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Drought effects on soil greenhouse gas fluxes in a boreal and a temperate forest

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Abstract Changing water regimes (e.g. drought) have unknown long-term consequences on the stability and resilience of soil microorganisms who determine much of the carbon and nitrogen exchange between the biosphere and atmosphere. Shifts in their activity could feedback into ongoing climate change. In this study, we explored soil drought effects on soil greenhouse gas (GHG; CO_2, CH_4, N_2O) fluxes over time in two sites: a boreal, coniferous forest in Finland (Hyytiälä) and a temperate, broadleaf forest in Austria (Rosalia). Topsoil moisture and topsoil temperature data were used to identify soil drought events, defined as when soil moisture is below the soil moisture at the permanent wilting point. Data over multiple years from automated GHG flux chambers installed on the forest floor were then analyzed using generalized additive models (GAM) to study whether GHG fluxes differed before and after drought events and whether there was an overall, multiyear temporal trend. Results showed CO_2 and N_2O emissions to be more affected by drought and long-term trends at

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Hyytiälä with increased CO_2 emission and decreased N_2O emissions both following drought and over the entire measurement period. CH_4 uptake increased at both sites both during non-drought periods and as an overall, multiyear trend and was predominantly affected by soil moisture dynamics. Multiyear trends also suggest an increase in soil temperature in the boreal forest and a decrease in soil moisture in the temperate forest. These findings underline forests as an important sink for CH_4, possibly with an increasing rate in a future climate.

Keywords Soil greenhouse gas fluxes · Carbon dioxide · Methane · Nitrous oxide · Boreal forest · Temperate forest · Drought events

Introduction

The current climate crisis will shift biogeochemical processes involved in the exchange and transformation of carbon (C) and nitrogen (N) in directions yet unknown despite these processes being not yet fully elucidated (Costa et al. 2021). Alongside global warming, precipitation patterns are predicted to become more erratic and extreme (Dai 2013). More frequent and severe drought, for example, is becoming an ever more common feature of climate change (IPCC 2022). Europe, for example, experienced in August 2022 the worst drought in the last 500 years, with low soil moisture and high vegetation stress due to wide and persistent lack of precipitation combined with a sequence of heatwaves (Toreti et al. 2022).

Soils are a central playing field for biogeochemical processes and act as important sources and sinks for elements (Zechmeister-Boltenstern et al. 2018), through the regulation of these processes by microorganisms. The microbes are essential for releasing elements into the soil that can be taken up by other microorganisms and plants, stored in the soil, emitted into the atmosphere in a gaseous form, or leached from the soil (Coleman and Wall 2015; Lladó et al. 2017).

Soil microorganisms are influenced by changing climatic and water regimes that have so far unknown consequences on their stability and resilience (Jansson and Hofmockel 2020). Soil microbial activity and taxonomic composition are influenced by soil moisture, the severity and duration of drought events, as well as soil re-wetting (Schimel 2007, 2018; Bardgett and Caruso 2020; Jansson and Hofmockel 2020). Microbially-driven biogeochemical cycling, for example, ceases under severe water stress, leading to reduced C and N loss from the system (Heimann and Reichstein 2008; Schimel 2018). Microbial responses are influenced by the drought duration, severity, and frequency, which affect the diffusion rate and availability of resources to microorganisms and the scale of microbial mortality (Göransson et al. 2013; Kakumanu et al. 2013; Meisner et al. 2015, 2017). Extreme precipitation on dry soils also presents a large challenge for microbial survival and activity. Rapid re-introduction of water into the soil forces microorganisms to quickly re-establish osmotic equilibrium to avoid cell lysis and mortality (Schimel 2007). Concurrently, there is a large pool of substrate that suddenly becomes bio-available, which can lead to a large increase in microbial activity (Borken and Matzner 2009; Schimel 2018) and a strong GHG pulse after rewetting (Birch 1958; Schimel 2007; Leitner et al. 2017a). Moreover, a high influx of water could also lead to inundated and therefore anaerobic soil conditions, which decreases microbial access to gaseous and volatile solutes (Schimel 2018) and could increase denitrification and methanogenesis rates (Schulze 2000; Serrano-Silva et al. 2014). Thus, the overall effect of a larger heterogeneity in moisture distribution on the soil GHG balance will depend on microbial adaptations during drought as well as the magnitude of the GHG pulses following rewetting (Bardgett and Caruso 2020). In systems not adapted to drought, despite CO_2 and N_2O flushes often see after rewetting (e.g. the Birch effect), reduced microbial biomass will likely lead to overall reduced microbial activity (Ren et al. 2018).

Indeed, soil responses to disturbances in water availability also differ depending on the temporal scale. Changes to biogeochemical processes are often non-linear in time, and the result of accumulated effects only becomes apparent after long time scales (Wollast and Mackenzie 1989; Schlesinger and Bernhardt 2013). Soil microbial communities can express varying levels of resistance and resilience to stress events that helps maintain functional stability, but repeated stress exposure can push them beyond a tipping point (Griffiths and Philippot 2013). Long-term monitoring of these processes is therefore

paramount to identifying and understanding patterns and responses. Most research projects are funded for short periods (3–5 years), meaning measurements are only conducted at most for a couple of years, which is often too short to observe significant or long-lasting responses to climate change (Shaver et al. 2000) or potentially identify tipping points for ecosystems (Reyer et al. 2015). Drought and short-term rewetting effects are well-studied, but whether soil drought effects on microbial activity are persistent after a drought, i.e. multiple months or years, and whether soil drought effects accumulate over multiple drought seasons is still a considerable knowledge-gap.

Both temperate and boreal forest soils are widely distributed globally, store large amounts of carbon (Crowther et al. 2019), and are important CH_4 sinks (Liu et al. 2019). At the same time, they have different soil drought exposure and will face different future soil drought patterns (Dai 2013). Understanding how the soil microbial activity from these habitats are influenced by long-term drought effects is paramount in predicting future shifts in GHG fluxes.

Here, we used long-term soil GHG flux data to investigate soil drought effects on biogeochemical processes by comparing GHG fluxes before, during, and after soil drought events in a boreal, coniferous forest in Finland (Hyytiälä) and a temperate, broadleaf forest in Austria (Rosalia). In this study, soil drought was defined as when soil moisture dropped below the permanent wilting point which indicates when microbial activity is limited and plants wilt permanently (Skopp et al. 1990; Davidson et al. 1998). The boreal forest is only sporadically and shortly subjected to meteorological drought; in the temperate forest, periods with little or no precipitation are recurrent. We hypothesized that (1) at the boreal forest site, soil CO_2 and N_2O emissions will decrease after the first soil drought event measured compared to 'initial' rates (i.e. rates before the first measured drought), but emissions will be the same or increase with subsequent droughts likely due to an already soil drought-adapted microbial community. For the temperate forest site, more drought exposed, we hypothesized that (2) soil CO_2 and N_2O emissions will not be significantly different during the rewetted periods after the first few droughts as compared to the initial period, likely to an already soil drought-adapted microbial community. For CH_4 fluxes, we hypothesized that at both sites (3) CH_4 uptake will remain relatively stable in non-drought periods compared to initial rates, likely because the re-increase of soil moisture will limit CH_4 diffusion. We further hypothesized that at both sites (4) there will be an increase in CO_2 and N_2O emissions and in CH_4 uptake over the entire multiyear period, likely due to long-term increase in soil temperature creating more favorable microbial conditions.

Materials and methods

Site descriptions

The SMEAR II LTER site (Station for Measuring Ecosystem-Atmosphere Relations; https://deims.org/663dac80-211d-4c19-a356-04ee0da0f0eb) is situated close to Hyytiälä Forestry Field Station of the University of Helsinki in southern Finland (Fig. 1). The site has a boreal climate and is dominated by even-aged *Pinus sylvestris* L. (Scots pine) with other prevalent species including *Picea abies* (L.) H. Karst. (Norway spruce), *Betula pendula* Roth (silver birch), and *Betula pubescens* Ehrh. (downy birch) and some *Juniperus communis* L. (common juniper), *Salix* sp. L. (willow), and *Sorbus aucuparia* L. (mountain ash) (Ilvesniemi et al. 2009). The study site was established by sowing after clear-felling, prescribed burning, and light soil preparation in 1962 (Hari et al. 2013). The understory plant species composition consisted of *Vaccinium myrtillus* L. (European blueberry), *Vaccinium vitis-idaea* L. (lingonberry), *Polytrichum commune* Hedw. (common haircap moss), *Pleurozium schreberi* (Brid.) Mitt. (red-stemmed feathermoss), *Hylocomium splendens* (Hedw.) Schimp (mountain fern moss), and *Deschampsia flexuosa* (L.) Trin. (wavy hair-grass) (Kulmala et al. 2008). Further site characteristics can be found in Table 1.

