

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

Helena Rautakoski¹, Mika Korkiakoski¹, Jarmo Mäkelä², Markku Koskinen³, Kari Minkkinen⁴, Mika Aurela¹, Paavo Ojanen^{4,5}, Annalea Lohila^{1,6}

¹Finnish Meteorological Institute, P.O. Box 503, FI-00101 Helsinki, Finland

²Advanced Computing Facility, CSC – IT Center for Science Ltd, P.O. Box 405, FI-02101 Espoo, Finland

³Department of Agriculture, University of Helsinki, Viikinkaari 9, FI-00790 Helsinki, Finland

⁴Department of Forest Sciences, University of Helsinki, P.O. Box 27, FI-00014 Helsinki, Finland

⁵Natural Resources Institute Finland, Viikinkaari 4, FI-00790 Helsinki, Finland

⁶Institute for Atmospheric and Earth System Research, University of Helsinki, Gustaf Hällströmin katu 2, P.O. Box 64, FI-00014 Helsinki, Finland

Correspondence to: Helena Rautakoski (helena.rautakoski@fmi.fi)

Abstract: The urgent need to mitigate climate change has evoked a broad interest in better understanding and 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 delayed relationships between N₂O flux and environmental conditions across seasons and years.

The spatio-temporal variation of the N₂O flux was large, with daily mean N₂O flux varying between –10 and +1760 µg N₂O m⁻² h⁻¹ and annual N₂O budgets of different chambers between +60 and +2110 mg N₂O m⁻² y⁻¹. Spatial differences in fluxes persisted through years of different environmental conditions. Soil moisture, WTL and air temperature were the most important variables explaining the temporal variation of N₂O fluxes. N₂O fluxes responded to precipitation events with peak fluxes measured on average 4 days after peaks in soil moisture and water table level. The length of the time lags varied in space and between seasons indicating possible interactions with temperature and other soil conditions.

The high temporal variation in N₂O flux was related to a) temporal variation in environmental conditions, with the highest N₂O fluxes measured after summer precipitation events and winter soil freezing, and b) to annually varying seasonal weather conditions, with the highest N₂O emissions measured during wet summers and winters with discontinuous snow cover. Climate change may thus increase winter N₂O emissions, which may be offset by lower summer N₂O emissions in dry years. The high sensitivity of N₂O fluxes to seasonal weather conditions suggests increasing variability in annual peatland forest N₂O budgets as the frequency of extreme weather events, such as droughts, is predicted to increase.

37 1. Introduction

38 Among the greenhouse gases whose emissions contribute to climate change, nitrous oxide (N₂O) is one of
39 the most potent, with a 100-year global warming potential 273 times greater than that of carbon dioxide (Forster et
40 al., 2021). A major part of N₂O emissions originates from soils (Butterbach-Bahl et al., 2013; Davidson and Kanter,
41 2014). Human impact through altered nitrogen (N) cycling, land use and climate change affect the soil N₂O emissions
42 in both natural and managed ecosystems (Tian et al., 2018, 2020). The urgent need to mitigate climate change has
43 evoked a broad interest in better understanding and estimating N₂O emissions of different ecosystems (Thompson et
44 al., 2019; Shakoor et al., 2021). However, the accurate estimation of N₂O emissions has remained a challenge and
45 emissions estimates continue to have relatively high uncertainties (Tian et al., 2020). A large part of the uncertainty
46 in N₂O emission estimates is due to inadequate understanding of the temporal and small-scale spatial variability of
47 N₂O fluxes (Sutton et al., 2007; Groffman et al., 2009; Kuzyakov and Blagodatskaya, 2015; Wang et al., 2020).

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

60 Temporal variation of soil conditions can lead to a high temporal variation of N₂O flux within a year
61 (Groffman et al., 2009; Kuzyakov and Blagodatskaya, 2015). Soil freeze-thaw and dry-wet cycles are examples of
62 changes in soil conditions shown to shape seasonal variation in N₂O emissions (Risk et al., 2013; Congreves et al.,
63 2018). High temporal variation of N₂O flux has been shown to be typical for several ecosystems (Luo et al., 2012;
64 Molodovskaya et al., 2012; Anthony and Silver et al., 2021), but understanding related to the temporal variation of
65 N₂O production is limited by sparse sampling intervals of manual flux measurements, lack of short-interval
66 measurements and poor temporal coverage of data from all parts of the year (Barton et al., 2015; Grace et al., 2020).
67 Since short periods of high N₂O fluxes can account for a substantial amount of the annual N₂O budget (Molodovskaya
68 et al., 2012; Ju and Zhang, 2017; Anthony and Silver, 2021), capturing N₂O flux peaks and understanding the causes
69 of temporal variation of N₂O flux are essential for estimating annual emissions accurately.

70 High spatial variation is also typical for N₂O flux and occurs on multiple spatial scales from large-scale
71 variation between ecosystems to small-scale variation within a few meters (Groffman et al., 2009; Krichels and Yang,
72 2019). High N₂O fluxes are typically measured in ecosystems with high N availability, such as in agricultural fields
73 and in drained organic soils where fertilization and organic matter mineralization provide N supply for N₂O production

74 (Maljanen et al., 2003; Reay et al., 2012; Leppelt et al., 2014; Pärn et al., 2018). Within an ecosystem, varying soil
75 properties and conditions such as organic matter content, soil moisture or pH can create spatial variability in the N₂O
76 fluxes (Jungkunst et al., 2012; Giltrap et al., 2014). Although the small-scale spatial variation of N₂O flux can be large
77 and exceed the spatial variation between more distant parts of the same ecosystem (Yanai et al., 2003; Jungkunst et
78 al., 2012; Giltrap et al., 2014), the causes of small-scale spatial variability of N₂O flux are poorly known and little
79 studied, especially with short-interval measurements. Several questions related, for example, to the persistence of
80 spatial patterns over time and linkages between the spatial and temporal variation of N₂O flux are little understood.

81 Drained peatland forests are examples of ecosystems with relatively high N₂O fluxes and high spatio-
82 temporal variation of those fluxes (Maljanen et al., 2003; Minkkinen et al., 2020; Pärn et al., 2018). In Finland, about
83 60 % of the original peatland area has been drained for forestry (Korhonen et al., 2021), which has resulted in a
84 lowered groundwater level and increased N availability for N₂O production from the decomposing peat. Drainage has
85 led to increased N₂O fluxes, especially in nutrient-rich peatland forests with a low C:N ratio (Martikainen et al., 1993;
86 Laine et al., 1996; Klemedtsson et al., 2005). The focus of previous studies on peatland forest N₂O fluxes has been
87 mainly on understanding the large-scale spatial variation of N₂O fluxes between different peatland forests
88 (Klemedtsson et al., 2005; Ojanen et al., 2010; Minkkinen et al., 2020) and reporting N₂O flux response to forest
89 harvesting or other forestry operations (Maljanen et al., 2003; Huttunen et al., 2003; Korhonen et al., 2019, 2020).
90 Temporal variation has been mainly studied with sparse-interval chamber measurements (Maljanen et al., 2010;
91 Pihlatie et al., 2010).

92 For the first time in boreal drained peat soils, we use multiple years (2015–2019) of automated chamber N₂O
93 fluxes to investigate the characteristics of temporal and small-scale spatial variation in N₂O flux. We link the temporal
94 variation of N₂O flux to seasonally and annually variable environmental conditions including immediate and time-
95 lagged responses. This is done to provide a more comprehensive understanding of the spatio-temporal dynamics of
96 N₂O flux and to reduce uncertainties in current and future N₂O emission estimates in boreal peatland forests and
97 beyond.

98

99 **2. Materials and methods**

100 **2.1. Site description**

101 The flux measurements were conducted between the 1st of June, 2015 and 29th of September, 2019 in a
102 drained nutrient-rich peatland forest located in southern Finland (Lettosuo, 60°38' N, 23°57' E). The mean annual
103 temperature in the area is 5.2 °C and the mean annual precipitation 621 mm according to the long-term weather record
104 from the nearest automatic weather station (Jokioinen Ilmala, 1991–2020, 35 km from the study site). The site was
105 initially drained in the 1930s and more intensively in 1969 to promote tree growth. Ditches were dug about 1 m deep
106 and 45 m apart. The site was fertilized with phosphorus and potassium after the later drainage. Drainage lowered the
107 groundwater table, resulting in a transition to boreal-forest-like vegetation. The relatively low C:N ratio reflects the
108 fen history of the site (Table 1).

109 Before March 2016, the site was a mixed forest with an overstory dominated by Scots pine (*Pinus sylvestris*)
110 and an understory dominated by Norway spruce (*Picea abies*). Both overstory and understory contained a small

111 amount of downy birch (*Betula pubescens*). Overstory pines were removed during a selection harvest in March 2016
 112 (70 % of the total stem volume; Korhonen et al., 2020, 2023). The surroundings of the measurement chambers used
 113 in this study were harvested more lightly, and the chamber area continued to have a high coverage of spruce and birch.
 114 The selection harvest did not affect N₂O fluxes according to the previous study from the site (Korhonen et al., 2020),
 115 and the effect of the harvest was left out of the focus of this study.

