



Exploring temporal and spatial variation of nitrous oxide flux using several years of peatland forest automatic chamber data

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Abstract: The urgent need to mitigate climate change has evoked a broad interest in better understanding and
15 estimating nitrous oxide (N₂O) emissions from different ecosystems. Part of the uncertainty in N₂O emission
estimates still comes from an inadequate understanding of the temporal and small-scale spatial variability of N₂O
fluxes. Using 4.5 years of N₂O flux data collected in a drained peatland forest with six automated chambers, we
explored temporal and small-scale spatial variability of N₂O fluxes. A Random forest with conditional inference
trees was used to find immediate and time-lagged relationships between N₂O flux and environmental conditions
20 across seasons and years with different environmental conditions.

The temporal variation of N₂O flux was large, and the daily mean flux varied between –11 and 1760 μg
N₂O m⁻² h⁻¹. Three of the six measurement chambers had a maximum N₂O flux of less than 400 μg N₂O m⁻² h⁻¹,
while the fluxes in the other three chambers exceeded 1000 μg N₂O m⁻² h⁻¹. Spatial differences in the flux persisted
over time, and despite the high small-scale spatial variability, the temporal patterns of the fluxes were relatively
25 similar across the chambers. Soil moisture as well as air and soil surface temperature were the most important
variables in the random forest, with lagged soil moisture also considered important. N₂O flux responded to soil
wetting with a time lag of 1–7 days, but the length of the time lag varied spatially and between seasons indicating
interactions with other spatially and temporally variable environmental conditions.

The high temporal variation in N₂O flux was related to a) seasonally variable environmental conditions,
30 with the highest N₂O fluxes measured after summer dry-wet cycles and winter soil freezing, and b) to annually
variable seasonal weather conditions, which lead to high year-to-year variability in N₂O budget. Changes especially
in the frequency of summer precipitation events and in winter temperature and snow conditions may increase the
variability of annual N₂O emissions if the variability in summer and winter weather conditions increases due to
climate change.

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1. Introduction

Among the greenhouse gases, whose emissions contribute to climate change, one of the most potent is nitrous oxide (N₂O), with a global warming potential 260 times stronger than carbon dioxide (Myhre et al., 2013). A major part of the emissions of N₂O originates from soils (Butterbach-Bahl et al., 2013; Davidson and Kanter, 2014), and human impact through altered nitrogen (N) cycle, land use and climate change affect the soil N₂O emissions both in natural and managed ecosystems (Tian et al., 2018, 2020). The urgent need to mitigate climate change has evoked a broad interest in better understanding and estimating N₂O emissions of different ecosystems (Thompson et al., 2019; Shakoor et al., 2021). However, the accurate estimation of N₂O emissions has remained a challenge and emissions estimates continue to have relatively high uncertainties (Tian et al., 2018, 2020). A large part of the uncertainty in N₂O emission estimates comes from inadequate understanding of the temporal and small-scale spatial variability of N₂O fluxes (Sutton et al., 2007; Groffman et al., 2009; Kuzyakov and Blagodatskaya, 2015; Wang et al., 2020).

N₂O is formed in multiple processes, each favored by different soil conditions (Butterbach-Bahl et al., 2013). The main processes producing N₂O in soils are nitrification and denitrification (Bollmann and Conrad, 1998; Zhu et al., 2013; Hu et al., 2015). Nitrifying bacteria turn ammonium into nitrate in aerobic conditions. Nitrate produced in nitrification can further be reduced to nitric oxide, N₂O and gaseous nitrogen (N₂) in oxygen-limited or anaerobic conditions (Wrage et al., 2001; Zhu et al., 2013; Wrage-Mönnig et al., 2018), making oxygen content a key control of N₂O flux (Song et al., 2019). Oxygen limitation in soil and substrate availability for microbes is affected by soil water content, which makes N₂O production also sensitive to varying soil moisture conditions (Butterbach-Bahl et al., 2013). Along with soil moisture, substrate availability is widely affected by human actions, such as fertilization, nitrogen deposition and drainage of organic soils, which are all linked to increased N₂O fluxes (Pärn et al., 2018; Tian et al., 2020; Lin et al., 2022). Soil temperature regulates microbial activity in the soil, but it also shapes microbial community composition and affects N₂O production through, for example, frost, ice formation and thaw (Holtan-Hartwig et al., 2002; Risk et al., 2013; Wagner-Riddle et al., 2017).

Temporal variation of soil conditions and substrate availability can lead to a high temporal variation of N₂O flux within a year (Groffman et al., 2009; Kuzyakov and Blagodatskaya, 2015). Soil freeze-thaw and dry-wet cycles are examples of changes in soil conditions shown to shape seasonal variation in N₂O emissions (Risk et al., 2013; Congreves et al., 2018). High temporal variation has been shown to be typical for N₂O flux in several ecosystems (Luo et al., 2012; Molodovskaya et al., 2012; Anthony and Silver et al., 2021), but understanding related to the temporal variation of N₂O production is limited by sparse sampling intervals of manual flux measurements, lack of short-interval measurements and poor temporal coverage of data from all parts of the year (Barton et al., 2015; Grace et al., 2020). Since short periods of high N₂O fluxes can account for a substantial amount of the annual N₂O budget (Molodovskaya et al., 2012; Ju and Zhang, 2017; Anthony and Silver, 2021), capturing N₂O flux peaks and understanding the causes of temporal variation of N₂O flux are essential for estimating annual emissions accurately.

Similar to temporal variation, high spatial variation is common for N₂O flux (Groffman et al., 2009). Estimating N₂O emissions accurately requires integrating information about the temporal and spatial dynamics. Variation in N₂O flux occurs on multiple spatial scales, from large-scale variation between ecosystems to small-



scale variation within a few meters (Ojanen et al., 2010; Krichels and Yang, 2019). High N₂O fluxes are typically measured in ecosystems with high N availability, such as in agricultural fields and in drained organic soils where
75 fertilization and organic matter mineralization provide N supply for N₂O production (Maljanen et al., 2003; Reay et al., 2012; Leppelt et al., 2014; Pärn et al., 2018). Within an ecosystem, varying soil properties and conditions such as organic matter content, soil moisture or pH can create spatial variability in the N₂O fluxes (Jungkunst et al., 2012; Giltrap et al., 2014). Although the small-scale spatial variation of N₂O flux can be large and exceed the spatial variation between more distant parts of the same ecosystem (Yanai et al., 2003; Jungkunst et al., 2012; Giltrap et al.,
80 2014), the causes of small-scale spatial variability of N₂O are poorly known and little studied, especially with short-interval measurements. Several questions related, for example, to the persistence of spatial patterns over time and linkages between the spatial and temporal variation of N₂O flux are little understood.

Drained peatland forests are examples of ecosystems with relatively high N₂O fluxes and high spatio-temporal variation of those fluxes (Maljanen et al., 2003; Ojanen et al., 2010; Pärn et al., 2018). In Finland about 60
85 % of the original peatland area has been drained for forestry (Korhonen et al., 2021). The drainage has resulted in a lowered groundwater level and increased N availability from the decomposing peat, leading to increased N₂O fluxes, especially in nutrient-rich peatland forests with a low C:N ratio (Martikainen et al., 1993; Laine et al., 1996; Klemetsson et al., 2005). The focus of previous studies on peatland forest N₂O fluxes has been on understanding the large-scale spatial variation of N₂O fluxes between peatland forests (Klemetsson et al., 2005; Ojanen et al.,
90 2010; Minkinen et al., 2020) and reporting N₂O fluxes for the studied peatland forest sites in response to harvesting (Huttunen et al., 2003; Korhonen et al., 2019, 2020). The temporal variation of N₂O flux as well as its linkages to smaller-scale spatial variation of the flux are not well understood, and only one snapshot of short-interval N₂O measurements is available from drained boreal peatland forest (Pihlatie et al., 2010).

For the first time in boreal peatlands and non-agricultural boreal ecosystems, we use several years (2015–
95 2019) of automated chamber measured N₂O flux to gain a more comprehensive understanding of the spatio-temporal dynamics of N₂O flux. We investigate the characteristics of temporal and small-scale spatial variation in N₂O flux and link the temporal variation of N₂O flux to seasonally and annually variable environmental conditions including immediate and time-lagged responses. This is done to form a more comprehensive understanding about the spatio-temporal dynamics of N₂O flux and to decrease uncertainties in current and future N₂O emission estimates in boreal
100 peatland forests and beyond.

2. Materials and methods

2.1. Site description

The measurements were made in 2015–2019 in Lettosuo, a drained nutrient-rich peatland forest located in
105 southern Finland (60°38' N, 23°57' E). The annual mean temperature in the area is 5.2 °C, and the mean annual precipitation is 621 mm according to long-term weather record from the nearest automatic weather station (Jokioinen Ilmala, 1991–2020). The site was first drained in the 1930s and more intensively in 1969 to enhance tree growth. The site was fertilized with phosphorus and potassium after the later drainage. The relatively low C:N ratio reflects the fen history of the site (Table 1). Ditches were dug in 1969 about 1 m deep with 45 m spacing. Drainage



110 lowered the groundwater level, resulting in a transition to boreal-forest-like vegetation. The ground vegetation
consisted mainly of dwarf shrubs (*Vaccinium myrtillus*, *Vaccinium vitis-idaea*) and herbaceous plants (*Lysimachia*
europaea, *Dryopteris carthusiana*) with sedges (*Carex globularis*, *Eriophorum vaginatum*) and Sphagnum mosses
(*Sphagnum russowii*, *Sphagnum girgensohnii*) in patches. Before March 2016, the site was a mixed forest dominated
by Scots pine (*Pinus sylvestris*) as an overstory, while the understory consisted of mostly Norway spruce (*Picea*
115 *abies*). Both over and understory included a small number of Downy birch (*Betula pubescens*). In March 2016,
overstory pine trees were harvested (70 % of the total stem volume; Korhonen et al., 2020, 2023), but the
surroundings of the measurement chamber used in this study were harvested more lightly. The study plots continued
to have high coverage of spruce and birch after the overstorey pine trees were removed in the harvesting. The partial
harvesting did not affect N₂O fluxes according to the previous study from the site (Korhonen et al., 2020), and the
120 effect of the harvesting was left out of the focus of this study.

