

Dissertationes Forestales 383

**Revealing drivers of nitrous oxide (N_2O) fluxes in a
thawing sub-Arctic permafrost peatland**

Nathalie Ylenia Triches

Department of Forest Sciences
Faculty of Agriculture and Forestry
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry,
for public examination in the Building EE, Walter Hall, University of Helsinki,
on 29 January 2026, at 12 o'clock noon.

Title of dissertation: Revealing drivers of nitrous oxide (N₂O) fluxes in a thawing sub-Arctic permafrost peatland

Author: Nathalie Ylenia Triches

Dissertationes Forestales 383

<https://doi.org/10.14214/df.383>

© Author

Licensed [CC BY-NC-ND 4.0](https://creativecommons.org/licenses/by-nd/4.0/)

Thesis Supervisors:

Dr. Mathias Göckede, Max Planck Institute for Biogeochemistry, Germany

Prof. Timo Vesala, Institute for Atmospheric and Earth System Research/Physics, University of Helsinki, Finland

Dr. Maija E. Marushchak, Department of Environmental and Biological Sciences, University of Eastern Finland, Finland

Dr. Anna-Maria Virkkala, Woodwell Climate Research Center, USA and Institute for Atmospheric and Earth System Research, University of Helsinki, Finland

Custos:

Prof. Jaana Bäck, Institute for Atmospheric and Earth System Research/Forest Sciences, University of Helsinki, Finland

Pre-examiners:

Prof. Frank Berninger, University of Eastern Finland, Finland

Dr. Christof Ammann, Agroscope, Switzerland

Opponent:

Dr. Christof Ammann, Agroscope, Switzerland

ISSN 1795-7389 (online)

ISBN 978-951-651-856-8 (pdf)

Publishers:

Finnish Society of Forest Science

Faculty of Agriculture and Forestry of the University of Helsinki

School of Forest Sciences of the University of Eastern Finland

Editorial Office:

Finnish Society of Forest Science

Viikinkaari 6, 00790 Helsinki, Finland

<https://www.dissertationesforestales.fi>

Triches NY (2026) Revealing drivers of nitrous oxide (N_2O) fluxes in a thawing sub-Arctic permafrost peatland. *Dissertationes Forestales* 383. 33 p. <https://doi.org/10.14214/df.383>

ABSTRACT

Nitrous oxide (N_2O) is the third most important anthropogenic greenhouse gas, with atmospheric concentrations increasing from 273 to 336 ppb since 1800, primarily due to the use of agricultural fertilisers. While N_2O fluxes from managed agricultural soils are well-studied, recent studies have shifted focus toward nutrient-rich Arctic soils. However, the majority of Arctic soils remain nutrient-poor, and low N_2O fluxes are poorly understood. This thesis advances our understanding of low N_2O fluxes in a nutrient-poor, highly heterogeneous Arctic peatland through three years of repeated manual chamber measurements across the snow-free season.

A key challenge in quantifying low fluxes is methodological sensitivity. We evaluated the performance of a novel portable gas analyser (Aeris MIRA Ultra N_2O/CO_2) under laboratory and field conditions, confirming its suitability for manual chamber measurements in the Arctic. We developed practical guidelines for instrument setup, chamber closure times, and the critical need to measure N_2O fluxes under both light (transparent chambers) and dark (opaque chambers) conditions.

We demonstrate that a nutrient-poor peatland acts as a continuous, non-negligible yet small sink for N_2O during the snow-free season—first *in-situ* evidence of sustained uptake in Arctic peatlands. However, we also identify a localised N_2O hot spot, showing that a single site could transform the ecosystem from a net sink to a net source. Using random forest models, we identify photosynthetically active radiation (PAR) and net ecosystem exchange as the dominant drivers of low N_2O fluxes, with consistent differences between light and dark conditions (Wilcoxon rank-sum test: 0.37, $p < 0.001$).

This work provides robust methodological guidance, reveals a persistent N_2O sink and unexpected hot spots, and identifies key environmental drivers of low N_2O fluxes. It underscores the necessity of repeated, paired light–dark measurements and sufficient replication to detect hot spots in variable Arctic ecosystems. These findings are relevant to Arctic and other nutrient-poor ecosystems globally.

Keywords: nitrous oxide, Arctic, PAR, peatland, Aeris MIRA Ultra N_2O/CO_2

ACKNOWLEDGEMENTS

*There is a bond between human beings and their environment —
with nature, if you will. I don't know much about your world,
but I believe you see nature as something that was just good enough to create you,
and now just good enough to be made to serve you;
to be exploited, twisted, and changed however you like.
But that attitude is wrong.*

*We are a part of nature, perhaps not even an important part,
and we are bound to it more strongly than most of us suspect.*

translated from Wolfgang and Heike Hohlbein, Die Zauberin von Märchenmond

This thesis was my attempt to understand one specific ecosystem in one specific area, the Stordalen palsa mire in northern Sweden, a little bit better. Although I am thankful and a wee bit proud of the scientific data we collected there- especially since one of the main findings was discovered in the field-, it was simply the amount of time spent in the mire and the region that taught me most about it. Palsa mires in Fennoscandia are beautiful little islands of a vanishing ecosystems, and even if we tried to mitigate the impacts of global warming, they will disappear. For some, this is a challenge to model the greenhouse gas emissions as accurately as possible, or give numbers on how much Stordalen has degraded over the last years. For me, it is a very obvious picture of how other mammals, plants, and whole ecosystems have to adapt to how humans exploited, twisted, and changed the world. It makes me sad to know that all these living beings will go through many changes, some good, some bad, to adapt to a new world. Unfortunately, our research will not change anything about that. Nevertheless, I hope that the magic of the mire touches the hearts of many scientists enough to see nature as a gift, for us and our children, and to realise that indeed, we are bound to any part of the world more strongly than most of us suspect.

I am extremely grateful to my main supervisor Mathias, who supported me in many difficult situations and called me at 7:15 a.m. during a field campaign to make sure I was alright. Kiitos to the best shrink at INAR (someone has to say it), Timo, for dry Finnish humour, advertising the University of Helsinki during the ICOS winter school, listening to my complaints, challenging me, and listening to my complaints (did I say that twice? There must be a reason.). Kiitos to Maija for her extensive help during the first field campaigns, an inspiring research stay, and sharing all her extensive knowledge on N₂O fluxes with me. Kiitos Anna, for all advice on how to deal with a PhD life and for sharing the passion for good statistics. Many thanks also to Martin, for his valuable input during the PAC meetings and his "just-chill-and-don't-worry-about-it" attitude.

Because five supervisors clearly aren't enough to get through a PhD, this list goes on. Kiitos Jaana for your help and patience in finishing this thesis. Thanks to Renate Ellinger and Claudia Trojandt for teaching me how to effectively speak German in Germany, communicate more efficiently, and take better care of myself. Herzlichen Dank to Anita Maercker, Ulli Schleier, Martin Hertel, Kristian Schufft, and the IPAS team for helping me to organise my field campaigns, and understand and visualise my data. Tack så mycket Mattias, Emily, and Niklas, who helped me with all big and small issues during my field campaigns, and made Abisko my real home. Kiitos Mirkka for being the best field helper, a good friend, and, most likely, the funniest person on the whole globe. Going to Abisko so regularly also meant stopping by in Copenhagen: mersi viiu mau, Fabia, for providing the most delicious vegan food, best company, and a welcoming home away from home. Grazie mille Fabio for dealing

with us "f*king morons" for four days and taking so many beautiful and useful photos for us. Jan, tausend Dank for all your patience, critique, and support. As always, a million thanks to my wee sis, Janoika, Evi and my mum for pulling me back up so many times, listening to my drama, still loving me and accepting me as who I am- muchas gracias, dankuwel, und mersi viiu, viiu mau. Last, but not least, thanks Apo, for being there more times than I can count, helping, annoying, and making me laugh on a daily basis, and being the best Schatz anyone could ask for. Teşekkürler, aşkim.

Oh, and- thanks to myself for not giving up and going through this despite an inability to think in equations and numbers, and Ursula Le Guin, Cornelia Funke, Christopher Paolini, Kai Meyer, Sebastien De Castell, and many other fantastic authors writing fantasy books out there, providing me with the perfect worlds to escape into when this one gets too depressing. You, along with my cats and other beloved four-legged friends, some great sports teachers and my escapes into the beautiful northern landscapes made sure I wouldn't go completely nuts during this PhD journey.

Jena, October 2025, Nathalie Ylenia Triches

LIST OF ORIGINAL ARTICLES

This dissertation is based on the following articles, which are referred to by bold Roman numerals in the text:

- I **Triches, N. Y.**, Engel, J., Bolek, A., Vesala, T., Marushchak, M. E., Virkkala, A.-M., Heimann, M., and Göckede, M. (2025) Practical guidelines for reproducible N₂O flux chamber measurements in nutrient-poor ecosystems. *Atmospheric Measurement Techniques*, 18, 3407–3424, <https://doi.org/10.5194/amt-18-3407-2025>
- II **Triches, N. Y.**, Bolek, A., Rovamo, M., Lamprecht, R. E., Ivanova, K., Hashmi, W., Yazbeck, Y., Eves, N. J., Virkkala, A.-M., Vesala, T., Biasi, C., Marushchak, M. E., and Göckede, M. Between light and dark, source and sink: N₂O dynamics in a subarctic, nutrient-poor permafrost peatland. *Manuscript*.
- III Paul, D., Hashmi, W., **Triches, N. Y.**, Znaminko, M., Siljanen, H. M. P., Mammarella, I., Göckede, M., Biasi, C., Marushchak, M. E. Unraveling the microbial mechanisms responsible for diurnal dynamics of N₂O fluxes in a nutrient-poor subarctic permafrost environment. *Manuscript*.

Author's contributions:

- I The author designed the study, conducted the gas flux measurements (3 months in total), created the software used for gas flux calculations and simulations, analysed the data, interpreted the results, wrote the article, and was the corresponding author.
- II The author helped to design the study, conducted the gas flux measurements (5 months in total), updated the software used for gas flux calculations, analysed the data, interpreted the results, wrote the article, and will be the corresponding author.
- III The author contributed to the conception of the work, participated in the gas flux measurements and calculated the flux rates, and contributed to the data analysis and writing of the flux analyses parts of article. All microbial analyses were led and interpreted by Dhiraj Paul.

Contents

ABSTRACT	3
ACKNOWLEDGEMENTS	4
LIST OF ORIGINAL ARTICLES	6
1 INTRODUCTION	9
1.1 What is the Arctic and why does it matter?	9
1.2 Global and Arctic N₂O fluxes	9
<i>1.2.1 How have we measured N₂O fluxes in the Arctic so far?</i>	10
<i>1.2.2 How is N₂O in soils produced and consumed?</i>	11
<i>1.2.3 What drives Arctic N₂O fluxes?</i>	12
2 AIMS OF THIS STUDY	13
3 MATERIALS AND METHODS	14
3.1 Study site	14
3.2 GHG flux measurements	15
<i>3.2.1 Flux sampling</i>	15
<i>3.2.2 Flux calculations</i>	16
3.3 Nutrient and microbial sampling	16
<i>3.3.1 Nutrient sampling</i>	16
<i>3.3.2 Microbial sampling</i>	17
3.4 Statistical analyses	17
4 OVERVIEW OF KEY RESULTS & DISCUSSION	18
4.1 Practical guidelines for successfully measuring N₂O in the Arctic	18
<i>4.1.1 Performance of Aeris MIRA Ultra N₂O / CO₂</i>	18
<i>4.1.2 Ideal chamber closure time and flux calculation</i>	18
4.2 Thawing permafrost peatland as continuous N₂O sink	20
4.3 PAR drives N₂O fluxes	22
4.4 Heterogeneous Arctic landscape and other drivers of N₂O fluxes	23
5 CONCLUSION	25
REFERENCES	27

1 INTRODUCTION

1.1 What is the Arctic and why does it matter?

The Arctic refers to the polar region of the Earth which surrounds the North Pole; however, a uniform definition of it does not exist. The extent of the terrestrial Arctic region can be described according to four definitions: 1. the astronomically distinguished line of latitude, i.e. the area above the Arctic circle ($66^{\circ}33'N$); 2. the climatological area in the Northern Hemisphere where the average temperature for the warmest month, July, is below $10^{\circ}C$; 3. the (geo)botanical criteria of the northern boundary of the tree line extent (Przybylak 2016), and the hydrological drainage basin, i.e. the watersheds which drain into the Arctic ocean (McGuire et al. 2010). Independent of the definition, areas on the borders of the Arctic circle can serve as precursor regions to anticipate potential changes further north.

