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Forest-floor greenhouse gas fluxes in a subalpine spruce forest: Continuous multi-year measurements, drivers, and budgets

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Abstract. Forest ecosystems play an important role in the global carbon (C) budget by sequestering a large fraction of anthropogenic carbon dioxide (CO_2) emissions and by acting as important methane (CH_4) sinks. The forest-floor greenhouse gas (GHG; CO_2, CH_4 and nitrous oxide N_2O) flux, i.e., from soil and understory vegetation, is one of the major components to consider when determining the C budget of forests. Although winter fluxes are essential to determine the annual C budget, only very few studies have examined long-term, year-round forest-floor GHG fluxes. Thus, we aimed to i) quantify the seasonal and annual variations of forest-floor GHG fluxes; ii) evaluate their drivers, including the effects of snow cover, timing, and amount of snow melt, and iii) calculate annual budgets of forest-floor GHG fluxes for a subalpine spruce forest in Switzerland. We measured GHG fluxes year-round during four years with four automatic large chambers at the ICOS Class 1 Ecosystem station Davos (CH-Dav). We applied random forest models to investigate environmental drivers and to gap-fill the flux time series. Annual and seasonal forest-floor CO_2 emissions responded most strongly to soil temperature and snow depth (2.34±0.20 kg CO_2 m^{-2} yr^{-1}). No response of forest-floor CO_2 emissions to leaf area index or photosynthetic photon flux density was observed, suggesting a strong direct control of environmental factors and a weak or even lacking indirect control of canopy biology. Furthermore, the forest-floor was a consistent CH_4 sink (-19.1±1.8 g CO_2-eq m^{-2} yr^{-1}), with annual fluxes driven mainly by snow depth. Fluxes during winter were less important for the CO_2 budget (6.0–7.3 %), while they contributed substantially to the annual CH_4 budget (14.4–18.4 %). N_2O fluxes were very low, negligible for the forest-floor GHG budget at our site. In 2022, the warmest year on record with also below-average precipitation at the Davos site, we observed a substantial increase in forest-floor CO_2 emissions compared to other years. The mean forest-floor GHG budget indicated emissions of 2317±200 g CO_2-eq m^{-2} yr^{-1} (mean±standard deviation over four years), with CO_2 fluxes dominating and CH_4 offsetting a small proportion (0.8 %) of the GHG budget. Due to the relevance of snow cover, we recommend year-round measurements of GHG fluxes with high temporal resolution. In a future with increasing temperatures and less snow cover due to climate change, we expect increased forest-floor CO_2 emissions even at this subalpine site, with negative effects on its carbon sink behaviour.

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1 Introduction

Carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) are the three main greenhouse gases (GHGs) driving global warming. Forest ecosystems play an important role in the global carbon (C) cycle by sequestering a large fraction of anthropogenic CO_2 emissions and by acting as an important CH_4 sink (Borken et al., 2006; Ni and Groffman, 2018). The GHG flux of the forest-floor, i.e., soil and understory vegetation, is one of the major components to consider when determining the C budget of forests, since soil respiration is the second largest terrestrial C flux and accounts for approximately 70 % of CO_2 losses in temperate forests (IPCC, 2021; Yuste et al., 2005). However, how forest-floor GHG fluxes will respond to climate change is still largely unknown.

Global warming particularly affects high latitude and high altitude forests (IPCC, 2021), altering snowfall, length and timing of snow cover as well as melting and soil freeze-thaw cycles (CH2018, 2018; Klein et al., 2016). Nevertheless, there have been very few studies that examined continuous, year-round and long-term forest-floor GHG fluxes in high latitude or high altitude forests (Barba et al., 2019; Luo et al., 2011). Unfortunately, measurements during periods with snow cover are challenging and thus often lacking due to logistical reasons, leading to winter fluxes missing even from multi-year studies (e.g., Richardson et al., 2019).

The forest-floor's CO_2 fluxes involve the processes of photosynthetic CO_2 uptake by plants as well as autotrophic and heterotrophic respiratory losses from plants and soils, respectively (Hanson et al., 2000). All three processes and their contributions to the total soil CO_2 fluxes depend on biotic and abiotic factors. For example, autotrophic respiration is mainly driven by plant activity and hence linked to photosynthesis and solar energy (Högberg et al., 2001; Janssens et al., 2001), whereas, heterotrophic respiration is strongly controlled by soil conditions (i.e., temperature and moisture), substrate availability, and the microbial community (e.g., Janssens et al., 2001; Scott-Denton et al., 2006). Furthermore, winter dynamics can impact soil respiration rates through changes in snow cover, soil freezing and thawing cycles (Reinmann and Templer, 2018; Schindlbacher et al., 2007). Especially, freeze-thaw events have recently been the focus of research because they cause abrupt changes in biophysical soil conditions which can alter autotrophic and heterotrophic soil respiration rates (Song et al., 2017). How the two components of soil respiration respond to climate change is however subject to major uncertainties with many studies showing contradictory results. Some studies demonstrated no significant increase of soil respiration to experimental warming in forest soils (Bradford et al., 2008; Carey et al., 2016), while others observed higher soil respiration rates (Bond-Lamberty et al., 2018; Crowther et al., 2016; Karhu et al., 2014). Among those reporting higher rates, there is disagreement on whether long-term adaptation can occur. In some studies, the higher respiration rates were sustained over several years (Melillo et al., 2017), while in others they declined again to previous levels (Eliasson et al., 2005; Hartley et al., 2007).

Forest soils have been shown to act as an atmospheric CH_4 sink (Dutaur and Verchot, 2007). The uptake of CH_4 in oxic soils occurs due to the presence of methanotrophic bacteria (Saunois et al., 2020). It is highly dependent on environmental factors, including soil temperature (T_{soil}), soil texture (transport of CH_4 into the soil), soil moisture (transport of CH_4 into the soil and

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limitation of bacterial activity), and soil nitrogen (N) content (Borken et al., 2006; Luo et al., 2013; Ni and Groffman, 2018). Furthermore, biotic factors such as plant cover can affect CH_4 consumption of the forest floor through the presence of *Sphagnum* moss species which are inhabited by methane-oxidizing bacteria (Basiliko et al., 2004). Generally, in temperate forests, CH_4 uptake increases in warmer and drier soils (Borken et al., 2006; Ni and Groffman, 2018). Winter dynamics further impact CH_4 fluxes, with frozen soil and snow cover affecting microbial activity and gas transport (Blankinship et al., 2018; Borken et al., 2006). Understanding the drivers of forest-floor CH_4 fluxes, including the complex interplay between biotic and abiotic factors, is vital for accurately modeling and predicting the role of forest ecosystems in the global CH_4 cycle.

Moreover, the forest-floor can act as a source or sink of N_2O (Chapuis-Lardy et al., 2007; Goldberg et al., 2010). Soil temperature, soil moisture, and N availability significantly influence N_2O fluxes through regulating the microbial processes which are mainly responsible for N_2O production in soils, i.e., nitrification and denitrification (Schaufler et al., 2010). High N_2O emission rates in temperate forests have been found under warm and moist conditions (Luo et al., 2013). Furthermore, studies have revealed that high N_2O emissions occur during freezing-thawing cycles and rewetting events, when abrupt changes in temperature and moisture conditions promote microbial activity and thus the release of N_2O (Goldberg et al., 2010; Papen and Butterbach-Bahl, 1999; Liu et al., 2018). Understanding the dynamics of these processes and drivers, particularly during freezing-thawing cycles, is crucial for estimating N_2O emissions from forests.

In this study, we investigated combined measurements of CO_2, CH_4 and N_2O forest-floor fluxes in a subalpine Norway spruce forest (Davos, CH-Dav, ICOS Class 1 Ecosystem station), in response to biotic and environmental drivers, based on four years of continuous measurements (2017, 2020-2022). Our objectives were to i) quantify seasonal and annual variations in climate variables and forest-floor CO_2, CH_4 and N_2O fluxes; ii) evaluate the drivers of forest-floor GHG fluxes, including effects of snow cover, timing and amount of snow melt; and iii) calculate the annual budgets of forest floor GHG fluxes.

2 Methods

2.1 Study site

The study site is a subalpine evergreen coniferous forest, located in the eastern Swiss Alps at a mean altitude of 1640 m a.s.l. (Davos Seehornwald; CH-Dav; 46°48’55.2” N, 9°51’21.3” E). The total annual precipitation is 876 mm, and the mean annual temperature is 4.3 °C (1997–2022). The site is certified as ICOS (Integrated Carbon Observation System) Class 1 Ecosystem station for eddy-covariance flux measurements since 2019. The dominant species is Norway spruce (*Picea abies* (L.) Karst), with an average tree height of 18 m (max. 35 m), and a mean tree age of approx. 100 years (with some specimens reaching over 300 years). Understory vegetation covers about 30 % of the surface and is mainly composed of blueberry (*Vaccinium myrtillus* and *Vaccinium gaulterioides*) and mosses (*Sphagnum* sp. Ehrh.). CH-Dav is a sustainably managed forest according to the Swiss National Forest Protection Law (1876; Tschopp, 2012). The soil types are chromic cambisol and rustic podzol (FAO classification; Jörg, 2008; Tab. 1).