The Lehrforst Rosalia LTER site (https://deims.org/77c127c4-2ebe-453b-b5af-61858ff02e31) is located in the eastern part of Austria (Fig. 1), is part of the University of Natural Resources and Life Sciences, Vienna, and has a Pannonian climate. All major tree species and forest types in Austria are present at the site: *Picea abies* (L.) H. Karst., *Abies alba* Mill. (European silver fir), *Larix decidua* Mill. (European larch), *Pinus sylvestris* L., *Fagus sylvatica* L., and *Quercus* sp. (oak). The site has been forested since at least the end of the 19th century, probably for

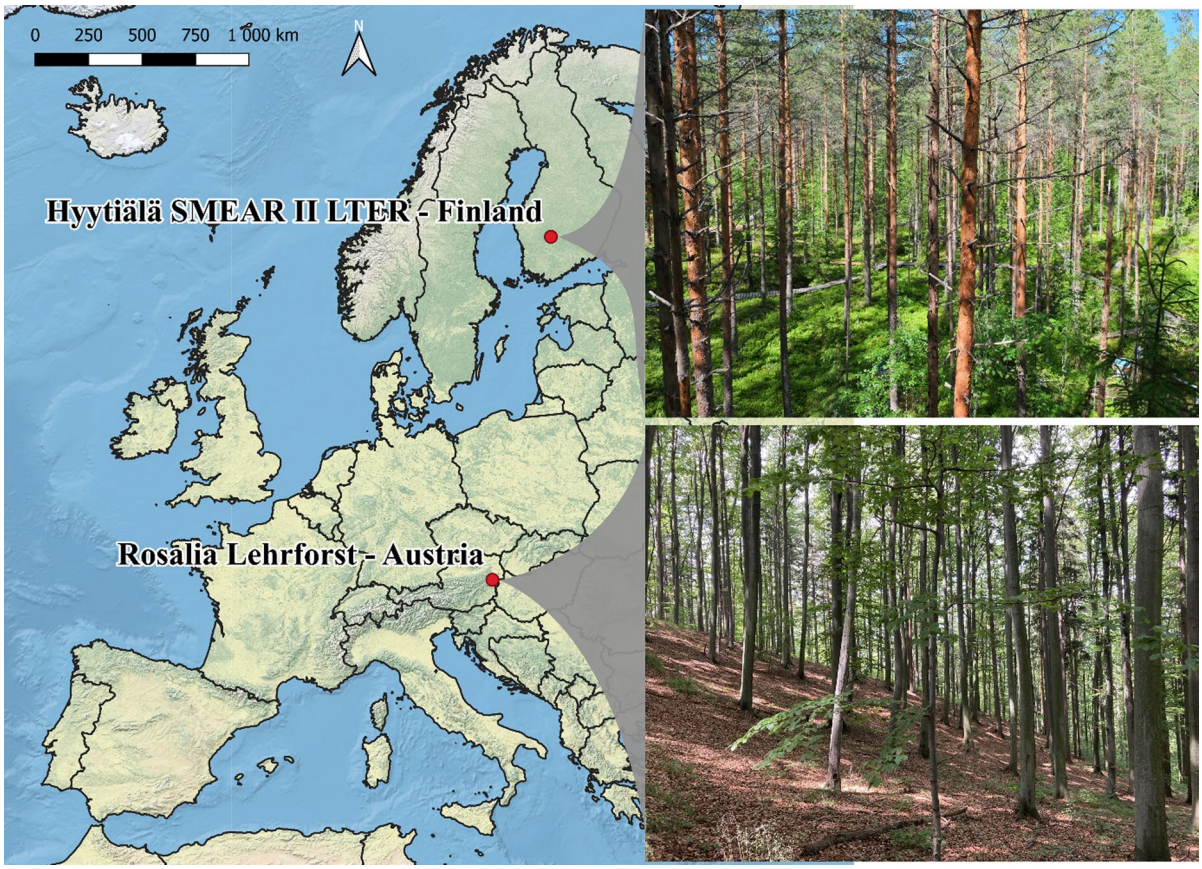


Fig. 1 Location of the two investigated sites: Hyytiälä SMEAR II in Finland and Lehrforst Rosalia in Austria. Map created with qGIS (version 3.28.0, QGIS Development Team 2023) and opensource basemap from naturalearthdata.com. Hyytiälä SMEAR II photo taken by Juho Aalto, and Lehrforst Rosalia photo taken by Eugenio Díaz-Pinés.

longer. The study location (DRAIN; https://deims.org/locations/b7008603-fca2-452f-9b3d-aad30cdafc7a) is in a mature *F. sylvatica* stand aged between 90 and 110 years. There is no understory beyond a small amount of *Rubus fruticosus* L. (European blackberry). Further site characteristics can be found in Table 1.

In addition to having contrasting climates, the sites also had differences in topography (Hyytiälä is on a flat hilltop, whereas Rosalia is on a west-facing slope), tree types (pine vs. beech), undergrowth species, and organic layer (Hyytiälä having thicker F and H layers). However, the sites have fairly similar soil characteristics. The two sites have low clay percentages and comparable silt and sand percentages that are over 40%. The soil pH and bulk density are relatively close, both soils being acidic with low bulk density. Hyytiälä SMEAR II soil C and N contents are both lower than at Lehrforst Rosalia, and Hyytiälä SMEAR II has a higher C:N ratio (32.4 versus 18.2, respectively).

Soil greenhouse gas flux measurements

At Hyytiälä SMEAR II, soil CO_2 fluxes were measured with three (2009–2014) or two (2015–2017) automated, static chambers (total chamber volume 10 L, enclosed soil surface area 0.05 m^2) placed on an aluminum collar inserted max. 5 cm deep into the soil to avoid cutting roots and minimize sideways gas diffusion that could influence measured fluxes (Hutchinson and Livingston 2001). On the collar was a chamber made of acrylic glass that automatically closed every 30 min for 3.5 min (Fig. S1). The chamber was equipped with a fan to ensure headspace air mixing and a small vent hole to minimize pressure

Table 1 Site characteristics for Hyytiälä SMEAR II in Finland and Lehrforst Rosalia in Austria

	Unit	Hyytiälä SMEAR II	Lehrforst Rosalia
Country		Finland	Austria
Coordinates		61°51'N, 24°17'E	47°42'N, 16°17' E
Elevation range	m a.s.l.	140–200	300–720
Elevation of measurements	m a.s.l.	181	600
Annual precipitation	mm	711	785
Mean annual air temperature	°C	3.5	6.5
Slope	°	0	14
Orientation		Not applicable	West-facing
Bedrock		Granite	Metamorphic crystalline
Soil type*		Haplic Podzol	Podsolic cambisol
Clay**	%	9	7
Silt**	%	40	47
Sand**	%	52	46
Bulk density	g cm^{-3}	0.74	0.60
Soil pH		3.41	3.84
Soil C	%	3.89	4.55
Soil N	%	0.12	0.25

Soil parameters are from the first 10 cm

**Percent weight; FAO classification (Jahn et al. 2006)

*According to WRB classification

disturbances in the chamber headspace. While the chamber was closed, headspace CO_2 concentration was measured using a GMP343 diffusion type CO_2 probe (Vaisala Oyj, Vantaa, Finland, NDIR sensor), and the data were recorded at 5 s intervals by AD converters (Nokeval, Nokeval Oy, Nokia, Finland). Headspace temperature and relative humidity were measured using a thermocouple type K sensor and a semiconductor sensor (HIH-4000, Honeywell International, Inc.), respectively. The setup is described in detail by (Pumpanen et al. 2015). Fluxes (mg CO_2–C m^{-2} h^{-1}) were calculated from the change in CO_2 concentration over time from outlier-filtered raw data collected between 40 and 170 s after chamber closing using linear fit and corrected for air temperature and atmospheric pressure (Metcalfe et al. 2007). The chambers were initially transparent and later covered (on May 18, 2010) with aluminum foil for darkening. Only measurements at night (i.e. when the solar elevation angle was <0 degrees) and with dark chambers were included in this dataset. CO_2 fluxes from different chambers were averaged to have a single flux estimate.

Hyytiälä SMEAR II soil N_2O and CH_4 fluxes were measured from 2007 to 2014 with one stainless steel, automated, static chamber, consisting of a permanent collar installed in the soil 5 cm deep and a chamber that was closed on top of the collar (total volume 83 L, enclosed soil surface area 0.32 m²). This was a different collar than for the CO_2 fluxes. The chamber was equipped with a fan and a vent-tube to minimize pressure disturbances. Headspace temperature was measured using a thermocouple. The headspace gas was sampled automatically into vials 7 or 8 times during a 45 min closing time once per day. The concentrations of N_2O and CH_4 were analyzed with a gas chromatograph (GC) equipped with a ^{63}Ni electron capture detector (ECD) and a flame ionization detector (FID, all Hewlett Packard 6890). Fluxes were then calculated from the concentration change from outlier-filtered raw data collected using linear fit for N_2O fluxes (μg N_2O–N m^{-2} h^{-1}) and CH_4 fluxes (μg CH_4–C m^{-2} h^{-1}) and corrected for pressure. Negative values of flux rates denote net GHG uptake by the soil from the atmosphere.

