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RESEARCH ARTICLE

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Key Points:

- Permafrost peatlands acted as sinks of nitrous oxide; thermokarst and wildfire caused increased and reduced uptake rates, respectively
- Uptake of nitrous oxide in peat plateaus and thermokarst bogs increased with soil temperature, suggesting sensitivity to climate warming
- Impacts of thermokarst and wildfire on nitrous oxide fluxes were minor compared to methane when expressed in carbon dioxide equivalents

Supporting Information:

Supporting Information may be found in the online version of this article.

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Nitrous Oxide Fluxes in Permafrost Peatlands Remain Negligible After Wildfire and Thermokarst Disturbance

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Abstract The greenhouse gas (GHG) balance of boreal peatlands in permafrost regions will be affected by climate change through disturbances such as permafrost thaw and wildfire. Although the future GHG balance of boreal peatlands including ponds is dominated by the exchange of both carbon dioxide (CO₃) and methane (CH_4) , disturbance impacts on fluxes of the potent GHG nitrous oxide (N₂O) could contribute to shifts in the net radiative balance. Here, we measured monthly (April to October) fluxes of N₂O, CH₄, and CO₂ from three sites located across the sporadic and discontinuous permafrost zones of western Canada. Undisturbed permafrost peat plateaus acted as N₂O sinks ($-0.025 \text{ mg N}_2\text{O m}^{-2} \text{d}^{-1}$), but N₂O uptake was lower from burned plateaus ($-0.003 \text{ mg N}_2\text{O} \text{ m}^{-2} \text{ d}^{-1}$) and higher following permafrost thaw in the thermokarst bogs $(-0.054 \text{ mg N}_2\text{O m}^{-2} \text{d}^{-1})$. The thermokarst bogs had below-ambient N₂O soil gas concentrations, suggesting that denitrification consumed atmospheric N₂O during reduction to dinitrogen. Atmospheric uptake of N₂O in peat plateaus and thermokarst bogs increased with soil temperature and soil moisture, suggesting sensitivity of N_2O consumption to further climate change. Four of five peatland ponds acted as N_2O sinks (-0.018 mg N_2O $m^{-2} d^{-1}$), with no influence of thermokarst expansion. One pond with high nitrate concentrations had high N₂O emissions (0.30 mg N_2 O m⁻² d⁻¹). Overall, our study suggests that the future net radiative balance of boreal peatlands will be dominated by impacts of wildfire and permafrost thaw on CH_4 and CO_2 fluxes, while the influence from N₂O is minor.

Plain Language Summary The peatlands in the boreal biome of northwestern Canada have been a sink of the potent greenhouse gases (GHG) carbon dioxide (CO₂) and nitrous oxide (N₂O), and a source of methane (CH₄) for many millennia. Now, climate change is transforming these boreal peat landscapes as more severe and frequent wildfires burn the forests and ground ice-rich permafrost thaws. Wildfires and permafrost thaw alter soil biogeochemical conditions such as soil temperature, soil moisture, and water table depth. The changing conditions have immediate effects on GHG production, transport, and consumption in the soil, which are reasonably well understood for CO₂ and CH₄ but not for N₂O. By measuring soil GHG concentrations at different depths and GHG exchange between soil and atmosphere with static chambers, we showed that N₂O exchange from different peat surfaces responded differently depending on the two disturbance types. While burned peatland areas were close to neutral regarding N₂O, the wet, thaw-affected areas showed increased N₂O uptake driven by high soil moisture contents, soil temperatures, and below-atmospheric N₂O soil gas concentrations. However, this minor N₂O uptake can only offset less than 1% of the global warming potential of CH₄ emissions from the thawing peatlands studied here.

1. Introduction

Northern peatlands cover ~ 3 million km² (Olefeldt et al., 2021) and impacts of climate change on their future greenhouse gas (GHG) balance may be of global significance (Koven et al., 2015; Lenton et al., 2008; Schuur et al., 2013, 2015). Peatland biogeochemistry is strongly influenced by often waterlogged, cold and nutrient poor soils, which can result in both atmospheric uptake and emissions of all three major GHGs; carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) (Frolking et al., 2006, 2011). Of these, N₂O fluxes have been the least studied and impacts of disturbances such as permafrost thaw and wildfires are not well understood across the





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Writing – review & editing: Christopher Schulze, Oliver Sonnentag, Carolina Voigt, Lauren Thompson, Lona van Delden, Liam Heffernan, Guillermo Hernandez-Ramirez, McKenzie Kuhn, Sisi Lin, David Olefeldt circumpolar region (Martikainen et al., 1993; Voigt et al., 2020; Voigt, Marushchak, et al., 2017). The discontinuous permafrost zone of the Taiga Plains ecozone in western Canada is the second largest peatland region in Canada with ~250,000 km² of peatlands (Olefeldt et al., 2021). Northwestern Canada is currently experiencing some of the fastest climate warming compared to both, the rest of the globe (Rantanen et al., 2022) and across Northern Canada (Bush & Lemmen, 2019), accelerating permafrost thaw (Chasmer & Hopkinson, 2017; Gibson et al., 2018), and intensifying fire regimes (Coogan et al., 2019; Turetsky et al., 2011), with uncertain net effects on the GHG balance.

Ecosystem disturbances, such as wildfires and permafrost thaw, can cause long-term shifts in CO_2 , CH_4 , and N_2O fluxes, potentially shifting from net emission to net uptake or vice versa (Helbig, Chasmer, Desai, et al., 2017; Helbig, Chasmer, Kljun, et al., 2017; Helbig et al., 2016; Voigt et al., 2020). To understand the net effect of an altered GHG balance on atmospheric radiative forcing, it is necessary to account for the differences in sustained global warming (emission) and cooling (uptake) potential (SGWP, SGCP) for each GHG (Neubauer & Megonigal, 2015, 2019). Although N_2O fluxes from pristine, boreal peatlands are generally small (Maljanen et al., 2010; Martikainen et al., 1993; Nadelhoffer et al., 1991), the SGWP and SGCP for N_2O fluxes are 6 and 270 times greater than for CH_4 and CO_2 , respectively, when considered on a 100-year horizon (Neubauer & Megonigal, 2019). Thus, even small shifts in N_2O fluxes could affect the net radiative balance of boreal peatlands and the overall impact of disturbances.

Net N_2O emissions from soils are influenced by the balance between N_2O production through both denitrification and nitrification and N_2O consumption which only occurs through denitrification (Butterbach-Bahl et al., 2013; Schlesinger, 2013; Voigt et al., 2020). Nitrification is an aerobic process where ammonium (NH_4^+) is oxidized to nitrate (NO_3^-), with N_2O as a potential by-product. Denitrification is an anaerobic process which involves both reduction of NO_3^- to N_2O , and reduction of N_2O to nitrogen gas (N_2). Suboxic conditions can favor the initial reduction of NO_3^- to N_2O , and lead to high N_2O emissions (Hendzel et al., 2005; Marushchak et al., 2011; Regina et al., 1998), while fully anoxic conditions under long-term water-saturated conditions favor the complete reduction of NO_3^- to N_2 . Fully anoxic conditions can also lead to N_2O uptake when NO_3^- availability is low and the reduction to N_2 uses atmospheric N_2O that diffuses into the soil (Chapuis-Lardy et al., 2007). Net N_2O emissions from peatlands, including the occurrence of hot spots and hot moments (McClain et al., 2003) of N_2O emissions, are thus driven by complex interactions between soil moisture, availability of inorganic nitrogen (N), competition for inorganic N between microbes and plants, soil temperature, and physical constraints on gas diffusion (Gil et al., 2017, 2021; Marushchak et al., 2021; Repo et al., 2009; Voigt et al., 2020).

Permafrost thaw in peatlands can lead to deepening and warming of the seasonally thawed active layer, but also complete thaw and collapse of the surface which leads to the development of thermokarst bogs and ponds (Quinton et al., 2009). The effect of peatland permafrost thaw on the GHG balance thus varies depending on impacts on environmental conditions and vegetation. Permafrost peatlands, including peat plateaus, are often dominated by lichens, shrubs, and stunted trees and have relatively dry soils, yielding a low rate of soil carbon (C) accumulation and low or negligible CH₄ emissions (Helbig, Chasmer, Kljun, et al., 2017; Helbig et al., 2017; Treat et al., 2016; Turetsky et al., 2020). Collapse into thermokarst bogs causes soil saturation and a shift in vegetation to dominance of Sphagnum mosses, leading to increased CH₄ emissions and increased rate of peat accumulation—although the net effect on the CO₂ balance is uncertain due to potential mineralization of deep peat layers (Jones et al., 2017). Peatland ponds with thermokarst expansion often emit large amounts of CH_4 and have net emissions of CO₂ (Elder et al., 2021; Walter Anthony et al., 2018), while the effects on pond N₂O fluxes are unknown. Studies of boreal peatland N₂O fluxes in permafrost regions come primarily from northern Europe and have shown generally low N₂O emissions from intact peat plateaus and palsas, but at times very high emissions during initial stages of permafrost thaw and soil warming associated with increased availability of inorganic N and increases in pH (Takatsu et al., 2022; Voigt, Lamprecht, et al., 2017). Thermokarst wetlands with mineral soils have in some regions led to high N_0 emissions (Abbott & Jones, 2015; Marushchak et al., 2021; Yang et al., 2018), but N₂O emissions did not increase with the development of Tibetan thermokarst bogs (Sun et al., 2021). Lab mesocosm experiments have suggested that development of thermokarst bogs may even lead to N₂O uptake (Voigt et al., 2019), suggesting that impacts of permafrost thaw on N₂O fluxes from peatlands will vary depending on environmental conditions during and after thaw, which may lead to distinct regional differences.

Wildfire in permafrost peatlands causes large immediate emissions of CO_2 through combustion (Mack et al., 2021; Walker et al., 2019, 2020) but can also influence CO_2 fluxes for decades after the fire due to a warmer peat profile and slow vegetation regeneration (Estop-Aragonés et al., 2018; Gibson et al., 2019). The effect of wildfire on N₂O

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fluxes in permafrost peatlands is unknown, but wildfire has been shown to cause N_2O emissions in burned upland forests (Köster et al., 2017). Absence of vegetation in degrading permafrost peatlands has been linked to high N_2O emissions, due to reduced competition for NO_3^- between plants and denitrifying bacteria (Voigt, Lamprecht, et al., 2017; Voigt, Marushchak, et al., 2017). Whether the same processes result in elevated N_2O emissions from permafrost peatlands in the years after wildfire is unknown.

The objective of this study was to assess the impacts of wildfire and permafrost thaw and thus thermokarst development on the GHG balance of peatlands, with a focus on N_2O fluxes. We measured monthly growing season N_2O , CH_4 , and CO_2 fluxes from different peat landforms (peatland stages) at three sites across the sporadic and discontinuous permafrost zones of the Taiga Plains ecozone in western Canada, including intact permafrost peat plateaus, peat plateaus affected by wildfire, thermokarst bogs, and peatland ponds. We monitored soil environmental conditions, nutrient availability, and dissolved soil GHG concentrations to assess controls on the GHG fluxes. Using SGWP and SGCPs we compared the net effect on the net radiative balance caused by impacts of wildfire and permafrost thaw on N_2O and CH_4 fluxes. We hypothesized that wildfire would cause increased N_2O emissions due to increased microbial availability and decreased competition for inorganic N, while thermokarst bogs and ponds would have reduced N_2O emissions or even uptake due to stable anoxic conditions favoring complete denitrification to N_2 .