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2.2 Chamber flux measurements

2.2.1 Chamber setup

Forest-floor CO_2, CH_4 and N_2O fluxes were measured during the years 2017 and 2020–2022 using a fully automated system with four chambers (FF1 to FF4) distributed within an area of 3600 m^2 in the forest, representative for the eddy-covariance footprint. Concentrations of CO_2, CH_4 and N_2O were measured with a Dual Laser Trace Gas Analyzer (TILDAS, Aerodyne Research, Billerica, USA) since 2017. Since January 2021, these measurements were reduced to measure CH_4 only, due to failure of one of the lasers. In addition, since November 2019, CO_2 concentrations in the chambers were measured with an infrared gas analyzer (LI-840, LI-COR Biosciences, Lincoln NE, USA). For the year 2020, CO_2 chamber measurements from both QCL and LIL-840 were available and used for further analyses. Chambers were designed according to Brümmer et al. (2017), following the ICOS RI protocol for chamber measurements (Pavelka et al., 2018). The opaque PVC chambers rested on aluminum frames, inserted 10 cm in the soil, sealed with EPDM (ethylene propylene diene monomer) gaskets, and had the dimension of 75 cm x 75 cm x 50 cm height (thus approx. 281 dm^3). They were equipped with a pressure vent, as well as air temperature and pressure sensors (BME280, Bosch Sensortec GmbH, Reutlingen, Germany). During the winter periods with snowfall, extension frames (2 x 50 cm height) allowed to increase their height. A 17 Watt geared electric motor (80807021, Crouzet, Valence, France) was used to move the entire PVC chamber vertically and horizontally by about 190 cm and 70 cm, respectively. One webcam per chamber allowed remote observation of the operation and estimate of snow cover and depth (see below). Since the vegetation inside the chamber frames was not cut, the chamber set-up measured forest-floor GHG fluxes (and not only soil fluxes). Due to their opaque material, no understory photosynthesis was measured with the chambers. Soil and vegetation cover inside the chambers (differentiated into three plant functional types: moss, grass, blueberry) were assessed visually in June 2022, when also the leaf area index (LAI) of the spruce forest was measured using digital photography above the chamber locations (Fuentes et al., 2008). One chamber cycle fit within 10 minutes, including closing and opening operations (controlled by an Arduino Ethernet), with an actual measurement period of 180 s when the chamber resided on the frame. The air from the chamber was fed to the gas analyzers in 6 mm OD tubing (Synflex 1300, Eaton, Dublin, Ireland) and pumped back to the chamber, forming a closed system. Switching of the air stream between the different chambers and the gas analyzers was accomplished using rotary selector valves (Valco Selectors, VICI AG International, Schenkon, Switzerland). Chamber cycles (lasting app. 1 h for four chambers) were repeated every 3 hours for each gas analyzer individually, leading to total 16 cycles per chamber and day (eight per gas analyzer). Chambers leakage tests of all four chambers were performed in 2019. Variations caused by possible leakage were below 3% of the measured flux, as required by the ICOS RI protocol (Pavelka et al., 2018).

Tab. 1: Site characteristics of the four chambers (FF1 to FF4). Annual means and standard deviations are shown for soil temperature (T_{soil}) and water filled pore space (WFPS) at 5 cm, soil depth, and days with snow cover. LAI, soil, and vegetation cover inside each

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chamber were determined in June 2022. Soil data (bulk density, pH, C and N stocks in the topsoil, i.e., litter, organic material layers, and 0–20 cm depth of mineral soil) were taken from Jörg (2008).

Site characteristics	FF1	FF2	FF3	FF4	Mean
T_{soil} at 5cm (°C)					
2017	4.44 ± 4.67	4.16 ± 4.84	4.29 ± 4.86	4.56 ± 4.52	4.36 ± 0.17
2020	4.66 ± 4.32	4.40 ± 4.46	4.46 ± 4.34	4.87 ± 4.15	4.60 ± 0.22
2021	4.18 ± 4.25	3.80 ± 4.48	3.74 ± 4.84	4.26 ± 4.20	3.99 ± 0.26
2022	5.15 ± 4.70	4.83 ± 4.96	4.70 ± 5.38	5.18 ± 4.61	4.97 ± 0.24
WFPS at 5 cm (%)					
2017	20.1 ± 5.09	17.2 ± 4.30	21.3 ± 6.82	22.5 ± 7.42	20.3 ± 2.27
2020	15.9 ± 2.88	15.5 ± 3.85	9.8 ± 0.69	23.9 ± 9.55	16.3 ± 5.79
2021	16.8 ± 3.88	14.5 ± 3.88	11.8 ± 4.45	25.0 ± 10.5	17.0 ± 5.70
2022	15.1 ± 4.19	12.7 ± 3.27	10.4 ± 3.56	21.3 ± 7.16	14.9 ± 4.70
Snow depth (cm)					
2017	5.8 ± 8.4	6.4 ± 9.8	4.5 ± 6.4	3.9 ± 6.2	5.1 ± 1.2
2020	4.3 ± 7.0	8.6 ± 12.1	4.2 ± 7.0	3.5 ± 6.0	5.2 ± 2.3
2021	17.6 ± 25.0	22.2 ± 29.5	14.6 ± 22.7	14.8 ± 21.0	17.3 ± 3.6
2022	5.1 ± 9.3	8.3 ± 14.1	6.1 ± 11.7	4.9 ± 9.5	6.1 ± 1.6
Days with snow cover					
2017	152	159	152	148	153 ± 5
2020	126	142	123	117	127 ± 11
2021	172	189	161	169	173 ± 12
2022	138	145	134	132	137 ± 6
Leaf area index (LAI)	2.9	4.2	3.1	2.9	3.3 ± 0.6
Soil cover inside chamber (%)					
bare soil	0	50	70	0	30 ± 36
moss	90	50	20	90	63 ± 34
grass	5	1	0	0	2 ± 2
Vaccinium	60	0	10	30	25 ± 26
Bulk density at 5 cm (g cm^{-3})	0.27	0.35	0.32	0.35	0.32 ± 0.04
pH	2.8–3.1	3.0–3.4	2.8–3.1	3.0–3.4	
C stock (t/ha)	93.5	147.7	135.4	105.8	120.6 ± 25.2
N stock (t/ha)	3.54	5.74	4.47	3.52	4.32 ± 1.05

2.2.2 Data processing and quality assessment

The concentration increase in the chamber headspace over time was used to determine the respective flux F using Eq. (1):

$$F = \frac{\frac{\partial C}{\partial t}\frac{V}{A}\frac{m}{V_m}\frac{p}{p_0}\frac{T_0}{T}}{m} \qquad (1)$$

where $\frac{\partial C}{\partial t}$ is the concentration change over time (mol mol^{-1} s^{-1}), V the actual chamber volume (m^3), A the forest-floor area within the chamber frame (m^2), m the molecular mass (dimensionless), V_m the molar volume (m^3 mol^{-1}) of the respective gas,

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p the mean chamber pressure (Pa), p_0 the standard pressure (1013.25 Pa), T_0 the standard temperature (273.15 K), and T the mean chamber temperature (K). We fitted a linear regression to the change in concentration of the respective gas over time ($\frac{\partial c}{\partial t}$) during the closed period of the chamber (180 s), excluding the first 20 s after closing. The R^2 of the fit was later used for the quality assessment and filtering of the calculated fluxes (see below). A positive flux means release from the forest floor to the atmosphere, and a negative flux indicates uptake by the forest floor.

The quality of the calculated fluxes was ensured by removing negative CO_2 fluxes (Step 1), removing outliers (Step 2, despiking), and applying a filter based on R^2 (Step 3). (1) We excluded any negative CO_2 fluxes (about 2 % of all fluxes). (2) We then despiked the flux data set with a running mean algorithm using a width of 30 days. (3) For the growing period (May to November) and the dormant period (December to April) separately, we removed fluxes with a R^2 value below the 10^{th} percentile of all R^2 values in the respective period (except if $R^2 > 0.9$), to avoid setting a fixed threshold for an acceptable R^2. These three steps were applied to each chamber and GHG separately. The 10^{th} percentile of R^2 values ranged from 0.001 to 0.99, being lower during the dormant compared to the growing period and particularly for N_2O fluxes (Tab. 2).

Tab. 2: 10^{th} percentiles of R^2 values from linear regressions used for flux calculations per gas, given separately for each chamber (FF1 to FF4) and growing and dormant periods. Percentiles were applied as quality thresholds.

Gas	Period	FF1	FF2	FF3	FF4
CO_2	growing period	0.97	0.98	0.98	0.99
	dormant period	0.35	0.48	0.47	0.68
CH_4	growing period	0.92	0.96	0.92	0.93
	dormant period	0.41	0.26	0.21	0.61
N_2O	growing period	0.022	0.001	0.001	0.003
	dormant period	0.042	0.002	0.003	0.002

Initially, the time series consisted of 40’426 CO_2 (in 2020 from both gas analyzers), 31’998 CH_4 and 14’309 N_2O flux measurements over the four years. After the quality checks described above, 37’596 CO_2 (93 %) and 26’565 CH_4 (83 %) flux measurements remained, which resulted in 4446 and 3972 daily means, respectively. Due to Step 3, we excluded the forest-floor N_2O fluxes from further driver and budget analyses.