At Lehrforst Rosalia, soil CO_2, CH_4, and N_2O fluxes were measured with an automated soil-atmosphere GHG flux detection system as explained in(Butterbach-Bahl et al. 1998) and with subsequent system applications and settings (Díaz-Pinés et al. 2017; Dannenmann et al. 2018). The system encompasses 12 automated, static chambers and is part of a climate manipulation experiment (Leitner et al. 2017b). For this work, we included data from four of the chambers, corresponding to the environmental control (no manipulation of the

precipitation). The chamber had a total volume of 37.5 L (enclosed surface area 0.25 m^2) and was made of transparent acryl glass with a stainless-steel frame installed on a stainless-steel frame inserted 5 cm into the ground (Fig. S1). The chambers were equipped with fans for air mixing and with a non-force open vent for headspace pressure equilibration. Three chambers closed for 45 min during which the air in each chamber was sampled four times. The gas samples were transported from the chambers *via* stainless-steel tubes to a central valve switching unit using a gas pump (flow rate 250 ml min^{-1}, NMP 830 154 KNDC, KNF Neuberger GmbH, Freiburg in Breisgau, Germany). A gas aliquot was then transferred to a non-dispersive infrared CO_2 analyzer (LI-840 A CO2/H2O analyzer, LI-COR, Lincoln, NE, USA) and another aliquot was diverted to a SRI 8610 GC (SRI Instruments Europe GmbH, Bad Honnef, Germany) for detection of CH_4 (FID) and N_2O (ECD) concentrations. CO_2 was removed from the gas aliquot measured in the GC with an Ascarite (sodium hydroxide-coated silica) column. Calibration gas (400 ppb N_2O, 3 ppm CH_4 and 400 ppm CO_2 in N_2, Linde Gas GmbH, Stadl-Paura, Austria) was added every 45 min by duplicate. The four air samples taken during a chamber closure created a linear change of gas concentrations, the slope of which was used to calculate the gas flux rates (mg CO_2–C m^{-2} h^{-1}, µg CH_4–C m^{-2} h^{-1}, µg N_2O–N m^{-2} h^{-1}) which were corrected for air temperature and atmospheric pressure (Metcalfe et al. 2007). For CO_2 calculation, only outlier-filtered raw data collected between 40 and 170 s after chamber closing to avoid over-saturation of the chamber, a linear approach with a high R^2 threshold (0.9) was then used. The data collected from entire closing period was used for the CH_4 and N_2O fluxes. For CH_4 and N_2O fluxes, estimates with a determination coefficient (R^2) < 0.9 were discarded, except in those cases with flux estimates below the minimum detectable flux, which was estimated to be about 6 µg CH_4–C m^{-2} h^{-1} and 3 µg N_2O–N m^{-2} h^{-1}. Each chamber was measured every 3 h, thus eight flux measurements per chamber per day were produced. The GHG fluxes from all the chambers were averaged together to have a single flux value data per day. CO_2 efflux included respiration of ground vegetation, but only a few blades of grass were present on the forest floor at the site, and the influence of plants on the estimated CO_2 fluxes is therefore considered to be negligible.

At both sites, low temperatures, and/or snow cover prevented the continuation of the measurements during winter. Soil CO_2 flux was measured nine months per year over nine years and CH_4 and N_2O fluxes for eight months per year at Hyytiälä SMEAR II over seven years, usually conducted from April to November. At Lehrforst Rosalia, fluxes of CO_2 were measured ten months per year over three years and CH_4 and N_2O for nine months per year over three years, usually from March to December.

Topsoil moisture and temperature measurements

At Hyytiälä SMEAR II, soil water content and soil temperature were measured at several locations (spatial replicates) within ~900 m^2 intensively monitored plot where the chamber collars were located. Topsoil water content was measured at five locations between 2 and 6 cm depth with a Time Domain Reflectometer (TDR-100, Campbell Scientific, Campbell Scientific, Inc, Logan USA) connected to datalogger (Campbell 21X), multiplexers (SDMX50) and probes by the CO_2, CH_4, and N_2O chambers. In a soil pit, 15 cm-long, two-rod type probes were installed. The datalogger controlled the measurement sequence and applied algorithms that determined the apparent probe length and soil water content (Ledieu et al. 1986). Topsoil temperature was measured between 2 and 5 cm depth using silicon temperature sensors (Philips KTY81-110) connected to serial data transmitters (Nokeval 5020) and then to the main computer through a RS232 line, where the temperature channels were read at 15 min intervals. Matlab scripts and functions were used to remove periods of instrument malfunctions or other known severe quality issues in the data, signal conversion from mV to appropriate physical units, and calibration correction. A basic quality check was also conducted to remove unrealistic values and spikes by running mean or median filter applied to each sensor's data. The discontinuity in topsoil moisture time series caused by the 2011–2012 soil measurement renovation was corrected by adjusting the signals of the channels consistent with pre-2011 data using the continuous time series of soil moisture near the automated CH_4 and N_2O chamber and soil water potential data as the baselines. That is to

say, the signal conversions of the new sensors were adjusted to make the post-renovation moisture data consistent with the old data.

In Lehrforst Rosalia, topsoil moisture (TDR theta. ML2x probes, METER ENVIRONMENT, Munich, Germany) and topsoil temperature (thermistor Th2-f probes, METER ENVIRONMENT) were measured at 10 cm depth every 1 min and 30 min averages were stored. Probes were located within the same plot < 2 m from the chamber measurements, and data were visually inspected and quality controlled.

All topsoil temperature and topsoil moisture measurements were averaged by day to correspond with the daily GHG flux measurements. Henceforth, 'topsoil' and 'soil' will be used interchangeably.

Defining topsoil drought events

In this study, the soil moisture volumetric percent at the permanent wilting point (PWP; soil moisture at 4.2 pF, − 15 bar) was used to indicate below what moisture threshold the soil was considered in a drought event. This was chosen since the PWP is the soil water potential threshold below which microbial activity is limited and a plant wilts permanently (Skopp et al. 1990; Davidson et al. 1998). So, when the soil water moisture dropped below this threshold, concurrently with relatively high soil temperatures (i.e., above the annual average, 8 °C at Hyytiälä and 10 °C at Rosalia; as to filter out winter droughts), the soil was considered in a drought. Winter droughts were not considered since biogeochemical activity is already very low due to low soil temperatures, and measuring equipment was usually not operational in winter months. At Hyytiälä SMEAR II, the PWP was obtained by laboratory measurement using a pressure plate extractor (Soilmoisture Equipment Corp., Goleta, CA) (Mecke et al. 2002). In Lehrforst Rosalia, the PWP was estimated using the Saxton-Rawls method, which is a predictive moisture regression using soil texture and organic matter (Saxton and Rawls 2006). The volumetric soil moisture contents at the PWP were 10% soil water content for Hyytiälä SMEAR II and 12% for Lehrforst Rosalia. The drought duration was defined as the number of consecutive days the soil moisture percent was at or below the threshold. Severity was defined as the percent the soil water content dropped below the threshold. The period before the first measured drought was labelled the 'initial period', each period below the PWP was labelled a 'drought period' and numbered consecutively, the period following a drought period was labelled a 'non-drought period' and again labelled consecutively. If a rewetting event occurred in the middle of a drought event (i.e., soil was rewetted but soil moisture immediately declined back down below the threshold) this was not considered a non-drought period, and the drought periods before and after this rewetting were considered a single drought period. This categorical variable, termed 'soil moisture status', was then included in the statistical models described below to compare the initial period with subsequent periods (see Table S1 for period durations). This categorical method of exploring soil moisture effects on GHG fluxes allowed us to focus on specific periods of different soil moisture levels (i.e. drought and non-drought periods) as opposed to a general soil moisture effect, which is already well established.

Meteorological data

At Hyytiälä SMEAR II, precipitation (liquid water equivalent) was measured cumulatively (mm) over a 1 min period using a Vaisala FD12P weather sensor at 18 m height. Air temperature (°C) measurements were made at 4.2 m height with a Pt100 sensor (platinum resistance thermometers) protected from solar radiation and ventilated by fans.

Lehrforst Rosalia air temperature and precipitation data were obtained from the nearby Heuberg Meteorological Station (~ 500 m away). Precipitation was measured by weight with a Sartorius QS8 (precipitation collected in 200 cm^2 collector) at 1.50 m height with a 30 min sum value. Air temperature was measured with an UMS RFT-2 at 2 m height with a 30 min average from 1 min resolution measurements. Precipitation data for both sites are open precipitation and do not reflect throughfall.

Statistics

All statistical analyses and figures were run or created using R (version 4.2.1; R Core Team 2022) and RStudio (version 2022.7.2.576, RStudio Team 2015). Removal of unrealistic data or data with some other issues was conducted with the quality checks described above. Data was then gap-filled

using interpolation 'na_kalman' (imputation by structural model & kalman smoothing) and 'na_seadec' (seasonally decomposed missing value imputation) functions in the imputeTS package (version 3.3, Moritz and Bartz-Beielstein 2017). This was done only for the measuring season, i.e., data was not gap-filled before or after the first and last measurements of the year. This was done because there was no way to verify function extrapolations during these periods. At Hyytiälä, gap-filled observations made up 20%, 23%, and 31% of CO_2, CH_4, and N_2O observations, respectively (Fig. S2). At Rosalia, gap-filled observations made up 18%, 40%, and 36% of CO_2, CH_4, and N_2O observations, respectively (Fig. S3). The number of gap-filled observations were generally similar between months and years for each GHG at each site.