Table 1: Soil properties at the study site. Values represent general soil properties at the study site before forest harvesting was done. Data from Korhonen et al. (2019).

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Depth	Total-N (%)	Total-C (%)	C:N	Bulk density (g cm ⁻³)
Humus	1.7 ± 0.4	56.2 ± 2.3	33.2 ± 2.3	0.01 ± 0.003
0–10 cm	2.2 ± 0.2	55.2 ± 2.1	24.9 ± 2.1	0.12 ± 0.03
10–20 cm	2.5 ± 0.2	58.9 ± 1.6	23.8 ± 1.6	0.18 ± 0.02

2.2. Automatic chamber measurements

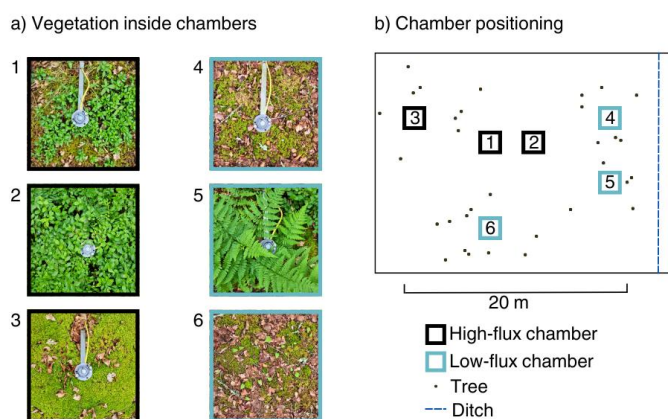
130 N₂O flux between the forest floor and atmosphere was measured with six automatically operating chambers. The
transparent, acrylic, rectangular cuboid chambers with the dimensions 57 x 57 x 40 cm (length x width x height)
were placed to sample the spatial variation of the ground vegetation composition and were located within an area of
15 x 20 m (Fig. 1). Distance to the closest ditch and trees also varied between chambers (Table S1). The chambers
were placed on permanently installed steel collars that were inserted into the soil to about 2 cm depth. All the
135 chambers closed automatically for six minutes once an hour year-round resulting in 6 x 24 flux measurements per
day. Chambers had temperature sensors measuring the headspace temperature and a fan to mix the air inside the
chamber headspace. N₂O concentration of the chamber headspace air was measured using a continuous-wave
quantum cascade laser absorption spectrometer (LGR-CW-QCL N₂O/CO-23d, Los Gatos Research Inc., Mountain
View, CA, USA) that was placed in the measurement cabin close to the chambers. The sample air was pumped into
140 the analyzer and back to the chamber headspace through plastic tubes (length 15 m). The same chamber
measurement system was used also in other studies covering N₂O, CO₂ and CH₄ fluxes of the same site (Koskinen et
al., 2014; Korhonen et al., 2017, 2020).

N₂O fluxes were calculated using a linear fit to the N₂O concentration change during the chamber closure.
Calculated fluxes were filtered using normalized root mean square error threshold and iterative standard deviation
145 filter to remove erroneous fluxes resulting from chamber malfunction. A more detailed description of the flux



calculation and filtering can be found in Korhonen et al., (2020). The fact that the fans were not adjusted according to the wind conditions likely created some diurnal cycle in the flux, as discussed previously for CO₂ and CH₄ fluxes at the same site (Koskinen et al., 2014; Korhonen et al., 2017). To minimize the possible effect of artificial diurnal variation in N₂O flux, daily mean fluxes were used in this study.

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Figure 1: a) Vegetation inside the six chambers and b) the positioning of the chambers on the forest floor in relation to the nearest ditch and trees. Chambers are named from one to six based on the maximum measured flux with Chamber 1 having the highest measured flux. Chambers 1–3 with black edges are classified as high-flux chambers and Chambers 4–6 with blue edges as low-flux chambers (Sect. 3.2).

2.3. Environmental variables

Several environmental variables were measured to link the temporal variation of N₂O fluxes with the environmental conditions. Air temperature was measured at 2 m height below the forest canopy (HMP45D, Vaisala Oyj, Vantaa, Finland). Soil surface temperature was measured at 2 cm depth in each chamber and the soil temperature at 5 cm depth at one location close to the chambers (Pt100, Nokeval Oy, Nokia, Finland). Soil moisture was measured at one location about 75 m from the chamber measurement location at 7 and 20 cm depths (Delta-T ML3, Delta-T Devices Ltd, Cambridge, UK). The soil moisture data were used to describe the temporal variation of soil moisture rather than the absolute level of soil moisture at the chamber location. We assumed that the measured soil moisture conditions represent the conditions near the chambers relatively well since the microtopography, surface vegetation and shading by the canopy were relatively similar in both locations.

Water table level (WTL) below the soil surface was measured hourly using automatic probes (TruTrack WT-HR, Intech Instruments Ltd, Auckland, New Zealand; Odyssey Capacitance Water Level Logger, Dataflow Systems Ltd, Christchurch, New Zealand) placed into dipwells that were installed into the ground. Chambers 1–2 and 3–4 shared a WTL sensor that was placed in between the two chambers, and Chambers 3 and 6 had their own WTL sensors next to the chamber collar. Since WTL measurements for Chambers 3, 4, 5 and 6 started in December 2015, WTL before that was modeled for each chamber using Random forest with conditional inference trees (Hothorn et al., 2006). Other WTL measurements near the automatic chambers, precipitation and soil moisture were used as explanatory variables in the models (evaluation data R² = 0.90–0.97).



175 Precipitation was measured at the site (Casella Tipping Bucket Rain Gauge, Casella Solutions Ltd,
Bedford, UK; OTT Pluvio2 L 400 RH, OTT Hydromet Ltd, Kempten, Germany) and daily cumulative precipitation
used. The precipitation data measured in the nearest weather station was used to gap-fill winters and other
measurement gaps in precipitation data measured at the site (correlation of precipitation between sites 0.65, $p <$
0.05). Snow depth was measured in the nearest weather station and used to describe general snow conditions
180 experienced each winter.

Thermal seasons were used to analyze the seasonality of N₂O fluxes. The thermal seasons were defined
according to typical Finnish standards (Ruosteenoja et al., 2011; Finnish Meteorological Institute, 2023), and by
using air temperature data of the site (Appendix A). During thermal winter, daily mean air temperature was
persistently below 0 °C, during summer above 10 °C and during thermal spring and autumn between 0 and 10 °C.
185 Seasons based on months are used to compare conditions measured at the site with seasonal long-term averages
reported for the nearest automatic weather station.

2.4. Identifying high-flux periods

The term high-flux period was used to describe periods of elevated flux, including periods from moderately
190 increased flux to the highest flux peaks. The term high-flux period was used instead of a commonly used hot
moment term because the definition of a hot moment largely varies between studies, with sometimes only extremely
high fluxes being considered as hot moments (Molodovskaya, 2012; Krichels et al., 2019; Anthony and Silver,
2021; Song et al., 2022).

To identify high-flux periods and to numerically describe the temporal patterns of N₂O fluxes, different
195 thresholds to separate high-flux days from the baseline days were tested. Finally, a common percentile threshold of
70 % was used in all chambers. High fluxes were measured less frequently compared to the more common low
fluxes, which made high-flux days distinct from the more common baseline days in flux histograms of all chambers
(Fig. S2). Any percentile threshold between 60–80 % separated high-flux days from the baseline relatively well, and
the mean of these (70 %) was used. The mean N₂O flux of the study period was close to the chosen 70 % percentile
200 threshold in all chambers. Days with the mean flux above the 70 % percentile were classified as high-flux days.

The length of each high-flux period was the number of days the flux remained above the 70 % percentile,
including possible data gaps within this period. The high-flux period was set to continue over the data gap if three
days before and after the data gap were classified as high-flux days. A three-day marginal was chosen to ensure that
short one-to-two-day peaks would not create long-lasting high-flux periods over the data gaps. If the high-flux
205 period started from a data gap or ended to it, the start or end date of the high-flux period was set to the first or last
measured day, respectively.

Pearson correlation was used to test correlation between N₂O flux time series of different chambers and
multiple linear regression was used to test if each environmental variable could explain differences in the flux
patterns between chambers. In the multiple linear regression, N₂O flux of each chamber was explained by flux of
210 one other chamber, and ability of each environmental variable to explain the remaining variance was tested one
environmental variable at the time.



2.5. Machine learning

Machine learning models were used to improve understanding of the temporal controls on N₂O flux, including a possible effect of time lags between environmental conditions and N₂O. Since the models were run separately for the six chambers, the models also allowed estimation of whether the temporal variation is controlled similarly in the different chambers. The machine learning approach was used because machine learning models do not rely on mathematical functions to describe relationships between variables and are able to account for interactions between variables without having to include them in the equation by hand (Olden et al., 2008). This is particularly useful when using a large dataset with multiple environmental variables to model N₂O fluxes whose controls and mathematical forms of responses are not yet fully understood.

The Random forest algorithm, developed by Breiman (2001), is a classification tree-based method that uses bootstrap aggregation of a model training data and a randomly chosen subset of explanatory variables (*mtry*) to train each classification tree. In bootstrap aggregation, a subset of data is taken from the model training data with or without returning it to the original training data. The part of data that is not bootstrapped to train trees is called out-of-bag (OOB). OOB data can be used to evaluate model performance since this part of the data is not used during the model training phase. In each Random forest tree, the bootstrapped data are classified into subgroups and further to smaller subgroups by setting threshold values for the randomly chosen subset of explanatory variables. The setting of the threshold values is done to maximize the information gain until no further thresholds, also called splits, can be made. After a selected number of trees are built, the final model prediction can be made using the average of all the trees (continuous response) or the most common outcome (categorical response).

