Greenhouse gases flux dynamics and controlling environmental factors in Northern wetlands

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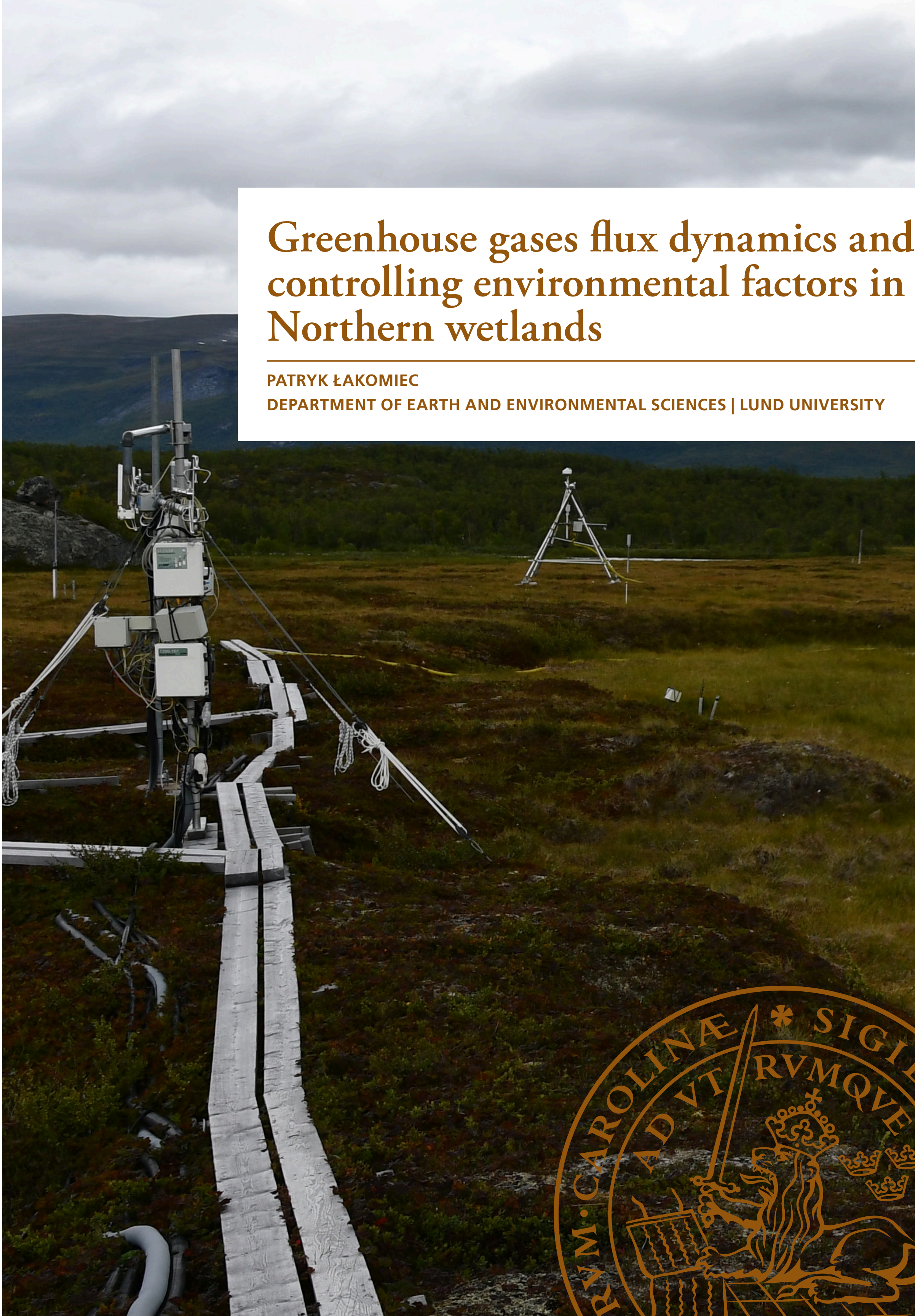

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DOCTORAL DISSERTATION

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Abstract: Methane (CH_4) and carbon dioxide (CO_2) emissions from northern peatlands are important components of the global greenhouse gas (GHG) balance and are highly sensitive to climate change and permafrost degradation. This thesis investigates spatial and temporal patterns of GHG fluxes across peatland ecosystems, with a particular focus on the environmental controls regulating CH_4 and CO_2 exchange.

Field measurements were conducted across Swedish peatlands using chamber systems and eddy covariance observations. Chamber measurements were used to study small-scale spatial variability in CH_4 fluxes and supported isotopic analyses of CH_4. Ecosystem-scale flux data from the ICOS Sweden station at Abisko-Stordalen were used to quantify annual GHG budgets across contrasting permafrost landforms, including palsa, thawing permafrost areas, and fully thawed fens. The study further evaluated how environmental drivers such as peat temperature, hydrology, light availability, and growing season length influence carbon exchange dynamics.

The thesis also examines methodological challenges in peatland GHG research. In particular, the role of gap-filling approaches in reducing uncertainties and highlighting the importance of methodological choices for reliable annual budget estimates. In addition, stable isotope analyses ($\delta^{13}C$-CH_4) were used to explore whether peatland CH_4 processes and carbon dynamics can be adequately represented by single isotopic value. Temporal and spatial variations in isotopic composition were linked to environmental conditions, substrate availability, and microbial community composition.

The results demonstrate that permafrost thaw strongly make changes in carbon cycling in peatlands by increasing CH_4 emissions and modifying CO_2 exchange patterns. Fully thawed systems showed greater CO_2 uptake during the growing season, but also higher ecosystem respiration rates, compared with palsa and partially thawed systems. CH_4 emissions were primarily controlled by peat temperature and hydrological conditions, while CO_2 dynamics were more strongly linked to growing season length and light availability. Furthermore, the findings emphasize that both spatial heterogeneity and methodological decisions significantly influence the interpretation of peatland carbon dynamics and GHG budgets.

By integrating flux measurements, isotopic analyses, and methodological evaluation, this thesis provides new insights into the controls on GHG emissions in northern peatlands undergoing climate warming, extreme events such as drought and permafrost degradation.

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Table of Contents

Abstract

Methane (CH_4) and carbon dioxide (CO_2) emissions from northern peatlands are important components of the global greenhouse gas (GHG) balance and are highly sensitive to climate change and permafrost degradation. This thesis investigates spatial and temporal patterns of GHG fluxes across peatland ecosystems, with a particular focus on the environmental controls regulating CH_4 and CO_2 exchange.

Field measurements were conducted across Swedish peatlands using chamber systems and eddy covariance observations. Chamber measurements were used to study small-scale spatial variability in CH_4 fluxes and supported isotopic analyses of CH_4. Ecosystem-scale flux data from the ICOS Sweden station at Abisko-Stordalen were used to quantify annual GHG budgets across contrasting permafrost landforms, including palsa, thawing permafrost areas, and fully thawed fens. The study further evaluated how environmental drivers such as peat temperature, hydrology, light availability, and growing season length influence carbon exchange dynamics.

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By integrating flux measurements, isotopic analyses, and methodological evaluation, this thesis provides new insights into the controls on GHG emissions in northern peatlands undergoing climate warming, extreme events such as drought and permafrost degradation.

Popular summary

Northern peatlands store huge amounts of carbon. While climate is warming and permafrost is thawing, they can release increasing amounts of greenhouse gases (GHG) such as methane (CH_4) and carbon dioxide (CO_2). So stored carbon can be released and amplify global warming. This thesis investigates how these emissions vary across different peatland types in northern Sweden and what environmental factors control them.

Using ecosystem observations and methane isotope analyses, controlling factors were examined. Impact how temperature, water levels, sunlight, and the length of the growing season affect GHG emissions were tested. Different data-processing methods and their influence on of annual carbon budgets estimation were evaluated.

The natural isotopic composition of methane ($\delta^{13}C-CH_4$) was used to better understand how CH_4 is produced and consumed within peatlands. These isotopic "fingerprints" provide information about the biological processes happens below the surface and how they respond to changing environmental conditions.

The results show that permafrost thaw is a major driver of changes in peatland carbon cycling. Fully thawed peatlands absorbed more CO_2 during the growing season but also released more carbon through ecosystem respiration. CH_4 emissions increased with warmer and wetter conditions. The study shows that peatlands are highly variable in space and time. Making careful measurement and analysis is essential for producing reliable GHG estimates. The results showed that CH_4 isotopic composition varies across different peatland habitats and over time, indicating that a single isotopic value cannot accurately represent the complexity of peatland CH_4 cycling.

This thesis improves our understanding how northern peatlands respond to climate warming, drought, and permafrost degradation. These findings will help to improve predictions of future GHG emissions and their role in global climate change.

List of papers

Paper I

Łakomiec, P., Holst, J., Friborg, T., Crill, P., Rakos, N., Kljun, N., Olsson, P.-O., Eklundh, L., Persson, A., and Rinne, J.: Field-scale CH_4 emission at a subarctic mire with heterogeneous permafrost thaw status, Biogeosciences, 18, 5811–5830, https://doi.org/10.5194/bg-18-5811-2021, 2021.

