



# Conceptualising carbon cycling pathways across different land-use types based on rates and ages of soil-respired CO<sub>2</sub>

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**Abstract.** Soil carbon dioxide (CO<sub>2</sub>) efflux constitutes a major carbon (C) transfer from terrestrial ecosystems to the atmosphere, driven by numerous metabolic and allocation processes in the plant-soil system. Land use affects key components of C cycling pathways through vegetation type, C allocation, abiotic conditions, and management impacts on soil organic matter (SOM). However, systematic comparisons of these pathways among land uses remain scarce. In two contrasting seasons, we measured respiration rates and C isotopic signatures (<sup>14</sup>C, <sup>13</sup>C) of in situ soil-respired CO<sub>2</sub> and its autotrophic and heterotrophic sources derived from incubations at 16 sites across Switzerland, covering temperate and alpine grasslands, forests, croplands, and managed peatlands. Our findings revealed significant differences in the rates, ages, and sources of soil-respired CO<sub>2</sub> between land-use types, reflecting variations in C cycling dynamics. We propose that respiration rates and ages of soil-respired CO<sub>2</sub> serve as comprehensive indicators to categorize C cycling into:

1. High-throughput systems (temperate grasslands) where high respiration rates of young (<10 years) CO<sub>2</sub> reveal rapid C cycling.

2. Temperature-constrained retarding systems (alpine grasslands) where the respiration of decadal- to centennial-old CO<sub>2</sub> reveals slow C cycling mainly due to cooler climatic conditions.
3. Input-constrained retarding systems (forests) where decadal-old CO<sub>2</sub> reflects a delayed C transfer of assimilates back to the atmosphere through soil respiration.
4. C-depleted systems (croplands) where reduced C inputs and tillage lead to C depletion and to respiratory losses of centennial-old C.
5. Hotspots of C release (managed peatlands) where ancient C is lost through respiration due to disturbances in natural C cycling by drainage.

Our results suggest that the relationship between rates and ages of soil-respired CO<sub>2</sub> can serve as a robust indicator of C retention and loss along the trajectory from natural to anthropogenically disturbed systems on a global scale.

## 1 Introduction

Soil carbon dioxide (CO<sub>2</sub>) efflux is one of the largest carbon (C) fluxes between terrestrial ecosystems and the atmosphere with CO<sub>2</sub> release from soils exceeding fossil fuel CO<sub>2</sub> emissions (IPCC, 2021; Nissan et al., 2023). Soil CO<sub>2</sub> fluxes (i.e., soil respiration) originate from root activity related to the metabolic processing and allocation of C in plants (i.e., autotrophic respiration), as well as the mineralization of various soil organic matter (SOM) compounds by microorganisms (i.e., heterotrophic respiration) (Kuzyakov, 2006; Trumbore, 2006). In this study, we refer to rhizosphere respiration as all respiratory processes within the rhizosphere, including autotrophic respiration by root activity as well as heterotrophic respiration related to the consumption of root exudates by mycorrhizal fungi and other rhizosphere microorganisms (Hanson et al., 2000; Trumbore, 2006). Relative source contributions are essential to determine the pathways and velocity of belowground C cycling. A dominance of autotrophic respiration indicates high gross primary productivity (GPP) (Schulze et al., 2009) or rapid cycling of plant assimilates through the plant-soil system (Diao et al., 2022; Fuchslueger et al., 2016; Gao et al., 2021), largely bypassing storage in soil. In contrast, a higher contribution of heterotrophic respiration indicates that a large fraction of C enters the soils as plant detritus, which is then respired during degradation and transformation processes.

Land use impacts soil respiration and its source contributions through various factors such as vegetation type, root density, nutrient input, and management practices, altering soil structure and C cycling pathways within the plant-soil system (e.g., Oertel et al., 2016; Rong et al., 2015; Schaufler et al., 2010; Xiao et al., 2021). In Europe, grasslands have the highest soil respiration rates, followed by wetlands, croplands, and forests (Schaufler et al., 2010). Grasslands are among the most productive land-use types in Europe, due to their high GPP and net primary productivity (NPP) (Schulze et al., 2009), high belowground C allocation (Fuchslueger et al., 2016; Hagedorn and Joos, 2014; Wang et al., 2021a), dense rooting system, and rapid fine root turnover (Leifeld et al., 2015; Solly et al., 2013) which together accelerate C cycling through the plant-soil system. In forests, aboveground C inputs are greater than in agricultural systems, where aboveground biomass is regularly removed (Hiltbrunner et al., 2013; Keel et al., 2019). These inputs – particularly woody debris and conifer litter – decompose slowly and lead to the formation of organic layers (Hiltbrunner et al., 2013; Tangarife-Escobar et al., 2024; Zanella et al., 2011), reducing the rate of C release back to the atmosphere. In arable land used for crop production, tillage and biomass removal disturb natural C cycling and induces the depletion of SOC stocks (Keel et al., 2019), especially in managed C-rich peatlands (Leifeld et al., 2005). Swiss peatlands, which store large amounts of C on a per area basis, have been intensively used for agriculture over the past century. Conversion of the

majority (82 %) of these peatlands to other land uses has led to severe degradation, causing high C losses (Wüst-Galley et al., 2020).

Despite their relevance in the global C cycle, soil CO<sub>2</sub> fluxes and their sources remain one of the greatest sources of uncertainty in global C budgets and in understanding climate feedbacks (Konings et al., 2019; Li et al., 2016; Tharammal et al., 2019). One reason is the methodological challenge of quantifying the sources of soil-respired CO<sub>2</sub> under natural conditions. Common approaches rely on destructive techniques such as trenching or girdling (e.g., Diao et al., 2022; Shi et al., 2022; Wunderlich and Borken, 2012), are constrained by their short-term nature such as <sup>13</sup>C pulse-labelling (Gao et al., 2021; Wang et al., 2021a), or by their differences in natural abundance  $\delta^{13}\text{C}$  signatures which do not allow for distinction of autotrophic sources from the decomposition of young SOC compounds (e.g., Diao et al., 2022; Millard et al., 2010). Radiocarbon (<sup>14</sup>C) analysis provides a powerful tool to determine the age of respired CO<sub>2</sub>, which in turn corresponds to the mean transit time of C – the time C spends in the terrestrial ecosystem from photosynthesis until respiration (Bolin and Rodhe, 1973; Eriksson, 1971; Sierra et al., 2017). Nuclear weapons testing in the 1950s and 1960s led to nearly a doubling in the amount of atmospheric <sup>14</sup>CO<sub>2</sub> in the Northern hemisphere (commonly known as the “bomb-spike”), inadvertently serving as a large-scale tracer experiment. Since then, atmospheric <sup>14</sup>CO<sub>2</sub> levels have been diluted due to the emission of <sup>14</sup>C-free fossil fuels (Schoor et al., 2016) and the incorporation of <sup>14</sup>CO<sub>2</sub> into the ocean and terrestrial ecosystems. The <sup>14</sup>C bomb-spike can be used to investigate C incorporation and cycling in terrestrial ecosystems on decadal time scales (Graven et al., 2024). In combination with stable carbon (<sup>13</sup>C) isotope analysis, <sup>14</sup>C measurements of CO<sub>2</sub> from in situ soil respiration as well as autotrophic and heterotrophic respiration from incubations provide a non-destructive approach to determine source contributions to total soil respiration based on their distinct isotopic signatures (e.g., Borken et al., 2006; Schoor and Trumbore, 2006). Soil incubation experiments under controlled conditions can further inform about SOC decomposability, the SOC fraction that is potentially readily available for microbial decomposition, by relating rates of heterotrophic respiration to SOC contents of the soil samples (Schädel et al., 2020). High SOC decomposability suggests a large fraction of readily available organic matter, whereas low SOC decomposability indicates greater persistence and stability of SOC and/or advanced decomposition of more labile SOM.

Radiocarbon and stable isotopic approaches have been used to investigate the age and source contributions of respired CO<sub>2</sub> in natural ecosystems (Hicks Pries et al., 2013; Phillips et al., 2013; Schoor and Trumbore, 2006; Wunderlich and Borken, 2012). However, these techniques have not yet been used in agro-ecosystems such as intensely managed grasslands, croplands, and drained peatlands. In our study, we investigated the magnitude, velocity, and pathways of C

cycling across five dominant land-use types in Switzerland which span a gradient from natural to intensely managed and disturbed ecosystems: grasslands (temperate and alpine), forests, croplands, and managed peatlands. We measured soil respiration rates and C isotopic signatures ( $\Delta^{14}\text{CO}_2$  and  $\delta^{13}\text{CO}_2$ ) of total soil respiration and its sources and used Bayesian mixing models to determine the age and source contribution for each land-use type. Our main goals were (i) to assess how the flux rates, ages, and source contributions of soil-respired  $\text{CO}_2$  vary across dominant land-use types in Switzerland, (ii) to determine how these variables change seasonally, and (iii) to develop a conceptual framework to describe how  $\text{CO}_2$  age and soil respiration rates can be used to identify and characterise C cycling pathways in various land-use types, in order to detect SOC losses, and to assess the vulnerability of C cycling in these systems to land-use and climate change.