The Arctic plays a key role in the global carbon (C) and nitrogen (N) cycles (Schuur et al. 2022), and can considerably affect the global climate. Ecosystems at high latitudes are experiencing warming at rates two to four times greater than the global average (Hugelius et al. 2020; Rantanen et al. 2022), leading to permafrost thaw and soil warming, especially in regions like northern Sweden (Biskaborn et al. 2019; Strand et al. 2021). Permafrost soils store an estimated 1000 ± 200 Pg of organic C and 60 ± 20 Pg of N within the upper 3 m, with roughly one third stored in peatlands (Palmtag et al. 2015; Palmtag et al. 2022). Including the stocks below 3 m, these soils represent the largest terrestrial C and N reservoir on Earth (Strauss et al. 2021). Warming can boost microbial activity and the decomposition of soil organic matter, thereby unlocking this huge reservoir of C and N and increasing emissions of greenhouse gases (GHGs) such as carbon dioxide (CO_2), methane (CH_4) and nitrous oxide (N_2O) (Palmtag et al. 2022). The release of these GHGs to the atmosphere would result in a positive feedback loop that intensifies global climate change and further accelerates global warming (Turetsky et al. 2020).

1.2 Global and Arctic N_2O fluxes

With a global warming potential almost 300 times stronger than CO_2 over a period of 100 years, N_2O is the third most important GHG on this planet (Intergovernmental Panel On Climate Change (Ipcc) 2023). It stays in the atmosphere for more than 100 years, and its concentration in the atmosphere has increased by nearly 25% since 1750 (Thoning et al. 2022). According to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (Intergovernmental Panel On Climate Change (Ipcc) 2023), N_2O emissions contributed 6.4% to the total effect of GHGs on global warming since pre-industrial times. Most of this increase is due to the introduction of synthetic N fertilisers in agriculture in the 1910s-1920s (Maaz et al. 2021), which is also the reason why most N_2O research has, so far, focussed on managed agricultural soils (De Klein et al. 2020). Nevertheless, natural sources dominate the global N_2O budget, contributing $11.8 \text{ Tg N yr}^{-1}$ (Tian et al. 2020). About half of these emissions originate from soils, with tropical soils exhibiting the highest fluxes among natural soils, while permafrost soils account for roughly 4% of global N_2O emissions (Tian et al. 2020, 2024). However, the magnitude of the Arctic N_2O budget is highly uncertain (Hugelius et al. 2024). Anthropogenic sources follow, contributing 6.5 Tg N yr^{-1} , of which agriculture is responsible for more than half (3.6 Tg N yr^{-1}) (Tian et al. 2024).

While the majority of Arctic research has focussed on CO₂ and CH₄ fluxes, N₂O fluxes have been previously neglected. This is mainly due to the traditional assumption that Arctic soils generally have a low availability of reactive N (Martikainen et al. 1993; Christensen et al. 1999), until more recent research challenged this view, especially under global warming. Since 2009, several studies have reported high N₂O emissions from organic-rich ecosystems and in the Arctic, with flux rates similar to those from agricultural soils (Repo et al. 2009; Elberling et al. 2010; Marushchak et al. 2011). High N₂O emissions have also been reported from disturbed soils following permafrost thaw (Yang et al. 2018; Marushchak et al. 2021). These findings have shifted the focus to selected high-nutrient areas within the Arctic. However, it is equally important to report and understand near-zero N₂O fluxes from nutrient-poor ecosystems to avoid a biased site selection favouring high-emitting areas (Voigt et al. 2020). In addition, low N and especially wet ecosystems could favour N₂O uptake (Martikainen et al. 1993), which has, to date, not been confirmed in Arctic field studies (Schlesinger 2013; Buchen et al. 2019). Along these lines, studies exploring N₂O processes in nutrient-poor Arctic ecosystems are rare and mostly laboratory-based (Palmer et al. 2012; Song et al. 2022). As a result, the highly heterogenous Arctic landscapes and high temporal and spatial variability of N₂O fluxes still make it challenging to assess the magnitude and impact of individual drivers on N₂O fluxes (Butterbach-Bahl et al. 2013; Voigt et al. 2020).

1.2.1 *How have we measured N₂O fluxes in the Arctic so far?*

The most widely used method to measure gas fluxes from the soil surface are chambers (Rapson and Dacres 2014). During closed chamber measurements, a chamber of a known volume is placed onto the soil to enable the accumulation or depletion of gases in or out of the chamber. Until recently, N₂O concentrations in the Arctic were determined by collecting (typically) between four and six air samples with a syringe from the head space of a closed flux chamber, and then analysing the samples using a gas chromatography (GC) in the laboratory (Denmead 2008; Hensen et al. 2013; Pavelka et al. 2018). This is the traditional approach when using portable chambers, and even though it has been used for decades, it is known that differences in low flux concentrations are hard, if not impossible to capture with this method (Hübschmann 2015; Fiedler et al. 2022). This is because so few samples drawn from a fluctuating time series may not display a linear trend, especially for N₂O (Hübschmann 2015). On top of that, the GC method includes the handling of gas samples and is prone to human error, making the detection limits of this method lower (Fiedler et al. 2022). Additionally, the large majority of N₂O fluxes was measured using opaque chambers, thus artificially excluding sunlight and seldom separating light and dark periods (Stewart et al. 2012). Recent advances in laser spectroscopy led to novel, portable (<15 kg), and fast-responding (1 Hz, i.e., sampling every second) GHG analysers, offering new possibilities for measuring low N₂O concentrations in the field (Subke et al. 2021). These analysers have lower detection limits and provide a higher precision method that allows for near-continuous monitoring of concentration changes in the field (Hensen et al. 2013). The detection limit was a significant constraint, as many reported N₂O fluxes were below the threshold of the GC method and made it impossible to investigate drivers of low N₂O fluxes accurately. With these recent advances, however, studies are needed to evaluate the performance of such instruments in different ecosystems.

1.2.2 How is N_2O in soils produced and consumed?

The primary sources of N_2O in natural soils are nitrification and denitrification, both of which are mediated by soil microbes (Butterbach-Bahl et al. 2013). However, there are many other pathways that have been reported in the last decade, and perhaps many that still remain unknown (Butterbach-Bahl et al. 2013). On top of that, because soils are so heterogenous, many contrasting micro-environments (e.g., aerobic and anaerobic) can co-occur on a small scale, and allow N transformation processes to happen at the same time (Bhattarai et al. 2022).

To understand the complexity of N_2O fluxes, it is essential to consider the main soil N cycling processes. These include inputs through atmospheric deposition and biological N_2 fixation, plant uptake, microbial immobilisation, mineralisation, nitrification, and denitrification (Robertson and Groffman 2024). Atmospheric deposition (from lightning, combustion, and long-range transport) introduces reactive N forms to soils. Plant uptake and microbial immobilisation remove available N, while mineralisation converts organic N to inorganic forms, supplying substrates for nitrification and denitrification. Nitrification is a mostly aerobic, autotrophic process in which nitrifying microbes oxidise ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-), resulting in the release of N_2O (Robertson and Groffman 2024). In contrast, denitrification occurs under anaerobic conditions, where denitrifying microbes use NO_3^- as an electron acceptor instead of O_2 when degrading organic compounds (Firestone and Davidson 1989). This process can result in either incomplete denitrification, leading to N_2O emissions, or complete denitrification, which closes the N cycle by releasing N_2 back into the atmosphere (Robertson and Groffman 2024).

On the other hand, the ability of soils to take up N_2O has been recognized for years (Firestone and Davidson 1989). N_2O uptake has been observed in Arctic and boreal ecosystems, particularly in soils with limited N availability and high moisture levels (Martikainen et al. 1993; Brummell et al. 2012, 2014; Voigt et al. 2020). Under these conditions, denitrifying microbes can take up atmospheric N_2O as an alternative electron acceptor when O_2 and NO_3^- are absent (Martikainen et al. 1993; Brummell et al. 2012; Voigt et al. 2020). The only pathway known for this N_2O uptake is the microbial-mediated reduction of N_2O to N_2 . This process is carried out by the enzyme N_2O reductase, and it is the *nosZ* gene that contains the DNA for making this enzyme (Sanford et al. 2012). It can be divided in two clades, which are groups of genes that share a common evolutionary origin: clade I, hosted by microbes who can both produce and consume N_2O , and clade II, hosted mainly by microbes consuming N_2O from the atmosphere (Sanford et al. 2012; Jones et al. 2013). When we differentiate between incomplete and complete denitrification, other genes, namely *nirK* and *nirS*, also play a role: in incomplete denitrification, the absence of *nosZ* and presence of *nir* lead to N_2O emissions, while in complete denitrification, nitrite reductase *nirK* and *nirS* genes produce NO, further converted to N_2O , part of which can be reduced to N_2 (Graf et al. 2014). The balance between N_2O producing and N_2O consuming genes can be expressed as $(nirK + nirS)/nosZ$ gene ratio. This ratio largely determines how much N_2O is produced as the net sum of the production and consumption processes (Jones et al. 2013). Overall, the balance between *nosZ* genes (complete denitrification or direct consumption of N_2O) and *nirK + nirS* genes (incomplete or complete denitrification), influenced by environmental factors such as nutrient availability and soil moisture, determines if an ecosystem is a source or sink of N_2O (Jones et al. 2013). Given the complexity, relatively little is known about microbial processes producing or consuming low N_2O fluxes in the Arctic region.

1.2.3 What drives Arctic N_2O fluxes?

N_2O fluxes – and the underlying production and consumption processes that regulate them – are controlled by many interacting environmental drivers (Butterbach-Bahl et al. 2013). To understand the mechanisms underlying N_2O fluxes, it is essential to consider the key drivers that influence soil microbial activity, which plays a central role in regulating N_2O fluxes (Butterbach-Bahl et al. 2013). In permafrost soils, the most studied of these are soil moisture, soil temperature, and the availability of nitrogen (N) and carbon (C) substrates, all of which are strongly modulated by vegetation cover (Voigt et al. 2020). Three primary factors contribute to elevated N_2O emissions:

- (a) optimal soil moisture, which creates an environment that supports both aerobic and anaerobic microbial activities. Intermediate water-filled pore space values (60–70 %) have been shown to promote coupled nitrification and denitrification, resulting in net N_2O release (Voigt et al. 2017a).
- (b) high soil temperatures, which increase microbial activity and, consequently, N_2O emissions. Higher soil temperatures are consistently associated with increased N_2O emissions when soil moisture or N availability are not limiting (Koponen et al. 2006; Voigt et al. 2017a; Wu et al. 2017).
- (c) sufficient supply of N and C, which fuels heterotrophic denitrifying and autotrophic nitrifying microbes. Enhanced mineral N availability in the form of NH_4^+ and NO_3^- , triggered by increased mineralisation and further nitrification and denitrification, can promote N_2O emissions (Voigt et al. 2020).

These factors are interconnected and influenced by various environmental parameters. For example, vegetation affects N_2O exchange by competing for reactive N, modifying soil temperature through shading, and altering soil moisture through transpiration (Marushchak et al. 2011; Voigt et al. 2017a). Bare peat surfaces, in particular, can act as hot spots due to high mineral N availability in the absence of plants. Thawing permafrost may further amplify these effects, leading to large emissions from drier palsu mounds on thawing permafrost peatlands, while collapsed, wetter areas typically show low fluxes (Elberling et al. 2010; Voigt et al. 2017b). By understanding the complex interplay between these factors, we can better comprehend the mechanisms controlling N_2O fluxes in permafrost regions and predict how they may respond to environmental changes.