Generalized additive models (GAM) were run, using the 'gam' function in the mgcv package (version 1.8.40; Wood 2011), to analyze changes in GHG fluxes, soil moisture content, and soil temperature variables over the measured period. GAM was chosen to take into account the seasonal variability of these timeseries data (Wood 2017). Independent models were created for each GHG, soil moisture, and soil temperature for each site. In the GHG flux models, the moisture status was included as a categorical explanatory variable to see whether the fluxes were different between the 'initial period' and the 'drought periods' and 'non-drought periods', i.e., before, during, and after drought events. Smooth functions, which helps indicate important data patterns to the model (e.g. seasonal patterns), were applied to month, time, soil moisture, and soil temperature individually. The time, soil moisture, and soil temperature splines explored overall temporal trends that covered the entire, multi-year measurement period, while month with a cyclic cubic spline and the number knots equaling the number of measured months took into account seasonality.

Model structure:

$$y_i = x_1 + f_1(x_{2i}) + f_2(x_{3i}) + f_2(x_{4i}) + f_2(x_{5i}) + \epsilon_i$$

where y_i is the response variable CO_2, CH_4, or N_2O flux, x_{1i} is the categorical covariate 'moisture status', x_{2i} is the covariate 'month' with f_1, a penalized smoothing basis cyclic cubic regression spline (the dimension of the basis used to represent the smooth terms, 'k', was set as the number of months), x_{3i}, x_{4i}, and x_{5i} are the covariates 'time', 'soil moisture', and 'soil temperature, respectively, each with a penalized smoothing basis cubic regression spline, and ε_i indicates the error term. When there was autocorrelation, determined by visual inspection of auto-correlation function (afc) and partial auto-correlation function (pafc) graphs created using the stats package (version 4.2.1), generalized additive mixed models were run using the 'gamm' function (mgcv package) with the addition of the correlation function 'corAR1' with a form of ~1|month. Model assumptions and fit were verified using the 'gam.check' function (mgcv package), plotting the residuals, and R^2 were used to check model fit following the process described in Zuur and Ieno (Zuur and Ieno 2016). Soil moisture and soil temperature were analyzed using the same model structure but excluding the soil moisture status.

Results

Using the topsoil drought threshold defined here, five drought periods were identified for Hyytiälä SMEAR II. The CO_2 flux measurement period overlapped all five droughts, while CH_4 and N_2O flux measurement periods only overlapped the first three soil droughts. The precipitation, air temperature, soil moisture, and soil temperature of the initial period were representative of long-term conditions (previous decade) at the site. In Lehrforst Rosalia, three topsoil drought periods were identified, and all three GHG measurement periods overlapped these three soil droughts. The precipitation and air temperature of the initial period were representative of long-term conditions (previous decade) at the site; soil moisture and soil temperature data do not exist preceding this study. Figure 2 shows daily precipitation and air temperature values during these drought events.

Hyytiälä SMEAR II LTER

Over the measurement period, soil moisture was $24.8 \pm 6.9\%$ on average. Moisture content was 4% higher in the non-drought 5 period as compared to the initial period that preceded all measured droughts (Fig. 3a), but this did not translate to a significant

increase over time ($p > 0.05$; Table 2). Soil moisture content was the highest during non-drought 2 (9% higher than initially). Soil temperature was 8.4 ± 4.2 °C on average over the measurement period and showed a significant temporal increase (i.e. time smooth; Fig. 3b), with non-drought periods having higher soil temperatures than the initial period (0.2 to 1.1 °C higher).

Over the nine years measured, the soils emitted an average of 120.0 ± 71.6 mg CO_2–C m^{-2} h^{-1} during the measured growing season. There was a 13% increase in CO_2 emissions between the initial period (i.e., before drought 1) and last non-drought period (i.e., non-drought 5; from 109.0 ± 70.1 up to 123.0 ± 70.7 mg CO_2–C m^{-2} h^{-1}, respectively; Fig. 3c), with a significant time smooth effect, and a 2.8% increase between the first and last years 2009 and 2017 (from 107.0 ± 69.0 to 110 ± 69.8 mg CO_2–C m^{-2} h^{-1}, respectively). Indeed, there was a significant difference between the initial flux period and the final non-drought period (non-drought 5; Table 3). No other period, drought or non-drought, was significantly different after autocorrelation was taken into account.

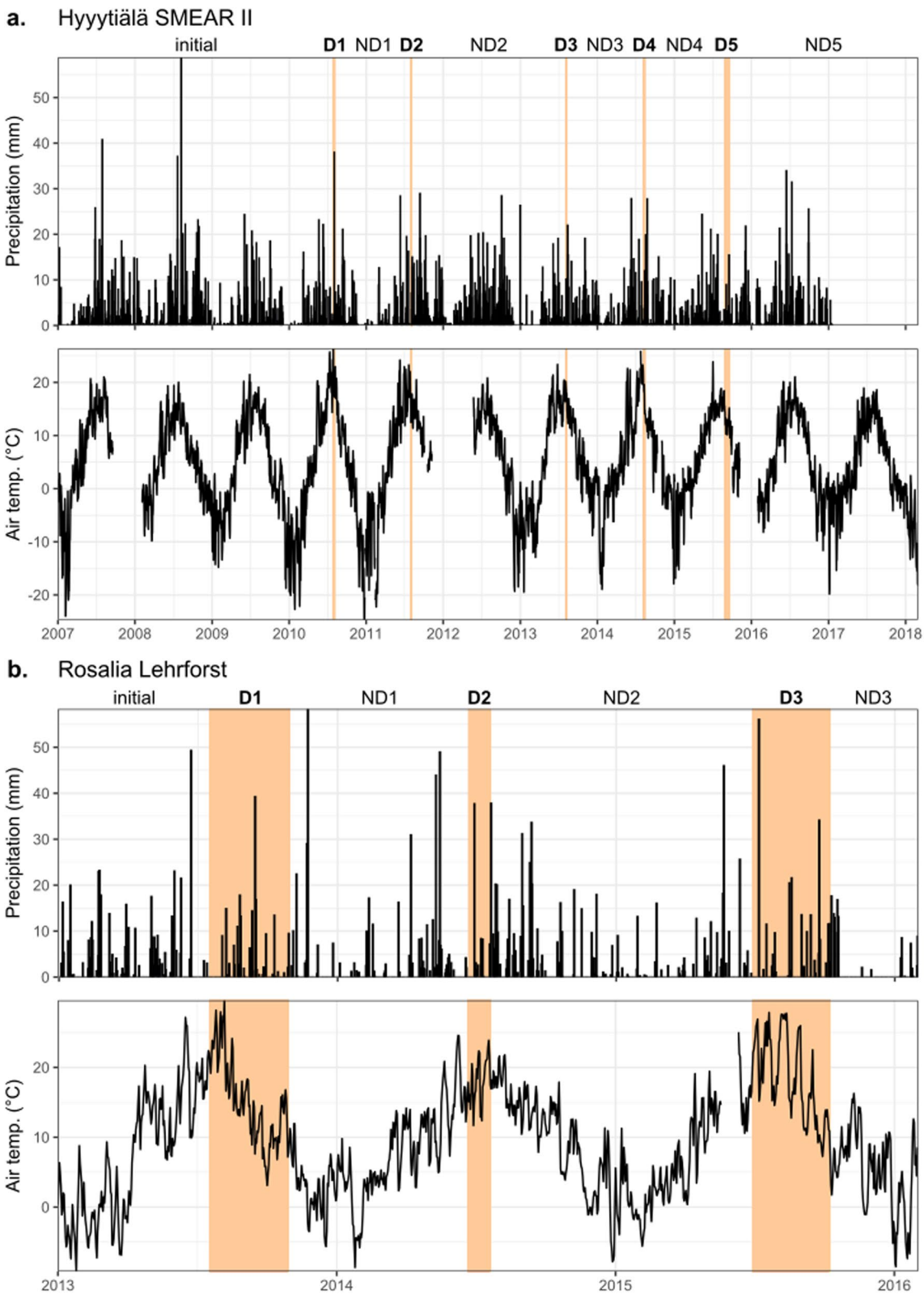
Over the 7 years measured, the soils took up a net average of 103.0 ± 33.6 µg CH_4–C m^{-2} h^{-1} during the measured growing season with an 8% increase in uptake between the initial and final moisture status periods (from 98.2 ± 30.4 to 106.0 ± 47.9 µg CH_4–C m^{-2} h^{-1}) and 16% increase between the first and last years 2007 and 2013 (from − 84.8 ± 14.2 to 98.4 ± 46.5 µg CH_4–C m^{-2} h^{-1}; Fig. 3d). During the initial period, all soil CH_4 fluxes, excluding a single observation, were uptake (average 84.8 ± 14.2 µg CH_4–C m^{-2} h^{-1}). As time progressed, the soil progressively started to show episodes of CH_4 emissions but concurrently took up more CH_4, leading to an overall increase in variability in observations. The model results supported the significant difference between the initial fluxes and most subsequent periods, with a continuous increase in CH_4 uptake (Table 3). Even though the occurrence of soil CH_4 emissions increased with time, there was an increase in the net CH_4 uptake with time, as indicated by a significant time smooth effect and a strongly significant ($p = 0.0001$) negative decrease between the initial and final periods (initial period and non-drought 3, respectively). Overall, time and soil moisture status period (i.e., drought, non-drought, etc.) explained relatively little of the CH_4 flux variance ($R^2 = 0.29$).