Random forest variable importance (VI) metrics show the importance of each explanatory variable in explaining variation in the response variable. Variable importance metrics can be biased if the data type and scale of the explanatory variables vary or if there is a correlation between explanatory variables (Strobl et al., 2007). Therefore, we used Random forest with conditional inference trees (Hothorn 2006) that allowed us to get more accurate variable importance measures in the presence of correlated explanatory variables and their time-lagged versions. Compared to trees in Random forest, conditional inference trees use a p-value-based splitting criterion to classify the bootstrap aggregated data in the building phase of each tree. As suggested by Strobl et al. (2007), in the presence of correlated explanatory variables, variable importance metrics from the conditional inference trees were calculated using conditional permutation importance.

Chamber-specific models had N₂O flux as the response variable and the measured temperature variables (air, 2, 5 cm), soil moisture (7 and 20 cm), WTL and daily cumulative precipitation as explanatory variables. Time lags of 1–7 days were added as additional explanatory variables for all the explanatory variables. The imbalanced distribution of N₂O fluxes as model predictors were corrected with the SMOGN algorithm (Abd Elrahman and Abraham, 2013). The subset of data to train each tree was bootstrapped without replacement with a sample size 0.632 times the size of the training dataset, as suggested by Strobl (2007). Models were trained with 500 trees and Random forest default *mtry* for continuous response variable was used (*mtry* = number of explanatory variables / 3).



The first three years of data were utilized as the model training period (1 June 2015–1 June 2018), and this data were further split into 70 % training data and 30 % evaluation data to test model performance within the training period. The fourth year of measurements until soil moisture measurements ended (1 June 2018–4 April 2019) was left aside for evaluation to test model performance outside the training period. The prediction accuracy of the models in each evaluation data was analyzed using R squared (R^2) and root mean squared error (RMSE). Evaluation results are presented in appendices (Appendix B). Variable importance values were scaled between zero and one to enable comparison between chambers. The Accumulated local effects (ALE) method by Apley and Zhu (2020) was used to visualize the response of N_2O flux to environmental conditions and their lags.

2.6. Gap-filling and N_2O budgets

Data gaps covered 12–24 % of the study period depending on the chamber. Most gaps occurred at the same time in all chambers. Notable is that measurements in Chamber 6 ended six months earlier in 2019 than measurements in other chambers. N_2O flux time series were gap-filled to calculate N_2O budgets. In other analysis, gap-filled data were not used to avoid additional uncertainty of the results arising from the gap-filling.

Gap-filling was done by training the Random forest with conditional inference trees on the whole measurement period (4.5 years) data with 30 % data excluded for evaluation. The same explanatory variables were used in the models as in the analysis, including time-lagged variables. Evaluation results of gap-filling models are shown in Appendices (Appendix B). Gap-filled daily mean N_2O fluxes were used to calculate cumulative N_2O flux for each chamber in each thermal season and year. The uncertainties related to the N_2O budgets were assumed to be a combination of uncertainty related to flux measurement and uncertainty related to gap-filling. Detailed information about the calculation of the uncertainty can be found in Korhikoski et al. (2017).

Flux calculation was performed in the Python programming language version 2.7 (Van Rossum and Drake, 1995). Data preparation and analysis were performed in R statistical software version 1.4.1 (R core team, 2021). Cforest in the party package (Hothorn et al., 2006; Strobl et al., 2007; Zeileis et al., 2008) was used for Random forest with conditional inference trees.

3. Results

3.1. Environmental conditions

The seasonal temperature conditions were variable for the years 2015–2019 (Fig. 2). The summers (June, July, August) 2015 (14.1 °C) and 2017 (14.4 °C) were colder than the long-term average (15.6 °C), while winters (December, January, February) 2015–2016 (–3.4 °C), 2016–2017 (–3 °C) and 2018–2019 (–3.5 °C) were warmer than the long-term average (–4.3 °C) (Jokioinen Ilmala, 1991–2020). Temperatures in all seasons during the years 2018 and 2019 were warmer than the long-term average, with summer (17.2 °C) and autumn (6.7 °C) 2018 being especially warm (long-term average temperatures 15.6 °C and 5.4 °C, respectively).

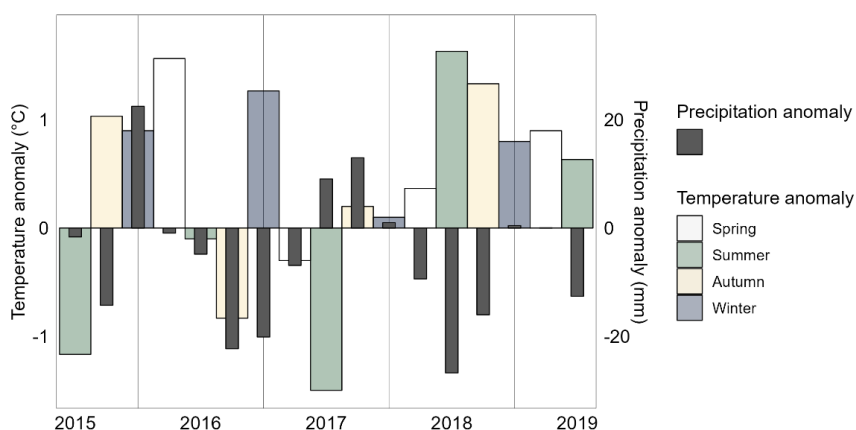
The area received the least amount of precipitation in 2018 (434 mm) and the most precipitation in 2017 (657 mm), when the long-term annual average was 621 mm. Winter 2015–2016 (67 mm) was wet, while autumn



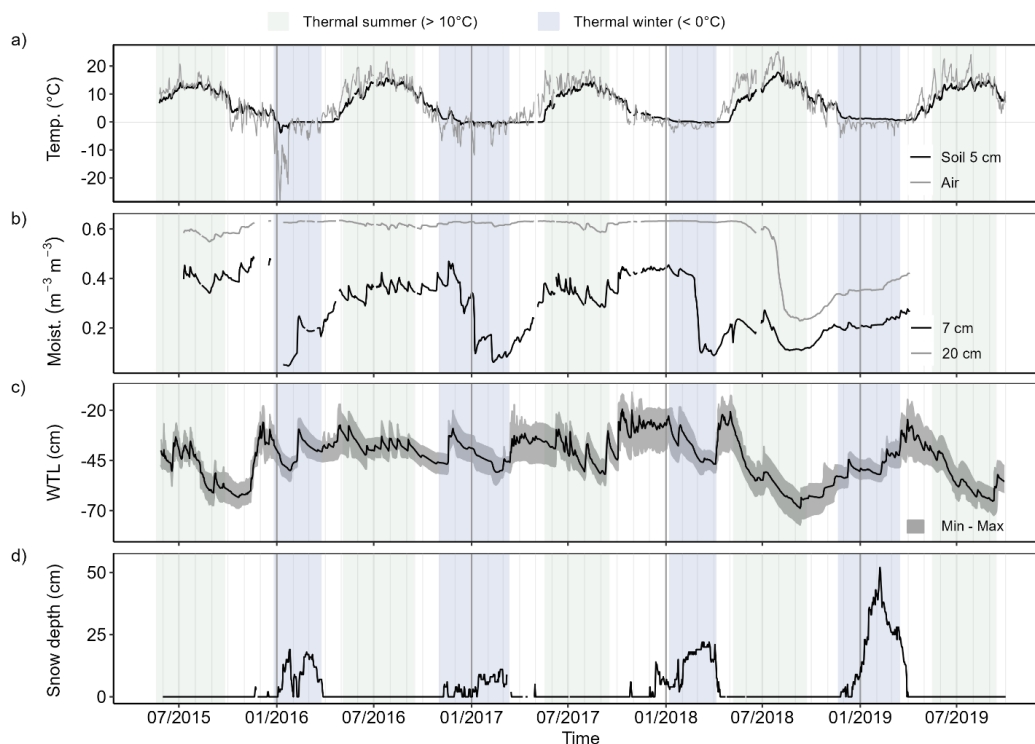
285 2016 (36 mm), winter 2016–2017 (24 mm) and summer 2018 (44 mm) were dry compared to the long-term averages (winter 44 mm, autumn 58 mm and summer 71 mm).

Soil conditions measured at the site varied between seasons and years (Fig. 3). Soil moisture at 7 cm was on average lower in winters ($0.26 \text{ m}^{-3} \text{ m}^{-3}$) and springs ($0.22 \text{ m}^{-3} \text{ m}^{-3}$) compared to summers ($0.31 \text{ m}^{-3} \text{ m}^{-3}$) and autumns ($0.33 \text{ m}^{-3} \text{ m}^{-3}$). Soil moistures at 7 cm and 20 cm were continuously lower than the means of the measurement period (0.28 and $0.56 \text{ m}^{-3} \text{ m}^{-3}$, respectively) from the summer 2018 until the end of the measurement period. WTL was deeper than the mean of the study period (-36 cm) in the summer and autumn 2015 as well as in the summers 2018 and 2019. Soil surface temperatures varied on average between $-0.6 \text{ }^\circ\text{C}$ in winter and $14.0 \text{ }^\circ\text{C}$ in summer with small differences in soil surface temperatures between chambers. Soil temperatures at 5 cm reached below zero temperatures in winters 2015–2016 (min $-3.8 \text{ }^\circ\text{C}$), 2016–2017 (min $-1.8 \text{ }^\circ\text{C}$) and 2017–2018 (min $-0.33 \text{ }^\circ\text{C}$) with most days with negative soil 5 cm temperatures in winters 2015–2016 and 2016–2017. Temporal variation in air and soil temperatures was greater in winters 2015–2016 and 2016–2017 compared to the latter two years of the measurement period. All winters had a period or periods of snow cover with the maximum measured snow depth being the greatest in winter 2018–2019 (52 cm) and the lowest in winter 2016–2017 (11 cm). Winters 2015–2016 (85 days) and 2016–2017 (93 days) had days with snow cover less than winters 2017–2018 (125 days) and 2018–2019 (116 days).