116
 117 **Table 1: Soil properties at the study site. Values represent general soil properties at the study site before**
 118 **the selection harvest was done. Data from Korhonen et al. (2019).**

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

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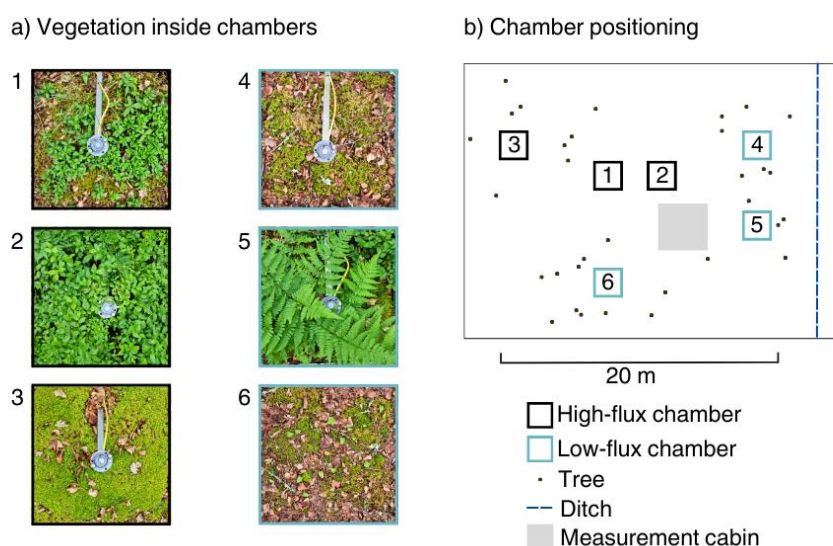
124 2.2. Automatic chamber fluxes

125 The N₂O flux between the forest floor and the atmosphere was measured using six automated chambers. The
 126 transparent, acrylic, rectangular cuboid chambers with the dimensions 57 x 57 x 40 cm (length x width x height) were
 127 placed to sample the spatial variation of the ground vegetation composition within an area of 15 x 20 m (Fig. 1). The
 128 chambers were placed on permanently installed steel collars that were inserted into the soil to a depth of 2 cm. All the
 129 chambers closed for six minutes once an hour year-round. The chambers had an air temperature sensor and a fan to
 130 mix the air inside the chamber headspace. During winters, chambers were cleaned from snow and ice every 1–3 weeks
 131 and snow depth inside the chambers was measured to account for the effect of snow depth on chamber volume. During
 132 the winter 2016–2017, extension collars were used to better allow snow to fit inside the chambers.

133 The N₂O concentration of the chamber headspace air was measured using a continuous wave quantum
 134 cascade laser absorption spectrometer (LGR-CW-QCL N₂O/CO-23d, Los Gatos Research Inc., Mountain View, CA,
 135 USA) that was placed in a measurement cabin close to the chambers (Fig. 1b). The analyzer had an accuracy of 0.01
 136 ppb per second, corresponding to a minimum detectable flux (Nickerson, 2016) of 0.06 μg N₂O m⁻² h⁻¹ in our chamber
 137 system. During each chamber closure, air from the closed chamber was pumped into the analyzer and back to the
 138 chamber headspace through plastic tubes (length 15 m, flow about 1 l/min). After each chamber closure, the airflow
 139 was switched to the next chamber. Ambient air was measured for at least 1 min between the chamber closures to allow
 140 concentrations in the tubes to stabilize back to the ambient level. Concentration data from the first 30 s of each chamber
 141 closure were not used in flux calculation to avoid possible pressure disturbance caused by the closing chamber
 142 affecting the flux (Pavelka et al., 2018). For more information about the automatic chamber system, see the previous
 143 studies from the same site (Koskinen et al., 2014; Korhonen et al., 2017, 2020). Measurements in Chamber 6 ended
 144 six months earlier (April 2019) than measurements in other chambers due to problems in chamber functioning.

145 N₂O fluxes were calculated similarly to Korhonen et al. (2017), but by using a linear fit. The mean
 146 headspace temperature of the closure and air pressure measured at the site were used in the flux calculation. Calculated
 147 fluxes were filtered using normalized root mean square error and an iterative standard deviation filter to remove

148 erroneous fluxes resulting from chamber malfunction (Korkiakoski et al., 2017). Daily mean N₂O fluxes from each
 149 chamber were used in the analysis because the automatic chamber system seemed to create an artificial diurnal cycle
 150 of N₂O from which the possible natural diurnal cycle could not be separated. The artificial diurnal cycle was caused
 151 by the difference in turbulence between the ambient air and chamber headspace, as previously reported for CO₂ and
 152 CH₄ (Koskinen et al., 2014; Korkiakoski et al., 2017). During calm periods, especially during summer nights, the
 153 transfer of N₂O from soil pores to the atmosphere slowed down, leading to increased N₂O concentration in the soil.
 154 When the chamber closed and the turbulence increased because of the fan, the N₂O from the soil pores was vented to
 155 the chamber headspace air, leading to overestimated flux. The opposite phenomenon probably occurred in windy
 156 conditions, resulting in underestimated flux. Based on our experience, automatic chamber fluxes measured in drained
 157 peatlands with dry and porous peat soil are particularly sensitive to this phenomenon (Koskinen et al., 2014;
 158 Korkiakoski et al., 2017). Hourly N₂O flux peaks were not typical in the flux data, and daily mean N₂O fluxes thus
 159 well represent the main characteristics of the temporal variation. It should be noted that the artificial diurnal cycle
 160 creates an additional source of uncertainty in the reported N₂O budgets.
 161



162
 163 **Figure 1: (a) Vegetation inside the six chambers and (b) the positioning of the chambers on the forest floor**
 164 **in relation to the nearest ditch and trees. Chambers are named from one to six based on the maximum**
 165 **measured flux with Chamber 1 having the highest measured flux. Chambers 1–3 with black edges are**
 166 **classified as “high-flux chambers” and Chambers 4–6 with blue edges as “low-flux chambers”.** For more
 167 **information on chamber vegetation, ditches and trees, see Table S1.**
 168

169 2.3. Environmental variables

170 Several environmental variables were measured to link the temporal variation of N₂O fluxes with the
 171 environmental conditions. Air temperature was measured at 2 m height below the forest canopy (HMP45D, Vaisala
 172 Oyj, Vantaa, Finland). Soil surface temperature was measured at 2 cm depth in each chamber and the soil temperature
 173 at 5 cm depth at one location close to the chambers (Pt100, Nokeval Oy, Nokia, Finland). Soil moisture was measured
 174 at one location about 75 m from the chamber measurement location at 7 and 20 cm depths (Delta-T ML3, Delta-T
 175 Devices Ltd, Cambridge, UK). The soil moisture data were used to describe the temporal variation of soil moisture,

176 assuming that the soil moisture had relatively similar temporal patterns across the study site. The absolute level of soil
177 moisture in each chamber may have differed from the measured soil moisture, and the possibility of differences in the
178 temporal variation of soil moisture between the logger and the chambers cannot be excluded. Soil moisture data were
179 used together with water table level and precipitation data to strengthen the conclusions related to soil water
180 conditions. The measurements of air and soil temperatures were ongoing throughout the study period, but the soil
181 moisture measurements ended half a year earlier than automatic chamber measurements (April 2019).

182 Water table level (WTL) below the soil surface was measured using automatic loggers (TruTrack WT-HR,
183 Intech Instruments Ltd, Auckland, New Zealand; Odyssey Capacitance Water Level Logger, Dataflow Systems Ltd,
184 Christchurch, New Zealand). Chambers 1–2 and 4–5 shared a WTL logger that was placed between the chamber pairs.
185 Chambers 3 and 6 had WTL loggers next to the chambers. WTL measurements for Chambers 3–6 started half a year
186 later than chamber measurements (December 2015). WTL during this and other data gaps was modeled using random
187 forest with conditional inference trees (Hothorn et al., 2006). WTL data from Chambers 1–2, seven other WTL loggers
188 at the study site and precipitation were used as explanatory variables in the gap-filling model. Modeling was done first
189 for the logger with the least amount of missing data, after which the gap-filled WTL time series was added to the
190 model as an explanatory variable to increase the predictive power of the model for the variables with more missing
191 data (evaluation data $R^2 = 0.90\text{--}0.97$).

192 Precipitation was measured at the site throughout the study period (Casella Tipping Bucket Rain Gauge,
193 Casella Solutions Ltd, Bedford, UK; OTT Pluvio2 L 400 RH, OTT Hydromet Ltd, Kempten, Germany) and daily
194 precipitation sum was calculated. The precipitation data measured at the nearest weather station was used to gap-fill
195 winters and other measurement gaps in precipitation data (correlation of precipitation between sites 0.65, $p < 0.05$).
196 Snow depth measured at the nearest weather station was used to describe general snow conditions experienced each
197 winter. Thermal seasons were used to analyze the seasonality of N_2O fluxes. The thermal seasons were defined
198 according to typical Finnish standards (Ruosteenoja et al., 2016; Finnish Meteorological Institute, 2023) by using air
199 temperature data from the site (Appendix A). Seasons based on months were used to compare conditions measured at
200 the site with long-term averages reported monthly for the nearest weather station.

201

202 **2.4. Identifying high-flux periods**

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

208 To identify the high-flux periods, their length, seasonality and starting conditions, different thresholds to
209 separate high-flux days from the baseline days were tested. High fluxes were measured less frequently compared to
210 the more common low fluxes (Fig. S2). Any percentile threshold between 60–80 % separated high-flux days from the
211 more common baseline fluxes relatively well, and the mean of these (70 %) was used. Days with the mean flux above
212 the 70 % percentile were classified as high-flux days and the rest of the days as baseline days. The length of each

213 high-flux period was the number of days the flux remained above the 70 % percentile, including possible data gaps
214 within this period. The high-flux period was set to continue over a data gap if three days before and after the data gap
215 were classified as high-flux days. A three-day marginal was chosen to ensure that short one-to-two-day peaks would
216 not create long-lasting high-flux periods over data gaps. If the high-flux period started from a data gap or ended to it,
217 the start or end date of the high-flux period was set to the first or last measured day, respectively. Pearson correlation
218 was used to test how similar the temporal patterns of N₂O flux were between chambers.

219

220 **2.5. Machine learning**

221 Machine learning models were used to improve understanding of the temporal controls on N₂O flux,
222 including a possible effect of time lags between environmental conditions and N₂O flux. The machine learning
223 approach was used because machine learning models do not rely on mathematical functions to describe relationships
224 between variables and are able to account for interactions between variables flexibly (Olden et al., 2008). The Random
225 forest algorithm, developed by Breiman (2001), is a classification tree-based method that uses bootstrap aggregation
226 of a model training data and a randomly chosen subset of explanatory variables (*mtry*-parameter) to train each
227 classification tree. In bootstrap aggregation, a subset of data is taken from the model training data with or without
228 returning it to the original training data. The part of data that is not bootstrapped to train trees is called out-of-bag
229 (OOB) data and it can be used to evaluate model performance. In each random forest tree, the bootstrapped data are
230 classified into subgroups and further into smaller subgroups by setting threshold values for the randomly chosen subset
231 of explanatory variables. The setting of the threshold values is done to maximize the information gain until no further
232 thresholds, also called splits, can be made. After a selected number of trees are built, the final model prediction can
233 be made using the average of all the trees (continuous response) or the most common outcome (categorical response).

