was additionally quantified under standardized conditions of temperature and moisture as an indicator for SOC stability. We
105 hypothesized that (i) the stability of SOC increases with depth, (ii) the influence of land use on SOC mineralization will be detectable up to 1 m depth, and (iii) the subsoil may exhibit higher mineralization rates than topsoil both during cold winter and dry summer conditions and thus due to more favorable thermal and moisture conditions.

2 Methods

2.1 Study area

110 The study area was in the Fichtelgebirge Mountains in northeastern Bavaria, Germany, within a 20 × 20 km squared area surrounding the Großer Waldstein peak (877 m a.s.l.). The climate is temperate with a mean annual temperature of approximately 6.5 °C and a mean annual precipitation ranging between 800 and 1000 mm (Bayerisches Landesamt für Umwelt, 2018a). The Fichtelgebirge is a low mountain range, mainly covered with coniferous forest, which extends diagonally from the southwest to the northeast across the study area and is surrounded by cropland, small forest patches, grassland and small
115 villages (Bayerisches Landesamt für Umwelt, 2018b). The soils developed mainly from metamorphic parent materials such as gneiss, phyllite, and mica schist. The characteristic dome-shaped mountains of the Fichtelgebirge Mountains are predominantly composed of granite (Bayerisches Landesamt für Umwelt, 2018b). On these bedrocks, the dominant soil types are Cambisols, Podzolic Cambisols, and Gleysols, while Regosols mainly occur at higher elevations (FAO classification).

2.2 Sampling design

120 The field campaign took place over a period of one year (December 2021 - December 2022) to capture seasonal variations. Measurements were conducted approximately once per week at one plot of each land-use type (cropland, meadow, and coniferous forest). To capture spatial and temporal variability across seasons (spring: March–May, summer: June–August, fall:



September–November, winter: December–February), seven new plots per land use type were selected within the study area for each season. In addition, three permanent plots per land use type were sampled once per season (Figure 1). In total we sampled 120 plots, 10 per season and land use type. To ensure randomization and spatial representativeness, the study area was divided into 64 grid cells. Each week, one cell per land use type was randomly selected. Within each cell, the exact sampling location was determined based on accessibility and landowner permission. Each grid cell was sampled only once per land use category to prevent spatial overlap, except for the permanent plots. Results from single sampling plots and repeatedly measured permanent plots were included in this study; however, we do not focus on the differences between these two sampling approaches. Sampling was restricted to terrestrial soils, primarily Cambisols and Cambic Podzols with loamy textures (FAO classification). Forest samples were collected from coniferous stands dominated by Norway spruce (*Picea abies*).

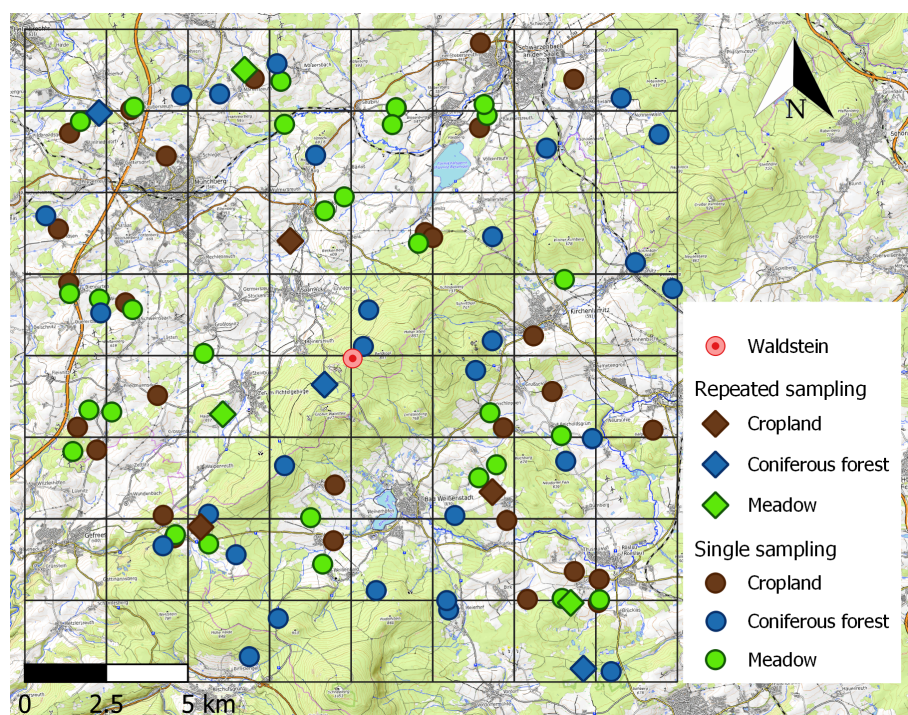


Figure 1. Map of the study area with an 8x8 grid used for plot selection (coordinates: 11.72° E–11.99° E, 50.05° N–50.24° N). Squares indicate plots that were sampled repeatedly (once per season; "permanent plots"), whereas circles indicate plots sampled only once. Blue symbols represent coniferous forest plots, brown symbols cropland plots, and green symbols meadow plots. The red double circle marks the location of Großer Waldstein. Base map: OpenTopoMap © OpenStreetMap contributors 2025, EPSG:3857

2.3 Soil sampling and determination of basic soil properties

On each plot two soil cores up to 1 m were taken with a soil column cylinder auger (Eijkelkamp, Netherlands, Ø 8 cm sampling size) and a gasoline driven hammer (Cobra 148, Atlas Copco). Each core was sliced in 10 cm increments, respectively, directly



135 in the field (Figure A1). To assess soil temperature and moisture in each 10 cm increment, a probe (Drill & Drop Probe RS232, Sentek Technologies, Australia) was inserted into the soil at least three days before the sampling and within a radius of 3 m. The probes measured the mean soil temperature and volumetric water content within a 10 cm diameter at 10 cm increments along a total length of 90 cm (Baumberger et al., 2024). Because soil moisture relative to the water holding capacity (WHC) is ecologically relevant for microbial respiration (Gulledge and Schimel, 1998), we determined the WHC and expressed actual soil
140 moisture as a percentage of WHC (%WHC), following the procedure described by Alef and Nannipieri (1995). The measured soil moisture was then expressed as a percentage of WHC. According to Grundmann et al. (1995), WHC values below 40% or above 60% are associated with reduced microbial activity. Soil pH was measured in deionized water at a soil-to-solution ratio of 1:2.5. Carbon and nitrogen contents, as well as SOC stocks, were determined following the methodology described by Haas et al. (2026).

145 **2.4 SOC mineralization at in situ temperature and moisture conditions**

Each 10 cm soil increment was prepared for SOC mineralization measurement shortly after sampling, i.e. typically within 2 hours. Soil increments were broken vertically into two parts and weighed (Figure A1). One part was used for the incubation and carefully placed in a jar by gently breaking it into two parts to facilitate the release of produced CO₂ while minimizing any disturbance to the soil structure ("field-like soil"). The other part was sieved (2 mm) for later measurements of mineralization
150 under standardized conditions. During this sieving, roots were carefully separated from the sample and used for root respiration measurement. For the incubation, the jars with the "field-like" soil and the extracted roots were put into a water bath. Each 10 cm soil increment was incubated in a separate water bath adjusted to the original soil temperature at the respective depth, which was measured by the temperature probe at the time when the sample was taken. Before the soil respiration was measured, the soil jars were flushed for at least 2 h with ambient air to allow any previously accumulated CO₂ to outgas. Pre-measurements
155 (not shown) were performed to ensure that only newly produced CO₂ will be measured after the flushing. Soil respiration was measured with a Li-Cor 6252 portable infrared gas analyzer (IRGA, Lincoln, NE, USA). Air circulated with a flow rate of 0.5 l min⁻¹ between the jar and the analyzer. A logger recorded the increasing CO₂ concentration every 10 seconds for multiple minutes to measure root respiration and soil respiration. From these measurements, soil respiration rates were derived from the linear increase (Eq. 1) in CO₂ concentration over time ($\Delta c/\Delta t$) and the molecular weight of carbon (M_i), and corrected for
160 jar volume (V), dry mass of the incubated soil (G), air temperature (T), and atmospheric pressure (p_a) in the head space. Soil respiration was normalized per gram of dry soil (SR_{grav}).

$$SR_{grav} [C\ mg * soil\ kg^{-1} * h^{-1}] = \frac{\Delta c [ppm] * 10^{-6}}{\Delta t [h]} * \frac{V [m^3]}{G [kg]} * \frac{p_a [Pa] * M_i [g/mol]}{8.314 * T [K]} \quad (1)$$

Soil respiration per unit area [$C\ g * ha^{-1} * h^{-1}$] and root respiration were calculated analogously to soil respiration per soil mass, but replacing the dry soil mass (G) with the soil surface area or the dry mass of roots, respectively. SOC mineraliza-
165 tion was defined as soil respiration minus root respiration, scaled by the amount of roots present in the incubated soil. This subtraction-based approach, using excised root respiration to estimate the root-derived fraction of total soil CO₂ release, is



conceptually similar to established root-exclusion and component integration methods used to partition soil respiration into autotrophic and heterotrophic sources (Hanson et al., 2000; Subke et al., 2006).