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305 **Figure 2: Seasonal temperature and precipitation anomalies during the measurement period. The seasonal mean air temperature and seasonal cumulative precipitation of each year is compared to the long-term seasonal averages at the nearest weather station (1991–2020). Seasons are based on months (autumn: September–November, winter: December–February, spring: March–May and summer: June–August).**



310 **Figure 3:** (a) Daily mean air and soil temperatures (5 cm depth), (b) soil moisture (7 and 20 cm depth), (c) water table level (WTL) and (d) snow depth. WTL is the mean of the values measured next to the different chambers with variation between the lowest and highest WTL indicated with shading. Snow depth was measured at the nearest weather station. Data are not gap-filled. For the definition of thermal winter and summer, see Sect. 2.3).

315 3.2. Temporal and spatial variation of N₂O flux

Daily mean N₂O flux varied between -10 and +1760 μg N₂O m⁻² h⁻¹ during the 4.5 years of measurements (Fig. 4), and chamber mean N₂O flux between +20 (Chamber 6) and +140 μg N₂O m⁻² h⁻¹ (Chamber 1) (Table 2). The annual mean flux was the highest in 2016 or 2017, depending on the chamber, and smallest in all chambers (Table S3.1). Mean fluxes in 2015 (June–December) were lower than in the whole years of 2016 and 2017 but higher than in 2018. Mean fluxes in 2019 (January–September) were generally higher than the mean fluxes in the whole year 2018.

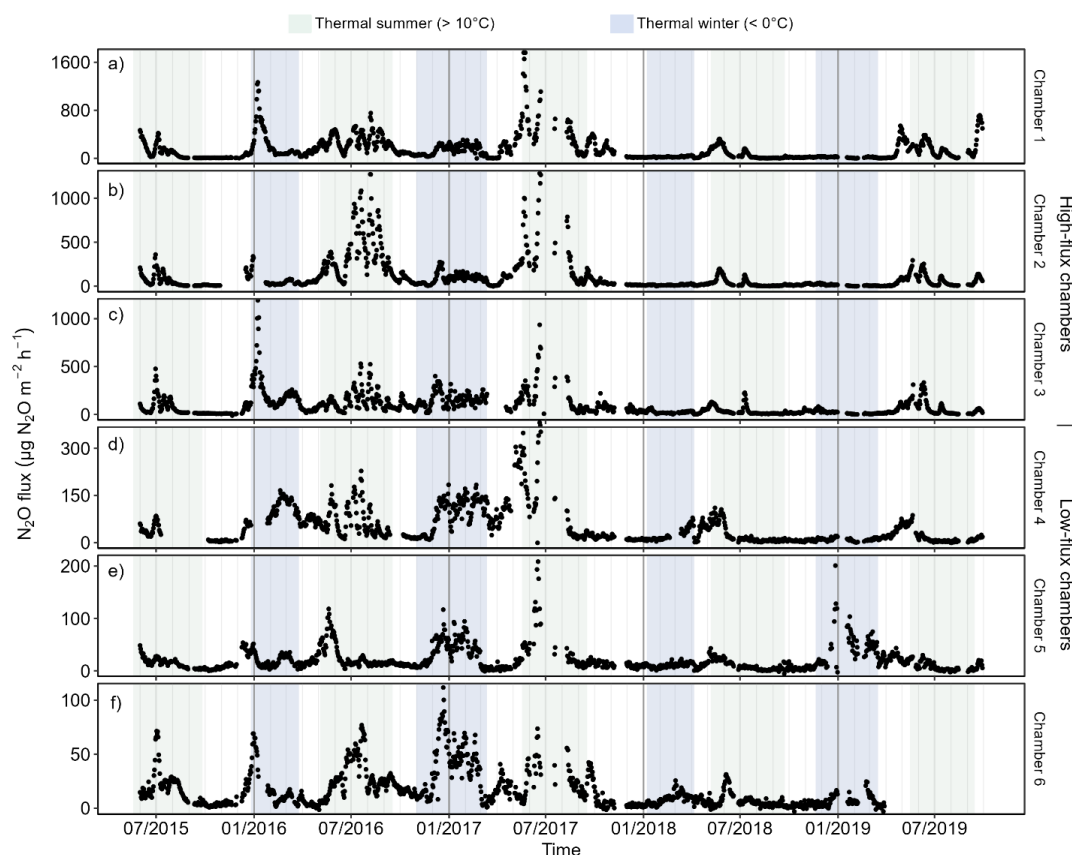
Three chambers (Chambers 1, 2 and 3) had maximum daily mean fluxes larger than 1100 μg N₂O m⁻² h⁻¹, while the other three chambers (Chambers 4, 5 and 6) had maximum daily fluxes smaller than 400 μg N₂O m⁻² h⁻¹. The mean and the range of the daily mean N₂O fluxes varied between years and chambers, but the high-flux chambers generally had a range and mean flux higher than the low-flux chambers in all years (Table S3.1). Differences in the mean and the range of the mean daily flux between high-flux and low-flux chambers were the largest in 2016 and 2017 and the smallest in 2018 and 2019. Based on the differences especially in the maximum



fluxes and in the range of the flux variation, Chambers 1–3 were classified as high-flux chambers and Chambers 4–6 as low-flux chambers.

330 Chamber-specific 70 % percentiles that were used to define high-flux periods from the baseline periods (Sect. 2.4) ranged from 20 to 170 $\mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$ (Table 2). The length of the individual baseline periods varied between 1 and 330 days with a mean of 26 days, while the length of the high-flux periods varied between 1 and 134 days with a mean of 11 days.

335 The correlations of the flux time series for each pair of chambers were positive and varied between 0.79 (Chambers 1 and 2) and 0.29 (Chambers 1 and 4) (Table S4.1). Correlations were the highest between the chambers with a similar range of N_2O flux: among high-flux chambers, correlations varied between 0.64–0.79 and among low-flux chambers, between 0.46–0.49. Soil surface and soil 5 cm temperatures explained the differences in N_2O fluxes between most chamber pairs statistically significantly (Fig. S4.2).



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Figure 4: Daily mean N_2O flux measured in the six automatic chambers in 2015–2019. Fluxes from different chambers are shown in panels (a–f) ordered by maximum daily mean N_2O flux. Chambers are grouped into low-flux (Chamber 1, 2 and 3) and high-flux chambers (Chamber 4, 5 and 6). The scale of the y-axis is chamber specific and fluxes are not gap-filled. Thermal winter refers to a period with daily mean air



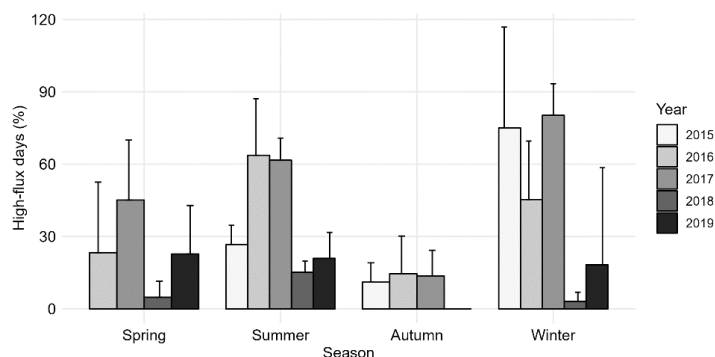
345 temperature persistently $< 0\text{ }^{\circ}\text{C}$ and thermal summer to a period with daily mean air temperature
 persistently $> 10\text{ }^{\circ}\text{C}$.

350 **Table 2: Minimum, maximum, mean, median, 70 % percentile and standard deviation of daily mean N_2O
 fluxes over 4.5 years for each chamber. Unit of the flux is $\mu\text{g N}_2\text{O m}^{-2}\text{ h}^{-1}$. Percentile thresholds (70 %) were
 used to define high-flux periods.**

Source	Min	Max	Mean	Median	Percentile 70 %	SD
Chamber 1	-1	1761	143	73	168	193
Chamber 2	-1	1282	99	34	88	171
Chamber 3	-12	1192	87	46	100	112
Chamber 4	-1	381	48	22	58	57
Chamber 5	-5	244	20	13	20	23
Chamber 6	-3	112	17	11	19	17

3.3. Seasonality of N_2O flux

The highest daily fluxes were measured during the thermal summers (Chambers 1, 2, 4 and 5) or winters
 355 (Chambers 3 and 6) depending on the chamber. The mean seasonal N_2O fluxes calculated for thermal seasons were
 also the highest for the thermal summers or winters throughout the study period. The mean N_2O flux was the
 smallest in autumn in all years and chambers. The percentage of measurement days identified as high-flux days was
 on average 24 % in spring, 38 % in summer and 44 % in winter, while the thermal autumns had 9 % days identified
 as high-flux days (Fig. 5). The proportion of high-flux days in each season varied between years with the highest
 360 proportions of winter high-flux days measured in 2015 and 2017, and the highest proportions of summer high-flux
 days measured in summers 2016 and 2017. Variation in the percentage of high-flux days between chambers was
 greatest for thermal winters.

