



Soil GHG dynamics after water level rise – Impacts of selection harvesting in peatland forests

Mikko Peltoniemi^{a,*}, Qian Li^a, Pauliina Turunen^{a,b}, Boris Tupek^a, Päivi Mäkiranta^a, Kersti Leppä^a, Mitro Müller^a, Antti J. Rissanen^{a,c}, Raija Laiho^a, Jani Anttila^a, Jyrki Jauhiainen^a, Markku Koskinen^b, Aleksi Lehtonen^a, Paavo Ojanen^a, Mari Pihlatie^b, Sakari Sarkkola^a, Elisa Vainio^b, Raisa Mäkipää^a

^a Natural Resources Institute Finland (Luke), Latokartanonkaari 9, 00790 Helsinki, Finland

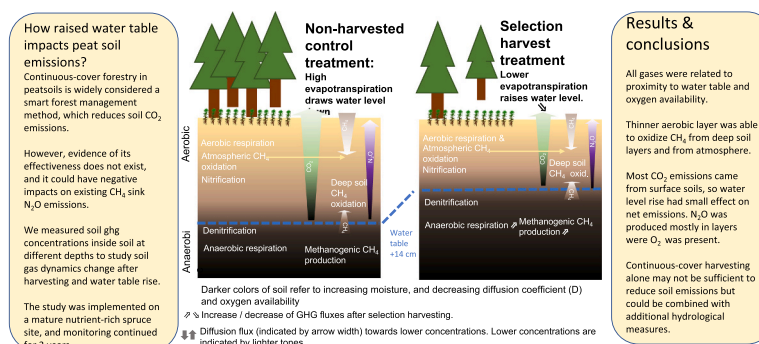
^b Environmental Soil Science, Department of Agricultural Sciences, University of Helsinki, Viikinkaari 9, 00790 Helsinki, Finland

^c Faculty of Engineering and Natural Sciences, Bio and Circular Economy research group, Tampere University, Korkeakoulunkatu 8, 33720 Tampere, Finland

HIGHLIGHTS

- Experimental selection harvesting of trees raised soil water table by 14 cm.
- Soil [GHG] profiles showed sustained CH₄ sinks in topsoils and near water table.
- Topsoils emitted CO₂ and N₂O, which were little affected by water table rise.
- Selection harvesting alone had only minor impact on emissions

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Jan Vymazal

Keywords:

Peatland hydrology
Gradient method
Continuous cover forestry
Norway spruce mire
Climate smart forestry
Soil greenhouse gas emissions

ABSTRACT

Managed boreal peatlands are widespread and economically important, but they are a large source of greenhouse gases (GHGs). Peatland GHG emissions are related to soil water-table level (WT), which controls the vertical distribution of aerobic and anaerobic processes and, consequently, sinks and sources of GHGs in soils. On forested peatlands, selection harvesting reduces stand evapotranspiration and it has been suggested that the resulting WT rise decreases soil net emissions, while the tree growth is maintained. We monitored soil concentrations of CO₂, CH₄, N₂O and O₂ by depth down to 80 cm, and CO₂ and CH₄ fluxes from soil in two nutrient-rich Norway spruce dominated peatlands in Southern Finland to examine the responses of soil GHG dynamics to WT rise. Selection harvesting raised WT by 14 cm on both sites, on average, mean WT of the monitoring period being 73 cm for unharvested control and 59 cm for selection harvest. All soil gas concentrations were associated with proximity to WT. Both CH₄ and CO₂ showed remarkable vertical concentration gradients, with high values in the deepest layer, likely due to slow gas transfer in wet peat. CH₄ was efficiently consumed in peat layers near and above WT where it reached sub-atmospheric concentrations, indicating sustained oxidation of CH₄ from both atmospheric

* Corresponding author.

E-mail address: mikko.peltoniemi@luke.fi (M. Peltoniemi).

<https://doi.org/10.1016/j.scitotenv.2023.165421>

Received 13 January 2023; Received in revised form 13 June 2023; Accepted 7 July 2023

Available online 18 July 2023

0048-9697/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

and deeper soil origins also after harvesting. Based on soil gas concentration data, surface peat (top 25/30 cm layer) contributed most to the soil-atmosphere CO₂ fluxes and harvesting slightly increased the CO₂ source in deeper soil (below 45/50 cm), which could explain the small CO₂ flux differences between treatments. N₂O production occurred above WT, and it was unaffected by harvesting. Overall, the WT rise obtained with selection harvesting was not sufficient to reduce soil GHG emissions, but additional hydrological regulation would have been needed.

1. Introduction

In the boreal zone of the northern hemisphere, peatlands are widespread (Nichols and Peteet, 2019; Xu et al., 2018) and much of the peatland area has a forest cover (e.g., Vitt, 2006; Vompersky et al., 2011). During the past century, the share of peatland forests has increased by systematic drainage by ditching to improve forest growth: altogether, there are currently ca 15 Mha of drained peatland forests in the boreal and temperate zones. In addition, global change is resulting in increased woody vegetation in previously open peatlands (Hedwall et al., 2017; Ratcliffe et al., 2017). Warming climate, and increasing canopy cover are associated with lowering soil water-table level (WT) due to increasing evapotranspiration (Sarkkola et al., 2010). In densely forested nutrient-rich sites, especially, the WT, under which the peat soil carbon (C) has been safely stored, can fall so deep that efficient aerobic decomposition in the oxic layer far surpasses C input to soil through plant litter above and below ground (e.g., Ojanen et al., 2013). While lowering WT is associated with increased soil CO₂ emission (Ojanen and Minkinen, 2019), it leads to a decreasing methane (CH₄) emission, and under dense forest the peat soil can be a small sink of atmospheric CH₄ (Ojanen et al., 2013, 2010). Suitable conditions for N₂O production should extend down to WT level until denitrification has stable conditions and it can consume N₂O. Altogether, lowered WTs in drained nutrient-rich peatland forests are associated with higher net soil greenhouse gas emissions, and even though tree biomass accumulation may maintain a net greenhouse gas sink for quite long (Ojanen et al., 2013), the soil emissions typically make such sites net sources over a forest rotation period (Ahtikoski et al., 2022; Shanin et al., 2021).

Ecosystem restoration that involves rewetting would lead to reduced climate warming impact of the high-emission sites in long term (Ojanen and Minkinen, 2020). Yet, the nutrient-rich peatland forests with high productivity make an important source of timber in some regions. For both economic and environmental reasons, immediate restoration of the whole area is thus not a likely option, but alternative ways to reduce the climate impact is being sought, since currently applied rotation forestry results very high emissions especially after clear-cutting (Korkiakoski et al., 2019). In continuous-cover forestry that applies selection harvesting, which decreases the canopy cover and evapotranspiration of trees and, consequently, raises the WT, the net soil emissions may be reduced, while economic timber production is continued (Nieminen et al., 2018a). However, verification of the success of tree density manipulation in reducing soil emissions takes time. For faster progress, we need to understand the changes in the in-soil production and fluxes of greenhouse gases in relation to changes in WT.

Soil CO₂ emissions mainly consist of aerobic heterotrophic respiration from organic matter decomposition and autotrophic respiration by plant roots. The activity of microbes that are responsible for the decomposition of litter and peat, and the consequent CO₂ emissions, increases with temperature (Davidson and Janssens, 2006; Mäkiranta et al., 2009). Heterotrophic respiration is highest at intermediate moisture levels but decreases when the soil becomes anoxic due to waterlogging, which also means low redox potential (Mäkiranta et al., 2009; Moore and Dalva, 1993). On the other hand, litter and peat decomposition may also slow down if the soil becomes too dry (Mäkiranta et al., 2009). Decomposition rates are also affected by substrate quality (Straková et al., 2012), fresh detritus decomposing faster than old material all other factors being equal. Methane (CH₄; and

simultaneously also some CO₂), on the other hand, is produced in anoxic conditions where fermentation and methanogenesis are the only available pathways for microbial energy acquisition. Microbes participating in methane production, i.e. methanogenic archaea, are obligate anaerobes, which only survive at anoxic conditions when redox is very low. In peatlands, the soil water table (WT) level variation drives the changes of oxygen status in soil, which affects the availability of alternative (to CO₂) inorganic (e.g. NO₂⁻, Fe³⁺, SO₄²⁻) and organic (e.g. quinones) electron acceptors. They divert the flow of electrons (from H₂, volatile fatty acids, alcohols) generated by fermenting bacteria to other anaerobic respiration processes (Klöpfer et al., 2014), which inhibits methanogenesis. On the other hand, methanogenesis can be stimulated by higher temperature, rhizodeposition (root exudates) (Waldo et al., 2019) and litter inputs (Corteselli et al., 2017).

Aerobic autotrophic nitrification and anaerobic heterotrophic denitrification are considered the most important N₂O producing processes in soils, although other processes (e.g. nitrifier-denitrification and abiotic denitrification) affect N₂O production as well (Butterbach-Bahl et al., 2013). In oxic conditions, in nitrification, ammonium (NH₄⁺) originating from organic N via decomposition, is oxidized via nitrite (NO₂⁻) to nitrate (NO₃⁻), producing N₂O as a by-product. In anoxic conditions, N₂O is produced as an intermediate product of sequential denitrification of NO₃⁻ to N₂. In stable anoxic conditions, N₂O emissions are usually low because anoxia and lack of NO₃⁻ limit nitrification and denitrification, respectively (Leppelt et al., 2014). In contrast, in forestry-drained peatlands, WT has drawn down and mineralization-nitrification actively releases NO₃⁻ from N-rich organic matter. The fluctuating WT level, however, leads to varying soil moisture and the mineralized NO₃⁻ can become available for denitrification occurring deeper in soil. Low WT, and the temporal variation of moisture, could thus favor high N₂O production. Earlier field studies have indeed observed that peatland N₂O emissions are high when WT is low in fertile peat soils (Martikainen et al., 1993; Ojanen and Minkinen, 2020; Pärn et al., 2018; Regina et al., 1996).

Current knowledge about peatland forest GHG responses to WT changes largely stems from the flux measurements made using open-bottom chambers and/or eddy covariance. These methods are, however, restricted to observing aggregate result of gas generating processes at the soil-atmosphere or ecosystem-atmosphere interface. Soil gas concentrations, on the other hand, record the current state of gas production, consumption, and transport within soils. If the measurements are placed vertically, sinks and sources of gases inside soils can be resolved, as well as fluxes at soil-atmosphere interface partitioned using the gradient method (Davidson and Trumbore, 1995; Jong and Schappert, 1972; Sotta et al., 2007). Generally, flux rates estimated with the gradient method have compared well with the estimates made with open-bottom chambers (Maier and Schack-Kirchner, 2014).

Studies using concentrations gradients in open peatland types in temperate zone have shown that soil CH₄ and CO₂ concentrations tend to increase with depth (Clymo et al., 1995; Elberling et al., 2011; Nilsson and Bohlin, 1993). They have also indicated that CH₄ is mainly produced just below WT, and at lower rates also deeper in soils (Clymo et al., 1995). CH₄ is effectively consumed in a thin layer above WT where both O₂ and CH₄ exist (Watson et al., 1997), but the consumption zone can extend below WT where O₂ is hardly detectable (Elberling et al., 2011). Forested peatlands, however, differ from open peatland types markedly. WT is considerably lower, peat material well decomposed and

fine structured, and they often lack vegetation with aerenchymous tissue such as *Carex* spp., which offers efficient gas exchange route between subsurface layers and atmosphere (Schimel, 1995; Shannon and White, 1994). Consequently, gas concentration could potentially experience steeper gradients, and sink-source distribution of gases differ from those in open peatlands/wetlands. A study on a forested bog in Ontario, Canada, showed a steep increase in CH₄ concentrations from unsaturated zone to below WT, and oxidation of CH₄ within 20 cm above WT (Roulet et al., 1993). No studies, however, have investigated associations between CH₄, CO₂, N₂O, and O₂ sink-source distributions together, or related them to soil-atmosphere fluxes when hydrological conditions change.

The objectives of this study are to provide understanding on how WT level raise associated with selection harvesting impacts 1) GHG (CO₂, CH₄ and N₂O) and O₂ concentrations (hereafter [CO₂], [CH₄] and [N₂O], [O₂], respectively) in soil profile; 2) the vertical distribution of GHGs' production and consumption processes in soil; 3) fluxes of GHGs at soil-atmosphere interface, and 4) to identify drivers of these processes. We hypothesized that

- i) CO₂, CH₄, and N₂O concentrations are decoupled, as they are generated in different soil processes with distinct favorable conditions; CO₂ is mostly produced in heterotrophic respiration under oxic conditions, CH₄ is produced through anaerobic methanogenesis, while N₂O is produced in incomplete nitrification or denitrification processes in dynamic moisture environment.
- ii) The selection harvesting and the subsequent WT raise decrease the CO₂ emission from the soil, as topsoil becomes moister and O₂ less abundant.
- iii) The selection harvesting decreases the CH₄ sink function or reverses the soil to a CH₄ source, because the shallower oxic layer increases [CH₄] near the soil surface and the topsoil does not consume all CH₄ produced below the WT.
- iv) N₂O concentrations are highest near the WT where moisture conditions alternate from completely anoxic to (partially) oxic. Due to the selection harvesting and raising WT, the source of N₂O emissions to atmosphere shifts closer to the soil surface than before harvest.

2. Materials and methods

2.1. Site description and measurement locations

The study was conducted in two forestry-drained peatland sites in Finland where harvesting experiments were established earlier (Table 1).