We hypothesized that  $\text{CO}_2$  age and soil respiration rates under different land-use types are driven by the interplay of vegetation (productivity, belowground allocation, litter quality), climate, soil physicochemical properties, and management practices. Specifically, we expected that (i) temperate grasslands predominantly respire young, few year old  $\text{CO}_2$  at a high rate due to high belowground C allocation and high autotrophic contributions driven by abundant fine root biomass; (ii) alpine grasslands respire decadal-old  $\text{CO}_2$  because colder climate slows down C turnover in the plant-soil system; (iii) forests respire decadal-old  $\text{CO}_2$  at lower rates than grasslands, due to slower litter decomposition and a higher proportion of heterotrophic respiration, (iv) croplands release decadal- up to centennial-old  $\text{CO}_2$  at low rates, because of reduced C inputs and tillage, which deplete soils in labile C and leave behind persistent, older SOC; and finally (v) managed peatlands release the oldest up to millennial-old  $\text{CO}_2$  at high rates, driven by the decomposition of preserved C and high heterotrophic respiration following drainage.

## 2 Materials and methods

### 2.1 Study sites

We sampled soil-respired  $\text{CO}_2$ , roots, and soil from 16 sites of five dominant land-use types in Switzerland: grasslands (temperate and alpine), forests, intensively managed croplands, and managed peatlands (drained and used as croplands). Land-use types were chosen based on established classifications following the Land use, land-use change and forestry (LULUCF) categories defined by the IPCC (IPCC, 2021, 2003), with an additional distinction between temperate and alpine grasslands to account for climatic differences. The 16 sites vary in their physicochemical soil properties, span a climatic as well as elevational gradient from 393 to 2630 m above sea level (a.s.l.) and encompass four of Switzerland's five ecoregions (Table 1, Supplement Fig. S1).

Site properties are typical for the respective land-use type across Switzerland. Generally, croplands and managed peatlands are found under relatively similar environmental conditions of the Swiss Plateau, whereas grasslands and forests occur across a broader range of climate conditions. We deliberately chose sites from Swiss monitoring programs to capture variability in climate and soil properties allowing us to test the robustness of land-use type effects on rates, ages, and source contribution of respired  $\text{CO}_2$ . Grasslands were either used as meadows (Chamau, Muldain) in the lowlands, including mowing and manure application, or as pasture (Jaun, alpine grasslands), including grazing. The three cropland sites resemble each other in crop type (July/August: maize, March: wheat; Table 1) and management practices, and are part of long-term field trials of the Swiss Federal Research Institute Agroscope, Switzerland, established 35 and 49 years ago (for Changins: e.g., Maltas et al., 2018; for Altwi, Reckenholz: e.g., Hirte et al., 2021). As part of the Swiss Plateau near settlements, the sites had been used as grassland, orchards and vineyards until the 19th century and had then been converted to croplands before they were used for the long-term cropping trials (Oberholzer et al., 2014). All cropland sites were treated with mineral fertilizer according to the Swiss fertilization guidelines (Flisch et al., 2009) and regularly ploughed before sowing to a soil depth of approximately 25 cm. The managed peatlands were drained in the second half of the 19th century and have been used for crop production ever since (Leifeld et al., 2011). Crop types differ between each peatland site and season, with most of the cultivated crops being vegetables (Table 1).

### 2.2 In situ $\text{CO}_2$ flux measurements and gas sampling

We measured rates and sampled  $\text{CO}_2$  from total soil respiration in situ at all sites during two sampling campaigns: one in July/August 2023 and another in March 2024. These months were selected to capture the greatest variability in the soil environmental conditions while avoiding snow cover and melt. Severe climatic conditions precluded a sampling in March at the three alpine grassland sites.

At each of the 16 sites, we inserted three opaque cylindrical PVC frames ( $\text{Ø} = 30$  cm; height = 15–25 cm; volume  $\sim 15$  L) approximately 3–5 cm deep into the soil and 1–2 m apart to account for soil heterogeneity. Chambers were installed 1–2 weeks before sampling to allow soil respiration to re-equilibrate after installation disturbance. To exclude the contribution of above-ground plant respiration, vegetation inside the chamber was clipped at installation and before sampling if plants had regrown.

We measured  $\text{CO}_2$  fluxes for each of the three chambers via a flow-through system using a LI-COR gas analyser (LI-8100A, LI-COR<sup>®</sup>).  $\text{CO}_2$  fluxes were calculated as the rate of change in concentration over time in the chamber headspace using a linear approach while correcting for air pressure and mean chamber temperature using Gay-Lussac's ideal gas law

**Table 1.** Site specific information on climate, soil type, and vegetation/crop type.

Land-use type	Site name	Location			Climate			Soil properties			Soil type (WRB classification)	Vegetation/Crop type	
		Lat	Lon	Elevation [m a.s.l.]	MAP [mm]	MAT [°C]	pH (0–10 cm)	SOC (0–10 cm) [%]	N (0–10 cm) [%]		July/August	March	
Grassland	Chamau	47.2102	8.4104	393	1134	9.9	6.3	2.9	0.3	Cambisol/Gleysol	Italian ryegrass, white clover		
	Vaz Muldau	46.6903	9.5196	1200	1040	4.9	7.0	7.1	0.9	Gleyic Fluvisol	mixed grasses		
	Jaun	46.6114	7.2727	1500	1712	6.0	5.2	5.8	0.6	Eutric Cambisol	mixed grasses		
Alpine	Flielapass	46.7433	9.9632	2320	1622 <sup>a</sup>	0.4 <sup>a</sup>	3.5	6.3	0.5	–	mixed grasses		
	Büelenhorn	46.6791	9.7793	2340	1622 <sup>a</sup>	−0.1 <sup>a</sup>	6.6	1.2	1.5	–	mixed grasses		
	Raddörl	46.7118	9.9387	2340	1622 <sup>a</sup>	0.4 <sup>a</sup>	3.7	15.0	1.0	–	mixed grasses		
	Schwarzhorn	46.7335	9.9530	2630	1622 <sup>a</sup>	−1.2 <sup>a</sup>	4.0	7.6	0.6	–	mixed grasses		
Forest	Beatenberg	46.7003	7.7625	1511	1725	4.7	3.1	6.6	0.3	Podzol	Norway Spruce		
	Pfynwald	46.3031	7.6121	615	575	10.6	6.2	11.9	0.5	Pararendzina	Scots pine		
	Hölslein	47.4381	7.7769	550	1009 <sup>b</sup>	9.0 <sup>b</sup>	5.2	6.2	0.5	–	European beech, Norway Spruce		
Cropland	Reckenholz	47.4307	8.5220	440	1050	9.4	5.5	2.4	0.3	Eutric Gleysol	summer maize		
	Altwi	47.4386	8.5255	493	1050	9.4	7.4	1.4	0.2	Calcic Cambisol	summer maize		
	Changins	46.3820	6.2389	446	994	10.7	7.1	0.9	0.1	Calcic Cambisol	summer maize		
Managed peatland	Lindergut	46.9797	7.0983	430	1030 <sup>c</sup>	10.7 <sup>c</sup>	7.0	11.5	0.9	Histosol	mixed grasses		
	Rimmermatte	47.0117	7.0772	432	1030 <sup>c</sup>	10.7 <sup>c</sup>	7.0	10.4	0.8	Histosol	onion		
	Urdert Site	47.0245	7.2044	438	1030 <sup>c</sup>	10.7 <sup>c</sup>	7.1	17.5	1.5	Histosol	summer maize		

<sup>a</sup> Alpine sites: MAP from Meeoswiss station Weissflühorn (2690 Hm), MAT from IMIS stations (FL02 for Flielapass and Raddörl; DAV2 for Büelenhorn; ZNZ2 for Schwarzhorn). <sup>b</sup> Hölslein: MAP and MAT from Meeoswiss station Basel-Bimingen. <sup>c</sup> Managed peatlands: MAP from Meeoswiss station Aarberg, MAT from Meeoswiss station Neuchâtel.

(Butterbach-Bahl et al., 2011). Chamber closure times during flux measurements were 3–10 min. After flux measurements, chambers were flushed with CO<sub>2</sub>-free air five times the chamber volume (ca. 75 L) and sealed until CO<sub>2</sub> levels reached ~ 1000 ppm for subsequent <sup>14</sup>C analysis. Air from all three chambers was composited into a 2 L air bag (Cali-5-Bond, Calibrated Instruments, LLC, USA). A detailed description of the sampling procedure is presented in Supplement Sect. S1 and Fig. S2. For <sup>13</sup>C analysis, we sampled gas from each of the three chambers separately, transferring headspace air into pre-evacuated 12 mL Exetainer<sup>®</sup> vials using a 60 mL syringe. The lack of spatial and temporal replicates for each site is a consequence of the limited capacity of <sup>14</sup>C measurements. In March, we repeated the CO<sub>2</sub> sampling and subsequent isotopic analysis for three spatial replicates at the forest sites Hölstein and Pfywald. Results of the spatial replication are presented in Sect. S6, Fig. S9, and Table S6.

For atmospheric background <sup>14</sup>CO<sub>2</sub> measurements, ambient air (~ 20 cm above the soil surface) was sampled into 5 L air bags (Cali-5-Bond, Calibrated Instruments, LLC, USA). Soil environmental conditions were monitored before and after gas sampling. Ambient air temperature was measured at the height of the chamber (~ 15 cm above soil surface). Soil temperature and volumetric water content (VWC) were monitored at 10 cm soil depth using a thermometer and HH2 moisture meter (Delta-T Devices Ltd), respectively.