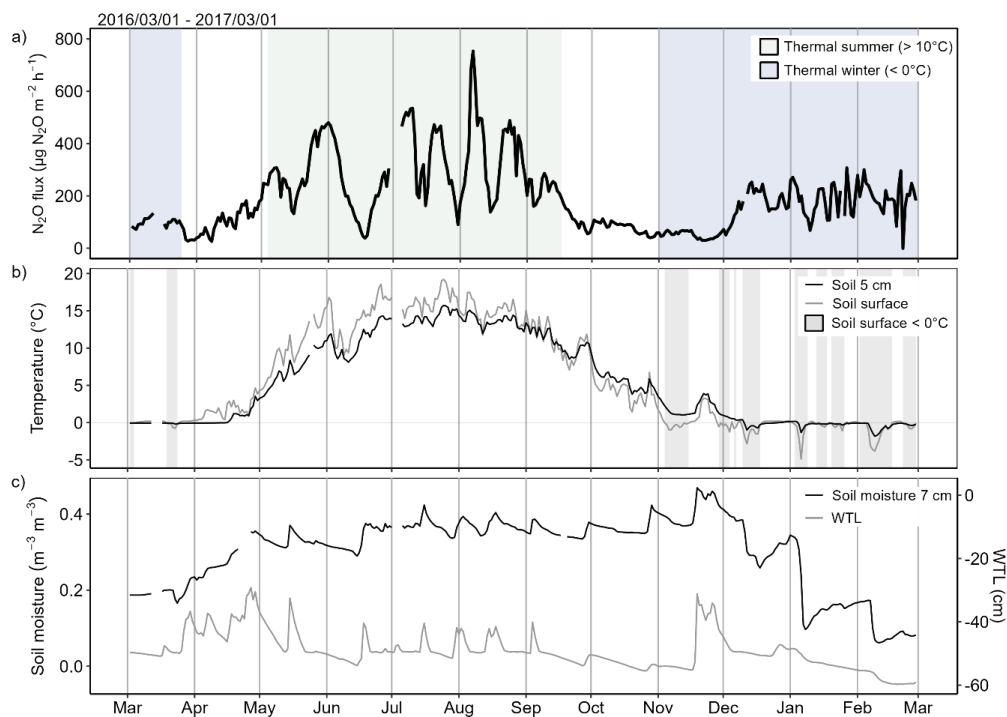


365 **Figure 5: Mean occurrence of high-flux days out of measured days in different thermal seasons and
 standard deviation between chambers.**

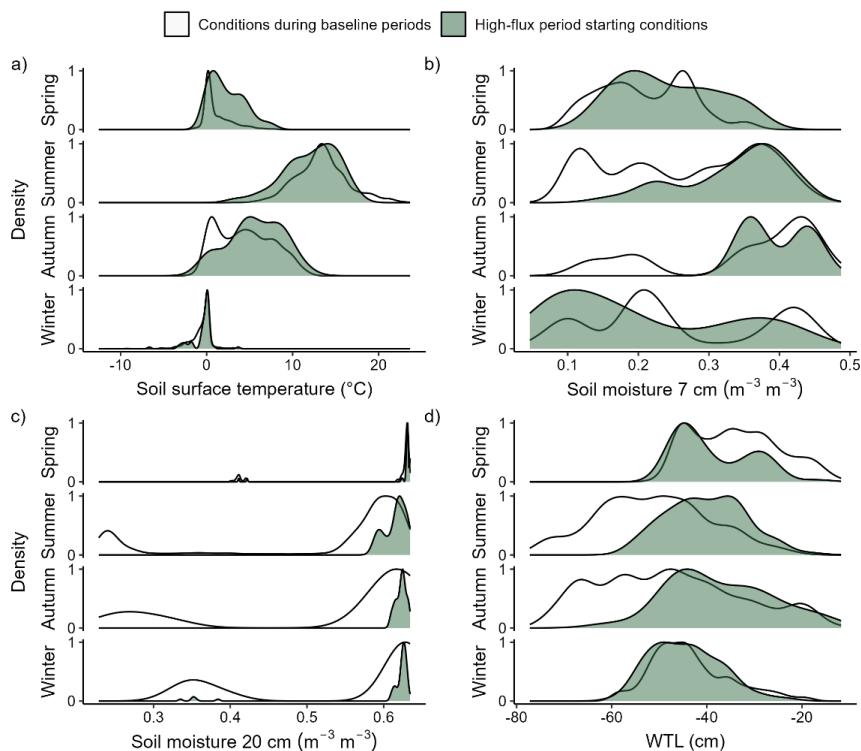


In spring, N₂O fluxes started to increase when soil surface temperature increased above zero (Fig. 6 and S5), with most of the spring high-flux periods starting at soil surface temperatures 0–2 °C (Fig. 7). Spring N₂O fluxes steadily increased with increasing soil temperatures, and flux peak top was reached in late spring or early summer. Increased summer N₂O fluxes were measured after peaks in soil moisture and WTL, the highest N₂O fluxes being reached typically several days after soil moisture and WTL peak. Most summer high-flux periods started when soil moisture at 7 cm was 0.37–0.41 m⁻³ m⁻³ and WTL between –35 and –50 cm. Autumn high-flux period starting conditions for soil moisture and WTL were similar to the summer, but increased N₂O fluxes were reached a longer period of time after soil moisture and WTL peak. Soil temperatures at the start of the high-flux periods were lower in autumn compared to summer.

In early winter, the N₂O fluxes increased when soil temperatures at the soil surface and 5 cm depth decreased close to zero and below that, with further increase in flux measured if soil temperature also at 5 cm depth decreased below zero (Fig. 6, 7, S5). After the initial freezing peak, early winter N₂O flux started to decrease after the soil temperatures increased close to or above zero. Later during the winter, increased N₂O fluxes were measured during periods of soil freezing or when soil temperatures increased close to or above zero after soil freezing. Freezing of the soil surface did not typically lead to high N₂O fluxes without temperatures being below zero also at 5 cm. An exception to that was Chamber 5 during winter 2018–2019, where high N₂O fluxes were measured during the mid-winter despite freezing temperature measured only at the surface soil. Temporal variation of N₂O fluxes within winter were also related to the temporal variation in soil surface and air temperature, with N₂O fluxes varying more in winters 2015–2016 and 2016–2017 with higher temporal variation in temperature compared to other winters.



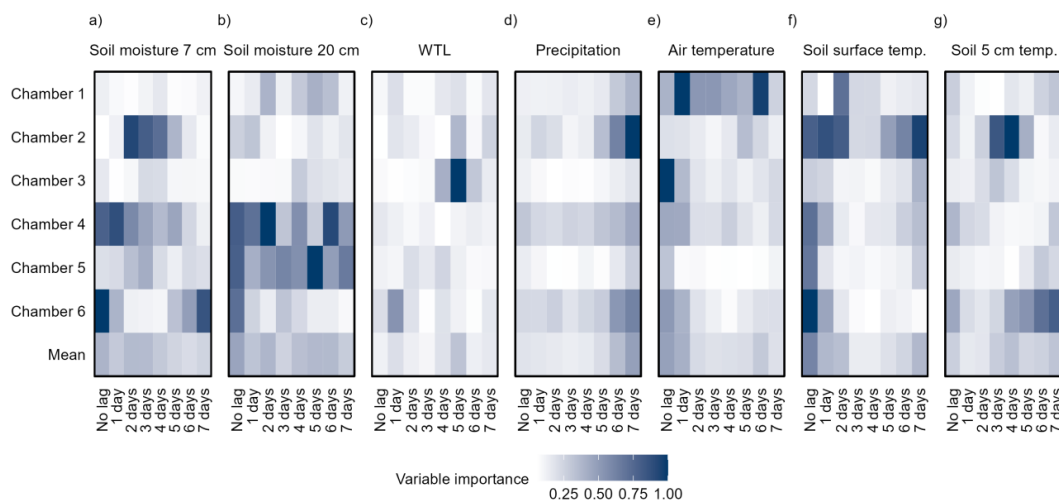
390 **Figure 6: a) Daily mean N₂O flux, b) soil surface temperature and temperature at 5 cm depth with**
highlighted freezing periods (soil surface temperature < 0°C), and c) soil moisture and water table level
(WTL) from February 2016 to March 2017 in Chamber 1. The temporal variation of N₂O flux in Chamber 1
was similar to other chambers, but the range of flux variation was larger compared to low-flux chambers.
The shown temporal dynamics of N₂O flux were measured in a year with relatively wet summer and warm
395 **winter. Data are not gap-filled. Figures for other chambers are presented in the supplements (S5).**



400 **Figure 7: Seasonal density distributions of high-flux periods starting in different a) soil surface temperatures, (b) soil moistures at 7 cm depth, (c) soil moistures at 20 cm depth, (d) and water table levels (WTL). Panels in each plot show density distribution for each thermal season. For comparison, the variation in soil conditions during baseline periods are also shown. All years and high-flux periods of all chambers are included. Density distribution values on y-axis are scaled (0–1).**

3.4. Modelling results

405 Unlagged soil moistures at 7 cm and 20 cm had mean variable importance (VI) scores 0.43 and 0.45 (respectively, 0 = lowest importance, 1 = highest importance) when VI scores were averaged across chambers (Fig. 8). Lagged (1–7 days) soil moisture variables received on average VI score of 0.31 (7 cm soil moisture) and 0.33 (20 cm soil moisture). The average VI score for unlagged air temperature was 0.45 and for soil surface temperature 0.24 and the variable importance generally decreased with increasing lag time. Unlagged soil temperature at 5 cm
410 received VI score of an average 0.27 and increased VI scores also for lagged variables with the mean across lags 0.25. VI scores for WTL were on average 0.04 with little importance for lagged WTL in most chambers. Precipitation received VI score of 0.06 and increasing importance with increasing lag time. The most important variable and the importance of their individual lags varied between chambers with either soil moisture, WTL or air temperature receiving the highest VI score. High-flux chambers received high VI scores also for lagged temperature
415 variables that were less important in low-flux chambers.