2.5 SOC mineralization under standardized conditions

170 To derive potential SOC mineralization under standardized conditions, a subset of the soil samples (10 plots of each land use type, including all available 10 cm increments) were sieved (2 mm) and frozen on the same day of sampling. Before measurement, samples were defrosted for 2-3 days, and soil moisture was adjusted to 50 % of water holding capacity. The samples were incubated for a week at 20 °C before the potential SOC mineralization at 22 °C was measured for three days in a respirometer (Respicond, Nordgren Innovations AB, Sweden), which allows incubating 96 samples simultaneously and
 175 assessing CO₂ release by trapping CO₂ in KOH solution (Nordgren, 1988).

2.6 Data Analysis

To test the effects of land use and season on SOC mineralization, we applied generalized linear mixed models (GLMMs) using the glmmTMB package (McGillcuddy et al., 2025) in R Statistical Software v.4.2.2 (Team, 2021). To ensure sufficient replication and statistical power for comparisons among depth categories, individual depth increments were aggregated into broader
 180 depth intervals: topsoil (0–30 cm), subsoil (30–70 cm), and deep subsoil (70–100 cm). Model assumptions were evaluated using residual diagnostics implemented in the DHARMA package (Hartig, 2022). The response variable, SOC mineralization, was square-root transformed to reduce heteroskedasticity and residual skewness. The model included depth (interval) and land use type as fixed effects and plot ID as a random intercept. For analyses examining seasonal variability in SOC mineralization, season and depth were included as fixed effects, while plot ID and land use were treated as random effects. If required,
 185 heteroscedasticity was accounted for by specifying a dispersion formula.

Significant differences among factor levels were assessed using pairwise comparisons based on estimated marginal means (EMMs) calculated with the emmeans package (Lenth and Piaskowski, 2025), which allows robust comparisons while accounting for co-variables included in the model. All figures were generated using the ggplot2 package (Wickham, 2016).

3 Results

190 3.1 Soil properties

The C/N ratio in the coniferous forest decreased continuously with depth, from 24.8 in the organic layer to 13.8 in the mineral deep subsoil (Table 1). In meadow and cropland soil the C/N ratio varied between 8.1 and 13.4 with higher values within the first 50 cm (12.1 - 13.1) and lower values in the last 50 cm (8.1-12.0). The pH-value in coniferous forest increased with depth from 3.8 to 4.7, indicating acidic conditions. Such acidity was not observed in the agricultural soils, where pH values ranged
 195 from 5.7 to 6.4 and remained within a weak acidic range throughout the profile. SOC concentrations decreased continuously with depth in coniferous forest and meadow soils, whereas in cropland soils they remained relatively constant within the upper



30 cm before decreasing with depth. Across all depths, SOC concentrations were highest in coniferous forests, followed by meadows and croplands. SOC stocks in the topsoil (0–30 cm) were highest in meadow soils. Below 30 cm, forest soils generally exhibited the highest SOC stocks, except in the deepest increment (90–100 cm).

Table 1. Soil properties derived from soil core increments. In total, 32 soil cores were sampled for each land use type, respectively. The number of replicates slightly decreases with sampling depth, as reaching bedrock before 100 cm prevented sampling at lower depths, thereby reducing the number of replicates in deeper layers (Haas et al., 2026). The mean and standard deviation was calculated for C/N ratio, pH-Value, SOC content and SOC stocks per 10 cm increment for cropland (Crop), forest (For) and meadow (Mea).

Depth [cm]	C/N ratio			pH-Value (H2O)			SOC content [%]			SOC stock [t ha ⁻¹]		
	Crop	For	Mea	Crop	For	Mea	Crop	For	Mea	Crop	For	Mea
Organic layer	-	24.8 ±3.1	-	-	3.8 0.3	-	-	33.47 ±9.80	-	-	55.8 ±37.2	-
0-10	12.2 ±1.2	23.9 ±3.6	12.1 ±1.0	6.4 ±0.5	4.1 ±0.2	6.1 ±0.5	2.48 ±0.65	4.77 ±1.81	4.90 ±1.69	22.1 ±6.3	24.8 ±10.8	38.3 ±10.7
10-20	12.1 ±1.0	22.9 ±4.9	12.4 ±1.6	6.3 ±0.5	4.3 ±0.2	6.2 ±0.4	2.34 ±0.43	2.48 ±1.26	2.87 ±0.99	22.4 ±3.9	16.8 ±6.5	27.1 ±8.8
20-30	13.0 ±3.8	21.3 ±5.4	13.4 ±3.0	6.3 ±0.6	4.4 ±0.2	6.2 ±0.5	1.68 ±0.56	1.66 ±0.88	1.43 ±0.66	16.9 ±6.7	11.5 ±6.7	14.6 ±6.9
30-40	13.0 ±4.5	19.7 ±5.6	12.9 ±4.3	6.2 ±0.7	4.4 ±0.2	6.2 ±0.6	0.79 ±0.42	1.2 ±0.77	0.79 ±0.73	7.9 ±4.6	9.6 ±7.8	8.4 ±7.8
40-50	13.1 ±4.6	17.6 ±4.7	12.2 ±4.2	6.2 ±0.7	4.4 ±0.3	6.2 ±0.6	0.54 ±0.31	0.92 ±0.78	0.62 ±0.69	5.2 ±3.2	7.0 ±6.4	7.2 ±8.9
50-60	12.0 ±3.5	16.6 ±5.4	11.8 ±3.8	6.0 ±0.8	4.5 ±0.4	5.9 ±0.7	0.41 ±0.29	0.64 ±0.54	0.35 ±0.28	4.0 ±3.0	4.8 ±5.8	4.1 ±3.9
60-70	11.2 ±3.1	16.2 ±6.1	11.6 ±4.0	5.8 ±0.7	4.6 ±0.5	5.9 ±0.6	0.31 ±0.27	0.44 ±0.29	0.28 ±0.18	2.7 ±2.2	3.0 ±3.5	3.3 ±2.3
70-80	11.5 ±3.8	16.3 ±10.0	11.0 ±4.1	5.8 ±0.7	4.7 ±0.5	5.9 ±0.6	0.26 ±0.25	0.33 ±0.32	0.26 ±0.3	1.8 ±1.5	2.1 ±2.9	2.9 ±3.6
80-90	10.0 ±3.8	15.4 ±9.8	9.8 ±3.6	5.7 ±0.7	4.9 ±0.5	5.8 ±0.6	0.20 ±0.17	0.38 ±0.37	0.19 ±0.09	1.6 ±2.1	1.0 ±2.2	1.6 ±1.1
90-100	8.1 ±3.2	13.8 ±6.9	10.5 ±5.0	5.7 ±0.7	4.7 ±0.6	5.8 ±0.8	0.14 ±0.07	0.23 ±0.13	0.16 ±0.09	0.7 ±1.0	0.2 ±0.8	1.2 ±1.4

200 3.2 Potential SOC-specific mineralization under standardized temperature and moisture conditions

The potential SOC-specific mineralization under standardized condition (50% WHC and 22 °C) was significantly different depending on depth and land use (Figure 2).

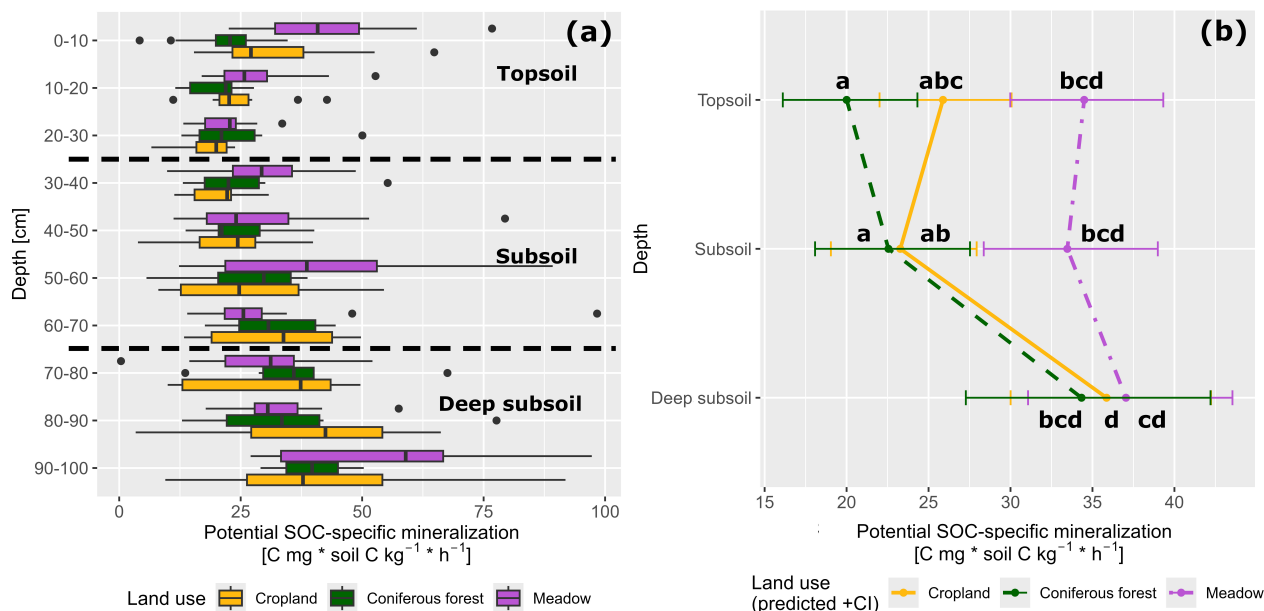


Figure 2. Potential SOC-specific mineralization across soil depth and land use. Boxplots (a) show the distribution and mean SOC mineralization rates normalized by SOC of soils incubated at 50% of their water holding capacity (WHC) and 22 °C for each 10 cm depth increment. Panel (b) presents the predicted mean mineralization for aggregated soil intervals (topsoil: 0–30 cm, subsoil: 30–70 cm, deep subsoil: 70–100 cm) with corresponding confidence intervals (error bars). Means not sharing a common letter differ significantly ($p < 0.05$). Comparisons were made across depth and land-use types; thus, all predicted means can be compared with each other for statistical significance.