2.3 Environmental data

Each of the chambers had measurements of soil water content (SWC; EC-5, Decagon Devices Inc.) and T_{soil} (107, Campbell Scientific Ltd.) at 5 cm soil depth in close vicinity (< 2 m away from the chamber). To account for potential drivers of canopy photosynthesis modulating forest-floor fluxes, photosynthetic photon flux density (PPFD; PAR LITE, Kipp & Zonen), air temperature (TA; HygroClip HC2-S3, Rotronic AG), and precipitation (PREC; 1518H3, Lambrecht Meteo GmbH) data were used as well, measured at the tower above the tree canopy at 35 m height (precipitation at 25 m height).

We calculated water-filled pore space (WFPS) from the soil water content (SWC) measurements using Eq. (2):

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$$WFPS = \frac{SWC}{1 - \frac{BD}{PD}} \times 100 \quad (2)$$

Bulk density (BD) was calculated using the data from a soil sampling campaign done in July 2018 according to ICOS RI standards (Arrouays et al., 2018). Soil data were used from soil profiles closest to the respective chambers (in total, data from six profiles were used). Particle density (PD) was assumed to be constant at 2.65 g cm^{-3} (Danielson and Sutherland, 2018). The mean daily snow cover and snow depth per chamber was derived from webcam images using a custom-made python image analysis tool, deriving snow depth from a scale installed in vicinity to each chamber within the image section.

2.4 Statistical analyses

2.4.1 Driver analysis

We used conditional random forests (RF) to model daily forest-floor CO_2 and CH_4 fluxes (based on all years and chambers) and investigate their environmental drivers. We selected predictors which were known from the literature, i.e., daily averages of T_{air}, T_{soil} at 5 cm depth, WFPS at 5 cm depth, and PPFD as well as their one- and four-day leads (meaning that we shifted the variables forward in time by one and four days). Furthermore, we added snow depth and changes in snow depth from one day to another (Δ snow depth) to the predictor set. To account for factors which could explain differences in the GHG fluxes among the chambers, we included several chamber-specific characteristics (Tab. 1), i.e., the LAI, the bare soil fraction in the chambers, and the total C and N stocks in the topsoil (litter, organic material layers, and 0–20 cm depth of mineral soil). We applied the function *cforest* from the R-package "party" which can deal with highly correlated predictor variables (v1.3.10; Strobl et al., 2008, 2007). Prior to model development, predictors and target variables were centered and scaled using the "caret" *preProcess* function, which brings all variables and measurements from different sensors and locations into the same range improving performance of the RF models (v6.0.93; Kuhn, 2008). The hyperparameter fitting was done using the train function from the R-package "caret" (see Appendix for final model setup) using 10-fold cross-validation. The assessment of driver importance in the RF model was done using the R package "permimp" which accounts for correlated variables within the predictor set (v.1.0.2; Strobl et al., 2007; Debeer and Strobl, 2020; Debeer et al., 2021). The calculated values for driver importance were rescaled to values between 0 and 1 using a min-max normalization.

We developed RF models separately for daily CO_2 and CH_4 fluxes (N = 4446 and 3972, respectively). The training of the RF was done using only a fraction of the data set (70 %). The remaining 30 % of the data set was used as test dataset to evaluate model performance. Centering and scaling were done separately for training and test datasets to avoid data leakage. The performance of the RF models was assessed using R^2 and random mean square errors (RMSE). During model development, we tested several different predictor sets. Furthermore, to optimize the models and to evaluate the robustness of model results, we evaluated the RF models trained on data sets separated by year of measurement or by chamber, and compared their accuracy to the model that was built using data from all years and all chambers. In total, 17 predictor variables entered the models (including the leads). RF models were also trained on seasonal data (i.e., spring, summer, autumn, winter; defined according to the meteorological definition) to investigate differences in drivers among the seasons. For the seasonal RFs, we used the

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same predictor sets as for the RFs developed on the entire data set. We calculated partial dependence (PD) plots of the conditional RFs using the "moreparty" package (v0.3.1; Robette, 2023) which is based on the "pdp" package (v0.8.1; Goldstein et al., 2015; Greenwell, 2017) to assess the relationships between the four most important predictors and the predictions. The PD is calculated as the change in the average predicted value, while the predictor at interest is varied over its marginal distribution.

2.4.2 Flux gap-filling and budget calculation

The gap-filling of CO_2 and CH_4 fluxes was done using the RF models developed above. Missing values in the predictor variables (gap length < 3 days) were linearly interpolated using the R package "chillR" (v0.72.8, Luedeling and Fernandez, 2022). The gap-filled flux data were then used to calculate the annual forest-floor GHG budgets per chamber. Since we estimated the annual forest-floor GHG budget for the study area, we report the mean over the four chambers. To be able to compare CO_2 and CH_4 budgets, we converted the CH_4 budgets into CO_2-equivalents (CO_2-eq) using the 100-year global warming potential of methane of 27 (IPCC, 2021).

In addition, we modeled the daily CO_2 fluxes using a Q_{10} model according to Eq. (3):

$$R_S = R_{ref} \times Q_{10}^{\frac{T_{soil} - 10}{10}} \quad (3)$$

where R_{ref} is the modeled R_S at a T_{soil} of 10°C, and Q_{10} is the temperature sensitivity. We developed one model for the full dataset (all years and all four chambers together). The annual budgets calculated with the Q_{10} modeled fluxes were then compared to the annual budgets from the RF gap-filling. All statistical analyses were performed using R Statistical Software (v4.2.0, R Core Team, 2022).

3 Results

3.1 Seasonal and interannual variability of environmental conditions and GHG fluxes

The seasonal courses of T_{air} and T_{soil} were very pronounced during the four years of the study, with highest temperatures in July and August, and lowest temperatures in January (Fig. 1a). All years showed highly variable WFPS with large differences among chambers (i.e., up to 35 % difference; Fig. 1b), with highest values during the snowmelt period, i.e., March to May. While the snow-covered periods usually started in November and lasted until April or May (Fig. 1c), the snow depths were much higher during winter 2020/2021 (reaching snow depths of over 1 m) compared to the other winters. Overall, the year 2022 was by far the warmest year ever recorded at the Davos research site, with an annual mean T_{air} of 5.6 °C (vs. the long-term mean of 4.3 °C; station data 1997–2022). Accordingly, annual mean T_{soil} at 5 cm was highest in 2022 for all chambers (annual mean T_{soil} over all chambers was 5.0 °C; Tab. 1). At the same time, precipitation in 2022 was low (773 mm vs. long-term mean of 876 mm; station data 1997–2022), which led to comparably dry soil conditions (annual mean WFPS over all chambers was lowest in 2022 (14.9 %) compared to that of the other years).

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On the one hand, the forest floor at the Davos Seehornwald site was a source of CO_2 during all four years, independent of the season (Fig. 1d). Typically, forest-floor CO_2 fluxes were very low in winter (mean CO_2 flux ± standard deviation (SD): 0.46±0.14 µmol m^{-2} s^{-1}), increased in spring after the snow melt, and reached their maximum values in June to September (mean CO_2 flux over all years: 3.50±0.84 µmol m^{-2} s^{-1}). Lowest forest-floor CO_2 emissions were measured in January 2021 (min. CO_2 flux: 0.06 µmol m^{-2} s^{-1}), highest CO_2 fluxes were observed in July 2022 (max. CO_2 flux: 6.54 µmol m^{-2} s^{-1}).

On the other hand, the forest floor was a consistent sink for CH_4, despite large short-term variations (days to weeks; Fig. 1e) and a few short peaks of CH_4 emissions in winter and spring. Seasonality of forest-floor CH_4 fluxes was very pronounced, with highest uptake in summer (mean CH_4 flux: -2.11±0.28 nmol m^{-2} s^{-1}), and still high CH_4 uptake rates during autumn and early winter (October to December; most clearly seen in 2022). Lowest CH_4 uptake was measured in the months of February to March (mean CH_4 flux: -0.44±0.22 nmol m^{-2} s^{-1}). With increasing duration of winter (March to May; Fig. 1e), the CH_4 sink strength further decreased. However, at the end of winter, between April and end of May (depending on the year), CH_4 uptake rates increased sharply.

Based on quality check 3, we did not consider the N_2O fluxes any further. The decision was driven by the observed low 10th percentiles of the R^2 values (Tab. 2), which indicated that the flux calculations frequently failed to yield satisfactory fits due to very low forest-floor N_2O fluxes (Appendix Fig. A.1), often below the minimum detectable flux of N_2O. This minimum reliable flux was estimated with the specifications of the TILDAS instrument (precision of 0.03 ppb), i.e., any change of N_2O concentrations in the chamber headspace during the measurement period had to be > 0.06 ppb (McManus et al., 2006) or > 29.1 nmol N_2O m^{-2} h^{-1}.