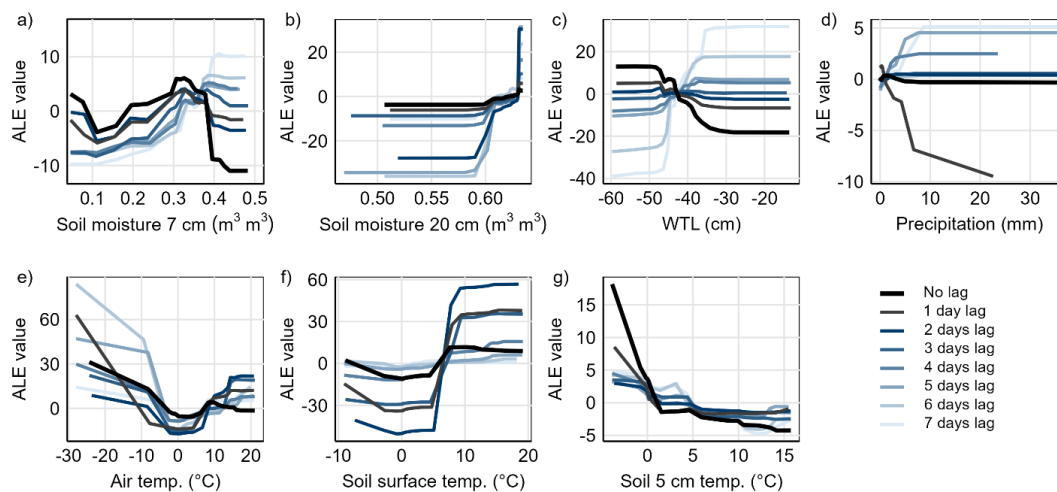


420 **Figure 8: Variable importance (VI) scores of different environmental variables and their lagged versions in explaining the temporal variation of N₂O.** The matrix plot shows VI values separately for different chambers (Chambers 1–6) as well as the mean VI across all the chambers (Mean). VI values are means across 10 runs of Random forest with conditional inference trees. VI scores are scaled between 0 and 1 (0 = lowest importance, 1 = highest importance) per chamber to make VI scores comparable across chambers.

425 ALE curves for unlagged 7 cm soil moisture showed the highest N₂O fluxes generally predicted on soil moisture values close to 0.3 m⁻³ m⁻³ or below 0.1 m⁻³ m⁻³ (Fig. 9 and S6). On moist conditions (> 0.3 m⁻³ m⁻³), the highest fluxes were predicted for lagged soil moisture. Predicted flux was typically the highest if soil moisture had been greater than 0.4 m⁻³ m⁻³ 3–7 days ago. On low 7 cm soil moistures (< 0.3 m⁻³ m⁻³), the highest N₂O fluxes were predicted for unlagged soil moisture with little differences between chambers. On high 20 cm soil moisture (> 0.6 m⁻³ m⁻³), predicted N₂O flux increased with increasing soil moisture in all chambers. Predicted flux on high 20 cm soil moisture was the highest for lagged soil moisture only in two chambers. For WTL, the predicted flux was the highest when WTL had been closer to the soil surface than –30 cm 3–7 days ago. The highest flux for unlagged WTL was typically predicted for WTL deeper than –50 cm. In all chambers, N₂O flux was predicted to be the highest for 4–7 days lagged precipitation if rainfall had been about 5 mm or more.

435 On temperatures above 5°C, the predicted N₂O fluxes increased with increasing air and soil surface temperatures with the highest predicted fluxes taking place when air and soil temperature exceeded 15 °C and 10 °C, respectively. Below about 0–2 °C temperatures, the predicted N₂O fluxes increased with decreasing air, soil surface and soil 5 cm temperature. In most chambers, increase in the predicted flux on soil 5 cm temperature at 0–2°C was especially strong with differences in the responses between immediate and lagged variables between chambers. Responses between lagged and unlagged soil surface and air temperature variables also varied between chambers.

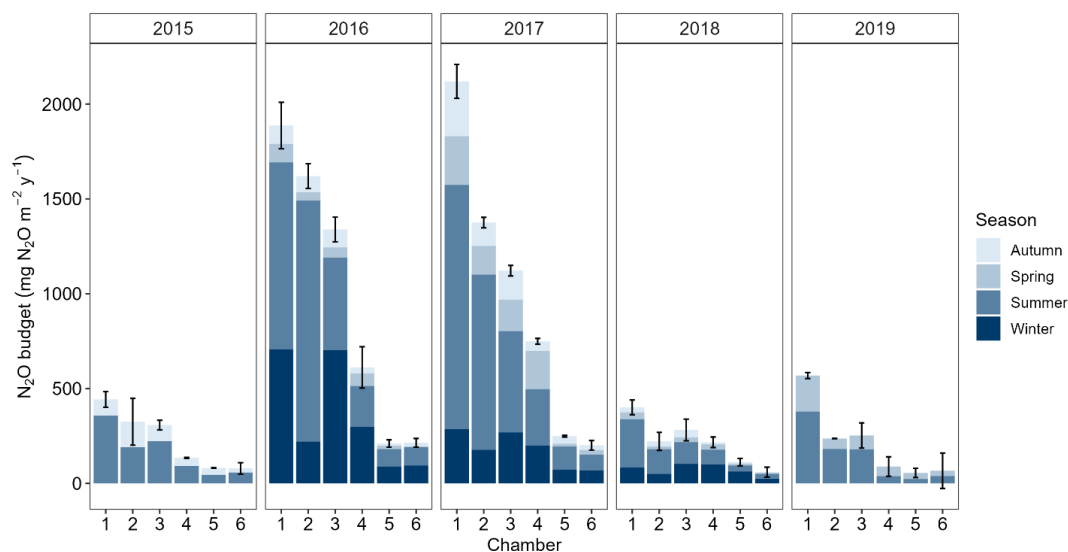
440



445 **Figure 9: Response curves between N₂O flux and environmental variables for Chamber 1 visualized using Accumulated Local Effects (ALE). Figures illustrate how the predicted N₂O flux values deviate from the mean predicted flux (ALE = 0) along the gradients of a) soil moisture at 7 cm depth, b) soil moisture at 20 cm depth, c) water table level (WTL), d) precipitation, e) air temperature, f) soil surface temperature and g) soil temperature at 5 cm. ALE responses for unlagged and lagged variables (1–7 days) are included. Lines represent the mean ALE values of 10 model runs. ALE responses for Chambers 2–6 are presented in supplements (S6).**

450 3.5. N₂O budgets

Annual N₂O budgets varied between 60 and 2110 mg N₂O m⁻² y⁻¹ when considering the three full measurement years 2016, 2017 and 2018 (Fig. 10, Tables S7). Annual N₂O budgets were higher than 1000 mg N₂O m⁻² y⁻¹ in high-flux chambers (Chambers 1–3) in 2016 and 2017, but less than 500 mg N₂O m⁻² y⁻¹ in all chambers in 2018. Winters and summers contributed generally the most to the annual N₂O budgets in all three years, with summers contributing on average 48 % and winters 34 % (Tables S7). The seasonal contributions to the annual N₂O budgets were, on average, 9 % for spring and autumn. Summer N₂O budgets in partially measured years 2015 and 2019 were smaller than in 2016 and 2017 but, especially in high-flux chambers, greater than in 2018.



460 **Figure 10: Annual N₂O budgets for each chamber and measurement year with seasonal contributions. Only**
461 **seasons that were completely within the measurement period (4.5 years) are included. The N₂O budget for**
462 **the year 2015 only includes summer and autumn, and the N₂O budget for the year 2019 only spring and**
463 **summer. Thermal seasons are used. Error bars denote total uncertainty related to the total N₂O budget of**
464 **the year.**

465

4. Discussion

4.1. Temporal variation of N₂O fluxes

The measured peatland forest N₂O fluxes were relatively high compared to N₂O fluxes from most of the other boreal and temperate forests on peat or mineral soils. The N₂O budgets of boreal peatland forests have mainly varied between -30 and 920 mg N₂O m⁻² y⁻¹ (Alm et al., 1999; Arnold et al., 2005; Minkinen et al., 2020; Butlers et al., 2023). The N₂O budgets of temperate mineral soil forests have varied within a similar range (Papen and Butterbach-Bahl, 1999; Luo et al., 2012). While the annual N₂O budgets in the present study were below 500 mg N₂O m⁻² y⁻¹ in 2018 in all measurement chambers, the annual N₂O budgets for three of the chambers exceeded 1000 mg N₂O m⁻² y⁻¹ in two years (2016 and 2017) out of the three full measurement years (Fig. 10). Similarly high or higher fluxes have been previously measured in peatland forest after clear-felling of the trees with especially logging residues linked with increased N₂O fluxes (Mäkiranta et al., 2012; Korhonen et al., 2019).

Nutrient-rich peat with relatively low C:N ratio likely explains high N₂O budgets of the study site. Low C:N ratio may have also increased sensitivity of N₂O fluxes to temporal variation in soil conditions (Klemetsson et al., 2005; Pihlatie et al., 2010; Hu et al., 2015). Although the partial harvesting done at the site in spring 2016 did not increase N₂O budget of the harvested area compared to the control site according to Korhonen et al., (2020), the effect of harvesting on N₂O fluxes of individual chambers cannot be completely excluded. Since N₂O budgets increased after harvesting both in harvested site and in the control (see Korhonen et al., 2020), most of the

480



increase in N₂O budgets in the years 2016 and 2017 is likely explained by year-to-year variation in environmental conditions.