234 Random forest variable importance (VI) metrics show the importance of each explanatory variable in
235 explaining variation in the response variable. VI metrics can be biased if the explanatory variables correlate (Strobl et
236 al., 2007). Therefore, we used random forest with conditional inference trees (Hothorn et al., 2006) that allowed us to
237 get more accurate VIs in the presence of correlated explanatory variables and their time-lagged versions. Compared
238 to trees in random forest, conditional inference trees use a p-value-based splitting criterion to classify the bootstrap
239 aggregated data in the building phase of each tree. As suggested by Strobl et al. (2007), in the presence of correlated
240 explanatory variables, variable importance metrics from the conditional inference trees were calculated using
241 conditional permutation importance.

242 Chamber-specific models had daily mean N₂O flux as the response variable and the measured temperature
243 variables (air, soil 2 cm and 5 cm depths), soil moisture (7 and 20 cm depths), WTL and daily cumulative precipitation
244 as explanatory variables. Periods of missing data in environmental variables were gap-filled using the random forest
245 proximity tool RFimpute (Liaw and Wiener, 2002). One-to-seven days' time-lagged versions of each environmental
246 variable were added as explanatory variables to the models besides unlagged environmental variables. The imbalanced
247 distributions of N₂O fluxes were corrected with the SMOGN algorithm (Abd Elrahman and Abraham, 2013). The
248 subset of data to train each tree was bootstrapped without replacement with a sample size 0.632 times the size of the

249 training dataset, as suggested by Strobl (2007). Models were trained with 500 trees and random forest default *mtry* for
250 continuous response variable was used ($mtry = \text{number of explanatory variables} / 3$).

251 The first three years of data were utilized as the model training period (June 2015 – June 2018), and this data
252 were further split into 70 % training data and 30 % evaluation data to test model performance within the training
253 period. The fourth year of measurements until soil moisture measurements ended (June 2018 – April 2019) was left
254 aside for evaluation to test model performance outside the training period. The performance of the models on different
255 evaluation datasets was analyzed using R squared (R^2) and root mean squared error (RMSE). R^2 was used to compare
256 model performance between chambers. Variable selection was not done. Evaluation results are presented in
257 appendices (Appendix B).

258 VIs and accumulated local effects (ALE) were used to interpret the modeling results. For easier comparison
259 of VIs across chambers, the VIs of each chamber were scaled from zero to one (0 = least important variable, 1 = most
260 important variable) and the total VIs of each variable were calculated (total VI = VI of unlagged variable + VIs of
261 lags). The ALE method by Apley and Zhu (2020) was used to visualize the response of N_2O flux to environmental
262 conditions and their lags in the models. In ALE figures, ALE value (y-axis) zero refers to the mean predicted N_2O
263 flux, with a positive ALE value meaning larger and a negative value lower predicted N_2O flux in a specific
264 environmental condition (x-axis). ALE values for lagged environmental variables indicate the response of predicted
265 N_2O flux to previous environmental conditions. From the unlagged and lagged versions of each environmental
266 variable, the one that received the highest ALE value for a given environmental condition was considered to represent
267 the typical response time of N_2O flux to that condition. In this article, the response time, or lag length in the presence
268 of at least a one-day lag, refers to the time it takes for N_2O to reach peak flux after the onset of a given environmental
269 condition. The reported evaluation results (RMSE, R^2), VIs, and ALE values are averages over 10 model runs.

270

271 **2.6. N_2O budgets**

272 Data gaps covered 12–24 % of the study period depending on the chamber. Daily mean N_2O flux time series
273 were gap-filled to calculate N_2O budgets. Gap-filled data were not used in other analyses to avoid additional
274 uncertainty arising from the gap-filling. The same models and explanatory variables were used as in the machine
275 learning part, including time-lagged variables. The fourth measurement year previously left for evaluation was also
276 included in the training data for gap-filling. To test the performance of the gap-filling model, separate models were
277 run with 70 % and 30 % split to the training data and evaluation data, respectively. Evaluation metrics (RMSE, R^2) of
278 gap-filling models are shown in Appendices (Appendix B). Gap-filled daily mean N_2O fluxes were used to calculate
279 N_2O budgets for each chamber in each thermal season. The uncertainty related to the N_2O budgets was assumed to be
280 a combination of uncertainty related to flux measurement and uncertainty related to gap-filling. Detailed information
281 about the calculation of the uncertainty can be found in Korkiakoski et al. (2017).

282 Flux calculation was performed in the Python programming language version 2.7 (Van Rossum and Drake,
283 1995). Data preparation and analysis were performed in R statistical software version 4.0.5 (R core team, 2021).
284 Cforest-command in the party package (Hothorn et al., 2006; Strobl et al., 2007; Zeileis et al., 2008) was used to

285 perform random forest with conditional inference trees. Data and simplified R-code about the machine learning part
286 of the study are made freely available (See Sect. 7).

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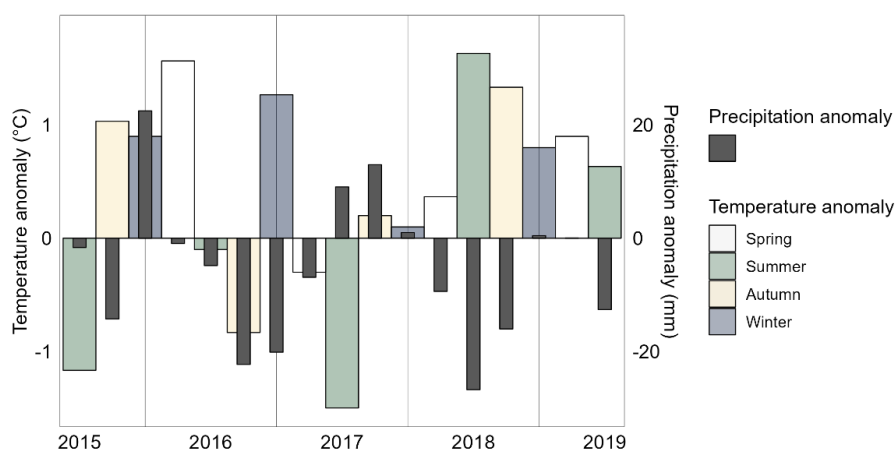
288 3. Results

289 3.1. Environmental conditions

290 The summers (June, July, August) 2015 and 2017 were colder (seasonal means 14.1 °C and 14.4 °C,
291 respectively) than the long-term average (15.6 °C, Jokioinen-Ilmala 1991–2020), and winters (December, January,
292 February) 2015–2016, 2016–2017 and 2018–2019 were warmer (seasonal means –3.4 °C, –3.0 °C and –3.5 °C,
293 respectively) than the long-term average (–4.3 °C) (Fig. 2). Temperatures were warm in all seasons in 2018 and 2019,
294 with the summer (seasonal mean 17.2 °C) and autumn (seasonal mean 6.7 °C) 2018 being particularly warm compared
295 to the long-term averages (summer 15.6 °C and autumn 5.4 °C). The area received the least amount of precipitation
296 in 2018 (annual sum 434 mm) and the most precipitation in 2017 (annual sum 657 mm) with the long-term annual
297 average being 621 mm. The summer 2018 (seasonal sum 44 mm) was especially dry compared to the long-term
298 average summer precipitation of 71 mm. The drought that began in the spring 2018 continued until autumn.

299 Soil moisture was continuously lower than the mean of the study period from the summer 2018 until the end
300 of the study period (Fig. 3), with the study period mean being 0.28 m⁻³ m⁻³ for 7 cm soil moisture and 0.56 m⁻³ m⁻³ for
301 20 cm soil moisture. WTL was on average –36 cm and continuously deeper than that in the summer and autumn 2015
302 as well as in the summers 2018 and 2019. Soil temperatures at 5 cm depth reached freezing temperatures in winters
303 2015–2016 (min. –3.8 °C), 2016–2017 (min. –1.8 °C) and 2017–2018 (min. –0.33 °C). Variation of air and soil
304 surface temperatures was high in winters 2015–2016 and 2016–2017. The snow cover was thickest in winter 2018–
305 2019 (max. 52 cm) and thinnest in winter 2016–2017 (max. 11 cm). The number of days with snow cover was lower
306 in winters 2015–2016 (85 days) and 2016–2017 (93 days), and higher in winters 2017–2018 (125 days) and 2018–
307 2019 (116 days).