Within individual land use types, the potential SOC-specific mineralization was significantly lower in the topsoil and subsoil than in the deep subsoil for both cropland and coniferous forest soils. In contrast, meadow soils showed no significant change in mineralization rates with increasing depth.

In the topsoil (0–30 cm) and subsoil (30–70 cm), the potential SOC-specific mineralization was significantly lower in coniferous forest soils than in meadow soils. Mineralization rates in cropland soils were intermediate between those of coniferous forest and meadow soils and did not differ significantly from either. In the deep subsoil (70–100 cm), the mineralization rates were comparable across all land use types and no significant differences were detected.

3.3 SOC mineralization at in situ temperature and moisture conditions across land use types

Mean annual SOC mineralization differed significantly among land use types across the entire 1 m soil profile (Figure 3). Coniferous forest and cropland soils consistently exhibited significantly lower mineralization rates than meadow soils at all depth intervals, while no significant differences were observed between forest and cropland.

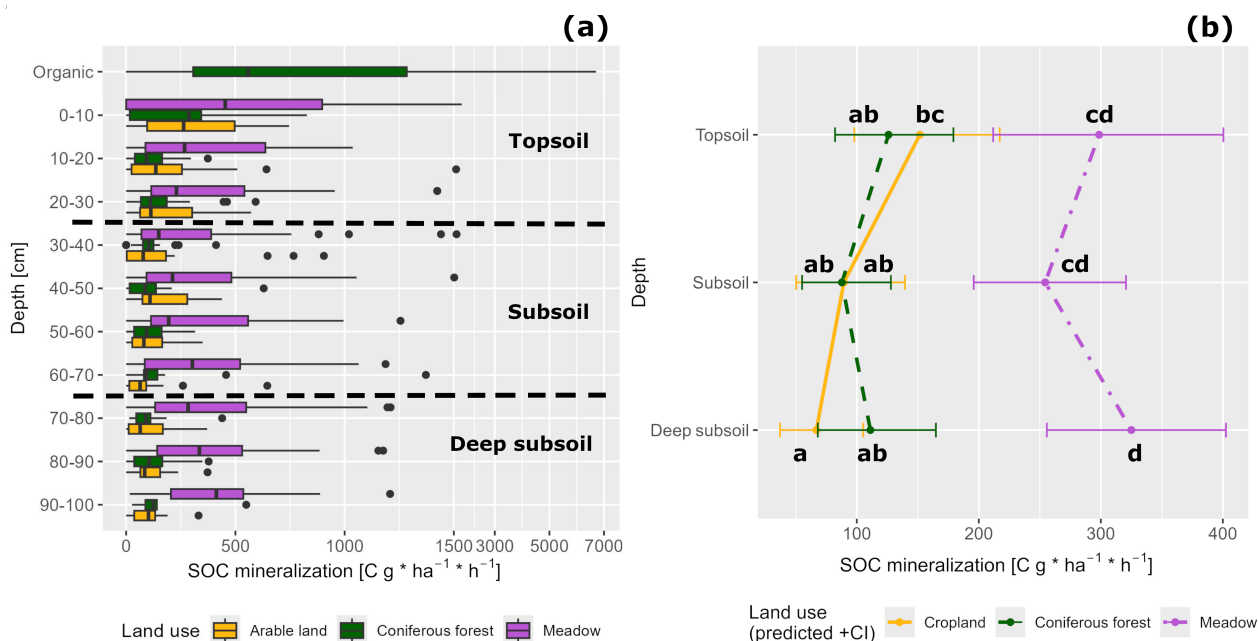


Figure 3. SOC mineralization at in situ soil temperature and soil moisture conditions across depths and land use types (cropland, coniferous forest, meadow). Boxplots (a) show the annual mean mineralization per 10 cm depth increment and land use type. Panel (b) presents predicted annual mean mineralization for aggregated soil intervals (topsoil: 0–30 cm, subsoil: 30–70 cm, deep subsoil: 70–100 cm) with corresponding confidence intervals (95 %, error bars). Letters indicate significant differences among land use types and aggregated soil depth increments. Means not sharing a common letter differ significantly ($p < 0.05$). Comparisons were made across depth and land-use types; thus, all presented means can be compared with each other for statistical significance.

Within land use types, cropland soils showed a significant decline in mineralization from the topsoil to the deep subsoil. In contrast, mineralization in both coniferous forest and meadow soils remained relatively constant with depth, with no significant differences among soil intervals.

3.4 Seasonal variation in SOC mineralization at in situ temperature and moisture conditions

Soil temperature and soil moisture exhibited temporal variation over the course of the year (Figure 4). In spring, mean soil temperatures ranged between 5.7 and 5.9 °C and soil moisture in the mineral soil ranged between 46–51 % WHC. During summer, mean temperatures increased to 15.1–16.1 °C in the mineral soil, while soil moisture ranged from about 20 % WHC in the upper layers to around 40 % WHC in the subsoil. In fall, soil moisture in the topsoil increased again across all depths (35–42 % WHC), while soil temperatures decreased to 8 °C in the upper 10 cm to 12 °C in the 90–100 cm layer. This vertical



temperature gradient became more pronounced in winter, when the upper 10 cm had a mean temperature of 1 °C, whereas the 90–100 cm layer reached 6 °C. Soil moisture increased again from fall to winter, ranging between 41 % and 55 % WHC in the
225 mineral soil. The organic layer was consistently drier than the mean moisture of the upper 10 cm of the mineral soil (6–17 %), except in summer, where both reached 21 % WHC.