### 2.3 Soil sampling and analysis

During the July/August sampling campaign, we sampled soil at the centre of each PVC frame after the gas sampling was completed. Soil cores were taken with a Humax corer (Ø = 5 cm) down to 52 cm soil depth. Sampling was continued as deep as possible (maximum depth = 90 cm) using a soil auger (Ø = 5 cm). Soil samples were stored at 2 °C until further processing. We split the mineral soil samples from the three soil cores into depth intervals of 0–5, 5–10, 10–20, 20–40, and 40–90 cm for all sites. At the forest sites, we additionally sampled organic layers (i.e., litter (L), fermented horizon (F), and humified horizon (H; only present at Beatenberg)). Alpine grassland sites were sampled separately by excavating soil profiles and taking volume-proportional samples for the pre-defined depth intervals. Volumes were estimated by simple measurements of the excavated areas and samples were weighed and sieved to 4 mm in the field prior to processing in the laboratory.

For further analysis, we pooled and homogenized the soil of the three cores and corresponding depths to yield one composite sample per depth and site. In order to measure the released CO<sub>2</sub> by heterotrophic respiration during incubation, we removed the roots and skeleton by sieving subsample at 4 mm. We acknowledge that sieving can disrupt soil structure and expose otherwise protected SOC but was necessary to remove roots contributing to the CO<sub>2</sub> release. However, we tried to limit aggregate disruption by careful sieving at

4 mm compared to the standard 2 mm-sieving. Subsamples were dried at 40 °C, sieved them to 2 mm, and ground to fine powder using a ball mill (MM2000, Retsch).

Gravimetric water content (GWC) was determined for each soil sample by drying a subsample of 6–10 g of fresh soil at 105 °C for 48 h. Bulk density was obtained by calculating the dry soil weight for each depth layer. Fine soil mass in each layer was determined by subtraction of the weight of the skeleton (> 2 mm). The volume of the skeleton was calculated by assuming a density of 2.65 g cm<sup>-3</sup> for stones (Walthert et al., 2002).

### 2.4 Root and soil incubations

We determined isotopic signatures of autotrophic and heterotrophic endmembers by conducting short-term root and soil incubations. Root incubations were prepared during the sampling campaigns in situ. We excavated fine roots (< 2 mm), including mycorrhizae within the chambers at 0–10 cm soil depth after the gas sampling. We carefully removed soil particles and rinsed the roots in an ultrapure water bath while keeping the root system as intact as possible. Roots from all three chambers were combined into one composite sample and incubated instantly, as the δ<sup>13</sup>C value of excised roots can slightly change after a few minutes (Midwood et al., 2006). We placed approximately 10 g of fresh roots into 2 L glass bottles that were wrapped in aluminium foil to exclude light. We immediately flushed the glass bottles with CO<sub>2</sub>-free air until all ambient air was removed. Roots were incubated overnight at approximately 22 °C, followed by gas sampling into a 2 L air bag using a flow-through system. A detailed description of the sampling procedure from incubations is presented in Sect. S2. Gas for <sup>13</sup>C analysis was sampled thereafter as described for in situ soil respiration.

Soil incubations were performed for each depth layer using the same procedure as for root incubations. Depending on the depth layer and their SOC contents, we incubated soil corresponding to dry soil weights between 30 and 250 g. Soils were incubated at 22 °C and field soil moisture levels. Depending on the respiration rates, the incubation time varied between one day and four weeks. We calculated basal respiration rates for each soil incubation by integrating the entire incubation period. Basal respiration was used as a proxy for SOC decomposability by relating it to the SOC content.

### 2.5 Isotopic analysis of gas samples

The <sup>13</sup>CO<sub>2</sub> contents of all gas samples were measured by an isotope-ratio mass spectrometer (IRMS Gas-Bench II coupled with a Delta-V Advanced IRMS, Thermo GmbH, Germany) at the Swiss Federal Research Institute of Forest, Snow and Landscape WSL. Graphitization and <sup>14</sup>C measurements were performed at the Laboratory of Ion Beam Physics, ETH Zurich, Switzerland.

For  $^{14}\text{C}$  analysis, gas samples were graphitized using an Air Loading Facility (ALF; Gautschi et al., 2021) coupled to an Automated Graphitization Equipment (AGE3, ETH Zurich, Switzerland; Wacker et al., 2010a) with an integrated zeolite trap to adsorb  $\text{CO}_2$  from the sampling bag. The  $^{14}\text{CO}_2$  contents of all gas samples were measured using a Mini radioCarbon Dating System (MICADAS, ETH Zurich, Switzerland; Synal et al., 2007) or a Low Energy AMS (LEA, ETH Zurich & IonPlus AG, Switzerland; Ramsperger et al., 2024). Measurement uncertainties were  $< 2\%$ . For data evaluation, the standard Oxalic Acid II (Mann, 1983) and blank material from the  $^{14}\text{C}$ -free phthalic anhydride (PhA) were measured alongside the samples and evaluated with the BATS software (Wacker et al., 2010b).

## 2.6 Isotopic analysis of bulk soil

Bulk soil samples were analysed for total and organic C, and  $\delta^{13}\text{C}$  by dry combustion with an automated elemental analyser – continuous flow isotope ratio mass spectrometer (Euro-EA 3000, HEKAtech GmbH, Germany, interfaced with a Delta-V Advanced IRMS, Thermo GmbH, Germany). Measurements were corrected against primary reference materials (VPDB and AIR). Measurement uncertainties were  $< 0.3\%$ . Samples with  $\delta^{13}\text{C}$  values exceeding  $-25\%$ , which suggest a potential contribution of inorganic C, were additionally analysed after fumigation with 37% HCl to remove inorganic C (Walthert et al., 2010).

For  $^{14}\text{C}$  analysis, potential inorganic C was removed for all samples by fumigation with 37% HCl (Komada et al., 2008; Walthert et al., 2010). Samples were acidified for 72 h at 60 °C and neutralized with NaOH pellets (72 h, 60 °C). All glassware was combusted at 550 °C for 5 h prior to use.  $^{14}\text{C}$  measurements in SOC of bulk soil were performed on a MICADAS featuring a gas ion source and coupled to an Elemental Analyser (EA vario MICRO cube, Elementar, Germany; Ruff et al., 2010) at the Laboratory of Ion Beam Physics, ETH Zurich, Switzerland. Measurement uncertainties were 6%–8%.

Comparisons of isotopic signatures from heterotrophically respired  $\text{CO}_2$  and SOC revealed possible contributions of carbonate weathering to  $\text{CO}_2$  for some sites and depths. We assumed contributions of carbonate weathering in cases where  $\Delta^{14}\text{C}$  signatures indicated  $\text{CO}_2$  age  $>$  SOC age and/or in cases where  $\delta^{13}\text{CO}_2 > \delta^{13}\text{C}$  of SOC (except croplands and managed peatlands). Although we estimated carbonate contributions with certain limitations (Sect. S7), we were unable to accurately correct the  $^{14}\text{C}$  signature of heterotrophically respired  $\text{CO}_2$  because the isotopic signatures of endmembers required for this correction (i.e., carbonate, SOC-derived  $\text{CO}_2$ ) could not be sufficiently constrained. Nevertheless, we provide estimated contributions and corrected  $\Delta^{14}\text{CO}_2$  signatures in Table S2. Our estimations revealed that the mean effect of carbonate weathering on total heterotrophic res-

piration and on in situ soil respiration was  $< 5 \pm 3\%$  and  $< 2 \pm 1\%$ , respectively (Table S2).

## 2.7 Estimation of ages from $\Delta^{14}\text{CO}_2$ signatures

We estimated ages of  $\text{CO}_2$  from heterotrophic respiration (total, topsoil and subsoil layers) and total soil respiration using carbonate-corrected  $\Delta^{14}\text{CO}_2$  values with the web-based OxCal software (2024; Bronk Ramsey, 2009) using the Bomb21NH1 calibration curve (Hua et al., 2022). In cases where the  $\Delta^{14}\text{CO}_2$  values were outside the calibration range (younger than 2019), ages were derived by comparing  $\Delta^{14}\text{CO}_2$  values with extended bomb curve data. The curve Bomb21NH1 was extended with  $\Delta^{14}\text{CO}_2$  values measured at Jungfraujoch, Switzerland by ICOS between 2022 to 2023 (Emmenegger et al., 2025) and in 2024 by Geissbühler et al. (2026). A detailed description of the approach is presented in Sect. S3.

## 2.8 Source partitioning using Bayesian mixing models and correction for atmospheric background

The soil respired  $\text{CO}_2$  (SR) that we captured in situ from the chamber headspace was partitioned into autotrophic (AR) and heterotrophic (HR from each depth layer) sources, as well as residual atmospheric air (ATM) using Bayesian mixing model approaches: MixSIAR (R package MixSIAR, version 3.1.12; Moore and Semmens, 2008; Stock et al., 2018) and an implementation using Python. Partitioning was performed for each site separately. The models use Markov Chain Monte Carlo to sample possible distributions so that:

$$\Delta^{14}\text{CO}_{2\text{SR}} = f_{\text{ATM}}\Delta^{14}\text{CO}_{2\text{ATM}} + f_{\text{AR}}\Delta^{14}\text{CO}_{2\text{AR}} + \sum_{\text{depth}=1}^n f_{\text{HR,depth}}\Delta^{14}\text{CO}_{2\text{HR,depth}} \quad (1)$$

$$\delta^{13}\text{CO}_{2\text{SR}} = f_{\text{ATM}}\delta^{13}\text{CO}_{2\text{ATM}} + f_{\text{AR}}\delta^{13}\text{CO}_{2\text{AR}} + \sum_{\text{depth}=1}^n f_{\text{HR,depth}}\delta^{13}\text{CO}_{2\text{HR,depth}} \quad (2)$$

$$1 = f_{\text{ATM}} + f_{\text{AR}} + \sum_{\text{depth}=1}^n f_{\text{HR,depth}} \quad (3)$$