Over the seven years, the soils emitted on average 0.6 ± 1.1 µg N_2O–N m^{-2} h^{-1} during the measured growing season with a decrease between the initial and final soil moisture periods (from 0.82 ± 1.1 down to 0.14 ± 1.3 µg N_2O–N m^{-2} h^{-1}, respectively; Fig. 3e). This trend was supported by the significant time smooth effect in the model results (Table 3). There were also significant declines between the initial period and all non-drought periods, with what appears to be stronger effects (estimate value) with each subsequent drought. Overall, like CH_4 fluxes, time and soil moisture status explained relatively little of the N_2O flux variance ($R^2 = 0.15$).

Lehrforst Rosalia

Over the three growing seasons measured, the soil moisture content averaged 17.8 ± 6.1% with a 40% decline between the initial and last periods (from 23.8 ± 3.7 to 14.2 ± 1.0%, respectively) and an 18% decline between the first and last year (from 18.0 ± 6.8 to 14.5 ± 4.0%, respectively; Fig. 4a). Model results supported a significant decline in soil moisture over the measured period (Table 2). Soil temperature averaged 10.2 ± 4.1 °C with a decrease between initial and final periods (from 9.0 ± 4.0 to 8.0 ± 1.6 °C, respectively; Fig. 4b) but an increase between the first and last years (from 9.9 ± 4.4 to 10.3 ± 4.2 °C, respectively). Model time smooth results supported a general temporal increase in soil temperature (Table 2).

The soils emitted an overall average of 71.7 ± 36.1 mg CO_2–C m^{-2} h^{-1} during the measured growing season. There was a 50% decrease between the initial and last non-drought period (from 83.9 ± 36.7 to 41.5 ± 15.4 mg CO_2–C m^{-2} h^{-1}, respectively), whereas the second non-drought period showed a 22% increase (from 83.9 ± 36.7 to 102.0 ± 5.1 mg CO_2–C m^{-2} h^{-1}; Fig. 4c). Between the first and last years, 2013 and 2015, there was a 13% decrease in CO_2 fluxes during the measured growing season. During the first drought, there was a decline in CO_2 fluxes. Short rewetting events occurred during the second and third droughts, which were related to an increase in CO_2 fluxes during the second drought and likely the cause of the plateau seen at the beginning of the


a.
Hyyytiälä SMEAR II
initial
D1
ND1
D2
ND2
D3
ND3
D4
ND4
D5
ND5
Precipitation (mm)
Air temp. (°C)
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
b.
Rosalia Lehrforst
initial
D1
ND1
D2
ND2
D3
ND3
Precipitation (mm)
Air temp. (°C)
2013
2014
2015
2016

◂ **Fig. 2** Open precipitation (mm) and air temperature (°C) at **a** Hyytiälä SMEAR II and **b** Lehrforst Rosalia. Orange, shaded periods indicate when the soil system was considered in a drought

third drought. Although, fluxes appeared more influenced by seasonal trends than by drought periods. Model results did not show a significant soil CO_2 flux trend between the initial period or any subsequent drought or non-drought periods (Table 4).

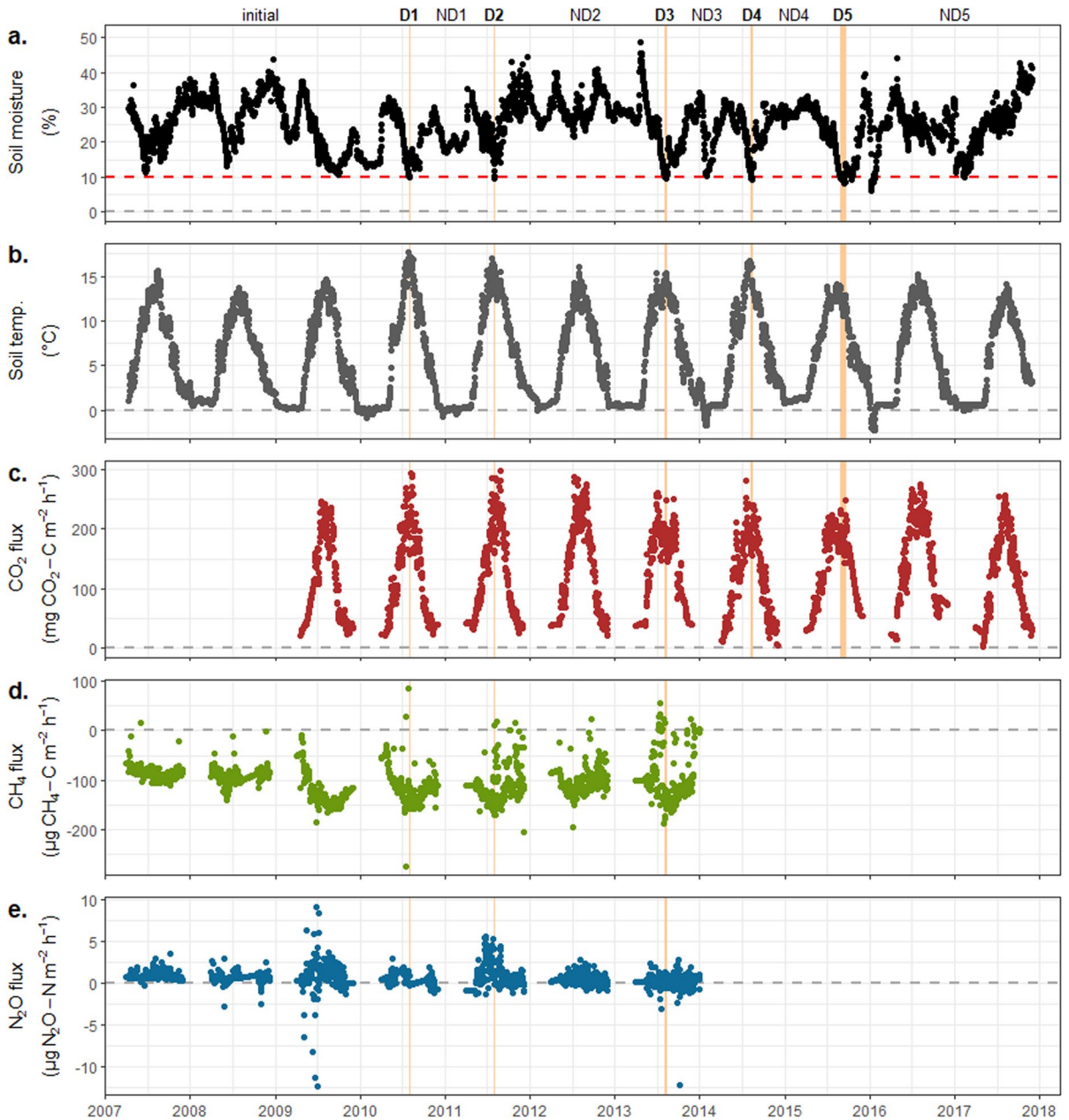


Fig. 3 Hyytiälä SMEAR II **a** CO_2 fluxes (mg CO_2–C m^{-2} h^{-1}), **b** CH_4 fluxes (µg CH_4–C m^{-2} h^{-1}), and **c** N_2O fluxes (µg N_2O–N m^{-2} h^{-1}) over time. Red data points indicate observations that were gap-filled using interpolation. Orange shaded periods indicate when the soil system was considered in a drought (winter 'droughts' were not considered here), and soil moisture status periods are labelled above (*D* drought period, *ND* non-drought period). The red, dashed line on the soil moisture figure indicates the soil moisture threshold