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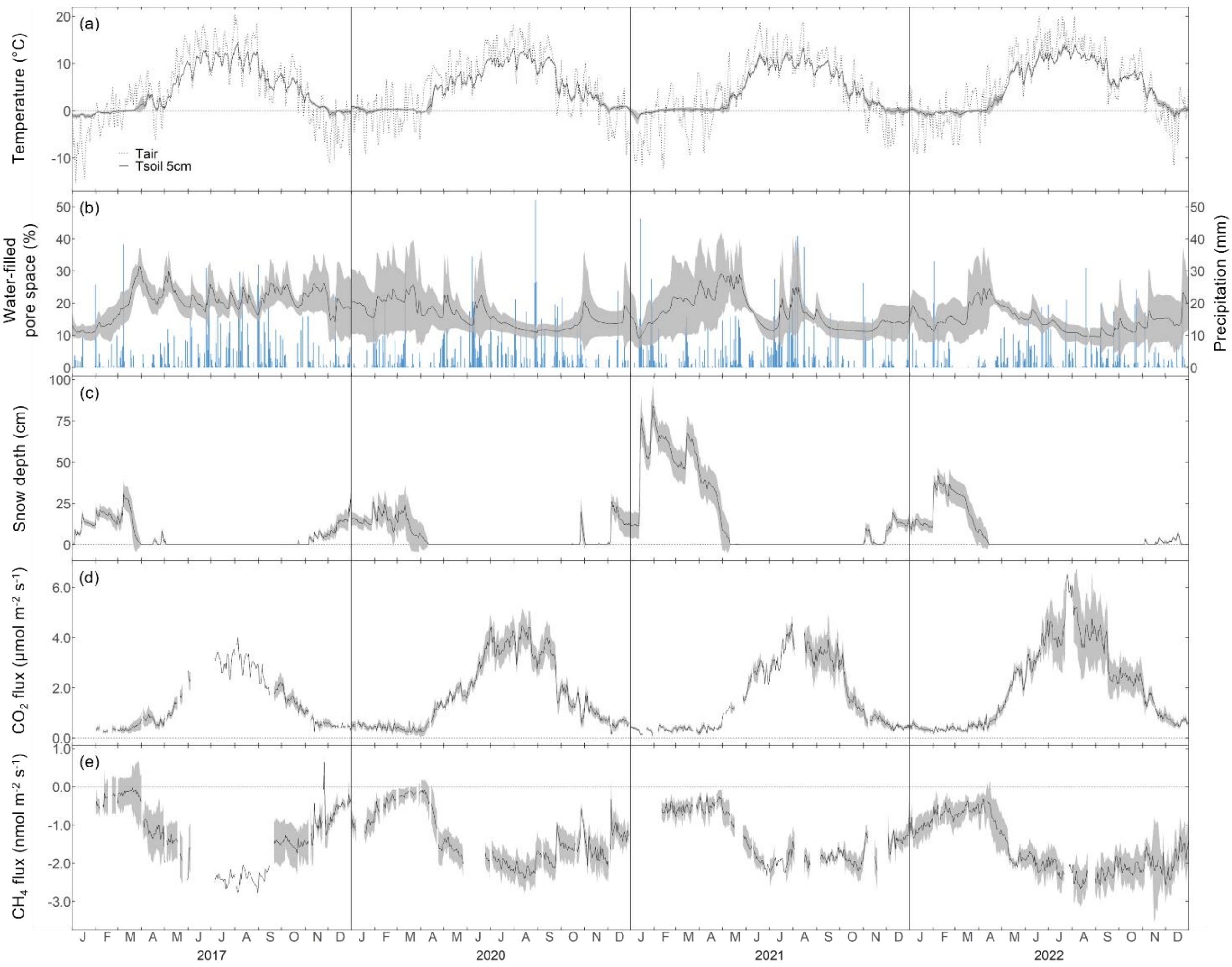

Fig. 1: Daily mean a) air temperature and soil temperature at 5 cm depth, b) water-filled pore space at 5 cm depth (left axis) and daily sum of precipitation (right axis), c) snow depth, and daily mean forest-floor d) CO_2 fluxes (not gap-filled), and e) CH_4 fluxes (not gap-filled), for the years 2017, 2020, 2021, and 2022. Black lines show means over four chambers, grey bands show standard deviations among four chambers. All data shown were quality-checked as described in the main text.

3.2 Driver analyses with random forest models

The RF models captured the temporal dynamics and absolute magnitudes of the observed forest-floor CO_2 and CH_4 fluxes very well, with R^2 values of 0.95 and 0.87, respectively (relationships of observed vs. predicted fluxes from test datasets) and RSME of 0.32 µmol m^{-2} s^{-1} and 0.27 nmol m^{-2} s^{-1}, respectively (Fig. A.2). Also the seasonal RF models for forest-floor CO_2 fluxes yielded high R^2 values of 0.94, 0.73, 0.90 and 0.63 for spring, summer, autumn and winter, respectively (Tab. A.1).

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Similarly, forest-floor CH_4 fluxes during spring, summer, autumn and winter were predicted well, with R^2 values of 0.80, 0.76, 0.72 and 0.73, respectively. Thus, the RF model performance was very good, also when shorter time periods were considered. Forest-floor CO_2 fluxes combined for all four years and seasons were predominantly driven by T_{soil} at 5 cm depth: T_{soil} at the time of the flux measurements was the most important driver, but also T_{soil} with a four-day (second most important) and with a one-day lead were relevant (Fig. 2). Furthermore, WFPS at 5 cm with a four-day lead played an important role. As expected, higher T_{soil} lead to higher CO_2 emissions, while higher WFPS reduced CO_2 emissions. No emissions of drivers enhancing canopy photosynthesis, i.e., LAI or PPFD, were observed. Separating the forest-floor CO_2 fluxes into seasonal fluxes resulted in a clear distinction of drivers in winter compared to the other seasons (Fig. 2). Winter CO_2 fluxes were mainly driven by snow depth (most important driver; higher snow depth leading to lower CO_2 fluxes), while T_{soil} played a smaller role. As for the overall fluxes, summer forest-floor CO_2 fluxes were mainly driven by T_{soil}, but also total N stocks were highly relevant (higher total N stock leading to lower CO_2 fluxes), much in contrast to the fluxes during spring and fall (Fig. 2).

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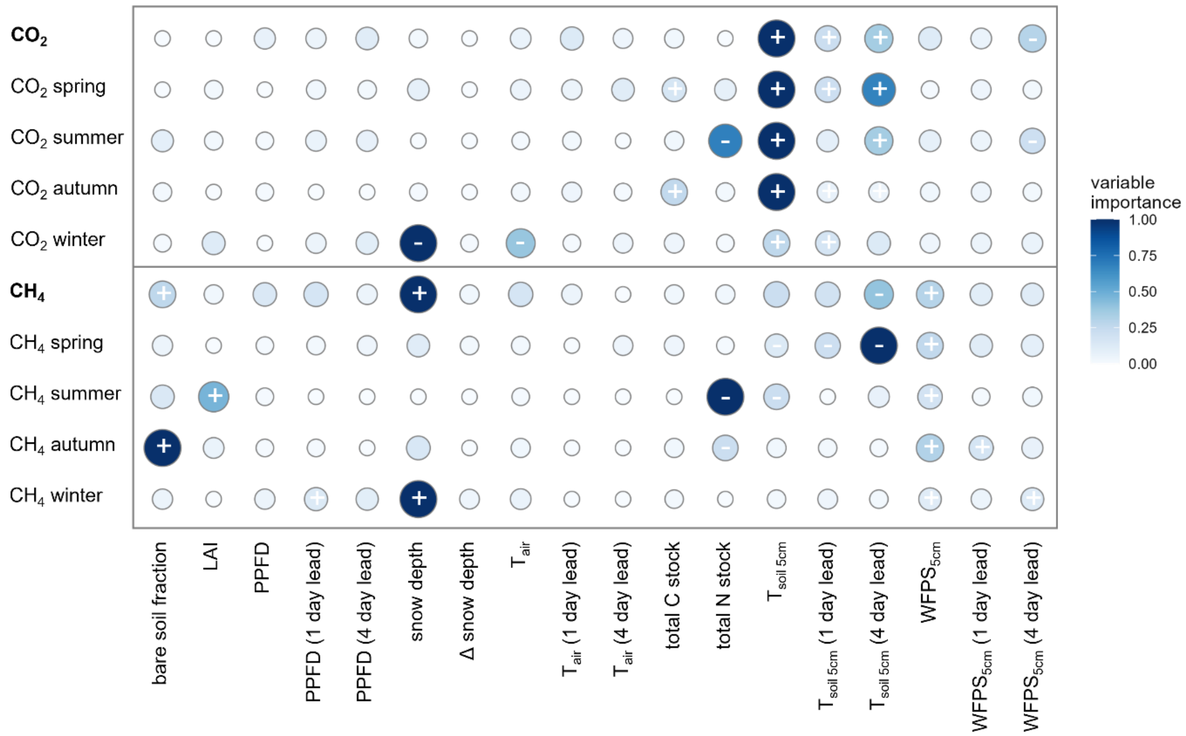