The Lettosuo study site locates in Tammela municipality (Table 1). It was originally a sparsely treed mesotrophic fen before drainage, but not quite as nutrient rich as Paroninkorpi. Drainage history of the site started in the 1930's, but more intensive drainage was done in 1969. Now it was classified as a *Vaccinium myrtillus* type II site (Mtkg II). The peat layer thickness varies between 1.5 and 2.5 m. The ditches were approximately 1 m deep and their spacing was 45 m. The dominant tree species were Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies* (L.) H. Karst) and pubescent birch (*Betula pubescens*). Ground vegetation was patchy and consisted of dwarf shrubs such as *Vaccinium myrtillus* and herbs such as *Trientalis europaea* and *Dryopteris carthusiana* (Bhuiyan et al., 2017). The moss layer was dominated by *Pleurozium schreberi* and *Dicranum polysetum*, as well as some *Sphagnum* species (e.g. *Sphagnum angustifolium* and *S. russowii*). The average area-specific biomass of living moss layer was 155 g/m² and it ranged between 67 and 406 g/m². The soil quality information of Lettosuo was listed in Table 2.

Lettosuo had two harvesting treatments: selection harvesting, clear-cutting and non-harvested control. The measurements of this study were conducted in selection harvesting area (called "Harvest") and non-harvested area (called "Control"; Fig. 1). The selection harvesting was conducted during February–March 2016. The average stand volume was decreased from 278 m³ ha⁻¹ to 208 m³ ha⁻¹ after harvesting with ~75 % of basal area of trees (BA) of the dominant pine trees were removed. During the harvesting, the proportions of Scots pine, Norway spruce and pubescent birch were decreased from 60 %, 20 % and 20 % to 2 %, 51 % and 47 % (BA), respectively.

Paroninkorpi study site locates in Janakkala (Table 1). It was originally a sparsely treed mesotrophic fen with herbs and tall sedges characterizing the ground vegetation. The site was ditched to increase forest growth in 1940s with the ditch network complemented in 1960s. Altered by drainage, the site was classified as Herb-rich type II drained peatland forest according to the Finnish classification system (Vasander and Laine, 2008). The peat layer was >1.5 m deep. The ditch spacing

Table 1
Information about the study sites.

Site	Location, ETRS-TM35FIN	Site type ^a	Peat type	Annual/Jun-Sep mean temperature (°C) ^b	Annual mean Precipitation (mm) ^b
Lettosuo	60.63° N, 23.95° E	Mtkg II	Carex	4.6/13.9	627
Paroninkorpi	61.01° N, 24.75° E	Rhtkg II	Carex	4.2/13.7	645

^a According to Finnish site type classification system for drained peatlands (Vasander and Laine, 2008).

^b Pirinen et al., 2012.

Table 2

Peat quality parameters, mean with standard deviation in parentheses. According to Anova, the means of C, N, and C:N differed significantly across the sites (all $p < 0.003$), but not across the treatments. pH did not differ significantly across sites or treatments.

Site	Depth ^a , cm	C, g/kg	N, g/kg	C:N	pH (CaCl ₂)
Lettosuo	0–10	546 (4.4)	22.4 (2.29)	24.7 (2.42)	2.62 (0.0501)
	10–20	586 (10.1)	24.4 (1.89)	24.3 (2.34)	2.67 (0.0566)
	20–30	583 (5.95)	21.6 (1.92)	27.3 (2.73)	2.75 (0.0731)
	30–40	582 (2.54)	19.7 (0.878)	29.5 (1.38)	2.84 (0.092)
	40–50	582 (15.3)	18 (0.765)	32.5 (1.64)	2.96 (0.111)
Paroninkorpi	0–10	520 (6.77)	18.5 (2.23)	28.3 (3.67)	2.74 (0.281)
	10–20	534 (7.1)	18 (2.23)	30 (3.63)	2.5 (0.0791)
	20–30	549 (10.9)	18.3 (2.12)	30.2 (2.99)	2.57 (0.0906)
	30–40	566 (8.71)	17.2 (2.88)	33.7 (5.09)	2.77 (0.117)
	40–50	565 (7.57)	17.8 (2.64)	32.3 (5.32)	2.91 (0.261)

^a Depth for peat quality samples measured below the living moss layer.



Fig. 1. Locations of study sites in Finland (left), harvest experiment layout and measurement locations in Paroninkorpi (middle) and Lettosuo (right) forestry-drained peatland forests.

was approximately 60–70 m, and the depth was 0.55–0.7 m. The dominant tree species is Norway spruce (*Picea abies* (L.) H. Karst) with heights of 20–22 m. Ground vegetation was composed of mosses (mostly *Sphagnum girgensohnii*, also *Hylocomium splendens*, *Pleurozium schreberi* were abundant), dwarf shrubs (mostly *Vaccinium myrtillus*), and some herbs (e.g. *Trientalis europaea*, *Oxalis acetosella*). Mean biomass of living moss layer was 203.5 g/m² and it ranged between 10.2 g/m²–357.6 g/m². The soil quality information of Paroninkorpi was listed in Table 2.

The selection harvesting treatments in Paroninkorpi were executed in February 2017. Before harvesting, the latest forest management operations on this site were conducted in the 1980s. Non-harvested control (called ‘Control’) and harvest treatments with two harvesting intensities (‘Harvest’) were established on 40 × 40 m plots. Plots were separated by buffer zones (approximately 10–20 m) with intact forest structure, with ditches separating blocks of three plots arranged in a row (Fig. 1), achieving hydrological separation of the blocks. The stand characteristics measurements of this study were conducted on two locations in plot 1 (harvest, pre-harvest basal area (BA) was 24.5 m² and LAI was 5.7 m²/m², post-harvest BA was 16.9 m² and LAI was 3.8 m²/m²), one location in plot 5 (harvest, pre-harvest BA was 24.7 m² and LAI was 5.5 m²/m², post-harvest BA was 11.6 m² and LAI was 2.6 m²/m²), and three locations in plot 6 (control, BA 23.6 m² and LAI 5.2 m²/m²) (Laurila et al., 2021; Leppä et al., 2020).

2.2. Concentration profile measurements

2.2.1. Set up and installation of gas collectors

To collect soil gas samples from different depths, silicon rubber tubes were inserted in soil. Gas concentrations in the silicon rubber tubes equilibrate with the gas concentrations in the surrounding soil environment. There is evidence that silicon rubber tubes are a reliable method for measuring gas concentrations from soil atmosphere (Jacinthe and Dick, 1996), and they are comparable with the gas extraction equilibration technique which has been often used for measuring dissolved gas contents in liquids (Jacinthe and Groffman, 2001). Each collector was made from gas-permeable 220 cm silicone rubber tube (inner d = 10 mm, outer d = 15 mm) with a total volume of approximately 165 cm³. For sampling, a shorter (55–105 cm) non-permeable PTFE tube (inner d = 4 mm, outer d = 6 mm) with three-way faucet was connected with the silicon rubber tube and drawn to

the soil surface. The other end of the silicon rubber tube was sealed. Connections and sealings were made with sealing tape, cable ties, heat shrinkable plastic tubes and metal tighteners. The gas collectors were tested for waterproofness before field use. Gas collectors were placed inside hoover tubes to prevent the compression of silicon rubber tubes in soil.

Six gas collector systems with measurement depths of 25, 45, and 65 cm were installed in Lettosuo selection harvest plot (*N* = 3) and control plot (*N* = 3) in 2016. Installations in Paroninkorpi were made in two stages. First, we installed 3 collector systems with measurement depths of 30, 50 and 80 cm in plots 1, 5 and 6 during 26–27th July 2018. After preliminary data analyses from Paroninkorpi, we installed additional gas collectors on 2nd May in 2019, supplementing the existing measurement set ups in Paroninkorpi with additional gas collectors at 10 cm depth, and installed three new collector systems with measurement depths 10, 30, and 50 cm (high WT prevented installing collectors to 80 cm). Two of these collector systems located in plot 6 and one in plot 1. After supplementary installations, both control and harvest treatments in Paroninkorpi had 3 soil gas profile measurement systems. The new collectors were installed without hoover tube covers, as none of the gas collectors showed symptoms of compression.

To install the gas collectors deep in soil, square-shaped pits were excavated. The locations of the pits were selected carefully to represent the typical conditions of treatments and to avoid major roots of living trees, which could prevent excavation. During excavation, soil was removed using spades and organized carefully to a sheet next to the pit so that it could be placed back after the installation of the collectors. The collectors were installed by carefully carving into the pit wall so that the surrounding soils were kept intact.

2.2.2. Collection of gas samples

The gas samples from collectors were sampled during the growing season (May–October) after the installation of the collector systems. Gas samples were taken using 60 ml syringes (SOL-M™). The sample was immediately injected into pre-vacuumed 12 ml glass vials (Labco Exetainer® vials with pierceable gray chlorobutyl septa for Standard Exetainer® caps). The sample in the first vial was used for concentration analysis, and the second for isotope analysis. Different syringes and needles were used for collecting gases from different depths. Between the samplings of different collectors, the syringes were flushed twice

with fresh air to avoid the influence of the previous sample.

In 2019 and 2020, gas samples were also taken inside the moss layer, at 1 cm depth, using a syringe and injected into the glass vials. Atmospheric reference concentrations of CH₄ and CO₂ were measured with air at 2 m above the sampling locations under each treatment in both study sites in June, July and August in 2019.

2.2.3. Analyses of GHG and O₂ concentrations

The CO₂, CH₄, N₂O and O₂ concentrations of the collected gas samples were analyzed by gas chromatograph (GC, Agilent 7890A, Agilent Technologies, California, USA). A volume of injected gas sample (1 ml) was evenly divided up into two columns in GC and CH₄ and CO₂ concentrations were measured with flame ionization detector (FID) by each column (Pihlatie et al., 2013; Vainio et al., 2021). O₂ concentration was measured using thermal conductivity detector (TCD), and N₂O was measured with an electron capture detector (ECD) in the other column. The lowest detectable concentration of CH₄ for this instrument was 0.10 ppm, and 151 ppm for CO₂ (Vainio et al., 2022).

2.3. Chamber measurements of gas fluxes

The gas flux between soil and atmosphere were measured biweekly during May–November 2020. For each measurement, an opaque chamber (0.3 m in diameter and 0.295 m in height) was placed on top of the soil surface (incl. understorey vegetation) and the evolution of CO₂ and CH₄ concentrations in chamber were measured with a LI-COR LI-7810 CH₄/CO₂/H₂O Trace Gas Analyzer (LI-COR Biosciences; Lincoln, NE, USA). The chamber was equipped with a thermometer to measure the temperature inside and a low-speed battery-operated electric fan for mixing air inside the chamber during measurement. Each measurement lasted for at least 3 min and the gas concentration was recorded by one second interval. The fluxes were calculated by first estimating the rate of gas ratio change (in ppm) in the chamber by linear regression, and then converting to concentration evolution using the ideal gas law, where we used mean chamber temperature and standard atmospheric pressure. The concentration measured during the initial 30 s period of pressure equalization was always removed from the flux calculation.

2.4. Monitoring of water table (WT) level, soil temperature, redox, and other environmental parameters

Water table (WT) level was manually measured biweekly during the growing seasons by the perforated plastic dipwells installed next to gas collector / flux measurement sites in Paroninkorpi during 2019–2020. In addition, it was also automatically recorded hourly by data loggers (Tru Track WT-HR-loggers and Odyssey Capacitance Water Level Loggers). Continuously measured data was calibrated with the manually observed data to create continuous WT time series (daily average) for each plot. In Lettosuo, plot average WT was calculated from data produced by four Odyssey data loggers that were located near gas collectors and flux measurement spots.

Soil temperature data were monitored with Thermochron® iButton® sensors (DS1921G) (Maxim Integrated Products, Inc.) at depth of 30 cm near gas collectors. In Lettosuo, temperature loggers were only near sample points 1A and 2B in 2019 and near points 1A, 2B and 2C in 2020. During the chamber flux measurements (see 2.3), soil temperature was also manually measured at 5 cm and 30 cm depth.

The redox potential (Eh) at 10, 30, 50, 80 cm depths in Paroninkorpi were measured using Paleo Terra redox sensors (PaleoTerra, Amsterdam, The Netherlands). The reference electrode was an Ag-AgCl electrode immersed in a saturated KCl solution. The redox potential relative to reference electrode were measured with three connected Pt electrodes per depth and averaged for each sensor system and depth. The measured redox potentials were converted to Standard Hydrogen Electrode (SHE) using a fixed potential difference of 213 mV, and they represent values at pH = 7. The measured values were not corrected with temperature in

this study, as temperature differences at deep soil layers were small. The accuracy of this sensor can be ± 10 meV in field conditions, while it can be larger in our condition due to lack of correction with temperature.

The precipitation of Paroninkorpi was monitored by the Lammi weather station which was <10 km away from the study site. For Lettosuo, it was monitored by Salkola weather station which was <4 km away from the study site. Air temperature was measured at both study sites. Further information about these measurements was described in (Laurila et al., 2021).

Data used in the analyses is shared openly in a Zenodo online repository (Peltoniemi et al., 2022).

2.5. Environmental conditions during the field measurements

The daily mean air temperature and rainfall showed similar values and seasonal patterns in the two study sites during 2018–2020 (Fig. 2). Water table (WT) fell deeper as the summer progressed, and simultaneously the WT differences between the treatments increased; these developments were interrupted by occasional rainfalls. Dynamics of WT seemed slower in Paroninkorpi than in Lettosuo (Fig. 2). On average, selective harvesting treatment had 10.3 and 13.6 cm higher WT than the unharvested controls during 2018–2020 in Lettosuo and Paroninkorpi, respectively (mean WT was -46.2 and -56.5 cm in Lettosuo and -56.8 and -70.4 cm in Paroninkorpi for harvest treatment and control, respectively). Corresponding rises of WT calculated for the soil gas sampling dates were 14 cm, mean levels being -55.8 and -69.6 cm in Lettosuo, and -62.3 , and -76.3 cm in Paroninkorpi. Redox potential at 10 and 80 cm depth in Paroninkorpi were less affected by WT, while it clearly increased with decreasing WT in the middle soil layers (Fig. 2), creating a logistic relationship with distance to WT (Supplementary B Fig. 1).