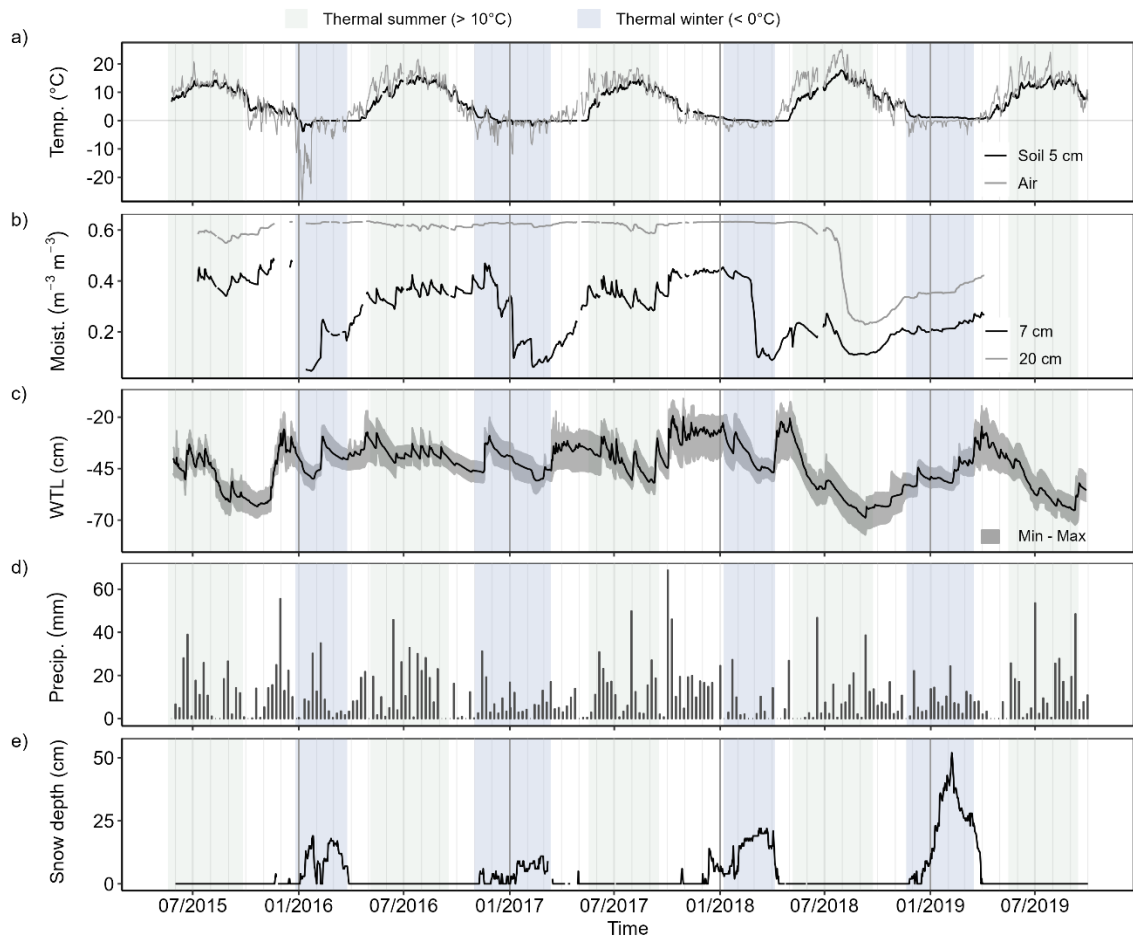
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310 **Figure 2: Difference of seasonal mean air temperature and precipitation sum from the long-term average.**
311 **The long-term averages from the nearest weather station are used (Jokioinen Ilmala, 1991–2020). Seasons are**
312 **based on months (autumn: September–November, winter: December–February, spring: March–May and**
313 **summer: June–August).**

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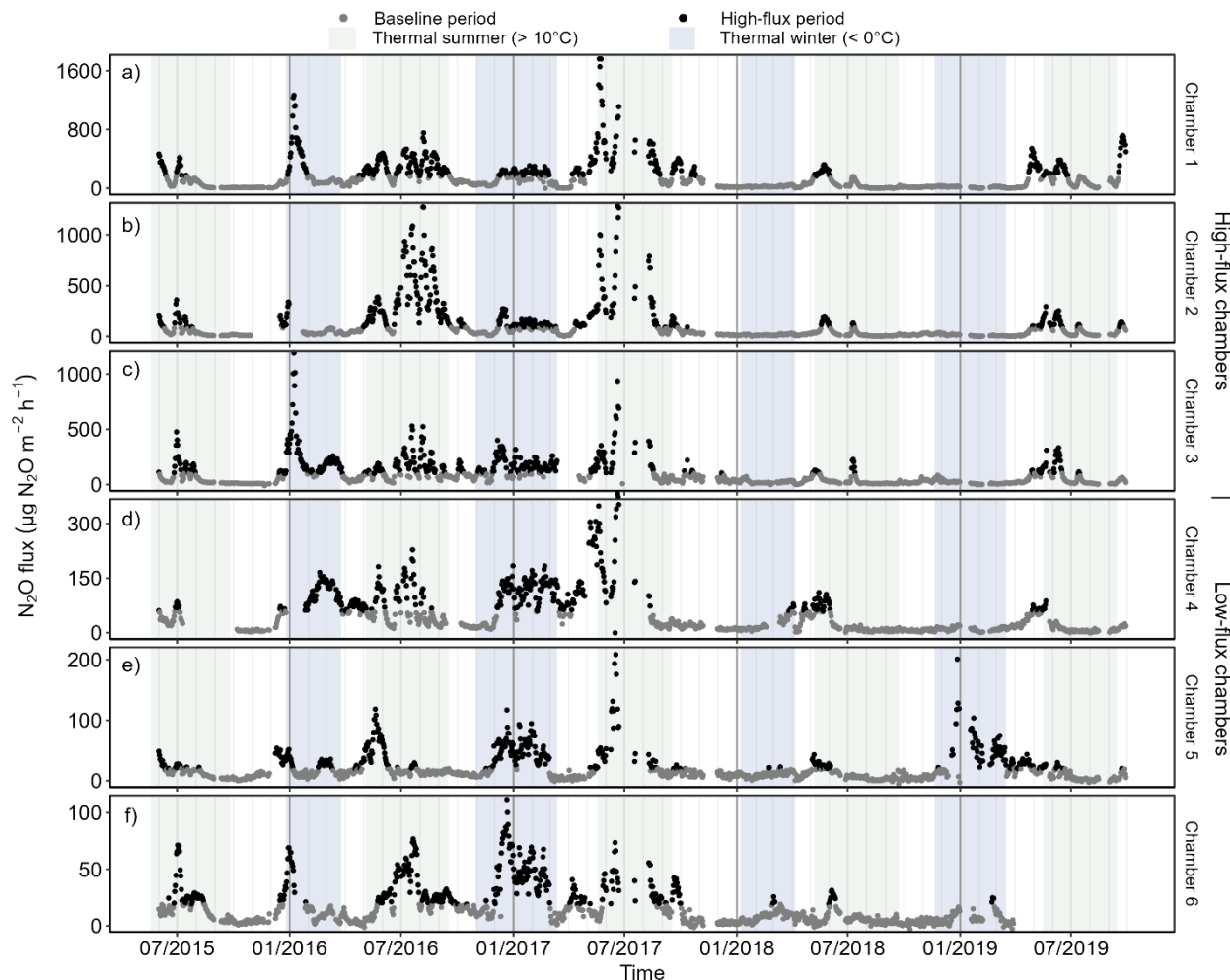
Figure 3: (a) Daily mean air and soil temperatures (5 cm depth), (b) soil moisture (7 and 20 cm depths), (c) water table level (WTL), (d) weekly precipitation sum and (e) daily mean snow depth. WTL is the mean of the chambers with gray shading showing the range of WTL between different chambers. Snow depth was measured at the nearest weather station. Data are not gap-filled.

322 3.2. Temporal and spatial variation of N₂O flux

323 The daily mean N₂O flux varied between -10 and +1760 $\mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$ during the 4.5 years of measurements
324 (Fig. 4). Three chambers (Chambers 1, 2 and 3) had maximum daily mean fluxes greater than 1100 $\mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$,
325 and the other three chambers (Chambers 4, 5 and 6) had maximum daily mean fluxes less than 400 $\mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$
326 (Table 2). Chambers 1–3 also had a higher mean flux than Chambers 4–6 in all years (Table S3.1). The annual mean
327 flux was the highest in 2016 or 2017, depending on the chamber, and lowest in 2018 or 2019. Based on the differences
328 in the maximum flux, standard deviation and the range of the flux variation, Chambers 1–3 were classified as “high-
329 flux chambers” and Chambers 4–6 as “low-flux chambers”.

330 The chamber-specific 70 % percentiles that were used to define the high-flux periods from the baseline
331 periods ranged from 20 (Chamber 5 and 6) to 170 $\mu\text{g N}_2\text{O m}^{-2} \text{h}^{-1}$ (Chamber 1, Table 2). The length of the individual
332 baseline periods varied from 1 to 330 days with a mean of 26 days, while the length of the high-flux periods varied

333 between 1 and 134 days with the mean of 11 days. The correlation of flux time series between chambers varied
 334 between 0.79 (Chambers 1 and 2) and 0.29 (Chambers 1 and 4) (Table S4). Correlation was the highest between the
 335 chambers with a similar range of N₂O flux: among high-flux chambers, correlation varied between 0.64–0.79 and
 336 among low-flux chambers, between 0.46–0.49. Differences in WTL between chambers were statistically significant
 337 but were not associated with the spatial variation of N₂O flux.
 338



339
 340 **Figure 4: Daily mean N₂O flux measured in the six automatic chambers in 2015–2019. Fluxes from different**
 341 **chambers are shown in panels (a–f) ordered by maximum daily mean N₂O flux. Chambers are grouped into**
 342 **high-flux (Chambers 1, 2 and 3) and low-flux chambers (Chambers 4, 5 and 6). The scale of the y-axis is**
 343 **chamber specific and fluxes are not gap-filled. Periods with the daily mean fluxes > 70 % percentile are**
 344 **classified as high-flux periods.**
 345

346 **Table 2: Minimum, maximum, mean, median, 70 % percentile and standard deviation (SD) of daily mean**
 347 **N₂O fluxes over the study period. The unit of the flux is µg N₂O m⁻² h⁻¹. Percentile thresholds (70 %) were**
 348 **used to define high-flux periods. Year-specific statistics can be found in Table S3.1.**
 349

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

350

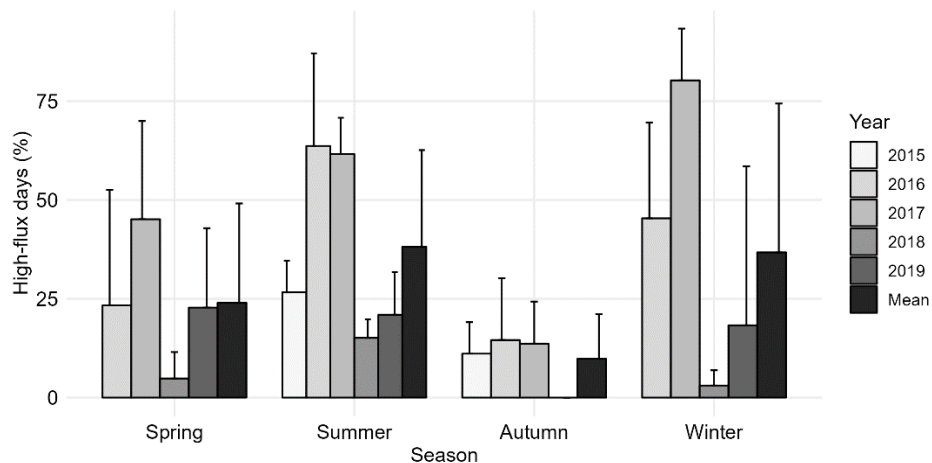
351 3.3. Seasonality of N₂O flux

352 The highest N₂O fluxes were measured during thermal summers (Chambers 1, 2, 4 and 5) or winters
 353 (Chambers 3 and 6). The fluxes were also on average the highest in summers and winters, and the lowest in autumns
 354 (Tables S3). The percentage of measurement days identified as high-flux days averaged 24 % in spring, 38 % in
 355 summer and 44 % in winter and 9 % in autumn (Fig. 5). The highest proportion of winter and summer high-flux days
 356 were measured in 2016 and 2017, and the lowest proportion in 2018.