where  $0 \leq f \leq 1$  is the proportional contribution of each endmember to total soil respiration and  $n$  is the number of incubated depth layers. Input data were  $\Delta^{14}\text{CO}_2$  values and associated measurement errors ( $\sim 2\%$ ) as well as  $\delta^{13}\text{CO}_2$  values and associated standard deviations of three replicates ( $\sim 0\%$ – $1\%$ ) for mixtures and sources. Constraints and modification of input data are presented in Sect. S4. To estimate the heterotrophic contribution of each depth layer to in situ soil respiration, respiration rates measured at 22 °C were adjusted to field temperature using a uniform  $Q_{10}$  of 2.4 (Raich and Schlesinger, 1992), together with depth-related temperature corrections (Bourletsikas et

al., 2023). The resulting temperature-adjusted rates were then used as weighting factors in the Bayesian mixing model to improve model performance. In the Bayesian mixing model in Python, we treated heterotrophic respiration from each depth layer as a separate source and added weighted respiration rates as deterministic predictors (assumed uncertainty = 10 %). In MixSIAR, we aggregated depths to topsoil (0–5, 5–10 cm) and subsoil (10–20, 20–40, 40–maximum depth cm) layers to reduce the number of sources in favour of the model performance. Respective isotopic endmember values (topsoil and subsoil) were calculated using a mass balance approach. Isospace plots of MixSIAR are presented in Figs. S10–S18. In MixSIAR we used weighted contributions of topsoil and subsoil to total heterotrophic respiration to set up an informative prior with the flat Dirichlet distribution, so that:  $\alpha = (f_{\text{ATM}}, f_{\text{AR}}, \sum f_{\text{HR,depth}})$  corresponds to  $\alpha = (1, 1, 1)$ . Model convergence was assessed via Gelman-Rubin (values < 1.05) and Geweke diagnostics. Further information on model settings is given in Table S1. We combined the mean values and standard deviations of both models to account for specific model restrictions and variability in model outputs. A detailed description of the differences and limitations of the two approaches (MixSIAR and implementation in Python) is given in Sect. S5.

To exclude atmospheric contribution to total soil respiration, we adjusted mean values and standard deviations of autotrophic and heterotrophic contributions so that:

$$f_{\text{AR}_{\text{corr}}} = \frac{f_{\text{AR}}}{1 - f_{\text{ATM}}} \quad (4)$$

$$\sum_{\text{depth}=1}^n f_{\text{HR,depth}_{\text{corr}}} = \frac{\sum_{\text{depth}=1}^n f_{\text{HR,depth}}}{1 - f_{\text{ATM}}} \quad (5)$$

We further corrected  $\Delta^{14}\text{CO}_2$  and  $\delta^{13}\text{CO}_2$  values of in situ soil respiration for the effect of atmospheric background using the proportions of source contributions from the model outputs. We calculated the corrected isotopic values ( $\text{SR}_{\text{corr}}$ ) as:

$$\Delta^{14}\text{CO}_{2\text{SR}_{\text{corr}}} = \frac{\Delta^{14}\text{CO}_{2\text{SR}} - (\Delta^{14}\text{CO}_{2\text{ATM}} \times (1 - f_{\text{SR}}))}{f_{\text{SR}}} \quad (6)$$

$$\delta^{13}\text{CO}_{2\text{SR}_{\text{corr}}} = \frac{\delta^{13}\text{CO}_{2\text{SR}} - (\delta^{13}\text{CO}_{2\text{ATM}} \times (1 - f_{\text{SR}}))}{f_{\text{SR}}} \quad (7)$$

where  $f_{\text{SR}}$  is the fraction of soil-derived  $\text{CO}_2$  calculated as the sum of autotrophic and heterotrophic source proportions as initially derived from the model outputs.

### 3 Results

#### 3.1 In situ soil respiration rates across land-use types and seasons

Average in situ respiration rates across land-use types ranged from 125 to 363  $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in July/August and from 91 to 191  $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in March (Table 2, Fig. 1). Forests exhibited the lowest respiration rates in both seasons. In July/August, managed peatlands had the highest respiration rates, however, this was mainly related to very high respiration at one of the sites (Lindergut). While the effects of land-use types on in situ soil respiration were not significant ( $p = 0.133$ ), seasonality had a significant effect ( $p < 0.001$ ) (Table S4). In agreement with the seasonality, in situ respiration rates were affected significantly by soil temperature ( $p < 0.001$ ) and soil water content ( $p = 0.002$ ) (Table S3). While grasslands had soil water contents above 45 vol %, forest and cropland sites exhibited particularly low soil water contents in July/August (< 20 vol %; Fig. 1).

#### 3.2 $\Delta^{14}\text{CO}_2$ values in total soil respiration across land-use types and seasons

The soil-respired  $\Delta^{14}\text{CO}_2$  values measured in situ varied significantly across land-use types ( $p = 0.001$  and  $p = 0.002$  with and without managed peatlands (Table S4), with the highest  $\Delta^{14}\text{CO}_2$  values in forests, followed by grasslands, croplands, and managed peatlands. The latter showed strongly  $^{14}\text{C}$ -depleted values (i.e.,  $\Delta^{14}\text{CO}_2 < -50\%$ ; Fig. 2).

The in situ soil-respired  $^{14}\text{CO}_2$  in croplands and grasslands exhibited modern values, close to the contemporary atmospheric  $^{14}\text{CO}_2$ , corresponding to ages < 10 years (Table 2). Within grasslands,  $\Delta^{14}\text{CO}_2$  values significantly increased ( $p = 0.006$ ) with elevation (Fig. S3, Table S5). Forest soils released  $\text{CO}_2$  with positive  $\Delta^{14}\text{C}$  values, indicative of bomb-derived, decadal-old  $\text{CO}_2$  (Table 2). In managed peatlands, soil-respired  $\text{CO}_2$  had very low  $\Delta^{14}\text{CO}_2$  values, corresponding to mean ages of approximately 1500 years (Table 2).

The  $\Delta^{14}\text{CO}_2$  values of total soil respiration differed significantly between July/August and March ( $p = 0.001$ ) with  $\Delta^{14}\text{CO}_2$  values being generally closer to atmospheric  $\text{CO}_2$  in March. However, the effect of seasonality varied significantly across land-use types ( $p < 0.001$ ). While managed peatlands exhibited the largest seasonal changes in soil-respired  $\Delta^{14}\text{CO}_2$ , temperate grasslands and forests showed the lowest seasonal variation (Fig. 2, Table 2).

#### 3.3 Isotopic signatures of atmosphere, autotrophic, and heterotrophic respiration

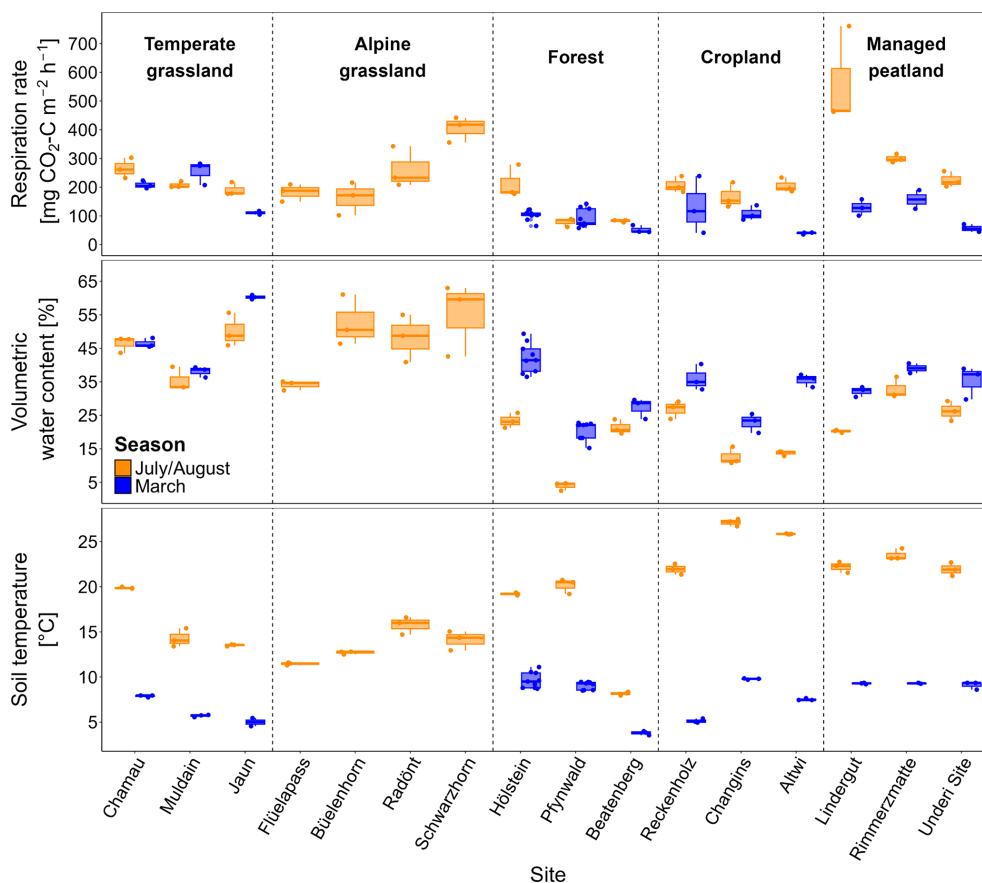
Our results showed seasonal variation in  $\Delta^{14}\text{CO}_2$  values of atmosphere and autotrophic respiration (Fig. S4). In the atmosphere, the mean  $\Delta^{14}\text{CO}_2$  value was more depleted in

**Table 2.** Mean soil respiration rates,  $\Delta^{14}\text{CO}_2$  values, estimated ages and relative source contribution of heterotrophic and autotrophic sources across land-use types. Carbonate-corrected  $\Delta^{14}\text{CO}_2$  values were used for the estimation of ages (Table S2). Data is reported as means  $\pm$  standard deviations across sites within land-use types.