Paper II

Łakomiec, P., Holst, J., Rakos, N., Lundin, E., Crill, P., Friborg, T., Jin, H., Eklundh, L., and Rinne, J.:CO_2 exchange at a subarctic mire complex with varying permafrost status (under preparation)

Paper III

Rinne, J., Łakomiec, P., Vestin, P., White, J. D., Weslien, P., Kelly, J., Kljun, N., Ström, L., and Klemedtsson, L.: Spatial and temporal variation in δ^{13}C values of methane emitted from a hemiboreal mire: methanogenesis, methanotrophy, and hysteresis, Biogeosciences, 19, 4331–4349, https://doi.org/10.5194/bg-19-4331-2022, 2022.

Paper IV

J. Rinne, J.-P. Tuovinen, L. Klemedtsson, M. Aurela, J. Holst, A. Lohila, P. Weslien, P. Vestin, P. Łakomiec, M. Peichl, E.-S. Tuittila, L. Heiskanen, T. Laurila, X. Li, P. Alekseychik, I. Mammarella, L. Ström, P. Crill, M. B. Nilsson; Effect of the 2018 European drought on methane and carbon dioxide exchange of northern mire ecosystems. Phil. Trans. R. Soc. B 26 October 2020; 375 (1810): 20190517. https://doi.org/10.1098/rstb.2019.0517

Paper V

Menoud, M., van der Veen, C., Lowry, D., Fernandez, J. M., Bakkaloglu, S., France, J. L., Fisher, R. E., Maazallahi, H., Stanisavljević, M., Nęcki, J., Vinkovic, K., Łakomiec, P., Rinne, J., Korbeń, P., Schmidt, M., Defratyka, S., Yver-Kwok, C., Andersen, T., Chen, H., and Röckmann, T.: New contributions of measurements in Europe to the global inventory of the stable isotopic composition of methane, Earth Syst. Sci. Data, 14, 4365–4386, https://doi.org/10.5194/essd-14-4365-2022, 2022.

Author contributions

Paper I

PŁ, JH, TF, PC, and JR analyzed and interpreted the data. **PŁ**, JH, PC, and JR wrote the manuscript. TF, PC, and NR designed the measurements. NK was responsible for the footprint calculation and its interpretation. POO and LE were responsible for interpreting UAV data. AP provided support with the water table level data.

Paper II

PŁ, JH, TF, PC, ER, and JR analyzed and interpreted the data. **PŁ**, JH, PC, ER, and JR wrote the manuscript. TF, PC, ER, and NR designed the measurements. HJ and LE were responsible for interpreting NDVI data.

Paper III

JR, NK, and LK designed the study. PV and PW collected the methane emission and isotopic data by the CRDS system. **PL** collected the isotopic data analyzed by isotope ratio mass spectrometry. JDW, LS, and LK collected the genetic data. JK collected the remote sensing data on mire microtopography. **PL** processed the methane emission and isotope data. JR analyzed the methane emission and isotopic data. JDW processed and analyzed the genetic data. LS analyzed the plant composition of chamber plots. JR, JDW, and JK wrote the first version of the manuscript. All coauthors contributed to interpretation of the results and commented on the manuscript at different stages.

Paper IV

J.R. designed the study, analysed and interpreted the data and wrote the manuscript. J.P.T. provided the RF model runs, interpreted the results and co-wrote the ms. M.A., A.L., P.W., M.P., L.H., T.L. and P.A. collected the data and interpreted the results. J.H., P.V., **P.L**., X.L. and I.M. processed the data and interpreted results. L.S. provided vegetation analysis. L.K., P.C. and M.N. interpreted the results and co-wrote the ms.

Paper V

MM, CvdV, DL, JMF, SB, JLF, and REF performed the isotopic measurements. MM, TR, DL, JLF, SB, JMF, REF, HM, MS, JN, KV, **PŁ**, PK, MS, SD, and TA took part in the collection of samples. MM gathered and analysed the data and prepared the figures; TR and DL contributed to the interpretation of the data. MM prepared the paper with contributions from TR, DL, JR, MS, **PŁ**, SB, HM, JMF, and HC.

List of figures

Abbreviations

ANN	Artificial Neural Network
CALM	Circumpolar Active Layer Monitoring
CH_4	Methane
CO_2	Carbon dioxide
CRDS	Cavity Ring-Down Spectroscopy
EC	Eddy Covariance
GHG	Greenhouse Gas
GLM	Generalized Linear Model
GPP	Gross Primary Productivity
GWP	Global Warming Potential
ICOS	Integrated Carbon Observation System
IRMS	Isotope Ratio Mass Spectrometry
MDS	Marginal Distribution Sampling
MDV	Mean Diurnal Variation
NEE	Net Ecosystem Exchange
NDVI	Normalized Difference Vegetation Index
OH	Hydroxyl radical
PAR	Photosynthetically Active Radiation

Reco	Ecosystem Respiration
SMHI	Swedish Meteorological and Hydrological Institute

Introduction

CO_2 is the most important anthropogenic GHG contributing to global warming. Unlike CH_4, which has a relatively short atmospheric lifetime, a substantial fraction of emitted CO_2 remains in the atmosphere for centuries to millennia due to slow exchanges among the atmosphere, oceans, and terrestrial biosphere (IPCC, 2021). Atmospheric CO_2 concentrations have increased dramatically since the pre-industrial era, rising from approximately 280 ppm in the mid-18th century to more than 420 ppm today (figure1), primarily because of fossil fuel combustion, cement production, deforestation, and land-use change (Friedlingstein et al., 2023). Since the beginning of industrialization, anthropogenic CO_2 emissions have continuously increased despite short-term variability associated with economic activity, volcanic eruptions, and large-scale climate oscillations. Approximately half of emitted CO_2 is currently absorbed by terrestrial ecosystems and the oceans. The remaining fraction stays in the atmosphere, amplifying the greenhouse effect (Le Quéré et al., 2018; Friedlingstein et al., 2023). Rising CO_2 concentrations contribute not only to increasing global temperatures but also to ocean acidification, changes in hydrological cycles, and ecosystem functioning. Consequently, reducing net CO_2 emissions is considered essential for limiting long-term climate change and achieving international climate targets such as those established under the Paris Agreement.

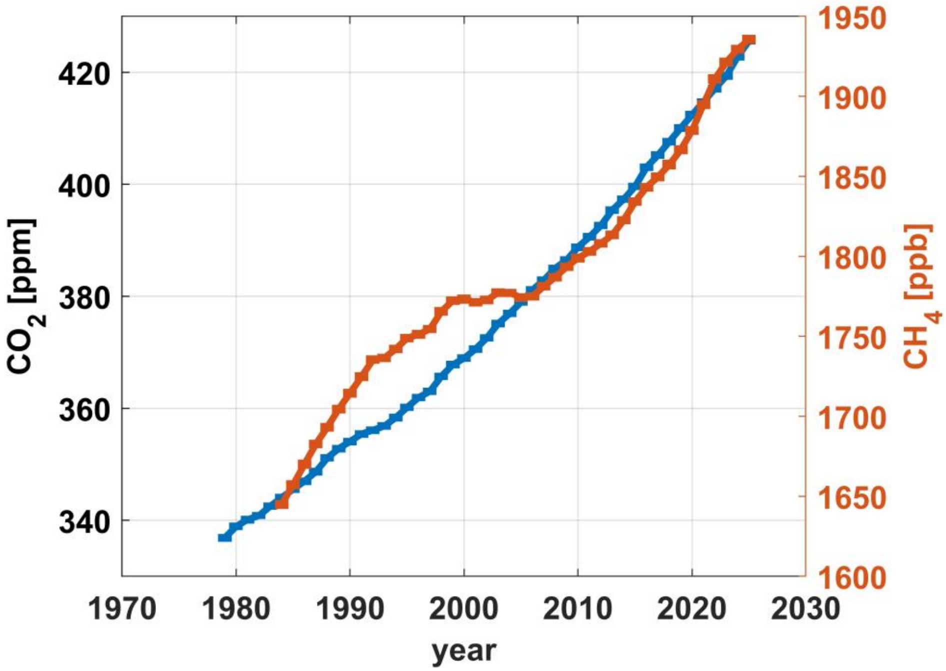

Figure 1. Trends in global annual mean atmospheric concentrations of CO_2 (blue line) and CH_4 (orange line). Data are yearly averaged and marked with error bars. Lan et al. (2022).

CH_4 is the second most important GHG contributing to global warming after CO_2. Its global warming potential (GWP) is 28 over a 100-year timescale and 84 over a 20-year timescale, with an atmospheric lifetime of approximately 11.8 years (IPCC, 2013). Atmospheric CH_4 concentrations have increased rapidly during the 21st century, highlighting CH_4's growing importance in climate change (Figure 1). After a period of relatively stable concentrations in the early 2000s, global atmospheric CH_4 began increasing again around 2007, followed by an accelerated growth rate after 2014 (Nisbet et al., 2019; Saunois et al., 2020). Global mean CH_4 concentrations exceeded 1900 ppb in 2021, compared with pre-industrial levels of approximately 720 ppb, representing an increase of more than 160% since the industrial revolution (IPCC, 2021). The annual atmospheric growth rate has increased in recent years, reaching level of more than 15 ppb yr^{-1} during 2020 and 2021 (Lan et al. 2022).