***Fig. 2:** Relative variable importance (rescaled to 0–1) according to the random forest driver analysis for CO_2 (top) and CH_4 (bottom) fluxes (not gap-filled; shown for the entire year, and per season). The direction of the effect of each predictor variable on the fluxes is shown by + (positive correlation) and – (negative correlation) signs, i.e., + indicates increased CO_2 emissions or decreased CH_4 uptake (increased CH_4 emissions). Signs are given for the four most important predictors which was investigated using partial dependence plots. See Materials and Methods for variable abbreviations.*

Forest-floor CH_4 fluxes combined for all four years and seasons were mainly driven by the snow depth (higher snow depth leading to more positive CH_4 fluxes and thus less CH_4 uptake; Fig. 2). Furthermore, the four-day lead of T_{soil} at 5 cm, WFPS at 5 cm, and the bare soil fraction inside the chamber strongly impacted the fluxes. We found that the drivers of the forest-floor CH_4 fluxes changed profoundly among seasons. Spring CH_4 fluxes were mainly temperature-driven (higher temperatures leading to more CH_4 uptake). In summer, forest-floor CH_4 fluxes were mainly driven by total N stocks (higher N stocks leading to more negative CH_4 fluxes and thus higher uptake) and by LAI (higher LAI leading to more positive CH_4 fluxes and thus lower uptake), reflecting spatial variability among chambers. In addition, CH_4 fluxes were influenced by an interaction of several drivers such as T_{soil} (higher T_{soil} leading to higher uptake) and WFPS (higher WFPS leading to lower uptake). For autumn CH_4 fluxes, bare soil fraction was the most important driver (more bare soil – and thus smaller moss cover (Tab. 1) – leading to more positive CH_4 fluxes and thus less CH_4 uptake), but also WFPS played an important role. Winter CH_4 fluxes responded mainly to snow depth (higher snow depth leading to less CH_4 uptake; Fig. 2).

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3.3 Forest-floor CO_2 and CH_4 budgets

The forest floor of this subalpine spruce forest was a net source of CO_2 and a net sink of CH_4 for all years of the study (averaged over all four chambers; Tab. 3). Mean annual forest-floor CO_2 and CH_4 budgets were 2.33±0.20 kg CO_2 m^{-2} yr^{-1} and -0.71±0.06 g CH_4 m^{-2} yr^{-1}, respectively. The annual forest-floor CO_2 budgets were mainly determined by summer and early autumn fluxes (i.e., June to September). The interannual variability (SD) of forest-floor CO_2 budgets was approx. 0.2 kg CO_2 m^{-2} yr^{-1} (8.6 %) during the four years of the study, with 2017 and 2021 showing smaller and 2022 the highest emissions. The annual CO_2 budgets calculated with the Q_{10} modeled data (2.42±0.21 kg CO_2 m^{-2} yr^{-1}; Tab. 3) agreed well with the CO_2 budgets based on the gap-filled fluxes using RF, also showing highest fluxes in 2022. A similar interannual variability (SD) as for the CO_2 budgets was found for the CH_4 budgets, with 8.5 % (0.06 g CH_4 m^{-2} yr^{-1}). Comparing the magnitudes of the forest-floor CO_2 and CH_4 budgets (in CO_2-eq) clearly showed that the CO_2 budget determined the forest-floor GHG budget of the spruce forest, since the CH_4 uptake (-19.1 g CO_2-eq m^{-2} yr^{-1}) was about two orders of magnitude smaller than the CO_2 emissions (2336±200 g CO_2-eq m^{-2} yr^{-1}).

Tab. 3: Mean annual budgets (±standard deviation (SD) over four chambers) of CO_2 and CH_4 forest-floor fluxes (using gap-filled data). The Q_{10} budget was calculated with Eq. 3 (Q_{10} and R_{ref} estimates were 4.8 and 3.16, respectively; overall R^2 was 0.86).

Year	CO_2 budget (g CO_2 m^{-2} yr^{-1})	(g C m^{-2} yr^{-1})	Q_{10} budget (g CO_2 m^{-2} yr^{-1})	CH_4 budget (g CO_2-eq m^{-2} yr^{-1})	(g C m^{-2} yr^{-1})	(g CH_4 m^{-2} yr^{-1})	Net GHG budget (g CO_2-eq m^{-2} yr^{-1})
2017	2139±334	584± 91	2407±28	-17.1±3.6	-0.47±0.10	-0.63±0.13	2122±334
2020	2338±324	638± 89	2390±54	-18.7±3.3	-0.52±0.09	-0.69±0.12	2319±324
2021	2138±275	584± 75	2204±40	-18.3±2.7	-0.51±0.08	-0.68±0.10	2120±275
2022	2730±589	745±161	2687±40	-22.2±4.4	-0.62±0.12	-0.82±0.16	2708±579
Overall	2336±200	638±55	2422±21	-19.1±1.8	-0.53±0.05	-0.71±0.06	2317±200

The year 2022 can be considered an exceptional year, both in terms of annual forest-floor CO_2 and CH_4 fluxes (Tab. 3), but also in terms of temporal development (Fig. 3a). For CO_2, there were not only higher emission rates in summer, but also a faster increase in CO_2 emission rates already in mid-April and sustained higher emissions until later in the year (Fig. 3a). The exceptionally high CO_2 fluxes coincided with the higher-than-usual T_{soil} which was the main driver of spring, summer, and autumn CO_2 fluxes. For CH_4, we observed a considerably higher annual CH_4 uptake in 2022 compared to other years (Tab. 3), mainly due to higher uptake rates in summer as well as still high uptake rates in autumn and early winter (Fig. 3b). Apart from higher T_{soil} driving the higher summer CH_4 uptake, this was mainly connected to comparably low soil moisture in autumn 2022 and the exceptionally low snow amount in November and December 2022.

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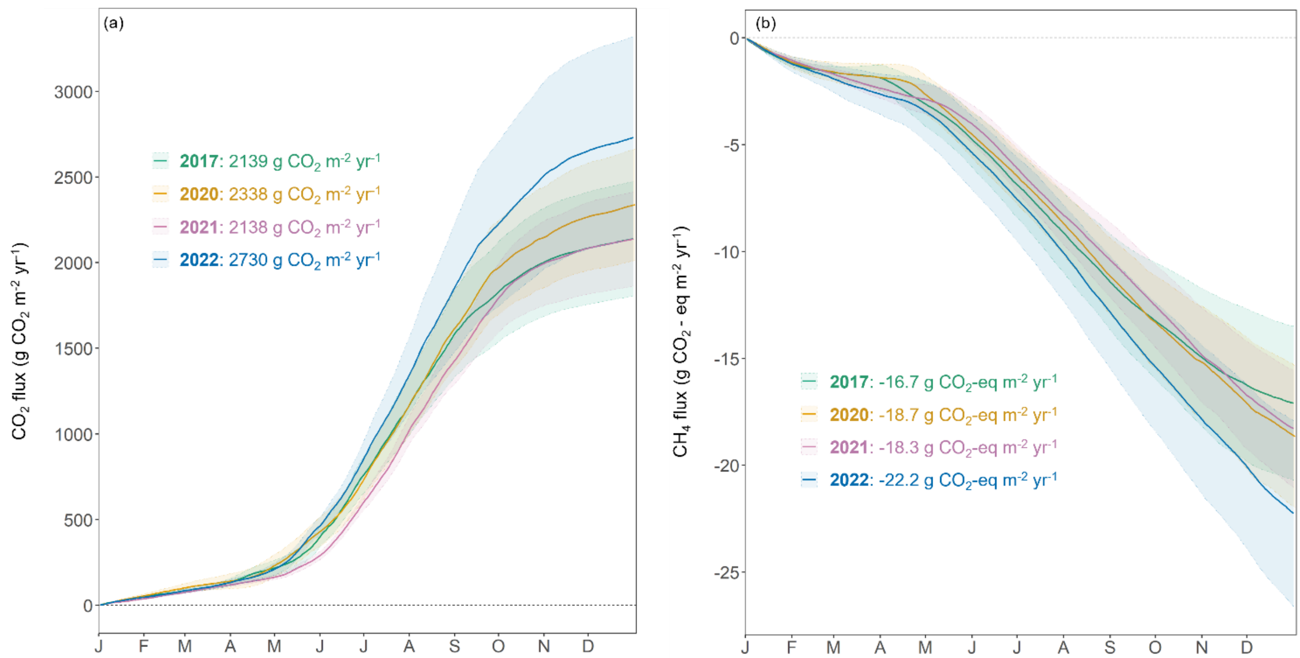

Fig. 3: Cumulative (a) CO_2 (g CO_2 m^{-2} yr^{-1}) and (b) CH_4 (g CO_2-eq m^{-2} yr^{-1}) forest-floor fluxes over four years. Lines show means of all four chambers; colored bands represent standard deviations among four chambers.