The redox potential in the soil profiles at Paroninkorpi was mostly in the range theoretically associated with O₂ reduction above the -80 cm level in 2019, and above the -50 cm level in 2020. Redox potential in the lowest depths was at the levels associated with NO₃⁻ or Fe(III) reduction. In general, redox potential was lower in the harvest plot than in the control plot, consistent with the generally higher WT in the harvested plot. The potential was never at the levels generally associated with CO₂ reduction.

2.6. Data analysis

2.6.1. Modelling of porosity, water content and diffusion of gases in soil

The bulk density of soil was measured from just below the (or 'the bottom of') living moss layer to 50 cm depth below this level by 10 cm intervals at both sites. The measured data were interpolated by Generalized additive model (GAM) to 1 cm intervals for the estimation of moisture and gas permeability in soil. The bulk density profiles showed that the density of peat increased then decreased with depth, and that peat was denser in Paroninkorpi than in Lettosuo (Supplementary A Fig. 1A).

First, the porosity and water retention curves (van Genuchten, 1980) for each 1 cm layer were obtained as a function of bulk density following (Päivänen, 1973). The calculations showed that porosity of peat in Lettosuo was larger throughout the soil profile than in Paroninkorpi (Supplementary A Fig. 1B). For the moss layer, where the bulk density was not measured, we applied the water retention curve with the poorest water retention for *Carex* peat (Päivänen, 1973).

Soil moisture of each soil layer at 1 cm interval was then derived based on their distance to WT, thus assuming the soil column is in hydraulic equilibrium (constant hydraulic head in vertical dimension) (Skaggs, 1980). Soil moisture was then estimated for each 1 cm soil layer for a range of WT values observed in the measurements. The pre-calculated and tabulated soil moisture estimates were used to calculate soil gas diffusivities during the soil gas sampling (see next section).

The in-soil fluxes of CO₂, CH₄ and N₂O between soil layers

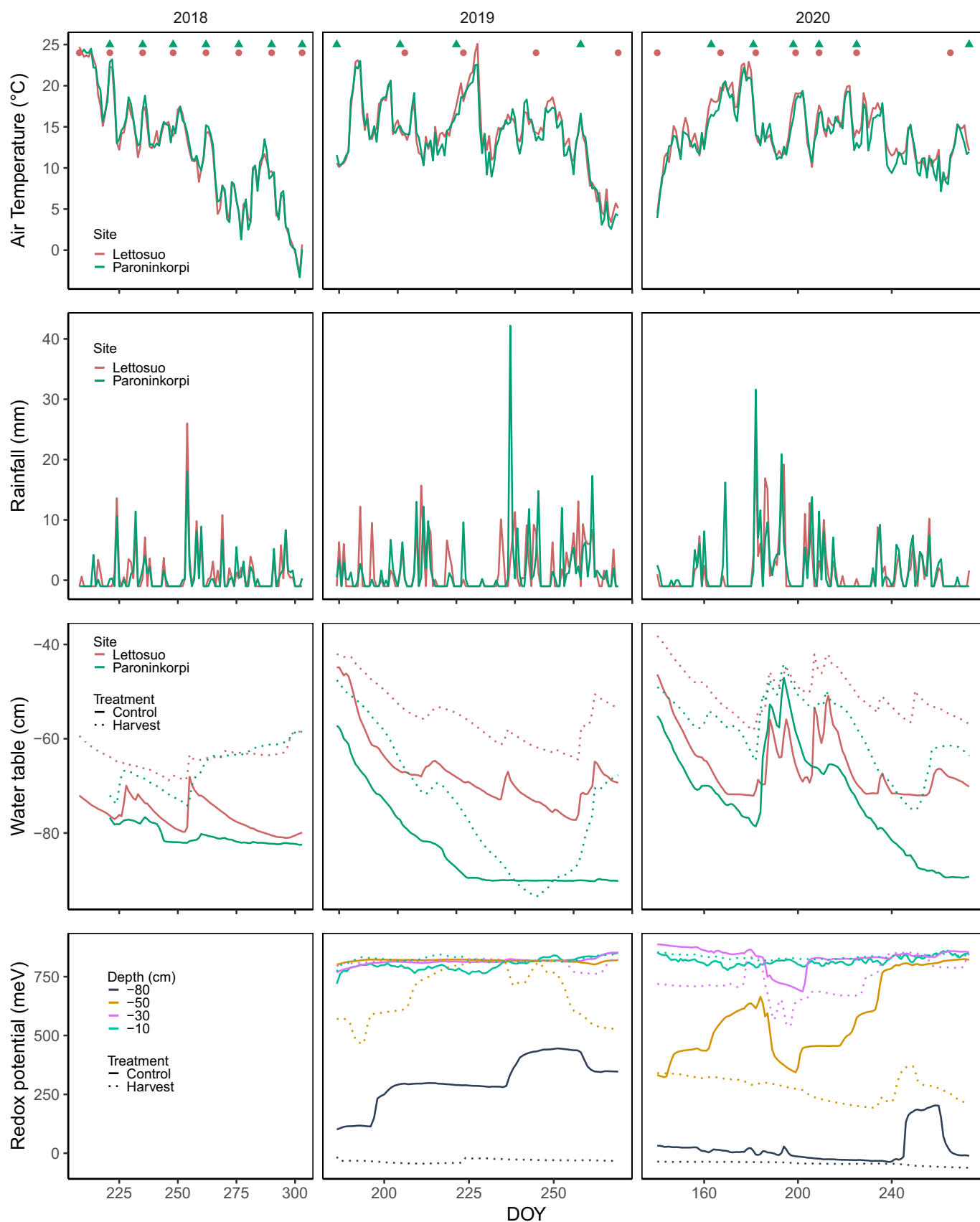


Fig. 2. Air temperature, precipitation, water table (WT) in Lettosuo and Paroninkorpi sites and redox potential in Paroninkorpi site in 2018–2020. Symbols in the top panel indicate the sampling dates for the gas concentrations.

were calculated for topsoil layer (25–1 cm in Lettosuo and 30–1 cm in Paroninkorpi); middle layer (45–25 cm in Lettosuo and 50–30 cm in Paroninkorpi) and deep soil layer (65–45 cm layers in Lettosuo and 80–50 cm in Paroninkorpi), assuming that diffusion dominates the vertical movement of gases. Diffusion is sensitive to soil moisture, so we used the modelled soil moisture and estimate porosity to adjust the diffusion coefficients at 1 cm interval for the entire soil column. Detailed calculation of diffusion using the Fick's equation, and the estimated diffusion coefficient profiles as a function of WT are presented in Supplementary A.

2.6.2. Statistical analysis

The treatment effect on gas concentrations in soil profile, in-soil fluxes between soil layers, and fluxes measured by chamber were analyzed using mixed effects models. Rather than trying to explain factors driving the differences in these variables we wanted to see if there are differences in the means of the gas concentrations by treatment and under high/low WT conditions (above/below –65 cm depth). General form of the fitted equations was

$$G(f(y_{ij})) \sim x_i + \epsilon_{ij},$$

where G is the distribution function and $f(\cdot)$ is either the identity function or $\log(y)$, x is a vector of explanatory variables at measurement location i , j identifies the repeated measure of the gas samples taken from the same measurement location and $\epsilon_{ij} \sim N(0, \sigma^2)$. The selection of G and $f(\cdot)$ was based on the best fitting found among various distributions using “fitdist” function under “fitdistplus” package in R (version 4.1.2, R Core Team, 2021). The fluxes measured with open-bottom chamber followed normal distribution, and the significance of treatment effect was analyzed by linear mixed model (LMM). The gas concentrations and in-soil fluxes between soil layers followed gamma distribution and generalized linear mixed model (GLMM) was used to study the effects of treatment and high/low WT (above/below 60 cm depth) conditions. The function `glmmTMB` in package “glmmTMB” was used to fit the models. The statistics were made for each study site and each soil layer separately.

The boosted regression trees (BRT) were used to evaluate the important environmental drivers of gas concentrations. Using BRT, we estimated the relative influences and functional responses of environmental factors on CO_2 , CH_4 , and N_2O concentrations in the soil profile. The BRT machine learning method combines regression (split tree) models and boosting (combining multiple tree models for improved prediction) and gives ecological insights and reveal nonlinearities and interactions among variables (Elith et al., 2008). The optimum number of trees and the final models were determined by a cross-validation method of the `gbm` package version 2.1.8 (Elith et al., 2008) for the analysis. We varied the learning rate, tree complexity, and bag fraction, which control the contribution of each tree, the number of splits (interaction depth), and the proportion of data used in fitting/validation, to see if model fits consistently improve with any of the parameters. No clear trends were found, so we fit the final model with learning rate set to 0.01, tree complexity to 3, and bag fraction to 0.75. The BRT analyses were also conducted in the R software environment.

3. Results

3.1. Gas concentration profiles

Soil CO_2 concentration ($[\text{CO}_2]$) increased steeply with depth under harvest treatment, while the depth profile was flatter under control treatments for both sites (Fig. 3 A-B). The $[\text{CO}_2]$ in the deepest layer was significantly increased by selection harvesting at both sites ($p = 0.001$ for 65 cm depth in Lettosuo; $p = 0.001$ for 80 cm depth in Paroninkorpi; Supplementary C Table 1.1).

CH_4 concentration ($[\text{CH}_4]$) was highest in the deepest soil layers, and lowest (sub-atmospheric concentration) in the middle layers (Fig. 3 C–D). Under control treatment, however, the sub-atmospheric concentrations even extended to the deepest soil layers in Lettosuo irrespective of the WT condition, and in Paroninkorpi when WT was low (Fig. 3 C–D). The harvest treatment significantly increased the $[\text{CH}_4]$ in the deepest layer in Lettosuo ($p < 0.001$ for 65 cm depth; Supplementary C Table 1.2). Although O_2 concentration ($[\text{O}_2]$) was low in the deepest layers at both sites (Fig. 3 G-H), high $[\text{CH}_4]$ values ($[\text{CH}_4] > 150$ ppm) were only observed under harvest treatment in Lettosuo with $[\text{CH}_4]:[\text{CO}_2]$ ratio higher than 0.1 (Supplementary B Fig. 3), indicating high methanogenic activity and small consumption of CH_4 .

N_2O concentration ($[\text{N}_2\text{O}]$) was highest in the middle layers (at 45 cm in Lettosuo and at 50 cm depth in Paroninkorpi) when WT was high (Fig. 3 E-F), while no consistent treatment effect was found (Supplementary C Table 1.3). $[\text{N}_2\text{O}]$ below 10 cm depth showed much higher level in Paroninkorpi than in Lettosuo (Fig. 3 E-F).

Temporal patterns in all gas concentrations profiles were consistent during the whole monitoring period but affected by fluctuating WT (Supplementary B Fig. 2.1–2.4). High $[\text{CH}_4]$ were observed when $[\text{CO}_2]$ was also high, although their correlations were only apparent in the selection harvesting treatments where $[\text{CH}_4]$ showed wider range (Fig. 4). Both $[\text{CO}_2]$ and $[\text{CH}_4]$ negatively correlated with $[\text{O}_2]$. Nevertheless, the co-variation of $[\text{N}_2\text{O}]$ with other gases was less clear, and high $[\text{N}_2\text{O}]$ were observed at both high and low $[\text{O}_2]$ conditions.

3.2. Emissions and in-soil fluxes of CO_2 , CH_4 and N_2O

The chamber measurements indicated that the soil of the harvest treatment was a smaller source of CO_2 to atmosphere than the control, but significant difference were only found in Paroninkorpi ($p = 0.012$; Fig. 5, see also Supplementary B. Fig. 4). The calculated in-soil CO_2 fluxes between soil layers showed that the CO_2 fluxes to atmosphere mostly originated from topsoil layers (Fig. 5), and the in-soil fluxes from topsoil layers showed a trend of decreasing when WT increasing in Paroninkorpi site (Supplementary B Fig. 5.1) While only a small fraction of CO_2 emission to atmosphere came from the deep soil layers studied (Fig. 5). The in-soil fluxes in the deepest soil layers studied were higher in the harvest treatment than control ($p = 0.002$ for Lettosuo and $p < 0.001$ for Paroninkorpi; Supplementary C Table 2.1).

Both sites were sinks of atmospheric CH_4 under both treatments showed by chamber measurements (Fig. 5, see also Supplementary B Fig. 4). In Paroninkorpi, the CH_4 sink was smaller in the harvest treatment than in the control ($p = 0.014$), but no significant difference was found in Lettosuo. The topsoil layers showed downward fluxes of CH_4 , corresponding to the sink measured with chamber. At both sites, we observed net CH_4 upwards fluxes in the deep soil layers and they increased with raising WT (Supplementary B Fig. 5.2), while the fluxes in middle layers were close to zero. These results imply that CH_4 produced in deep soil was also consumed in soil and that there was no net transfer of CH_4 from deep layer to upper layers. The CH_4 fluxes in deep soil layers were higher in the harvested plots than in the control at both sites ($p = 0.058$ for Lettosuo and $p < 0.001$ for Paroninkorpi; Supplementary C Table 2.2), indicating the WT raise after harvesting enhanced the CH_4 production from deep soil.

Upward N_2O fluxes existed between soil layers above WT (Fig. 5, also see Supplementary B Fig. 5.3). N_2O fluxes between different soil layers did not differ significantly between the treatments, but Paroninkorpi site exhibited higher fluxes than Lettosuo site. Neither of the sites showed clear net transport of N_2O from the deep soil layer to upwards (Fig. 5).