The main sink of atmospheric CH_4 is oxidation by hydroxyl (OH) radicals in the troposphere, which accounts for the majority of CH_4 removal. Additional sinks include oxidation in the stratosphere, soil uptake by methanotrophic bacteria, and minor losses in the marine boundary layer (Ciais et al., 2026). Emissions currently exceed total uptake, resulting in a net increase in atmospheric concentrations (Saunois et al., 2020).

Current global CH_4 emissions are estimated at approximately 576–737 Tg CH_4 yr^{-1}, with anthropogenic sources contributing roughly 60% of total emissions and natural sources accounting for the remainder (Saunois et al., 2020). Major anthropogenic CH_4 sources include fossil fuel production and distribution, agriculture (particularly enteric fermentation and rice cultivation), landfills, and biomass burning (figure2).

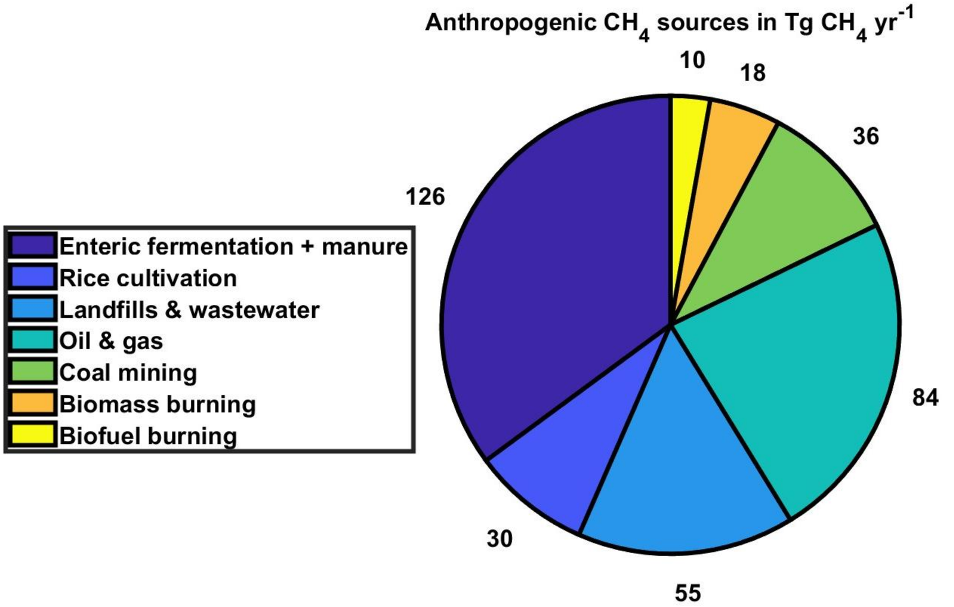

Figure2. Global anthropogenic CH_4 emissions by source sector presented in Tg CH_4 yr^{-1}. Adapted from Saunois et al. (2020).

Natural wetlands remain the single largest natural CH_4 source globally (figure3), contributing approximately 149–227 Tg CH_4 yr^{-1}, equivalent to nearly one-third of total global CH_4 emissions (Kirschke et al., 2013; Saunois et al., 2020).

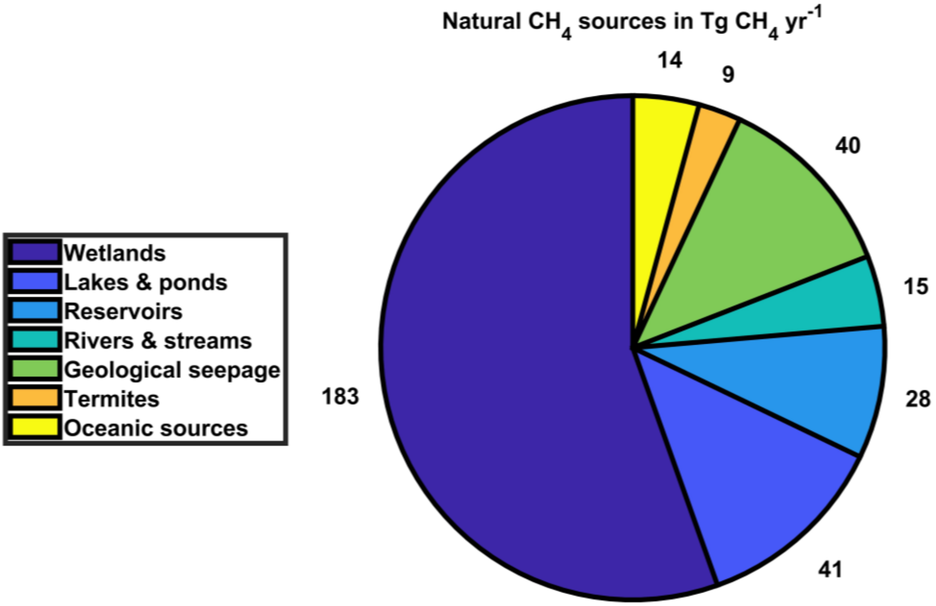

Figure3. Global natural CH_4 emissions by source category (Tg CH_4 yr^{-1}). Adapted from Saunois et al. (2020).

The causes of the CH_4 increase since 2007 are still not fully understood. Proposed explanations include increasing emissions from tropical wetlands driven by climate variability, expanding agricultural activities, fossil fuel extraction, and changes in atmospheric hydroxyl radical (OH) concentrations, which regulate CH_4 oxidation in the atmosphere (Schwietzke et al., 2016; Turner et al., 2019). Isotopic observations suggest that much of the recent atmospheric CH_4 growth may be linked to biogenic sources, particularly agriculture and wetlands, rather than fossil fuel emissions alone (Schaefer et al., 2016). The causes of the renewed increase in atmospheric CH_4 concentrations since 2007, and regrowth observed after 2019, remain an active area of research. Earlier hypotheses proposed increasing emissions from tropical wetlands driven by climate variability, expanding agricultural production, fossil fuel extraction, and changes in the atmospheric abundance of hydroxyl (OH) radicals, which regulate CH_4 oxidation (Schwietzke et al., 2016; Turner et al., 2019). Stable isotope observations have further suggested that much of the renewed atmospheric CH_4 growth may come from biogenic sources, such as wetlands and agriculture, rather than fossil fuel emissions alone (Schaefer et al., 2016). Recent studies suggest that no single mechanism can fully explain the observed increase. Ciais et al. 2026 showed that the CH_4 growth during the early 2020s resulted from a temporary reduction in atmospheric OH concentrations during 2020–2021. This weakened the

CH_4 sink. Also, wetland and inland water emissions have additional contribution. Their analysis also demonstrated strong regional variability, with increased emissions from northern tropical wetlands and the Arctic during this period. These findings highlight that recent atmospheric CH_4 trends come from a combination of changing emissions and atmospheric chemistry. This shows the complexity of the global CH_4 budget and the need for improved understanding of natural CH_4 sources and their environmental controls.

The global CH_4 budget is constrained using two main methodological approaches: bottom-up and top-down estimates. Bottom-up approaches rely on process-based models, emission inventories, and observational upscaling to quantify individual sources, while top-down approaches use atmospheric observations and inverse modelling to estimate emissions at different scales, from regional to global. Inconsistency between these approaches exist, largely due to uncertainties in natural emissions, particularly from wetlands and inland waters (Kirschke et al., 2013; Saunois et al., 2020).

Wetlands play a dual role in the global carbon cycle as both long-term carbon sinks and major CH_4 sources. They store large amounts of carbon, particularly in peatlands, which contain more than 600 Gt of carbon globally (Yu et al., 2011). Peatlands represent one of the largest and most efficient terrestrial carbon reservoirs on Earth despite covering only about 3% of the global land surface. Their waterlogged and oxygen-limited conditions slow organic matter decomposition, allowing partially decomposed plant material to accumulate as peat over thousands of years (Limpens et al., 2008; Loisel et al., 2021). As a result, peatlands store large quantities of soil carbon, estimated for nearly one-third of global soil carbon stocks, exceeding the amount of carbon stored in the world's forests (Gorham, 1991; Yu et al., 2011).