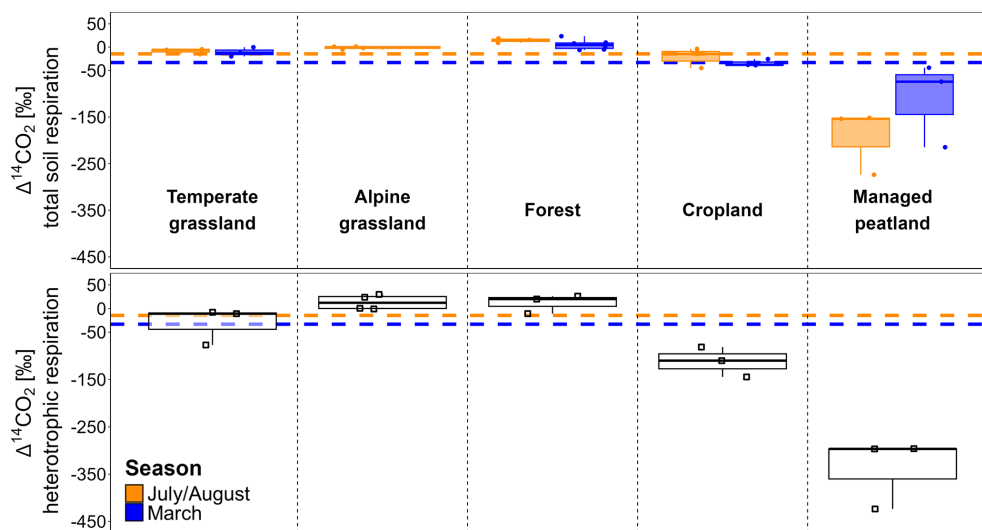
Season	Land-use type											
	Temperate grassland		Alpine grassland		Forest		Cropland		Managed peatland			
	July/August	March	July/August	March	July/August	March	July/August	March	July/August	March	July/August	March
Total soil respiration												
Respiration rate [ $\text{mg CO}_2\text{-C m}^{-2}\text{ h}^{-1}$ ]	221 $\pm$ 39	191 $\pm$ 73	253 $\pm$ 110	–	125 $\pm$ 76	91 $\pm$ 29	193 $\pm$ 22	93 $\pm$ 48	363 $\pm$ 178	144 $\pm$ 52		
$\Delta^{14}\text{CO}_2$ value [‰]	–9 $\pm$ 6	–11 $\pm$ 10	–1 $\pm$ 3	–	14 $\pm$ 5	5 $\pm$ 10	–21 $\pm$ 21	–34 $\pm$ 7	–193 $\pm$ 70	–111 $\pm$ 91		
Estimated age [yrf]	8 $\pm$ 1	7 $\pm$ 1	5	–	11 $\pm$ 1	9 $\pm$ 1	162 $\pm$ 127 $\pm$ 1*	230 $\pm$ 32/5*	1486 $\pm$ 47	828 $\pm$ 23		
Heterotrophic respiration												
Estimated $\Delta^{14}\text{CO}_2$ value [‰]												
Total	–32 $\pm$ 39	13 $\pm$ 16	12 $\pm$ 20	–112 $\pm$ 32	–339 $\pm$ 73							
Organic layer												
Topsoil	1 $\pm$ 13	31 $\pm$ 22	6 $\pm$ 18	23 $\pm$ 16	–109 $\pm$ 62	–167 $\pm$ 27						
Subsoil	–56 $\pm$ 58	–41 $\pm$ 17	–54 $\pm$ 83	–107 $\pm$ 50	–349 $\pm$ 75							
Estimated age [yrf]												
Total	9 $\pm$ 1	40 $\pm$ 3	11 $\pm$ 1	648 $\pm$ 32	3188 $\pm$ 46							
Organic layer												
Topsoil	7	12 $\pm$ 1	7	11 $\pm$ 1	241 $\pm$ 16	1394 $\pm$ 26						
Subsoil	39	387 $\pm$ 14	142 $\pm$ 4	729 $\pm$ 19	3294 $\pm$ 48							
Rel. source contribution [%]												
Total	40 $\pm$ 5	46 $\pm$ 5	37 $\pm$ 5	–	69 $\pm$ 7	53 $\pm$ 4	31 $\pm$ 1	11 $\pm$ 2	53 $\pm$ 7	23 $\pm$ 4		
Organic layer												
Topsoil	25 $\pm$ 4	21 $\pm$ 2	29 $\pm$ 4	–	44 $\pm$ 5	5 $\pm$ 0	18 $\pm$ 1	3 $\pm$ 2	5 $\pm$ 5	3 $\pm$ 3		
Subsoil	15 $\pm$ 2	24 $\pm$ 4	9 $\pm$ 2	–	5 $\pm$ 0	16 $\pm$ 0	12 $\pm$ 1	8 $\pm$ 1	48 $\pm$ 4	20 $\pm$ 2		
Autotrophic respiration												
Estimated $\Delta^{14}\text{CO}_2$ value [‰]	–12 $\pm$ 4	–15 $\pm$ 6	–6 $\pm$ 3	–	–4 $\pm$ 4	–9 $\pm$ 5	–13 $\pm$ 3	–32 $\pm$ 4	–14 $\pm$ 4	–34 $\pm$ 3		
Rel. source contribution [%]	60 $\pm$ 7	54 $\pm$ 5	63 $\pm$ 6	–	31 $\pm$ 5	47 $\pm$ 3	69 $\pm$ 6	89 $\pm$ 3	47 $\pm$ 6	77 $\pm$ 3		

\* For total soil respiration in croplands, two age ranges are possible. Highly  $\text{C}^{14}$  depleted atmospheric background samples for these sites make it difficult to interpret the depleted  $\Delta^{14}\text{CO}_2$  values of total soil respiration. The values are within a range that the comparison with the site-adjusted bomb curves would reveal ages of around 7 and 5 years in July/August and March, respectively. The low relative source proportion of heterotrophic respiration is further indicative of an overall respiration of younger  $\text{CO}_2$ .





**Figure 1.** Soil respiration rates ( $\text{mg CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ), volumetric water content (VWC; vol %), and soil temperature ( $^{\circ}\text{C}$ ) from in situ measurements in July/August and March across sites and land-use types. Dots indicate replicate measurements boxplots represent summary statistics for each site. VWC and soil temperature are presented for 0–10 cm of the mineral soil (excluding organic layers in forests).



**Figure 2.**  $\Delta^{14}\text{CO}_2$  values (‰) of total soil respiration (top) in both seasons and heterotrophic respiration (bottom) across land-use types. Dashed horizontal lines indicate mean atmospheric background  $\Delta^{14}\text{CO}_2$  levels across land-use types in July/August and March. Note that  $\Delta^{14}\text{CO}_2$  values of some sites and depths might be influenced by carbonate weathering, which can lower these values. However, the resulting effect on total heterotrophic and total soil respiration is small, and the overall trends remain unchanged (Table S2).

March than in July/August at all sites (mean across all sites:  $-14 \pm 10\%$  in July/August and  $-33 \pm 10\%$  in March), generally related to reduced respiratory activity and seasonal variation in atmospheric transport of CO<sub>2</sub> (Schoor et al., 2016). Due to the proximity of cropland sites to fossil CO<sub>2</sub> sources (i.e., highways, larger roads), their atmospheric  $\Delta^{14}\text{CO}_2$  values were more depleted than for other land-use types (Fig. S4). Autotrophic  $\Delta^{14}\text{CO}_2$  signatures were generally close to atmospheric  $\Delta^{14}\text{CO}_2$  values and followed their seasonal trend with more depleted  $\Delta^{14}\text{CO}_2$  values in March. In forests, however, autotrophic  $\Delta^{14}\text{CO}_2$  signatures in March were similar to those in July/August (Fig. S4).

Generally, the  $\Delta^{14}\text{CO}_2$  values from heterotrophic respiration indicate a continuous increase in the age of respired CO<sub>2</sub> with increasing soil depth, which was consistent across all land-use types (Fig. 3). However,  $\Delta^{14}\text{CO}_2$  values from two cropland sites increased from very depleted values at 0–5 cm to less depleted values at 5–10 cm soil depth.

The variation of  $\Delta^{14}\text{CO}_2$  values of total heterotrophic respiration across land-use types followed a similar pattern as that of total soil respiration. Temperate grassland soils released the most contemporary CO<sub>2</sub> with ages < 10 years, while alpine grassland and forest soils released bomb-derived, decadal-old CO<sub>2</sub> with average ages of ~40 and 11 years, respectively (Table 2). Within grasslands, heterotrophic respiration from topsoil layers exhibited an even stronger increase of  $\Delta^{14}\text{CO}_2$  values with elevation than in situ soil respired CO<sub>2</sub> ( $p = 0.056$ ; Figs. 3, S3, Table S5). In contrast, heterotrophic CO<sub>2</sub> in subsoil layers did not show an elevational pattern but showed depleted  $\Delta^{14}\text{C}$  values for all grassland sites corresponding to ages of 387 years (Fig. 3). Cropland soils released ~650-year-old CO<sub>2</sub> and managed peatland even emitted ~3200-year-old CO<sub>2</sub> ( $p_{\text{land-use type}} < 0.001$ ; Fig. 2, Tables 2, S4).