357 In spring, N₂O fluxes increased steadily as soil surface temperatures increased above zero (Fig. 6 and S5),
 358 with most of the spring high-flux periods starting at soil surface temperatures 0–2 °C (Fig. 7). Spring N₂O fluxes
 359 increased steadily with increasing soil temperatures, and flux peaks were reached in late spring or early summer.
 360 Summer high-flux periods started after precipitation events at moist soil conditions (0.37–0.41 m⁻³ m⁻³) and during
 361 relatively high WTL (–35 to –50 cm depth) (Fig. 7), but the peak fluxes were reached several days after the rain events.
 362 The starting conditions for soil moisture and WTL in the autumn high-flux periods were similar to those in summer,
 363 but the response to soil wetting was slower and fluxes were smaller.

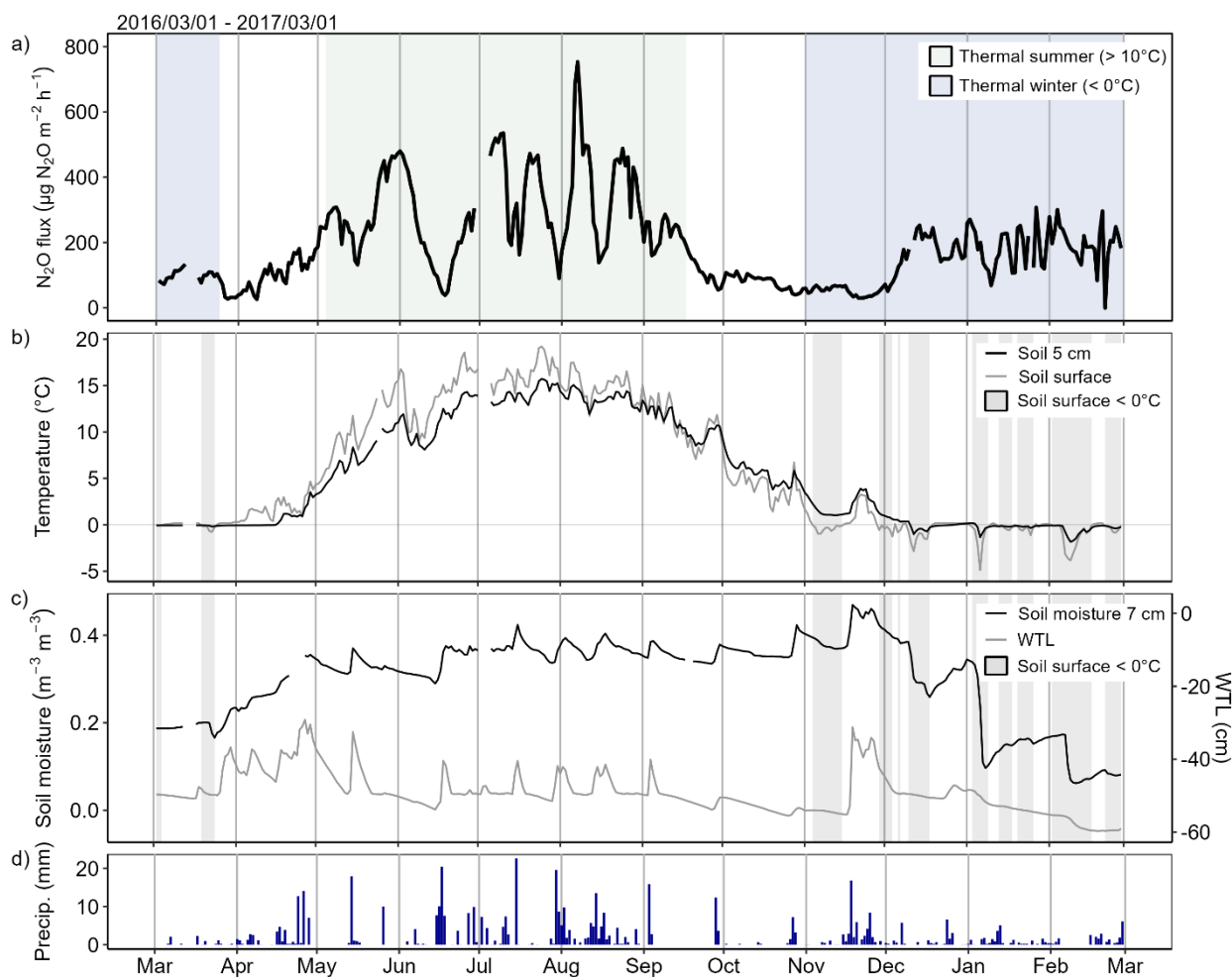
364 Winter high-flux periods started on soil temperatures close to 0 °C (Fig. 7). In early winter, N₂O fluxes
 365 increased when soil surface temperatures decreased to near zero and below that, with further increase in flux measured
 366 if soil temperature also at 5 cm depth decreased below zero (Fig. 6 and S5). Later in the winter, increased N₂O fluxes
 367 were measured during periods of soil freezing or when soil temperatures increased towards or above zero. Freezing
 368 of the soil surface did not typically lead to high N₂O fluxes without temperatures being below zero also at 5 cm depth.
 369 The response to soil freezing, especially in the early winter, was stronger than the response to soil thawing in terms of
 370 duration of the high-flux periods and peak flux.

371

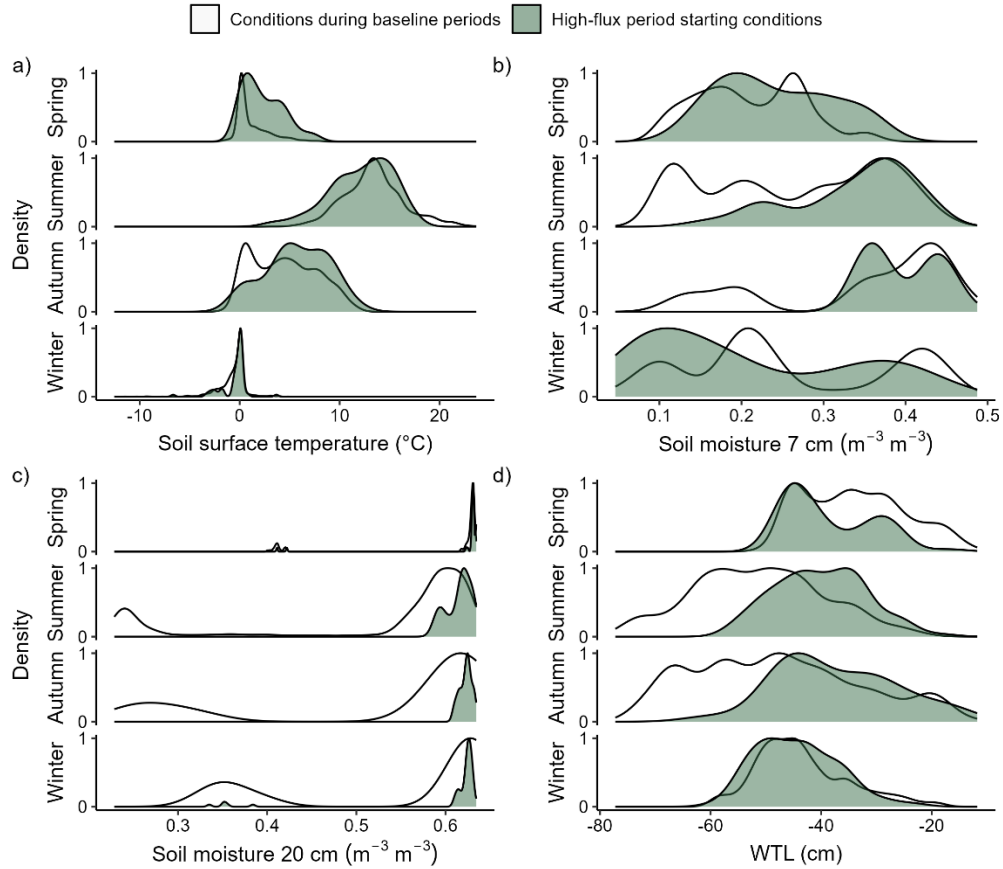


372

373 **Figure 5: Occurrence of high-flux days out of measured days in different thermal seasons. Bars show annual**
 374 **means across different chambers and error bars show standard deviation between chambers. Mean bars show**
 375 **the mean across the years. The bar for winter 2019 only contains winter days between January – March 2019.**
 376



377
 378 **Figure 6: (a) Daily mean N₂O flux, (b) soil surface temperature and temperature at 5 cm depth with**
 379 **highlighted freezing periods (soil surface temperature < 0 °C), (c) soil moisture and water table level (WTL),**
 380 **and (d) daily precipitation from March 2016 to March 2017 in Chamber 1. The temporal variation of N₂O**
 381 **flux in Chamber 1 was similar to the other chambers, but the range of flux variation was larger compared to**
 382 **the low-flux chambers. The shown temporal dynamics of N₂O flux were measured in a year with relatively**
 383 **wet summer and warm winter. Data are not gap-filled. Figures for other chambers are presented in the**
 384 **supplements (S5).**
 385