3.3. Drivers of gas concentration profiles

Based on the BRT analysis, the variables indicating the oxygenation status ($[\text{O}_2]$, distance to WT) of soils were the most important ones explaining the variation in $[\text{CH}_4]$ (log-transformed) and $[\text{N}_2\text{O}]$

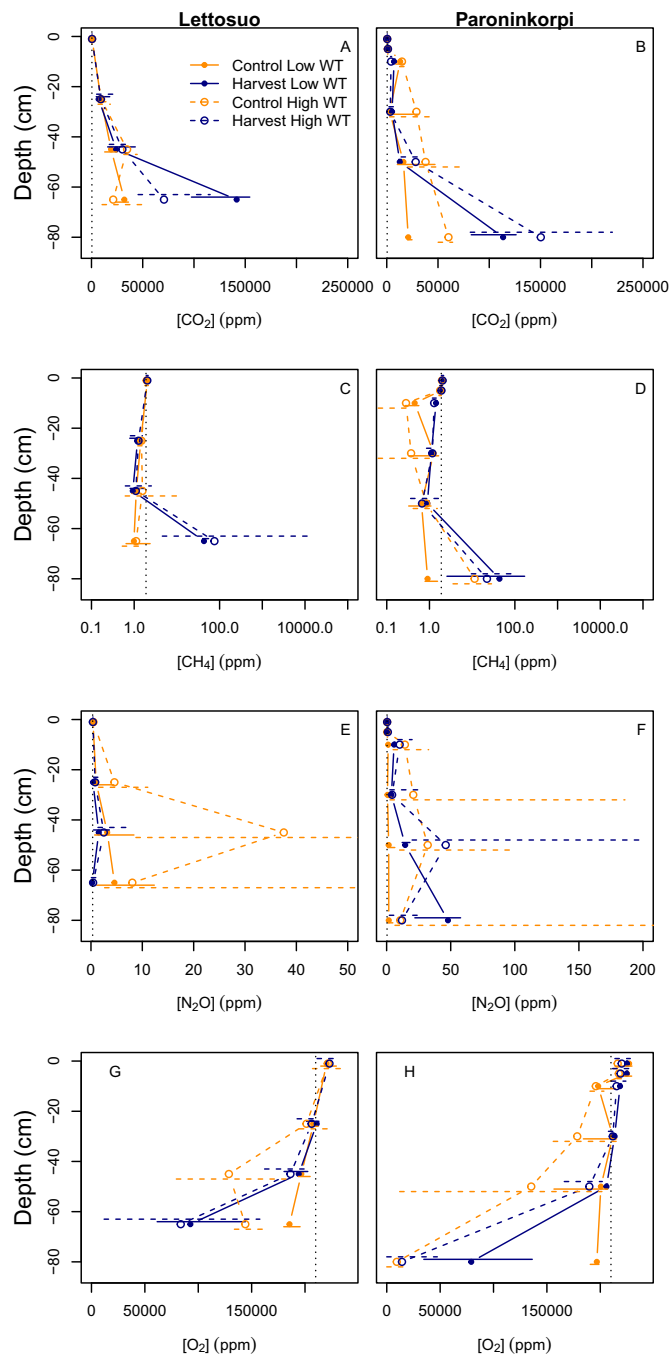


Fig. 3. Median soil gas concentrations by depth under control and harvest treatments and under high/low water table (WT) conditions (WT above/below -60 cm depth) in Lettosuo (left panels) and Paroninkorpi (right panels). Horizontal lines extend from 25 % to 75 % quantiles.

(Table 3). $[\text{CO}_2]$ (log transformed) was also linked with $[\text{O}_2]$, but the depth from soil surface was more important than the distance to WT in driving its changes. Air and soil temperature had small explanatory powers for the studied gases compared to aforementioned factors (Fig. 6).

The relationship of $[\text{CH}_4]$ with $[\text{O}_2]$ and distance to WT was nearly step like, indicating switch between aerobic and anaerobic soil processes. Increases of $[\text{CO}_2]$ were associated with decreasing $[\text{O}_2]$ somewhat linearly on back-transformed scale. The effect of depth on $[\text{CO}_2]$ decreased steeply near the soil surface, possibly indicating a sudden change in soil porosity and gas permeability. $[\text{CO}_2]$ also increased with

the increasing of $[\text{CH}_4]$. The patterns in $[\text{N}_2\text{O}]$ were more complex. $[\text{N}_2\text{O}]$ increased with decreasing $[\text{O}_2]$, and particularly near the WT level. The $[\text{N}_2\text{O}]$ linearly increased with increasing Eh until it peaked at 250 meV and suddenly dropped to lowest values in the Eh range (Fig. 6; see also Supplementary B Fig. 1).

The relationship between the gas concentrations and WT became apparent when they were plotted against the distance to WT (Fig. 7). $[\text{CO}_2]$ and $[\text{CH}_4]$ increased steeply near and below WT, when $[\text{O}_2]$ was also low. However, notably different behavior of concentrations was observed in Paroninkorpi control where the $[\text{O}_2]$ and $[\text{CH}_4]$ were lower, but $[\text{CO}_2]$ was higher throughout the profile all the way down to WT level than in other plots and treatments. $[\text{N}_2\text{O}]$ peaked approximately 10 cm above WT in the harvest treatment, where the redox was approximately 250 meV (Supplementary B Fig. 1).

4. Discussion

The dynamics of all studied GHGs were clearly regulated by the soil water table level (WT) and oxic/anoxic conditions ($[\text{O}_2]$), and $[\text{N}_2\text{O}]$ also by redox. High $[\text{CO}_2]$ and $[\text{CH}_4]$ co-occurred near WT and at low $[\text{O}_2]$, reflecting diffusion limitations of gas transport and methanogenic activity in deep soil when it was near saturation or submerged. High $[\text{N}_2\text{O}]$ showed up when other GHGs were at low to medium concentrations, but high $[\text{N}_2\text{O}]$ were still reached under both high and low $[\text{O}_2]$ conditions, suggesting complex and weak relationship with other gases. Production and consumption rates of gases differed vertically and were largely decoupled (hypothesis 1). Most CO_2 was produced near soil surface, CH_4 mainly below and near WT and effectively consumed near and above WT. N_2O was produced in a more extensive soil column, from WT level, up until soil surface, although its concentration accumulated near WT.

Selection harvest had modest impacts on soil CO_2 emissions (hypothesis 2). Surface soil layer produced largest emissions, which means that WT raise must be considerable to reduce its CO_2 production. In the WT range observed in our study, there was a decreasing trend in soil CO_2 flux with rising WT only between the surface soil layers on one of the sites (30–1 cm layer in Paroninkorpi) but not on the other site, while all chamber measurements and other layers did not have clear CO_2 flux trends with WT (Supplementary B Fig. 5.1). This also suggests that radical changes in WT are needed to significantly reduce surface soil CO_2 emissions. It should be noted that our study sites were both quite dry (deep WT), while peatland forests in general the average WT may vary widely (Ojanen et al., 2013). A rise of 14 cm (that we observed during the sampling dates, on average) could have more impact in sites that are initially wetter. High relative contribution of surface soil is also in line with earlier understanding on the factors affecting decomposition. First, surface soil was warmer during the measurement period than deep soil. Decomposition has a non-linear response to temperature (e.g. Davidson and Janssens, 2006), so based on temperature alone, top layers should release more heterotrophic CO_2 . Second, lack of oxygen decreases the microbial activity in deep soil but less in the surface soil. Third, root autotrophic respiration and fungal activity are confined to surface soil and contribute to CO_2 concentrations and fluxes, and they are thus part of the total emission flux calculated based on the concentration gradient-method and measured with chambers. Fungal and root activity are also known to speed up decomposition of organic matter (Kuzakov, 2010), although the stimulating effect has not been observed in drained peatland forests earlier (Linkosalmi et al., 2015). Fourth, surface-most soil contains fresh detritus and less decomposed organic matter than deeper in soil. Earlier studies have found that surficial peat decomposes faster than deep peat, and have related faster CO_2 production to chemical quality differences in peat (Leifeld et al., 2012; Reiche et al., 2010), although this may not hold in all types of peatlands. Here, surficial peat did have lower C:N ratios than measured for the deeper layers soil, which indicates that the substrate is more decomposable (Krüger et al., 2015; Kuhry and Vitt, 1996), unless the changing botanical origin of

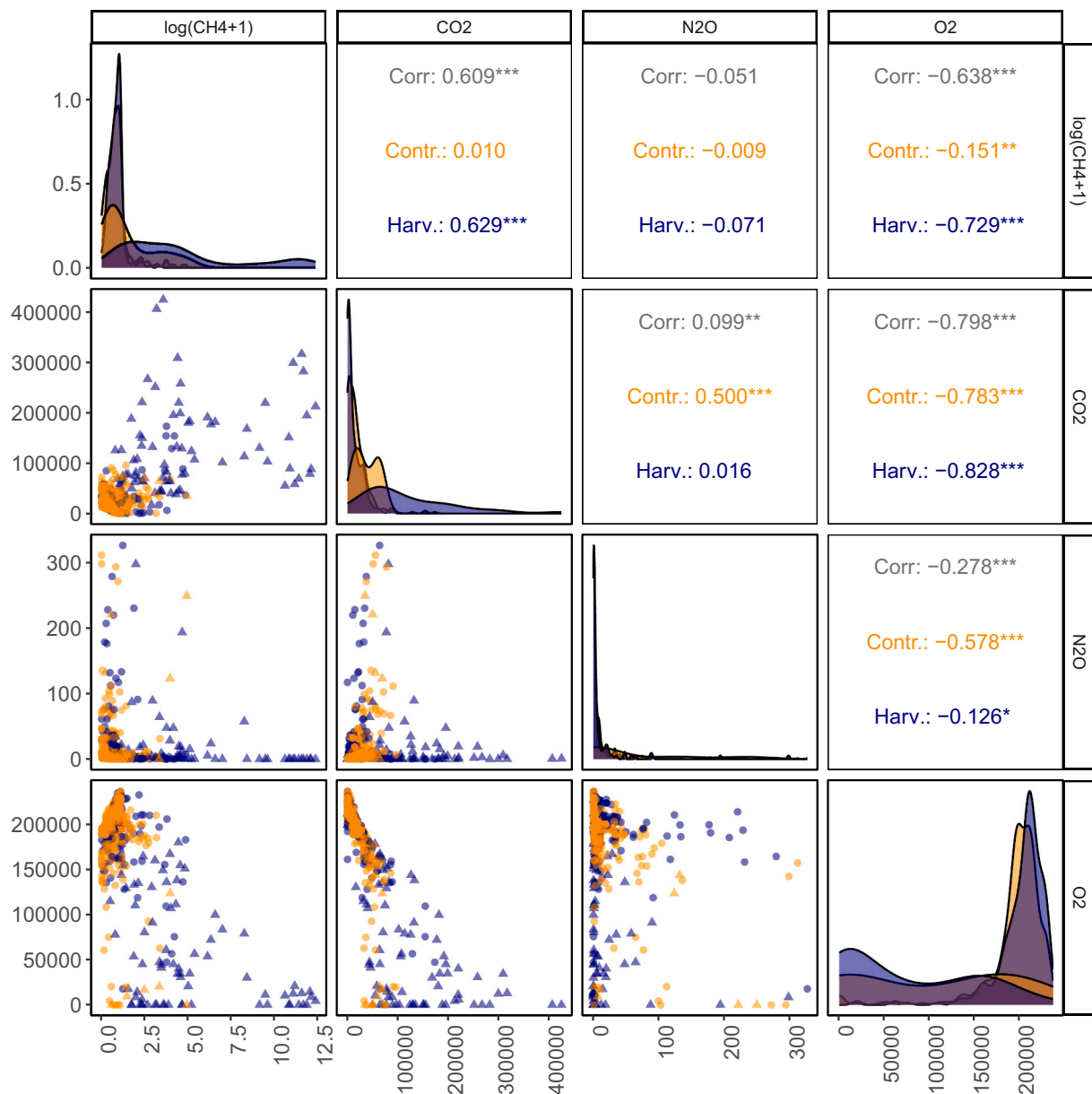


Fig. 4. Correlations of gas concentrations under control and harvest treatments. Round and triangle symbols indicate the gas was taken from the gas collector when it was above and below WT, respectively.

peat explains differences. Differences of C:N ratios to lower soil layers were not large, though. However, drying of peat and subsidence of peat could unlock carbon from deeper layers from these sites in future. The high $[\text{CO}_2]$ observed in deep soil are not in conflict with the estimated large contribution of the surface soils on the CO_2 emissions. High $[\text{CO}_2]$ can be built up in deep soil although its production would be relatively small because the diffusion non-linearly decreases with peat moisture.

How much WT should then raise to considerably reduce the heterotrophic CO_2 emissions from peatland forests? Based on our results, it is pivotal that WT raises more than we observed (14 cm). Earlier studies measuring and simulating WT changes after selection harvest (incl. sites in this study) have reported WT rises in the range of 4–18 cm, depending on the site and harvest intensity (Lepä et al., 2020). This is not sufficient on typical drained peatland forests, and the selection harvesting should be combined with at least partial ditch blocking to significantly raise WT, and to be effective in reducing heterotrophic CO_2 emissions. In the long run, continuous cover forestry and avoidance of the ditch network clearing may result shallower ditches and raised WT, but then

the impact on GHG fluxes is also delayed. It should be noted that the heterotrophic CO_2 emission is not the same as soil carbon balance, which is contributed to by litter inputs. These in turn largely depend on the vegetation type (Straková et al., 2010). Our concentration profile-based measurements, and also the chamber measurements miss some of the litter inputs.