### 3.4 SOC decomposability

SOC decomposability, measured by the CO<sub>2</sub> release from soils under standardized conditions, varied significantly across land-use types in both topsoil ( $p < 0.001$ ) and subsoil ( $p = 0.002$ ), following a general pattern of decreasing decomposability with increasing soil depth (Fig. 4, Table S4). Croplands and managed peatlands exhibited the lowest values (< 20–60  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ), while forests showed high decomposability in the organic layer (> 200  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ), but much lower levels in the mineral soil. In Pfywald, SOC decomposability in the organic layer was restricted due to low soil moisture conditions (Fig. 1). Temperate grasslands had intermediate decomposability in topsoil and lower values in subsoil. Alpine grasslands exhibited the highest values (46–257  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ), with increased decomposability at higher elevations.

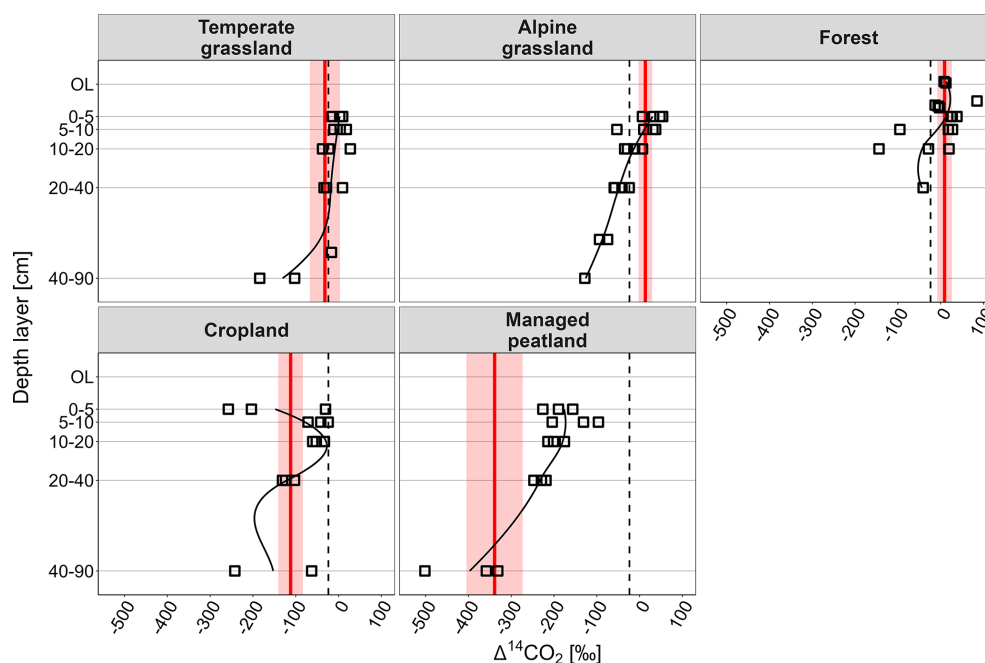
### 3.5 Changes in source contribution across land-use types

The  $\Delta^{14}\text{CO}_2$  signatures of total soil respiration fell between  $\Delta^{14}\text{CO}_2$  values of autotrophic and heterotrophic endmembers, indicating both contributed to total soil respiration (Fig. S6). Although the difference in source contribution across land-use types was not statistically significant ( $p = 0.071$ ), distinct patterns existed (Fig. 5, Table S4). Overall, autotrophic respiration was the dominant source of total soil respiration across all land-use types and both seasons (~60%) (Fig. 5, Table 2). The average autotrophic contribution was greatest in croplands (~80%) followed by managed peatlands and grasslands (~60%). Forest showed the smallest average autotrophic contribution (~40%) and accordingly, was the only land-use type where heterotrophic respiration dominated total soil respiration. The relative contribution of heterotrophic respiration was generally higher in July/August than in March for all land-use types except croplands (Fig. 5, Table 2). Managed peatlands showed the strongest seasonal variation of source contribution with an average heterotrophic contribution of 47% in July/August and 17% in March.

Measurements of the isotopic composition of heterotrophically respired CO<sub>2</sub> across various depths revealed differences in the contributions of organic layer, topsoil, and subsoil layers to total soil respiration among land-use types. Topsoils were the dominant heterotrophic source in grasslands (~26%) in both seasons and in forests during July/August (44%) (Table 2, Fig. 3). In forests, the organic layer contributed substantially to total soil respiration in both seasons (21% in July/August and 34% in March). In croplands, the generally low contribution of heterotrophic respiration showed similar contributions from top- and subsoil layers (Table 2, Fig. 3). Managed peatlands were almost entirely dominated by heterotrophic respiration from subsoil layers in July/August (48% of total soil respiration) while subsoil contributions were significantly reduced in March (Table 2).

## 4 Discussion

Our  $\Delta^{14}\text{CO}_2$  measurements clearly document that in situ soil respiration from all land-use types, except from managed peatlands, was dominated by relatively young C (< 12 years old). In addition, mineralized CO<sub>2</sub> from total heterotrophic respiration showed young C release (< 40 years old) from all land use types, except from managed peatlands and croplands. This pattern indicates that when C enters the soil system, the largest fraction gets rapidly respired back to the atmosphere. Although soil-respired CO<sub>2</sub> was predominantly young, estimated mean ages varied from < 10 years in grasslands to ~10 years in forests, and reached up to ~1500 years in managed peatlands. In conjunction with variations in soil respiration rates and SOC decomposability across land-



**Figure 3.** Depth profiles of  $\Delta^{14}\text{CO}_2$  signatures (‰) of heterotrophic respiration and weighted  $\Delta^{14}\text{CO}_2$  values of total heterotrophic respiration (red line) and error range (red shaded area). Dashed black vertical lines indicate the mean atmospheric  $\Delta^{14}\text{CO}_2$  value during our sampling campaigns across all land-use types and both seasons ( $-24$ ‰).

use types, the  $^{14}\text{C}$ -derived ages in soil-respired  $\text{CO}_2$  provide evidence that the magnitude, velocity, and pathways of C cycling within the plant-soil regime vary among these systems. Although there was variation in environmental conditions (i.e. soil moisture, soil temperature) within individual land-use types across different sites, the overarching patterns distinguishing land-use types remained consistent and site-level variability was accounted for in the statistical analysis. This suggests that land use played a more significant role in shaping respiration dynamics than site-specific environmental conditions.

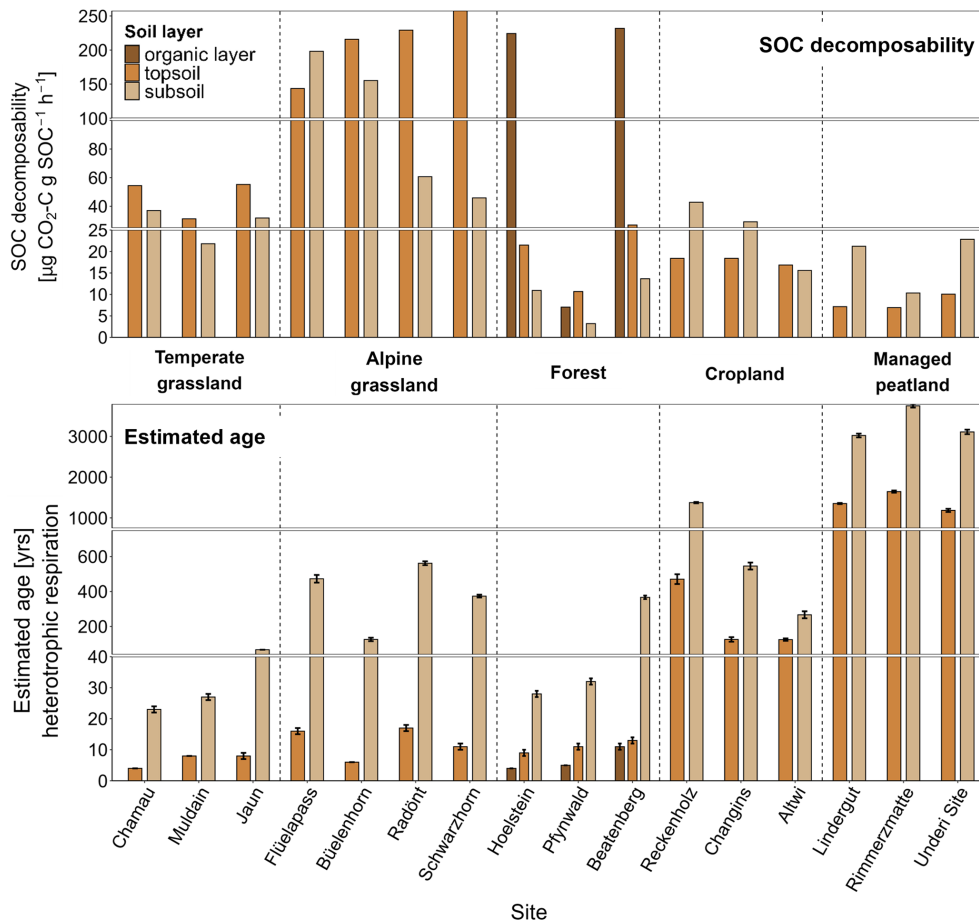
Here, we propose that SOC decomposability, in situ soil respiration rates and  $^{14}\text{C}$ -derived ages of soil-respired  $\text{CO}_2$  can serve as comprehensive indicators to categorize C cycling into five different systems: (1) high-throughput systems characterized by rapid C cycling – temperate grasslands, (2) temperature-constrained retarding systems characterized by slow C cycling – alpine grasslands, (3) input-constrained retarding systems with a delayed transfer of assimilates back to the atmosphere through soil respiration – forests, (4) C-depleted systems, where reduced C inputs result in the depletion of recent C material and SOC stocks – intensively managed croplands, and (5) hotspots of old soil C release due to significant disturbances in natural C cycling – managed peatlands.