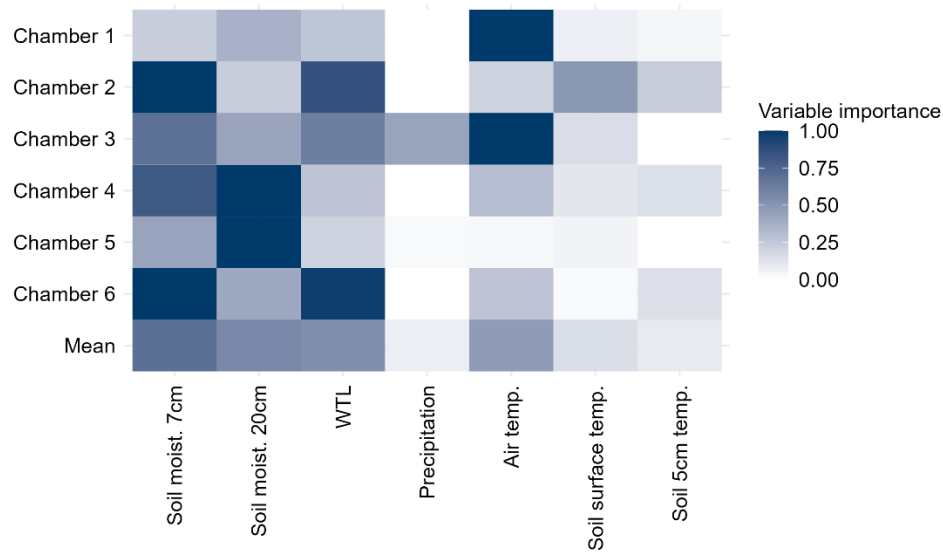


386

387 **Figure 7: High-flux period starting conditions in each season compared to conditions outside the high-flux**
 388 **periods. Density plots show the distribution of high-flux periods starting on different (a) soil surface**
 389 **temperature, (b) soil moisture at 7 cm depth, (c) soil moisture at 20 cm depth, (d) and water table level (WTL).**
 390 **The Y-axis shows scaled (0–1) proportion (%) of high-flux periods starting on conditions shown on the x-axis**
 391 **(1=most common high-flux periods starting condition, 0=no starting high-flux periods). For comparison, the**
 392 **variation in soil conditions during baseline periods is also shown (1=most common baseline period condition,**
 393 **0=no such condition measured during baseline periods). All years and chambers are included.**
 394

395 **3.4. Machine learning**

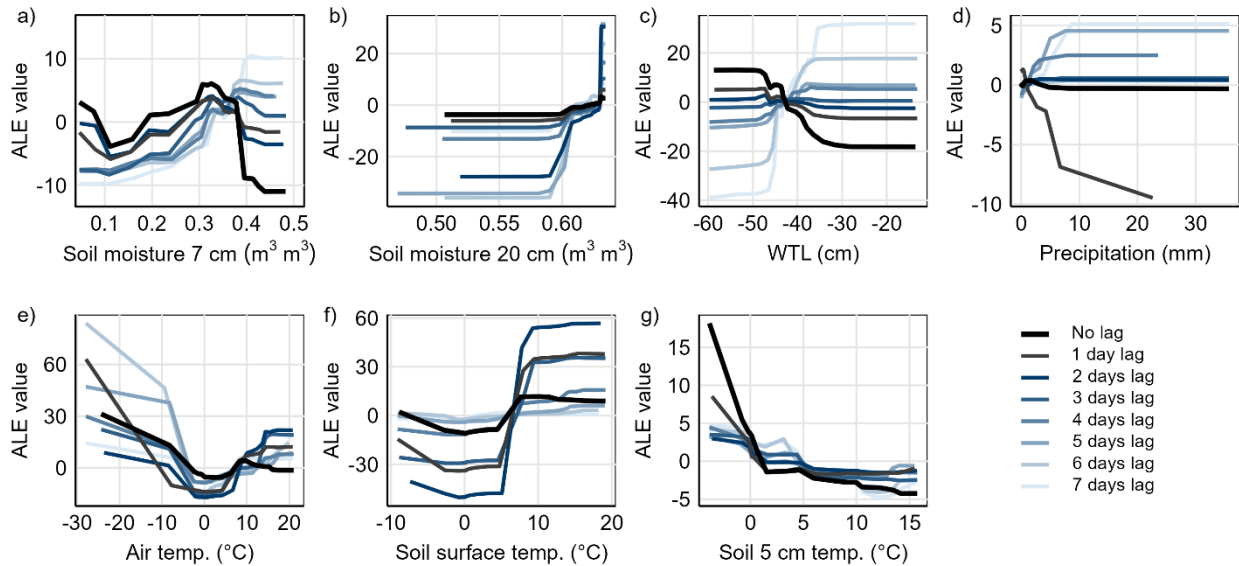
396 Soil moisture (both 7 and 20 cm), air temperature and WTL were considered to be the most important
 397 variables explaining the temporal variation of N₂O flux (Fig. 8) with the mean total variable importance (VI, 0 = no
 398 importance, 1 = high importance) being 0.7 and 0.6 for soil moisture (7 and 20 cm respectively) and 0.5 for air
 399 temperature and WTL. The mean VI of lags (1–7 days) for each environmental variable was the highest for 7 and 20
 400 cm soil moisture (mean VI 0.3 for both) with 5 cm soil temperature and air temperature also having importance on
 401 lags (mean VI 0.25 and 0.20, respectively, Fig. S6). Lags of other variables received mean VIs lower than 0.1, but
 402 precipitation had an increasing VI towards the longest lags (6–7 days).



403
 404 **Figure 8: Total variable importance (VI) of different environmental variables in explaining the temporal**
 405 **variation of N₂O flux in random forest with conditional inference trees. Total VI is the sum of VIs of unlagged**
 406 **and lagged (1–7 days) versions of the variable. Rows in the matrix plot show VIs for different chambers and**
 407 **the mean VIs across all the chambers (Mean). VI scores are scaled between 0 and 1 (0 = no importance, 1 =**
 408 **highest importance) per chamber. Lag-specific VIs are shown in Fig. S6.**
 409

410 Accumulated local effects (ALE) for 7 cm soil moisture showed that the highest fluxes were predicted for
 411 the 1–7 days lagged soil moisture when the soil was moist ($> 0.35 \text{ m}^{-3} \text{ m}^{-3}$). The lag with the highest predicted flux
 412 varied from 1 to 7 days between chambers with a mean lag of 4 days. Predicted fluxes were also high when soil
 413 moisture was low ($< 0.1 \text{ m}^{-3} \text{ m}^{-3}$, frozen soil). For WTL, the predicted flux was generally high when WTL was high
 414 ($> -45 \text{ cm}$), with the highest predicted flux on average for 4 days lagged WTL. The predicted flux for unlagged WTL
 415 was low at high WTL, while the predicted flux for unlagged WTL increased with decreasing WTL. N₂O flux was
 416 predicted to be the highest 4–7 days after precipitation with an average lag of 5 days between chambers when daily
 417 precipitation had been at least 5 mm.

418 For air and soil surface temperatures above 5 °C, the predicted fluxes increased with increasing temperature,
 419 with the highest predicted fluxes at air temperatures above 15 °C and soil temperatures above 10 °C. For air and soil
 420 temperatures (soil surface and 5 cm depth) below 0–2 °C, the predicted N₂O fluxes increased with decreasing
 421 temperature. In most chambers, the increase in predicted flux for soil 5 cm temperature at 0–2 °C was particularly
 422 strong. Responses between lagged and unlagged temperatures varied among chambers.

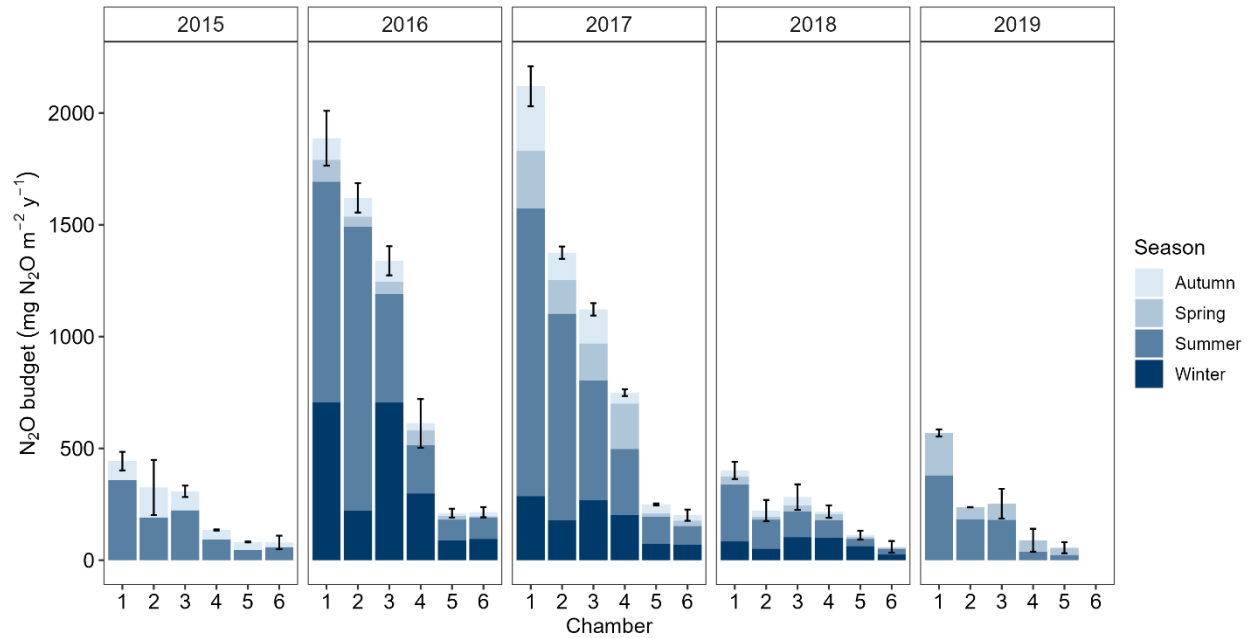


423

424 **Figure 9: Response of predicted N₂O flux to different environmental conditions for Chamber 1 visualized**
 425 **using Accumulated Local Effects (ALE). Figures illustrate how the predicted N₂O flux values deviate from the**
 426 **mean predicted flux (ALE = 0) along the gradients of (a) soil moisture at 7 cm depth, (b) soil moisture at**
 427 **20 cm depth, (c) water table level (WTL), (d) precipitation, (e) air temperature, (f) soil surface temperature**
 428 **and (g) soil temperature at 5 cm. ALE responses for unlagged and lagged variables (1–7 days) are included.**
 429 **ALE responses for Chambers 2–6 are presented in supplements (S7).**
 430