2. Materials and Methods

2.1. Study Sites and Sampling Design

Our study sites are three peatland complexes located within the sporadic and discontinuous permafrost zones of the Taiga Plains ecozone (Obu et al., 2019): Lutose (59.50°N, 117.20°W), Scotty Creek (61.30°N, 121.30°W), and Smith Creek (63.15°N, 123.25°W) (Figure 1a and Table S1 in Supporting Information S1). Mean annual air



temperature is -1.0° , -2.8° , -4.1° C at Lutose, Scotty Creek, and Smith Creek, respectively, while mean annual precipitation is ~380 mm at all sites with ~60% rainfall (Environment and Climate Change Canada, 2020). Peatland initiation occurred at Lutose and Scotty Creek sites ~8,500 cal yr BP (Heffernan et al., 2020; Pelletier et al., 2017), and was followed by transitions through marsh and fen stages until permafrost aggradation occurred ~1,800 and ~5,000 cal yr BP, respectively (Heffernan et al., 2020; Pelletier et al., 2017). The Smith Creek peatland initiation is yet to be studied. Peat depth is ~590, ~330, and ~150 cm at Lutose, Scotty Creek, and Smith Creek. Each peatland complex comprises permafrost-affected peat plateaus, and permafrost-free thermokarst bogs, channel fens, and shallow ponds. Ongoing and accelerating permafrost thaw, leading to the transition of peat plateaus into thermokarst bogs, fens and ponds has been documented at all sites (Chasmer & Hopkinson, 2017; Gibson et al., 2018; Heffernan et al., 2020; Holloway & Lewkowicz, 2020; Kuhn et al., 2021; Pelletier et al., 2017).

At each site, we established sampling transects (20–30 m in length) perpendicular to the peat plateau-thermokarst bog transition. Four distinct peatland stages were included: undisturbed permafrost peat plateau (Peat Plateau), thawing peat plateau edge (Plateau Edge), young thermokarst bogs adjacent to the plateau edge (Young Bog), and mature thermokarst bogs (Mature Bog) (Figure 1 and Figure S1 in Supporting Information S1). The vegetation composition of the peat plateaus at all three sites was comprised of stunted, open canopy of black spruce (*Picea mariana*), low woody shrubs (*Vaccinium vitis-idaea, Rhododendron groenlandicum, Vaccinium uliginosum*), and a ground cover of lichens (*Cladonia* spp.) and occasional hummocks (*Sphagnum fuscum, Sphagnum magellanicum*). The Plateau Edge was found only in a narrow transition (~2–4 m) between the Peat Plateau into Young Bog stage (Figures 1b and 1d) and had the same vegetation composition as the Peat Plateau, but some black spruce trees were tilted ("drunken trees") or showed evidence of stress from waterlogging. The Young Bog stage was the wettest stage, dominated by *Sphagnum fuscum* and rannock rush (*Scheuchzeria palustris*), while the drier Mature Bog stage was dominated by *Sphagnum fuscum* and *Sphagnum magellanicum*, bog-rosemary (*Andromeda polifolia*), leatherleaf (*Chameadaphne calyculata*), and hare's -tail cottongrass (*Eriophorum vaginatum*). Radiocarbon analysis at Lutose and Scotty Creek has dated the time since permafrost thaw to be 30–90 years for Young Bog and ~200–550 years for Mature Bog stages (Heffernan et al., 2020; Pelletier et al., 2017).

Two burned peat plateaus were also included in the study, both located <10 km from the Lutose peatland complex. One of sites burned in 2007 (2007 Burn) and has previously been studied (Estop-Aragonés et al., 2018; Gibson et al., 2018, 2019), and the other burned in 2019 (2019 Burn), that is, these sites burned 12 and <1 year prior to the study, respectively. The 2019 Burn had very limited vegetation regrowth and was largely covered by char and singed *Sphagnum fuscum* hummocks. The 2007 Burn had a dense shrub layer of Labrador tea (*Rhododendron groenlandicum*) and regrowth of <1 m tall black spruce. Wildfire changes the soil thermal regime of peat plateaus with ~60% deeper active layers (Gibson et al., 2018) and higher soil temperatures than unburned peat plateaus (Gibson et al., 2019); effects that last for up to 30 years (Gibson et al., 2018).

We also studied five peatland ponds (Figure S2 in Supporting Information S1), three at Lutose (L1, L2, and L4) and two at Smith Creek (W1 and W2), all of which have been part of previous studies (Kuhn et al., 2021; Thompson et al., 2023). All pond depths ranged from 0.5 to 2.5 m and were between 0.5 and 5 ha in area. Ongoing thermokarst expansion affected W1 and L1, as indicated by submerged and tilted black spruce trees. Ponds W2, L2, and L4 had no visible evidence of thermokarst expansion. The surroundings of pond L2 were burned in 2007 and L2 was the only pond with a beaver lodge. All ponds had thick organic sediments, up to 4 m depth above the underlying mineral sediment (Kuhn et al., 2022).

2.2. Greenhouse Gas Flux Measurements

Boardwalks were installed at each site to reduce trampling and minimize ebullitive GHG emissions. Plot-scale fluxes of N_2O , CH_4 , and CO_2 were measured using the static chamber technique (Crill, 1991; Norman et al., 1997; Subke et al., 2021). Flux measurements at Lutose and Smith Creek were made once per month between April and October in 2019 (seven sampling dates at Lutose, six at Smith Creek). At Scotty Creek, measurements were made only once in September 2018 and used different equipment described in the Supporting Information (Text S1). The chambers were opaque and the chamber-based flux measurements included ground cover and low-stature vegetation, but excluded the trees present in the peat plateaus; therefore, CO_2 fluxes are thereafter referred to as soil respiration. Circular PVC collars (0.12 m²) were inserted into the ground to a depth of 10 cm at least 24 hr prior to the first flux measurement and in few meters distance to the next collar. Each peatland stage was sampled at four collars. To create an adequate seal, each collar had a ring-formed edge filled with water before placing the chamber in the collar. We used chambers with heights of 19 or 38 cm (22.4 and 44.7 L, respectively). Vegetation height and distance

between the collar ring and peat surface were measured for each sampling occasion to account for different chamber volumes. Gas samples (20 mL) were extracted from chambers 5, 10, 15, 30, and 60 min after chamber closure and were subsequently transferred into pre-evacuated 12 mL glass vials (Labco, Lampeter, Wales, United Kingdom). Air temperature in the chambers was monitored during closure using outdoor thermometers with remote sensors (Bios Thermor, Newmarket, ON). A total of 290 chamber flux measurements from peat surfaces were conducted.

GHG concentrations from aquatic surfaces were taken from opaque floating chambers (0.06 m^2 , 13.6 L). The floating chambers were deployed in replicates of four along the edges of the ponds ($\sim 1 \text{ m}$ from the edge, avoiding the release of artificial bubbles from the sediment) and both chamber outlets were closed after pressure had equilibrated. We concentrated the floating chambers on the shorelines where active thermokarst was visible for the two thermokarst-affected ponds, L1 and W1. Gas sample collection from ponds followed the same protocols as the soil chambers. The calculated pond GHG fluxes were considered to represent total emissions (i.e., the sum of diffusive and ebullitive emissions). We collected a total of 86 chamber flux measurements from pond surfaces.

Gas samples from Smith Creek and Lutose (including pond gas samples) were analyzed at the University of Alberta, Edmonton, for N_2O , CH_4 , and CO_2 concentrations on a Varian Model 3800 gas chromatography with a Combi-Pal autosampler (CTC Analytics AG, Zwingen, Switzerland) and an electron capture detector (Varian Inc., Walnut Creek, CA). The instruments' minimum gas concentration detection limits were 0.010 parts per million (ppm) for N_2O , 0.085 ppm for CH_4 , and 8.846 ppm for CO_2 (Roman-Perez et al., 2021). Calibration curves were established using at least five standard gases, ranging from 0.25 to 9.77 ppm for N_2O , from 0.83 to 7.99 ppm for CH_4 , and from 282 to 10,099 ppm for CO_2 (Roman-Perez et al., 2021). The changes in gas concentrations over time were used to calculate peatland stage and pond GHG fluxes. Each time-series of five gas concentrations were inspected for outliers. For series with one or two outliers, these specific data points were removed prior to calculating fluxes. Series with more than two outliers were removed completely (18 fluxes). Fluxes were calculated using the method suggested by Hüppi et al. (2018), implemented in the R computing environment (R Core Team, 2020) package "gasfluxes" (Fu β , 2017). Air pressure used in the calculations was retrieved from nearby weather stations (Environment and Climate Change Canada, 2020).

We calculated the SGWP and SGCP of both N_2O and CH_4 fluxes according to Neubauer and Megonigal (2019), that is, we multiplied both CH_4 fluxes and N_2O fluxes by their corresponding 100-year time span factors 45 and 270, respectively (both emission and uptake). In this way, we obtained comparable GHG fluxes expressed in CO_2 -equivalents $m^{-2} d^{-1}$.

2.3. Environmental and Soil Data

Frost table, water table, soil moisture, and soil temperature were measured at each collar at each sampling occasion. Frost table position was measured with a 150 cm long probe inserted into the ground until it undoubtedly hit the frozen ground. The water table position was measured in pre-installed 5 mm diameter stilling wells with a blowing tube. Near-surface soil moisture (0–10 cm) was measured with a portable probe (Delta-T HH2, Delta, Cambridge, United Kingdom), averaging five readings around each collar for each occasion. Soil temperature was measured at 5, 10, 20, and 40 cm depths with handheld thermometers (Thermoworks, American Fork, UT). In addition, we inserted soil temperature loggers (Pendant HoboProV2, Onset Corp., Bourne, MA) at 5, 20, and 40 cm depths at one location in each stage. These temperature loggers were installed for a whole year and collected hourly temperature data to describe the soil temperature regimes.

Peat bulk densities (BD) and carbon-to-nitrogen ratios were determined for near-surface (0–20 cm) peat at each stage. We collected triplicate peat samples (est. volume of 200 cm³ pieces taken at 0–5, 5–10, and 10–20 cm depth using a bread knife to cut same-sized chunks) from each peatland stage. The peat samples were weighed both when wet and dried (65°C for over 48 hr) to establish soil water content and BD. According to Carter and Gregorich (2008), water-filled pore space (WFPS) was calculated from volumetric water content and BD, and C and N contents were determined by dry combustion with an elemental analyzer (Thermo Finnigan Flash EA 1112 Series, San Jose, CA).

2.4. Porewater Chemistry

Porewater was collected from each peatland stage at Lutose and Smith Creek during the monthly occasions using MacroRhizon samplers with a 0.15 μ m pore size (Rhizosphere Research, Wageningen, The Netherlands). The MacroRhizon samplers were inserted to yield porewater at 0–10 cm depth. Porewater samples were collected into two 60 mL acid-washed amber bottles, where one sample was acidified in the field with 0.2 mL 2M HCl.