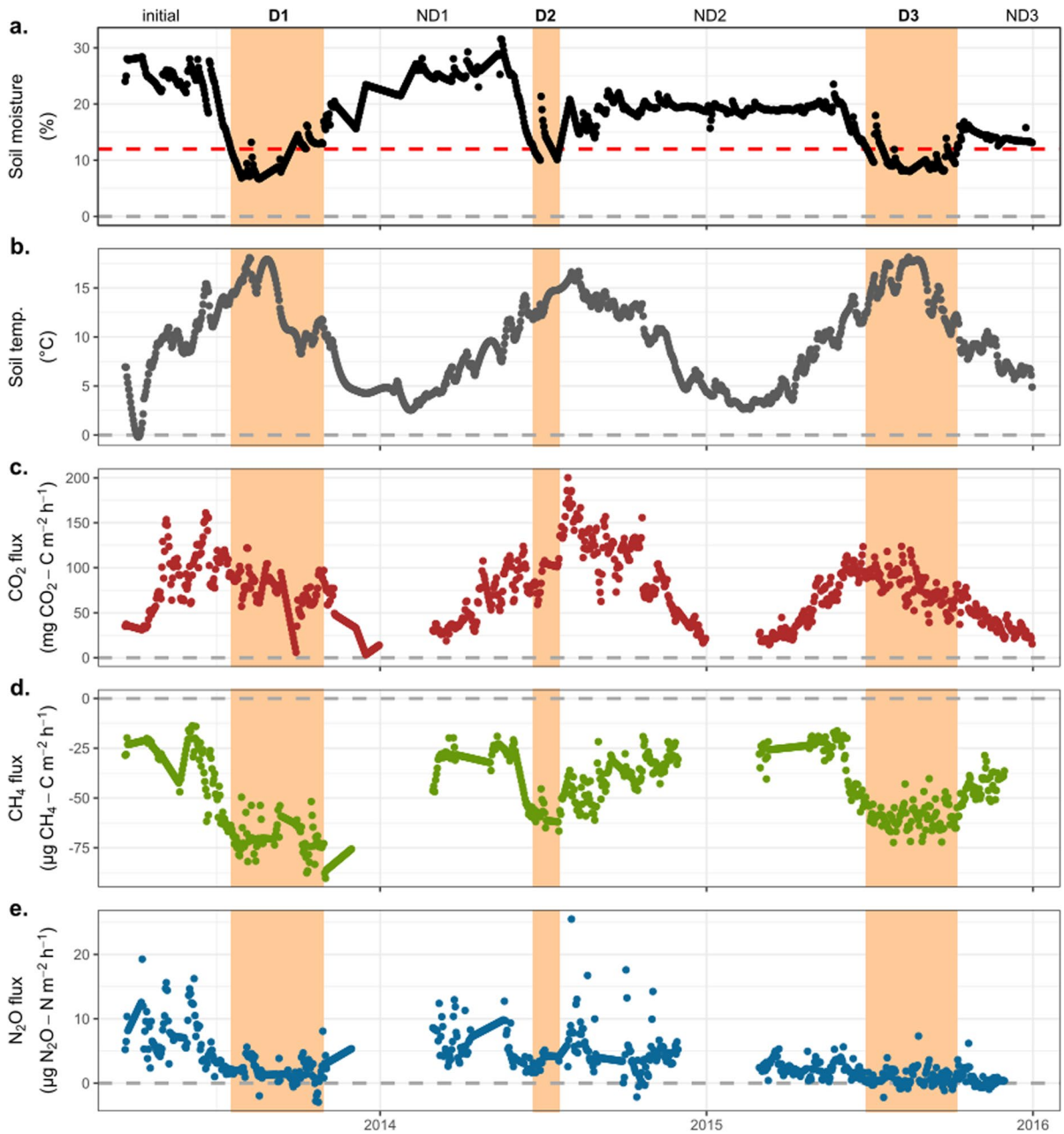


Fig. 4 Lehrforst Rosalia **a** CO_2 fluxes (mg CO_2–C m^{-2} h^{-1}), **b** CH_4 fluxes (µg CH_4–C m^{-2} h^{-1}), and **c** N_2O fluxes (µg N_2O–N m^{-2} h^{-1}) over time. Red data points indicate observations that were gap-filled using interpolation. Orange shaded periods indicate when the soil system was considered in a drought (winter 'droughts' were not considered here), and soil moisture status periods are labelled above (*D* drought period, *ND* non-drought period). The red, dashed line on the soil moisture figure indicates the soil moisture threshold

Overall, soils had a net uptake of 44.9 ± 18.3 µg CH_4–C m^{-2} h^{-1} during the measured growing season with a 33% increase in uptake between the initial and the last non-drought period (from 33.4 ± 13.9 to 44.7 ± 6.5 µg CH_4–C m^{-2} h^{-1} respectively) and a 20% decrease between the first and final years (53.8 ± 22.3

Table 2 Hyytiälä SMEAR II and Lehrforst Rosalia GAM results for soil moisture and soil temperature

Soil moisture content	edf	Ref.df	F	*p*-value		R-sq.(adj)
Hyytiälä SMEAR II						
s (Month)	2.07	6.00	0.92	0.03	*	0.11
s (Time)	1.00	1.00	0.21	0.64		
Soil temperature	edf	Ref.df	F	p-value		R-sq.(adj)
s (Month)	4.90	6.00	77.77	< 0.0001	***	0.83
s (Time)	7.78	7.78	18.12	< 0.0001	***	
Lehrforst Rosalia						
s (Month)	2.72	8.00	2.68	< 0.0001	***	0.60
s (Time)	2.00	2.00	162.78	< 0.0001	***	
Soil temperature	edf	Ref.df	F	p-value		R-sq.(adj)
s (Month)	4.37	8.00	18.08	< 0.0001	***	0.86
s (Time)	1.84	1.84	2.73	0.04	*	

The 's()' indicates the result of the variables included in the model with smoothing functions, which indicates the overall trend of the data over the entire, multi-year measurement period

The effective degrees of freedom (edf) represents the complexity of the smooth, a higher edf indicates more wiggly curves

Ref.df is the reference degrees of freedom

and 43.0 ± 16.1 μg CH_4–C m^{-2} h^{-1} in 2013 and 2015, respectively; Fig. 4d). The soil did not emit any CH_4 during the measurement period. CH_4 uptake was 38% higher during drought periods compared to non-drought periods (average 62.3 ± 5.1 μg CH_4–C m^{-2} h^{-1} vs. 45.2 ± 11.8 μg CH_4–C m^{-2} h^{-1}, respectively), with the increase starting before the drought period, i.e., before the soil moisture reached the permanent wilting point. Uptake decreased when the soil moisture content increased again. Model results showed significantly lower initial CH_4 uptake than most of the drought or non-drought periods (Table 4). The first drought and the last period (non-drought 3) were not significantly different from the initial period. The time smooth showed a significant change in CH_4 fluxes over the measured period.

Soils emitted an overall average of 3.8 ± 3.4 μg N_2O–N m^{-2} h^{-1} during the measured growing season with a decrease in emissions between the initial and last non-drought period (from 7.1 ± 3.7 to 0.7 ± 1.3 μg N_2O–N m^{-2} h^{-1}, respectively) and between the first and last years (4.6 ± 3.7 and 1.4 ± 1.4 μg CH_4–C m^{-2} h^{-1} in 2013 and 2015, respectively; Fig. 4e). The first and second droughts coincided with a decrease in N_2O emissions (average 1.8 ± 1.7 and 2.7 ± 0.6 μg N_2O–N m^{-2} h^{-1}, respectively), with an increase after the end of the drought. Fluxes were less affected by the third drought but were generally had lower emissions in year 3 likely due to the lower soil moisture. N_2O uptake occurred during the first and last drought periods as well as during the last non-drought period (average 1.3 ± 1.2, 0.5 ± 0.5, and 0.3 ± 0.3 μg N_2O–N m^{-2} h^{-1}, respectively). There appears to be a general decrease in emissions and an increase in uptake over time, but this is not supported by the GAM results (Table 4). There were no significant differences between N_2O fluxes during the initial period and any other period, and there was no significant time smooth effect.

Discussion

In this study, we explored the effects of drought events on soil GHG fluxes in two forests in two different climates: a boreal climate and a Pannonian climate. The boreal, coniferous forest site Hyytiälä SMEAR II has a lower mean annual precipitation

Table 3 Hyytiälä SMEAR II GAM results for CO_2, CH_4, and N_2O fluxes

Soil CO_2 flux	Estimate	Std. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	73.15	10.23	7.15	< 0.0001	***	0.92
Drought 1	− 0.39	9.45	− 0.04	0.97		
Non-drought 1	12.86	6.52	1.97	0.05	*	
Drought 2	20.3	12.35	1.65	0.10		
Non-drought 2	30.3	10.46	2.9	0.004	**	
Drought 3	6.11	14.38	0.43	0.67		
Non-drought 3	49.76	12.51	3.98	< 0.0001	***	
Drought 4	43.18	16.14	2.68	0.008	**	
Non-drought 4	55.1	15.55	3.54	0.0004	***	
Drought 5	95.59	17.86	5.35	< 0.0001	***	
Non-drought 5	97.97	17.67	5.55	< 0.0001	***	
	edf	Ref.df	F	*p*-value		
s (Month)	2.58	6.00	2.11	< 0.0001	***	
s (Time)	7.53	7.53	11.46	< 0.0001	***	
s (Soil temperature)	6.78	6.78	325.53	< 0.0001	***	
s (Soil moisture)	5.70	5.70	11.63	< 0.0001	***	
Soil CH_4 flux	Estimate	Sth. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	− 90.31	6.00	− 15.06	< 0.0001	***	0.38
Drought 1	− 19.52	21.98	− 0.89	0.37		
Non-drought 1	− 27.96	8.20	− 3.41	0.001	***	
Drought 2	− 33.12	21.05	− 1.57	0.11		
Non-drought 2	− 16.96	13.25	− 1.28	0.20		
Drought 3	− 57.49	22.13	− 2.60	0.01	**	
Non-drought 3	− 49.67	15.85	− 3.13	0.002	**	
	edf	Ref.df	F	*p*-value		
s (Month)	< 0.0001	6.00	0.00	0.89		
s (Time)	8.76	8.98	27.06	< 0.0001	***	
s (Soil temperature)	4.67	4.67	7.67	< 0.0001	***	
s (Soil moisture)	1.00	1.00	44.07	< 0.0001	***	
Soil N_2 O flux	Estimate	Sth. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	1.34	0.17	7.93	< 0.0001	***	0.16
Drought 1	− 0.97	0.96	− 1.01	0.31		
Non-drought 1	− 1.01	0.24	− 4.31	< 0.0001	***	
Drought 2	− 1.03	0.85	− 1.21	0.23		
Non-drought 2	− 1.71	0.37	− 4.57	< 0.0001	***	
Drought 3	− 1.06	0.89	− 1.19	0.24		
Non-drought 3	− 1.42	0.47	− 3.02	0.0003	**	
	edf	Ref.df	F	*p*-value		
s (Month)	1.03	6.00	0.38	0.08	.	
s (Time)	5.52	5.52	5.70	0.0002	***	
s (Soil temperature)	1.82	1.82	18.45	< 0.0001	***	
s (Soil moisture)	1.41	1.41	3.47	0.08	.	