The soil maintained a CH_4 sink function after selection harvesting (contrary to our initial hypothesis 3 of reduced sink), although the oxic layer where CH_4 oxidation occurs was shallower due to the rise of the WT. The measured WT level was still always below –35 cm depth in Lettosuo and –40 cm depth in Paroninkorpi for the selection harvested and non-harvested plots, which lead to the topsoil layer as a permanent aerobic layer thus consuming both atmospheric and deep soil CH_4 under all WT conditions we observed (Supplementary B Fig. 5.2). Therefore, the WT rise in our study hasn't resulted in the leakage of CH_4 produced in deep soil to atmosphere or reduced the atmospheric sink function of topsoil. Given that our study describes the typical conditions in well-drained peatland forests, we suggest that it is likely uncommon that

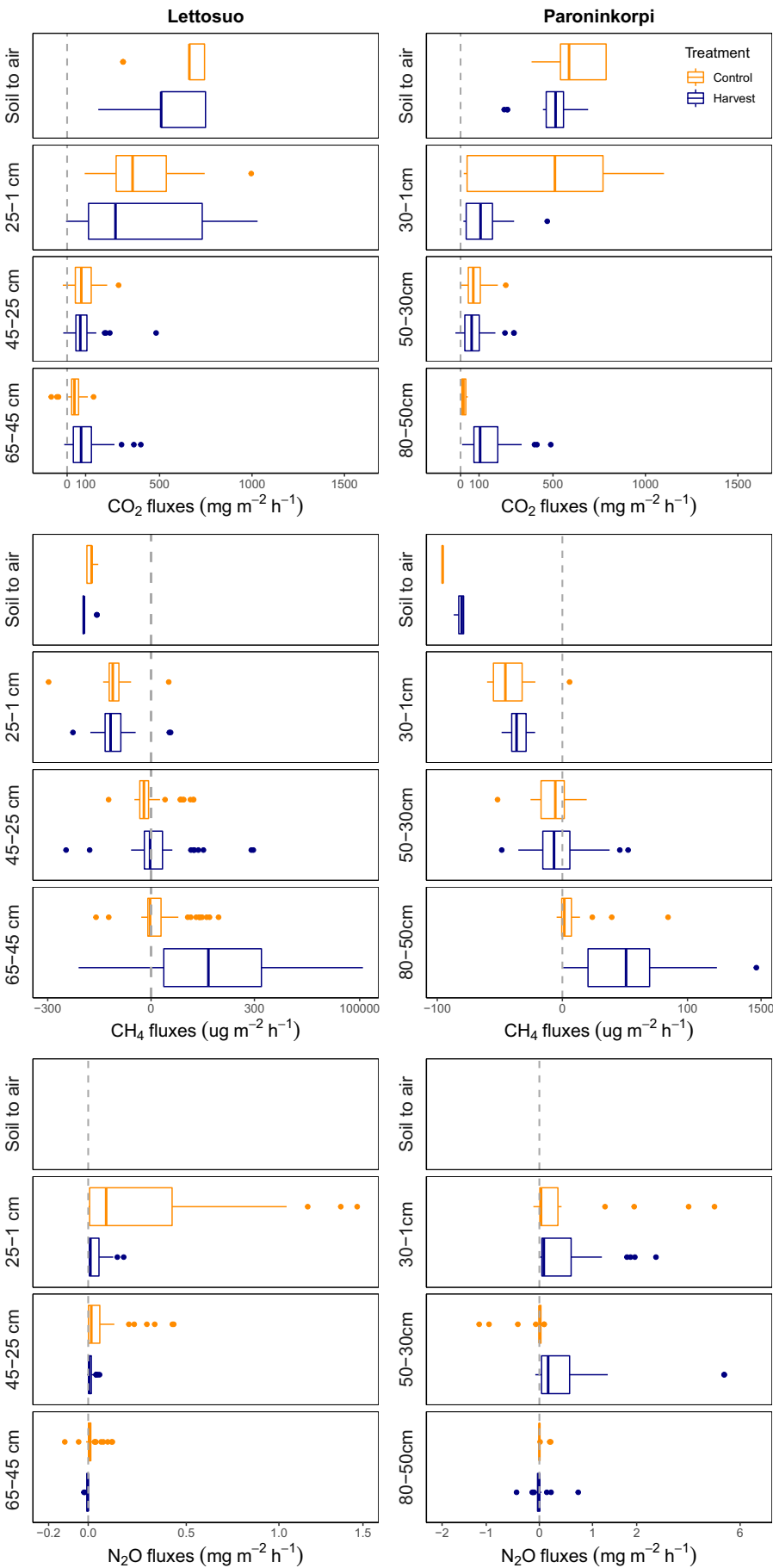


Fig. 5. Fluxes of CO₂ and CH₄ between soil-atmosphere measured by chamber and in-soil fluxes of CO₂, CH₄ and N₂O between soil layers estimated by soil gas concentrations and estimated soil gas permeability in Lettosuo (left panels) and Paroninkorpi (right panels). Thick black line shows the distribution of median, boxes show the interquartile range (IQR), and whiskers extend to 1.5 times of the IQR. Positive values indicate upward fluxes and negative values indicate downward fluxes.

Table 3

Statistics of BRT models for the greenhouse gases, and the most influential variables explaining variance in the gas concentration data. Variables included in the models for gases in the table columns: Oxygen concentration measured from the same sample ($[O_2]$), Methane concentration measured from the same sample ($[CH_4]$), Distance from WT (WTdist), Redox potential at pH = 7 (Eh), Sum of rainfall during the past week (Rain1w), Measurement depth from soil surface (Depth), Past week average air temperature (Tair1w), Soil temperature at measurement location at 30 cm depth from soil surface (T30cm), Past week redox potential average (Eh1w), Indicator for Lettosuo and Paroninkorpi (Site), Indicator for treatment harvest or control (Treatment), Current day rainfall (Rain), Current day air temperature (Tair).

Statistics	$\log ([CH_4] + 1)$	$\log ([CO_2] + 1)$	$[N_2O]$
N obs.	772.00	771.00	772.00
N trees	750.00	2700.00	1000.00
Mean tot. Dev.	3.03	2.92	54,771.04
Mean resid. Dev.	0.39	0.08	25,417.77
Estimated cv deviance	0.74	0.20	50,829.51
S.E.	0.11	0.03	32,066.03
Training data correlation	0.93	0.99	0.78
C.V. correlation	0.87	0.97	0.43
S.E.	0.02	0.01	0.09

$\log ([CH_4] + 1)$		$\log ([CO_2] + 1)$		$[N_2O]$	
Variable	Rel. influence	Variable	Rel. influence	Variable	Rel. influence
$[O_2]$	47.80	$[O_2]$	55.42	$[O_2]$	31.31
WTdist	21.31	Depth	33.26	WTdist	20.19
Site	17.12	$[CH_4]$	6.31	Eh	16.51
Tair	3.27	T30cm	1.31	Rain1w	7.58
T30cm	2.43	WTdist	1.13	Depth	6.92
Eh	1.73	Eh	0.73	Tair1w	6.73
Tair1w	1.52	Rain1w	0.54	T30cm	4.37
Rain1w	1.47	Tair	0.43	Eh1w	3.33
Depth	1.41	Tair1w	0.39	Site	0.93
Eh1w	0.87	Rain	0.22	Treatment	0.90
Rain	0.54	Eh1w	0.15	Rain	0.62
Treatment	0.52	Treatment	0.06	Tair	0.59

the WT rise after selection harvesting (see also Leppä et al., 2020) can reach to a level which is sufficient to reverse the topsoil CH_4 sink. Such conditions could occur after clearcutting, though (Korkiakoski et al., 2019; Mäkiranta et al., 2012). Based on earlier research from drained peatland forests, CH_4 emissions emerge when WT is higher than -30 cm (Ojanen et al., 2010), a condition which was not reached when our gas measurements were conducted.

The consumption of CH_4 at or above WT level was very efficient based on sub-atmospheric $[CH_4]$ and in-soil CH_4 fluxes being close to zero in the middle soil layers. This indicates net transfer of methane both from atmosphere, and from deeper soil to layers above WT. We also observed O_2 was available already just above the WT, allowing methanotrophic CH_4 consumption. These observations align with previous research from boreal forested bogs suggesting that methane from atmosphere was consumed within 15 cm of topsoil, while methane from deeper origins was consumed within 20 cm above WT (Roulet et al., 1993). Similar results have been obtained from open peatlands (Clymo et al., 1995; Watson et al., 1997), where the methane consumption with little leakage to atmosphere was attributed to hummocks above water table. Other studies have also indicated effective methane oxidation at close proximity just above the source that locates below the WT level (Sundh et al., 1994). Based on our study, it seems that the actual diffusion rates in wet peat are slow enough to allow immediate and effective methanotrophic consumption of CH_4 near its main source at or below WT, but diffusion rates are still not small enough to limit oxygen supply. Unfortunately, the depth resolution of our observations and other uncertainties did not allow resolving more accurately the net sink-source distribution within soils, so for future purposes, we suggest

increasing depth resolution of gas and WT measurements from what we had.

Besides sources of methane produced below WT, it has been suggested that methane production can occur above WT level in anoxic micro-pockets (Deppe et al., 2010; Silins and Rothwell, 1999). These pockets can extend 20–30 cm above WT during the drying cycle and 10 cm above during the wetting cycle (Kiuru et al., 2022). Based on the observed sub-atmospheric $[CH_4]$ and near-zero in-soil fluxes in middle soil layers, any methane produced in these pockets should also be effectively consumed by the nearby methane oxidation.

Regarding to hypothesis 4, we observed that the highest production of N_2O occurred between the middle and surficial soil layers. Earlier research has suggested that N_2O production is highest at intermediate moisture levels (Pärn et al., 2018), and that nitrification can reach maximum rates near water-filled pore space 60 % (Davidson et al., 2000; Parton et al., 2001). Such conditions range from shallow layers almost down to WT level, as peat effectively retains moisture. This creates a wide depth range of suitable conditions for N_2O production.

Based on our measurements, however, optimal redox conditions for N_2O production prevailed approximately 0–20 cm above WT. The redox potential is between 200 and 300 mV when NO_3^- is the dominant electron acceptor, a condition associated with high N_2O emissions (e.g. Włodarczyk et al., 2008). We also observed $[N_2O]$ peaking around 250 mV in the BRT analysis. Despite this, surficial layers were more important for N_2O production. While the redox conditions near WT were optimal, the differences of $[N_2O]$ between the layers near WT and more surficial layers were relatively small. This diminished the upward fluxes of N_2O between the gradient end points, particularly due to the low gas permeability of peat matrix in the lowest soil layers. It is also possible that only little nitrification occurs in deeper soil due to increasingly anaerobic conditions, and that the lack of nitrate limits denitrifier- N_2O production in the deep layers, but the low gas permeability of peat effectively blocks the gas transport and keeps the concentrations at highest levels.

Interestingly, we also observed that N_2O was present at high and low $[O_2]$ (Fig. 4). It seems that the importance of processes releasing N_2O is segregated vertically, nitrification dominating production at upper layers, while the role of incomplete denitrification being larger in the deep soil – when not limited by the availability of NO_3^- . In surficial layers, decomposition actively releases ammonium (NH_4^+), which is then oxidized via nitrite (NO_2^-) to nitrate (NO_3^-), producing N_2O as a by-product. While the dominance of processes producing N_2O differed by depth, the transition is likely smooth. It is also likely that nitrification and denitrification co-occur at nearby microsites/pockets (Nielsen et al., 1996), and particularly in conditions where O_2 availability is very low but not zero. At low O_2 availability, the $N_2O:NO_x^-$ ratios of nitrification are also known to increase (Khalil et al., 2004; Parton et al., 2001), and that small concentrations of O_2 inhibit N_2O reduction (to N_2) during denitrification (Babbitt et al., 2015; Ji et al., 2015; Otte et al., 1996), both promoting N_2O production.

The changes of N_2O fluxes due to selection harvesting remained unclear. Based on our study, moderate and persistent WT raises did not have significant effect on N_2O fluxes. Only a peak of N_2O fluxes from topsoil layers was found when WT around 65 cm depth in Lettosuo site (Supplementary B Fig. 5.3). Earlier multisite study has reported that peatland N_2O emissions are higher at deeper WT (Minkkinen et al., 2020) but not all other studies have found clear differences between sites with difference WT status (Tupek et al., 2015). It is possible that either moderate changes of WT like in our study, and which occur deep (< 50 cm) in soil, do not generate remarkable N_2O flux changes to atmosphere (or between 25/30 cm to 1 cm layer, which was our proxy to flux to atmosphere). Logging residues left in the recent selection harvest (3–5 yrs. ago) could also stimulate N_2O production, and compensate any decreases caused by raising WT. Indeed, earlier studies have observed that logging residues increase N_2O production in peatland soils (Mäkiranta et al., 2012) and also in mineral soils with some delay