#### 4.1 High-throughput systems – temperate grasslands

Among all land-use types, temperate grasslands represent the land-use type with the highest rates and the youngest age of soil-respired  $\text{CO}_2$ , characterizing them as high-throughput systems. The high respiration rates in grasslands are consistent with those observed across European land-use types (Schaufler et al., 2010). Here, we show that temperate grasslands have high contributions of autotrophic respiration (60%), indicating that a large fraction of their high GPP (Schulze et al., 2009) is rapidly allocated to the belowground, where it is metabolized and respired. Among land-use types, grasslands typically show the densest rooting system, the highest root turnover (Solly et al., 2014), rapid belowground C allocation (Fuchslueger et al., 2016) and a particularly high rhizodeposition (Wang et al., 2021a). Our study reveals young ages of heterotrophically respired  $\text{CO}_2$  and in bulk SOC in topsoil layers (Figs. 3, S7), indicating that plant-derived C inputs into the soil are rapidly processed by soil microbes. Overall, this results in rapid C cycling through the plant-soil system in temperate grasslands.

#### 4.2 Temperature-constrained retarding systems – alpine grasslands

Our assessment of grassland sites, spanning an elevation gradient from 390 to 2630 m a.s.l., shows increasing  $^{14}\text{C}$ -derived ages of soil-respired  $\text{CO}_2$  and SOC with elevation (Fig. S3). Since autotrophic respiration dominated irrespective of ele-



**Figure 4.** SOC decomposability (top;  $\mu\text{g CO}_2\text{-C g SOC}^{-1} \text{h}^{-1}$ ) and estimated ages of heterotrophic respiration (bottom) across land-use types and individual sites for organic layers, topsoil, and subsoil. Error bars for estimated ages represent propagated uncertainties corresponding to the OxCal confidence intervals derived from seasonal estimates. Note that the breaks in the y-axes have different scales for better visualisation.

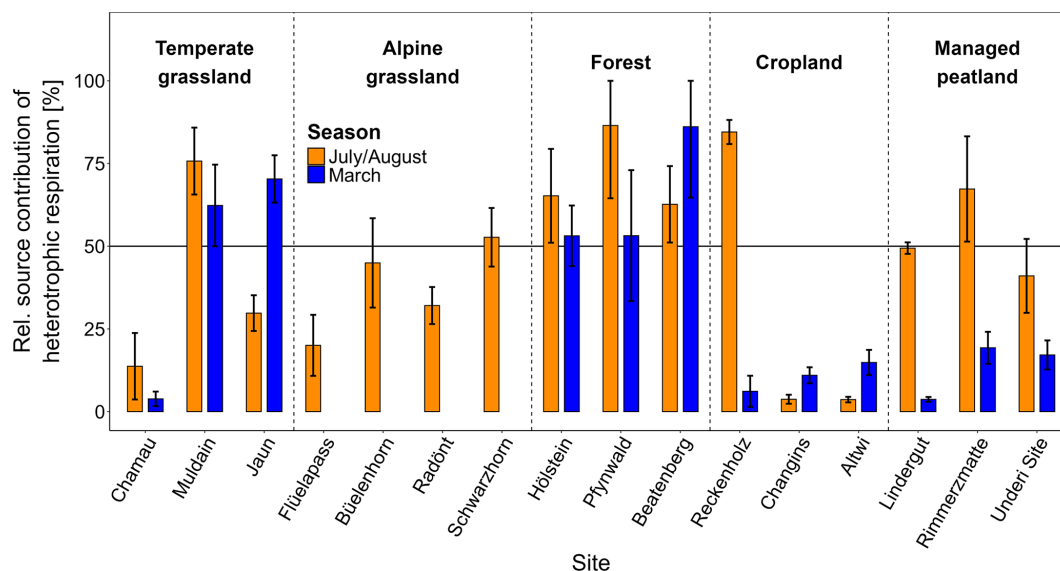
vation, the increasing age of in situ soil-respired  $\text{CO}_2$  with elevation derives from microbial processing of older SOC at higher elevation. In support, the  $\Delta^{14}\text{C}_{\text{CO}_2}$  values of heterotrophic respiration in topsoil layers increased with elevation (Fig. S3), indicating enhanced respiration of bomb-derived, decadal-old C. At the same time, Bayesian mixing models showed topsoil layers to contribute more strongly to heterotrophic respiration with increasing elevation. Overall, these findings indicate a slowing of C cycling towards colder climatic conditions in alpine grasslands, reaching MAT's as low as  $-1.4^\circ\text{C}$ , with shallower and more acidic soils (Table 1). In support, Leifeld et al. (2009) observed an increasing age in particulate organic matter in grassland soils especially in deeper soils, which was related to the reduced productivity in alpine grasslands, a shallower rooting depth, and a low microbial activity at low mean annual temperatures. Our finding of the highest SOC decomposability in alpine grasslands among all land-use systems shows that these soils contain the largest amount of readily decomposable SOC (Fig. 4). Along with their high  $^{14}\text{C}$ -derived ages in SOC, this suggests that

the retarded processing of C inputs into the soil has led to the retention and accumulation of labile C. This, in turn, indicates that alpine grasslands are particularly vulnerable to C cycle perturbations induced by climate warming or by disturbances, potentially leading to losses of old but non-stabilized C.

### 4.3 Input-constrained retarding systems – forests

In comparison to the other land-use types, forests showed the lowest respiration rates, the greatest contribution of heterotrophic respiration and released the oldest  $\text{CO}_2$  via in situ soil respiration among undisturbed ecosystems.

The low respiration rates and high relative contributions of heterotrophic respiration is likely the combined effect of a less dense, but deeper rooting system (Jackson et al., 1996), the retarded assimilate transfer to the rhizosphere (Gao et al., 2021) and a larger aboveground C allocation (Schaufler et al., 2010), as well as high heterotrophic contributions from the organic layer (21 %–34 %) to total soil respiration.



**Figure 5.** Relative source contribution of heterotrophic respiration in July/August and March across all land-use types and individual sites. Bars represent combined mean values and error bars combined standard deviations from the model outputs.

Beyond the lower and slower belowground C allocation, elevated  $\Delta^{14}\text{CO}_2$  values of heterotrophic respiration indicate that the release of older  $\text{CO}_2$  from forest soils also derives from the decomposition of decadal-old SOC compared with temperate grasslands (Fig. S7). This, in turn, implies slower turnover of plant-derived C in SOC in forests as compared to other land-use types (for croplands and managed peatlands the very old age of heterotrophically respired  $\text{CO}_2$  primarily derives from the decomposition of preserved, old C). While slower turnover in alpine grasslands can be associated with colder climatic conditions, higher ages of SOC and respired  $\text{CO}_2$  in forests likely derive from both the input of older below- and aboveground C to the soil (Solly et al., 2013) and its lower quality slowing decomposition. Forest litter is often enriched in lignin and polyphenols, and nutrient-poorer than grassland litter, and thus more recalcitrant (Zhang et al., 2008). In addition, an acidic soil environment induced by needle litter in coniferous forests, together with cold and moist conditions, suppresses microbial and faunal activity (Desie et al., 2020; Zhang et al., 2008), which results in a build-up of thick organic layers (as in Beatenberg) (Hiltbrunner et al., 2013). Our source partitioning revealed that organic layers were major contributors to total heterotrophic respiration ( $\sim 30\%$  in July/August and  $\sim 60\%$  in March). Combined with the substantial contributions of total heterotrophic respiration (53%–69%), this resulted in the highest  $^{14}\text{C}$ -derived age of in situ soil-respired  $\text{CO}_2$  among semi-natural ecosystems.

Although climatic differences among forest sites, ranging from hot, dry summer conditions in inner-alpine valleys to cold, wet conditions in subalpine forests, resulted in variations in in situ respiration rates and SOC decomposability,

the ages and source contributions of respired  $\text{CO}_2$  remained relatively consistent across sites. This suggests that land-use type exerts a stronger control on C cycling pathways than short-term climatic variability, even though the latter affects instantaneous respiration fluxes.

#### 4.4 C-depleted systems – intensively managed croplands

Our results show that while croplands had  $\Delta^{14}\text{CO}_2$  values in in situ soil respiration close to atmospheric  $\Delta^{14}\text{CO}_2$  values, their heterotrophically respired  $\text{CO}_2$  and bulk SOC had pre-bomb  $^{14}\text{C}$  levels and were thus depleted in  $^{14}\text{C}$  compared to forests and grasslands (Figs. 2, S7). This overall pattern reveals a high autotrophic contribution in croplands, releasing contemporary C, as well as a long-term depletion of SOC. The latter is likely caused by continuous biomass removal during harvest and the small belowground C input reducing SOC storage (Don et al., 2011; Keel et al., 2019). Losses of SOC can additionally be fostered by soil tillage destroying soil aggregates (e.g., Six et al., 1999), generally leaving SOM with a relatively larger fraction of persistent, old C. In agreement, our study shows that along with the depletion of  $^{14}\text{C}$  in soil-respired  $\text{CO}_2$  and SOC compared to forests and grasslands, cropland soils also showed a low SOC decomposability and the smallest SOC stocks among all land-use types (Figs. 5, S8). This suggests that these cropland soils are subjected to net C losses, aligning with observations from Swiss long-term experiments that show declining SOC stocks in intensively managed croplands, which had previously been used as grasslands (Keel et al., 2019). The depletion of labile SOC is likely particularly pronounced in the investigated croplands, as they have been continuously man-

aged as croplands for more than 35 years, likely even more than 100 years.