Because most N_2O studies measured N_2O fluxes only in dark conditions (by adding a light-reflective tarpaulin on the chamber or using opaque chambers), the relationship between photosynthetically active radiation (PAR) and N_2O fluxes is complex and understudied, particularly in Arctic ecosystems (Shurpali et al. 2016; Keane et al. 2018). This is because soil N_2O fluxes are a result of multiple production and consumption processes, none of which are currently known to be completely suppressed in dark conditions, unlike gross primary production (GPP). Stewart et al. 2012 reported light-dependent N_2O fluxes from High Arctic polar-desert soils, with N_2O sources under dark, and N_2O sinks under light conditions. They suggested that the effect of light on N_2O fluxes is highly site and condition dependent, with vegetation and soil moisture playing an important role (Stewart et al. 2012); however, their results were not statistically significant. As a driver of photosynthetic activity, PAR has been shown to stimulate root exudation in agricultural soil by increasing the discharge of readily available C from plant roots which is supplied to denitrifying microbes (Keane et al. 2018; Wu et al. 2021). C availability drives denitrification both directly (Firestone and Davidson

1989) an indirectly by depleting the soil of O₂ through microbial respiration (Farquharson and Baldock 2008), and can therefore lead to higher N₂O emissions (Wu et al. 2021). In addition to PAR, the N₂O–CO₂ flux relationship remains poorly understood, despite its importance for global carbon–nitrogen interactions (Xu et al. 2008). Across ecosystems, CO₂ fluxes (both net ecosystem exchange (NEE) and ecosystem respiration (ER)) were significantly positively correlated to N₂O fluxes and explained 52–84% of N₂O variation, likely due to root-zone oxygen concentrations, root exudation of labile C by plants (Xu et al. 2008), or vegetation-driven N uptake (Zona et al. 2013). While CO₂ fluxes are routinely partitioned into gross primary production (GPP) and ecosystem respiration (ER), N₂O studies are seldom separated into light and dark measurement periods (Stewart et al. 2012). Chamber measurements during light conditions are crucial to fully understand this relationship, but have been rarely conducted in high-latitude ecosystems.

2 AIMS OF THIS STUDY

The overall aim of this study was to bring forward our knowledge on N₂O fluxes in Arctic regions by detailed studies on a subarctic palsa mire. Specifically, my study introduces new, practical guidelines on how to successfully measure N₂O fluxes in Arctic and other nutrient-poor ecosystems (**I**), investigates drivers of both Arctic N₂O emissions and uptake using a unique, extensive dataset (n = 1483) from seven field campaigns covering all months between May and September (**II, III**), and examines the impact of microbes on N₂O fluxes during differing light conditions (**III**):

- I How can we best measure low N₂O fluxes in the Arctic? (Study **I**)
- II How do micro habitat properties, microbial activity, and seasonal weather conditions affect N₂O fluxes at the Stordalen mire? (Study **II, III**)
- III Can microbes explain the effects of differing light conditions on N₂O fluxes? (Study **III**)

Study **I** focussed on practical guidelines, including optimal chamber closure times, and the recommendation to include both light (transparent) and dark (opaque) measurements. We further tested the performance of the N₂O/CO₂ portable gas analyser (Aeris MIRA Ultra) in Arctic ecosystems. Having found a significant difference between light and dark measurements on N₂O fluxes during the first test field campaign, study **II** focussed on the effect of micro habitat properties and environmental variables (PAR, CO₂, as well as soil temperature, soil moisture, soil nutrient availability, and vegetation) on N₂O fluxes, providing novel insights on drivers of N₂O fluxes in the Arctic. Study **III** completes the dissertation by analysing the impact of microbes on the light and dark difference.

3 MATERIALS AND METHODS

We use the terminology proposed by Fiedler et al. (2022), with location describing the area where sampling occurs ("Stordalen mire"), site describing a vegetation unit within the location ("palsa lichen", "palsa moss", "bog", "fen"), and chamber base position (i.e. plot) for the exact spot where N_2O was measured. With "chamber closure time", we specify the time frame a chamber was closed onto the soil; one of these periods is then called "measurement period".

3.1 Study site

We collected the majority of our data at the Stordalen mire, a complex palsa mire underlain by sporadic permafrost located in subarctic Sweden ($68^{\circ} 20.0' \text{ N}$, $19^{\circ} 30.0' \text{ E}$), 10 km east of Abisko (Ábeskovvu in Northern Sámi language). Here, the classification as "subarctic" follows the updated Köppen-Geiger climate classification, indicating cold summers and winters and no significant precipitation difference between seasons (Peel et al. 2007). Permafrost has been thawing rapidly at this location over the last decades, and only remains in the dry uplifted areas on the peatland (palsas) (Sjögersten et al. 2023). Palsas are raised peat mounds that form when frozen ice lenses push peat layers upward (Seppälä 2011). They are a common - but disappearing - landscape feature in Fennoscandia. For our study, we randomly selected 24 chamber base positions in three transects on a dry-to-wet thawing gradient from palsa to bog to fen, with 6 replicates for each land cover type: palsa lichen, palsa moss, bog, and fen (Figure 1). Vegetation on the palsa is mainly dominated by lichen (*Cladonia spp.*), shrubs (*Empetrum hermaphroditum*, *Betula nana*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Rubus chamaemorus*) and some mosses (*Dicranum elongatum*, *Sphagnum fuscum*). Both bogs and fens contain peat-forming mosses (*Sphagnum balticum*, *S. lindbergii*, *S. riparium*), with the dominant vascular plants on fens being cotton grass (*Eriophorum vaginatum*, *E. angustifolium*) and in bogs sedges (*Carex rotundata*, *C. rostrata*). The soils in the area are classified as organic

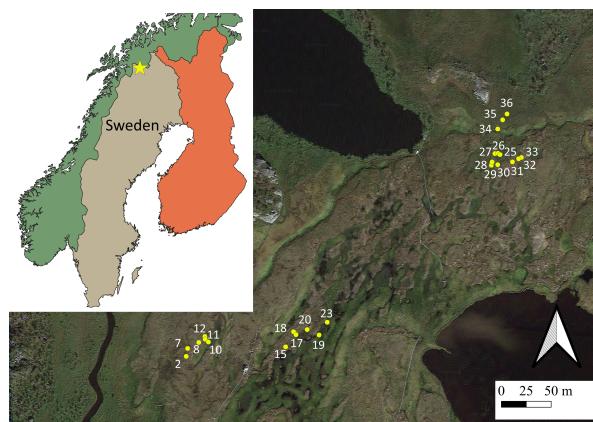


Figure 1: Three transects with chamber base positions in Stordalen overlaid on satellite image from ©Google Maps. The location of the Stordalen mire is marked with a star. Here, micro habitats are represented with different colours and symbols for clarity. The spatial data of each country can be found at <https://simplemaps.com>, last access: 17/09/2024 (I)

histosols or, if permafrost occurs within 2 m of cryoturbation activities, as cryosols (Siewert 2018). Transects 1 and 2 each contain 6 chamber base positions and are located in the northern centre of the mire, within the footprint of an Integrated Carbon Observation System (ICOS, SE-Sto) eddy covariance tower which has been operating since 2014 (Lundin 2022, Figure 1). Transect 3 lies in the most north-eastern part of the palsa (Figure 1). We further conducted some "hot spot screening" all over the palsa, during which we lowered the chamber on bare soil patches to specifically look for hot spots.

To test if our hypothesis about the light dependency of N_2O fluxes holds true for other peatlands as well, we further collected data at the Storflakket mire ($68^\circ 20.8' \text{ N}$, $18^\circ 58.3' \text{ E}$) near Stordalen during two days in June and July 2024.

3.2 GHG flux measurements

3.2.1 Flux sampling

Data were collected in September 2022, May, June, July, and September 2023, and June, July, and August 2024. For our measurements, we used a custom-built static, non-steady state, non-flow-through chamber (Livingston and Hutchinson 1995) made from acrylic glass (Göli GmbH, Germany) with a height of 250 mm and a diameter of 250 mm (Figure 2). The chamber was equipped with a fan (SUNON Maglev, 80 mm x 80 mm x 25 mm, 2000 RPM) to ensure well-mixed conditions within the chamber during the measurements, a relative humidity (RH) and temperature probe (EE08, E+E Elektronik, Germany), and a pressure sensor (61402V, RM Young). As complementary variables, we measured soil temperature at 15 cm depth (PT100 4-wire sensors, JUMO GmbH & Co. KG) at each quadrant outside of the plot, soil moisture at 12 cm and 30 cm (CS655-DS and CS650-DS, Campbell Scientific), and photosynthetically active radiation (PAR) (PQS1, Kipp and Zonen). To measure N_2O and CO_2 concentrations within the chamber head space, we used the Aeris MIRA Ultra $\text{N}_2\text{O}/\text{CO}_2$ analyser (Aeris Technologies; sensitivity: 0.2 ppb/s for CO_2 and N_2O , frequency: 1 Hz). To measure CO_2 and CH_4 , we used the Li-7810 $\text{CH}_4/\text{CO}_2/\text{H}_2\text{O}$ Trace Gas Analyser from LI-COR. For the dark measurements, a custom-made, reflective, light-impermeable tarpaulin was placed on top of the transparent chamber. We used a chamber closure time of 5 min (**II**, **III**) and 10 min for testing purposes (**I**), respectively.



Figure 2: Chamber setup during measurement period, with soil moisture and soil temperature sensors installed in the soil, and all inlets connected. Photo: Fabio Cian, "Ubiquitous Anomaly", CC BY-NC-ND 4.0 (**I**)

3.2.2 Flux calculations

In our study (**I**, **II**, **III**), we calculated N_2O fluxes using *all data points* from one measurement period, rather than subjectively selecting suitable parts of the curve as is commonly done for other GHG (Jentzsch et al. 2025). We removed 8 secs in the start of the measurement period to account for the time delay until the concentration from the chamber reached the cell of the gas analyser. An extra 7 secs were removed for opaque measurements, since we needed more time in the field to cover the chamber with the reflective tarpaulin. To calculate the fluxes with both linear (LM) and non-linear (HM) methods in a reproducible way, we used the R package goFlux (v0.2.0, (Rheault et al. 2024)). The linear equation was applied as follows in Eq. 1:

$$F(t) = \frac{dC(t)}{dt} \frac{V}{A} \quad (1)$$

where $F(t)$ is the gas flux rate at a given location during the chamber closure time (t), $\frac{dC(t)}{dt}$ is the mass concentration change with time, V is the volume of the chamber, and A the area of the soil covered by the collar (Subke et al. 2021). To report our flux rates, we used the atmospheric sign convention, i.e. negative signs for an uptake of N_2O into the soil, and positive signs for emissions.

The HM model approach in goFlux is based on the Hutchinson and Mosier 1981 approach as given in Eq. 2:

$$C(t) = \varphi + (C_0 - \varphi)e^{-\kappa t} \quad (2)$$

Here, φ is the assumed constant gas concentration of the source within the soil (Pedersen et al. 2010); C_0 is the gas concentration in the chamber at the moment of chamber closure; and κ is the model parameter. An improved version of the HM model approach (Hüppi et al. 2018) is further implemented into the package.

3.3 Nutrient and microbial sampling

3.3.1 Nutrient sampling

From June to September 2024, we added six Plant Root Simulator (PRS[®], Western AG, Canada) probes (3 anion- and 3 cation adsorbing) next to each chamber base position to get more information on the nutrients. These PRS[®] probes are *in-situ* ion exchange resin membranes that measure the ion supply in soils by adsorbing cations and anions (Sharifi et al. 2009). We added them for 2-3 weeks during and in between the measurement campaigns in 2024 (**II**).