The unacidified sample was analyzed for concentrations of NH_4^+ , NO_3^- , and phosphate (PO_4^{3-}) using a Thermo Scientific Gallery Beermaster Plus Photometric Analyzer (Thermo Fisher Scientific, Waltham, MA), while the acidified samples were analyzed for non-purgeable organic carbon (NPOC) and total dissolved nitrogen (TDN) concentrations using a Shimadzu TOC-L CHP Analyzer (Shimadzu Corporation, Kyoto, Japan). Trace element concentrations including, amongst others, iron (Fe) and copper (Cu) were determined by ICP-OES (iCAP6300 Duo, Thermo Fisher Scientific, Waltham, MA). Pond surface water samples were collected, filtered using a 0.7 μ m pore size GF/F filter, and then handled and analyzed in the same way as the porewater samples. The electrical conductivity (EC) and pH of porewater and pond water samples were measured on-site with calibrated PT1 and PT2 Ultrapens (Myron L Company, Carlsbad, CA).

Soil nutrient supply rates were estimated using Plant Root Simulator (PRS) probes (Western AG Innovations, Saskatoon, SK) at Smith Creek and Lutose at each collar. The PRS probes hold ion exchange resins which exchange ions at a rate that depends on the ion activity and diffusion in soils, thus integrating physical, chemical, and biological factors to provide an in situ relative measure of nutrient supply (Sharifi et al., 2009; M. Wang et al., 2018; Western Ag Innovations, 2000). Paired sets of PRS probes encompassing both cations and anions were inserted at 5 cm depth into the peat adjacent to each flux collar. All PRS probes samplers were kept installed over 40 days, starting mid-July 2019. After rinsing with distilled water, the PRS probes were shipped to and analyzed by Western AG Innovations for supply rates of NH_4^+ -N and NO_3^- -N, and PO_4^{3-} -P as well as other ions.

2.5. Soil Gas Concentration Profiles

Soil gas concentration profiles were measured once at all sites. We sampled near the end of the growing season, on 13 September 2018 at Scotty Creek, 19 August 2019 at Lutose, and 26 August 2019 at Smith Creek. We extracted soil gases using vertical metal soil gas probes, with samples from 2, 5, 10, and 20 cm following Marushchak et al. (2021). Each peatland stage had five replicates of depth profiles. In the moist, anoxic peatland stages with the water table near the surface, there was often porewater instead of gas in the attached 35 mL syringe, which was then shaken for one minute to equilibrate the gas concentration of 7 mL porewater with the remaining 28 mL headspace gas. Distributed over the day and different peatland stages, we also took ambient air samples. All gas samples were stored in 12 mL glass vials (Labco, Lampeter, Wales) and analyzed in the same way as the gas samples from Scotty Creek, outlined in Supporting Information S1.

2.6. Statistical Analyses

All statistical analyses were done using the R computing environment (R Core Team, 2020). Linear regressions were done to relate peatland fluxes of N_2O , CH_4 , and CO_2 to soil temperature at 5 or 40 cm, and to growing season averages of WFPS using "stat cor" function in R. To assess for differences between sites and peatland stages, we first averaged measurements of GHG fluxes for each collar over the growing season. Data from Scotty Creek was not included in further analysis since we only had one sampling occasion in September 2018. We then checked the data distribution of nutrient concentrations, supply rates, and fluxes of N₂O, CH₄, and CO₂ for normality with the Shapiro-Wilk test using the "rstatix" package (Kassambara, 2021). Next, we ran a two-way ANOVA assessing differences in nutrient concentrations, nutrient supply rates, and GHG fluxes among sites (Lutose and Smith Creek) and among peatland stages (Peat Plateau, Plateau Edge, Young Bog, and Mature Bog), including their interactions. The 2019 Burn and 2007 Burn data was not included in the two-way ANOVA since no burned site was present at the Smith Creek site. In most cases there was no influence of site, and we therefor combined data from peatland stages (Peat Plateau, Plateau Edge, Young Bog, Mature Bog) at Smith Creek and Lutose along with data from the 2019 Burn and 2007 Burn stages into a one-way ANOVA, using the "rstatix" package (Kassambara, 2021). Lastly, to test for differences based on type of disturbance, we ran a one-way ANOVA to test for differences between the intact peat plateau stages (Peat Plateau and Plateau Edge combined), the thermokarst bog stages (Mature Bog and Young Bog combined) and the burned peat plateau stages (2019 Burn and 2007 Burn combined). Combining peatland stages was justified by their similar soil environmental conditions and vegetation composition within the three combined groups.

3. Results

3.1. Environmental Conditions

There was a consistent order in BD across the three sites with the highest BDs in Peat Plateaus and the lowest in Young Bogs (Table 1). Soil temperature, water table position, and WFPS also had consistent order across sites

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Peatland Stage Properties and Growing Season Environmental Characteristics

Site and peatland		Pully density	WEDSa	Watar tabla	A ativa lavar	Soil temperature ^a [°C]		
stage	pH ^a	[g cm ⁻³]	[%]	depth ^a [cm]	[cm]	5 cm	20 cm	40 cm
Lutose								
2019 Burn	$4.10\pm0.30^{\rm d}$	0.07	16 ± 4^{d}	29 ± 19^{d}	74	12.2 ^d	5.6 ^d	2.5 ^d
2007 Burn	4.75 ± 0.61	NA	26 ± 16	51 ± 13	107	10.6	5.3	4.0
Peat Plateau	4.63 ± 0.91	0.06	19 ± 5	>40	77	10.3	4.3	1.9
Plateau Edge	3.95 ± 0.06	0.08	25 ± 7	27 ± 10	>150	10.4	5.5	6.0
Young Bog	4.85 ± 0.34	0.02	85 ± 22	7 ± 6	-	11.8	10.0	9.9
Mature Bog	4.91 ± 1.25	0.05	22 ± 8	24 ± 12	-	10.7	6.9	7.4
Scotty Creek								
Peat Plateau	4.39 ^e	0.11 ^f	10 ^g	NA	68 ^g	NA	NA	NA
Plateau Edge	NA	0.11 ^f	29 ^g	NA	65 ^g	NA	NA	NA
Young Bog	NA	0.03 ^f	66 ^g	NA	-	NA	NA	NA
Mature Bog	4.79 ^e	0.05^{f}	60 ^g	NA	-	NA	NA	NA
Smith Creek								
Peat Plateau	5.46 ± 1.92	0.06	19 ± 15	21 ± 14	47	8.2	2.2	0.0
Plateau Edge	4.79 ± 0.30	0.09	40 ± 29	11 ± 5	66	8.0	3.6	1.5
Young Bog	4.34 ± 0.62	0.02	100 ± 0	0 ± 1	-	10.1	7.4	5.2
Mature Bog	4.49 ± 0.80	0.04	79 ± 15	5 ± 4	_	12.8	9.6	8.2

Note. There is no active layer in both permafrost-free bog stages (= -). NA = No data available.

^aGrowing season averages (mean \pm standard deviation) of pH, water-filled pore space (WFPS), water table depth, and soil temperatures are based on measurements done during each sampling occasion. ^bBulk densities are averaged for 0–10 cm depth to allow comparison between different sites/approaches. ^cActive layer depth is the average of at least four frost table measurements in September/October. ^dMonthly measurements at 2019 Burn only started in July 2019. ^eThompson et al. (2022). ^fPelletier et al. (2017). ^gMeasured only in September 2018.

over the growing season, with the warmest and wettest conditions in Young Bogs, followed by Mature Bogs, Plateau Edges, and driest and coolest soils in Peat Plateaus. The 2019 Burn and 2007 Burn had warmer soils than unburned Peat Plateaus (Figure S3 in Supporting Information S1). The more southern Lutose site generally had warmers soils than the more northern Smith Creek site. The exception was the Mature Bog, which was wetter and warmer at Smith Creek than at Lutose (Table 1). The three peatland complexes had acidic soils with pH between 3.95 and 5.46, with no consistent pattern along the thaw transects. The peatland ponds all had pH between 7.4 and 7.9, but concentrations of nutrients varied greatly among ponds (Table 1).

3.2. Porewater Nutrient Concentrations and Supply Rates

Concentrations of NO₃⁻, NH₄⁺, and PO₄³⁻ in porewater were highly variable and had only a few consistent trends among peatland sites or peatland stages (Figures 2a, 2c, 2e) (Complete ANOVA results in Tables S2 and S3 in Supporting Information S1). Concentrations of NO₃⁻ were around two times higher at Lutose than at Smith Creek (two-way ANOVA, $F_{1,33} = 7.02$; p < 0.05), but there were no differences between peatland stages ($F_{3,33} = 1.53$; p = 0.23). Concentrations of NH₄⁺ did not vary among sites ($F_{1,33} = 3.37$; p = 0.08) or peatland stages ($F_{3,33} = 0.43$; p = 0.73). Concentrations of PO₄³⁻ did not vary between sites ($F_{1,33} = 2.01$; p = 0.17), but among peatland stages ($F_{3,33} = 5.10$; p < 0.01). A one-way ANOVA showed that burned stages had 12 to 25 times higher PO₄³⁻ than intact and thermokarst stages ($F_{2,47} = 10.62$; p < 0.001, Tukey HSD p < 0.001).

Supply rates of NO₃⁻, NH₄⁺, and P did not differ between the Lutose and Smith Creek sites, and only differed for a few peatland stages (Figures 2b, 2d, 2f) (Tables S2 and S3 in Supporting Information S1). Nutrient supply rates of NO₃⁻ varied between peatland stages ($F_{3,24} = 4.48$; p = 0.012) with lower rates for Young Bogs than Mature Bogs and Plateau Edges. No differences among peatland stages were found for supply rates of NH₄⁺





Figure 2. Porewater concentrations and supply rates of (a, b) nitrate (NO_3^-), (c, d) ammonium (NH_4^+), (e) phosphate (PO_4^{-3-}), and (f) phosphorus (P) across all peatland stages, that is, 2019 Burn (B19), 2007 Burn (B07), Peat Plateau (P), Plateau Edge (PE), Young Bog (YB), and Mature Bog (MB) at Lutose and Smith Creek. Measurements were collected over the 2019 growing season. Note the logarithmic scale of all *y*-axes.

 $(F_{3,24} = 4.48; p = 0.012)$, but we note the high supply rates for the Young Bog at Lutose and the Mature Bog at Smith Creek which both were fully saturated for much of the growing season. A one-way ANOVA showed that burned stages had higher supply rates of P than either the intact permafrost stages and thermokarst stages $(F_{3,39} = 5.30; p = 0.009)$.

3.3. Soil Gas Concentrations

Concentrations of N_2O below the water table were lower than ambient atmospheric N_2O concentrations in all Young Bog and Mature Bog profiles (Figure 3a). We observed a decreasing gradient in N_2O concentrations with depth below the water table, while the drier profiles had lesser and more gradual decreases. Out of 60 soil gas concentration profiles, only two Peat Plateau profiles had N_2O concentrations higher than ambient at 20 cm depth (Figure 3a). In contrast to N_2O , CH₄ concentrations in the Young Bog and Mature Bog increased with depth, especially below the water table, and ranged from ambient concentrations at 2 ppm to 30,000 ppm (Figure 3b). Under



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Figure 3. Soil gas concentrations of (a) nitrous oxide (N_2O), (b) methane (CH_4), and (c) carbon dioxide (CO_2) for Peat Plateau, Plateau Edge, Young Bog, and Mature Bog depth profiles from three peatland sites (Lutose, Scotty Creek, and Smith Creek). Measurements were done at the end of the growing season, in September 2018 at Scotty Creek and in August 2019 at Lutose and Smith Creek. Water table position is shown for every soil profile, indicated to be above or below the gas sampling depths (2, 5, 10, and 20 cm). Note the logarithmic scale for the CH₄ and CO₂ soil gas concentrations.