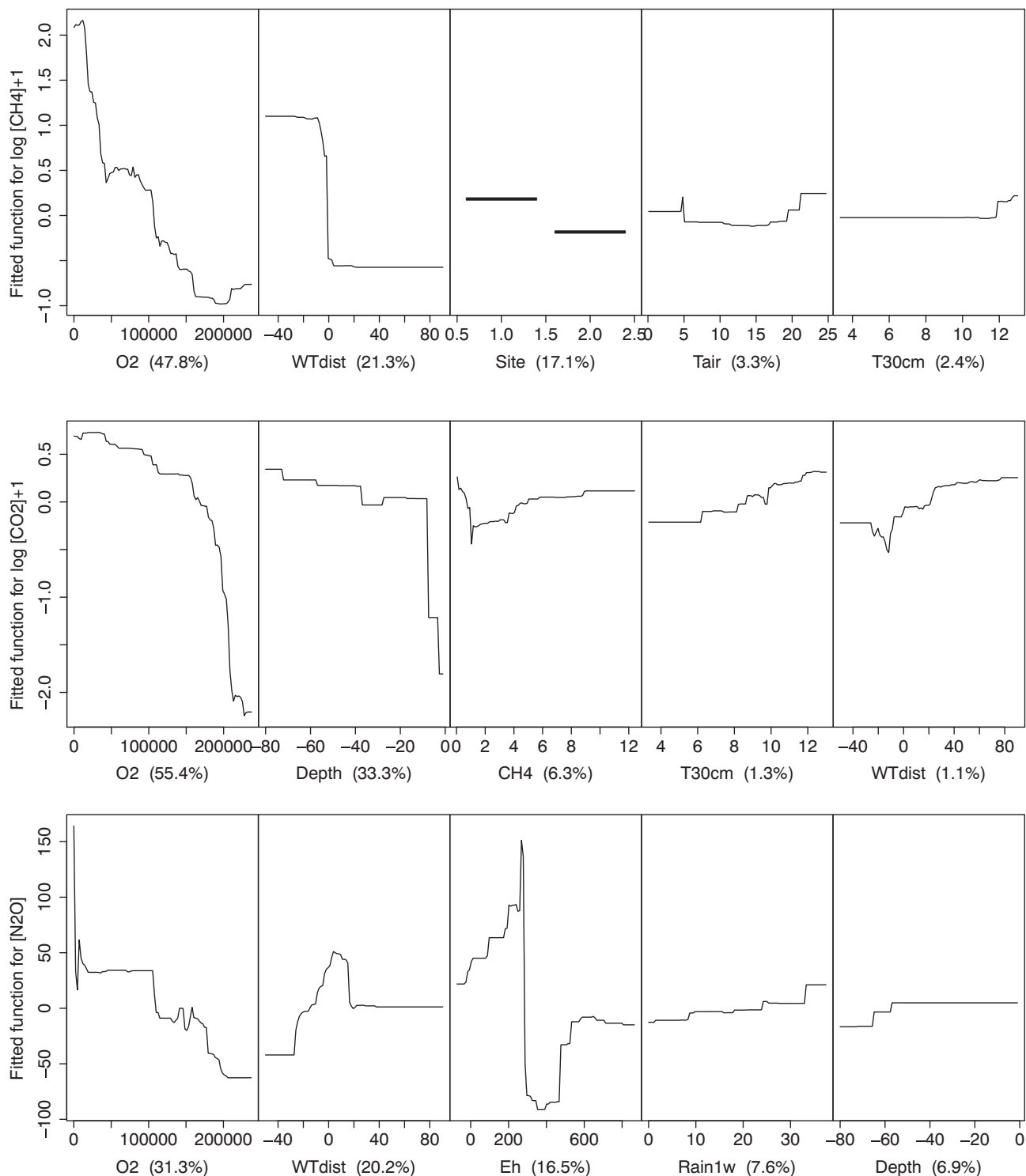
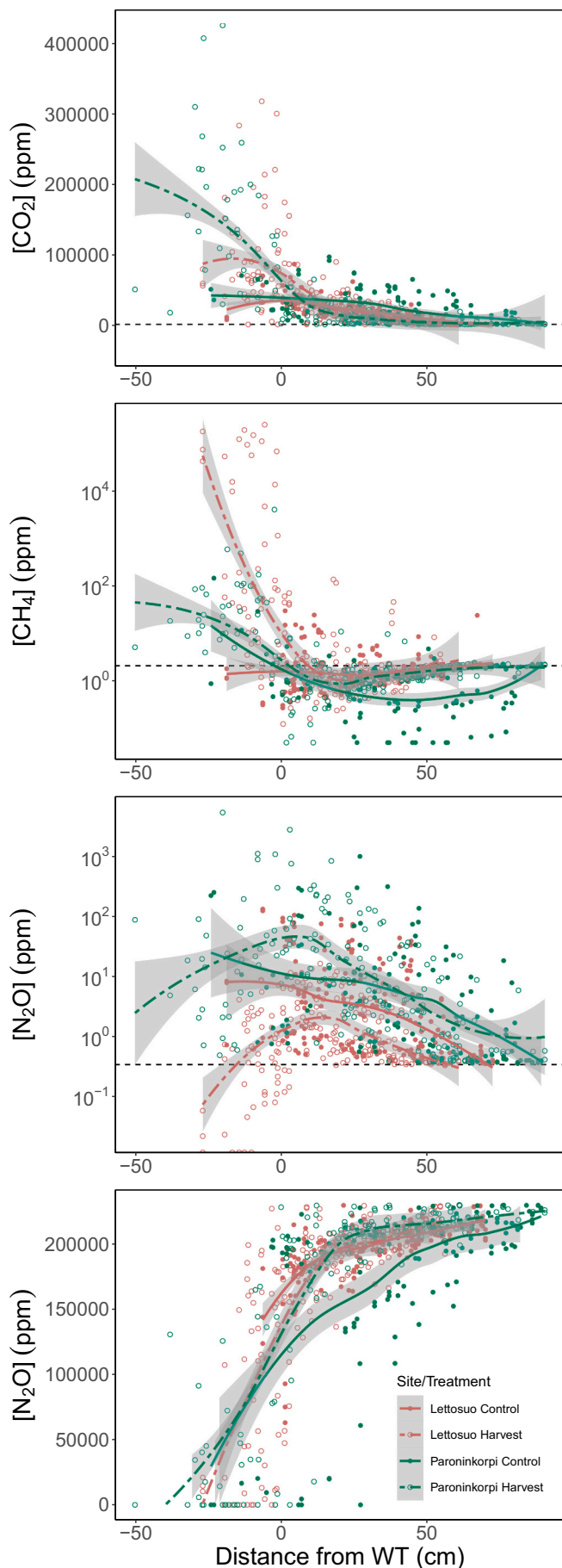


Fig. 6. Main variables explaining the gas concentrations in soil and their partial dependence plots (PDP) based on the boosted regression tree method (BRT). PDP depicts the effect of a variable on the response when the average effects of all other variables are accounted for. Value in parentheses are relative influences of variable to the fit. See Table 3 for fit statistics and estimates of relative influences of other variables used in the BRT.

(Törmänen et al., 2020). It seems based on our study, and also based on earlier study (Minkkinen et al., 2020) that sites with high soil N and low C:N also have higher N_2O production (Ojanen et al., 2010; Pärn et al., 2018). This suggests that studying WT effects should focus on nutrient rich sites. Further research is also required on how temporal WT variation, and not only its persistent change, affects the N_2O production.

Our measurement set up does suffer from some uncertainties. First,

when comparing data, it should be noted that the inaccuracy of the depths of both gas sampling depths and WT measurements is roughly 10 cm. This is caused by variability of soil surface. WT is also known to be spatially and temporally variable due to the time-dynamics of gas and pressure inside peat even in short distances (Kellner et al., 2005). However, we consider these uncertainties do not influence our main results and conclusions on gas concentrations and in-soil fluxes, and



(caption on next column)

Fig. 7. Relationship between soil gas concentrations and distance from water table (WT). Zero at x axis indicates WT level, and positive and negative values indicate that gas was collected above and below WT, respectively. Lines and confidence (gray) intervals are based on `stat_smooth()` in `ggplot()` in R with default parameters, and only intended to visual examination of the change of mean value with distance from WT. Horizontal dash line indicate the mean GHG concentrations at 1 m above soil in Lettosuo during the dates when soil gas samples were collected.

their relationship with WT, although they limit the quantification of their relationships. Second, it is also important to note that the gas permeability of the soil matrix near collectors could be impacted due to the disturbance of soil when installing gas collectors, although the collectors were gently inserted into pit walls and the removed soil was carefully put back. This may have short-term impacts on the gas concentrations, which may be observed in the data collected in 2018 in Paroninkorpi site, where the pits were dug in July 2018 and gas sampling started in August. Third, we could not avoid cutting roots of plants near gas collectors. However, during the excavation, we found out that roots below 30 cm were rare, in line with earlier observations that most of the coarse roots (Heikurainen, 1955) and fine roots (Bhuiyan et al., 2017) are in top soil layers in peatland forests. Moreover, roots remained intact on the other face of the collector, which was carved into the pit wall.

We assumed soil gases are transported in soil via diffusion, whereas in fact other transportation modes also exist, which likely render the calculated in-soil gas fluxes underestimates. Some plants, like sedges, are known to transport CH_4 from the deep soil anoxic conditions to the atmosphere (Schimel, 1995). However, these types of plants were not abundant in our measurement plots. The plots were dominated by *Sphagnum* spp., which are known to host methanotrophs (Larmola et al., 2010; Raghoebarsing et al., 2005). Our study suggests that moss-associated methanotrophs consume atmospheric methane rather than deep soil methane at these sites, as methane concentrations were even smaller in deep soil than in the surface 30 cm. We also observed stronger CH_4 sink with chambers compared with the estimated in-soil fluxes at topsoil layer, which could indicate the existence of additional sink in moss capitulum, which was the upper end point of the topmost concentration gradient. In addition, gases can be transported by the movement of water in soil in dissolved form. Depending on the direction of water movement, it can either increase or decrease the fluxes between soil layers. However, it should not significantly affect the effective fluxes between the soil layers as soil air gas concentrations should stabilize with their partial pressures in water soon following WT movements. Gases can also accumulate in deep soil due to low gas permeability of soil layers, and then be released as bubbles if conditions change (Brown et al., 1989; Windsor et al., 1992), e.g., if water table changes (Männistö et al., 2019; Moore and Roulet, 1993; Roulet et al., 1993). Ebullition effect has partially been captured by our silicon rubber tube sampling in cases where very high concentrations were measured. In our study, we accounted for the direct effect of peat structure and moisture on diffusion coefficient but not the indirect effect which may exist. Gas diffusivity rates in soil can be affected by WT movement and consequent impacts on soil microstructure and porosity after flooding (Elberling et al., 2011). Diffusion rates also exhibit hysteresis, which is related to moisture content development in drying and wetting cycles of peat (Kiuru et al., 2022), and also to the presence of gas bubbles clogging pore spaces (Kellner et al., 2005). These effects obviously increase the uncertainty of our in-soil gas transfer rates.

The permeability of silicon rubber tubes defines the low limit of meaningful gas sampling intervals from the tubes, but we do not consider it significantly adds to the uncertainties. The diffusion coefficients of CO_2 and N_2O in silicon rubber are close to their diffusion coefficients in water (Bruins, 1929; Grable, 1966; Holter, 1990), which allows a frequent sampling of gases. Thus, our biweekly to monthly

sampling frequency clearly exceeded this limit. It has been estimated that it takes 4.4 h and 22 h for N₂O concentrations to equilibrate with surrounding conditions through a silicon rubber tube of thickness 2.4 mm (vs. 2.5 mm for tubes used in this study) under 22 °C and 4 °C, respectively (Jacinthe and Dick, 1996), which well covers the temperature range in this study. Based on the Graham's Law, the diffusion rates of gases are expected to be proportional to their molecular masses. Given that all other gases we studied have molecular masses close or lower than N₂O, we do not expect that any of the gases significantly differs from each other in terms of their diffusion through silicon tube wall. Moreover, the inlet and valves were made from less diffusive material than silicon rubber, so there was sufficient volume of samples in tubes and we did not encounter failures of the system, which allowed us to consider that samples represent at least diel averages of true gas concentrations in soil preceding the sampling. The silicon rubber tubes, and relatively fast gas exchange could also allow to build a continuous monitoring system for soil gases.

Although we found simplified description of soil hydrology and the concentration-gradient-based measurements for estimating fluxes informative, more elaborated models are required to integrate other possible gas transport routes (convection with WT, plant transport) to actual sink-source mechanisms (respiration, methanotrophic consumption, biochemical reactions) occurring in peat soils. Such models exist, e.g. Himmeli model has been developed for these purposes, but so far it has been calibrated only using emission data from natural peatlands (Raivonen et al., 2017). With higher depth resolution of measurements, this would be effective way to estimate the distribution of consumption and production processes of gases in soils, which is needed for informed predictions of soil GHG emissions in changing conditions. Currently, we are using data assimilation to calibrate Himmeli model using the data used in this study. The data is also shared online to facilitate development and calibration of other models (Peltoniemi et al., 2022).

5. Conclusions

Our study showed that emissions and vertical patterns of soil GHG concentrations are affected by the distance to water table depth. Consequently, water table raise should decrease or reverse soil CH₄ sink, decrease soil CO₂ and N₂O emissions. However, at our sites, surface peat layers were able to consume all CH₄, and soils remained CH₄ sinks after modest water table raise caused by the selection harvesting and decreased transpiration. Soils produced nearly as much CO₂ in the selection harvested as in the unharvested controls, since surface soil produced largest emissions and modest WT raise had little direct impact on that layer. N₂O dynamics were closely associated with site fertility, poor redox conditions near but above water table, and not clearly associated with harvest treatment. These results suggest that raising WT by controlling stand density and evapotranspiration may not be sufficient to reduce peat soil emissions in nutrient-rich peatland forests. Other complementary methods like partial blocking of ditches should be considered, too, particularly on well-drained soils where the soil water table is initially low. It will be important to find suitable combinations of hydrological control for different types of peatland sites to protect the accumulated C in peat, particularly as climate change increases evapotranspiration and temperatures raise and speed up soil heterotrophic processes.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.165421>.

CRediT authorship contribution statement

Mikko Peltoniemi: Conceptualization, Methodology, Data Curation, Visualization, Supervision, Investigation, Formal analysis, Project administration, Writing- Original Draft

Qian Li: Data Curation, Writing- Original Draft, Visualization, Investigation, Formal analysis

Pauliina Turunen: Methodology, Data Curation, Visualization
Boris Tupek: Formal analysis, Software, Methodology
Päivi Mäkiranta: Investigation, Project administration
Kersti Leppä: Formal analysis, Software
Mitro Müller: Methodology, Investigation
Antti J. Rissanen: Investigation, Writing- Review & Editing
Raija Laiho: Writing- Review & Editing, Funding acquisition
Jani Anttila: Formal analysis, Software
Jyrki Jauhainen: Investigation, Funding acquisition
Markku Koskinen: Investigation, Review & Editing
Aleksi Lehtonen: Funding acquisition, Review & Editing
Paavo Ojanen: Investigation, Writing - Review & Editing
Mari Pihlatie: Conceptualization, Methodology
Sakari Sarkkola: Investigation, Writing - Review & Editing
Elisa Vainio: Methodology, Writing - Review & Editing
Raisa Mäkipää: Funding acquisition, Project administration, Writing - Review & Editing

Financial support

The financial support for the study was received from the Strategic Research Council at the Academy of Finland (project SOMPA, decision no. 312912 and 336570), EU Horizon 2020 (Holisoils, GA No. 101000289), Academy of Finland Flagship Programme (UNITE, decision no. 337655), and LIFE18 CCM/LV/001158 LIFE OrgBalt.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

We have opened the data in Zenodo, see DOI in the manuscript. Codes shared on request.