The *p*-values and asterisks indicate significant difference as compared to the intercept, i.e. the initial period

The 's()' indicates the result of the variables included in the model with smoothing functions, which indicates the overall trend of the data over the entire, multi-year measurement period

The effective degrees of freedom (edf) represents the complexity of the smooth, a higher edf indicates more wiggly curves

Ref.df is the reference degrees of freedom

Table 4 Lehrforst Rosalia GAM results for CO_2, CH_4, and N_2O fluxes

Soil CO_2 flux	Estimate	Std. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	63.04	11.03	5.72	< 0.0001	***	0.78
Drought 1	− 12.51	6.59	− 1.9	0.06	.	
Non-drought 1	4.84	8.46	0.57	0.57		
Drought 2	3.76	12.54	0.3	0.76		
Non-drought 2	9.71	13.68	0.71	0.48		
Drought 3	14.33	23.04	0.62	0.53		
Non-drought 3	14.71	25.09	0.59	0.56		
	edf	Ref.df	F	*p*-value		
s (Month)	2.50	8.00	0.86	0.03	*	
s (Time)	1.00	1.00	1.89	0.17		
s (Soil temperature)	1.90	1.90	72.99	< 0.0001	***	
s (Soil moisture)	1.77	1.77	4.84	0.03	*	
Soil CH_4 flux	Estimate	Sth. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	− 34.13	5.87	− 5.82	0	***	0.82
Drought 1	− 0.1	3.9	− 0.03	0.98		
Non-drought 1	− 13.32	5.51	− 2.42	0.02	*	
Drought 2	− 22.98	7.16	− 3.21	0.001	**	
Non-drought 2	− 25.66	7.93	− 3.24	0.001	**	
Drought 3	− 44.1	14.18	− 3.11	0.002	**	
Non-drought 3	− 37.17	16.27	− 2.29	0.02	*	
	edf	Ref.df	F	*p*-value		
s (Month)	3.52	7.00	2.73	3.52	***	
s (Time)	2.92	2.92	14.48	2.92	***	
s (Soil temperature)	1.00	1.00	17.9	1.00	***	
s (Soil moisture)	1.00	1.00	16.42	1.00	***	
Soil N_2 O flux	Estimate	Sth. Error	*t*-value	*p*-value		R-sq.(adj)
(Intercept)	6.06	1.61	3.76	0.0002	***	0.71
Drought 1	0.19	1.03	0.18	0.85		
Non-drought 1	− 1.94	1.31	− 1.48	0.14		
Drought 2	− 1.40	1.96	− 0.71	0.48		
Non-drought 2	− 2.29	2.10	− 1.09	0.28		
Drought 3	− 4.73	3.57	− 1.33	0.18		
Non-drought 3	− 6.47	3.83	− 1.69	0.09	.	
	edf	Ref.df	F	*p*-value		
s (Month)	2.12	7.00	1.11	0.009	**	
s (Time)	1.00	1.00	1.33	0.25		
s (Soil temperature)	1.98	1.98	34.25	< 0.0001	***	
s (Soil moisture)	1.00	1.00	16.91	< 0.0001	***	

The *p*-values and asterisks indicate significant difference as compared to the intercept, i.e. the initial period

The 's()' indicates the result of the variables included in the model with smoothing functions, which indicates the overall trend of the data over the entire, multi-year measurement period

The effective degrees of freedom (edf) represents the complexity of the smooth, a higher edf indicates more wiggly curves

Ref.df is the reference degrees of freedom

than the Pannonian, broadleaf site Lehrforst Rosalia, however the latter is much more exposed to drought (Metzger et al. 2005).

The soil drought periods (i.e., when soil moisture content dropped below the soil moisture percent at the PWP), do not appear to coincide strongly with low precipitation but do appear to occur shortly after periods of high air temperature even after temperatures decline. Thus, the concept of soil drought surely is influenced by the amount of rain in a given time period, but also by the water losses (i.e. evapotranspiration, which is likely enhanced at high air temperature and high vapor pressure deficit). Indeed, meteorological droughts (rainfall deficit) do not necessarily propagate to agricultural droughts (soil moisture too low for adequate plant performance) (Fuentes et al. 2022) and lends support for our choice to use soil moisture as a drought indicator for the soil microbial community, whose activity greatly drives GHG fluxes, oppose to other drought indices (e.g., Palmer's Drought Severity Index). In Lehrforst Rosalia, soil drought duration was much longer and drought severity (soil moisture content below the soil moisture drought threshold) higher than in Hyytiälä SMEAR II. The measurement period at Hyytiälä SMEAR II allowed more soil drought events to be included in the analyses, and the drought events appear to occur more frequently, with longer durations, and with more severity as time progressed. Although our data are limited to one single site, they are contrary to the general decrease in drought observations in northern Europe but consistent with an increase in heat extremes observations and predictions (IPCC 2022).

Soil moisture did not significantly change over the nine-year measurement period in Hyytiälä SMEAR II, while soil temperature showed a small but significant increase. In contrast, soil moisture in Lehrforst Rosalia significantly decreased over the three-year measurement period along with an increase in soil temperature. These findings are in line with predictions that soil moisture drought is increasing more in central compared to northern Europe (Lehner et al. 2017; Grillakis 2019). For soil temperature, despite the known importance for microbial C and N cycling and thus climate change (Jansson and Hofmockel 2020), few global, continental-scale, or even regional-scale model trends and predictions are available outside regions with permafrost, which impedes our ability to compare our results to future predictions.

Soil CO_2 fluxes

CO_2 fluxes were significantly higher during all non-drought periods than the initial period, and fluxes increased in Hyytiälä SMEAR II from 2009 to 2017. These results partially support our first hypothesis predicting a significant decrease in CO_2 emissions after the first drought event but no difference or increased emissions subsequent droughts and supports our fourth hypothesis predicting significant increased CO_2 emissions over the entire, multiyear period. The fluxes from the first non-drought period were not lower than the initial period, but higher, which suggest that the microbial community is already drought adapted to some extent, due to the exposure to drought events that occurred preceding our study. The observed increasing CO_2 emissions could be in response to the increasing soil temperatures seen at this site, leading to improved conditions for microbial activity (Karhu et al. 2014). In other studies conducted at Hyytiälä SMEAR II in 2012 and in 2017–2018, soil CO_2 fluxes ranged from approximately 43 CO_2–C m^{-2} h^{-1} in winter to 324 CO_2–C m^{-2} h^{-1} in summer (Pumpanen et al. 2015; Ryhti et al. 2022), similar to what was measured here. However, soil moisture dropped lower on average in our study than in the study by Pumpanen et al. (2015), which could explain why the summer peaks measured in summer were lower in our study (average of 274.0 CO_2–C m^{-2} h^{-1}). In Lehrforst Rosalia, there was no significant difference between the initial period or subsequent periods, which supports our second hypothesis predicting that CO_2 fluxes emissions would not be significantly different after the first few droughts at Lehrforst Rosalia. There was also no significant difference over the entire, multiyear period, contrary to what we predicted in our forth hypothesis, i.e. a long-term increase in CO_2 emissions at the site. This was potentially due to the truncated measurement periods at the beginning and end of the study (initial and non-drought 3 periods), which did not permit a "full picture" comparison. Visual observation of the data and the overall temporal trend analysis (i.e., time smooth) suggests a possible ($p = 0.08$) decline in soil CO_2 fluxes with time. This might have been significant with a longer

measurement period and in correlation with the decreasing soil moisture, allowing more drought events to be included and enough time to observe significant shifts in soil microbial activity (Shaver et al. 2000). The small rewetting and subsequent rapid re-drying events that happened during the drought periods at Rosalia might have also alleviated some drought stress and reduced soil drought effects. The average soil CO_2 flux measured here (71.7 mg CO_2–C m^{-2} h^{-1}) was lower than the flux measured in the same stand but in different plots between July 2012 and February 2013 (128 mg CO_2–C m^{-2} h^{-1}; (Leitner et al. 2016). Differences are likely due to measurement periods covering different portions of the year (our study covering the vegetation period over multiple years and the other study covering periods outside the vegetation period over a couple of months), and varying environmental conditions (Ettema and Wardle 2002; Baldrian 2017), as well as due to different methods (smaller and manual chambers). The CO_2 fluxes measured at both sites include both heterotrophic and autotrophic respiration. Indeed, it has been found that autotrophic respiration was more sensitive to drought than heterotrophic respiration (Huang et al. 2018), but, with our study design, we are unable to confirm that the autotrophic community was in drought stress (ecosystem drought) during our defined droughts (topsoil drought).