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Figure 4. Fluxes and temperature dependency of (a, b) nitrous oxide (N_2O), (c, d) methane (CH₄), and (e, f) soil respiration (CO₂) from peatland stages, that is, 2019 Burn (B19), 2007 Burn (B07), Peat Plateau (P), Plateau Edge (PE), Young Bog (YB), and Mature Bog (MB) at three sites (Lutose, Scotty Creek and Smith Creek). Each symbol is an individual flux measurement, collected monthly throughout the growing season from April to October 2019 from Lutose (n = 7) and Smith Creek (n = 6), but only once in September 2018 at Scotty Creek. Linear regressions use data from all three sites and show the relationship between soil temperature at 5 cm and N_2O and soil respiration, while the temperature at 40 cm is used for CH₄ fluxes.

oxic conditions in the peat plateaus, CH_4 concentrations declined with depth to a minimum of 1.5 ppm CH_4 . Only a few Peat Plateau and Plateau Edge profiles had elevated CH_4 concentrations, associated with wetter locations. The CO_2 concentrations had similar patterns as CH_4 concentrations in wet sites, with increasing concentrations up to 180,000 ppm below the water table (Figure 3c). In contrast to CH_4 , CO_2 increased with depth also above the water table, for example, in dry Peat Plateaus, and CO_2 concentrations were never below ambient.

3.4. Greenhouse Gas Fluxes

There were no differences in N_2O , CH_4 , or CO_2 (soil respiration) fluxes between the Lutose and Smith Creek sites when comparing peatland stages present at both sites; Peat Plateau, Plateau Edge, Young Bog, and Mature Bog (Figure 4, two-way ANOVA results in Table S4 in Supporting Information S1). Average growing season N_2O uptake was greatest from the combined thermokarst bog stages (Mature Bog and Young Bog, -0.054 mg





Figure 5. Relationship between nitrous oxide (N_2O) fluxes and near-surface soil water-filled pore space (WFPS). Each symbol represents the growing season average N_2O flux and WFPS for individual collars located in different peatland stages, including burned peat plateaus (2019 Burn, 2007 Burn) along with Peat Plateau, Plateau Edge, Young Bog, and Mature Bog. Note the logarithmic scale for the WFPS. Logarithmic regressions are shown for each of the six peatland stages (colored lines, p > 0.05), and for the combined data (black line, p < 0.001).

N₂O m⁻² d⁻¹), followed by the peat plateau stages (Peat Plateau and Plateau Edge, $-0.025 \text{ mg N}_2\text{O} \text{ m}^{-2} \text{ d}^{-1}$), and least for the burned peat plateau stages (2019 Burn and 2007 Burn, -0.003 mg N₂O m⁻² d⁻¹) (one-way ANOVA, $F_{2.45} = 15.1$; p < 0.001, Table S5 in Supporting Information S1). Fluxes from Scotty Creek were not included in statistical analysis since measurements were only done once in September 2018, but we noted some distinct patterns-including N₂O emissions rather than N₂O uptake from the Peat Plateau and Plateau Edge (Figure 4a). Uptake of N₂O increased significantly with higher soil temperature at 5 cm depth in the Peat Plateau and Plateau Edge (Figure 4b), leading to a seasonal trend of highest uptake in July and August. The influence of soil temperature on N₂O uptake was weaker for Mature Bog and Young Bog and absent at the 2019 Burn and 2007 Burn stages (Figure 4b). Seasonal average N2O uptake was greater from collars with higher near-surface WFPS (Figure 5). This trend was present but non-significant within each peatland stage, but significant ($R^2 = 0.24$, p < 0.001) when assessed across all collars from all peatland stages.

Emissions of CH₄ were highest from the thermokarst bog stages, where emissions generally increased with higher soil temperatures at 40 cm (Figure 4d). Average growing season CH₄ emissions were greatest from the thermokarst bog stages (Mature Bog and Young Bog, 34 and 31 mg CH₄ m⁻² d⁻¹, respectively), while there was no significant difference between the intact peat plateau (Peat Plateau and Plateau Edge, -0.07 and 10.3 mg CH₄ m⁻² d⁻¹, respectively) and burned peat plateau stages (2019 Burn and 2007 Burn, 3.2 and -0.54 mg CH₄ m⁻² d⁻¹, respectively) (one-way ANOVA, $F_{2,45} = 15.1$; p < 0.001, Table S5 in Supporting Information S1). The ranking of average CH₄ emissions among stages closely followed the average water table position (Table 1). Emissions of CH₄ from Scotty Creek were not included in the analysis but had a similar pattern.

Soil respiration (dark chamber CO₂ fluxes) had a strong seasonal trend linked to soil temperature at 5 cm at all peatland stages, except at the 2019 Burn stage (Figure 4f). The 2019 Burn stage also had the lowest average growing season soil respiration (1,200 mg CO₂ m⁻² d⁻¹), while the 2007 Burn (3,400 mg CO₂ m⁻² d⁻¹) was not different from either the peat plateau stages (Peat Plateau and Plateau Edge, 3,900 and 4,100 mg CO₂ m⁻² d⁻¹, respectively) or the thermokarst bog stages (Mature Bog and Young Bog, 5,200 and 3,300 mg CO₂ m⁻² d⁻¹, respectively) (one-way ANOVA, $F_{5,42} = 3.79$; p = 0.006, Table S5 in Supporting Information S1).

3.5. N₂O Fluxes From Peatlands Ponds

Four out of five ponds had N₂O uptake, with average rates similar to the peatland stages ($-0.018 \text{ mg N}_2\text{O} \text{m}^{-2} \text{d}^{-1}$), and no difference between ponds with stable edges and active thermokarst expansion (Figure 6). Pond L2 had high average N₂O emissions (0.30 mg N₂O m⁻² d⁻¹), and emissions could reach up to 1.00 mg N₂O m⁻² d⁻¹. Ponds near Lutose generally had higher EC, NPOC, TDN, and inorganic nutrients compared to ponds near Smith Creek (Table 2). Whether ponds had stable edges or actively thermokarst expansion did not have consistent influences on water chemistry. The L2 pond near Lutose, affected by beaver activity and within a 2007 wildfire, had the highest PO₄³⁻ and the highest ratio between NO₃⁻ and NH₄⁺ (Table 2).

3.6. Impact of Wildfire and Permafrost Thaw on the Net Radiative Balance

We used SGCP and SGWP to assess impacts on the net radiative balance from shifts in CO_2 , CH_4 , and N_2O fluxes due to wildfire and permafrost thaw (Figure 7). The CO_2 fluxes we report only represent soil respiration, and not the full net ecosystem exchange, and can thus not be directly compared to the shifts in CH_4 and N_2O fluxes. Comparing the burned peat plateau stages (2019 Burn and 2007 Burn) with Peat Plateau and Plateau Edge, we found that wildfire led to reduced uptake of N_2O representing +5.9 mg CO_2 -eq. m⁻² d⁻¹ (emissions). The reduction of soil respiration between the 2019 Burn and the intact counterpart was -2,700 mg CO_2 m⁻² d⁻¹ but does



Figure 6. Nitrous oxide (N_2O) fluxes from five peatland ponds with different forms of disturbance (Intact = L4, W2, Beaver/2007 Burn = L2, Thermokarst = L1, W1). Flux measurements were done on six occasions between May and October 2019 for all sites except pond L2 which was visited three times between July and October 2019.

not represent the full CO₂ balance. Comparing the thermokarst bog stages (Mature Bog and Young Bog) with Peat Plateaus and Plateau Edges, we found that thermokarst led to increased N₂O uptake representing -7.8 mg CO₂-eq. m⁻² d⁻¹ (uptake), while a shift from minor to large CH₄ emissions represented +1,200 mg CO₂-eq. m⁻² d⁻¹ (emissions). Hence, the influence of greater N₂O uptake offset less than 1% of the increased CH₄ emissions following thermokarst bog development, when estimated as CO₂-eq.

4. Discussion

Here, we explored the impacts of permafrost thaw and wildfire on N_2O , CH_4 , and CO_2 fluxes from boreal peatlands in western Canada, with a focus on controls on N_2O fluxes and their contribution to the overall GHG balance. Generally, we observed N_2O uptake rather than emissions from different peatland stages and peatland ponds, and that the rate of N_2O uptake in the studied nutrient-poor peatlands increased with higher soil temperatures and higher soil moisture. As a result, permafrost thaw and development of thermokarst bogs led to increased N_2O uptake, although accompanying increases of CH_4 emissions had a much greater influence on the net radiative balance. In contrast, we found that wildfire led to reduced N_2O uptake, minor changes to CH_4 fluxes, and reduced soil respiration in the first year after fire. We found N_2O uptake from most of the studied peatland ponds, with no clear influence of thermokarst pond expansion, but also that one pond acted as a N_2O emission hot spot.

Table 2 Peatland Pond Characteristics									
Site and			Nutrient c			oncentrations [µg L ⁻¹]			
peatland pond	pН	EC [µS cm ⁻¹]	Fe ^a [mg L ⁻¹]	NPOC [mg L ⁻¹]	TDN [mg L ⁻¹]	NO ₃ -	$\mathrm{NH_4^+}$	PO ₄ ³⁻	
Lutose									
L1 ^b	7.89 ± 0.97	366 ± 93	0.1	48.3 ± 15.5	3.04 ± 1.39	25 ± 36	984 ± 1,239	126 ± 163	
L2 ^c	$7.54 \pm 0.06^{\rm d}$	144 ± 5^{d}	1.3 ^d	$44.2 \pm 1.4^{\rm d}$	$1.41 \pm 0.27^{\rm d}$	129 ± 139^{d}	97.7 ± 29.7^{d}	195 ± 109^{d}	
L4	7.43 ± 0.94	660 ± 87	0.1	41.3 ± 9.0	2.06 ± 0.56	3.2 ± 2.4	226 ± 323	8.5 ± 7.1	
Smith Creek									
W1 ^b	7.27 ± 0.89	111 ± 17	< 0.001	18.8 ± 1.7	0.83 ± 0.14	6.3 ± 9.4	50.7 ± 37.7	5.3 ± 1.9	
W2	7.20 ± 0.50	90 ± 22	0.1	18.6 ± 1.5	0.88 ± 0.19	7.0 ± 7.7	78.2 ± 85.7	4.5 ± 0.8	

Note. Growing season averages (mean \pm standard deviation) of pH, electrical conductivity (EC), Total dissolved nitrogen (TDN), non-purgeable organic carbon (NPOC), nitrate (NO₃⁻), ammonium (NH₄⁺), and phosphate (PO₄³⁻) are based on monthly measurements between May and September/October 2019.

^aConcentrations of iron (Fe) were only measured once in 2019. ^bFloating chambers placed at actively expanding thermokarst edges. ^cSituated in 2007 Burn fire scar and beaver activity. ^dMonthly measurements at L2 only started in July 2019.