In August 2024, we combined flux measurements with soil sampling for geochemical and microbial analyses (**III**). We sampled approximately 20 g of soil next to each chamber base position during both day and night flux measurements by transparent chambers. In the laboratory, we measured soil pH and electrical conductivity (EC), and extracted nitrite (NO_2^-), nitrate (NO_3^-), sulfate (SO_4^{2-}), phosphate (PO_4^{3-}), chloride (Cl^-), dissolved organic carbon (DOC), and dissolved nitrogen (DN) content. We calculated dissolved organic nitrogen (DON) as the difference between total dissolved nitrogen (DN) and inorganic nitrogen. For carbon

and nitrogen analysis, we ground oven-dried samples and measured them using an elemental analyser coupled to isotope ratio mass spectrometry (EA-IRMS).

3.3.2 Microbial sampling

We extracted total community DNA and RNA from all 48 samples (2 per day (day and night) \times 4 micro habitats \times 2 depths \times 3 replicates), and assessed their quality (III). We quantified the extracted RNA and DNA and, for consecutive qPCR analyses, treated some RNA with DNase to remove residual DNA. We used quantitative real-time Polymerase Chain Reaction (qPCR) to quantify key functional genes involved in denitrification (*nirS* and *nirK*) and N₂O consumption (*nosZ* clade I and *nosZ* clade II). We further extracted community DNA through metagenome sequencing and assembly. In total, we used 8 samples (4 micro habitats \times 2 depths, 2 and 15 cm) for sequencing (III).

3.4 Statistical analyses

All data were processed in R (version 4.5.0; R Core Team, 2025) and version controlled in GitLab (for more information, see <https://git.bgc-jena.mpg.de/ipas/fluxprogeniereleases>). A filter script was applied to pre-process and quality-control the raw data, such as removing data points within a specific time interval at the start of the measurement period to account for the time lag of gases moving through the tubes to reach the laser cell. The filter script also included quality control of other parameters by, *e. g.*, removing implausible values (*e.g.*, -9999), replacing negative PAR values with 0, averaging soil temperature gained from the four sensors, and setting minimum and maximum values for all parameters (I, II, III).

We used our openly available script to show differences between chamber closure times (I, see chapter 4.1.2. and Figure 3). First, we calculated all fluxes using a 10-minute chamber closure time. To see how different closure times affect N₂O fluxes, we shortened the closure time by 1 minute at a time, starting from 9 minutes, and recalculated the fluxes for each new time (*e.g.*, 9 minutes = 540 sec, 8 minutes = 480 sec, etc.). We compared how chamber closure time affects flux rates during light and dark measurements, and identified the number of fluxes above the minimum detectable flux based on the goFlux output. While calculating our fluxes, we became aware of one chamber base position acting as a hot spot, *i.e.* showing much higher flux rates than the other chamber base positions. Since we wanted to focus our analyses on low fluxes, we removed this hot spot from analyses in the first study (I), and conducted statistical analyses for the second study separately for low and high N₂O fluxes (II). The hotspot was also excluded from the third study (III).

We examined how N₂O fluxes varied across micro habitats and environmental conditions using a combination of statistical tests and modelling approaches (II, III, see chapters 4.3 and 4.4). To compare average flux rates between micro habitats, we applied a one-way ANOVA followed by Tukey's HSD post-hoc test (see chapter 4.2 and Figures 4A and 5). Differences between light and dark chamber measurements were assessed with a Wilcoxon rank-sum test (II). To analyse the impact of PAR on N₂O fluxes, we calculated non-linear light-response models of N₂O fluxes against PAR for each microhabitat and for the pooled dataset, using a Michaelis–Menten type function (II). To explore environmental drivers of low N₂O fluxes, we trained a random forest model using PAR, CO₂ fluxes, green canopy cover, active layer depth, soil moisture, and soil temperature as predictors (II). Finally, we investigated the relationships between the high N₂O flux (hot spot) and environmental variables by fitting exponential

regression models (on log-transformed fluxes) separately for light and dark conditions. Model fit was summarised by sample size, R^2 , and p -values, enabling comparisons across predictors (II, see chapter 4.4 and Figure 7).

4 OVERVIEW OF KEY RESULTS & DISCUSSION

4.1 Practical guidelines for successfully measuring N₂O in the Arctic

4.1.1 Performance of Aeris MIRA Ultra N₂O / CO₂

Before taking an instrument to the field, it is important to test its performance in the laboratory; key aspects include checking for the drift of the instrument, and its sensitivity to water (I). In our 10 h sampling period, the Aeris MIRA Ultra N₂O / CO₂ showed a very stable signal with no apparent drift, and a low standard deviation of 0.29 ppb. The Allan deviation plot showed low instrument noise of approximately 0.18 pbb at 2 secs averaging. We further tested the sensitivity of the Aeris MIRA Ultra N₂O / CO₂ towards fluctuations in water vapour concentrations using a standard gas, since this is a commonly known issue of portable gas analysers (Webb et al. 1980; Crosson 2008). We conducted our tests with four relative humidity (RH) levels of approximately 28%, 45%, 60%, and 83% and found that our analyser was insensitive to differing RH levels with mean N₂O concentrations of 332.7, 332.6, 332.7, and 332.5 ppb, respectively. Overall, with low noise and water interference along with negligible signal drift after the warm-up period, we decided that the Aeris MIRA Ultra N₂O / CO₂ was a suitable instrument for measuring low N₂O fluxes in Arctic ecosystems (I).

4.1.2 Ideal chamber closure time and flux calculation

One key aspect of successful chamber measurements is the chamber closure time, which, ideally, should be kept as short as possible to minimise disturbances between soil-air conditions and observational artefacts. These include potential impacts when closing the chamber, e.g., pushing atmospheric air or flushing soil gas into the chamber, or increasing temperature and humidity inside the chamber due to soil and plant evaporation caused by the chamber's transparency acting as a greenhouse (Rochette and Eriksen-Hamel 2008; Subke et al. 2021). Our results suggest that for measurements of low N₂O fluxes with a small chamber (height and diameter 25 cm), a minimum of 4 min and 3 min closure time is required for light (transparent) and dark (opaque) measurements, respectively (Figure 3, I). Below this time, the amount of flux rates for light measurements below the minimal detectable flux (MDF) may be too large, or the time may not be sufficient to achieve a change in the N₂O concentrations high enough to detect a significant trend over the measurement noise (Figure 3 a). For dark measurements, longer chamber closure times may lead to an underestimation of the N₂O sink (Figure 3 b). This is because N₂O availability through soil diffusion is often the limiting factor for N₂O uptake by N₂O-reducing microbes (Liu et al. 2022), so that when the chamber is closed, the uptake rate decreases due to the concentration gradient between soil and chamber head space and the resulting substrate limitation. For an optimal balance between detection sensitivity and measurement efficiency, we recommend a standard 5 min closure time for all measurements with smaller chambers, which allows to detect most N₂O fluxes (I, II, III).

With 300 data points collected during a 5-min chamber closure time, we further recom-

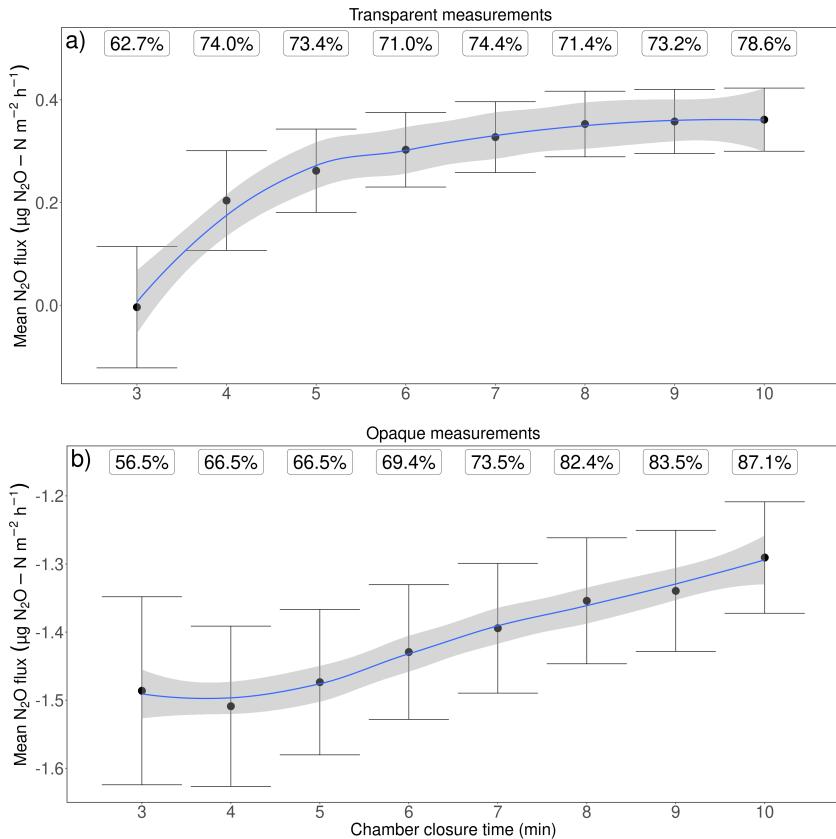


Figure 3: Mean N_2O fluxes (note: not concentrations) for transparent and opaque measurements, with number of measurement periods above the minimal detectable flux (MDF, %). Note the different y-axes for the upper and lower plots. The range indicates the upper and lower limit of the 95% confidence interval (I).

mend to use *all available data points* for non-linear flux calculation for all (low) N_2O flux measurements (I, II, III). Using all data points, after filtering out unrealistic values and visual verification of flux estimates, enhances the reproducibility and consistency of future Arctic N_2O fluxes, as well as their comparison. This can be improved by using novel software packages, which offer the possibility to calculate fluxes both linearly and non-linearly, and report these flux rates in a reproducible way (Rheault et al. 2024). Linear and non-linear approaches may typically be seen as alternatives and not as complimentary approaches. However, the non-linear fitting includes the linear fitting as a special case when flux rates are low. In that case, if data points show a linear trend, the exponential fitting will automatically reduce to a linear fitting with the same slope. This special case was confirmed in our data set, where all N_2O fluxes could be calculated with the non-linear approach, which was reduced to the linear approach in 41 % of all fluxes ($n = 1728$, I). We encourage future research to provide reproducible ways of calculating fluxes, and testing optimal chamber closure times for other low-nutrient ecosystems. We further recommend that future Arctic studies measure N_2O fluxes with high-precision portable gas analysers in low- and high-nutrient ecosystems.

4.2 Thawing permafrost peatland as continuous N_2O sink

Our results confirmed that the nutrient-poor Stordalen permafrost peatland can act as a continuous, non-negligible sink of N_2O , with a mean / median flux and standard error (SE) across all years, measurement campaigns, and sites of $-0.57 / -0.38 \pm 0.05 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ($n = 1383$) (Figure 4 NET N_2O FLUX panel and 5, I, II). Because we tested the suitability of our instrument to measure low N_2O fluxes (I) and repeatedly measured N_2O uptake, we are confident that our results indicate an actual biological process rather than an methodological artefact (I, II). Palsa lichen plots (mean / median flux of $-0.29 / -0.25 \pm 0.07 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$; $n = 379$) showed a significantly lower sink than bog ($-0.71 / -0.44 \pm 0.10 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$; $n = 378$) and fen ($-0.71 / -0.46 \pm 0.12 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$; $n = 331$), respectively (Figure 4A). Palsa moss plots were not different from others (mean / median flux of $-0.59 / -0.47 \pm 0.10 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$; $n = 295$). This sink for dry palsa lichen and palsa moss habitats is particularly interesting, as this has not been reported previously.