Peatlands also play a critical role in regulating hydrology, biodiversity, and climate feedback. Peatlands function as natural water reservoirs by retaining and slowly releasing water, reducing flood risk and maintaining regional hydrological stability. Plant and microbial communities are adapted to acidic, nutrient-poor, and water-saturated conditions. Drainage, peat extraction, wildfire, and permafrost thaw expose previously frozen or waterlogged organic matter to aerobic decomposition, rapidly releasing CO_2 and CH_4 into the atmosphere (Bridgham et al., 2013; Turetsky et al., 2020). Peat accumulation occurs over millennial timescales, the carbon stored in peatlands represents a long-term sink of carbon that is extremely vulnerable to disturbance. Global CH_4 assessments shows that northern wetlands are among the fastest-growing natural CH_4 sources under climate warming (Saunois et al., 2025). Hydrological changes associated with permafrost thaw amplify CH_4 emissions even when annual CO_2 balances remain relatively stable (McNicol et al., 2023; Delwiche et al., 2025). These findings highlight that ecosystem climate feedback cannot be evaluated using CO_2 exchange alone.

Climate warming has impact on the peatland GHGs emission stability, especially in northern high-latitude and permafrost regions. Rising temperatures and declining water tables can enhance microbial decomposition and CH_4 production (Perryman et al., 2022). Thawing permafrost gives access to carbon pools that have been long term stored (Hugelius et al., 2020). Models suggest that continued warming may shift many peatlands from long-term carbon sinks to net GHG sources, creating positive feedback that could amplify global climate change (Malmer et al., 2005; Bridgham et al., 2013).

CH_4 emissions from wetlands are driven by three key processes: production (methanogenesis), oxidation (methanotrophy), and transport to the atmosphere (Lai, 2009). CH_4 transport occurs via diffusion, ebullition, and plant-mediated pathways through aerenchyma tissues (Figure 4).

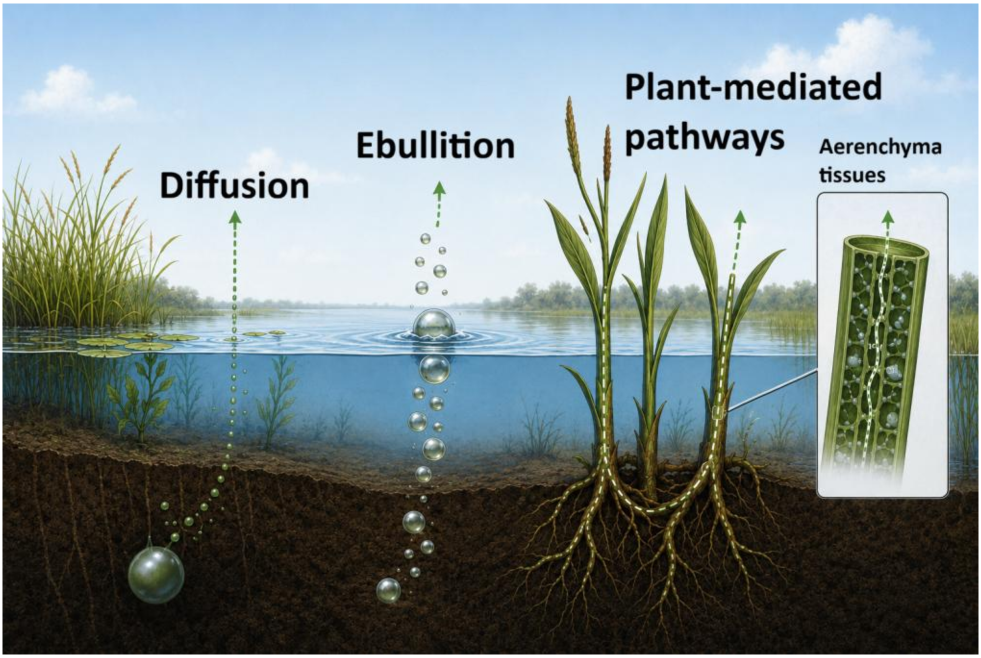

Figure4. Major CH_4 transport pathways in wetlands: diffusion through soil and water, ebullition, and plant-mediated transport via aerenchyma. AI generated

Each pathway has impact on the magnitude, timing, and variability of CH_4 fluxes. Diffusion is the slowest pathway and develop along concentration gradients through soil pore water and the water column. CH_4 diffuses slowly through soil, and it is oxidized by methanotrophic bacteria in oxygen surface layers before reaching the atmosphere. Diffusive transport results in relatively low and continuous CH_4 emissions (Whalen, 2005; Tveit et al., 2019).

Ebullition happens when dissolved CH_4 concentrations exceed saturation thresholds in pore water, leading to bubble formation that rapidly transports CH_4 to the atmosphere. This pathway skips aerobic oxidation zones and contributes to total CH_4 fluxes, especially under high CH_4 production rates, elevated temperatures, or falling hydrostatic pressure (Strack et al., 2013). Ebullition is episodic and spatially heterogeneous, often producing short-term emission peaks that dominate wetland CH_4 budgets during certain periods (Tokida et al., 2007).

Plant-mediated transport through aerenchyma tissues is frequently the dominant pathway in vegetated wetlands. Wetland plants have gas conducting tissues that transport oxygen from shoots to roots while simultaneously providing a path for CH_4 movement from anaerobic soils to the atmosphere. This pathway can account for more than 90% of total ecosystem CH_4 emissions in some wetlands. It bypasses the oxic surface layer, where CH_4 oxidation would happen (Bhullar et al., 2014; Pangala et al., 2017). Plant-mediated transport influences CH_4 fluxes in several contrasting ways. Vascular plants enhance emissions by directly venting CH_4 to the atmosphere. However, oxygen released from roots into the rhizosphere can stimulate methanotrophy and reduce net emissions locally (Whalen, 2005; Bhullar et al., 2014). The balance between these opposing effects depends strongly on plant species, root structure and water table depth.

Hydrological conditions regulate each pathway. High water tables promote anoxic conditions and CH_4 production while limiting oxygen penetration into soils and reducing CH_4 oxidation. In this conditions, plant-mediated transport and ebullition dominates emissions. Lower water tables extend aerobic zones and favour diffusive transport with greater CH_4 oxidation losses (Christensen et al., 2003; Rinne et al., 2007). Temperature affects all transport pathways indirectly by stimulating microbial CH_4 production and influencing gas solubility and bubble formation dynamics.

Methanogenesis is carried out by anaerobic archaea under oxygen-limited conditions, mainly in water-saturated soils where alternative electron acceptors such as nitrate, sulphate, and ferric iron have been depleted. CH_4 is produced through two metabolic pathways: acetoclastic methanogenesis, in which acetate is converted to CH_4 and CO_2, and hydrogenotrophic methanogenesis, where CO_2 is reduced using H_2 (Segers, 1998; Le Mer & Roger, 2001).

A part of the CH_4 produced in wetland soils is consumed through methanotrophy before reaching the atmosphere. Methanotrophic bacteria oxidize CH_4 to CO_2 in aerobic microsites, near the soil surface and within the rhizosphere where oxygen is supplied by plant roots (Whalen, 2005). Aerobic methanotrophs can oxidize between significant amount of the CH_4 generated in wetlands (Le Mer & Roger, 2001; Nazaries et al., 2013). CH_4 oxidation rates are regulated by oxygen availability, temperature, soil moisture, and redox conditions. (Whalen, 2005)

Methanogenesis pathways show a strong control on the stable isotopic composition of emitted CH_4, particularly the ratios of carbon isotopes ($\delta^{13}C$-CH_4) and hydrogen isotopes (δD-CH_4). The two main microbial pathways—acetoclastic and hydrogenotrophic methanogenesis (figure5)—produce CH_4 with different isotopic signatures because of variation in enzymatic fractionation during substrate utilization. These isotopic differences are used to distinguish CH_4 production pathways (Whiticar, 1999; Conrad, 2007).

Acetoclastic methanogenesis is the conversion of acetate into CH_4 and CO_2:

$CH_3COOH \rightarrow CH_4 + CO_2$

In this pathway, the methyl group of acetate is directly converted into CH_4, producing CH_4 that is isotopically less depleted in ^{13}C, with $\delta^{13}C$-CH_4 ranging between −50‰ and −65‰ (Whiticar, 1999). Acetoclastic methanogenesis typically dominates in nutrient-rich freshwater wetlands and environments with high acetate availability (Conrad, 2007).

Hydrogenotrophic methanogenesis, by contrast, reduces CO_2 using hydrogen as an electron donor:

$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O$

This pathway produces CH_4 that is more depleted in ^{13}C because methanogens preferably use the lighter isotope during CO_2 reduction. Typical $\delta^{13}C$-CH_4 values from hydrogenotrophic methanogenesis range from −60‰ to −110‰ (Whiticar, 1999; Hornibrook et al., 1997). Hydrogenotrophic methanogenesis commonly dominates in acidic peatlands, northern bogs, and nutrient-poor wetlands where acetate concentrations are limited and fermentation products are rapidly consumed (Chasar et al., 2000).