Figure 7. Greenhouse gas balances in CO_2 -equivalents among peatland stages (in the order from left to right: 2019 Burn, 2007 Burn, Peat Plateau, Plateau Edge, Young Bog, and Mature Bog), comparing (a) soil respiration, (b) CH_4 fluxes, and (c) N_2O fluxes. Boxplots use all flux data measured throughout the 2019 growing season, with black crosses indicating the averages. Conversion to CO_2 -equivalents use sustained global warming and cooling potentials (SGWP, SGCP) based on a 100-year time span for CH_4 (45) and N_2O (270) (Neubauer & Megonigal, 2019). Note the difference in the scale of the *y*-axes. Outliers are not shown.

Below we discuss the controls on the GHG balance of each of the studied peatland stages, and the implications of thermokarst and wildfire for the future net radiative balance.

4.1. Greenhouse Gas Balance of Peat Plateaus

In the intact Peat Plateaus, the presence of permafrost leads to dry, low nutrient conditions, as displayed by the lowest soil moisture content and soil temperatures in connection with the shallowest active layer when compared to the burned counterparts. The Plateau Edges as the transition zone to the thermokarst bogs had similar vegetation than the plateaus but displayed a deepened active layer and a water table closer to the surface due to ground subsidence. Thus, Peat Plateaus and their Plateau Edges had mostly oxic conditions at shallow depths that facilitate aerobic processes and exhibited near zero N_2O fluxes or small N_2O uptake.

 N_2O uptake increased significantly with higher soil temperatures in both, peat plateaus and plateau edges. Soil temperature has been identified as a key control of N_2O fluxes previously (Butterbach-Bahl et al., 2013; Voigt, Lamprecht, et al., 2017). As such, Siljanen et al. (2020) concluded that N_2O production processes in boreal forests are more temperature-sensitive than N_2O consumption processes, as they found N_2O emissions during the warm, dry summer months and N_2O uptake during the wetter, colder shoulder season. However, our results showed the opposite as overall N_2O uptake, and thus N_2O consumption increased with surface soil temperatures during the peak growing season. Emissions of N_2O are subject to high temporal (hot moments) and spatial (hot spots) variability (Fiencke et al., 2022; Marushchak et al., 2011; McClain et al., 2003). Although we did not observe high N_2O emissions at the soil surface of our study sites, we measured increased N_2O soil gas concentrations at depth in two out of 15 Peat Plateau plots, indicating active N_2O production. In fact, N_2O produced at depth may not necessarily reach the soil surface (Arah et al., 1991). Siljanen et al. (2020) suggested that acid-tolerant denitrifiers, as identified in arctic wetlands (Palmer et al., 2012), consume N_2O via reductase and thus exceed N_2O production.

Besides soil temperatures, porewater nutrient concentrations and soil moisture content usually control the N₂O balance. The effect of active layer deepening caused increased nutrient supply of NO₃⁻ and NH₄⁺ in the Plateau Edges but did not lead to N₂O emissions. In contrast, the Plateau Edges showed slightly increased, non-significant uptake of N₂O consistent over all three sites as the Plateau Edges are slightly wetter than the Peat Plateaus. Thus, we conclude that the effect of soil moisture exceeded the effect of nutrient supply rates under generally low availability of NO₃⁻ and NH₄⁺. The Peat Plateaus in this study had the lowest P supply and PO₄³⁻ porewater concentrations compared to the other stages, which could have limited N₂O emissions (Liimatainen et al., 2018). Besides N₂O uptake, we also observed CH₄ uptake by the peat plateaus due to the oxic soil conditions, similar to other studies on boreal forests (Siljanen et al., 2020) and tundra peat plateaus (Voigt, Lamprecht, et al., 2017). As in Gibson et al. (2019) and Estop-Aragonés et al. (2018), soil respiration was higher in the Peat Plateaus than in burned stages but was lower than in the thermokarst stages.



4.2. Greenhouse Gas Balance of Burned Peat Plateaus

We expected wildfire disturbance to lead to increased N_2O emissions linked to enhanced availability of NH_4^+ and NO_3^- , possibly caused by (a) reduced plant demand due to a lack of vegetation as observed from bare peat surfaces on palsa and peat plateau surfaces in Eurasia (Fiencke et al., 2022; Marushchak et al., 2011; Repo et al., 2009; Voigt et al., 2017), (b) mineralization of organic matter during combustion (Walker et al., 2019, 2020), and (c) increased soil mineralization in the years after wildfire due to warmer soils and a deeper active layer (Gibson et al., 2018), potentially resulting in a flush of higher nutrient supply, specifically inorganic N, from recently thawed, deeper soil layers (Ackley et al., 2021; Keuper et al., 2012; Ramm et al., 2022; Salmon et al., 2018). In addition to inorganic N, the availability of PO_4^{3-} supply can fuel nitrification and enhance N₂O production (Liimatainen et al., 2018) by stimulating microbial activity (F. Wang et al., 2014). Although our results confirmed an increased supply of phosphorus post-fire, we did not observe N₂O emissions, but observed near zero N₂O fluxes from burned peat plateaus.

Three reasons could contribute to the lack of N_2O emissions from the burned peat plateaus. First, although soil respiration almost reached pre-burn rates 12 years after wildfire and increased with soil temperature, N_2O uptake by the wildfire-affected plateaus was not correlated with soil temperature, unlike the intact Peat Plateaus and Plateau Edges. We attribute the absence of temperature sensitivity of N_2O uptake to the fact that microbial communities might have been affected by the fire and require extended time to re-establish. Similarly, high N_2O emissions from thawing yedoma permafrost only occurred in revegetated soils several years after thaw, with re-establishment of the soil microbial communities involved in N-cycling (Marushchak et al., 2021). Köster et al. (2017) found that N_2O emissions only reached pre-fire rates in boreal mineral soils 40 years after fire.

Second, burned wood ash can inhibit N_2O production during nitrification and denitrification in acidic boreal peat soils (Liimatainen et al., 2014). In addition, the loss of labile soil C from combustion could also influence microbial communities to reduce their ability for CH_4 and N_2O uptake, limiting denitrification as well as nitrification and CH_4 oxidation (Gibson et al., 2019; Köster et al., 2017). The lack of labile soil C a has been attributed to lower soil respiration following wildfire than unburned surfaces (Gibson et al., 2019).

Lastly, the burned peat plateau stages had the deepest water table and driest conditions (WFPS <30%) in the soil profile. Soil moisture has been identified as an important regulator of N₂O fluxes in permafrost-affected soils (optimum WFPS for N₂O emissions: 40%–60%), frequently overruling the effect of temperature (Voigt et al., 2020). Like recent post-wildfire studies on arctic mineral soils in Greenland (Hermesdorf et al., 2022) and subarctic upland forest soils in Northern Canada (Köster et al., 2017), we conclude here that soil moisture also controlled N₂O fluxes in wildfire-affected peatlands in the western Canadian boreal zone, possibly limiting both, emissions and uptake of N₂O.

4.3. Greenhouse Gas Balance of Thermokarst Bogs

The development of thermokarst bogs leads to saturated conditions of the peat profile, particularly during the first few decades. We found that thermokarst formation and subsequent wet conditions promote N_2O uptake in peatlands in the Taiga Plains, which were up to three times greater than uptake from the Peat Plateau and Plateau Edge. Despite the relative differences in soil moisture regimes across the sites, the observed trends of increased N_2O uptake and below ambient N_2O porewater concentrations under anoxic conditions were consistent for all three sites.

Although N_2O uptake can also occur under oxic conditions, observed in polar desert soils (Brummell et al., 2014), the anoxic conditions suggest the prevalence of denitrification, particularly in the mostly anoxic Young Bog stage. Nitrification only produced limited NO_3^- and N_2O under wet conditions, so that concentrations and supply rates of NO_3^- were low. The small amounts of available NO_3^- and N_2O were reduced to N_2 in the denitrification process under the anoxic conditions, which is a typical wetland process also found in thawing yedoma permafrost (Marushchak et al., 2021). In conclusion, the limitations of both NO_3^- and oxygen promote the favorability of N_2O as a terminal electron acceptor, which is eventually reduced to N_2 (Butterbach-Bahl et al., 2013; Voigt et al., 2020). Besides low NO_3^- , the anoxic conditions also lead to high NH_4^+ , aligning with results from an incubation study with peat samples from a collapse-scar bog (Morison et al., 2018) and suggesting well-established and effective denitrification and/or inhibited nitrification under anoxic conditions. Both thermokarst stages had a higher phosphorus supply than the Peat Plateaus, associated with increased productivity driven by higher soil temperatures (Figure 4f and Figure S3 in Supporting Information S1); except for the Young Bog at Smith Creek, where inundation cut off respiration (Figure 4e).

Besides WFPS and its effects on redox conditions and nutrient supply, we consider the elevated soil temperatures in the thermokarst bogs as a secondary driver of the increased N₂O uptake, despite non-significant correlations. Although well-established in literature (e.g., Jones et al., 2017), CH_4 emissions also correlated weakly with soil temperatures at 40 cm depth. Therefore, as expected with climate change, longer, wetter, and warmer summers could further amplify the thermokarst areas' N₂O uptake and CH_4 emissions, respectively.

4.4. Greenhouse Gas Balance of Peatland Ponds

Boreal peatland ponds have been identified as potential hot spots for N_2O , CH_4 , and CO_2 emissions (Huttunen et al., 2002; Kortelainen et al., 2020; Kuhn et al., 2021) with thermokarst activity enhancing CH_4 and CO_2 emissions (Kuhn et al., 2022). In our study, four of five ponds had minor N_2O uptake similar to the peatland stages. We also found no differences in N_2O exchange between thermokarst and stable edges, despite previous studies on these ponds found higher CH_4 emissions from thermokarst edges (Kuhn et al., 2022), suggesting different controls on CH_4 and N_2O emissions in boreal ponds.

One pond, L2, had N_2O emissions (~0.30 mg N_2O m⁻² d⁻¹) similar to those reported for agricultural wetlands (0.27 mg N_2O -N m⁻² d⁻¹; Pennock et al., 2010) and was within the global range reported for ponds (0.12–0.56 mg N_2O -N m⁻² d⁻¹; DelSontro et al., 2018). L2 had distinct water chemistry compared to both the four other ponds in this study and to 20 other ponds in the study region (Kuhn et al., 2021), as L2 had five to fifty times higher dissolved NO_3^- and iron concentrations. Differences in NO_3^- concentrations and net emission of N_2O were possibly driven by the pond's proximity to a twelve-year-old fire scar or linked to beaver activity. The potential liberation of inorganic N through wildfire has been shown to enhance downstream N_2O emissions from water bodies (Soued et al., 2016). However, this study did not find higher inorganic N concentrations in recently burned peat plateaus for downstream transport into ponds. Further, L2 was the only pond with known beaver activity. The presence of beavers has been shown to alter the biogeochemistry of ecosystems, enhancing N inputs in ponds (Naiman & Melillo, 1984), and potentially driving the observed high N_2O emissions.

Notably, the high magnitude of N_2O released from ponds like L2 can potentially offset all N_2O uptake from thermokarst bog expansion, as L2's relative N_2O -related net radiative balance (not shown) is five to 15 times larger than any other measured net radiative balance in this study (Figure 7). However, since we only found N_2O emissions from one out of five ponds, further work is required to identify N_2O hot spots amongst the peatland ponds, which constitute less than 1% of the area in peatland complexes (Olefeldt et al., 2021). In comparison, 5.3% of the unburned area and 8.3% of the burned areas transitioned into young bogs within the Taiga Plains over 30 years (Gibson et al., 2018).