4 Discussion

4.1 Interannual variability in forest-floor GHG fluxes

Over the four-year measurement period (2017 and 2020–2022), we acquired high-resolution forest-floor GHG flux data for four distinct years allowing comprehensive year-round analyses. Notably, 2022 emerged as the warmest year ever recorded at the Davos site, coinciding with remarkably low precipitation levels. Despite these counteracting environmental conditions, forest-floor CO_2 emissions in 2022 exceeded the other three years by approximately 20 %. Concurrently, we observed the highest forest-floor CH_4 uptake in 2022. Anjileli et al. (2021) reported that even during extreme heat events soil respiration increased by approximately 25 % compared to average conditions, emphasizing the dominating influence of temperature on CO_2 emissions also under extreme dry conditions. Additionally, Borken et al. (2006) indicated that droughts can enhance the soil CH_4 sink in temperate forests. In contrast, the year 2021 was the coldest year among the four years we investigated, with an annual mean T_{air} of 3.9 °C mainly driven by below-average spring temperatures. This was reflected clearly in the GHG fluxes with below-average CO_2 emissions (approximately 30 % lower compared to the four-year mean) and below-average CH_4 uptake in spring 2021 (approximately 20 % lower compared to the four-year mean). Moreover, 2021 was an exceptional year in terms of snow amount (snow depth in winter and spring exceeded the four-year average by 87 % and 145 %, respectively), relevant drivers identified in this study.

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While the year 2020 was also characterized by a warm weather, its summer temperatures were less extreme than those in 2022. Our findings revealed that the CO_2 emissions in 2020 did not reach the levels observed in 2022, supporting our driver analyses, clearly indicating that the exceptionally high summer temperatures experienced in 2022 were the primary driving force behind the 2022 annual CO_2 emissions. The RF models for 2022 resulted in slightly lower forest-floor CO_2 fluxes than measured, suggesting that no overfitting had occurred (Fig. A.3, A.4). Moreover, these results highlight the critical role played by extreme summer temperatures in shaping the C dynamics of this subalpine spruce ecosystem and underscore the significance of understanding their implications for future C budgets, potentially reducing the overall C sink behavior observed so far in this forest (Zielis et al., 2014).

4.2 Drivers of forest-floor GHG fluxes

Forest-floor GHG fluxes were shown to have very distinct drivers across the different season. Consistent with our expectations, soil temperature predominantly controlled forest-floor CO_2 fluxes, thereby influencing the annual CO_2 budget at annual as well as seasonal scales (except winter season). In contrast, no effects of drivers known to enhance canopy photosynthesis (i.e., LAI, PPFD) and thus below-ground allocation and soil respiration (Högberg et al., 2001) were observed on the forest-floor CO_2 fluxes for any time in this spruce forest, suggesting a strong direct control of environmental factors and a weak or even lacking indirect control of canopy biology. Drivers of forest-floor CH_4 fluxes were much more variable compared to those for CO_2 fluxes, with winter CH_4 fluxes being affected by the same driver (snow depth) as the annual fluxes. In addition, CH_4 fluxes responded most strongly to WFPS in autumn. These findings support the hypothesis proposed by Borken et al. (2006), which emphasized the role of factors influencing the diffusion rates of atmospheric CH_4 into the soil, such as soil water content and snow cover, in determining CH_4 uptake in forest soils. Notably, previous studies have also reported a close relationship between CH_4 fluxes and seasonal changes in soil moisture (Ni and Groffman, 2018; Ueyama et al., 2015). However, our results indicated that in spring and summer, T_{soil} rather than WFPS played a more important role in driving forest-floor CH_4 uptake. Additionally, we identified a notable influence of soil N on summer CH_4 fluxes, with higher N stocks, and thus most likely higher N mineralization during the summer months, corresponding to enhanced CH_4 uptake. This aligns with previous findings in forest ecosystems, where soil mineral N has been shown to stimulate CH_4 oxidation (Goldman et al., 1995; Martinson et al., 2021). Moreover, we found a positive correlation between bare soil fraction and forest-floor CH_4 uptake, i.e., less bare soil and thus higher moss cover leading to higher forest-floor CH_4 uptake. This is in line with the findings that *Sphagnum* mosses can promote CH_4 oxidation (Basiliko et al., 2004). Also for forest-floor CH_4 fluxes, hardly any effect of canopy biology was detected (except for summer). Thus, a strong direct control of environmental factors on both GHG fluxes was observed, increasing the vulnerability of the forest C sink with future climate change (IPCC, 2021).

4.3 Forest-floor GHG budgets

The overall forest-floor GHG budget showed a total emission of 2317±200 g CO_2-eq m^{-2} yr^{-1}, dominated by the annual CO_2 budget (2.34±0.20 kg CO_2 m^{-2} yr^{-1}), which was within the range of studies conducted in temperate, subalpine or boreal forests

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which we consider comparable to our site (1.07–2.91 kg CO_2 m^{-2} yr^{-1}; Gaumont-Guay et al., 2014; Groffman et al., 2006; Schindlbacher et al., 2007, 2014; Wang et al., 2013; Xu et al., 2015). Also our estimate of annual CH_4 budget at the site (-0.71±0.06 g CH_4 m^{-2} yr^{-1}) fell within the range of -1.6 to -0.18 CH_4 m^{-2} yr^{-1} observed in other forest studies (Borken et al., 2006; Luo et al., 2013; Ueyama et al., 2015; Yu et al., 2017), offsetting a mere 0.8 % of the CO_2 emissions. Winter fluxes contributed a large fraction to the overall CH_4 budget (14.4–18.4 %), but played a less important role for the CO_2 budget (6.0–7.3 %), similar to the CO_2 contribution in other mid latitude and temperate ecosystems (5.5–8.9 %; Gao et al., 2018; Wang et al., 2013) but smaller than some high latitude and other subalpine ecosystems (12–20 %; Kim et al., 2017; Schindlbacher et al., 2007; Xu et al., 2015).

To date, only a few studies have examined soil or forest-floor GHG fluxes in subalpine, temperate, or boreal forests measuring CO_2, CH_4 *and* N_2O fluxes in parallel (Tab. 4). Moreover, it is noteworthy that the integration of year-round and temporally highly resolved measurements remains rather uncommon; to our knowledge, only two other studies with year-round measurements exist apart from the current study (Luo et al., 2011; Pilegaard et al., 2003). On the one hand, previous studies frequently measured fluxes for only a limited period of the year, often excluding the dormant season. On the other hand, many of the studies adopted a weekly to monthly measurement frequency, consequently being unable to detect any short-term hot moments, and thus potentially underestimating the flux magnitude. If year-round measurements of forest-floor CO_2 fluxes are not feasible, using Q_{10} models might be a viable option, if the annual temperature range is being well covered, as seen in the agreement between our gap-filled continuous measurements and the Q_{10} budget. However, although T_{soil} was identified as the primary driver of CO_2 emissions, it was not the only one. Thus, neglecting other potential drivers might reduce the reliability and increase the uncertainty of any (modeled) annual CO_2 budget. Moreover, identifying important drivers for GHG fluxes is the more reliable, the longer and thus typically the more frequent measurements were done. Additionally, to effectively capture the dynamic nature of soil GHG fluxes, it is essential to use of automatic chambers with high temporal resolution, preferentially opaque to exclusively quantify respiration. Therefore, we recommend continuous, year-round measurements to reliably estimate annual forest-floor GHG budgets, particularly when large seasonal variability of potential drivers is expected, or when the duration of the active period, i.e., start and end of the snow-free period, is highly variable like in high elevation or high latitude ecosystems. Particularly with the anticipated impacts of future climate change (IPCC, 2021), duration of growing periods will change, and winter fluxes (or the lack thereof) will gain increasing importance (Xie et al., 2017).

Tab. 4: Previously published studies investigating forest-floor or soil CO_2, CH_4 *and* N_2O fluxes in parallel in temperate, subalpine, or boreal forests using automatic or static chambers.