CH_4 could be produced by methanogenic archaea during the anaerobic degradation of organic matter and is characterized by distinct isotopic signatures, typically showing strong depletion in ^{13}C and D relative to thermogenic CH_4 (Milkov and Etiope, 2018)

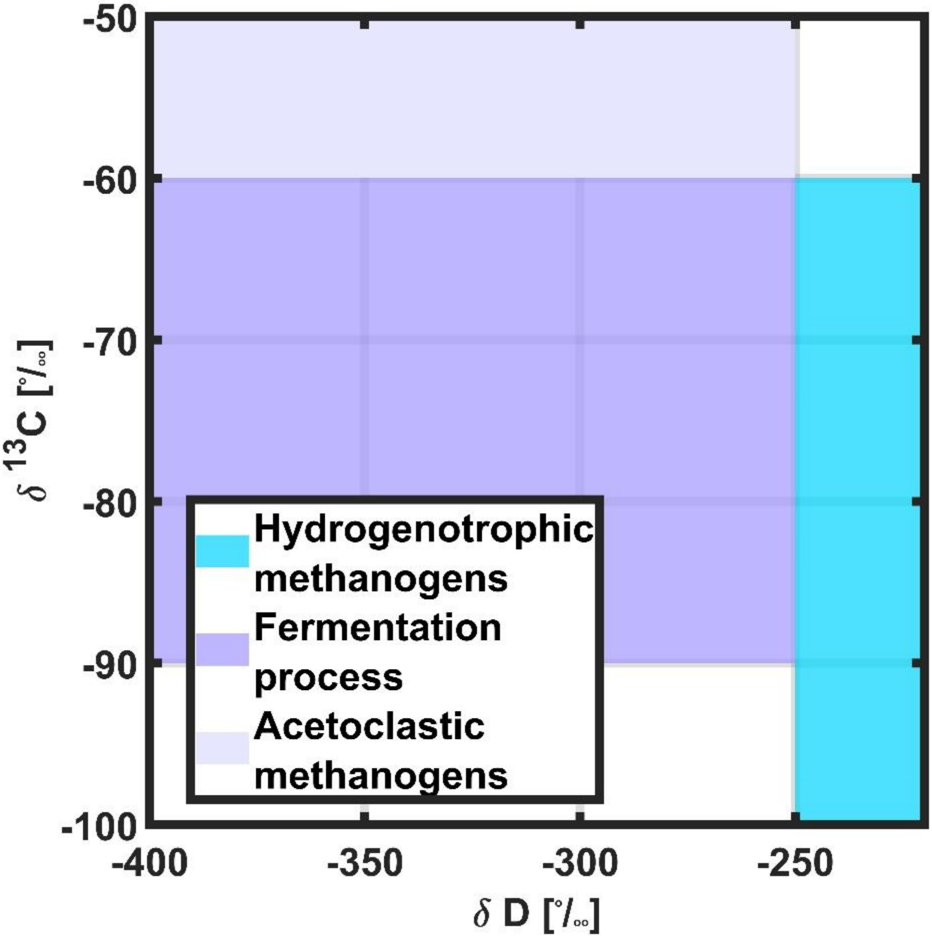

Figure5. Microbial CH4 production $\delta^{13}C$ and δD signatures. Adapted from Whiticar (1999), Chanton et al. (2005), and Milkov & Etiope (2018).

Environmental factors such as substrate quality, temperature, pH, and vegetation composition can shift the relative importance of these pathways and change the isotopic composition of emitted CH_4. Colder temperatures and low-pH conditions prefer hydrogenotrophic methanogenesis, leading to more ^{13}C-depleted CH_4 emissions from northern peatlands (Hornibrook et al., 1997).

Methanotrophy further modifies CH_4 isotopic signatures because methanotrophic bacteria prefer to oxidize lighter CH_4. As CH_4 oxidation proceeds, the remaining CH_4 becomes progressively enriched in ^{13}C and deuterium, increasing $\delta^{13}C$-CH_4 and δD-CH_4 values in emitted fluxes (Bastviken et al., 2002). Isotopic measurements of CH_4 emitted from wetlands reflect not only production pathways but also oxidation during transport through soils and the rhizosphere.

Nordic peatlands play a major role in regional and global carbon cycling because they exchange CO_2 with the atmosphere through photosynthesis and ecosystem respiration. In boreal and subarctic peatlands, carbon is accumulated in long-term, because plant CO_2 uptake is higher than respiratory carbon losses under waterlogged and oxygen-limited conditions (Lund et al., 2009; Aurela et al., 2007). The annual CO_2 sink strength of Nordic peatlands is small and highly sensitive to variations in temperature, hydrology, vegetation composition, and snow cover duration.

Temperature regulates CO_2 exchange in northern peatlands by affecting both photosynthesis and respiration. Warmer growing season can enhance plant productivity and increase CO_2 uptake. It stimulates microbial activity and decomposition rates. In many Nordic peatlands, respiration responds strongly to warming than photosynthesis, particularly when connected with decreasing soil moisture, potentially weakening the long-term peatland carbon sink (Lund et al., 2009; Korrensalo et al., 2020).

Vegetation form strongly influences CO_2 fluxes across peatland microforms. Hummocks, lawns, and hollows support different plant communities with distinct carbon dynamics. Hummocks are typically dominated by dwarf shrubs and *Sphagnum* species adapted to drier conditions, results in higher respiration rates. Wetter lawns and hollows are dominated by sedges and moisture-tolerant mosses that promote greater net CO_2 uptake and reduced peat decomposition (Krohn et al., 2017; Korrensalo et al., 2020). These differences in vegetation structure and hydrology make peatland microtopography an important control on ecosystem carbon balance.

Light availability is a driver of CO_2 exchange in peatlands. It regulates photosynthesis and GPP. During the growing season, increased photosynthetically active radiation enhances CO_2 uptake by peatland vegetation. In boreal bogs and fens, the response of CO_2 fluxes to light is strongly influenced by hydrology, vegetation composition, and temperature. Long-term changes in water-table depth also modify plant communities and has impact on peatland sensitivity to incoming radiation (Kokkonen et al., 2022). Northern European peatlands show that light and water conditions are crucial to determine NEE. Wetter peatlands often functioning as stronger CO_2 sinks under favourable light conditions (Metzger et al., 2015). These findings suggest that future changes in cloud cover, warming, and drainage may change the light-driven carbon balance of Nordic peatlands.

Permafrost thaw increases peat decomposition and has impact on the local hydrology, potentially mobilizing large stores of previously frozen organic carbon.

Some northern peatlands currently remain net CO_2 sinks during the growing season, increasing winter respiration and thaw-induced decomposition may offset summer carbon uptake in the future (Virkkala et al., 2018). Recent studies indicate that northern peatland carbon balances are becoming increasingly variable under ongoing climate change, with considerable uncertainty surrounding whether these ecosystems will continue to function as long-term carbon sinks (Loisel et al., 2022)

Understanding CH_4 dynamics in wetlands is essential for predicting future climate feedback. Given the large uncertainties associated with natural CH_4 and CO_2 sources and their sensitivity to environmental drivers, continued research is needed to improve process understanding, refine global CH_4 and CO_2 budgets, and assess ecosystem responses under future climate scenarios.

One of the most common methods to quantify CH_4 and CO_2 fluxes is EC. This is microecological method suitable for long-term measurements. However, continuous EC flux datasets contain gaps due to instrument failure, power interruptions, low turbulence conditions, sensor icing, and quality filtering, particularly during nighttime and winter periods (Falge et al., 2001; Aubinet et al., 2012). In EC studies of wetland GHG exchange, gap-filling is more than a technical procedure. It is a critical methodological step that directly influences annual CO_2 and CH_4 budgets, and uncertainty quantification. Cumulative CO_2 and CH_4 balances are highly sensitive to missing data treatment, the selection of gap-filling method is crucial. A gap-filling in wetland is challenging because GHG fluxes show strong temporal variability driven by hydrology, temperature sensitivity, and episodic CH_4 release events such as ebullition. Simple interpolation methods may fail to reproduce nonlinear ecosystem responses and extreme flux events, leading to systematic under- or overestimation of annual balances (Moffat et al., 2007). EC studies treat gap-filling uncertainty as an integral component of total flux uncertainty rather than a preprocessing step.

Several statistical and process-based methods have been developed to address these uncertainties. Common approaches include mean diurnal variation (MDV), look-up tables, nonlinear regression models, artificial neural networks, and marginal distribution sampling (MDS) (Reichstein et al., 2005). These methods attempt to reconstruct missing fluxes based on relationships with environmental drivers such as temperature, radiation, vapor pressure deficit, and water table depth. Studies have shown that different gap-filling techniques can produce substantially different annual carbon budgets, particularly when datasets contain long gaps or highly variable CH_4 fluxes (Moffat et al., 2007; Knox et al., 2016).

Aim

The aims of this thesis are to improve our understanding of how permafrost thaw influences GHG fluxes across peatland ecosystems and to evaluate the environmental factors that control these fluxes on temporal and spatial scales. This thesis focuses on the responses of CO_2 and CH_4 fluxes to ecosystem changes connected with permafrost degradation and global warming. The role of simplifying isotopic approaches and gap-filling methods in reducing uncertainties in GHG budgets were investigated. This thesis specifically uses spatial variability to improve understanding of carbon cycling. Moreover, it shows how methodological choices influence our interpretation of carbon cycling in peatland ecosystems. This thesis aims to answer the following research questions:

- What are the spatial and temporal dynamics of GHG fluxes in peatlands?
- What are the main controlling factors regulating GHG fluxes in heterogeneous ecosystems such as peatlands?
- Is gap-filling a technical procedure, or is it a critical step for understanding and quantifying uncertainty in GHG flux estimates?
- Can peatland processes and carbon dynamics be adequately represented by a single isotopic signature?