4.5. Implications of Climate Change on the Net Radiative Balance

Although we did not determine the net ecosystem CO_2 exchange of the peat surfaces, it is likely that CO_2 rather than CH_4 dominates shifts in the net radiative balance for wildfire-affected areas, as differences in CH_4 fluxes from the burned plateau and the Peat Plateau were minor. As gross primary production is reduced due to the lack of vegetation, soil respiration will drive net ecosystem exchange post-wildfire disturbance. Previous work showed soil respiration from burned peat plateaus to be lower than the intact Peat Plateau in Lutose (Gibson et al., 2019). Effects of thermokarst bog expansion have shown CH_4 to dominate net radiative forcing rather than CO_2 in the first few decades after permafrost thaw (Helbig, Chasmer, Desai, et al., 2017; Helbig, Chasmer, Kljun, et al., 2017), both governed by the water table position in the peat landscape. The growing season of 2019 was relatively dry, with low water tables compared to site observations at Lutose since 2015 (Heffernan et al., 2021). There, soil respiration signaled high productivity in the thermokarst bog stages (Estop-Aragonés et al., 2018), aligning with the observed N₂O uptake observed in our study. The shallow water table at Smith Creek inhibited soil respiration and moss photosynthesis in the Young Bog (Kou et al., 2022). Except for the inundated Young Bog at Smith Creek, soil respiration in this study showed an inverse correlation to N₂O uptake.

We also found an inverse relationship between N_2O and CH_4 for the peatland stages, in both soil gas concentrations and fluxes. Fundamental biogeochemical redox processes are governed by water table depth and soil moisture



contents, controlling the typically inverse CH_4 and N_2O production (Frolking et al., 2011; Maljanen et al., 2010). Completely anoxic conditions in fully saturated soils are conducive to CH_4 production and, in turn, low CH_4 oxidation (Frolking et al., 2011; Maljanen et al., 2010), while the anoxic conditions would also be expected to lead to complete denitrification, producing N_2 rather than N_2O as gaseous end-product. While we found a similar range to a comparable study (Siljanen et al., 2020), N_2O uptake of the peat plateau was only around half of the CH_4 uptake from this yet intact peatland stage when expressed in CO_2 -eq. Regarding the thermokarst bogs, the increased N_2O uptake offset less than 1% of their CH_4 emissions. However, the measured N_2O uptake from all peat surfaces of the Taiga Plains (overall average: $-0.03 \text{ mg } N_2O \text{ m}^{-2} \text{ d}^{-1}$) was large compared to previous studies from across the circumpolar region (lower quartile: $-0.01 \text{ mg } N_2O \text{ m}^{-2} \text{ d}^{-1}$; Voigt et al., 2020).

Thus, we conclude that wildfire and thermokarst can shift CO₂, CH₄, and N₂O fluxes, dominated by enhanced CH₄ emissions following thermokarst compared to intact Peat Plateaus displaying uptake of both, N₂O and CH₄. CO₂ fluxes are rather impacted by wildfire, based on our findings and previous studies. Ongoing permafrost thaw is highly likely for at least 6% of the overall study area, that is, more than 22,000 km² (Gibson et al., 2021). Considering the vast areal extension of peatland thermokarst in the Taiga Plains (Helbig et al., 2016), our findings thus suggest a small counter acting N₂O feedback to the impacts of increasing CH₄ emissions, which has previously been unaccounted for.

5. Conclusion

We found a negative feedback from increased N_2O uptake upon thermokarst disturbance and a positive feedback from reduced N_2O uptake following wildfire in the Taiga Plains. Unlike previous studies on permafrost peatlands in northern Eurasia, where abundant hot spots of N_2O emissions have been found, we did not find any such evidence in western Canada. For thermokarst bogs, our results suggest WFPS and soil temperature as major drivers of altered N_2O fluxes in these nutrient-limited environments. Peatland ponds were generally neutral or sinks of N_2O , albeit with a wide range of fluxes and one N_2O hot spot driven by elevated NO_3^- supply. From a SGCP/ SGWP perspective, the effects of wildfire and permafrost thaw on GHG emissions from boreal peatlands in our study region are likely to be dominated by the responses of CH_4 and CO_2 , while N_2O uptake constituted less than 1% of CH_4 emissions from peatland thermokarst.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Additional Figures (S1–S3) and Tables (S1–S5) are available in the Supporting Information S1 to this journal article. The data set and metadata for this research is publicly available at the University of Alberta Libraries' Education & research archive under https://doi.org/10.7939/r3-5ce6-yx27 and is licensed under CC BY-NC 4.0. All statistic software and functions used in this study are available for download under https://cran.r-project.org/.

References

- Abbott, B. W., & Jones, J. B. (2015). Permafrost collapse alters soil carbon stocks, respiration, CH₄, and N₂O in upland tundra. *Global Change Biology*, 21(12), 4570–4587. https://doi.org/10.1111/gcb.13069
- Ackley, C., Tank, S. E., Haynes, K. M., Rezanezhad, F., McCarter, C., & Quinton, W. L. (2021). Coupled hydrological and geochemical impacts of wildfire in peatland-dominated regions of discontinuous permafrost. *Science of the Total Environment*, 782, 146841. https://doi.org/10.1016/j. scitotenv.2021.146841
- Arah, J. R. M., Smith, K. A., Crichton, I. J., & Li, H. S. (1991). Nitrous oxide production and denitrification in Scottish arable soils. Journal of Soil Science, 42(3), 351–367. https://doi.org/10.1111/j.1365-2389.1991.tb00414.x
- Brummell, M. E., Farrell, R. E., Hardy, S. P., & Siciliano, S. D. (2014). Greenhouse gas production and consumption in High Arctic deserts. Soil Biology and Biochemistry, 68, 158–165. https://doi.org/10.1016/j.soilbio.2013.09.034
 - Bush, E. & Lemmen, D. S. (Eds.) (2019). Canada's changing climate report (p. 444). Government of Canada. Retrieved from https://changingclimate.ca/CCCR2019/about/
 - 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? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1621), 20130122. https://doi.org/10.1098/rstb.2013.0122

Carter, M. R., & Gregorich, E. G. (2008). Soil sampling and methods of analysis (2nd ed.). Canadian Journal of Soil Science, Taylor & Francis Group, CRC Press. https://doi.org/10.1201/9781420005271

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- Chapuis-Lardy, L., Wrage, N., Metay, A., Chotte, J.-L., & Bernoux, M. (2007). Soils, a sink for N₂O? A review. *Global Change Biology*, 13(1), 1–17. https://doi.org/10.1111/j.1365-2486.2006.01280.x
- Chasmer, L., & Hopkinson, C. (2017). Threshold loss of discontinuous permafrost and landscape evolution. *Global Change Biology*, 23(7), 2672–2686. https://doi.org/10.1111/gcb.13537
- Coogan, S. C. P., Robinne, F.-N., Jain, P., & Flannigan, M. D. (2019). Scientists' warning on wildfire A Canadian perspective. Canadian Journal of Forest Research, 49(9), 1015–1023. https://doi.org/10.1139/cjfr-2019-0094
- Crill, P. M. (1991). Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles*, 5(4), 319–334. https://doi.org/10.1029/91GB02466
- DelSontro, T., Beaulieu, J. J., & Downing, J. A. (2018). Greenhouse gas emissions from lakes and impoundments: Upscaling in the face of global change. *Limnology and Oceanography Letters*, 3(3), 64–75. https://doi.org/10.1002/lol2.10073
- Elder, C. D., Thompson, D. R., Thorpe, A. K., Chandanpurkar, H. A., Hanke, P. J., Hasson, N., et al. (2021). Characterizing methane emission hotspots from thawing permafrost. *Global Biogeochemical Cycles*, 35(12), e2020GB006922. https://doi.org/10.1029/2020GB006922
- Environment and Climate Change Canada. (2020). *Historical data*. Environment and Climate Change Canada, 2020. Retrieved from https://climate.weather.gc.ca/historical_data/search_historic_data_e.html
- Estop-Aragonés, C., Czimczik, C. I., Heffernan, L., Gibson, C., Walker, J. C., Xu, X., & Olefeldt, D. (2018). Respiration of aged soil carbon during fall in permafrost peatlands enhanced by active layer deepening following wildfire but limited following thermokarst. *Environmental Research Letters*, 13(8), 85002. https://doi.org/10.1088/1748-9326/aad5f0
- Fiencke, C., Marushchak, M. E., Sanders, T., Wegner, R., & Beer, C. (2022). Microbiogeochemical traits to identify nitrogen hotspots in permafrost regions. *Nitrogen*, 3(3), 458–501. https://doi.org/10.3390/nitrogen3030031
- Frolking, S., Roulet, N., & Fuglestvedt, J. (2006). How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research*, 111(G1), G01008. https://doi.org/10.1029/2005JG000091
- Frolking, S., Talbot, J., Jones, M. C., Treat, C. C., Kauffman, J. B., Tuittila, E., & Roulet, N. (2011). Peatlands in the Earth's 21st century climate system. *Environmental Reviews*, 19(NA), 371–396. https://doi.org/10.1139/a11-014
- Fuß, R. (2017). gasfluxes: Greenhouse gas flux calculation from chamber measurements. Retrieved from https://cran.r-project.org/web/packages/ gasfluxes/index.html
- Gibson, C., Cottenie, K., Gingras-Hill, T., Kokelj, S. V., Baltzer, J., Chasmer, L., & Turetsky, M. (2021). Mapping and understanding the vulnerability of northern peatlands to permafrost thaw at scales relevant to community adaptation planning. *Environmental Research Letters*, 16(5), 055022. https://doi.org/10.1088/1748-9326/abe74b
- Gibson, C. M., Chasmer, L. E., Thompson, D. K., Quinton, W. L., Flannigan, M. D., & Olefeldt, D. (2018). Wildfire as a major driver of recent permafrost thaw in boreal peatlands. *Nature Communications*, 9(1), 3041. https://doi.org/10.1038/s41467-018-05457-1
- Gibson, C. M., Estop-Aragonés, C., Flannigan, M., Thompson, D. K., & Olefeldt, D. (2019). Increased deep soil respiration detected despite reduced overall respiration in permafrost peat plateaus following wildfire. *Environmental Research Letters*, 14(12), 125001. https://doi. org/10.1088/1748-9326/ab4f8d
- Gil, J., Pérez, T., Boering, K., Martikainen, P. J., & Biasi, C. (2017). Mechanisms responsible for high N₂O emissions from subarctic permafrost peatlands studied via stable isotope techniques. *Global Biogeochemical Cycles*, 31(1), 172–189. https://doi.org/10.1002/2015GB005370
- Gil, J. A., Marushchak, M. E., Rütting, T., Baggs, E. M., Pérez, T., Novakovskiy, A., et al. (2021). Sources of nitrous oxide and fate of mineral nitrogen in sub-Arctic permafrost peat soils. *Biogeosciences Discussions*, 1–25. https://doi.org/10.5194/bg-2021-228
- Heffernan, L., Estop-Aragonés, C., Knorr, K.-H., Talbot, J., & Olefeldt, D. (2020). Long-term impacts of permafrost thaw on carbon storage in peatlands: Deep losses offset by surficial accumulation. *Journal of Geophysical Research: Biogeosciences*, 125(3), e2019JG005501. https:// doi.org/10.1029/2019JG005501
- Heffernan, L., Jassey, V. E. J., Frederickson, M., MacKenzie, M. D., & Olefeldt, D. (2021). Constraints on potential enzyme activities in thermokarst bogs: Implications for the carbon balance of peatlands following thaw. *Global Change Biology*, 27(19), 4711–4726. https://doi. org/10.1111/gcb.15758
- Helbig, M., Chasmer, L. E., Desai, A. R., Kljun, N., Quinton, W. L., & Sonnentag, O. (2017). Direct and indirect climate change effects on carbon dioxide fluxes in a thawing boreal forest–wetland landscape. *Global Change Biology*, 23(8), 3231–3248. https://doi.org/10.1111/gcb.13638
- Helbig, M., Chasmer, L. E., Kljun, N., Quinton, W. L., Treat, C. C., & Sonnentag, O. (2017). The positive net radiative greenhouse gas forcing of increasing methane emissions from a thawing boreal forest-wetland landscape. *Global Change Biology*, 23(6), 2413–2427. https://doi. org/10.1111/gcb.13520
- Helbig, M., Pappas, C., & Sonnentag, O. (2016). Permafrost thaw and wildfire: Equally important drivers of boreal tree cover changes in the Taiga Plains, Canada. *Geophysical Research Letters*, 43(4), 1598–1606. https://doi.org/10.1002/2015GL067193.Received
- Helbig, M., Quinton, W. L., & Sonnentag, O. (2017). Warmer spring conditions increase annual methane emissions from a boreal peat landscape with sporadic permafrost. *Environmental Research Letters*, *12*(11), 115009. https://doi.org/10.1088/1748-9326/aa8c85
- Hendzel, L. L., Matthews, C. J. D., Venkiteswaran, J. J., st. Louis, V. L., Burton, D., Joyce, E. M., & Bodaly, R. A. (2005). Nitrous oxide fluxes in three experimental boreal forest reservoirs. *Environmental Science & Technology*, 39(12), 4353–4360. https://doi.org/10.1021/es049443j
- Hermesdorf, L., Elberling, B., D'Imperio, L., Xu, W., Lambæk, A., & Ambus, P. L. (2022). Effects of fire on CO₂, CH₄, and N₂O exchange in a well-drained Arctic heath ecosystem. *Global Change Biology*, 28(16), 4882–4899. https://doi.org/10.1111/gcb.16222
- Holloway, J. E., & Lewkowicz, A. G. (2020). Half a century of discontinuous permafrost persistence and degradation in western Canada. Permafrost and Periglacial Processes, 31(1), 85–96. https://doi.org/10.1002/ppp.2017
- Hugelius, G., Tarnocai, C., Broll, G., Canadell, J. G., Kuhry, P., & Swanson, D. K. (2013). The northern circumpolar soil carbon database: Spatially distributed datasets of soil coverage and soil carbon storage in the northern permafrost regions. *Earth System Science Data*, 5(1), 3–13. https://doi.org/10.5194/essd-5-3-2013
- Hüppi, R., Felber, R., Krauss, M., Six, J., Leifeld, J., & Fuß, R. (2018). Restricting the nonlinearity parameter in soil greenhouse gas flux calculation for more reliable flux estimates. *PLoS One*, 13(7), e0200876. https://doi.org/10.1371/journal.pone.0200876
- Huttunen, J. T., Väisänen, T. S., Heikkinen, M., Hellsten, S., Nykänen, H., Nenonen, O., & Martikainen, P. J. (2002). Exchange of CO₂, CH₄, and N₂O between the atmosphere and two northern boreal ponds with catchments dominated by peatlands or forests. *Plant and Soil*, 242(1), 137–146. https://doi.org/10.1023/A:1019606410655
- Jones, M. C., Harden, J., O'Donnell, J., Manies, K., Jorgenson, T., Treat, C., & Ewing, S. (2017). Rapid carbon loss and slow recovery following permafrost thaw in boreal peatlands. *Global Change Biology*, 23(3), 1109–1127. https://doi.org/10.1111/gcb.13403
- Kassambara, A. (2021). rstatix: Pipe-Friendly framework for basic statistical tests. Retrieved from https://CRAN.R-Project.Org/Package=rstatix Keuper, F., van Bodegom, P. M., Dorrepaal, E., Weedon, J. T., van Hal, J., van Logtestijn, R. S. P., & Aerts, R. (2012). A frozen feast: Thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, 18(6), 1998–2007. https://doi. org/10.1111/j.1365-2486.2012.02663.x