485 Considering nutrient-rich soil and the tendency for high temporal variation of N₂O flux in several
ecosystems (Maljanen et al., 2010; Luo et al., 2012; Molodovskaya et al., 2012; Anthony and Silver, 2021), the
complex temporal dynamics of N₂O fluxes within and between years were expected. The high-flux period starting
conditions and modelling results support previous evidence on the importance of freeze-thaw and dry-wet cycles
strongly impacting temporal variation of N₂O fluxes (Butterbach-Bahl et al., 2013; Risk et al., 2013; Wagner-Riddle
490 et al., 2017; Congreves et al., 2018). However, when comparing the temporal dynamics of N₂O flux with those
previously published from boreal and temperate regions (Maljanen et al., 2010; Pihlatie et al., 2010; Luo et al.,
2012; Molodovskaya et al., 2012; Anthony and Silver, 2021; Gerin et al., 2023), the present data underline the
importance of summer and winter N₂O fluxes contributing to the annual N₂O budget more than fluxes in spring.
Previously, several studies on both peat and mineral soils have emphasized the importance of spring N₂O fluxes in
495 the annual N₂O budget, with distinct spring N₂O peaks in some cases accounting for a large fraction of the annual
budget (Pihlatie et al., 2010; Luo et al., 2012; Wang et al., 2023). In the present study, only moderately high N₂O
flux peaks were measured in spring and early spring N₂O peaks were not typical. Year-to-year variation in N₂O
budgets was more attributed to variation in winter and summer N₂O fluxes than variation in spring N₂O fluxes.

During winters with discontinuous and shallow snow cover combined with high temporal variation in air
500 temperature below and above zero (2015–2016 and 2016–2017), the N₂O fluxes were higher compared to the
snowier winters with more stable temperature conditions (2017–2018 and 2018–2019). The insulating properties of
the thicker snowpack may have prevented the soil from freezing to deeper depth, decreasing N₂O fluxes during
winter (Maljanen et al., 2009; Ruan and Robertson, 2017). Thicker snowpack combined with less variable air
temperature conditions in the last two winters of the study period have likely decreased the number of freeze-thaw
505 cycles and decreased intensity of them leading to smaller total N₂O flux during winter.

High-flux periods, especially during summers were linked with precipitation events that increased soil
moisture and WTL. These high-flux events increased the total N₂O budget of the rainy summers (2016 and 2017),
while N₂O budget in dry summer (2018) was low. Precipitation events may have increased the number of anoxic
microsites in the soil favoring N₂O production also through denitrification (Congreves et al., 2019; Song et al.,
510 2022). Active peat decomposition in the warm soil during the summer has likely also decreased oxygen availability
in the soil and increased N availability from the mineralizing peat leading to high N₂O emissions after summer rain
events (Maljanen et al., 2003). Low surface soil moisture has likely limited N₂O production during drought, leading
to small N₂O budgets in dry summer (Borken and Matzner, 2009; Congreves et al., 2018; Harry et al., 2021).

Autumn and spring N₂O fluxes varied relatively little between years with different weather conditions,
515 indicating weaker sensitivity of spring and autumn N₂O fluxes to seasonal weather conditions. N₂O fluxes during
autumn have been low also in part of the previous studies (Maljanen et al., 2003; Luo et al., 2012), but Pihlatie et al.
(2007) and Alm et al. (1999) found increased autumn N₂O fluxes after litter fall in drained peatland forest sites. Site-
specific differences could alter contributions of different seasons to annual N₂O budgets and affect sensitivity of
N₂O budgets to differing conditions in different seasons.



520 As the climate changes, the typical weather conditions for each season are predicted to change. In northern
latitudes, winters are expected to become warmer and wetter, and summer droughts are expected to become more
frequent (Zhao and Dai, 2017; IPCC, 2021). The high year-to-year variability in N₂O fluxes, which was largely
attributed to variation in summer and winter weather conditions, may imply changes and increased variability in
annual N₂O budgets if weather patterns of these seasons change and the frequency of extreme weather events
525 increases due to climate change.

4.2. Linkages to spatial variation

Capturing temporal patterns of N₂O fluxes from six chambers allowed us to explore the linkages between
the spatial and temporal patterns of N₂O fluxes across different measurement years. Lower N₂O fluxes from three of
530 the chambers compared to high N₂O fluxes measured in the other three chambers demonstrate the often spatially
variable nature of N₂O even on a small scale within a few tens of meters (Groffman et al., 2009; Hénault et al.,
2012; Jungkunst et al., 2012).

What was notable was that the spatial differences in N₂O fluxes between chambers were persistent across
different years. The mean and the maximum daily mean fluxes were consistently larger for the high-flux chambers
535 (Chambers 1–3), although differences between chambers were smaller during the low-flux year 2018 due to a larger
decrease in N₂O fluxes in high-flux chambers compared to low-flux chambers. Despite large temporal variations in
flux within and between years, the spatial patterns of N₂O flux remained throughout the measurement period.

The persistence of spatial variation implies that spatial variation of N₂O flux is controlled by long-term
controls that persist throughout years with different weather conditions. The long-term controls could include, for
540 example, spatial variation in soil properties (e.g. pH, porosity, C and N content) or placement of plant roots that
have both been suggested to affect the spatial variation of N₂O fluxes even on a very small scale within the soil
(Butterbach-Bahl et al., 2002; Jungkunst et al., 2012; Kuzyakov and Blagodatskaya, 2015). However, it must be
noted that results regarding the causes of within-site spatial variation have been highly variable between different
studies, and few studies have managed to explain spatial variation well (Ball et al., 2000; Butterbach-Bahl et al.,
545 2002; Yanai et al., 2003; Giles et al., 2012; Jungkunst et al., 2012). The linkages between soil properties, vegetation
and N₂O fluxes are complex, with interactions making the relations between the N₂O flux and soil system difficult to
understand.

In the present study, the high-flux chambers had fewer trees near them than low-flux chambers, and the
distance to nearby trees was shorter in low-flux chambers (Fig. 1, Table S1). This could indicate the importance of
550 trees shaping the spatial patterns of peatland forest floor N₂O fluxes, similar as suggested by Butterbach-Bahl et al.
(2002) in mineral soil forest. Trees may have impacted the availability of nitrogen through nitrogen uptake and
nitrogen inputs to soil above and below ground (Kaiser et al., 2011; Kuzyakov and Blagodatskaya, 2015; Hu et al.,
2016). Since trees also affect the forest microclimate and soil conditions by shading and affecting transpiration and
distribution of rain fall in forest (Butterbach-Bahl et al., 2002; Aalto et al., 2022), variation in tree cover could have
555 contributed to the spatio-temporal dynamics of peatland forest N₂O fluxes.



Although the chambers had persistently different levels of the N₂O flux throughout the study period, the chambers had clear similarities in the temporal dynamics of the N₂O flux (Fig. 4). High-flux and baseline flux periods identified for each chamber occurred often at the same time. N₂O flux time series, especially among high-flux and small-flux chamber groups, also correlated, implying shared temporal patterns but stronger similarities between chambers with a more similar flux level. Similarities in the temporal flux patterns between the chambers indicate that the changes in the soil environmental conditions affect N₂O fluxes relatively similarly despite the large spatial variation in flux.

Previous studies using manual chambers in agricultural settings with more variable soil conditions have found partly opposing results. Temporal patterns have been either variable or shared across space (Velthof et al., 2000; Krichels et al., 2019), with both findings mainly attributed to the spatio-temporal variation of soil moisture conditions. Soil moisture data from the individual chambers were not available here, but the chambers seemingly reached soil conditions triggering N₂O production at similar times, although the resulting N₂O flux level varied between chambers. In the presence of more topographical variation as in the study by Krichels et al. (2019), spatial variation in soil conditions could have led to more variable temporal patterns in N₂O flux across space if triggering conditions of N₂O production were reached at different times in different parts of the area. In the present study area, the factors causing the high and temporally persistent spatial variation in flux have not affected the way fluxes respond to temporal variation in soil conditions leading to similarities in temporal dynamics of the flux.

Differences in the temporal patterns between the high-flux and low-flux chambers were mainly related to the length and relative height of the high-flux periods as well as to the exact timing of the peak top within the high-flux periods. This has likely decreased the correlation of the temporal flux patterns between high-flux chambers and low-flux chambers. Since soil temperature variables were able to explain differences in temporal patterns of N₂O flux between most chamber pairs, N₂O peak length, timing, and relative height of flux peaks could be further shaped by spatial differences in the magnitude by which N₂O fluxes respond to temperature conditions.

4.3. Freeze-thaw cycles

Increased winter N₂O fluxes occurred in different phases of freeze-thaw cycles; during the onset of freezing periods, during repeated freeze-thaw events in the middle of the winter and during or after thawing in late winter and spring. Increased N₂O fluxes in different phases of freeze-thaw periods can be seen, for example, in winter 2016–2017 (Fig. 6), with increased N₂O fluxes measured during the early winter freezing as well as during and after part of the short freezing periods later in winter and spring.

Previous results about the timing of increased N₂O fluxes regarding freeze-thaw cycles have been variable. Some studies report increased N₂O fluxes during the freezing period (Papen and Butterbach-Bahl, 1999; Teepe et al., 2001; Maljanen et al., 2009, 2010; Ruan and Roberston, 2017), while part of the studies report high fluxes mainly during and after the thawing (Koponen and Martikainen, 2004; Pihlatie et al., 2010; Luo et al., 2012; Molodovskaya et al., 2012). Although here, the spring thaw resulted in a steady increase in N₂O flux, with peak N₂O flux reached later in spring or early summer, short-term N₂O flux peak during soil melting was not observed. High



variability in the temporal patterns of winter and spring N₂O flux in different studies highlights the need to understand the causes of site-specific differences that create variable winter N₂O flux patterns.