It should be noted that the CO<sub>2</sub> released from two cropland sites (Altwi, Changins) is likely affected by carbonate weathering induced by liming practices, which led to relatively high <sup>13</sup>CO<sub>2</sub> and highly depleted <sup>14</sup>CO<sub>2</sub> values released from the topsoil (Fig. 4). However, isotope mixing revealed that potential carbonate weathering contributed < 1 % to total soil respiration in croplands. This is consistent with e.g., Schindlbacher et al. (2015, 2019) and Serrano-Ortiz et al. (2010) who suggest that CO<sub>2</sub> release from carbonates makes a minor contribution to soil-respired CO<sub>2</sub>. In addition, potential carbonate contribution did not affect estimates of autotrophic contributions to total soil respiration. <sup>14</sup>C-derived ages were estimated using carbonate-corrected <sup>14</sup>C values (Sect. S7, Table S2).

Autotrophic contributions in croplands found in this study (July/August: 69 %, March: 89 %) align with previous studies using <sup>14</sup>C and <sup>13</sup>C labelling approaches (Søe et al., 2004; Werth and Kuzyakov, 2008). Low heterotrophic contributions are likely due to small litter inputs and poor decomposability of the remaining old SOC (Fig. S7). We further assume that high relative autotrophic contributions are also related to hampered heterotrophic respiration due to adverse soil environmental conditions. The two sites, Altwi and Changins, with exceptionally high autotrophic contributions (96 %), exhibited very low water contents (< 15 vol %). In contrast, the Reckenholz site, with moderate moisture levels (27 vol %), showed a much lower autotrophic contribution of only 15 % (Figs. 1, 5). The low water contents in cropland surface soils are probably due to the sparse vegetation cover which enhances evaporative water losses.

#### 4.5 Hotspots of C release – managed peatlands

Despite the dominant contribution of autotrophic respiration to total soil respiration (mean across all managed peatland sites: 68 ± 19 %), managed peatlands released millennial-old CO<sub>2</sub> at a high rate which indicates substantial C losses and advanced degradation in these systems. The release of old, pre-bomb CO<sub>2</sub> has also been observed for other drained and managed peatlands in Switzerland (Bader et al., 2017; Wang et al., 2021b) and can be related to the ~ 150-year long aeration following drainage, which has induced the decomposition of peat material that had previously been protected by anaerobic water-saturated conditions. At our sites, the low SOC decomposability in conjunction with high Δ<sup>14</sup>CO<sub>2</sub>-derived ages (Fig. 5) indicates not only the immediate mobilization of older C following aeration, but also an advanced degradation stage of the peat soil.

The autotrophic contribution (47 % in July/August, 77 % in March) to total soil respiration that we estimated for managed peatlands agrees well with contributions found in natural peatlands during the growing season, where <sup>14</sup>C pulse-labelling and trenching approaches revealed autotrophic res-

piration to contribute between 35 % and 61 % (Crow and Wieder, 2005; Wunderlich and Borke, 2012) to total soil respiration. The observed seasonal differences in autotrophic contributions support that water table depth plays a crucial role for the sources of respired CO<sub>2</sub> (Rankin et al., 2023; Stuart et al., 2023). Counterintuitively, the autotrophic contribution to soil respiration was lower in July/August than in March, despite the high plant activity during the growing season. Lower heterotrophic contributions in March (Table 2) are likely because of higher water tables (Paul et al., 2021, 2024). Drier conditions in summer aerate larger portions of the peat, thereby enhancing peat decomposition (Rankin et al., 2023; Stuart et al., 2023). Source partitioning further revealed higher heterotrophic contribution from subsoil layers than from topsoil layers in managed peatlands, which contrasts with observations from all other land-use types (Table 2). Higher subsoil contributions likely result from pronounced increases in SOC stocks with depth (Figs. S8, 5). Respiratory C losses from deeper peat also contributed to the high in situ <sup>14</sup>CO<sub>2</sub>-ages of ~ 1500 years released from the managed peatlands in July/August.

#### 4.6 Seasonal dynamics in the age of soil respired CO<sub>2</sub> across land-use types

In March, Δ<sup>14</sup>CO<sub>2</sub> values were generally closer to atmospheric levels than in July/August which we attribute to higher contributions of autotrophic respiration in March. Higher autotrophic contributions in March than in July/August were unexpected, as heterotrophic respiration typically dominates respiration during winter months due to plant dormancy (Dörr and Münnich, 1986; Schindlbacher et al., 2009; Torn et al., 2009; Wang et al., 2000). We attribute these findings to a combined effect of plant phenology and temperature. Generally, autotrophic respiration is rather driven by plant phenology than by temperature (Atarashi-Andoh et al., 2012), thus we likely captured an active state of the phenology in March for grassland and forest sites. In addition, Marchand et al. (2025) revealed that root activity of deciduous tree species is not constrained by low temperatures. In forests, evergreen vegetation, as well as mosses and graminoids on the forest floor might have additionally contributed to autotrophic respiration. In addition to phenology, the greater autotrophic contribution in March could be related to the up to 9 °C higher air than soil temperatures (Fig. S5). While low soil temperature likely restricted heterotrophic respiration, vegetation was possibly metabolically active at higher air temperatures (Ferrari et al., 2018), which overall resulted in a relatively higher autotrophic respiration compared to microbial activity in cold soils. However, also in crop- and managed peatlands, total soil respiration showed more modern Δ<sup>14</sup>CO<sub>2</sub> values during March as compared to July/August. In addition, Bayesian models estimated high autotrophic contributions during March. For these vegetation-free arable systems, this may partly result

from the release of recent C during decomposition of residual plant material from the summer growing season, which was not adequately reflected in the incubation experiments.

#### 4.7 Study limitations

The present investigation comprises an extensive suite of C isotopic and supporting data from soils across diverse land-use types and ecoregions of Switzerland. Given the logistical and analytical constraints associated with  $^{14}\text{C}$  measurements, we strategically focused on sampling in July/August and March to capture the broadest variability in environmental conditions and plant physiological states. As a consequence, our study provides snapshots rather than continuous records of  $\text{CO}_2$  ages, source contributions, and soil respiration rates, resulting in limited spatial and temporal coverage. Despite the inherent limitations, the data reveal clear and robust patterns, offering novel and meaningful insights into C cycling pathways across different land-use types.

To exclude aboveground plant respiration from the in situ  $\text{CO}_2$  flux, vegetation inside the chamber was clipped 1–2 weeks prior to sampling and directly before if there was plant regrowth. While this approach helped isolate soil-respired  $\text{CO}_2$ , clipping may have influenced the contribution of autotrophic respiration. Some studies have shown that recent clipping can trigger a short-term increase in rhizosphere respiration (Wunderlich and Borke, 2012), potentially leading to an overestimation of autotrophic contributions. However, given the time allowed between clipping and sampling, we assume that the overall impact on autotrophic respiration in our study was limited. In addition, other studies suggest that such effects are only minor or transient (Bahn et al., 2006; Barneze et al., 2024; Zhou et al., 2007). Two additional sources of soil respiration that may contribute to  $\text{CO}_2$  sampled during soil incubations remain challenging to account for: carbonate weathering from natural or artificial (liming) sources, and the decomposition of recent plant assimilates, the latter particularly affecting crop- and managed peatlands. In these land-use types, model estimations of high autotrophic contributions during winter might be biased by the release of recent  $\text{CO}_2$  from decomposing plant residues from the last growing season, carrying a similar modern  $\Delta^{14}\text{C}$  than autotrophic respiration. Despite these limitations, clear patterns have emerged from the suite of measurements undertaken as part of this study, providing the basis for a proposed conceptual framework for land-use system categorization based on the rates and  $^{14}\text{C}$  signatures of soil respiration.

## 5 Conclusions

Our study demonstrates that combining measurements of respiration rates and  $^{14}\text{C}$  signatures of soil-respired  $\text{CO}_2$  – both in situ and under controlled incubations – provides valuable insights into C cycling pathways across contrasting land-

use types. This combined approach reveals how differences in C inputs, microbial processing, ecosystem-specific constraints, and management practices jointly shape the respiration rate, age, and sources of released  $\text{CO}_2$  – ranging from rapid, input-driven cycling of young C with high autotrophic contributions in temperate grasslands to the loss of ancient, previously preserved C via heterotrophic respiration through drainage in managed peatlands. The  $^{14}\text{C}$ -based respiration measurements provide a general framework for identifying systems in which soils retain SOC versus conditions that promote the decomposition and mobilization of older SOC. Applying this approach across broader climatic gradients, soil types, or management regimes could help define transferable indicators of soil C cycling. The integration of rate- and  $^{14}\text{C}$ -based measurements of soil respiration may enable more accurate predictions of how soils will respond to future environmental change.

*Code and data availability.* The data supporting this study, together with the codes used for the Bayesian mixing model, are publicly available in the open-access Zenodo repository under DOI: <https://doi.org/10.5281/zenodo.18067939> (Minich, 2025).

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