We also observed a pronounced seasonal course (Figure 5), with the sink strength peaking

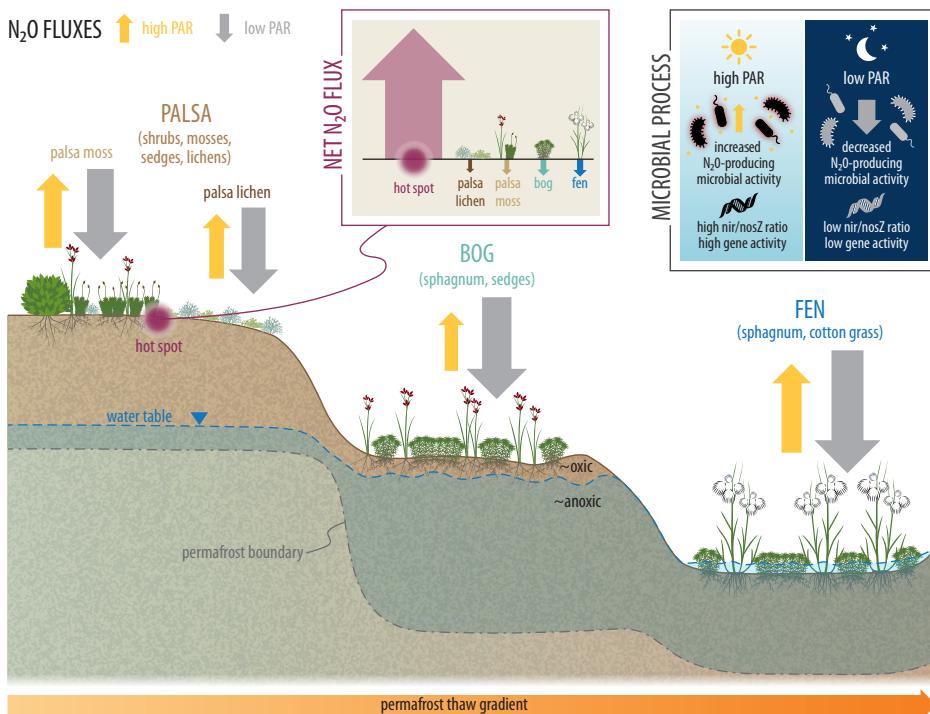


Figure 4: Overview figure of key results, with differences in micro topography, vegetation, water table, and permafrost boundary for the micro habitats palsa moss, palsa lichen, bog, and fen. Orange, upward-facing arrows show N_2O emissions during high photosynthetically active radiation (PAR), i.e. sunny conditions, whereas grey, downward-facing arrows indicate a sink during low PAR, i.e. dark conditions. A hot spot and its magnitude related to the other micro habitats is shown in the NET N_2O FLUX panel, with an overall N_2O sink for the micro habitats excluding the hot spot. The MICROBIAL PROCESS panel shows the microbial process responsible for at least part of the differences in high and low PAR N_2O fluxes. Illustration: Annett Boerner

for all micro habitats in the hot summer months June and July, and strongly reduced to near-neutral uptake or small emission in all other months (**II**). The vast majority of monthly mean fluxes were negative, except for net emissions observed from palsa lichen in May (median / mean: $0.3 / 0.18 \pm 0.10 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$), and from fen in September (median / mean: $0.11 / 0.14 \pm 0.10 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$).

It was not surprising to observe an N_2O sink in bogs and fens, given their high water tables and the resulting reducing soil conditions (Martikainen et al. 1993; Voigt et al. 2020). In these environments, where nitrate ($\text{NO}_3^- - \text{N}$) is absent (as indicated by our nutrient data), atmospheric N_2O can serve as the terminal electron acceptor in denitrification (Martikainen et al. 1993; Brummell et al. 2012). What is more unexpected, however, is the detection of a N_2O sink activity on dry palsa surfaces. To the best of our knowledge, this phenomenon has not yet been documented in field studies, although it was observed in a laboratory mesocosm experiment with soil from a Finnish permafrost peatland (Bhattarai et al. 2022). This thesis is thus the first one to report a persistent, non-negligible sink of N_2O in a sub-Arctic permafrost peatland over several years, including uptake in the drier parts of it. When we compare our values to a recent review, our results show a stronger sink than previously reported for wetlands (median (25-75 percentiles): $0.42 (-0.33, 4.83) \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$, (Voigt et al. 2020)), even when we include our hot spot (mean / median \pm standard error N_2O fluxes of $0.54 / -0.28 \pm 0.24 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ($n = 1462$)). This could be explained by methodological differences: with our portable gas analyser, we used much shorter chamber closure times, which are essential for measuring N_2O uptake because diffusion-limited N_2O is rapidly depleted, causing longer closure times to underestimate N_2O uptake rates (**I**). This could also be one of the reasons why we detected a sink in dry palsas, which on its own contributed to a stronger sink.

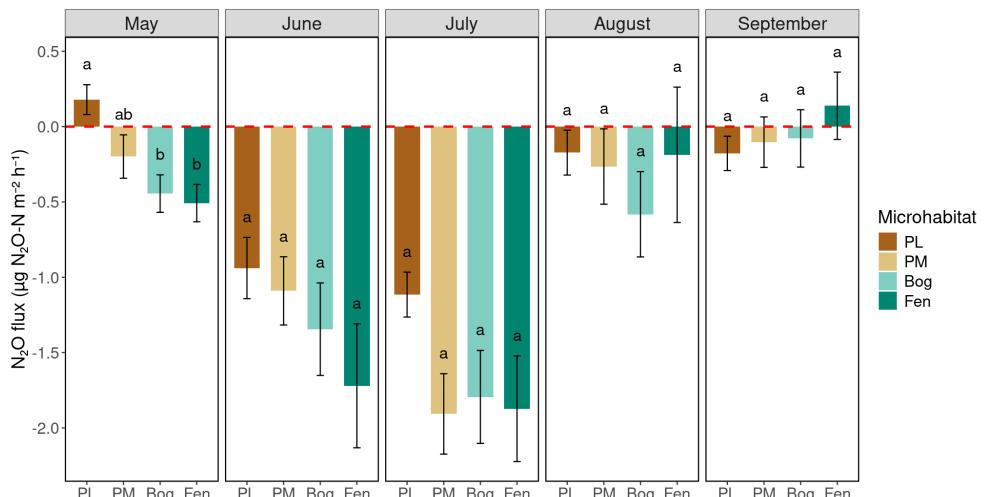


Figure 5: N_2O flux (mean \pm SE?) divided into months and micro habitats, excluding one hot spot (light and dark conditions combined). PL and PM indicate Palsa Lichen and Palsa Moss, respectively. Letters indicate significance according to ANOVA and Tukey HSD post-hoc tests, with differing letters between micro habitats indicating significant differences. The purple horizontal line indicates the border between a source (positive values) and sink (negative values) (**II**).

4.3 PAR drives N₂O fluxes

We found significant differences between mean N₂O fluxes during light and dark conditions across micro habitats (Wilcoxon signed rank test 0.37, $p < 0.001$), with a median and standard error (SE) of $0.42 \pm 0.06 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ for light ($n = 673$), and $-1.06 \pm 0.06 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ for dark fluxes ($n = 710$), respectively (Figure 4, **II**). Prompted by our observations in 2022 and 2023, we were curious to see if:

- (a) this phenomenon was specific to our site;
- (b) the differences in light and dark measurements would be confirmed during the night and could thereby exclude measurement artefacts;
- (c) microbes could explain the differences between day and night.

To investigate the influence of sampling location, we collected 24 daytime measurements (4 micro habitats x 6 replicates) on 16 June and 23 July 2024 in a nearby permafrost peatland to investigate if light and dark fluxes would show a similar pattern than at our site, which was indeed the case. We concluded that the phenomenon was not specific to our site (**II**). In June, July, and August 2024, we also conducted six night time measurements (19 / 20 June, 17 / 18 July, 20 / 21 August between 20:00 and 02:00 Swedish local time, UTC+2) to check if N₂O fluxes measured with a transparent chamber in naturally dark conditions during the night would be similar to those measured with an artificially darkened opaque chamber in the day time. We did these measurements in both polar day conditions in June and July (i.e., the sun did not set) and dark nights in August (**II, III**). In August, we further included microbial sampling. We found that during night time, N₂O was indeed taken up in palsas, bogs, and fens, with palsa lichen and palsa moss showing even a larger uptake during nights than fluxes measured in dark conditions during the day based on median flux rates in July. In bogs and fens, as well as in August (dark nights), night measurements showed lower uptake rates than dark measurements during the day (**II**).

To understand more about the mechanisms behind this, a closer look into the soil was needed. Our microbial analyses by qPCR showed that, although genes for both N₂O production (*nirK* and *nirS*) and N₂O uptake (*nosZ clade I and II*) were present at our site (DNA level), only the *nirK* and *nosZ clade I* genes were active (RNA level) (**III**). However, instead of, e.g., *nirK* being active during the day and *nosZ clade I* being active during the night, it was the *nirK / nosZ clade I* gene expression ratio that closely aligned with the diurnal pattern of N₂O fluxes (Figure 6). We found a high expression of both *nirK* and *nosZ clade I* during the day compared to a low expression during the night, indicating that microbes were more active in producing N₂O during the day (Figure 4 and 6). In other words, the differences in N₂O fluxes were driven primarily by N₂O production rather than reduction. Additionally, our nutrient analyses in August showed that the concentrations of dissolved organic carbon, NO₃⁻, and NH₄⁺ were higher during the day in fen and palsa moss (**III**). This aligns with patterns when fitting a light-response curve to our data (**II**): both fen and palsa moss follow a hyperbolic curve, suggesting that the effect of PAR is particularly strong at low values - during dark conditions. This similarity between palsa moss and fen may be explained by a higher green canopy cover in summers with temperatures above and soil moisture below average. In such canopy conditions, *Sphagnum spp.* mosses in bogs tend to dry out and become yellow, whereas shrubs in palsa moss and cotton grass in fens can tolerate more heat and drought, resulting in a higher green canopy for palsa moss and fen (**II**).

Based on the PAR dependence of N₂O flux and the close match between microbial gene expression and N₂O flux, we can conclude with a high certainty that the light-dark effect we

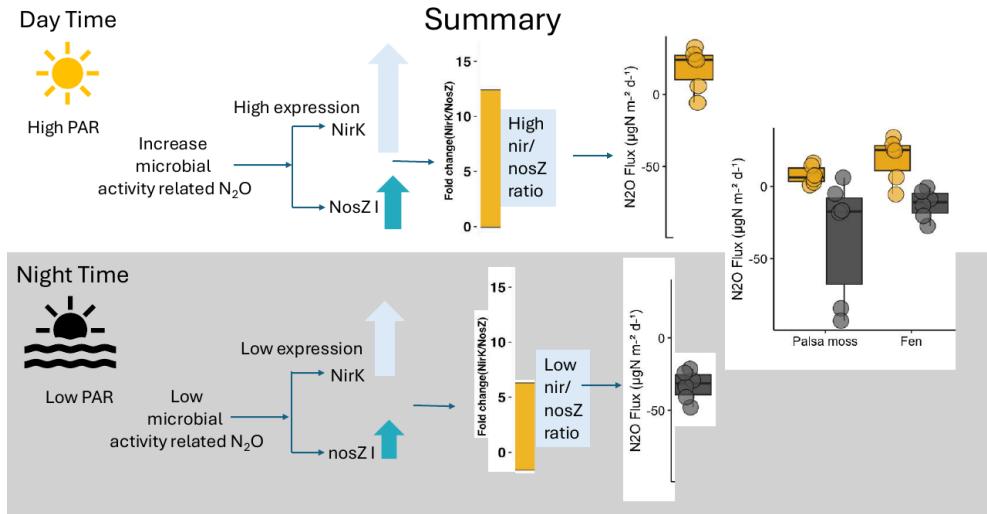


Figure 6: Overview of microbial activity, with high PAR at day time leading to increased microbial activity and a high expression of *nirK* and *nosZ clade I* genes, resulting in a high *nir/nosZ* ratio and N₂O emissions. Shaded in grey are night time conditions with low PAR, low microbial activity and a low expression of *nirK* and *nosZ clade I* genes, resulting in a low *nir/nosZ* ratio and N₂O uptake. Fold change refers to the ratio between the *nirK* and *nosZ* genes. Credits: Dhiraj Paul

observed is a real phenomenon, not a measurement artefact. Our analyses indicate that the light-dependent N₂O flux in a nutrient-poor thawing permafrost peatland is regulated by a combination of factors, including vegetation effects (potentially through root exudation or plant-mediated N₂O production) and microbial activity. This complex interplay contributes to the diurnal and seasonal patterns of net N₂O fluxes, and can even determine whether the ecosystem functions as a net sink or source of N₂O. This difference -although the opposite direction- had been reported from polar desert soils (Stewart et al. 2012), but without significance. Interestingly, Stewart et al. 2012 suggested that soil moisture and plant communities were the key drivers of these differences, with larger N₂O uptake in wet and dark conditions and larger N₂O emissions during light conditions, which aligns with our findings. They also hypothesised that the differences of N₂O fluxes in light and dark conditions can result from short-term effects of vegetation and soil microbes competing for resources in response to light-driven changes in O₂ availability (Stewart et al. 2012). Apart from our study, we are not aware of any studies following up on these hypotheses, and strongly recommend further studies to clarify the PAR effect on N₂O fluxes.