Soil CH_4 fluxes

Fluxes of CH_4 from the Hyytiälä SMEAR II soil were initially all uptake, excluding a single observation. Over time, there was an increase in CH_4 emissions from the soil, but this coincided with an increase in uptake, which maintained a net soil CH_4 uptake and an uptake rate higher than initial levels. The non-significant change in soil moisture in combination with increasing soil temperature could have helped periodically create the anaerobic conditions required for methanogenesis, leading to increased CH_4 emissions (Serrano-Silva et al. 2014). Soil moisture was measured here (6 and 10 cm) in this study; thus, we can only speculate that anaerobic conditions were present somewhere at deeper layers, generating CH_4 that was only partially consumed by methanotrophs, so that still a fraction of it was effectively released into the atmosphere. A significant difference between initial and non-drought values was detected following the first and third droughts as well. No difference was detected following the second drought as compared to the initial period. These results partially reject our third hypothesis predicting CH_4 uptake to remain relatively stable. The significant difference following drought one and three, but not following drought two, was potentially due to the lower soil moisture following drought one and three, where the topsoil drying alleviates diffusion limitations for methanotrophs deeper in the soil. Visual observation and the time smooth support a net increase in CH_4 uptake at the site over time, which supports our fourth hypothesis. A similar previous soil flux study at Hyytiälä using automated closed chambers measured an annual average uptake of 112.3 μg CH_4–C m^{-2} h^{-1} in 2006 and 2007 (Skiba et al. 2009), which, when compared to the initial (98.2 μg CH_4–C m^{-2} h^{-1}) and final (106.0 μg CH_4–C m^{-2} h^{-1}) rates measured here, does not support a long-term increase in CH_4 uptake at Hyytiälä. The results of our study suggest an overall increasing CH_4 sink potential at Hyytiälä. Indeed, Hyytiälä had the largest CH_4 sink activity of all studied sites in the aforementioned study (Skiba et al. 2009), which included forest, grassland, arable land, and wetland sites. In Lehrforst Rosalia, CH_4 uptake markedly increased during the drought periods and remained higher during the first and second non-drought periods compared to the initial period. These results do not support our third hypothesis predicting stable CH_4 fluxes. In the case following the second and third droughts, the increase in uptake could have been due to the lower soil moisture, which allowed increased diffusion. The truncated initial and final measurement periods may have affected GAM results. Despite strongly increased CH_4 uptake during drought events in Rosalia, the overall, multiyear trend appears to show a decrease in uptake with time, which does not support our fourth hypothesis predicting increased CH_4 uptake. In another study in the same forest stand, an average CH_4 uptake of 40.0 μg CH_4–C m^{-2} h^{-1} was measured between July 2012 and February 2013 (Leitner et al. 2016), which is comparable to the range of the fluxes measured here (from 33.4 to 44.7 μg CH_4–C m^{-2} h^{-1} during the initial and final periods, respectively). Unlike in Hyytiälä SMEAR II, there were no occurrences of soil CH_4 emissions in Lehrforst Rosalia likely because of its location on a slope which limits water stagnation and thus anaerobic conditions.

Soil N_2O fluxes

Uptake of N_2O in Hyytiälä SMEAR II, like for CH_4 fluxes, showed changes in rates of soil uptake and emission. Fluxes were significantly lower in non-drought periods compared to the initial period, with stronger effects for each subsequent non-drought period, which only partially supports our first hypothesis predicting that N_2O emissions would decrease after the first soil drought event but would be the same or increase with subsequent droughts. This decrease could be due to the relatively low soil moistures following drought two and three. This consistent decreasing trend is supported by the time smooth results, and there is a notable decrease in emissions with an increase in uptake. These results reject our fourth hypothesis predicting increased N_2O emissions over the multiyear period measured. A similar study at Hyytiälä SMEAR II in 2002 to 2003 using static gas flux chambers measured a mean N_2O emission of 0.35 µg N_2O–N m^{-2} h^{-1} (Pihlatie et al. 2007), while the 2006–2007 gas flux study measured a subsequently higher average of 0.6 µg N_2O–N m^{-2} h^{-1} (Skiba et al. 2009). Both are lower than the initial rate measured in our study (0.8 µg N_2O–N m^{-2} h^{-1}), higher than the final rates (0.1 µg N_2O-N m^{-2} h^{-1}), and lower or equal to the overall average rate (0.6 µg N_2O–N m^{-2} h^{-1}). This suggests a variable but overall stable N_2O flux rate in Hyytiälä with a potential decline in flux rates and thus a potential N_2O sink as suggested both by Pihlatie et al. (2007) and Skiba et al. (2009). In Lehrforst Rosalia, although GAM results did not show any significant differences between periods or a general trend, visually there appears to be the same trend as in Hyytiälä SMEAR II, a decline in N_2O fluxes with decreased emissions and increased uptake over time. Indeed, initial Lehrforst Rosalia N_2O fluxes were much higher than initial rates in Hyytiälä (7.1 versus 0.8 µg N_2O–N m^{-2} h^{-1}, respectively), but declined to be more comparable by the end (0.6 versus 0.1 µg N_2O–N m^{-2} h^{-1}, respectively). The results from the Leitner et al. (2016) study, average N_2O fluxes 5.7 µg N_2O–N m^{-2} h^{-1} between July 2012 and February 2013, also suggest a decrease in N_2O fluxes when compared to the fluxes from the first and last years measured here (4.6 and 1.4 µg CH_4–C m^{-2} h^{-1} in 2013 and 2015, respectively). Decreased N_2O fluxes would be consistent with decreasing soil moisture levels (Schindlbacher and Zechmeister-Boltenstern 2004).

Conclusion

In this study, we sought to identify the effects of soil drought events on soil GHG fluxes and general temporal trends over a multiyear period at a boreal forest and a temperate forest site. CO_2 and N_2O emissions were more affected by drought and long-term trends at Hyytiälä with increased CO_2 emission and decreased N_2O emissions both following drought and over the entire measurement period. CH_4 uptake increased at both sites both during non-drought periods and as an overall, multiyear trend and was predominantly affected by soil moisture dynamics. Multiyear trends also suggest an increase in soil temperature in the boreal forest and a decrease in soil moisture in the temperate forest. An advantage of in situ observations is that they estimate the 'actual' net effects of climate change in realistic settings and include all interacting factors. Indeed, manipulative drought experiments have been found to underestimate drought effects compared to observational studies (Kröel-Dulay et al. 2022). However, in parallel, the inability to control all environmental factors impedes the disentanglement of potential drivers of observed trends. Indeed, here, it was not possible to clearly distinguish between changes caused by the drought events themselves or by indirect climate change effects, e.g., via on-going decreased soil moisture, increased soil temperatures, or variables not measured here such as increased atmospheric CO_2 levels or N deposition. At Hyytiälä SMEAR II, for example, differences between initial and non-drought periods were found for all three GHG, but these results appear to be part of a larger, general trend as opposed to a direct drought effect, notably for CH_4 and N_2O fluxes where there were measurements years before a drought event. At Lehrforst Rosalia, the limited 3-year measuring period hindered a larger view of temporal trends. Exploring additional environmental factors may have reduced the uncertainty about the underlying drivers for the significant temporal changes in soil CO_2, CH_4, and N_2O fluxes that we observed over the measured timeframes and increased chamber numbers, notably at Hyytiälä SMEAR II, would better cover spatial

heterogeneity. Furthermore, our work underlines the importance of long-term measurement networks such as eLTER to be able to detect, quantify, and understand changes of biogeochemical processes. We conclude, that both boreal and temperate forests are potentially important CH_4 sinks, and the sink strength of boreal forest might even increase in the future. Indeed, the increasing CH_4 sink strength of Hyytiälä could outweigh the warming effects of its N_2O emissions. Although, this may coincide with increased CO_2 emissions. These results help elucidate how GHG fluxes from forest habitats may shift as drought frequency and global temperatures increase. Future studies should include more chamber replication to better cover potential special heterogeneity, a wider range of habitat types, and longer time durations.

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Data availability Hyytiälä SMEAR II meteorological data is available in the Fairdata.fi database (DOI: https://doi.org/10.23729/62f7ad2c-7fe0-4f66-b0a4-8d57c80524ec; https://doi.org/10.23729/62f7ad2c-7fe0-4f66-b0a4-8d57c80524ec). Hyytiälä gas flux data is available in the B2SHARE database: CO_2 flux data (DOI: https://doi.org/10.23728/b2share.e027118ea22148ef92789e740116711e), and CH_4 and N_2O flux data (DOI: https://doi.org/10.23728/b2share.c911e3614658465eafde6b60d9bf88ef). Lehrforst Rosalia data is available in the B2SHARE database: meteorological data (DOI: https://doi.org/10.23728/b2share.681966be29a34f3ebc6015ac255ab143; https://b2share.eudat.eu/records/681966be29a34f3ebc6015ac255ab143), and gas flux data (DOI: https://doi.org/10.23728/b2share.3983fd5a8c574e12af21c4a8682bac88).

Declarations

Conflict of interest The authors declare no conflict of interest.

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