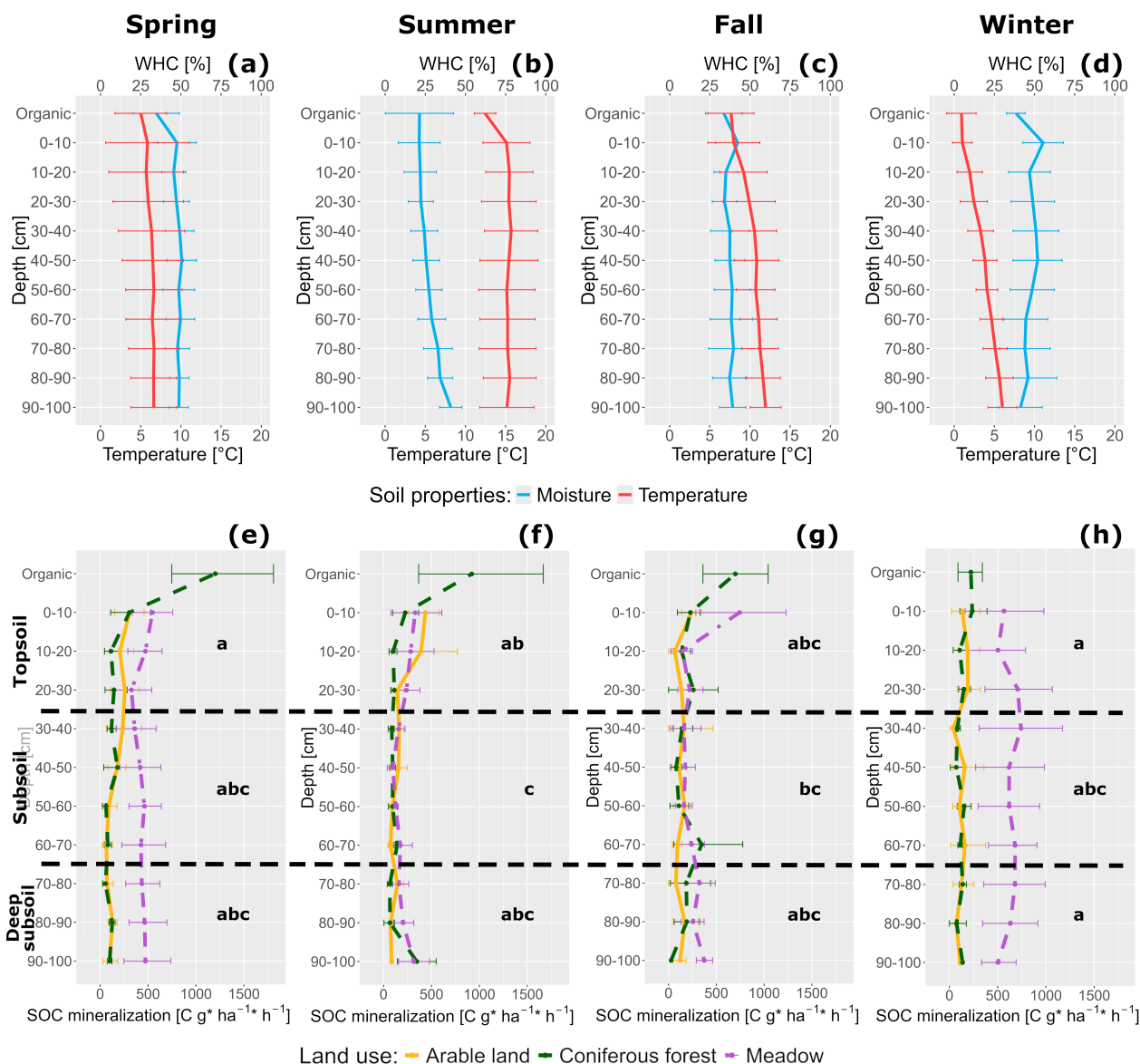


Figure 4. Seasonal (spring: a, e; summer: b, f; fall: c, g; winter: d, h) soil temperature, soil moisture, and SOC mineralization at in situ conditions. Panels a-d show the seasonal mean soil temperature and moisture for each 10 cm depth increment within the 1 m soil profile of each season. Panels e-h display the mean SOC mineralization at in situ soil temperature and soil moisture conditions with 95 % confidence intervals (error bars), shown as colored lines by land use type for each 10 cm depth increment and season. Letters indicate significant differences among seasons and aggregated soil depth increments (topsoil: 0–30 cm, subsoil: 30–70 cm, deep subsoil: 70–100 cm). Means not sharing a common letter differ significantly ($p < 0.05$). Comparisons were made across depth and seasons; thus, all presented means can be compared with each other for statistical significance.



There was no significant seasonal effect on SOC mineralization rates within the aggregated soil intervals (topsoil: 0–30 cm, subsoil: 30–70 cm, deep subsoil: 70–100 cm). For most of the year (i.e., spring, fall, and winter), SOC mineralization did not differ significantly among the topsoil (0–30 cm), subsoil (30–70 cm), and deep subsoil (70–100 cm). A significant difference was observed only in summer, when mineralization rates were higher in the topsoil than in the subsoil.

4 Discussion

4.1 Stability of SOC with depth

Topsoil typically respire more CO₂ per gram of soil under standardized conditions than subsoil, largely due to its higher carbon content (Fierer et al., 2003). This was also observed in our study. However, we hypothesized that this difference would become even more pronounced when mineralization was normalized by SOC content, assuming that potential SOC mineralization would decrease with depth. This expectation was based on the assumption that physical stabilization mechanisms become increasingly important in deeper soil layers, where mineral surfaces are more abundant relative to SOC (Schrumpf et al., 2013). Consequently, subsoil SOC is generally considered to be older and potentially more stable than topsoil SOC (Paul et al., 1997; Rumpel et al., 2002; Eusterhues et al., 2003; Schrumpf et al., 2013). Contrary to this hypothesis, potential SOC-specific mineralization rates under standardized moisture and temperature conditions did not decrease with depth in any of the land-use types. In meadow soils, mineralization remained relatively constant throughout the soil profile, with no significant differences among the aggregated depth intervals (topsoil: 0–30 cm, subsoil: 30–70 cm, deep subsoil: 70–100 cm). In contrast, coniferous forest and cropland soils showed significantly higher mineralization rates in the deep subsoil than in both the topsoil and subsoil. That shows that mineralization is influenced not only by the quantity of SOC but probably also by its chemical composition and by environmental conditions, including pH, tillage, and fertilization (Von Lützow et al., 2006; Adhikari et al., 2023). In coniferous forest soils, the increase in potential SOC-specific mineralization with depth coincided with increasing pH and a decreasing C/N ratio. This pattern suggests that changes in soil chemical conditions and SOC quality may have contributed to the higher mineralization rates observed in the deep subsoil. In meadow soils, in contrast, neither pH nor C/N ratio changed substantially with depth, which was consistent with the relatively constant potential mineralization rates. This may indicate that SOC quality and its accessibility to microorganisms did not change sufficiently with depth to cause a detectable change in mineralization rates. In cropland soils, however, potential mineralization increased with depth despite pH and C/N ratios being relatively similar to those of meadow soils. This pattern may partly reflect the effects of agricultural management, as land use intensity, particularly nitrogen fertilization, has been shown to decrease SOC mineralization, while tillage can reduce microbial activity and disrupt microbial habitats (Solly et al., 2014; Yao et al., 2019). Such effects may have been particularly pronounced in the topsoil and subsoil of the cropland plots, potentially contributing to the lower mineralization rates observed there compared to the deep subsoil. Similar increases in potential SOC-specific mineralization with depth have been reported by Wordell-Dietrich et al. (2017) and Salomé et al. (2010) for forest and cropland soils. These studies attributed the higher mineralization rates in subsoil to a relatively larger proportion of labile carbon and lower microbial carbon use efficiency. Under such conditions, microorganisms may need to mineralize a greater proportion of the available carbon to meet their



260 energy requirements, resulting in higher CO₂ production per unit SOC. This suggests that the physical stabilization in the subsoil is maybe less strong than expected or chemical quality and the less hostile for the microorganisms in the subsoil counteract the effects of physical protection.

Potential SOC-specific mineralization rates also differed among land use types, with the highest rates observed in meadows, followed by croplands and coniferous forests. Even where differences were not always statistically significant, the same ranking was observed by Woloszczyk et al. (2020) in a study area in Schleswig-Holstein, Germany. The significantly lower mineralization rates of forest soils compared with meadow soils in the topsoil and subsoil were likely related to their low pH and the higher recalcitrance of organic matter (Von Lützow et al., 2008). In addition, tree roots generally decompose more slowly than herbaceous roots, potentially contributing to lower microbial turnover in forest soils (Solly et al., 2014; Silver and Miya, 2001). Cropland soils, in contrast, exhibited higher pH values and generally less recalcitrant plant litter than coniferous forest soils (Osono et al., 2014). Nevertheless, potential mineralization rates in cropland were similarly low to those in forest soils and significantly lower than those in meadow soils in both the topsoil and subsoil. Higher mineralization rates in meadows compared with croplands have been attributed to a greater amount of particulate organic matter and enhanced microbial activity (Schlüter et al., 2022). In croplands, a substantial portion of aboveground plant biomass is removed during harvest, while tillage can decrease microbial activity (Yao et al., 2019; Graham et al., 2021). In addition, land use intensity, particularly nitrogen fertilization, has been shown to slow fine root decomposition (Solly et al., 2014). Together, these factors may explain the significantly lower mineralization rates observed in cropland topsoils and subsoils compared with meadow soils, and their similarly low rates to those of coniferous forests despite higher pH values and potentially less recalcitrant organic matter. Overall, our results do not support the initial hypothesis that potential SOC-specific mineralization decreases with depth. Instead, the depth pattern depended on land use, with higher rates in the deep subsoil (70-100 cm) of cropland and coniferous forest. This suggests that potential SOC stability is controlled by a combination of SOC quality, substrate accessibility, and microbial activity, rather than by soil depth alone, and that increasing soil depth does not necessarily imply greater SOC stability.

4.2 Land use effect on SOC mineralization under in situ conditions across soil depths

The hypothesis that land use influences SOC mineralization and that this effect persists down to 1 m depth is supported by our results. Mineralization differed significantly among land use types, with meadow soils exhibiting consistently higher mineralization rates than both cropland and coniferous forest soils. Higher mineralization rates in meadow soils likely reflect both a greater availability of readily decomposable SOC, as indicated by their higher potential SOC-specific mineralization, and generally larger SOC stocks throughout most of the soil profile (Haas et al., 2026). Similar patterns have frequently been attributed to the continuous input of high-quality root-derived carbon and the absence of soil disturbance under permanent grassland, which promote microbial activity and the accumulation of labile organic matter (Poeplau et al., 2018; Wiesmeier et al., 2019). In contrast, SOC mineralization under in situ conditions in cropland and forest soils appears to reflect the decline in SOC stocks with depth rather than the increase in potential SOC-specific mineralization. Long-term differences in tillage intensity, vegetation type, rooting depth, and the quantity and quality of below ground carbon inputs appear to shape SOC availability and microbial activity even in deep soil layers. Deep-rooted perennial vegetation likely enhances carbon inputs into



the subsoil, whereas in croplands, tillage concentrates organic matter near the surface, and soil compaction from agricultural
295 machinery further limits carbon transfer to deeper horizons (Abdalla et al., 2016). Consequently, land use influences not only
SOC stocks (Haas et al., 2026) but also SOC mineralization rates across the soil profile. The relatively constant mineralization
rates per unit area with depth in meadow and forest soils imply a larger subsoil contribution to total soil CO₂ release than
typically derived from in situ measurements of CO₂ concentrations within the soil profile, which attribute the majority of soil
CO₂ efflux to the upper 20–30 cm (Davidson et al., 2006b; Maier and Schack-Kirchner, 2014). Part of this difference may
300 reflect the disturbance and short-term character of our measurements (Chapter 4.3). However, gradient-based estimates inte-
grate root-derived and heterotrophic CO₂, depend on diffusivity models that are uncertain in heterogeneous and stony subsoils
(Maier and Schack-Kirchner, 2014), and have rarely been applied across land use types. Whole-soil warming experiments
using such in situ profile measurements have shown that subsoil SOC responds to warming at least as strongly as topsoil SOC
(Hicks Pries et al., 2017; Soong et al., 2021), our results add that, under ambient conditions, subsoil SOC in all three land use
305 types is mineralized at rates per unit SOC that are not lower than in the topsoil. The persistence of land use effects into the
deep subsoil suggests that management practices can influence carbon cycling beyond the topsoil. As a substantial proportion
of global SOC is stored below 30 cm depth, understanding the controls on subsoil mineralization is essential for predicting
long-term carbon sequestration and the response of SOC stocks to land use change.