431 3.5. N₂O budgets

432 The annual N₂O budgets of individual chambers varied between 60 (Chamber 6) and 2110 mg N₂O m⁻² y⁻¹
 433 (Chamber 1) when considering the three full measurement years 2016, 2017 and 2018 (Fig. 10, Tables S8). In 2016
 434 and 2017, annual N₂O budgets were 1120–2110 mg N₂O m⁻² y⁻¹ in the high-flux chambers and 200–740 mg N₂O m⁻²
 435 y⁻¹ in the low-flux chambers. In 2018, the N₂O budgets were lower than 400 mg N₂O m⁻² y⁻¹ in all chambers. Winters
 436 and summers generally contributed the most to the annual N₂O budgets in all three years, with summers contributing
 437 on average 48 % and winters 34 % (Tables S8). The contributions of spring and autumn to the annual N₂O budgets
 438 were on average 10 % per season.
 439



440

441 **Figure 10: Annual N₂O budgets for each chamber and measurement year with seasonal contributions. The**
 442 **N₂O budget for 2015 only includes summer and autumn, and the N₂O budget for 2019 spring and summer.**
 443 **Measurements in Chamber 6 ended in early 2019 and no budget is shown for that year. Thermal seasons are**
 444 **used. Error bars denote total uncertainty related to the total N₂O budget of the year.**

445

446 **4. Discussion**

447 The measured N₂O fluxes were relatively high compared to fluxes reported for other boreal and temperate
 448 forests on peat and mineral soils. The N₂O budgets of boreal peatland forests have mainly varied between 30 and 1200
 449 mg N₂O m⁻² y⁻¹ (Arnold et al., 2005; Minkinen et al., 2020; Butlers et al., 2023), and in a similar range also in
 450 temperate mineral soil forests (Papen and Butterbach-Bahl, 1999; Luo et al., 2012). The N₂O budgets of our six
 451 automatic chambers are unlikely able to represent the N₂O budget of the whole site, but the mean annual N₂O budget
 452 of the chamber area greater than 950 mg N₂O m⁻² y⁻¹ in the two full study years out of three underlines the role of
 453 drained nutrient-rich peatland forest as hotspots for N₂O emissions (Fig. 10).

454 Nutrient-rich peat with a relatively low C:N ratio likely explains the high N₂O budgets of the chamber area.
 455 Low C:N ratio may also have increased the sensitivity of the N₂O flux to temporal variation in soil conditions
 456 (Klemmedtsson et al., 2005; Pihlatie et al., 2010). Although the selection harvest done at the site in the spring 2016 did
 457 not increase the N₂O budget of the harvested area compared to the control site according to Korkiakoski et al. (2020),
 458 the effect of the harvest on N₂O fluxes of individual chambers cannot be completely excluded. Since the N₂O budgets
 459 increased after harvesting in both the harvested and the control site (Korkiakoski et al., 2020), most of the increase in
 460 N₂O budgets in the years 2016 and 2017 is likely explained by year-to-year variation in environmental conditions.

461

462 **4.1. Seasonal variation of N₂O fluxes**

463 Winters were characterized by N₂O flux peaks occurring during both freezing and thawing (Fig. 6, 7 and S5),
464 similar to those reported in earlier studies (Teepe et al., 2001; Maljanen et al., 2007; Maljanen et al., 2010). Freezing-
465 related N₂O emissions are likely explained by N₂O production in the remaining unfrozen water films that have
466 increased C and N content in the freezing soil (Maljanen et al., 2007; Congreves et al., 2018). Winter N₂O flux peaks
467 were measured when soil frost reached at least the 5 cm depth, whereas during winters with only shallow frost (< 5
468 cm, winters 2017–2018 and 2018–2019), high N₂O fluxes were less common. This indicates the importance of frost
469 depth for winter N₂O emissions. The importance of ground frost severity and depth has also been suggested by others
470 in several ecosystems (Nielsen et al., 2001; Koponen and Martikainen, 2004; Maljanen et al., 2007; Luo et al., 2012).
471 The importance of deeper soil freezing may indicate that the freezing-related N₂O fluxes mainly originate from the
472 freezing peat rather than from the surface litter layer, unlike suggested by Pihlatie et al. (2007) in a nutrient-poor
473 peatland forest. Low C:N ratio may have favored N₂O production in the nutrient-rich peat (Klemmedtsson et al., 2005).
474 Site-specific differences in nutrient availability may influence the sensitivity of winter N₂O fluxes to frost depth.

475 Winters with deeper soil frost and higher N₂O emissions (winters 2015–2016 and 2016–2017) were
476 characterized by discontinuous and shallow snow cover and variable temperature conditions (Fig. 3 and 4). Shallow
477 snow cover combined with alternating cold and warm weather in the first two winters of the study period have likely
478 increased the number of freeze-thaw cycles and their intensity leading to higher total N₂O fluxes (Maljanen et al.,
479 2007; Ruan and Robertson, 2017). The results suggest the possibility for increasing winter N₂O emissions from
480 drained peat soils if winters continue to warm, the occurrence of extreme temperature fluctuations increases and snow
481 cover in the southern boreal region becomes shallower.

482 Similar to freezing, soil thawing triggered N₂O emissions during winter freeze-thaw cycles, but emissions
483 ceased within a few days of the onset of the thawing phase even if soil temperature continued to rise (Fig. 6 and S5).
484 Similar short-term N₂O peaks in response to soil thawing have been measured also in laboratory experiments by Teepe
485 et al. (2001), and Koponen and Martikainen (2004). Thaw-related emissions have often been explained by increased
486 N availability in the thawing soil (Groffman et al., 2006; Wagner-Riddle et al., 2017), and the cause of the short pulse
487 of N₂O flux during winter thawing might be related to the rapid use of labile N made available during the soil freezing
488 period. Release of N₂O accumulated in the frozen soil might also explain some of the short-term N₂O flux peaks
489 during thaw (Maljanen et al., 2007; Pihlatie et al., 2010). The response of N₂O fluxes to soil thaw during winter was
490 weaker than the response especially to early winter soil freezing which highlights the importance of freezing-related
491 N₂O emissions in the studied ecosystem.

492 Previously, several studies on both peat and mineral soils have emphasized the importance of thaw-related
493 spring N₂O fluxes in the annual N₂O budgets, with pronounced spring N₂O flux peaks in some cases accounting for a
494 large fraction of the annual budget (Pihlatie et al., 2010; Luo et al., 2012; Wang et al., 2023). In the present study,
495 spring soil thaw triggered N₂O emissions, but emissions increased slowly with increasing soil temperature and peaked
496 in late spring or summer, significantly later after soil thaw than reported in previous studies (Fig. 6 and S5). The strong
497 temperature dependence of spring N₂O fluxes may indicate that the substrate for the spring N₂O production comes
498 from the decomposing peat and litter in the warming soil. Temperature dependence of spring fluxes could be related

499 to drained peat soil, where the major source of N is known to be decomposing peat (Martikainen et al., 1993). Different
500 responses to thawing in winter compared to spring might be related to decreasing availability of N from early winter
501 towards spring (Koponen and Martikainen, 2004; Congreves et al., 2018), which also likely explains the tendency for
502 stronger response to freeze-thaw cycles in early winter.

503 High-flux periods during the growing season, especially in the summer, were associated with precipitation
504 events that increased soil moisture and raised WTL (Fig. 6, 7 and S5). These high-flux periods increased the total N₂O
505 budget of the rainy summers (2016 and 2017), whereas the N₂O budget was low in the warm and dry summer 2018.
506 Precipitation events may have increased the number of anoxic microsites in the soil, favoring N₂O production also
507 through denitrification (Congreves et al., 2018). Fast peat decomposition in the warm soil during the summer likely
508 reduced oxygen availability in the soil and increased N availability from the mineralizing peat resulting in high N₂O
509 fluxes after summer rain events (Maljanen et al., 2003). Low N₂O fluxes during dry summer are likely explained by
510 low microbial activity and substrate availability in the dry soil (Borken and Matzner, 2009; Congreves et al., 2018).
511 Our results on summer and winter N₂O fluxes suggest that low N₂O fluxes during dry summers might offset the effect
512 of the increasing winter N₂O fluxes on annual N₂O budgets if dry summers become more frequent in the warming
513 climate.

514 N₂O fluxes during autumn were low and showed little year-to-year variability (Fig. 5, 6 and S5). Low autumn
515 N₂O emissions have also been measured in previous studies (Maljanen et al., 2003; Luo et al., 2012), although Pihlatie
516 et al. (2007) and Alm et al. (1999) found increased autumn N₂O fluxes after litter fall in drained peatland forests. The
517 low contribution of autumn N₂O fluxes to annual emissions in the present study is probably explained by the more
518 nutrient-rich peat and the lower importance of N₂O production in the litter layer in the total N₂O production
519 (Martikainen et al., 1993; Pihlatie et al., 2007). The results indicate that the site-specific differences in the peat nutrient
520 availability could alter the contributions of different seasons to annual N₂O budgets. High temporal variability of
521 fluxes and greater sensitivity of N₂O fluxes to environmental conditions in nutrient-rich peatland forests are likely to
522 increase the sensitivity of N₂O budgets to increasing variability in seasonal conditions in the changing climate.

523

524 **4.2. Linkages to spatial variation**

525 Lower fluxes from the three low-flux chambers (maximum flux < 400 μg N₂O m⁻² h⁻¹) compared to high
526 N₂O fluxes (maximum flux > 1100 μg N₂O m⁻² h⁻¹) measured in the three high-flux chambers demonstrate the spatially
527 variable nature of N₂O flux even on a small scale within a few meters (Groffman et al., 2009; Hénault et al., 2012;
528 Jungkunst et al., 2012). What was notable was that the spatial differences in N₂O fluxes between chambers were
529 persistent across years. The persistence of spatial variation implies that spatial variation of N₂O flux is controlled by
530 long-term controls that persist throughout years with different weather conditions.