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Chamber method	Location	Forest type	Years	Duration	# Chambers	Frequency	Reference
Automatic	46.82° N 9.86° E	Subalpine (spruce)	2017, 2020–2022	Year-round	4	3 h	This study
Automatic	39.09° N 75.44° W	Temperate (mixed)	2017	Apr–Jul	3	1 h	Barba et al., 2019
Static	43.23° N 3.20° W	Radiata pine, Douglas fir, beech	2010–2011	Year-round	6	Biweekly	Barrena et al., 2013
Static	37.07° N 119.19° W	Montane mixed-conifer (Mediterranean-type climate)	2010–2012	Year-round	24	Weekly–monthly	Blankinship et al., 2018
Static	35.66° S 148.15° E	Temperate (eucalypt)	2006	2 weeks in Nov	10	4 h	Fest et al., 2009
Static	43.93° N 71.75° W	Northern hardwood (beech, maple, birch)	1998–2000	Year-round	8	Weekly–monthly	Groffman et al., 2006
Static	42.40° N 128.10° E	Broad-leaved Korean pine mixed	2019	Mar–Oct	8	Twice a week–twice a month	Guo et al., 2020
Static	48.09° N 16.01° E	Temperate (beech)	1997	Apr–Nov	8	Biweekly	Hahn et al., 2000
Static	43.83° N 74.87° W	Temperate (mixed)	2008	May–Jul	15	Biweekly	Hopfensperger et al., 2009
Static	47.03° N 8.72° E	subalpine (spruce)	2007–2012	Year-round	10	Every 3 weeks	Krause et al., 2013
Automatic (CO_2), static (CH_4, N_2O)	48.50° N 11.17° E	Temperate (spruce)	1994–1997, 2000–2010	Year-round	5	1 h (CO_2), 2 h (CH_4, N_2O)	Luo et al., 2011
Static	46.67–47.93° N 91.75–92.52° W	Boreal-temperate (mixed)	2013	May–Oct	48	Monthly	Martins et al., 2017
Static	33.30–33.47° N 108.35–108.65° E	Temperate–cold temperate (deciduous broad-leaved & coniferous)	2012–2014	Year-round	60	Weekly–monthly	Pang et al., 2023
Automatic (CO_2), static (CH_4, N_2O)	55.48° N 11.63° E	Temperate (beech)	1998–1999, 2001	Year-round	5 (CO_2), 6 (CH_4, N_2O)	2 h (CO_2), biweekly (CH_4, N_2O)	Pilegaard et al., 2003

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Automatic	45.20° N 68.74° W	Sub-boreal (spruce, hemlock)	2013–2016	May–Nov	3-5	30 min	Richardson et al., 2019
Concentration profiles	41.33° N 106.33° W	Subalpine (spruce, fir)	1991–1992	Mar–May	2	Daily–biweekly	Sommerfeld, 1993
Static	49.26–52.20° N 74.03–76.07° W	Boreal (black spruce, jack pine, aspen, alder)	2007	May–Oct	48	Monthly	Ullah et al., 2009
Static	57.13° N 14.75° E	Cold temperate (coniferous)	1999–2002	Year-round	30	Weekly–biweekly	Von Arnold et al., 2005
Static	53.28–53.50° N 122.10–122.45° E	Cold temperate continental monsoon	2016–2018	Year-round	9	Weekly–monthly	Wu et al., 2019

5 Conclusions

We measured year-round GHG fluxes during multiple years with four large opaque automatic chambers and were able to identify their most important drivers. In the light of climate change-induced variations in the onset of the active growing season, growing season length, and winter conditions, we recommend to spatially expand the deployment of such chambers at research stations capable of year-round measurements, including the periods with snow cover. As temperatures will continue to rise due to climate change, and warm and dry conditions, such as in the previous summers, are projected to become more frequent and more severe, we expect an increase in forest-floor GHG emissions at the Davos and similar subalpine or high latitude sites. Anticipated milder winters with reduced snowfall, resulting in shorter snow cover duration and lower average snow depth, will likely contribute to enhanced forest-floor CO_2 emissions and increased forest-floor CH_4 uptake in the future. Since CO_2 emissions are typically much larger than the CH_4 uptake, such as at our site, we expect the forest floor to become a more substantial GHG source in the future, potentially reducing the overall C sink of this type of forest.

Data availability. The data used in this study will be made publicly available from the ETH Research Collection (https://doi.org/10.3929/ethz-b-000619728, preliminary link).

Author contributions. NB designed the study; PM, LK and SB conducted the field work; SB and LK processed the data; LK performed the data analyses, developed the models, and wrote the manuscript draft; SB, MG, PM, IF and NB commented on the manuscript and contributed substantially to discussions and revisions.

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

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inputs during the flux processing and data interpretation. Their contributions have greatly contributed to the progress of this study.

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A Appendix

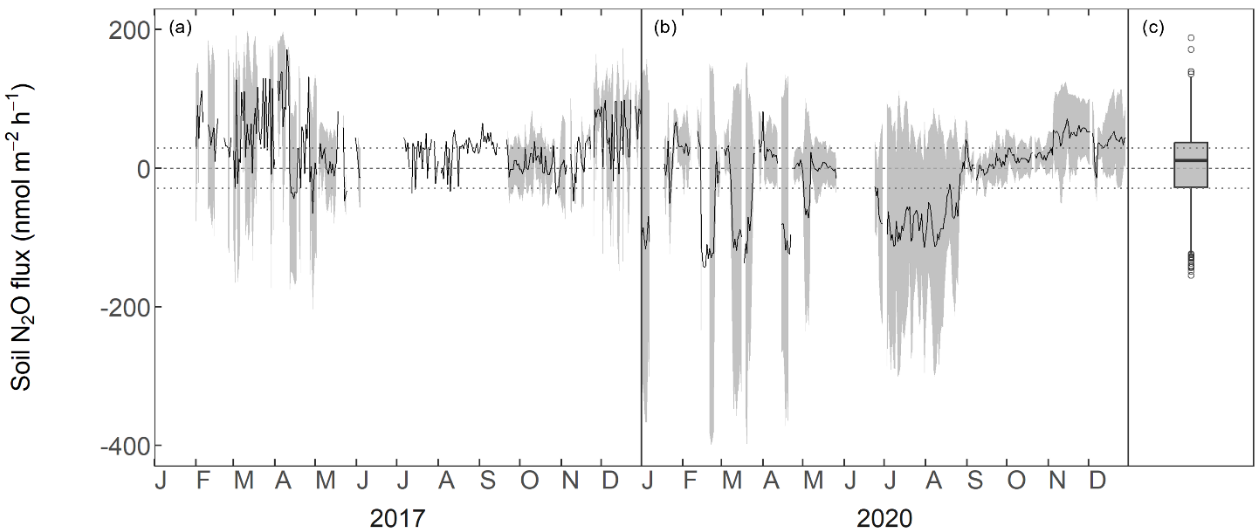

Fig. A.1: Forest-floor N_2O fluxes (nmol m^{-2} h^{-1}) for the years 2017 (a) and 2020 (b). Black lines show means over four chambers, grey bands show standard deviations among four chambers. Boxplot showing distribution of means over four chambers (c). The dotted lines depict the minimum flux which could be detected by the Dual Quantum Cascade Laser spectrometer.

Tab. A.1: Details of random forest models used for driver analysis and gap-filling for different time periods (entire year, separately for seasons). Number of observations used to train the models (training set), the hyperparameters "mtry" and "ntree" as well as the R^2 values for observed vs. predicted test data are given. "mtry" specifies how many variables were randomly sampled as candidates at each split, "ntree" indicates the number of trees.

Gas	Time period	No. observations in training set	mtry	ntree	test R^2
CO_2	entire year	3111	10	2000	0.95
	spring	860	18	2000	0.94
	summer	623	14	2000	0.73
	autumn	836	14	2000	0.90

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	winter	774	14	2000	0.63
CH_4	entire year	2799	14	2000	0.87
	spring	825	18	2000	0.80
	summer	520	18	2000	0.76
	autumn	772	10	2000	0.72
	winter	674	10	2000	0.73

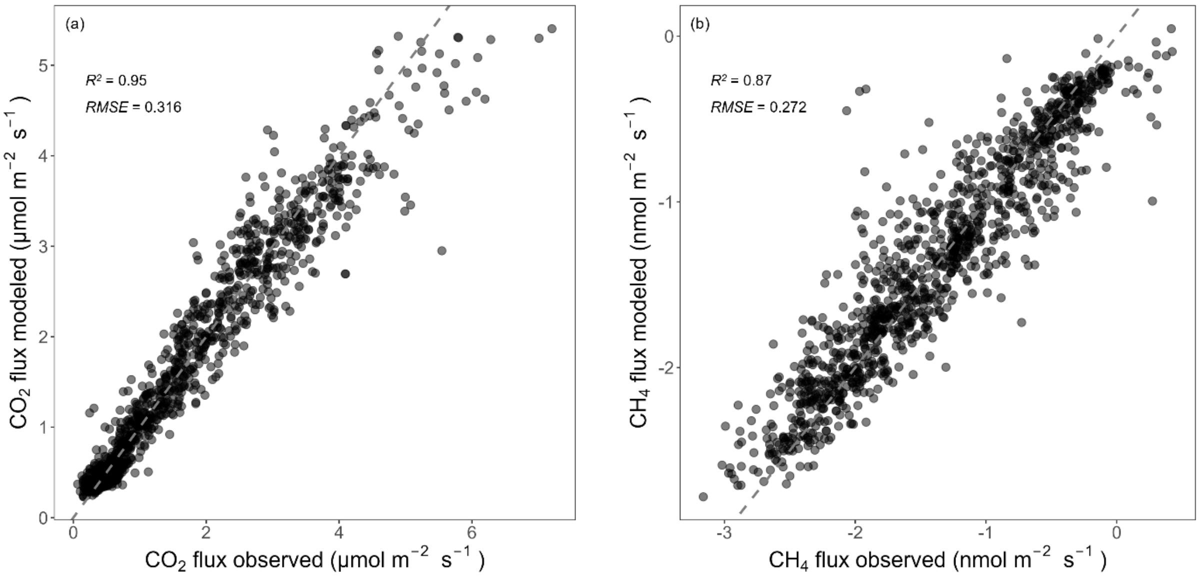

Fig. A.2: Relationships between observed and predicted (a) CO_2 and (b) CH_4 fluxes from the RF models used for gap filling (only showing test data). R^2 and RSME are given. Black dashed lines mark the 1:1 lines.