21698961,

- Kortelainen, P., Larmola, T., Rantakari, M., Juutinen, S., Alm, J., & Martikainen, P. J. (2020). Lakes as nitrous oxide sources in the boreal landscape. *Global Change Biology*, 26(3), 1432–1445. https://doi.org/10.1111/gcb.14928
- Köster, E., Köster, K., Berninger, F., Aaltonen, H., Zhou, X., & Pumpanen, J. (2017). Carbon dioxide, methane and nitrous oxide fluxes from a fire chronosequence in subarctic boreal forests of Canada. *Science of the Total Environment*, 601–602, 895–905. https://doi.org/10.1016/j. scitotenv.2017.05.246
- Kou, D., Virtanen, T., Treat, C. C., Tuovinen, J.-P., Räsänen, A., Juutinen, S., et al. (2022). Peatland heterogeneity impacts on regional carbon flux and its radiative effect within a boreal landscape. *Journal of Geophysical Research: Biogeosciences*, *127*(9), e2021JG006774. https://doi. org/10.1029/2021JG006774
- Koven, C. D., Schuur, E. A. G., Schädel, C., Bohn, T. J., Burke, E. J., Chen, G., et al. (2015). A simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. *Philosophical Transactions of the Royal Society A: Mathematical, Physical & Engineering Sciences*, 373(2054), 20140423. https://doi.org/10.1098/rsta.2014.0423
- Kuhn, M., Schmidt, M., Heffernan, L., Stührenberg, J., Knorr, K. H., Estop-Aragonés, C., et al. (2022). High ebullitive, millennial-aged greenhouse gas emissions from thermokarst expansion of peatland lakes in boreal western Canada. *Limnology & Oceanography*, 68(2), 498–513. https://doi.org/10.1002/ino.12288
- Kuhn, M. A., Thompson, L. M., Winder, J. C., Braga, L. P. P., Tanentzap, A. J., Bastviken, D., & Olefeldt, D. (2021). Opposing effects of climate and permafrost thaw on CH₄ and CO₂ emissions from northern lakes. AGU Advances, 2(4), e2021AV000515. https://doi. org/10.1029/2021AV000515
- Lenton, T. M., Held, H., Kriegler, E., Hall, J. W., Lucht, W., Rahmstorf, S., & Schellnhuber, H. J. (2008). Tipping elements in the Earth's climate system. Proceedings of the National Academy of Sciences of the United States of America, 105(6), 1786–1793. https://doi.org/10.1073/ pnas.0705414105
- Liimatainen, M., Martikainen, P. J., & Maljanen, M. (2014). Why granulated wood ash decreases N₂O production in boreal acidic peat soil? Soil Biology and Biochemistry, 79, 140–148. https://doi.org/10.1016/j.soilbio.2014.09.016
- Liimatainen, M., Voigt, C., Martikainen, P. J., Hytönen, J., Regina, K., Óskarsson, H., & Maljanen, M. (2018). Factors controlling nitrous oxide emissions from managed northern peat soils with low carbon to nitrogen ratio. Soil Biology and Biochemistry, 122, 186–195. https://doi. org/10.1016/j.soilbio.2018.04.006
- Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., & Miller, S. N. (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. *Science*, 372(6539), 280–283. LP – 283. https://doi.org/10.1126/science.abf3903
- Maljanen, M., Sigurdsson, B. D., Guðmundsson, J., Óskarsson, H., Huttunen, J. T., & Martikainen, P. J. (2010). Greenhouse gas balances of managed peatlands in the Nordic countries – Present knowledge and gaps. *Biogeosciences*, 7(9), 2711–2738. https://doi.org/10.5194/ bg-7-2711-2010
- Marshall, I. B., Schut, P. H., & Ballard, M. (1999). A national ecological framework for Canada. In Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch. Retrieved from https://sis.agr.gc.ca/cansis/nsdb/ecostrat/index.html
- 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(6450), 51–53. https://doi.org/10.1038/366051a0
- Marushchak, M. E., Kerttula, J., Diáková, K., Faguet, A., Gil, J., Grosse, G., et al. (2021). Thawing Yedoma permafrost is a neglected nitrous oxide source. *Nature Communications*, 12(1), 7107. https://doi.org/10.1038/s41467-021-27386-2
- Marushchak, M. E., Pitkämäki, A., Koponen, H., Biasi, C., Seppälä, M., & Martikainen, P. J. (2011). Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. *Global Change Biology*, 17(8), 2601–2614. https://doi.org/10.1111/j.1365-2486.2011.02442.x
- McClain, M. E., Boyer, E. W., Dent, C. L., Gergel, S. E., Grimm, N. B., Groffman, P. M., et al. (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, 6(4), 301–312. https://doi.org/10.1007/s10021-003-0161-9
- Morison, M. Q., Macrae, M. L., Petrone, R. M., & Fishback, L. (2018). Climate-induced changes in nutrient transformations across landscape units in a thermokarst subarctic peatland. Arctic Antarctic and Alpine Research, 50(1), e1519366. https://doi.org/10.1080/15230430.2018.1519366 Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., & Laundre, J. A. (1991). Effects of temperature and substrate quality on element mineralization
- in six arctic soils. *Ecology*, 72(1), 242–253. https://doi.org/10.2307/1.2404/bitects of temperature and substrate quanty on element initialization in six arctic soils. *Ecology*, 72(1), 242–253. https://doi.org/10.2307/1.2404/bitects of temperature and substrate quanty on element initialization bitmans, D. & Mullillo, J. M. (1094). Nitianona hudgets of a substrate strange situated by bases (Castor consideratio). *Ocealaria*, 62(2), 150–155.
- Naiman, R. J., & Melillo, J. M. (1984). Nitrogen budget of a subarctic stream altered by beaver (Castor canadensis). *Oecologia*, 62(2), 150–155. https://doi.org/10.1007/BF00379007
- Neubauer, S. C., & Megonigal, J. P. (2015). Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, 18(6), 1000–1013. https://doi.org/10.1007/s10021-015-9879-4. http://www.jstor.org/stable/43677758
- Neubauer, S. C., & Megonigal, J. P. (2019). Correction to: Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosystems*, 22(8), 1931–1932. https://doi.org/10.1007/s10021-019-00422-5
- Norman, J. M., Kucharik, C. J., Gower, S. T., Baldocchi, D. D., Crill, P. M., Rayment, M., et al. (1997). A comparison of six methods for measuring soil-surface carbon dioxide fluxes. *Journal of Geophysical Research*, 102(D24), 28771–28777. https://doi.org/10.1029/97JD01440 Obu, J., Westermann, S., Bartsch, A., Berdnikov, N., Christiansen, H. H., Dashtseren, A., et al. (2019). Northern Hemisphere permafrost map based
- on TTOP modelling for 2000–2016 at 1 km2 scale. *Earth-Science Reviews*, 193, 299–316. https://doi.org/10.1016/j.earscirev.2019.04.023
 Olefeldt, D., Hovemyr, M., Kuhn, M. A., Bastviken, D., Bohn, T. J., Connolly, J., et al. (2021). The boreal–arctic wetland and lake dataset
- (BAWLD). Earth System Science Data, 13(11), 5127-5149, https://doi.org/10.5194/essd-13-5127-2021
- Palmer, K., Biasi, C., & Horn, M. A. (2012). Contrasting denitrifier communities relate to contrasting N₂O emission patterns from acidic peat soils in arctic tundra. *The ISME Journal*, 6(5), 1058–1077. https://doi.org/10.1038/ismej.2011.172
- Pelletier, N., Talbot, J., Olefeldt, D., Turetsky, M., Blodau, C., Sonnentag, O., & Quinton, W. L. (2017). Influence of Holocene permafrost aggradation and thaw on the paleoecology and carbon storage of a peatland complex in northwestern Canada. *The Holocene*, 27(9), 1391–1405. https://doi.org/10.1177/0959683617693899
- Pennock, D., Yates, T., Bedard-Haughn, A., Phipps, K., Farrell, R., & Mcdougal, R. (2010). Landscape controls on N₂O and CH₄ emissions from freshwater mineral soil wetlands of the Canadian Prairie Pothole region. *Geoderma*, 155(3–4), 308–319. https://doi.org/10.1016/j. geoderma.2009.12.015
- Quinton, W. L., Bemrose, R. K., Zhang, Y., & Carey, S. K. (2009). The influence of spatial variability in snowmelt and active layer thaw on hillslope drainage for an alpine tundra hillslope. *Hydrological Processes*, 23(18), 2628–2639. https://doi.org/10.1002/hyp.7327
- Ramm, E., Liu, C., Ambus, P., Butterbach-Bahl, K., Hu, B., Martikainen, P. J., et al. (2022). A review of the importance of mineral nitrogen cycling in the plant-soil-microbe system of permafrost-affected soils changing the paradigm. *Environmental Research Letters*, 17(1), 13004. https://doi.org/10.1088/1748-9326/ac417e
- Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., et al. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. Communications Earth & Environment, 3(1), 168. https://doi.org/10.1038/s43247-022-00498-3