Methods

Study Sites

This thesis was mostly focused on two contrasting wetland ecosystems in Sweden, Abisko-Stordalen and Mycklemossen representing both sub-Arctic permafrost peatlands and temperate peatland environments. Together, these sites provide the opportunity to investigate GHG dynamics across strong climatic, hydrological, and ecological gradients. Results of this investigation improve understanding of how environmental conditions and permafrost degradation influence carbon cycling in northern wetlands. In addition to the main study sites, other sub-Arctic wetlands were included in the isotopic studies of CH_4 allowing the analysis of spatial variability in stable isotope signatures across different peatland systems. Those wetlands: Storflaket, Kursflaket, and Katterjåkk, are part of Circumpolar Active Layer Monitoring (CALM) program (Brown et al., 2000). Additional northern wetlands represent different hydrological, vegetation and permafrost conditions. The combined dataset represents both subarctic permafrost and non-permafrost peatlands and hemiboreal wetlands with contrasting vegetation communities and water-table conditions.

Abisko–Stordalen Mire

The main study site was the Abisko–Stordalen mire complex (figure6), located in northern Sweden (68°20′ N, 19°03′ E), approximately 10 km East of Abisko near Lake Torneträsk. The site is situated within the discontinuous permafrost zone and represents one of the most extensively studied sub-Arctic peatland systems in the Arctic region. Stordalen mire is characterized by a heterogeneous landscape composed of elevated palsa plateaus, partially thawed bogs, and fully thawed fens, representing different stages of permafrost degradation and hydrological development. This mosaic structure makes the site particularly suitable for studying the effects of permafrost thaw on GHG and ecosystem carbon dynamics.

Figure6. EC tower at the Abisko-Stordalen Site. On the left side of the tower is eleveted palsa and on the right side is the thawing area.

The region experiences a sub-Arctic climate with relatively low annual precipitation and large seasonal temperature variability. Historical mean annual air temperatures below 0 °C (−0.5 °C for 1912–2006), but temperatures have increased above 0 °C since the early 2000s, reaching 0.6 °C in 2006 (Callaghan et al., 2010). In recent decades, annual mean temperatures have exceeded the freezing threshold, contributing to permafrost degradation within the mire system. Mean annual precipitation is relatively low, ranging from approximately 300 to 340 mm, with a significant fraction falling as snow during winter.

The vegetation composition relates to local hydrological and permafrost conditions. Dry palsa plateaus are dominated by dwarf shrubs, lichens, and mosses, whereas wetter thawing areas are covered by Sphagnum mosses, sedges, and Ericaceous vegetation. Fully thawed fen systems are characterized by high water tables and dense graminoid vegetation, particularly sedge species such as Eriophorum and Carex, which helps CH_4 transport from deeper peat layers to the atmosphere. These vegetation differences contribute to the spatial variability in CH_4 and CO_2 fluxes observed across the mire.

An important characteristic of the Stordalen site is its topographic, where a mountain valley channels regional airflow. A single EC tower was used to investigate GHG exchange from two contrasting ecosystem sectors at the Stordalen Mire (Figure7). The study site is characterized by a bimodal wind regime caused by the surrounding Lake Torneträsk valley. The EC system can sample different surface types depending on wind direction. Westerly winds produced a footprint dominated by the permafrost palsa plateau, while easterly winds relate to thawing sector with smaller palsa patches. Fluxes come from these two sectors were separated using wind-sector filtering. It allows to analyse two ecosystems exposed to the same meteorological conditions. This approach give opportunity to exam the influence of permafrost thaw and hydrological conditions on GHG exchange.

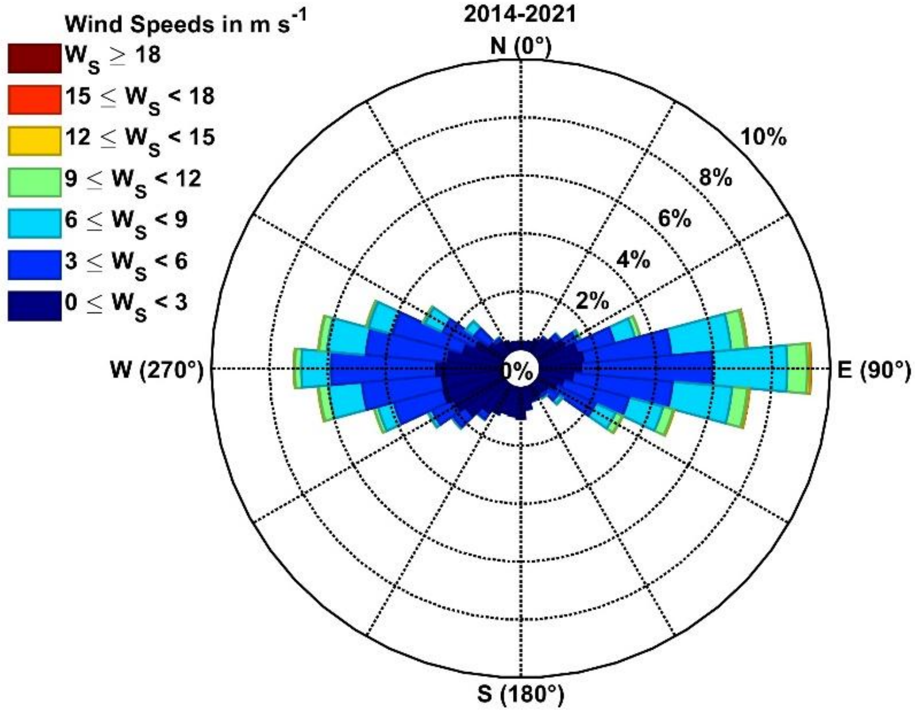

Figure7. Wind rose shows the bimodal wind regime for the Stordalen Mire for years 2014-2021

Due to ongoing permafrost thaw and hydrological changes, Abisko–Stordalen has become a key location for studying climate feedback mechanisms in northern ecosystems. The site is also part of several long-term international monitoring networks, including ICOS Sweden, enabling continuous observations of CO_2 and

CH_4 fluxes at ecosystem scale. These long-term datasets provide valuable opportunities to examine interannual variability, extreme climate events, and long-term trends in GHG.

Mycklemossen Mire

In addition to the sub-Arctic study site, field measurements were conducted at Mycklemossen mire (Figure8), a temperate poor fen located in south-western Sweden (58°21′ N, 12°10′ E). Compared with Stordalen, Mycklemossen represents a warmer and wetter peatland environment and therefore provides an important climatic contrast within this thesis.

Figure8. Mycklemossen Mire measurement site within the Skogaryd Research Catchment, southwestern Sweden. Mycklemossen is part of the SITES infrastructure and an ICOS Ecosystem Station (SE-Myc), where continuous GHG fluxes are measured using an EC tower. The site is also equipped with automatic chamber systems.

The site experiences a temperate climate with a mean annual air temperature of approximately 6.7 °C (1990–2019) and mean annual precipitation of around 1000 mm, according to long-term records from Vänersborg from the Swedish Meteorological and Hydrological Institute (SMHI). The relatively mild climate results in a substantially longer growing season compared with sub-Arctic peatlands, influencing vegetation productivity, peat decomposition, and GHG dynamics. Mycklemossen is a nutrient-poor fen dominated by peat-forming mosses and graminoid vegetation. The site is characterized by high-water tables and organic-rich peat soils, conditions that favour CH_4 production under anaerobic conditions (White et al., 2023).

Measurements conducted at Mycklemossen primarily focused on CH_4 flux variability and isotopic analyses. The site provided opportunities to investigate temporal variations in CH_4 emissions and stable isotope signatures under contrasting environmental conditions.

CALM sites

Storflaket, Kursflaket, and Katterjåkk are three peatland sites in northern Sweden that are part of the Circumpolar Active Layer Monitoring (CALM) program (Brown et al., 2000). Storflaket and Kursflaket are in the Abisko valley and have environmental conditions like those at Abisko–Stordalen. In contrast, Katterjåkk is outside the valley and its rain-shadow effect, resulting in a more maritime climate. Climatic conditions are different among the sites, influencing their permafrost dynamics. Mean winter (December–February) air temperatures are −10.0 °C at Katterjåkk (515 m a.s.l.; SMHI), −9.7 °C at the Abisko Scientific Research Station (ANS; ~385 m a.s.l.), which represents Kursflaket (ANS, 2020), and −11.1 °C at Storflaket. Annual precipitation (2010–2019) ranges from 848 mm at Katterjåkk to 358 mm at ANS (SMHI). Consequently, Katterjåkk has a deeper winter snowpack (approximately 80 cm; SMHI) than the more continental Storflaket and Kursflaket mires (approximately 10 cm at Storflaket; Johansson et al., 2013). Permafrost at Katterjåkk had completely thawed by 2010, where permafrost persists at Permafrost persists at Storflaket and Kursflaket, but the active layer has progressively thickened over recent decades, with reported rates of approximately 0.7–1.0 cm yr^{-1} at Storflaket and Kursflaket, respectively (Johansson et al., 2013).