4.4 Heterogeneous Arctic landscape and other drivers of N₂O fluxes

Our measurements highlight the importance of a sufficient amount of replicates in heterogeneous ecosystems like the Arctic: one of our chamber base positions, a vegetated area on palsa moss, acted as a continuous hot spot over the three years of our study (Figure 4). When we include this hot spot, our study site shows a mean / median flux of $0.61 / -0.25 \pm 0.25 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ($n = 1402$), with palsa moss showing both mean and median emissions of $4.24 / 0.12 \pm 0.25 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$ ($n = 344$). Motivated by this hot spot, we extended

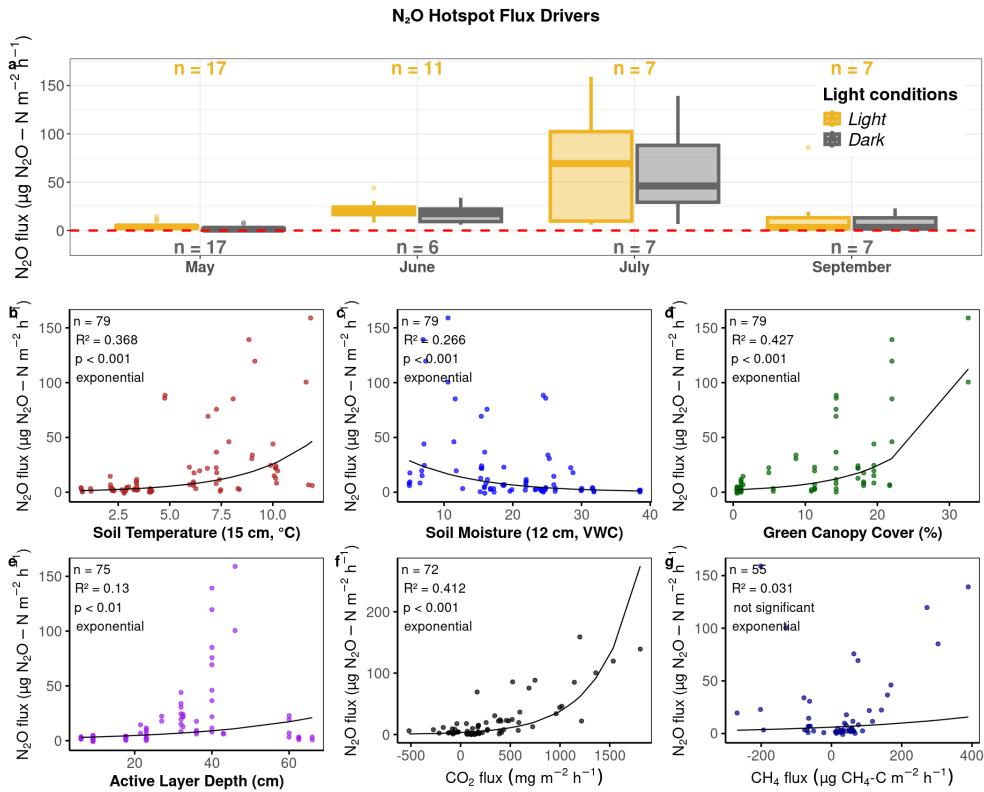


Figure 7: Drivers of the single palsa moss N₂O hot spot, with a) showing light (orange boxplots) and dark (grey boxplots) measurements during all measurement campaigns and the red dashed line indicating source (positive values) and sink (negative values). Other plots show simple regression models between the N₂O flux and b) Soil temperature at 15 cm depth, c) Volumetric Water content (%), i.e. soil moisture at 12 cm depth, d) Green canopy cover, e) Active layer depth, f) CO₂ flux, and g) CH₄ flux. We tested linear, quadratic, logarithmic and exponential models and compared them by AIC. The lowest AIC for all predictors were given by the exponential model: $y = e^{\beta_0 + \beta_1 x}$, where y is N₂O flux and x is the predictor.

our search across the site, including bare soils where hot spots have previously been observed Marushchak et al. 2011. Only one further hot spot was detected (Figure 4). Nevertheless, the presence of hot spots could significantly enhance the landscape-integrated N₂O emissions, and maybe even change the site from a net sink to a net source (II).

The hot spot at our site showed a clear pattern between light and dark fluxes, similar to the other plots, but with larger fluxes (Figure 7a). Opposite to the other plots, fluxes showed highest emissions in the peak summer (Figure 7a), although only few data points are available ($n = 14$ for July). This trend runs through most main drivers: while for the "low N₂O flux chamber positions", increasing CO₂ fluxes, green canopy cover, and soil temperatures lead to a higher N₂O flux uptake (II), the high N₂O emissions from the hot spot correlated positively with green canopy cover (Figure 7 d $R^2 = 0.43$, $p < 0.001$), CO₂ fluxes (Figure 7f $R^2 = 0.41$, $p < 0.001$), and soil temperature (Figure 7b $R^2 = 0.37$, $p < 0.001$). The positive temperature dependency has been previously reported from N₂O hot spots, suggesting that other factors such as soil moisture or N availability are not limiting N₂O production (Marushchak et al.

2011). When we exclude the influence of other predictors (partial regression), only GCC and CO₂ flux remain positively correlated with N₂O (Kendalls τ 0.32 and 0.28 with p-value < 0.01 and 0.01, respectively), and CH₄ becomes more important (Kendalls τ 0.18, p = 0.08, **II**).

The vegetation composition and green canopy cover on the hot spot was similar to other palsa moss replicates, and the hot spot did also not differ in nutrient concentrations at the peat surface, soil moisture, soil temperature, or any other measured environmental variable. While the exact cause of this hot spot remains unclear, its occurrence may be related to a barely visible, straight line on the ground surface—possibly an early-stage crack in the permafrost peatland (data not shown). One possibility is that in and next to this crack, the deeper layers within the peat profile are more aerated, which could boost both mineralisation and nitrification due to the higher mineral N contents and lower C/N ratios, and lead to N₂O emissions on the surface (Keuper et al. 2012). However, since N₂O flux rates are not consistently higher in late season with deeper active layers, it is likely that N₂O from deeper layers is not the only reason for the hot spot. As stated above, a hot spot has the potential to shift the net N₂O budget of an ecosystem; the vegetated hot spot in our study makes extrapolation efforts extremely uncertain since there is no easy option to tell the frequency of these hot spots and their emission strengths. One way forward may be airborne scanning of N₂O hot spots using drones, but it remains unclear if the N₂O concentrations are high enough to capture using this method.

5 CONCLUSION

This dissertation presents the most comprehensive dataset on Arctic N₂O fluxes to date, gathered using the manual chamber method. By repeatedly measuring the same plots over three years and during different parts of the snow-free period, we were able to use advanced statistical techniques to disentangle the complex drivers of low N₂O fluxes. Our findings highlight the high spatio-temporal variability of N₂O fluxes and underscore the challenges of analysing N₂O drivers in heterogeneous ecosystems like the Arctic.

With our results, we provide practical guidelines for successful Arctic N₂O studies, and emphasise the need to conduct both light and dark measurements, and, if possible, include simultaneous measurements of carbon fluxes. These recommendations are not only relevant to Arctic studies but also applicable to investigations of low N₂O fluxes in other ecosystems, such as peatlands and forests in temperate and boreal regions. The use of novel gas analysers, like the Aeris MIRA Ultra N₂O/CO₂, while adjusting chamber closure times to the size of the chamber and ecosystem, are crucial for accurate measurements. Our expertise with this analyser has already gathered international attention, with researchers from around the world seeking our advice on its use.

The N₂O sink we report from the Stordalen mire is stronger than previously reported values from sub-Arctic ecosystems. Combined with the fact that the large majority of these studies were conducted under dark conditions, it is possible that a) Stordalen really is indeed a stronger N₂O sink than other comparable ecosystems, or b) previous studies overestimated N₂O fluxes due to methodological limitations. Our two-days comparison measurements at the nearby Storflakket mire suggest that it may be an even stronger N₂O sink than Stordalen, but further measurements on other Arctic (palsa) peatlands are needed to confirm this. The large uncertainties associated with previous near-zero estimates of N₂O fluxes in sub-Arctic ecosystems, on the other hand, highlight the need for more accurate and comprehensive

measurements. This discrepancy may be due to the fact that most studies were conducted under dark conditions and without portable gas analysers, which could lead to underestimation of N₂O sink strength.

Our study makes a significant contribution to the field by demonstrating the importance of including N₂O measurements in soil-to-atmosphere flux studies, particularly in the Arctic. While our study focused on nutrient-poor peatlands, future research should also investigate mineral Arctic soils to determine if the processes we identified are similar to those in other nutrient-poor areas. Additionally, hot spots of N₂O emissions in Arctic ecosystems, including vegetated soils, should not be neglected, as they are crucial in determining the sink or source function of an ecosystem. To be able to detect low fluxes, high-precision, portable gas analysers must be prioritised to conduct measurements across multiple palsa peatlands and other Arctic ecosystems to improve estimates of the pan-Arctic N₂O budget. Our work has the potential to challenge current upscaling efforts, which may have systematically overestimated N₂O emissions in the Arctic.

Our dataset, although comprehensive, is limited to the snow-free season. Continuous measurements using automated chambers or eddy covariance towers could provide valuable insights into the temporal aspects of N₂O fluxes, complementing our spatially extensive dataset. Winter measurements, although challenging, are crucial for understanding the full range of N₂O fluxes in the Arctic. Easily accessible areas like the Stordalen mire can serve as ideal locations for these measurements. Furthermore, future chamber studies should investigate the light-dependency of N₂O fluxes across a range of ecosystems, ideally including microbial analyses to elucidate the underlying processes.

In summary, this dissertation presents a groundbreaking study on Arctic N₂O fluxes, providing critical insights into the complex drivers of these fluxes and highlighting the need for more accurate and comprehensive measurements. Our findings have far-reaching implications for the field, and we are confident that our research will contribute significantly to the advancement of N₂O research in the Arctic and beyond.

REFERENCES

Bhattarai HR, Marushchak ME, Ronkainen J, Lamprecht RE, Siljanen HMP, Martikainen PJ, Biasi C, and Maljanen M (2022) Emissions of atmospherically reactive gases nitrous acid and nitric oxide from Arctic permafrost peatlands. *Environ Res Lett* 17.: 024034. <https://doi.org/10.1088/1748-9326/ac4f8e>.

Biskaborn BK, Smith SL, Noetzli J, Matthes H, Vieira G, Streletschi DA, Schoeneich P, Romanovsky VE, Lewkowicz AG, Abramov A, Allard M, Boike J, Cable WL, Christiansen HH, Delaloye R, Diekmann B, Drozdov D, Etzelmüller B, Grosse G, Guglielmin M, Ingeman-Nielsen T, Isaksen K, Ishikawa M, Johannsson M, Johannsson H, Joo A, Kaverin D, Kholodov A, Konstantinov P, Kröger T, Lambiel C, Lanckman J.-P, Luo D, Malkova G, Meiklejohn I, Moskalenko N, Oliva M, Phillips M, Ramos M, Sannel ABK, Sergeev D, Seybold C, Skryabin P, Vasiliev A, Wu Q, Yoshikawa K, Zheleznyak M, and Lantuit H (2019) Permafrost is warming at a global scale. *Nat Commun* 10.: 264. <https://doi.org/10.1038/s41467-018-08240-4>.