Acknowledgements

We thank Petri Salovaara (Luke) and other technical staff for collecting measurements, and Matti Lopenen (UH) for technical assistance related to gas analyses.

References

- Ahtikoski, A., Rämö, J., Juutinen, A., Shanin, V., Mäkipää, R., 2022. Continuous cover forestry and cost of carbon abatement on mineral soils and peatlands. *Front. Environ. Sci.* 10 <https://doi.org/10.3389/fenvs.2022.837878>.
- Babbin, A.R., Bianchi, D., Jayakumar, A., Ward, B.B., 2015. Rapid nitrous oxide cycling in the suboxic ocean. *Science* 348, 1127–1129. <https://doi.org/10.1126/science.aaa8380>.
- Bhuiyan, R., Minkinen, K., Helmisaari, H.-S., Ojanen, P., Penttilä, T., Laiho, R., 2017. Estimating fine-root production by tree species and understorey functional groups in two contrasting peatland forests. *Plant Soil* 412, 299–316. <https://doi.org/10.1007/s11104-016-3070-3>.
- Brown, A., Mathur, S.P., Kushner, D.J., 1989. An ombrotrophic bog as a methane reservoir. *Glob. Biogeochem. Cycles* 3, 205–213. <https://doi.org/10.1029/GB003i003p0205>.
- Bruins, H.R., 1929. Coefficients of diffusion in liquids. In: Washburn, E.W. (Ed.), *International Critical Tables of Numerical Data, Physics, Chemistry and Technology*. MacGraw-Hill, London, pp. 63–75.
- Butterbach-Bahl, K., Baggs, E.M., Dannenmann, M., Kiese, R., Zechmeister-Boltenstern, S., 2013. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Phil. Trans. R. Soc. B* 368, 20130122. <https://doi.org/10.1098/rstb.2013.0122>.
- Clymo, R.S., Pearce, D.M.E., Conrad, R., Fowler, D., Jenkinson, D.S., Monteith, J.L., Unsworth, M.H., 1995. Methane and carbon dioxide production in, transport through, and efflux from a peatland. *Phil. Trans. Roy. Soc. London* 351, 249–259. <https://doi.org/10.1098/rsta.1995.0032>.
- Corteselli, E.M., Burtis, J.C., Heinz, A.K., Yavitt, J.B., 2017. Leaf litter fuels methanogenesis throughout decomposition in a forested peatland. *Ecosystems* 20, 1217–1232. <https://doi.org/10.1007/s10021-016-0105-9>.

- Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173. <https://doi.org/10.1038/nature04514>.
- Davidson, E.A., Trumbore, S.E., 1995. Gas diffusivity and production of CO₂ in deep soils of the eastern Amazon. In: *Tellus B: Chemical and Physical Meteorology*, 47, pp. 550–565. <https://doi.org/10.3402/tellusb.v47i5.16071>.
- Davidson, E.A., Keller, M., Erickson, H.E., Verchot, L.V., Veldkamp, E., 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides: using two functions based on soil nitrogen availability and soil water content, the hole-in-the-pipe model characterizes a large fraction of the observed variation of nitric oxide and nitrous oxide emissions from soils. *BioScience* 50, 667–680. [https://doi.org/10.1641/0006-3568\(2000\)050\[0667:TACMOS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0667:TACMOS]2.0.CO;2).
- Deppe, M., Knorr, K.-H., McKnight, D.M., Blodau, C., 2010. Effects of short-term drying and irrigation on CO₂ and CH₄ production and emission from mesocosms of a northern bog and an alpine fen. *Biogeochemistry* 100, 89–103. <https://doi.org/10.1007/s10533-010-9406-9>.
- Elberling, B., Askaer, L., Jørgensen, C.J., Joensen, H.P., Kühl, M., Glud, R.N., Lauritsen, F.R., 2011. Linking soil O₂, CO₂, and CH₄ concentrations in a wetland soil: implications for CO₂ and CH₄ fluxes. *Environ. Sci. Technol.* 45, 3393–3399. <https://doi.org/10.1021/es103540k>.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- van Genuchten, M.Th., 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Sci. Soc. Am. J.* 44, 892–898. <https://doi.org/10.2136/sssaj1980.03615995004400050002x>.
- Grable, A.R., 1966. Soil aeration and plant growth. In: Norman, A.G. (Ed.), *Advances in Agronomy*. Academic Press, pp. 57–106. [https://doi.org/10.1016/S0065-2113\(08\)60648-3](https://doi.org/10.1016/S0065-2113(08)60648-3).
- Hedwall, P.-O., Brunet, J., Rydin, H., 2017. Peatland plant communities under global change: negative feedback loops counteract shifts in species composition. *Ecology* 98, 150–161. <https://doi.org/10.1002/ecy.1627>.
- Heikurainen, L., 1955. Structure of Scots pine root systems in a pine swamp and effect of draining on the structure. *Silva Fennica* 65.
- Holter, P., 1990. Sampling air from dung pats by silicone rubber diffusion chambers. *Soil Biol. Biochem.* 22, 995–997. [https://doi.org/10.1016/0038-0717\(90\)90143-N](https://doi.org/10.1016/0038-0717(90)90143-N).
- Jacinto, P.-A., Dick, W.A., 1996. Use of silicone tubing to sample nitrous oxide in the soil atmosphere. *Soil Biol. Biochem.* 28, 721–726. [https://doi.org/10.1016/0038-0717\(95\)00176-X](https://doi.org/10.1016/0038-0717(95)00176-X).
- Jacinto, P.-A., Groffman, P.M., 2001. Silicone rubber sampler to measure dissolved gases in saturated soils and waters. *Soil Biol. Biochem.* 33, 907–912. [https://doi.org/10.1016/S0038-0717\(00\)00236-4](https://doi.org/10.1016/S0038-0717(00)00236-4).
- Ji, Q., Babbitt, A.R., Jayakumar, A., Oleynik, S., Ward, B.B., 2015. Nitrous oxide production by nitrification and denitrification in the Eastern Tropical South Pacific oxygen minimum zone. *Geophys. Res. Lett.* 42, 10,755–10,764. <https://doi.org/10.1002/2015GL066853>.
- Jong, E.D., Schappert, H.J.V., 1972. Calculation of soil respiration and activity from CO₂ profiles in the soil. *Soil Sci.* 113, 328–333.
- Kellner, E., Waddington, J.M., Price, J.S., 2005. Dynamics of biogenic gas bubbles in peat: potential effects on water storage and peat deformation. *Water Resour. Res.* 41. <https://doi.org/10.1029/2004WR003732>.
- Khalil, K., Mary, B., Renault, P., 2004. Nitrous oxide production by nitrification and denitrification in soil aggregates as affected by O₂ concentration. *Soil Biol. Biochem.* 36, 687–699. <https://doi.org/10.1016/j.soilbio.2004.01.004>.
- Kiuru, P., Palviainen, M., Grönholm, T., Raivonen, M., Kohl, L., Gauci, V., Urzainki, I., Laurén, A., 2022. Peat macropore networks – new insights into episodic and hotspot methane emission. *Biogeosciences* 19, 1959–1977. <https://doi.org/10.5194/bg-19-1959-2022>.
- Klüpfel, L., Piepenbrock, A., Kappler, A., Sander, M., 2014. Humic substances as fully regenerable electron acceptors in recently anoxic environments. *Nat. Geosci.* 7, 195–200. <https://doi.org/10.1038/ngeo2084>.
- Korkiakoski, M., Tuovinen, J.-P., Penttilä, T., Sarkkola, S., Ojanen, P., Minkkinen, K., Rainne, J., Laurila, T., Lohila, A., 2019. Greenhouse gas and energy fluxes in a boreal peatland forest after clear-cutting. *Biogeosciences* 16, 3703–3723. <https://doi.org/10.5194/bg-16-3703-2019>.
- Krüger, J.P., Leifeld, J., Glatzel, S., Szidat, S., Alewell, C., 2015. Biogeochemical indicators of peatland degradation – a case study of a temperate bog in northern Germany. *Biogeosciences* 12, 2861–2871. <https://doi.org/10.5194/bg-12-2861-2015>.
- Kuhry, P., Vitt, D.H., 1996. Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology* 77, 271–275. <https://doi.org/10.2307/2265676>.
- Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. *Soil Biol. Biochem.* 42, 1363–1371. <https://doi.org/10.1016/j.soilbio.2010.04.003>.
- Larmola, T., Tuittila, E.-S., Tirola, M., Nykänen, H., Martikainen, P.J., Yrjölä, K., Tuomivirta, T., Fritze, H., 2010. The role of Sphagnum mosses in the methane cycling of a boreal mire. *Ecology* 91, 2356–2365. <https://doi.org/10.1890/09-1343.1>.
- Laurila, T., Aurela, M., Hatakka, J., Hotanen, J.-P., Jauhainen, J., Korkiakoski, M., Korpela, L., Koskinen, M., Laiho, R., Lehtonen, A., Leppä, K., Linkosalmi, M., Lohila, A., Minkkinen, K., Mäkelä, T., Mäkiranta, P., Nieminen, M., Ojanen, P., Peltoniemi, M., Penttilä, T., Rainne, J., Rautakoski, H., Saarinen, M., Salovaara, P., Sarkkola, S., Mäkipää, R., 2021. Set-up and Instrumentation of the Greenhouse Gas Measurements on Experimental Sites of Continuous Cover Forestry, Natural Resources and Bioeconomy Studies. Natural Resources Institute Finland (Luke).
- Leifeld, J., Steffens, M., Galego-Sala, A., 2012. Sensitivity of peatland carbon loss to organic matter quality. *Geophys. Res. Lett.* 39. <https://doi.org/10.1029/2012GL051856>.
- Leppä, K., Hökkä, H., Laiho, R., Launiainen, S., Lehtonen, A., Mäkipää, R., Peltoniemi, M., Saarinen, M., Sarkkola, S., Nieminen, M., 2020. Selection cuttings as a tool to control water table level in boreal drained peatland forests. *Front. Earth Sci.* 8, 428. <https://doi.org/10.3389/feart.2020.576510>.
- Leppelt, T., Dechow, R., Gebbert, S., Freibauer, A., Lohila, A., Augustin, J., Drösler, M., Fiedler, S., Glatzel, S., Höper, H., Järveoja, J., Lærke, P.E., Maljanen, M., Mander, Ü., Mäkiranta, P., Minkkinen, K., Ojanen, P., Regina, K., Strömberg, M., 2014. Nitrous oxide emission budgets and land-use-driven hotspots for organic soils in Europe. *Biogeosciences* 11, 6595–6612. <https://doi.org/10.5194/bg-11-6595-2014>.
- Linkosalmi, M., Pumpanen, J., Biasi, C., Heinonsalo, J., Laiho, R., Lindén, A., Palonen, V., Laurila, T., Lohila, A., 2015. Studying the impact of living roots on the decomposition of soil organic matter in two different forestry-drained peatlands. *Plant Soil* 396, 59–72. <https://doi.org/10.1007/s11104-015-2584-4>.
- Maier, M., Schack-Kirchner, H., 2014. Using the gradient method to determine soil gas flux: a review. *Agric. For. Meteorol.* 192–193, 78–95. <https://doi.org/10.1016/j.agrformet.2014.03.006>.
- Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., Minkkinen, K., 2009. Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. *Soil Biol. Biochem.* 41, 695–703. <https://doi.org/10.1016/j.soilbio.2009.01.004>.
- Mäkiranta, P., Laiho, R., Penttilä, T., Minkkinen, K., 2012. The impact of logging residue on soil GHG fluxes in a drained peatland forest. *Soil Biol. Biochem.* 48, 1–9. <https://doi.org/10.1016/j.soilbio.2012.01.005>.
- Männistö, E., Korrensalo, A., Alekseychik, P., Mammarella, I., Peltola, O., Vesala, T., Tuittila, E.-S., 2019. Multi-year methane ebullition measurements from water and bare peat surfaces of a patterned boreal bog. *Biogeosciences* 16, 2409–2421. <https://doi.org/10.5194/bg-16-2409-2019>.
- Martikainen, P.J., Nykänen, H., Crill, P., Silvola, J., 1993. Effect of a lowered water table on nitrous oxide fluxes from northern peatlands. *Nature* 366, 51–53. <https://doi.org/10.1038/366051a0>.
- Minkkinen, K., Ojanen, P., Koskinen, M., Penttilä, T., 2020. Nitrous oxide emissions of undrained, forestry-drained, and rewetted boreal peatlands. *For. Ecol. Manag.* 478, 118494. <https://doi.org/10.1016/j.foreco.2020.118494>.
- Moore, T.R., Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *J. Soil Sci.* 44, 651–664. <https://doi.org/10.1111/j.1365-2389.1993.tb02330.x>.
- Moore, T.R., Roulet, N.T., 1993. Methane flux: water table relations in northern wetlands. *Geophys. Res. Lett.* 20, 587–590. <https://doi.org/10.1029/93GL00208>.
- Nichols, J.E., Peteet, D.M., 2019. Rapid expansion of northern peatlands and doubled estimate of carbon storage. *Nat. Geosci.* 12, 917–921. <https://doi.org/10.1038/s41561-019-0454-z>.
- Nielsen, T.H., Nielsen, L.P., Revsbech, N.P., 1996. Nitrification and coupled nitrification-denitrification associated with a soil-manure interface. *Soil Sci. Soc. Am. J.* 60, 1829–1840. <https://doi.org/10.2136/sssaj1996.036159950060060031x>.
- Nieminen, M., Hökkä, H., Laiho, R., Juutinen, A., Ahtikoski, A., Pearson, M., Kojola, S., Sarkkola, S., Launiainen, S., Valkonen, S., Penttilä, T., Lohila, A., Saarinen, M., Haahiti, K., Mäkipää, R., Miettinen, J., Ollikainen, M., 2018a. Could continuous cover forestry be an economically and environmentally feasible management option on drained boreal peatlands? *For. Ecol. Manag.* 424, 78–84. <https://doi.org/10.1016/j.foreco.2018.04.046>.
- Nilsson, M., Bohlin, E., 1993. Methane and carbon dioxide concentrations in bogs and fens—with special reference to the effects of the botanical composition of the peat. *J. Ecol.* 81, 615–625. <https://doi.org/10.2307/2261660>.
- Ojanen, P., Minkkinen, K., 2019. The dependence of net soil CO₂ emissions on water table depth in boreal peatlands drained for forestry. *Mires Peat* 1–8. <https://doi.org/10.19189/Map.2019.OMB.Sta.1751>.
- Ojanen, P., Minkkinen, K., 2020. Rewetting offers rapid climate benefits for tropical and agricultural peatlands but not for forestry-drained peatlands. *Glob. Biogeochem. Cycles* 34, e2019GB006503. <https://doi.org/10.1029/2019GB006503>.
- Ojanen, P., Minkkinen, K., Alm, J., Penttilä, T., 2010. Soil-atmosphere CO₂, CH₄ and N₂O fluxes in boreal forestry-drained peatlands. *For. Ecol. Manag.* 260, 411–421. <https://doi.org/10.1016/j.foreco.2010.04.036>.
- Ojanen, P., Minkkinen, K., Penttilä, T., 2013. The current greenhouse gas impact of forestry-drained boreal peatlands. *For. Ecol. Manag.* 289, 201–208. <https://doi.org/10.1016/j.foreco.2012.10.008>.
- Otte, S., Grobden, N.G., Robertson, L.A., Jetten, M.S., Kuenen, J.G., 1996. Nitrous oxide production by *Alcaligenes faecalis* under transient and dynamic aerobic and anaerobic conditions. *Appl. Environ. Microbiol.* 62, 2421–2426.
- Päivänen, J., 1973. Hydraulic conductivity and water retention in peat soils. *Acta For. Fenn.* 0. <https://doi.org/10.14214/aff.7563>.
- Pärn, J., Verhoeven, J.T.A., Butterbach-Bahl, K., Dise, N.B., Ullah, S., Aasa, A., Egorov, S., Espenberg, M., Järveoja, J., Jauhainen, J., Kasak, K., Klemetsson, L., Kull, A., Laggoun-Défarge, F., Lapshina, E.D., Lohila, A., Löhmus, K., Maddison, M., Mitsch, W.J., Müller, C., Niinemets, Ü., Osborne, B., Pae, T., Salm, J.-O., Sgouridis, F., Sohar, K., Soosaar, K., Storey, K., Teemusk, A., Tenywa, M.M., Tournebise, J., Truu, J., Veber, G., Villa, J.A., Zaw, S.S., Mander, Ü., 2018. Nitrogen-rich organic soils under warm well-drained conditions are global nitrous oxide emission hotspots. *Nat. Commun.* 9, 1135. <https://doi.org/10.1038/s41467-018-03540-1>.
- Parton, W.J., Holland, E.A., Del Grosso, S.J., Hartman, M.D., Martin, R.E., Mosier, A.R., Ojima, D.S., Schimel, D.S., 2001. Generalized model for NO_x and N₂O emissions from soils. *J. Geophys. Res. Atmos.* 106, 17403–17419. <https://doi.org/10.1029/2001JD900101>.