595 The highest winter N₂O fluxes typically occurred in the early winter soon after the soil freezing at the time when frost reached 5 cm depth (Fig. 6 and 7, S5). Winter high-flux periods with peak N₂O fluxes clearly elevated from the baseline flux level were generally only measured during winters when soil frost reached 5 cm depth several times (winters 2015–2016 and 2016–2017) and only during freeze-thaw cycles occurring at 5 cm depth (late winter 2016–2017). The importance of deeper soil freezing rather than freezing only of the soil surface may indicate that the winter N₂O fluxes during freezing may have originated from the freezing peat rather than from the freezing litter
600 at the surface of the soil. The importance of the severity of ground frost and frost depth affecting N₂O fluxes has also been suggested by others (Nielsen et al., 2001; Koponen and Martikainen, 2004; Luo et al., 2012). The conclusion about the possible source of winter N₂O fluxes in the topsoil peat rather than in the soil surface litter differs from the results of Pihlatie et al. (2010) in a nutrient-poor peatland forest site. More nutrient-rich peat with a low C:N ratio may have favored N₂O production in peat (Regina et al., 1998; Ojanen et al., 2010). Higher nitrogen
605 availability in peat may have enabled a stronger link between winter N₂O fluxes and conditions experienced in the peat. Site-specific differences in nutrient availability in different parts of the soil may affect the sensitivity of winter N₂O fluxes to frost depth.

4.4 Delayed responses and interactions

610 The results of this study indicate general importance of lagged soil moisture and WTL conditions affecting N₂O fluxes on the short time scale of 1–7 days. Peak N₂O fluxes were reached sometimes several days after the highest surface soil moisture and WTL values were measured (Fig. 9, S6). Studies mostly from mineral soils have found no lags or lags of a few hours between the soil moisture peak and the highest N₂O fluxes, while others have found lags of a maximum of two days (Firestone and Tiedje, 1979; Smith and Tiedje, 1979; Song et al., 2022). In
615 this study, the lag time between surface soil moisture peak and the peak N₂O fluxes was typically at least two days, with indications for longer lags than seven days in some chambers. Long delays between the soil moisture peak and peak N₂O fluxes may be due to the ability of peat to retain moisture and therefore retain anaerobic microsites in soil for a longer time compared to most mineral soils (Päivänen, 1973; Walczak et al., 2002).

Differences in the importance of different variables and their lags between chambers may indicate varying
620 lag-times and sensitivities to different soil moisture and WTL conditions across space. Despite spatial differences in lag times and differences in the most important variables for which the lags were identified, the highest N₂O fluxes on unfrozen soil were reached on intermediate soil moistures (0.3–0.4 m³ m⁻³) after the soil had started to drain and WTL started to decrease after a precipitation event. The optimal conditions for high N₂O fluxes on intermediate soil moistures could be explained by the simultaneous occurrence of oxic and anoxic soil microsites that allow
625 simultaneous nitrification and denitrification in draining soil (Bateman and Baggs, 2005; Wang et al., 2021; Song et al., 2022).

Although models were not run to different seasons separately, the response of N₂O fluxes to soil moisture peaks was slower in autumn. Lag times between peak N₂O fluxes and soil moisture peak increased and the height of



630 the N₂O flux peaks decreased from summer towards late autumn. Lower temperatures in autumn leading to
decreased microbial activity and decreasing availability of N from decomposing peat in colder soil may explain
lower fluxes and slow response of N₂O fluxes to soil moisture peaks in autumn (Holtan-Hartwig et al., 2002). The
finding reminds us of the importance of interactions affecting seasonal patterns of N₂O fluxes.

5. Conclusions

635 The study shows extremely high temporal and spatial variability in peatland forest N₂O fluxes with
persistent spatial patterns and common temporal dynamics across space. The considerable small-scale spatial
variation in N₂O fluxes was persistent in time and is therefore likely to be influenced by relatively long-term
controls in the soil. The temporal variation of N₂O flux was instead strongly influenced by seasonal weather
conditions such as precipitation, snow depth and drought. Temporally varying soil environmental conditions affect
640 N₂O fluxes through complex responses and interactions, leading to high temporal variation in N₂O flux between
years as well as within and between seasons. Responses of N₂O fluxes to environmental conditions include time lags
that further shape temporal patterns of N₂O fluxes.

The observed high peatland forest N₂O emissions highlight the role of N₂O emissions originating from non-
agricultural systems and the importance of considering the spatio-temporal dynamics of highly seasonally variable
645 N₂O fluxes, especially in boreal regions with strong seasonal patterns. The results indicate high importance of
summer precipitation and winter temperature and snow conditions for seasonal and annual N₂O budgets, and thus
the possibility of increased annual variability in N₂O emissions as seasonal weather conditions change in a warming
climate.

650 6. Appendices

Appendix A. Thermal seasons

Thermal winter was the season with daily mean air temperatures persistently below 0°C and thermal
summer a season with daily mean air temperatures persistently above 10°C (Ruosteenoja et al., 2011; Finnish
Meteorological Institute, 2023). During spring and autumn, temperatures varied between 0–10 °C. Cumulative
655 temperature sums of daily mean temperatures were then used to identify starting days of the thermal seasons at
which temperature goes persistently above or below the seasonal temperature threshold. The starting day of the
thermal winter was the day after the annual cumulative temperature sum reached the maximum. The starting day of
the thermal spring was the day after the minimum cumulative temperature sum was reached. Starting days of
thermal summer and autumn were calculated similarly but by extracting 10 °C from the air temperatures before
660 calculating the cumulative temperature sum (modified temperature sum). The day after the minimum modified
temperature sum was reached was defined as the starting date of the summer, while the maximum modified
cumulative temperature pointed the onset of thermal autumn.



Appendix B. Evaluating the model performance

665 R_2 of the chamber-specific models used in the analyses varied between 0.72 and 0.85 in OOB data, and
between 0.60 and 0.69 in training period evaluation data (30 % of training period data) (Table B1). When predicting
N₂O fluxes outside the training period (fourth measurement year), R_2 varied between 0.02 and 0.69. Performance of
N₂O gap-filling models was tested only using OOB data and evaluation data within the whole measurement period
(30 % of data). For gap-filling models, R_2 in OOB data varied between 0.71 and 0.84, while R_2 in evaluation data
670 varied between 0.67 and 0.78 (Table B2).

For the models used in the analysis, the poor prediction accuracy outside of training period, especially in
chambers 3, 4, and 6, was likely due to overestimation of the general flux level during the relatively dry year 2019,
which was excluded from the training period (Fig. S8). The model was also unable to predict anomalous high-flux
period in low-flux winter 2018–2019 in Chamber 5 likely due to a lack of chamber-specific soil temperature data
675 deeper in the soil. The temporal patterns of the flux otherwise followed temporal patterns of measured fluxes
relatively well. Poor prediction accuracy outside the training period in part of the chambers indicates that predicting
N₂O fluxes to a year with distinct environmental conditions compared to the years in the training data may lead to
large under or overestimation of N₂O fluxes. The used models could benefit from additional explanatory variables,
such as redox potential or availability of different forms of nitrogen (Rubol et al., 2012; Saha et al., 2020). Including
680 additional soil variables in the model could decrease the need to have excessively large model training periods to
accurately predict and gap-fill N₂O fluxes.

685 **Table B1: Model performance in evaluation datasets. Out of bag (OOB) data refers to data left outside
model training in Random forest with conditional inference trees, evaluation data within training period
refers to 30 % of data randomly left aside for model evaluation and evaluation data outside training period
refers to the fourth measurement year outside model training period (3 years).**

Chamber	Evaluation data	RMSE	R ²
1	OOB	138.8	0.75
	Within training period	134.9	0.60
	Outside training period	113.7	0.67
2	OOB	105.7	0.84
	Within training period	106.0	0.69
	Outside training period	85.1	0.69
3	OOB	81.0	0.72
	Within training period	93.7	0.64
	Outside training period	75.7	0.02
4	OOB	36.3	0.83
	Within training period	29.5	0.77
	Outside training period	56.6	0.01



5	OOB	14.5	0.85
	Within training period	12.7	0.65
	Outside training period	22.0	0.33
6	OOB	10.2	0.85
	Within training period	10.3	0.68
	Outside training period	17.0	0.03

690 **Table B2: Performance of gap-filling models on evaluation datasets. Out of bag (OOB) data refers to data left outside model training in Random forest with conditional inference trees and evaluation data within training period refers to 30 % of training period data that was randomly left aside for model evaluation. Training period of gap-filling models covers the total measurement period (4.5 years).**

Chamber	Evaluation data	RMSE	R ²
1	OOB	118.3	0.80
	Within training period	124.7	0.67
2	OOB	90.2	0.84
	Within training period	86.6	0.78
3	OOB	80.7	0.74
	Within training period	62.1	0.69
4	OOB	30.3	0.83
	Within training period	28.6	0.76
5	OOB	16.7	0.71
	Within training period	14.0	0.71
6	OOB	9.9	0.82
	Within training period	9.7	0.72

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7. Data availability

Flux data and supporting environmental data are available at: <https://doi.org/10.5281/zenodo.8142188> (Rautakoski et al., 2023a). R codes used in data analysis are available from the corresponding author by request. Python codes
 700 used in flux calculation and R codes used in data analysis are available from the corresponding author by request.

8. Supplement

The supplement of the article is available at: <https://doi.org/10.5281/zenodo.8141569> (Rautakoski et al., 2023b).

9. Author Contributions

705 AL, MA, MK and PO set up the study design. Field maintenance of measurement systems was carried out by MK, AL and PO. Fluxes were calculated by MK and filtered by HR. Data analysis and modelling was carried out by HR with the support of AL and JM. HR wrote the article with the help of co-authors.



10. Competing interests

710 The authors declare that they have no conflict of interest.

11. Acknowledgments

We thank the Academy of Finland (Biogeochemical and biophysical feedbacks from forest harvesting to climate change – BiBiFe, Grant no. 324259; Managing Forests for Climate Change Mitigation – FORCLIMATE, Grant no. 347794) and the Maj and Tor Nessling foundation (Grant no. 201700450) for funding the work. We also thank for the support by the ACCC Flagship funded by the Academy of Finland (Grant no. 337552) and the Ministry of Transport and Communications through the Integrated Carbon Observation System (ICOS) and ICOS Finland. DeepL Write (DeepL SE, 2023) was used to improve the language of the article.

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