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- R Core Team. (2020). R: A language and environment for statistical computing (3.6.3). R Foundation for Statistical Computing. Retrieved from https://www.r-project.org/
- Regina, K., Nykänen, H., Maljanen, M., Silvola, J., & Martikainen, P. J. (1998). Emissions of N₂O and NO and net nitrogen mineralization in a boreal forested peatland treated with different nitrogen compounds. *Canadian Journal of Forest Research*, 28(1), 132–140. https://doi. org/10.1139/x97-198
- Repo, M. E., Susiluoto, S., Lind, S. E., Jokinen, S., Elsakov, V., Biasi, C., et al. (2009). Large N₂O emissions from cryoturbated peat soil in tundra. *Nature Geoscience*, 2(3), 189–192. https://doi.org/10.1038/ngeo434
- Roman-Perez, C. C., Hernandez-Ramirez, G., Kryzanowski, L., Puurveen, D., & Lohstraeter, G. (2021). Greenhouse gas emissions, nitrogen dynamics and barley productivity as impacted by biosolids applications. *Agriculture, Ecosystems & Environment, 320*, 320. https://doi. org/10.1016/j.agee.2021.107577
- Salmon, V. G., Schädel, C., Bracho, R., Pegoraro, E., Celis, G., Mauritz, M., et al. (2018). Adding depth to our understanding of nitrogen dynamics in permafrost soils. *Journal of Geophysical Research: Biogeosciences*, 123(8), 2497–2512. https://doi.org/10.1029/2018JG004518
- Schlesinger, W. H. (2013). An estimate of the global sink for nitrous oxide in soils. *Global Change Biology*, 19(10), 2929–2931. https://doi.org/10.1111/gcb.12239
- Schuur, E. A. G., Abbott, B. W., Bowden, W. B., Brovkin, V., Camill, P., Canadell, J. G., et al. (2013). Expert assessment of vulnerability of permafrost carbon to climate change. *Climatic Change*, 119(2), 359–374. https://doi.org/10.1007/s10584-013-0730-7
- Schuur, E. A. G., McGuire, A. D., Schädel, C., Grosse, G., Harden, J. W., Hayes, D. J., et al. (2015). Climate change and the permafrost carbon feedback. *Nature*, 520(7546), 171–179. https://doi.org/10.1038/nature14338
- Sharifi, M., Lynch, D. H., Zebarth, B. J., Zheng, Z., & Martin, R. C. (2009). Evaluation of nitrogen supply rate measured by in situ placement of Plant Root SimulatorTM probes as a predictor of nitrogen supply from soil and organic amendments in potato crop. American Journal of Potato Research, 86(5), 356–366. https://doi.org/10.1007/s12230-009-9090-2
- Siljanen, H. M. P., Welti, N., Voigt, C., Heiskanen, J., Biasi, C., & Martikainen, P. J. (2020). Atmospheric impact of nitrous oxide uptake by boreal forest soils can be comparable to that of methane uptake. *Plant and Soil*, 454(1), 121–138. https://doi.org/10.1007/s11104-020-04638-6
- Soued, C., del Giorgio, P. A., & Maranger, R. (2016). Nitrous oxide sinks and emissions in boreal aquatic networks in Québec. *Nature Geoscience*, 9(2), 116–120. https://doi.org/10.1038/ngeo2611
- Subke, J.-A., Kutzbach, L., & Risk, D. (2021). Soil chamber measurements. In T. Foken (Ed.), Springer handbook of atmospheric measurements (pp. 1603–1624). Springer International Publishing. https://doi.org/10.1007/978-3-030-52171-4_60
- Sun, X., Wang, H., Song, C., Jin, X., Richardson, C. J., & Cai, T. (2021). Response of methane and nitrous oxide emissions from peatlands to permafrost thawing in Xiaoxing'an Mountains, Northeast China. Atmosphere, 12(2), 222. https://doi.org/10.3390/atmos12020222
- Takatsu, Y., Miyamoto, T., Tahvanainen, T., & Hashidoko, Y. (2022). Nitrous oxide emission in response to pH from degrading palsa mire peat due to permafrost thawing. *Current Microbiology*, 79(2), 56. https://doi.org/10.1007/s00284-021-02690-8
- Thompson, L. M., Kuhn, M. A., Winder, J. C., Braga, L. P. P., Hutchins, R. H. S., Tanentzap, A. J., et al. (2023). Controls on methylmercury concentrations in lakes and streams of peatland-rich catchments along a 1700 km permafrost gradient. *Limnology & Oceanography*, 68(3), 583–597. https://doi.org/10.1002/lno.12296
- Thompson, L. M., Olefeldt, D., Mangal, V., & Knorr, K. H. (2022). Soil and porewater chemistry from peatlands of the Interior Plains, Northwestern Canada (dataset). University of Alberta Education & Research Archive. https://doi.org/10.7939/r3-vp5e-aj53
- Treat, C. C., Jones, M. C., Camill, P., Gallego-Sala, A., Garneau, M., Harden, J. W., et al. (2016). Effects of permafrost aggradation on peat properties as determined from a pan-Arctic synthesis of plant macrofossils. *Journal of Geophysical Research: Biogeosciences*, 121(1), 78–94. https://doi.org/10.1002/2015JG003061
- Turetsky, M. R., Abbott, B. W., Jones, M. C., Anthony, K. W., Olefeldt, D., Schuur, E. A. G., et al. (2020). Carbon release through abrupt permafrost thaw. *Nature Geoscience*, 13(2), 138–143. https://doi.org/10.1038/s41561-019-0526-0
- Turetsky, M. R., Kane, E. S., Harden, J. W., Ottmar, R. D., Manies, K. L., Hoy, E., & Kasischke, E. S. (2011). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, 4(1), 27–31. https://doi.org/10.1038/ngeo1027
- Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – Carbon dioxide, methane, and nitrous oxide. *Global Change Biology*, 23(8), 2929–3432. https://doi.org/10.1111/gcb.13563
- Voigt, C., Marushchak, M. E., Abbott, B. W., Biasi, C., Elberling, B., Siciliano, S. D., et al. (2020). Nitrous oxide emissions from permafrost-affected soils. *Nature Reviews Earth & Environment*, 1(8), 420–434. https://doi.org/10.1038/s43017-020-0063-9
- Voigt, C., Marushchak, M. E., Lamprecht, R. E., Jackowicz-Korczyński, M., Lindgren, A., Mastepanov, M., et al. (2017). Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. *Proceedings of the National Academy of Sciences of the United States of America*, 114(24), 6238–6243. https://doi.org/10.1073/pnas.1702902114
- Voigt, C., Marushchak, M. E., Mastepanov, M., Lamprecht, R. E., Christensen, T. R., Dorodnikov, M., et al. (2019). Ecosystem carbon response of an Arctic peatland to simulated permafrost thaw. *Global Change Biology*, 25(5), 1746–1764. https://doi.org/10.1111/gcb.14574
- Walker, X. J., Baltzer, J. L., Cumming, S. G., Day, N. J., Ebert, C., Goetz, S., et al. (2019). Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature*, 572(7770), 520–523. https://doi.org/10.1038/s41586-019-1474-y
- Walker, X. J., Rogers, B. M., Veraverbeke, S., Johnstone, J. F., Baltzer, J. L., Barrett, K., et al. (2020). Fuel availability not fire weather controls boreal wildfire severity and carbon emissions. *Nature Climate Change*, 10(12), 1130–1136. https://doi.org/10.1038/s41558-020-00920-8
- Walter Anthony, K., Schneider von Deimling, T., Nitze, I., Frolking, S., Emond, A., Daanen, R., et al. (2018). 21st-century modeled permafrost carbon emissions accelerated by abrupt thaw beneath lakes. *Nature Communications*, 9(1), 3262. https://doi.org/10.1038/s41467-018-05738-9
- Wang, F., Li, J., Wang, X., Zhang, W., Zou, B., Neher, D. A., & Li, Z. (2014). Nitrogen and phosphorus addition impact soil N₂O emission in a secondary tropical forest of South China. Scientific Reports, 4(1), 5615. https://doi.org/10.1038/srep05615
- Wang, M., Talbot, J., & Moore, T. R. (2018). Drainage and fertilization effects on nutrient availability in an ombrotrophic peatland. Science of the Total Environment, 621, 1255–1263. https://doi.org/10.1016/j.scitotenv.2017.10.103
- Western Ag Innovations. (2000). Plant Root SimulatorTM (PRS) probes are an effective tool for measuring nutrient supplies to plant roots. Retrieved from https://www.westernag.ca/innovations/publications/techupdates?view=tu&id=3
- Yang, G., Peng, Y., Marushchak, M. E., Chen, Y., Wang, G., Li, F., et al. (2018). Magnitude and pathways of increased nitrous oxide emissions from uplands following permafrost thaw. *Environmental Science & Technology*, 52(16), 9162–9169. https://doi.org/10.1021/acs.est.8b02271