Chamber measurements

CH_4 fluxes were measured using automatic chamber systems (Figure8, Figure9), which give opportunity to do high-frequency and long-term observations of GHG exchange in heterogeneous peatland ecosystems. Chamber-based approaches are widely used in wetland studies because they allow measurements at spatial scales that capture the strong small-scale variability associated with vegetation composition, hydrology, and microtopography (Bubier et al., 2003; McCalley et al., 2014). In peatlands, where CH_4 emissions can vary substantially over distances of only a few meters, chamber measurements provide an important tool for investigation spatial heterogeneity that cannot be captured by ecosystem-scale methods alone

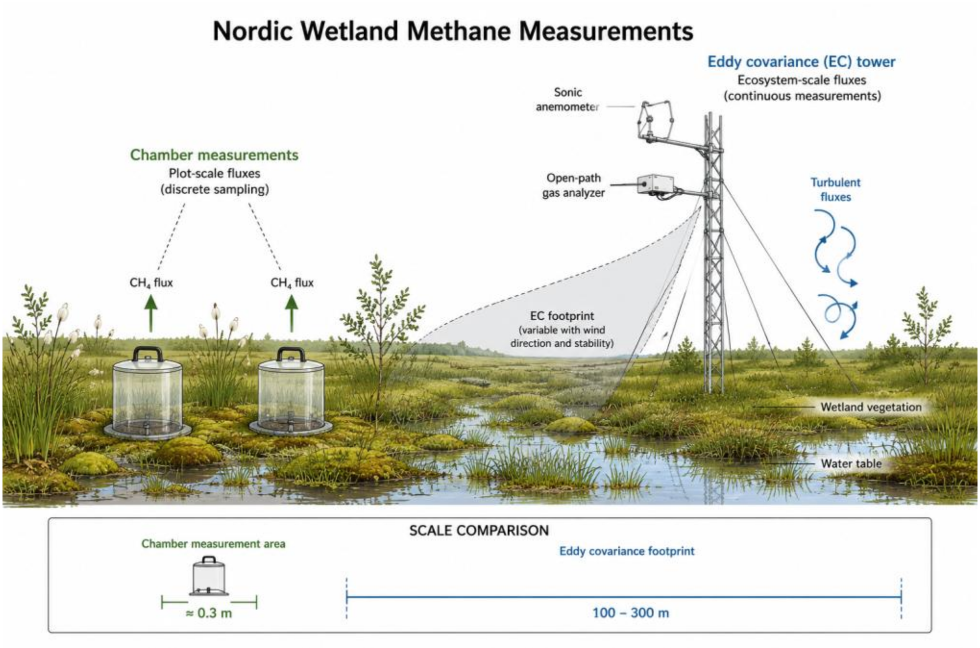

Figure9. Chamber systems and EC instrumentation used for GHG measurements at the peatland study sites. The approximate measurement scales of each method are included to illustrate the spatial extent of the observations. AI generated

The chamber systems used in this study contain permanently installed chambers connected to gas analysers through an automated switching system. Chambers were sequentially closed and sampled according to predefined measurement intervals, 25 minutes of sampling with closed lid and 5 minutes for the ventilation. Automatic chamber systems are easier to use in remote environments because they reduce the need for frequent manual sampling while providing measurements with high temporal resolution.

Second type, manual chambers were used for discrete flux measurements and isotopic sampling, allowing collection of gas samples for laboratory analyses.

During chamber closure, changes in gas concentrations within the chamber headspace were monitored continuously and used to calculate surface-atmosphere fluxes. Fluxes were derived from concentration changes over time using regression approaches. Both linear and non-linear fitting approaches are commonly applied in chamber studies, and methodological choices associated with flux calculation procedures can influence estimated CH_4 fluxes (Pirk et al., 2016; Korkiakoski et al., 2017).

Fluxes measured using closed chambers were calculated from the rate of change in gas concentration within the chamber headspace according to:

$$F=\frac{dC}{dt}\times\frac{VP}{ART}$$

where Fis the gas flux, $\frac{dC}{dt}$ is the rate of concentration change during chamber closure, V is the chamber volume, A is the enclosed surface area, P is atmospheric pressure, R is the universal gas constant, and T is air temperature in Kelvin.

Careful quality control procedures were applied throughout the study to minimize uncertainties associated with concentration fitting and chamber performance. Chamber measurements were combined with isotopic analyses and ecosystem-scale observations to improve the understanding of CH_4 dynamics across both spatial and temporal scales.

Despite these advantages, chamber-based approaches also have several important limitations that must be considered when interpreting flux measurements. Long-term deployment of fixed chambers can make changes in environmental conditions inside the measurement area. Chamber collars and infrastructure may influence snow accumulation, peat thermal properties, hydrology, and vegetation composition over time. Such disturbances can modify microbial activity and plant-mediated gas transport pathways, potentially introducing biases into measured fluxes. Chamber closure itself may additionally affect turbulence, pressure conditions, temperature, and light availability inside the chamber and influencing gas exchange processes during measurements.

Another important limitation concerns the spatial representativeness of chamber observations. Chamber measurements represent relatively small surface areas and therefore may not fully capture ecosystem-scale variability in highly heterogeneous peatlands. This issue is particularly relevant in northern wetlands where CH_4 emissions are often patchily distributed due to differences in microtopography and hydrological conditions. Consequently, a sufficiently large number of chambers and careful selection of chamber placement are required to adequately represent the spatial variability of GHG exchange.

Isotopic sampling and analysis

To complement chamber-based CH_4 flux measurements, isotopic analyses of CH_4 were conducted to improve the understanding of CH_4 production pathways, oxidation processes, and temporal variability in peatland carbon cycling.

Gas sampling was performed during chamber enclosure periods when CH_4 concentrations within the chamber headspace increased sufficiently for isotopic analysis. Samples were collected manually using 2 L inert foil gas sampling bags (Supel™ Inert Foil Gas Sampling Bags, Sigma-Aldrich, USA), which are designed to minimize gas permeability and isotopic fractionation during storage and transport. New bags were used to reduce contamination and memory effects.

Collected gas samples were transported to Utrecht University and Royal Holloway, University of London, where isotopic analyses were conducted using isotope ratio mass spectrometry (IRMS). Measurements of stable carbon isotope composition ($\delta^{13}C$-CH_4) followed established analytical methodologies described by Fisher et al. 2006 and Röckmann et al. 2016. IRMS is the standard analytical technique for high-precision CH_4 isotope measurements because of its excellent reproducibility and analytical sensitivity.

The isotopic composition of emitted CH_4 was determined using the Keeling plot approach (Keeling, 1958), which is commonly applied in atmospheric and ecosystem studies to estimate isotopic source signatures. In this method, measured isotopic values are plotted against the inverse of CH_4 concentration, and the isotopic composition of the CH_4 source is derived from the intercept of the linear regression.

The isotopic source signature was estimated using the Keeling plot relationship:

$$\delta^{13}C(x)=a+\frac{b}{x}$$

Here $\delta^{13}C(x)$ is the observed $\delta^{13}C$ value of CH_4 during sampling at the CH_4 mixing ratio of x and a and b are coefficients from linear fitting. The a is the intercept, which can be interpreted as the source isotopic signature

The Keeling plot approach assumes that observed CH_4 concentrations represent mixing between background atmospheric CH_4 and a locally emitted source. When inverse CH_4 concentration is equal to 0, our intercept, it gives the isotopic value only from the source. This is the most common method to separate background and source isotopic value.

Linear regression fitting and associated confidence intervals were calculated using the linfitxy function in MATLAB (Browaeys, 2021), which accounts for uncertainties in both CH_4 concentration and isotopic measurements. Incorporating uncertainties in both variables is important because errors associated with concentration measurements and isotopic analyses can significantly influence the calculated intercept values and the estimated isotopic source signatures.

To improve temporal resolution and continuous observations of isotopic variability, automated chamber systems were connected to a cavity ring-down spectroscopy (CRDS) analyser (Picarro G2201-i, Picarro Inc., USA). The CRDS system give opportunity of in situ measurements of CH_4 concentration and $\delta^{13}C\text{-}CH_4$ at high temporal frequency without the need for extensive laboratory processing. This approach allowed the investigation of short-term variability in CH_4 isotope signatures associated with diurnal cycles, environmental fluctuations, and episodic CH_4 emission events.

Compared with IRMS, CRDS measurements provide lower analytical precision and are more sensitive to instrumental drift and concentration dependencies. Nevertheless, CRDS systems offer advantages for field-based studies because they allow continuous, measurements under natural environmental conditions. Additionally, field deployment is also easier as it doesn’t require any cryogenic traps like IRMS. Previous studies have demonstrated that CRDS instruments can measure temporal variability in CH_4 isotopic composition with sufficient accuracy for ecosystem-scale applications, particularly when combined with data quality control.