Brummell ME, Farrell RE, Hardy SP, and Siciliano SD (2014) Greenhouse gas production and consumption in High Arctic deserts. *Soil Biol Biochem* 68: 158–165. <https://doi.org/10.1016/j.soilbio.2013.09.034>.

Brummell ME, Farrell RE, and Siciliano SD (2012) Greenhouse gas soil production and surface fluxes at a high arctic polar oasis. *Soil Biol Biochem* 52: 1–12. <https://doi.org/10.1016/j.soilbio.2012.03.019>.

Buchen C, Roobroeck D, Augustin J, Behrendt U, Boeckx P, and Ulrich A (2019) High N₂O consumption potential of weakly disturbed fen mires with dissimilar denitrifier community structure. *Soil Biol Biochem* 130: 63–72. <https://doi.org/10.1016/j.soilbio.2018.12.001>.

Butterbach-Bahl K, Baggs EM, Dannenmann M, Kiese R, and Zechmeister-Boltenstern S (2013) Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philos Trans R Soc Lond B Biol Sci* 368. Number: 1621: 20130122. <https://doi.org/10.1098/rstb.2013.0122>.

Christensen TR, Michelsen A, and Jonasson S (1999) Exchange of CH₄ and N₂O in a subarctic heath soil: effects of inorganic N and P and amino acid addition. *Soil Biol Biochem* 31: 637–641.

Crosson E (2008) A cavity ring-down analyzer for measuring atmospheric levels of methane, carbon dioxide, and water vapor. *Appl Phys B* 92.: 403–408. <https://doi.org/10.1007/s00340-008-3135-y>.

De Klein CAM, Harvey MJ, Clough TJ, Petersen SO, Chadwick DR, and Venterea RT (2020) Global Research Alliance N₂O chamber methodology guidelines: Introduction, with health and safety considerations. *J Environ Qual* 49.: 1073–1080. <https://doi.org/10.1002/jeq2.20131>.

Denmead OT (2008) Approaches to measuring fluxes of methane and nitrous oxide between landscapes and the atmosphere. *Plant Soil* 309. Number: 1-2: 5–24. <https://doi.org/10.1007/s11104-008-9599-z>.

Elberling B, Christiansen HH, and Hansen BU (2010) High nitrous oxide production from thawing permafrost. *Nat Geosci* 3.: 332–335. <https://doi.org/10.1038/ngeo803>.

Farquharson R and Baldock J (2008) Concepts in modelling N₂O emissions from land use. *Plant Soil* 309.: 147–167. <https://doi.org/10.1007/s11104-007-9485-0>.

Fiedler J, Fuß R, Glatzel S, Hagemann U, Huth V, Jordan S, Jurasinski G, Kutzbach L, Maier M, Schäfer K, Weber T, and Weymann D (2022) BEST PRACTICE GUIDELINE: Measurement of carbon dioxide, methane and nitrous oxide fluxes between soil-vegetation-systems and the atmosphere using non-steady state chambers.

Firestone MK and Davidson EA (1989) Microbiological Basis of NO and N₂O Production and Consumption in Soil. *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere (M.O., Andreae, D.S. Schimel, and G.P. Robertson (eds.))* New York, NY: John Wiley & Sons: 7–21.

Graf DRH, Jones CM, and Hallin S (2014) Intergenomic Comparisons Highlight Modularity of the Denitrification Pathway and Underpin the Importance of Community Structure for N₂O Emissions. *PLoS ONE* 9. Ed. by V De Crécy-Lagard: e114118. <https://doi.org/10.1371/journal.pone.0114118>.

Hensen A, Skiba U, and Famulari D (2013) Low cost and state of the art methods to measure nitrous oxide emissions. *Environ Res Lett* 8.: 025022. <https://doi.org/10.1088/1748-9326/8/2/025022>.

Hübschmann H.-J (2015) Handbook of GC-MS: Fundamentals and Applications. 1st ed. Wiley. <https://doi.org/10.1002/9783527674305>.

Hugelius G, Ramage J, Burke E, Chatterjee A, Smallman TL, Aalto T, Bastos A, Biasi C, Canadell JG, Chandra N, Chevallier F, Ciais P, Chang J, Feng L, Jones MW, Kleinen T, Kuhn M, Lauerwald R, Liu J, López-Blanco E, Luijckx IT, Marushchak ME, Natali SM, Niwa Y, Olefeldt D, Palmer PI, Patra PK, Peters W, Potter S, Poulter B, Rogers BM, Riley WJ, Saunois M, Schuur EAG, Thompson RL, Treat C, Tsuruta A, Turetsky MR, Virkkala A.-M, Voigt C, Watts J, Zhu Q, and Zheng B (2024) Permafrost Region Greenhouse Gas Budgets Suggest a Weak CO₂ Sink and CH₄ and N₂O Sources, But Magnitudes Differ Between Top-Down and Bottom-Up Methods. *Glob Biogeochem Cycles* 38.: e2023GB007969. <https://doi.org/10.1029/2023GB007969>.

Hugelius G, Loisel J, Chadbourn S, Jackson RB, Jones M, MacDonald G, Marushchak M, Olefeldt D, Packalen M, Siewert MB, Treat C, Turetsky M, Voigt C, and Yu Z (2020) Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proc Natl Acad Sci* 117.: 20438–20446. <https://doi.org/10.1073/pnas.1916387117>.

Hüppi R, Felber R, Krauss M, Six J, Leifeld J, and Fuß R (2018) Restricting the nonlinearity parameter in soil greenhouse gas flux calculation for more reliable flux estimates. *PLOS ONE* 13. Ed. by UM Sainju. Publisher: Public Library of Science (PLoS): e0200876. <https://doi.org/10.1371/journal.pone.0200876>.

Hutchinson GL and Mosier AR (1981) Improved Soil Cover Method for Field Measurement of Nitrous Oxide Fluxes. *Soil Sci Soc Am J* 45: 6.

Intergovernmental Panel On Climate Change (Ipcc) (2023) Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. 1st ed. Cambridge University Press. <https://doi.org/10.1017/9781009325844>.

Jentzsch K, Van Delden L, Fuchs M, and Treat CC (2025) An expert survey on chamber measurement techniques and data handling procedures for methane fluxes. *Earth Syst Sci Data* 17.: 2331–2372. <https://doi.org/10.5194/essd-17-2331-2025>.

Jones CM, Graf DRH, Bru D, Philippot L, and Hallin S (2013) The unaccounted yet abundant nitrous oxide-reducing microbial community: a potential nitrous oxide sink. *ISME J* 7.: 417–426. <https://doi.org/10.1038/ismej.2012.125>.

Keane BJ, Ineson P, Vallack HW, Blei E, Bentley M, Howarth S, McNamara NP, Rowe RL, Williams M, and Toet S (2018) Greenhouse gas emissions from the energy crop oilseed rape (*Brassica napus*); the role of photosynthetically active radiation in diurnal N₂ O flux variation. *GCB Bioenergy* 10.: 306–319. <https://doi.org/10.1111/gcbb.12491>.

Keuper F, Van Bodegom PM, Dorrepael E, Weedon JT, Van Hal J, Van Logtestijn RSP, and Aerts R (2012) A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Glob Change Biol* 18.: 1998–2007. <https://doi.org/10.1111/j.1365-2486.2012.02663.x>.

Koponen HT, Escudé Duran C, Maljanen M, Hytönen J, and Martikainen PJ (2006) Temperature responses of NO and N₂O emissions from boreal organic soil. *Soil Biol Biochem* 38.: 1779–1787. <https://doi.org/10.1016/j.soilbio.2005.12.004>.

Liu H, Li Y, Pan B, Zheng X, Yu J, Ding H, and Zhang Y (2022) Pathways of soil N₂O uptake, consumption, and its driving factors: a review. *Environ Sci Pollut Res* 29.: 30850–30864. <https://doi.org/10.1007/s11356-022-18619-y>.

Livingston GP and Hutchinson GL (1995) Enclosure-based measurement of trace gas exchange: applications and sources of error. *Biogenic Trace Gases: Measuring Emissions from Soil and Water (P.A. Matson and R.C. Harriss (eds.))* John Wiley & Sons: 14–51.

Maaz TM, Sapkota TB, Eagle AJ, Kantar MB, Bruulsema TW, and Majumdar K (2021) Meta-analysis of yield and nitrous oxide outcomes for nitrogen management in agriculture. *Glob Change Biol* 27.: 2343–2360. <https://doi.org/10.1111/gcb.15588>.

Martikainen PJ, Nykänen H, Crill P, and 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>.

Marushchak ME, Kerttula J, Diáková K, Faguet A, Gil J, Grosse G, Knoblauch C, Lashchinskiy N, Martikainen PJ, Morgenstern A, Nykamb M, Ronkainen JG, Siljanen HMP, Van Delden L, Voigt C, Zimov N, Zimov S, and Biasi C (2021) Thawing Yedoma permafrost is a neglected nitrous oxide source. *Nat Commun* 12.: 7107. <https://doi.org/10.1038/s41467-021-27386-2>.

Marushchak ME, Pitkämäki A, Koponen H, Biasi C, Seppälä M, and Martikainen PJ (2011) Hot spots for nitrous oxide emissions found in different types of permafrost peatlands: NITROUS OXIDE FLUXES FROM PERMAFROST PEATLANDS. *Glob Change Biol* 17.: 2601–2614. <https://doi.org/10.1111/j.1365-2486.2011.02442.x>.

McGuire AD, Macdonald RW, Schuur EA, Harden JW, Kuhry P, Hayes DJ, Christensen TR, and Heimann M (2010) The carbon budget of the northern cryosphere region. *Curr Opin Environ Sustainnmental Sustainability* 2.: 231–236. <https://doi.org/10.1016/j.cosus.2010.05.003>.

Palmer K, Biasi C, and Horn MA (2012) Contrasting denitrifier communities relate to contrasting N₂O emission patterns from acidic peat soils in arctic tundra. *ISME J* 6.: 1058–1077. <https://doi.org/10.1038/ismej.2011.172>.

Palmtag J, Hugelius G, Lashchinskiy N, Tamstorf MP, Richter A, Elberling B, and Kuhry P (2015) Storage, Landscape Distribution, and Burial History of Soil Organic Matter in Contrasting Areas of Continuous Permafrost. *Arct Antarct Alp Res* 47.: 71–88. <https://doi.org/10.1657/AAAR0014-027>.

Palmtag J, Obu J, Kuhry P, Richter A, Siewert MB, Weiss N, Westermann S, and Hugelius G (2022) A high spatial resolution soil carbon and nitrogen dataset for the northern permafrost region based on circumpolar land cover upscaling. *Earth Syst Sci Data* 14.: 4095–4110. <https://doi.org/10.5194/essd-14-4095-2022>.

Pavelka M, Acosta M, Kiese R, Altimir N, Brümmer C, Crill P, Darenova E, Fuß R, Gielen B, Graf A, Klemedtsson L, Lohila A, Longdoz B, Lindroth A, Nilsson M, Jiménez SM, Merbold L, Montagnani L, Peichl M, Pihlatie M, Pumpanen J, Ortiz PS, Silvennoinen H, Skiba U, Vestin P, Weslien P, Janous D, and Kutsch W (2018) Standardisation of chamber technique for CO₂, N₂O and CH₄ fluxes measurements from terrestrial ecosystems. *Int Agrophy* 32. Number: 4: 569–587. <https://doi.org/10.1515/intag-2017-0045>.

Pedersen AR, Petersen SO, and Schelde K (2010) A comprehensive approach to soil-atmosphere trace-gas flux estimation with static chambers. *Eur J of Soil Sci* 61.: 888–902. <https://doi.org/10.1111/j.1365-2389.2010.01291.x>.