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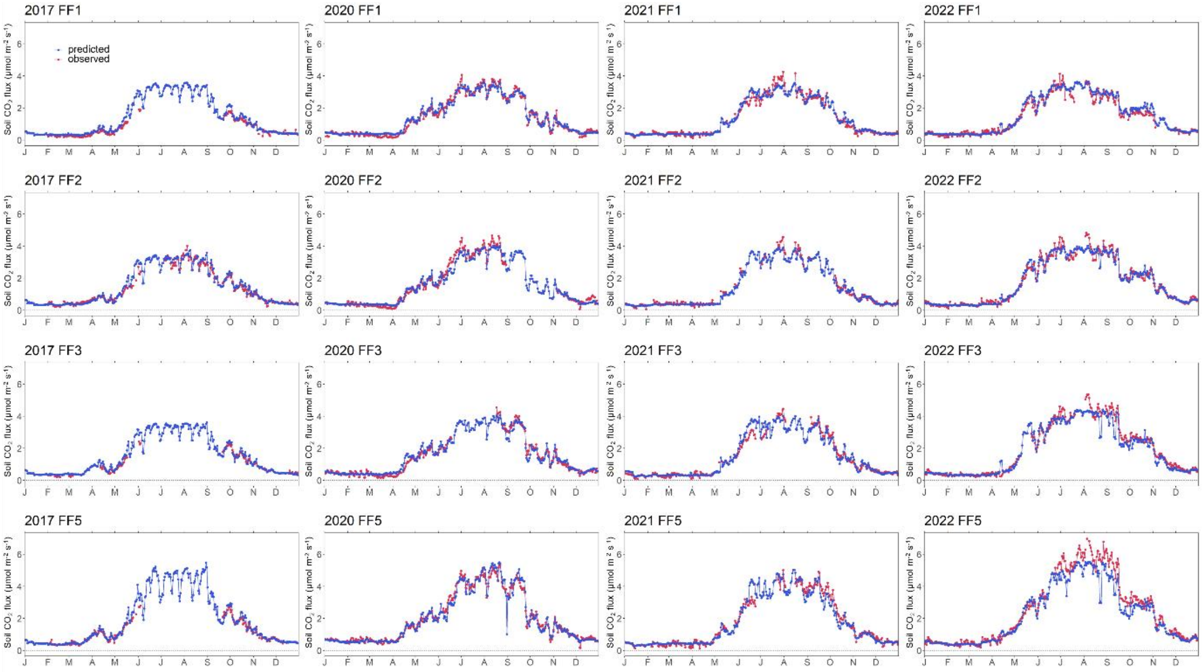

Fig. A.3: Time series of observed and predicted (using random forest model) forest-floor CO_2 fluxes for four years (2017, 2020–2022) and four chambers (FF1 to FF4).

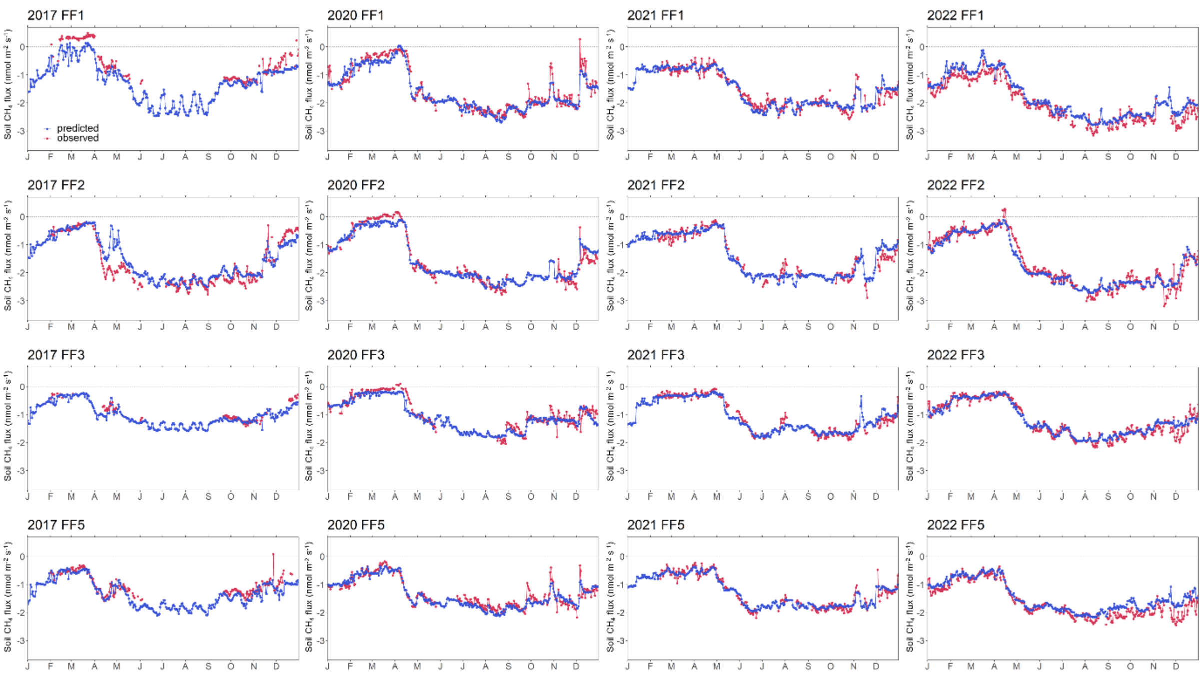

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Fig. A.4: Time series of observed and predicted (using random forest model) forest-floor CH_4 fluxes for four years (2017, 2020–2022) and four chambers (FF1 to FF4).

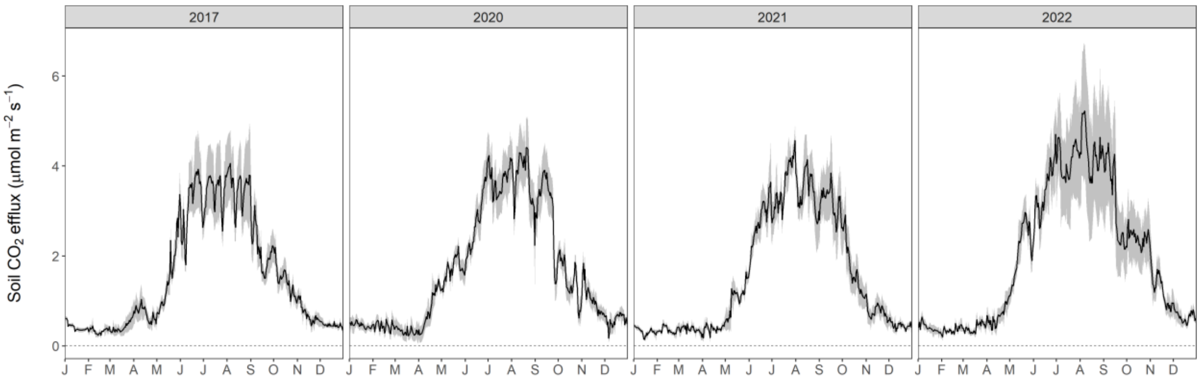

Fig. A.5: Gap-filled CO_2 fluxes over four years (grey area: min-max among four chambers).

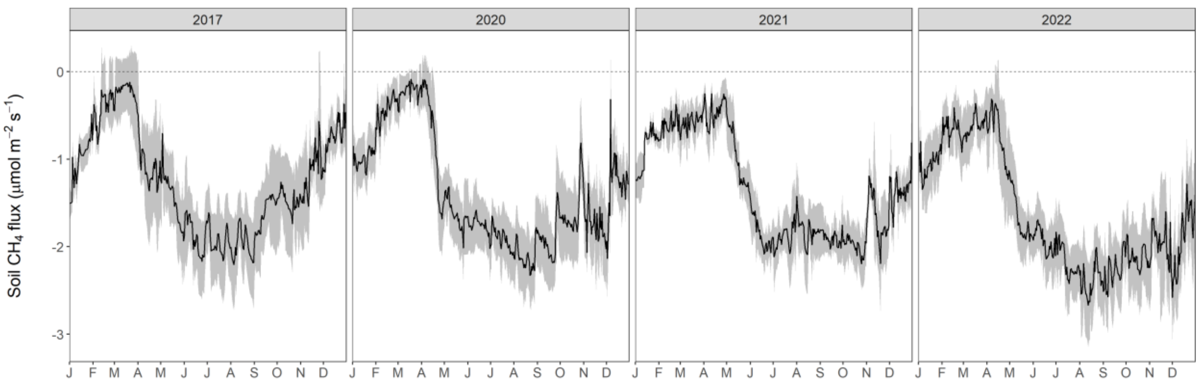

Fig. A.6: Gap-filled CH_4 fluxes over four years (grey area: min-max among four chambers).

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