4.3 Seasonal effect on SOC mineralization under in situ conditions of temperature and moisture

310 We hypothesized that subsoil may exhibit higher SOC mineralization rates than topsoil during cold winter and dry summer due
to more favorable thermal and moisture conditions. Despite pronounced seasonal variation in soil temperature and soil moisture,
we did not observe any seasonal effects on the mineralization at any depth. A likely explanation is the counteracting influence of
environmental constraints: warm but dry conditions in summer and fall versus moist but cold conditions in winter and spring.
Under such conditions, microbial activity may be limited either by low temperature or insufficient moisture. Optimal soil
315 moisture for aerobic microbial activity is typically reported at 40–60 % WHC (Meyer et al., 2018a; Grundmann et al., 1995),
whereas lower moisture levels can restrict water and nutrient availability and thus constrain microbial processes (Uhlřřová
et al., 2005; Papendick and Campbell, 1981). The limitation of microbial activity by soil moisture and temperature in our study
area was also supported by Baumberger et al. (2026), who measured total soil CO₂ efflux at the same plots and during the same
period as this study. Their chamber measurements showed that soil efflux were relatively low compared with those reported
320 from other areas in Germany. This finding is consistent with the prevailing environmental conditions: of the 1,096 observations,
only 569 exceeded 40 % WHC, and 421 of these occurred during spring and winter when soil temperatures were relatively
low. These contrasting seasonal effects were most pronounced in the topsoil, which exhibited the greatest variability (standard
deviation: 6.0 °C and 13 % WHC). In contrast, environmental conditions in the subsoil (standard deviation: 5.4 °C and 6 %
WHC) and deep subsoil (standard deviation: 4.8 °C and 4 % WHC) were considerably more stable, likely contributing to the
325 absence of significant seasonal variation in SOC mineralization at greater depths. Considering only soil samples with optimal
moisture conditions (40–60 % WHC), mean soil temperature was 4.0 °C in the topsoil, 6.5 °C in the subsoil, and 8.4 °C in
the deep subsoil. As higher temperatures promote microbial activity, this might explain why mineralization rates remained



similar despite the exponential decline in SOC stocks with depth in the subsoil. The only significant within-season difference was observed in summer, where SOC mineralization in the topsoil was significantly higher than in the subsoil. Although mean
 330 summer temperatures were similar in both layers (15.3 °C in the topsoil and 15.9 °C in the subsoil), the topsoil showed greater variability in soil moisture, including several observations above 40 % WHC, despite similar mean moisture values (16 % vs. 15 % WHC). Overall, unfavorable soil moisture and soil temperature conditions constrained microbial activity and SOC mineralization throughout much of the year and across all depths. Hence, we have to reject our hypothesis that subsoil or deep
 335 subsoil layers respire more CO₂ than the topsoil during winter. However, the lack of comparable data on **field-like**, depth-resolved SOC mineralization under field conditions limits direct validation and comparison of these findings, underscoring the importance of conducting incubations under realistic field moisture and temperature conditions.

The importance of moisture and/or temperature limitation for SOC mineralization is further illustrated by comparing mineralization rates measured of soil under field temperature and moisture conditions with mineralization rates determined under standardized laboratory conditions. In the topsoil, the mean SOC-specific mineralization rate (Figure A2) was only about half
 340 of the mineralization measured under near-optimal incubation conditions (Figure 2), indicating that microbial activity was substantially constrained by environmental conditions in situ. In contrast, mean SOC-specific mineralization rates in the subsoil and deep subsoil measured shortly after sampling under in situ temperature and moisture conditions exceeded mineralization rates determined under standardized laboratory conditions by approximately two- and threefold, respectively. This finding was unexpected, as the standardized incubation conditions (e.g., 50 % WHC and relatively high temperature) should have pro-
 345 moted near-maximal microbial activity. Several explanations can be considered. A methodological artifact caused by residual ("legacy") CO₂ outgassing is unlikely, as preliminary tests confirmed that the head space flushing period was sufficient to remove accumulated CO₂ before measurements commenced (data not shown). Oxygen limitation is also an unlikely explanation because subsoils in well-aerated soils are generally not oxygen limited (Schlüter et al., 2022; Angert et al., 2015; Salomé et al., 2010), a conclusion further supported by our pre-experiments using oxygen-free flushing. Moreover, the soil structure
 350 was largely preserved during sampling, which limits, although does not exclude, disturbance effects on microbial activity. Soil samples were taken with an auger and only gently broken before incubation, and roots were excised from a separate sample of the same depth increment (Chapter 2.4), so that the incubated soil itself remained almost undisturbed. Nevertheless, sampling can stimulate CO₂ release by exposing previously protected organic matter and releasing CO₂ stored in the pore space (Kuziyakov and Larionova, 2005; Salomé et al., 2010), particularly during the first hours after sampling. The rates reported here
 355 therefore represent "field-like" rather than true in situ mineralization rates and may slightly overestimate in situ mineralization. In addition, root respiration measured on excised roots from a separate sample can only approximate the root-derived fraction of total CO₂ release (Chapter 2.4, (Hanson et al., 2000)), so that partitioning errors propagate into the SOC mineralization estimates, most strongly in the root-rich topsoil. Given the minimal disturbance of the incubated soil, however, these effects are unlikely to explain the differences between the two incubation approaches. A more plausible explanation is the difference in
 360 substrate availability between the two approaches. As discussed above, microorganisms in the subsoil likely depend primarily on root exudates and dissolved organic carbon (DOC) leached from the topsoil. Prior to standardized mineralization measurements, however, the soil was sieved, thereby removing roots and interrupting the continuous supply of DOC. Also, samples



were pre-incubated for one week before start of the measurement at standardized conditions. Consequently, the availability of readily accessible carbon substrates may have declined substantially during the incubation period, leading to reduced microbial activity after several days. In contrast, mineralization measurements performed shortly after sampling likely captured microbial activity before these labile carbon pools were depleted. Thus, both physical disturbance and delays between sampling and mineralization measurements may lead to an underestimation of the mineralization potential, particularly in the subsoil (Salomé et al., 2010; Schroeder et al., 2021). In addition, field conditions rarely reached the optimal range for microbial activity, suggesting that actual mineralization in situ may be strongly constrained by temperature and moisture.

Overall, our findings indicate that SOC mineralization across the soil profile was constrained by the opposing effects of temperature and moisture, with no consistent seasonal enhancement of subsoil mineralization. The contrast between field-condition and standardized-incubation measurements further suggests that sample disturbance and depletion of readily available substrates may underestimate subsoil mineralization potential. These results highlight the need for depth-resolved measurements using fresh, minimally disturbed soils under realistic field temperature and moisture conditions.

5 Conclusion

This study shows that the potential stability of SOC may depend more on SOC quality than on SOC quantity and soil depth. Despite lower SOC contents in the subsoil, potential SOC-specific mineralization remained similarly high or even increased. This resulted in similar SOC mineralization rates across the soil profile under in situ field conditions, despite decreasing SOC stocks in meadow and coniferous forest soils. Annual mean SOC mineralization rates decreased with depth only in cropland soils, indicating that land use can influence SOC mineralization throughout the 1 m soil profile and highlighting the importance of considering subsoil processes when assessing SOC dynamics. Meadow soils exhibited consistently higher SOC mineralization rates than cropland and coniferous forest soils, likely reflecting both greater availability of readily decomposable SOC and generally larger SOC stocks. The persistence of these differences into the deep subsoil suggests that land-use-related differences in carbon inputs and management shape SOC cycling beyond the topsoil. Measurements under in situ conditions over the year showed no clear seasonal variation in SOC mineralization, probably due to soil moisture and/or temperature limitations. These limiting conditions were more pronounced in the topsoil and may partly explain why SOC mineralization rates remained similar in the subsoil.

This study provides insights into the controls of SOC mineralization across soil depths and land-use types in the Fichtelgebirge Mountains, highlighting the importance of considering subsoil processes and in situ environmental conditions when assessing SOC dynamics. As the study was conducted within a single low-mountain landscape, further investigations across different landscapes, climatic conditions, and soil types are needed to assess the generality of these patterns and improve predictions of the future role of subsoil SOC under a changing climate. In particular, studies combining measurements of field-like soils under in situ temperature and moisture conditions with experiments under standardized or manipulated conditions could help disentangle the mechanisms controlling SOC mineralization in subsoils.



395 *Data availability.* The datasets will be published at PANGAEA after acceptance.