531 The long-term controls could include, for example, spatial variation in soil properties (e.g. pH, bulk density,
532 availability of different forms of N) or placement of plant roots both of which have been suggested to influence the
533 spatial variation in N₂O fluxes even at very small scales within the soil (Butterbach-Bahl et al., 2002; Jungkunst et al.,
534 2012; Kuzyakov and Blagodatskaya, 2015). In the present study, the high-flux chambers had fewer trees nearby than
535 low-flux chambers, and the distance to nearby trees was greater (Fig. 1, Table S1). Tree roots may have affected the

536 availability of different forms of nitrogen through nitrogen uptake and nitrogen inputs to soil (Kaiser et al., 2011;
537 Kuzyakov and Blagodatskaya, 2015; Hu et al., 2016), resulting in higher fluxes further away from the trees in this
538 case. Because trees affect the forest floor microclimate, ground vegetation and soil conditions through transpiration
539 and by influencing the distribution of rainfall and light in the forest (Butterbach-Bahl et al., 2002; Aalto et al., 2022),
540 variation in the tree cover may also have contributed to the spatio-temporal dynamics of N₂O fluxes. Although the
541 distance to trees seemed to explain some of the spatial variation in N₂O flux, the spatial variation, especially within
542 the small and high-flux chamber groups, remained unexplained. Ground vegetation was also not linked to spatial
543 variation of N₂O. The results emphasize the importance of comprehensive soil sampling (e.g. N forms, bulk density,
544 pH, C:N, root density) and chamber-specific measurements of environmental variables (e.g. soil moisture, soil
545 temperature, WTL), when studying spatio-temporal variation of N₂O flux, especially in the forested study sites with
546 variable microclimate.

547 Despite the large spatial variation in the N₂O flux, the high-flux periods identified for each chamber typically
548 occurred at similar times, although the exact length and timing of the high-flux periods varied (Fig. 4, Table S4).
549 Similarities in the temporal variation of fluxes suggest that temporal changes in the soil environmental conditions
550 affected N₂O fluxes relatively similarly across space. In previous studies, temporal patterns within sites were either
551 variable or common across space (Velthof et al., 2000; Krichels and Yang, 2019), with both findings mainly attributed
552 to the spatio-temporal variation of soil moisture. Stronger similarities in the temporal variation of N₂O flux within the
553 low and high-flux chamber groups indicate that some differences in the response of N₂O flux to environmental
554 conditions may be related to the overall spatial variation of the flux.

555

556 **4.3 Delayed responses**

557 The results indicate that N₂O flux has a delayed response to precipitation events with peak N₂O fluxes
558 measured on average 4 days after soil moisture and WTL peaks, and 5 days after rainfall (Fig. 9 and S7). Studies
559 mostly conducted on mineral soils in laboratories have found short time lags from the onset of anaerobiosis or water
560 saturation to the highest measured N₂O production, with lags ranging from few hours to less than two days (Firestone
561 and Tiedje, 1979; Smith and Tiedje, 1979; Russow et al., 2000; Song et al., 2019). Compared to the previous studies,
562 the observed lag times are long, with indication for even longer lags than seven days in some chambers.

563 The present data only allow us to hypothesize the causes of the long lag times after precipitation events. The
564 ability of peat to retain moisture and thus anaerobic microsites in the soil means that anaerobic conditions for
565 denitrification are maintained and the possible co-occurrence of nitrification and denitrification can last for longer
566 than in most mineral soils (Päivänen, 1973; Wrage et al., 2001; Walczak et al., 2002). The highest N₂O fluxes during
567 the growing season were reached on intermediate soil moisture (0.3–0.4 m⁻³ m⁻³) after the soil had started to drain and
568 WTL had started to decrease after a precipitation event (Fig. 7 and 9, S7). Based on this study and previous laboratory
569 studies, we suggest that after a period of high N₂O reduction activity and therefore relatively low N₂O fluxes from
570 denitrification in the wet soil soon after rain, N₂O production in the draining soil increased (Firestone and Tiedje,
571 1979; Russow et al., 2000; Congreves et al., 2018). As soil continued to drain, conditions for simultaneous nitrification
572 and denitrification became optimal (Bateman and Baggs, 2005; Wang et al., 2021; Song et al., 2022), further increasing

573 N₂O production and leading to the peak N₂O flux some days after rain. The ability of peat to retain moisture could
574 extend the time for soil drainage after rainfall and thus time before optimal conditions for N₂O production are reached.
575 Hydrophobic properties of dry peat soils can also extend the time before N₂O fluxes respond to soil wetting (Borken
576 and Matzner, 2009) contributing to longer lag times. To determine exact lag times in response to soil moisture peaks,
577 chamber-specific soil moisture data would be required.

578 Although models were not run for different seasons separately, the response of N₂O fluxes to precipitation
579 events seemed to be slower during autumn and resulted in lower N₂O flux peaks (Fig. 6 and S5). Lower temperatures
580 in autumn likely decreased microbial activity and mineralization of N from decomposing peat, which could explain
581 lower fluxes and slower response of N₂O fluxes to precipitation events in autumn (Holtan-Hartwig et al., 2002).
582 Chamber differences in the lag times associated with precipitation events and differences in the variable importance
583 of different environmental variables (Fig. 8 and S6) may also indicate varying sensitivities of N₂O production to
584 spatially varying soil conditions. These differences may be related to different microbial community, substrate
585 availability or soil properties that have been identified as important controls of N₂O production (Hénault et al., 2012;
586 Butterbach-Bahl et al., 2013; Hu et al., 2015) and are likely to shape the response of N₂O production to environmental
587 conditions.

588

589 **5. Conclusions**

590 This study shows high temporal and spatial variability in peatland forest N₂O fluxes with persistent spatial
591 patterns across years with different environmental conditions. The temporal variation of N₂O flux was strongly
592 influenced by seasonal weather conditions, especially precipitation, snow depth and drought. Temporally varying soil
593 conditions affect N₂O fluxes through complex responses that include delayed responses to soil wetting. Interactions
594 between spatially and temporally varying soil conditions, such as temperature, further shape the spatio-temporal
595 patterns of N₂O flux. The considerable small-scale spatial variation in N₂O fluxes is likely to be influenced by
596 relatively long-term controls such as soil properties and positioning of trees.

597 The observed high N₂O fluxes from the peatland forest highlight the role of nutrient-rich drained peat soils
598 as hotspots for N₂O emissions in the boreal region. The dependence of N₂O budgets on seasonally varying weather
599 conditions suggests high sensitivity of peatland forest N₂O budgets to changing climate. Winter N₂O emissions will
600 likely increase in the future due to warming winters with shallow and discontinuous snow cover. Summer N₂O
601 emissions may decrease and possibly offset the effect of warming winters on annual N₂O budgets in dry years. Year-
602 to-year variation in N₂O emissions will likely increase as extreme weather events are predicted to become more
603 frequent.

604

605 **6. Appendices**

606 **Appendix A. Thermal seasons**

607 Thermal winter was the season with daily mean air temperatures persistently below 0 °C and thermal summer
608 season with daily mean air temperatures persistently above 10 °C (Ruosteenoja et al., 2016; Finnish Meteorological

609 Institute, 2023). During spring and autumn, temperatures varied between 0–10 °C. Cumulative temperature sums of
 610 daily mean temperatures were then used to identify the starting days of the thermal seasons at which temperature went
 611 persistently above or below the seasonal temperature threshold (0 or 10 °C). The starting day of the thermal winter
 612 was the day after the annual cumulative temperature sum reached the maximum. The starting day of the thermal spring
 613 was the day after the minimum cumulative temperature sum was reached. Starting days of thermal summer and autumn
 614 were calculated similarly but by extracting 10 °C from the air temperatures before calculating the cumulative
 615 temperature sum (modified temperature sum). The day after the minimum modified temperature sum was reached was
 616 defined as the starting date of the summer, while the maximum modified cumulative temperature pointed the onset of
 617 thermal autumn.

618

619 **Appendix B. Evaluating the model performance**

620 R_2 of the chamber-specific models used in the analyses varied between 0.72 and 0.85 in OOB data, and
 621 between 0.60 and 0.69 in training period evaluation data (30 % of training period data) (Table B1). When predicting
 622 N_2O fluxes outside the training period (fourth measurement year), R_2 varied between 0.02 and 0.69. The performance
 623 of gap-filling models was tested only using OOB data and evaluation data within the whole study period (30 % of
 624 data). For gap-filling models, R_2 in OOB data varied between 0.71 and 0.84, while R_2 in evaluation data varied between
 625 0.67 and 0.78 (Table B2).

626 For the models used in the analysis, the poor prediction accuracy outside of the training period, especially in
 627 Chambers 3, 4, and 6, was likely due to overestimation of the general flux level during the relatively dry year 2019,
 628 which was excluded from the training period (Fig. S9). The model was also unable to predict anomalous high-flux
 629 period in low-flux winter 2018–2019 in Chamber 5 likely due to a lack of chamber-specific soil temperature data
 630 deeper in the soil. The temporal patterns of the flux otherwise followed temporal patterns of measured fluxes relatively
 631 well. Poor prediction accuracy outside the training period in part of the chambers indicates that predicting N_2O fluxes
 632 to a year with distinct environmental conditions compared to the years in the training data may lead to large under or
 633 overestimation of N_2O fluxes. The used models could benefit from additional explanatory variables, such as redox
 634 potential or the availability of different forms of nitrogen (Rubol et al., 2012; Saha et al., 2020). Including additional
 635 soil variables in the model could decrease the need to have excessively large model training periods to accurately
 636 predict and gap-fill N_2O fluxes.

637

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

642

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

643

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

648

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

649

650

651 7. Data availability

652 Flux data and supporting environmental data are available at: <https://doi.org/10.5281/zenodo.8142188> (Rautakoski
653 et al., 2023a). Simplified R code of the machine learning part of the study is made freely available at:

654 https://github.com/helenemilii/N2O_modeling. Python codes used in flux calculation and R codes used in data
655 analysis are available from the corresponding author by request.

656

657 **8. Supplement**

658 The supplement of the article is available at: <https://doi.org/10.5281/zenodo.10533480> (Rautakoski et al., 2023b).

659 **9. Author Contributions**

660 AL, MA, MK and PO set up the study design. Field maintenance of measurement systems was carried out by MK,
661 AL and PO. Fluxes were calculated by MK and filtered by HR. Data analysis, modeling and writing of the article
662 were done by HR with the support of AL and other co-authors.

663 **10. Competing interests**

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

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673

674 **12. References**

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