Peel MC, Finlayson BL, and McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci* 11.: 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>.

Przybylak R (2016) The Climate of the Arctic. Vol. 52. Atmospheric and Oceanographic Sciences Library. Cham: Springer International Publishing. <https://doi.org/10.1007/978-3-319-21696-6>.

Rantanen M, Karpechko AY, Lipponen A, Nordling K, Hyvärinen O, Ruosteenaja K, Vihma T, and Laaksonen A (2022) The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ* 3.: 168. <https://doi.org/10.1038/s43247-022-00498-3>.

Rapson TD and Dacres H (2014) Analytical techniques for measuring nitrous oxide. *TrAC - Trends Anal Chem* 54: 65–74. <https://doi.org/10.1016/j.trac.2013.11.004>.

Repo ME, Susiluoto S, Lind SE, Jokinen S, Elsakov V, Biasi C, Virtanen T, and Martikainen PJ (2009) Large N₂O emissions from cryoturbated peat soil in tundra. *Nat Geosci* 2.: 189–192. <https://doi.org/10.1038/ngeo434>.

Rheault K, Christiansen JR, and Larsen KS (2024) goFlux: A user-friendly way to calculate GHG fluxes yourself, regardless of user experience. *J Open Source Softw* 9.: 6393. <https://doi.org/10.21105/joss.06393>.

Robertson G and Groffman P (2024) Nitrogen transformations. *Soil Microbiology, Ecology and Biochemistry*. Elsevier: 407–438. <https://doi.org/10.1016/B978-0-12-822941-5.00014-4>.

Rochette P and Eriksen-Hamel NS (2008) Chamber Measurements of Soil Nitrous Oxide Flux: Are Absolute Values Reliable? *Soil Sci Soc Am J* 72.: 331–342. <https://doi.org/10.2136/sssaj2007.0215>.

Sanford RA, Wagner DD, Wu Q, Chee-Sanford JC, Thomas SH, Cruz-García C, Rodríguez G, Massol-Deyá A, Krishnani KK, Ritalahti KM, Nissen S, Konstantinidis KT, and Löffler FE (2012) Unexpected nondenitrifier nitrous oxide reductase gene diversity and abundance in soils. *Proc Natl Acad Sci* 109.: 19709–19714. <https://doi.org/10.1073/pnas.1211238109>.

Schlesinger WH (2013) An estimate of the global sink for nitrous oxide in soils. *Glob Change Biol* 19.: 2929–2931. <https://doi.org/10.1111/gcb.12239>.

Schuur EA, Abbott BW, Commane R, Ernakovich J, Euskirchen E, Hugelius G, Grosse G, Jones M, Koven C, Leshyk V, Lawrence D, Loranty MM, Mauritz M, Olefeldt D, Natali S, Rodenhizer H, Salmon V, Schädel C, Strauss J, Treat C, and Turetsky M (2022) Permafrost and Climate Change: Carbon Cycle Feedbacks From the Warming Arctic. *Annu Rev Environ Resourc* 47.: 343–371. <https://doi.org/10.1146/annurev-environ-012220-011847>.

Seppälä M (2011) Synthesis of studies of palsa formation underlining the importance of local environmental and physical characteristics. *Quat Res* 75.: 366–370. <https://doi.org/10.1016/j.yqres.2010.09.007>.

Sharifi M, Lynch DH, ZebARTH BJ, Zheng Z, and Martin RC (2009) Evaluation of Nitrogen Supply Rate Measured by in situ Placement of Plant Root Simulator™ Probes as a Predictor of Nitrogen Supply from Soil and Organic Amendments in Potato Crop. *Am J Potato Res* 86.: 356–366. <https://doi.org/10.1007/s12230-009-9090-2>.

Shurpali NJ, Rannik Ü, Jokinen S, Lind S, Biasi C, Mammarella I, Peltola O, Pihlatie M, Hyvönen N, Räty M, Haapanala S, Zahniser M, Virkajarvi P, Vesala T, and Martikainen PJ (2016) Neglecting diurnal variations leads to uncertainties in terrestrial nitrous oxide emissions. *Sci Rep* 6.: 25739. <https://doi.org/10.1038/srep25739>.

Siewert MB (2018) High-resolution digital mapping of soil organic carbon in permafrost terrain using machine learning: a case study in a sub-Arctic peatland environment. *Biogeosciences* 15.: 1663–1682. <https://doi.org/10.5194/bg-15-1663-2018>.

Sjögersten S, Ledger M, Siewert M, De La Barreda-Bautista B, Sowter A, Gee D, Foody G, and Boyd DS (2023) Optical and radar Earth observation data for upscaling methane emissions

linked to permafrost degradation in sub-Arctic peatlands in northern Sweden. *Biogeosciences* 20.: 4221–4239. <https://doi.org/10.5194/bg-20-4221-2023>.

Song Y, Cheng X, Song C, Li M, Gao S, Liu Z, Gao J, and Wang X (2022) Soil CO₂ and N₂O emissions and microbial abundances altered by temperature rise and nitrogen addition in active-layer soils of permafrost peatland. *Front Microbiol* 13: 1093487. <https://doi.org/10.3389/fmicb.2022.1093487>.

Stewart KJ, Brummell ME, Farrell RE, and Siciliano SD (2012) N₂O flux from plant-soil systems in polar deserts switch between sources and sinks under different light conditions. *Soil Biol Biochem* 48: 69–77. <https://doi.org/10.1016/j.soilbio.2012.01.016>.

Strand SM, Christiansen HH, Johansson M, Åkerman J, and Humlum O (2021) Active layer thickening and controls on interannual variability in the Nordic Arctic compared to the circum-Arctic. *Permafrost Periglac Process* 32.: 47–58. <https://doi.org/10.1002/ppp.2088>.

Strauss J, Abbott B, Hugelius G, Schuur E, Treat C, and Fuchs M (2021) Recarbonizing global soils – A technical manual of recommended management practices. FAO. <https://doi.org/10.4060/cb6378en>.

Subke J.-A, Kutzbach L, and Risk D (2021) Soil Chamber Measurements. *Springer Handbook of Atmospheric Measurements*. Ed. by T Foken. Series Title: Springer Handbooks. Cham: Springer International Publishing: 1603–1624. https://doi.org/10.1007/978-3-030-52171-4_60.

Thoning K, Dlugokencky E, Lan X, and NOAA Global Monitoring Laboratory (2022) Trends in globally-averaged CH₄, N₂O, and SF₆. <https://doi.org/10.15138/P8XG-AA10>.

Tian H, Pan N, Thompson RL, Canadell JG, Suntharalingam P, Regnier P, Davidson EA, Prather M, Ciais P, Muntean M, Pan S, Winiwarter W, Zaehle S, Zhou F, Jackson RB, Bange HW, Berthet S, Bian Z, Bianchi D, Bouwman AF, Buitenhuis ET, Dutton G, Hu M, Ito A, Jain AK, Jeltsch-Thömmes A, Joos F, Kou-Giesbrecht S, Krummel PB, Lan X, Landolfi A, Lauerwald R, Li Y, Lu C, Maavara T, Manizza M, Millet DB, Mühle J, Patra PK, Peters GP, Qin X, Raymond P, Resplandy L, Rosentreter JA, Shi H, Sun Q, Tonina D, Tubiello FN, Van Der Werf GR, Vuichard N, Wang J, Wells KC, Western LM, Wilson C, Yang J, Yao Y, You Y, and Zhu Q (2024) Global nitrous oxide budget (1980–2020). *Earth Syst Sci Data* 16.: 2543–2604. <https://doi.org/10.5194/essd-16-2543-2024>.

Tian H, Xu R, Canadell JG, Thompson RL, Winiwarter W, Suntharalingam P, Davidson EA, Ciais P, Jackson RB, Janssens-Maenhout G, Prather MJ, Regnier P, Pan N, Pan S, Peters GP, Shi H, Tubiello FN, Zaehle S, Zhou F, Arneth A, Battaglia G, Berthet S, Bopp L, Bouwman AF, Buitenhuis ET, Chang J, Chipperfield MP, Dangal SRS, Dlugokencky E, Elkins JW, Eyre BD, Fu B, Hall B, Ito A, Joos F, Krummel PB, Landolfi A, Laruelle GG, Lauerwald R, Li W, Lienert S, Maavara T, MacLeod M, Millet DB, Olin S, Patra PK, Prinn RG, Raymond PA, Ruiz DJ, Werf GR van der, Vuichard N, Wang J, Weiss RF, Wells KC, Wilson C, Yang J, and Yao Y (2020) A comprehensive quantification of global nitrous oxide sources and sinks. *Nature* 586. Number: 7828 Publisher: Nature Publishing Group: 248–256. <https://doi.org/10.1038/s41586-020-2780-0>.

Turetsky MR, Abbott BW, Jones MC, Anthony KW, Olefeldt D, Schuur EAG, Grosse G, Kuhry P, Hugelius G, Koven C, Lawrence DM, Gibson C, Sannel ABK, and McGuire AD

(2020) Carbon release through abrupt permafrost thaw. *Nat Geosci* 13.: 138–143. <https://doi.org/10.1038/s41561-019-0526-0>.

Voigt C, Lamprecht RE, Marushchak ME, Lind SE, Novakovskiy A, Aurela M, Martikainen PJ, and Biasi C (2017a) Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Glob Change Biol* 23. Number: 8 _eprint: <https://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.13563>: 3121–3138. <https://doi.org/10.1111/gcb.13563>.

Voigt C, Marushchak ME, Abbott BW, Biasi C, Elberling B, Siciliano SD, Sonnentag O, Stewart KJ, Yang Y, and Martikainen PJ (2020) Nitrous oxide emissions from permafrost-affected soils. *Nat Rev Earth Environ* 1.: 420–434. <https://doi.org/10.1038/s43017-020-0063-9>.

Voigt C, Marushchak ME, Lamprecht RE, Jackowicz-Korczyński M, Lindgren A, Masteponov M, Granlund L, Christensen TR, Tahvanainen T, Martikainen PJ, and Biasi C (2017b) Increased nitrous oxide emissions from Arctic peatlands after permafrost thaw. *Proc Natl Acad Sci* 114.: 6238–6243. <https://doi.org/10.1073/pnas.1702902114>.

Webb EK, Pearman GI, and Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Q J R Meteorol Soc* 106.: 85–100. <https://doi.org/10.1002/qj.49710644707>.

Wu D, Cárdenas LM, Calvet S, Brüggemann N, Loick N, Liu S, and Bol R (2017) The effect of nitrification inhibitor on N₂O, NO and N₂ emissions under different soil moisture levels in a permanent grassland soil. *Soil Biol Biochem* 113: 153–160. <https://doi.org/10.1016/j.soilbio.2017.06.007>.

Wu Y.-F, Whitaker J, Toet S, Bradley A, Davies CA, and McNamara NP (2021) Diurnal variability in soil nitrous oxide emissions is a widespread phenomenon. *Glob Change Biol* 27.: 4950–4966. <https://doi.org/10.1111/gcb.15791>.

Xu X, Tian H, and Hui D (2008) Convergence in the relationship of CO₂ and N₂ O exchanges between soil and atmosphere within terrestrial ecosystems. *Glob Change Biol* 14.: 1651–1660. <https://doi.org/10.1111/j.1365-2486.2008.01595.x>.

Yang G, Peng Y, Marushchak ME, Chen Y, Wang G, Li F, Zhang D, Wang J, Yu J, Liu L, Qin S, Kou D, and Yang Y (2018) Magnitude and Pathways of Increased Nitrous Oxide Emissions from Uplands Following Permafrost Thaw. *Environ Sci Technol* 52.: 9162–9169. <https://doi.org/10.1021/acs.est.8b02271>.

Zona D, Janssens IA, Gioli B, Jungkunst HF, Serrano MC, and Ceulemans R (2013) N₂ O fluxes of a bio-energy poplar plantation during a two years rotation period. *GCB Bioenergy* 5.: 536–547. <https://doi.org/10.1111/gcbb.12019>.