Appendix A

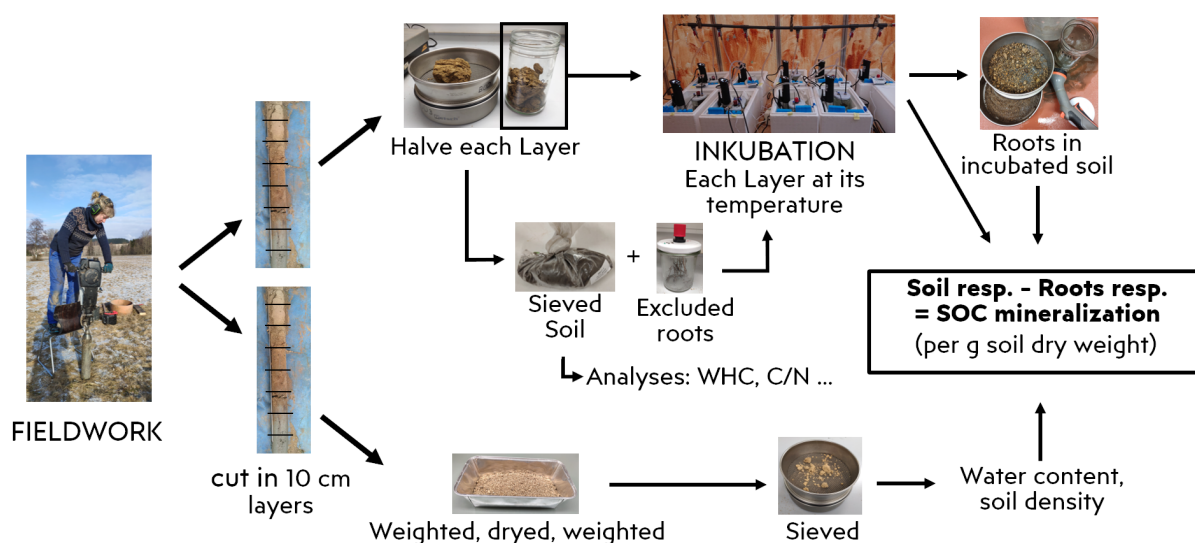


Figure A1. Flowchart of the field and laboratory workflow used to determine SOC mineralization based on measurements of total soil respiration and root respiration, including the assessment of relevant soil properties such as soil water content, water holding capacity (WHC), bulk density, and carbon and nitrogen contents.

Author contributions. BH: Writing – original draft, Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization. MB: Writing – review & editing, Investigation, Methodology. AR: Writing – review & editing, Investigation. JK: Writing – review & editing, Investigation. WB: Writing – review & editing, Conceptualization. HM: Writing – review & editing, Conceptualization, Funding acquisition, Supervision. NM: Writing – review & editing, Conceptualization, Funding acquisition, Methodology, Supervision.

Competing interests. The contact author has declared that none of the authors has any competing interests.

Acknowledgements. Karin Söllner, Uwe Hell, Mona Müller and the student assistants Arne Thomas, Leoni Koch, Jennifer Krüger, Sulari Anthony, Shahin Shahriari, Valentin Kurbel, Jens Hamberger, Serafina Anzinger, Silas Schmedt, Stefan Wirth, Lena Schumann and Henri

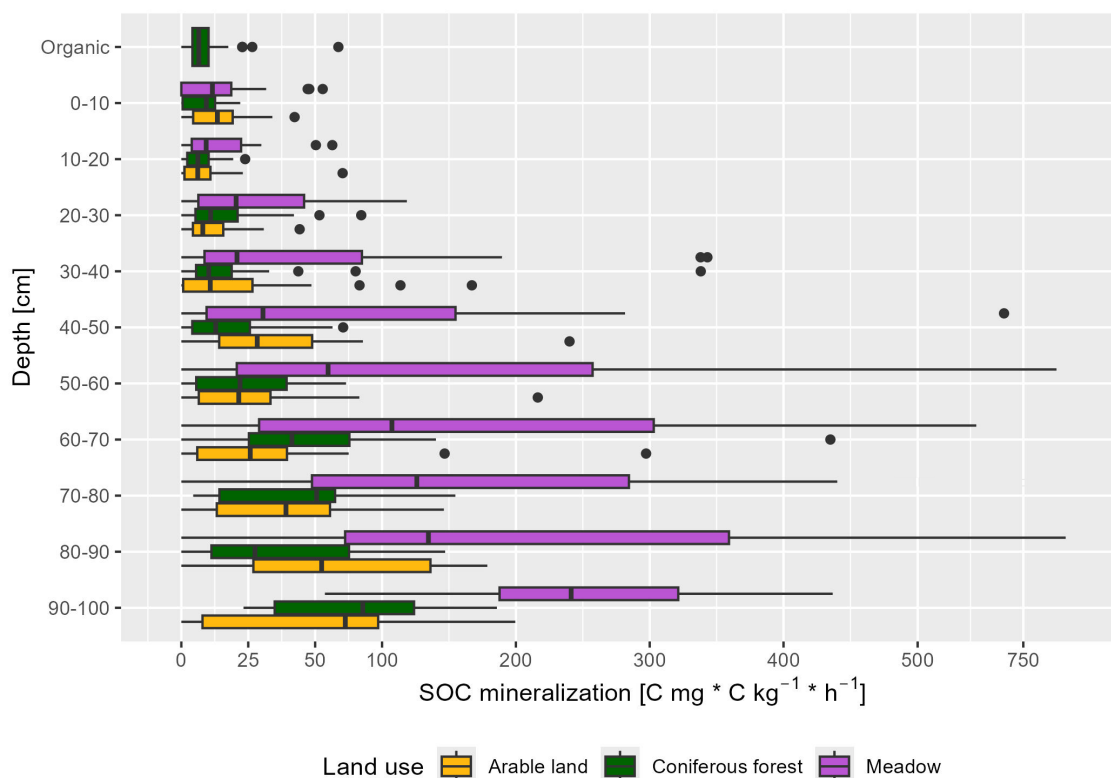


Figure A2. SOC-specific mineralization at in situ temperature and moisture conditions across depths and land use types (cropland, coniferous forest, meadow). Boxplots show the distribution and annual mean mineralization rates for each 10 cm depth increment. The dataset is the same as Figure 3 but normalized by SOC and expressed in a different unit.

405 Braunmiller are acknowledged for help with the laboratory and field work. We are grateful to all the farmers, landowners, and the Bavarian Forest Ministry for granting us access to their land and allowing us to conduct our fieldwork on their properties. We thank the German Research Foundation for funding (Project number 455085607). During the preparation of this work Bettina Haas used ChatGPT (OpenAI) to support language editing and to improve clarity and readability. After using this tool, Bettina Haas reviewed and edited the content as needed and takes full responsibility for the content of the published article.

410 The research was conducted in the project carbon4D, funded by the German Research Foundation (DFG; Project number 455085607).



References

- Abdalla, K., Chivenge, P., Ciais, P., and Chaplot, V.: No-tillage lessens soil CO₂ emissions the most under arid and sandy soil conditions: results from a meta-analysis, *Biogeosciences*, 13, 3619–3633, <https://doi.org/10.5194/bg-13-3619-2016>, 2016.
- 415 Adhikari, K., Anderson, K. R., Smith, D. R., Owens, P. R., Moore, P. A., and Libohova, Z.: Identifying key factors controlling potential soil respiration in agricultural fields, *Agricultural & Environmental Letters*, 8, e20 117, <https://doi.org/10.1002/ael2.20117>, 2023.
- Alef, K. and Nannipieri, P.: *Methods in Applied Soil Microbiology and Biochemistry*, Elsevier, ISBN 978-0-12-513840-6, <https://doi.org/10.1016/B978-0-12-513840-6.X5014-9>, 1995.
- Andruschkewitsch, R., Geisseler, D., Koch, H.-J., and Ludwig, B.: Effects of tillage on contents of organic carbon, nitrogen, water-stable
 420 aggregates and light fraction for four different long-term trials, *Geoderma*, 192, 368–377, <https://doi.org/10.1016/j.geoderma.2012.07.005>, 2013.
- Angert, A., Yakir, D., Rodeghiero, M., Preisler, Y., Davidson, E. A., and Weiner, T.: Using O to study the relationships between soil CO efflux and soil respiration, *Biogeosciences*, 12, 2089–2099, <https://doi.org/10.5194/bg-12-2089-2015>, 2015.
- Baumberger, M., Haas, B., Sivakumar, S., Ludwig, M., Meyer, N., and Meyer, H.: High-resolution soil temperature and soil
 425 moisture patterns in space, depth and time: An interpretable machine learning modelling approach, *Geoderma*, 451, 117 049, <https://doi.org/10.1016/j.geoderma.2024.117049>, 2024.
- Baumberger, M., Haas, B., Borken, W., Nowosad, J., Giese, L., Klein-Raufhake, T., Hamer, U., Meyer, N., and Meyer, H.: How the landscape influences soil respiration: Explaining spatio-temporal patterns with interpretable machine learning, *Geoderma*, 472, 117 904, <https://doi.org/10.1016/j.geoderma.2026.117904>, 2026.
- 430 Bayerisches Landesamt für Umwelt, G.: Frankenwald, Fichtelgebirge und Vogtland, https://www.lfu.bayern.de/boden/bodenreise/le_08.htm, 2018a.
- Bayerisches Landesamt für Umwelt, G.: UmweltAtlas Bayern, <https://www.umweltatlas.bayern.de>, 2018b.
- Bond-Lamberty, B., Bailey, V. L., Chen, M., Gough, C. M., and Vargas, R.: Globally rising soil heterotrophic respiration over recent decades, *Nature*, 560, 80–83, <https://doi.org/10.1038/s41586-018-0358-x>, 2018.
- 435 Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils, *Global Change Biology*, 15, 808–824, <https://doi.org/10.1111/j.1365-2486.2008.01681.x>, 2009.
- Cleveland, C. C., Nemergut, D. R., Schmidt, S. K., and Townsend, A. R.: Increases in soil respiration following labile carbon additions linked to rapid shifts in soil microbial community composition, *Biogeochemistry*, 82, 229–240, <https://doi.org/10.1007/s10533-006-9065-z>, 2007.
- 440 Cook, F. J. and Orchard, V. A.: Relationships between soil respiration and soil moisture, *Soil Biology and Biochemistry*, 40, 1013–1018, <https://doi.org/10.1016/j.soilbio.2007.12.012>, 2008.
- Crowther, T. W., Todd-Brown, K. E. O., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B., Snoek, B. L., Fang, S., Zhou, G., Allison, S. D., Blair, J. M., Bridgham, S. D., Burton, A. J., Carrillo, Y., Reich, P. B., Clark, J. S., Classen, A. T., Dijkstra, F. A., Elberling, B., Emmett, B. A., Estiarte, M., Frey, S. D., Guo, J., Harte, J., Jiang, L., Johnson, B. R., Kröel-Dulay, G., Larsen, K. S., Laudon, H., Lavallee, J. M., Luo, Y., Lupascu, M., Ma, L. N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L. L., Schmidt, I. K., Sistla, S., Sokol, N. W., Templer, P. H., Treseder, K. K., Welker, J. M., and Bradford, M. A.: Quantifying global soil carbon losses in response to warming, *Nature*, 540, 104–108, <https://doi.org/10.1038/nature20150>, 2016.



- Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10} , *Global Change Biology*, 12, 154–164, <https://doi.org/10.1111/j.1365-2486.2005.01065.x>, 2006a.
- 450 Davidson, E. A., Savage, K. E., Trumbore, S. E., and Borken, W.: Vertical partitioning of CO_2 production within a temperate forest soil, *Global Change Biology*, 12, 944–956, <https://doi.org/10.1111/j.1365-2486.2005.01142.x>, 2006b.
- Devine, S., Markewitz, D., Hendrix, P., and Coleman, D.: Soil Aggregates and Associated Organic Matter under Conventional Tillage, No-Tillage, and Forest Succession after Three Decades, *PLoS ONE*, 9, e84988, <https://doi.org/10.1371/journal.pone.0084988>, 2014.
- Eusterhues, K., Rumpel, C., Kleber, M., and Kögel-Knabner, I.: Stabilisation of soil organic matter by interactions
455 with minerals as revealed by mineral dissolution and oxidative degradation, *Organic Geochemistry*, 34, 1591–1600, <https://doi.org/10.1016/j.orggeochem.2003.08.007>, 2003.
- Fang, C. and Moncrieff, J. B.: The variation of soil microbial respiration with depth in relation to soil carbon composition, *Plant and Soil*, 268, 243–253, <https://doi.org/10.1007/s11104-004-0278-4>, 2005.
- Fierer, N., Allen, A. S., Schimel, J. P., and Holden, P. A.: Controls on microbial CO production: a comparison of surface and subsurface soil
460 horizons, *Global Change Biology*, 9, 1322–1332, <https://doi.org/10.1046/j.1365-2486.2003.00663.x>, 2003.
- Graham, C., Ramos-Pezzotti, M., and Lehman, M.: Short-term impacts to the soil microbial population during grassland conversion to cropland, *Soil and Tillage Research*, 206, 104839, <https://doi.org/10.1016/j.still.2020.104839>, 2021.
- Grundmann, G. L., Renault, P., Rosso, L., and Bardin, R.: Differential Effects of Soil Water Content and Temperature on Nitrification and Aeration, *Soil Science Society of America Journal*, 59, 1342–1349, <https://doi.org/10.2136/sssaj1995.03615995005900050021x>, 1995.
- 465 Grüneberg, E., Schöning, I., Riek, W., Ziche, D., and Evers, J.: Carbon Stocks and Carbon Stock Changes in German Forest Soils, in: Status and Dynamics of Forests in Germany, edited by Wellbrock, N. and Bolte, A., vol. 237, pp. 167–198, Springer International Publishing, Cham, ISBN 978-3-030-15732-6 978-3-030-15734-0, https://doi.org/10.1007/978-3-030-15734-0_6, series Title: Ecological Studies, 2019.
- Gulledge, J. and Schimel, J. P.: Moisture control over atmospheric CH_4 consumption and CO_2 production in diverse Alaskan soils, *Soil*
470 *Biology and Biochemistry*, 30, 1127–1132, [https://doi.org/10.1016/S0038-0717\(97\)00209-5](https://doi.org/10.1016/S0038-0717(97)00209-5), 1998.
- Haas, B., Baumberger, M., Müller, M., Schweers, J., Hülsmann, L., Lehdorff, E., Meyer, H., and Meyer, N.: Regional spatial and vertical patterns of SOC stocks in a low mountain landscape in Germany, *Geoderma Regional*, 46, e01102, <https://doi.org/10.1016/j.geodrs.2026.e01102>, 2026.
- Hanson, P., Edwards, N., Garten, C., and Andrews, J.: Separating root and soil microbial contributions to soil respiration: A review of
475 methods and observations, *Biogeochemistry*, 48, 115–146, <https://doi.org/10.1023/A:1006244819642>, 2000.
- Hartig, F.: DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models, <https://github.com/florianhartig/dharma>, 2022.
- Hicks Pries, C. E., Castanha, C., Porras, R. C., and Torn, M. S.: The whole-soil carbon flux in response to warming, *Science*, 355, 1420–1423, <https://doi.org/10.1126/science.aal1319>, 2017.
- 480 Hirano, T.: Seasonal and diurnal variations in topsoil and subsoil respiration under snowpack in a temperate deciduous forest, *Global Biogeochemical Cycles*, 19, 2004GB002259, <https://doi.org/10.1029/2004GB002259>, 2005.
- Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., and Piñeiro, G.: The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls, *Annual Review of Ecology, Evolution, and Systematics*, 48, 419–445, <https://doi.org/10.1146/annurev-ecolsys-112414-054234>, 2017.



- 485 Jobbágy, E. G. and Jackson, R. B.: The vertical distribution of soil organic carbon and its relation to climate and vegetation, *Ecological Applications*, 10, 423–436, [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2), 2000.
- Kalbitz, K., Kaiser, K., Bargholz, J., and Dardenne, P.: Lignin degradation controls the production of dissolved organic matter in decomposing foliar litter, *European Journal of Soil Science*, 57, 504–516, <https://doi.org/10.1111/j.1365-2389.2006.00797.x>, 2006.
- Kleber, M., Bourg, I. C., Coward, E. K., Hansel, C. M., Myneni, S. C. B., and Nunan, N.: Dynamic interactions at the mineral–organic matter
490 interface, *Nature Reviews Earth & Environment*, 2, 402–421, <https://doi.org/10.1038/s43017-021-00162-y>, 2021.
- Kuzyakov, Y.: Sources of CO₂ efflux from soil and review of partitioning methods, *Soil Biology and Biochemistry*, 38, 425–448, <https://doi.org/10.1016/j.soilbio.2005.08.020>, 2006.
- Kuzyakov, Y. and Larionova, A. A.: Root and rhizomicrobial respiration: A review of approaches to estimate respiration by autotrophic and heterotrophic organisms in soil, *Journal of Plant Nutrition and Soil Science*, 168, 503–520, <https://doi.org/10.1002/jpln.200421703>, 2005.
- 495 Kätterer, T., Bolinder, M. A., Andrén, O., Kirchmann, H., and Menichetti, L.: Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment, *Agriculture, Ecosystems & Environment*, 141, 184–192, <https://doi.org/10.1016/j.agee.2011.02.029>, 2011.
- Lenth, R. V. and Piaskowski, J.: emmeans: Estimated Marginal Means, aka Least-Squares Means, <https://CRAN.R-project.org/package=emmeans>, 2025.
- 500 Lloyd, J. and Taylor, J. A.: On the Temperature Dependence of Soil Respiration, *Functional Ecology*, 8, 315, <https://doi.org/10.2307/2389824>, 1994.
- Lomander, A., Kätterer, T., and Andrén, O.: Modelling the effects of temperature and moisture on CO₂ evolution from top- and subsoil using a multi-compartment approach, *Soil Biology and Biochemistry*, 30, 2023–2030, [https://doi.org/10.1016/S0038-0717\(98\)00077-7](https://doi.org/10.1016/S0038-0717(98)00077-7), 1998.
- Maier, M. and Schack-Kirchner, H.: Using the gradient method to determine soil gas flux: A review, *Agricultural and Forest Meteorology*, 192–193, 78–95, <https://doi.org/10.1016/j.agrformet.2014.03.006>, 2014.
- 505 Martens, D. A., Reedy, T. E., and Lewis, D. T.: Soil organic carbon content and composition of 130-year crop, pasture and forest land-use managements, *Global Change Biology*, 10, 65–78, <https://doi.org/10.1046/j.1529-8817.2003.00722.x>, 2004.
- Matzner, E. and Borken, W.: Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review, *European Journal of Soil Science*, 59, 274–284, <https://doi.org/10.1111/j.1365-2389.2007.00992.x>, 2008.
- 510 McGillicuddy, M., Warton, D. I., Popovic, G., and Bolker, B. M.: Parsimoniously Fitting Large Multivariate Random Effects in **glmmTMB**, *Journal of Statistical Software*, 112, <https://doi.org/10.18637/jss.v112.i01>, 2025.
- Meyer, N., Welp, G., and Amelung, W.: The Temperature Sensitivity (Q₁₀) of Soil Respiration: Controlling Factors and Spatial Prediction at Regional Scale Based on Environmental Soil Classes, *Global Biogeochemical Cycles*, 32, 306–323, <https://doi.org/10.1002/2017GB005644>, 2018a.
- 515 Meyer, N., Welp, G., Rodionov, A., Borchard, N., Martius, C., and Amelung, W.: Nitrogen and phosphorus supply controls soil organic carbon mineralization in tropical topsoil and subsoil, *Soil Biology and Biochemistry*, 119, 152–161, <https://doi.org/10.1016/j.soilbio.2018.01.024>, 2018b.
- Minasny, B., Malone, B. P., McBratney, A. B., Angers, D. A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.-S., Cheng, K., Das, B. S., Field, D. J., Gimona, A., Hedley, C. B., Hong, S. Y., Mandal, B., Marchant, B. P., Martin, M., McConkey, B. G., Mulder, V. L.,
520 O'Rourke, S., Richer-de Forges, A. C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V., Stockmann, U., Sulaeman, Y., Tsui, C.-C., Vågen, T.-G., Van Wesemael, B., and Winowiecki, L.: Soil carbon 4 per mille, *Geoderma*, 292, 59–86, <https://doi.org/10.1016/j.geoderma.2017.01.002>, 2017.