- Peltoniemi, M., Li, Q., Turunen, P., Müller, M., Anttila, J., Koskinen, M., Laiho, R., Lehtonen, A., Mäkiranta, P., Sarkkola, S., Tupek, B., Mäkipää, R., 2022. Soil Gas Concentration and Flux Data From Two Peatland Forest Harvesting Experiments in Southern Finland. <https://doi.org/10.5281/zenodo.7472653>.
- Pihlatie, M.K., Christiansen, J.R., Aaltonen, H., Korhonen, J.F.J., Nordbo, A., Rasilo, T., Benanti, G., Giebel, M., Helmy, M., Sheehy, J., Jones, S., Juszczak, R., Klefoth, R., Lobo-do-Vale, R., Rosa, A.P., Schreiber, P., Serça, D., Vicca, S., Wolf, B., Pumpanen, J., 2013. Comparison of static chambers to measure CH₄ emissions from soils. *Agric. For. Meteorol.* 171–172, 124–136. <https://doi.org/10.1016/j.agrformet.2012.11.008>.
- Raghoebarsing, A.A., Smolders, A.J.P., Schmid, M.C., Rijpstra, W.I.C., Wolters-Arts, M., Derksen, J., Jetten, M.S.M., Schouten, S., Sininghe Damsté, J.S., Lamers, L.P.M., Roelofs, J.G.M., Op den Camp, H.J.M., Strous, M., 2005. Methanotrophic symbionts provide carbon for photosynthesis in peat bogs. *Nature* 436, 1153–1156. <https://doi.org/10.1038/nature03802>.
- Raivonen, M., Smolander, S., Backman, L., Susiluoto, J., Aalto, T., Markkanen, T., Mäkelä, J., Rinne, J., Peltola, O., Aurela, M., Lohila, A., Tomasic, M., Li, X., Larmola, T., Juutinen, S., Tuittila, E.-S., Heimann, M., Sevanto, S., Kleinen, T., Brovkin, V., Vesala, T., 2017. HIMMEL v1.0: Helsinki Model of Methane build-up and emission for peatlands. *Geosci. Model Dev.* 10, 4665–4691. <https://doi.org/10.5194/gmd-10-4665-2017>.
- Ratcliffe, J.L., Creevey, A., Andersen, R., Zarov, E., Gaffney, P.P.J., Taggart, M.A., Mazei, Y., Tsyganov, A.N., Rowson, J.G., Lapshina, E.D., Payne, R.J., 2017. Ecological and environmental transition across the forested-to-open bog ecotone in a west Siberian peatland. *Sci. Total Environ.* 607–608, 816–828. <https://doi.org/10.1016/j.scitotenv.2017.06.276>.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Regina, K., Nykänen, H., Silvola, J., Martikainen, P.J., 1996. Fluxes of nitrous oxide from boreal peatlands as affected by peatland type, water table level and nitrification capacity. *Biogeochemistry* 35, 401–418. <https://doi.org/10.1007/BF02183033>.
- Reiche, M., Gleixner, G., Küsel, K., 2010. Effect of peat quality on microbial greenhouse gas formation in an acidic fen. *Biogeosciences* 7, 187–198. <https://doi.org/10.5194/bg-7-187-2010>.
- Roulet, N.T., Ash, R., Quinton, W., Moore, T., 1993. Methane flux from drained northern peatlands: effect of a persistent water table lowering on flux. *Glob. Biogeochem. Cycles* 7, 749–769. <https://doi.org/10.1029/93GB01931>.
- Sarkkola, S., Hökkä, H., Koivusalo, H., Nieminen, M., Ahti, E., Päivänen, J., Laine, J., 2010. Role of tree stand evapotranspiration in maintaining satisfactory drainage conditions in drained peatlands. *Can. J. For. Res.* 40, 1485–1496. <https://doi.org/10.1139/X10-084>.
- Schimmel, J.P., 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. *Biogeochemistry* 28, 183–200. <https://doi.org/10.1007/BF02186458>.
- Shanin, V., Juutinen, A., Ahtikoski, A., Frolov, P., Chertov, O., Rämö, J., Lehtonen, A., Laiho, R., Mäkiranta, P., Nieminen, M., Laurén, A., Sarkkola, S., Penttilä, T., Tupek, B., Mäkipää, R., 2021. Simulation modelling of greenhouse gas balance in continuous-cover forestry of Norway spruce stands on nutrient-rich drained peatlands. *For. Ecol. Manag.* 496, 119479. <https://doi.org/10.1016/j.foreco.2021.119479>.
- Shannon, R.D., White, J.R., 1994. A three-year study of controls on methane emissions from two Michigan peatlands. *Biogeochemistry* 27, 35–60. <https://doi.org/10.1007/BF00002570>.
- Silins, U., Rothwell, R.L., 1999. Spatial patterns of aerobic limit depth and oxygen diffusion rate at two peatlands drained for forestry in Alberta. *Can. J. For. Res.* 29, 53–61. <https://doi.org/10.1139/x98-179>.
- Skaggs, R.W., 1980. A water management model for artificially drained soils. *North Carolina. In: Agricultural Experiment Station. Technical Bulletin (USA)* 1–54.
- Sotta, E.D., Veldkamp, E., Schwendenmann, L., Guimarães, B.R., Paixão, R.K., Ruivo, M. de L.P., LOLA da COSTA, A.C., Meir, P., 2007. Effects of an induced drought on soil carbon dioxide (CO₂) efflux and soil CO₂ production in an Eastern Amazonian rainforest, Brazil. *Glob. Chang. Biol.* 13, 2218–2229. <https://doi.org/10.1111/j.1365-2486.2007.01416.x>.
- Straková, P., Anttila, J., Spetz, P., Kitunen, V., Tapanila, T., Laiho, R., 2010. Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. *Plant Soil* 335, 501–520. <https://doi.org/10.1007/s11104-010-0447-6>.
- Straková, P., Penttilä, T., Laine, J., Laiho, R., 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Glob. Chang. Biol.* 18, 322–335. <https://doi.org/10.1111/j.1365-2486.2011.02503.x>.
- Sundh, I., Nilsson, M., Granberg, G., Svensson, B.H., 1994. Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microb. Ecol.* 27, 253–265. <https://doi.org/10.1007/BF00182409>.
- Törmänen, T., Lindroos, A.-J., Kitunen, V., Smolander, A., 2020. Logging residue piles of Norway spruce, scots pine and silver birch in a clear-cut: effects on nitrous oxide emissions and soil percolate water nitrogen. *Sci. Total Environ.* 738, 139743. <https://doi.org/10.1016/j.scitotenv.2020.139743>.
- Tupek, B., Minkinen, K., Pumpanen, J., Vesala, T., Nikinmaa, E., 2015. CH₄ and N₂O dynamics in the boreal forest–mire ecotone. *Biogeosciences* 12, 281–297. <https://doi.org/10.5194/bg-12-281-2015>.
- Vainio, E., Peltola, O., Kasurinen, V., Kieloaho, A.-J., Tuittila, E.-S., Pihlatie, M., 2021. Topography-based statistical modelling reveals high spatial variability and seasonal emission patches in forest floor methane flux. *Biogeosciences* 18, 2003–2025. <https://doi.org/10.5194/bg-18-2003-2021>.
- Vainio, E., Haikarainen, I.P., Machacova, K., Putkinen, A., Santalahti, M., Koskinen, M., Fritze, H., Tuomivirta, T., Pihlatie, M., 2022. Soil-tree-atmosphere CH₄ flux dynamics of boreal birch and spruce trees during spring leaf-out. *Plant Soil*. <https://doi.org/10.1007/s11104-022-05447-9>.
- Vasander, H., Laine, J., 2008. Site type classification on drained peatlands. In: null, R.K., Korpela, Leila, Sarkkola, Sakari (Eds.), *Finland - Fenland. Finnish Peatland Society Maahenki, [Helsinki]*, pp. 146–151.
- Vitt, D.H., 2006. Functional characteristics and indicators of boreal peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), *Boreal Peatland Ecosystems, Ecological Studies*. Springer, Berlin, Heidelberg, pp. 9–24. https://doi.org/10.1007/978-3-540-31913-9_2.
- Vompersky, S.E., Sirin, A.A., Sal'nikov, A.A., Tsyganova, O.P., Valyaeva, N.A., 2011. Estimation of forest cover extent over peatlands and paludified shallow-peat lands in Russia. *Contemp. Probl. Ecol.* 4, 734–741. <https://doi.org/10.1134/S1995425511070058>.
- Waldo, N.B., Hunt, B.K., Fadely, E.C., Moran, J.J., Neumann, R.B., 2019. Plant root exudates increase methane emissions through direct and indirect pathways. *Biogeochemistry* 145, 213–234. <https://doi.org/10.1007/s10533-019-00600-6>.
- Watson, A., Stephen, K.D., Nedwell, D.B., Arah, J.R.M., 1997. Oxidation of methane in peat: kinetics of CH₄ and O₂ removal and the role of plant roots. *Soil Biol. Biochem.* 29, 1257–1267. [https://doi.org/10.1016/S0038-0717\(97\)00016-3](https://doi.org/10.1016/S0038-0717(97)00016-3).
- Windsor, J., Moore, T.R., Roulet, N.T., 1992. Episodic fluxes of methane from subarctic fens. *Can. J. Soil Sci.* 72, 441–452. <https://doi.org/10.4141/cjss92-037>.
- Włodarczyk, T., Szarlip, P., Brzezinska, M., Kotowska, U., 2008. Redox potential, nitrate content and pH in flooded Eutric Cambisol during nitrate reduction. *Res. Agric. Eng.* 53, 20–28. <https://doi.org/10.17221/2132-RAE>.
- Xu, J., Morris, P.J., Liu, J., Holden, J., 2018. PEATMAP: refining estimates of global peatland distribution based on a meta-analysis. *CATENA* 160, 134–140. <https://doi.org/10.1016/j.catena.2017.09.010>.