- Nordgren, A.: Apparatus for the continuous, long-term monitoring of soil respiration rate in large numbers of samples, *Soil Biology and Biochemistry*, 20, 955–957, [https://doi.org/10.1016/0038-0717\(88\)90110-1](https://doi.org/10.1016/0038-0717(88)90110-1), 1988.
- 525 Osono, T., Azuma, J.-i., and Hirose, D.: Plant species effect on the decomposition and chemical changes of leaf litter in grassland and pine and oak forest soils, *Plant and Soil*, 376, 411–421, <https://doi.org/10.1007/s11104-013-1993-5>, 2014.
- Papendick, R. I. and Campbell, G. S.: Theory and Measurement of Water Potential, in: *SSSA Special Publications*, edited by Parr, J., Gardner, W., and Elliott, L., vol. 9, pp. 1–22, Wiley, 1 edn., ISBN 978-0-89118-767-7 978-0-89118-904-6, <https://doi.org/10.2136/sssaspecpub9.c1>, 1981.
- 530 Paul, E. A., Follett, R. F., Leavitt, S. W., Halvorson, A., Peterson, G. A., and Lyon, D. J.: Radiocarbon Dating for Determination of Soil Organic Matter Pool Sizes and Dynamics, *Soil Science Society of America Journal*, 61, 1058–1067, <https://doi.org/10.2136/sssaj1997.03615995006100040011x>, 1997.
- Pisani, O., Haddix, M. L., Conant, R. T., Paul, E. A., and Simpson, M. J.: Molecular composition of soil organic matter with land-use change along a bi-continental mean annual temperature gradient, *Science of The Total Environment*, 573, 470–480, <https://doi.org/10.1016/j.scitotenv.2016.08.154>, 2016.
- 535 Poelplau, C., Zopf, D., Greiner, B., Geerts, R., Korvaar, H., Thumm, U., Don, A., Heidkamp, A., and Flessa, H.: Why does mineral fertilization increase soil carbon stocks in temperate grasslands?, *Agriculture, Ecosystems & Environment*, 265, 144–155, <https://doi.org/10.1016/j.agee.2018.06.003>, 2018.
- Rasse, D. P., Rumpel, C., and Dignac, M.-F.: Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation, *Plant and Soil*, 269, 341–356, <https://doi.org/10.1007/s11104-004-0907-y>, 2005.
- 540 Rayment, M. and Jarvis, P.: Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest, *Soil Biology and Biochemistry*, 32, 35–45, [https://doi.org/10.1016/S0038-0717\(99\)00110-8](https://doi.org/10.1016/S0038-0717(99)00110-8), 2000.
- Reichstein, M., Rey, A., Freibauer, A., Tenhunen, J., Valentini, R., Banza, J., Casals, P., Cheng, Y., Grünzweig, J. M., Irvine, J., Joffre, R., Law, B. E., Loustau, D., Miglietta, F., Oechel, W., Ourcival, J., Pereira, J. S., Peressotti, A., Ponti, F., Qi, Y., Rambal, S., Rayment, M., Romanya, J., Rossi, F., Tedeschi, V., Tirone, G., Xu, M., and Yakir, D.: Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices, *Global Biogeochemical Cycles*, 17, 2003GB002035, <https://doi.org/10.1029/2003GB002035>, 2003.
- 545 Rodeghiero, M. and Cescatti, A.: Spatial variability and optimal sampling strategy of soil respiration, *Forest Ecology and Management*, 255, 106–112, <https://doi.org/10.1016/j.foreco.2007.08.025>, 2008.
- 550 Rumpel, C. and Kögel-Knabner, I.: Deep soil organic matter—a key but poorly understood component of terrestrial C cycle, *Plant and Soil*, 338, 143–158, <https://doi.org/10.1007/s11104-010-0391-5>, 2011.
- Rumpel, C., Kögel-Knabner, I., and Bruhn, F.: Vertical distribution, age, and chemical composition of organic carbon in two forest soils of different pedogenesis, *Organic Geochemistry*, 33, 1131–1142, [https://doi.org/10.1016/S0146-6380\(02\)00088-8](https://doi.org/10.1016/S0146-6380(02)00088-8), 2002.
- Salomé, C., Nunan, N., Pouteau, V., Lerch, T. Z., and Chenu, C.: Carbon dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms, *Global Change Biology*, 16, 416–426, <https://doi.org/10.1111/j.1365-2486.2009.01884.x>, 2010.
- 555 Sanderman, J. and Amundson, R.: A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soils, *Biogeochemistry*, 89, 309–327, <https://doi.org/10.1007/s10533-008-9221-8>, 2008.
- Schlüter, S., Roussety, T., Rohe, L., Guliyev, V., Blagodatskaya, E., and Reitz, T.: Land use impact on carbon mineralization in well aerated soils is mainly explained by variations of particulate organic matter rather than of soil structure, *SOIL*, 8, 253–267, <https://doi.org/10.5194/soil-8-253-2022>, 2022.
- 560



- 24



- Von Lützow, M., Kögel-Knabner, I., Ludwig, B., Matzner, E., Flessa, H., Ekschmitt, K., Guggenberger, G., Marschner, B., and Kalbitz, K.: Stabilization mechanisms of organic matter in four temperate soils: Development and application of a conceptual model, *Journal of Plant Nutrition and Soil Science*, 171, 111–124, <https://doi.org/10.1002/jpln.200700047>, 2008.
- 600 Warner, D. L., Bond-Lamberty, B., Jian, J., Stell, E., and Vargas, R.: Spatial Predictions and Associated Uncertainty of Annual Soil Respiration at the Global Scale, *Global Biogeochemical Cycles*, 33, 1733–1745, <https://doi.org/10.1029/2019GB006264>, 2019.
- Wickham, H.: *ggplot2: elegant graphics for data analysis, Use R!*, Springer international publishing, Cham, second edition edn., ISBN 978-3-319-24277-4, <https://doi.org/https://doi.org/10.1007/978-3-319-24277-4>, 2016.
- Wiesmeier, M., Urbanski, L., Hobbey, E., Lang, B., Von Lützow, M., Marin-Spiotta, E., Van Wesemael, B., Rabot, E., Ließ, M., Garcia-
605 Franco, N., Wollschläger, U., Vogel, H.-J., and Kögel-Knabner, I.: Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales, *Geoderma*, 333, 149–162, <https://doi.org/10.1016/j.geoderma.2018.07.026>, 2019.
- Woloszczyk, P., Fiencke, C., Elsner, D.-C., Cordsen, E., and Pfeiffer, E.-M.: Spatial and temporal patterns in soil organic carbon, microbial biomass and activity under different land-use types in a long-term soil-monitoring network, *Pedobiologia*, 80, 150 642, <https://doi.org/10.1016/j.pedobi.2020.150642>, 2020.
- 610 Wordell-Dietrich, P., Don, A., and Helfrich, M.: Controlling factors for the stability of subsoil carbon in a Dystric Cambisol, *Geoderma*, 304, 40–48, <https://doi.org/10.1016/j.geoderma.2016.08.023>, 2017.
- Yan, Q. and Kumar, P.: Impacts of Landscape Evolution on Heterotrophic Carbon Loss in Intensively Managed Landscapes, *Frontiers in Water*, 3, 666 278, <https://doi.org/10.3389/frwa.2021.666278>, 2021.
- Yao, S.-H., Zhang, Y.-L., Han, Y., Han, X.-Z., Mao, J.-D., and Zhang, B.: Labile and recalcitrant components of organic matter of a Mol-
615 lisol changed with land use and plant litter management: An advanced ¹³C NMR study, *Science of The Total Environment*, 660, 1–10, <https://doi.org/10.1016/j.scitotenv.2018.12.403>, 2019.
- Zibilske, L. M. and Bradford, J. M.: Soil Aggregation, Aggregate Carbon and Nitrogen, and Moisture Retention Induced by Conservation Tillage, *Soil Science Society of America Journal*, 71, 793–802, <https://doi.org/10.2136/sssaj2006.0217>, 2007.