Eddy covariance measurements

Ecosystem-scale GHG exchange was measured using the EC technique, a micrometeorological method that allow for continuous, non-invasive measurements of net gas fluxes between terrestrial ecosystems and the atmosphere (Figure6, Figure9). The EC method is widely used for quantifying ecosystem-scale exchanges of CO_2, CH_4, water vapour, and energy because it allows direct measurements under natural environmental conditions with minimal disturbance to the ecosystem surface (Aubinet et al., 2012; Baldocchi, 2003).

The EC technique is based on the covariance between high-frequency measurements of vertical wind velocity and scalar concentrations, such as CO_2 or CH_4. Turbulent eddies transport gases vertically within the atmospheric boundary layer, and by measuring fluctuations in wind speed and gas concentration at frequencies typically at 10 Hz, net ecosystem-atmosphere fluxes can be quantified continuously over time. Compared with chamber-based methods, EC measurements integrate gas exchange over larger areas and provide more representative estimates of ecosystem-scale GHG budgets.

The turbulent flux of a gas is calculated as:

$F = \overline{w'c'}$

where F is the turbulent flux, w′ is the instantaneous deviation of vertical wind velocity from its mean, and c′ is the deviation in gas concentration. The overbar means averaging over a predefined period, typically 30 minutes. Positive fluxes represent emissions to the atmosphere, and negative values indicate net ecosystem uptake

Flux footprint analysis was used to determine the source area contributing to each half-hour flux measurement. The footprint describes the upwind area that contributes to the measured turbulent flux and varies according to atmospheric stability, wind speed, measurement height, and surface roughness.

One of the major advantages of the EC method is that measurements are performed continuously without physically disturbing the ecosystem surface. Long-term EC observations are particularly valuable for quantifying seasonal dynamics, interannual variability, and ecosystem responses to extreme climatic events. Continuous measurements are important for assessing the impacts of climate change and peatland carbon cycling.

The EC method also has several important limitations and methodological challenges. Reliable EC measurements require relatively flat and homogeneous terrain with steady and undisturbed airflow. In heterogeneous ecosystems such as peatlands, assumptions of horizontal homogeneity are not always met due to spatial variability in vegetation composition, hydrological conditions, and microtopography. EC measurements integrate fluxes across multiple surface types, and direct separation of fluxes from individual microtopographic units is not possible. This limitation can be avoided by flux partitioning based on wind direction. It can be applied to distinguish flux contributions originating from different sectors within the measurement footprint. This approach improves the information about ecosystems, because they are exposed for the same environmental conditions. However, this solution increases analytical complexity and results in additional data gaps due to sector filtering.

EC measurements additionally require extensive data processing and quality control procedures. High-frequency measurements must go under corrections before fluxes can be calculated. Standard processing steps include coordinate rotation, frequency response correction, time lag compensation, and density corrections accounting for fluctuations in temperature and water vapour (Webb et al., 1980; Aubinet et al., 2012). Quality filtering is applied to remove periods with insufficient turbulence, instrument malfunction, precipitation interference, or non-stationary atmospheric conditions. This filtering produces gaps in the dataset. However, annual GHG balances require continuous time series. These missing periods must be reconstructed using gap-filling approaches. Gap-filling represents an important step in EC studies and influence annual budget estimates and uncertainty assessments.

Several gap-filling methods have been developed for EC applications, each with specific advantages and limitations (Reichstein et al., 2005; Wutzler et al., 2018; Kim et al., 2020; Irvin et al., 2021; Vekuri et al., 2023). Traditional approaches include look-up table methods and marginal distribution sampling, where missing fluxes are estimated using relationships between observed fluxes and environmental drivers such as radiation, temperature, and vapour pressure deficit (Reichstein et al., 2005). More recently, machine learning approaches such as artificial neural networks have increasingly been applied because they can capture non-linear relationships between fluxes and environmental variables. Generalized linear models and empirical regression approaches are also commonly used for GHG flux reconstruction in peatland studies.

Gap-filling methods are necessary for generating complete annual dataset. However, they also introduce additional uncertainty into flux estimates. The performance of a gap-filling model strongly depends on the availability and quality of auxiliary environmental variables and on how well the selected predictors represent the ecosystem processes. Missing or poorly represented environmental drivers may increase uncertainty and introduce systematic biases into annual GHG budgets.

Results and discussion

Part I: Spatial variability and environmental drivers of CO_2 and CH_4 Fluxes (Paper I and Paper II)

The combined analysis of CH_4 and CO_2 fluxes across the palsa plateau, thawing bog, and fen demonstrates that these GHGs respond differently to permafrost degradation. Because these GHG are produced through different biological and physical processes. CO_2 is result of plant activity on the surface, while CH_4 relates to microbial activity inside soil.

The CO_2 measurements show that all investigated ecosystems functioned as net carbon sinks during most years, except for the thawing sector in 2014, which was a weak carbon source (Figure10). The strongest CO_2 uptake was observed in the fen, where maximum daytime NEE was approximately –7.6 µmol CO_2 m^{-2} s^{-1}, compared with –1.6 and –2.0 µmol CO_2 m^{-2} s^{-1} for the palsa plateau and thawing sector. Annual net CO_2 uptake in the fen, approximately –167 g C m^{-2} yr^{-1} was significantly higher than that of the palsa and thawing sector, approximately –31 g C m^{-2} yr^{-1}. No statistically significant differences in annual NEE, GPP or ecosystem respiration were detected between the palsa plateau and the partially thawed bog over the multi-year period, despite major differences in soil moisture, vegetation composition and thaw status. These findings suggest that moderate permafrost degradation alone does not necessarily change ecosystem-scale CO_2 exchange when vegetation productivity and respiration remain closely balanced.

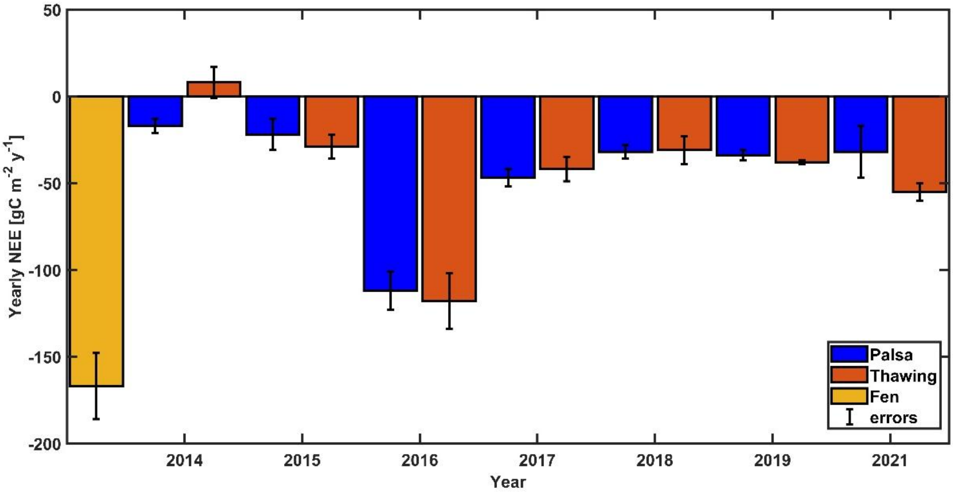

Figure10. Average annual NEE with the standard deviation for three different ecosystem, palsa, thawing sector and fen at the Abisko-Stordalen Mire. Presented values are mean value among three different gap-filling method, ANN, GLM and Jena-algorithm.

The CH_4 measurements show differences in CH_4 emissions between ecosystems with contrasting permafrost conditions. CH_4 emissions from the thawing sector were higher than those from the palsa plateau, with estimated annual emissions of approximately 8.2 and 2.7 g C m^{-2} yr^{-1}, respectively (Figure11). This indicate that permafrost degradation enhanced ecosystem-scale CH_4 release. Peak growing-season fluxes from the thawing surface reached around 40 mg C m^{-2} d^{-1}, more than twice those observed over the palsa plateau, approximately 19 mg C m^{-2} d^{-1}. The higher emissions from thawing areas related to warmer, wetter soil conditions that promoted methanogenesis, while GPP showed no significant relationship with CH_4 fluxes. In contrast to the no significant differences observed in CO_2 exchange between the palsa plateau and the thawing sector, CH_4 emissions responded strongly to permafrost thaw. It demonstrates that changes in hydrological conditions and active-layer development can increase CH_4 flux even when ecosystem CO_2 exchange remains unchanged. Winter emissions also represented a significant percentage of the annual CH_4 budget, contributing approximately 27–45 % of total annual CH_4 emissions. This agrees with recent Arctic syntheses demonstrating that cold-season emissions can contribute 15–50% of annual CH_4 emissions, with some high-latitude peatlands releasing more than half of their annual CH_4 budget outside the growing season (Pirk et al., 2017; Treat et al., 2018; Natali et al., 2019).

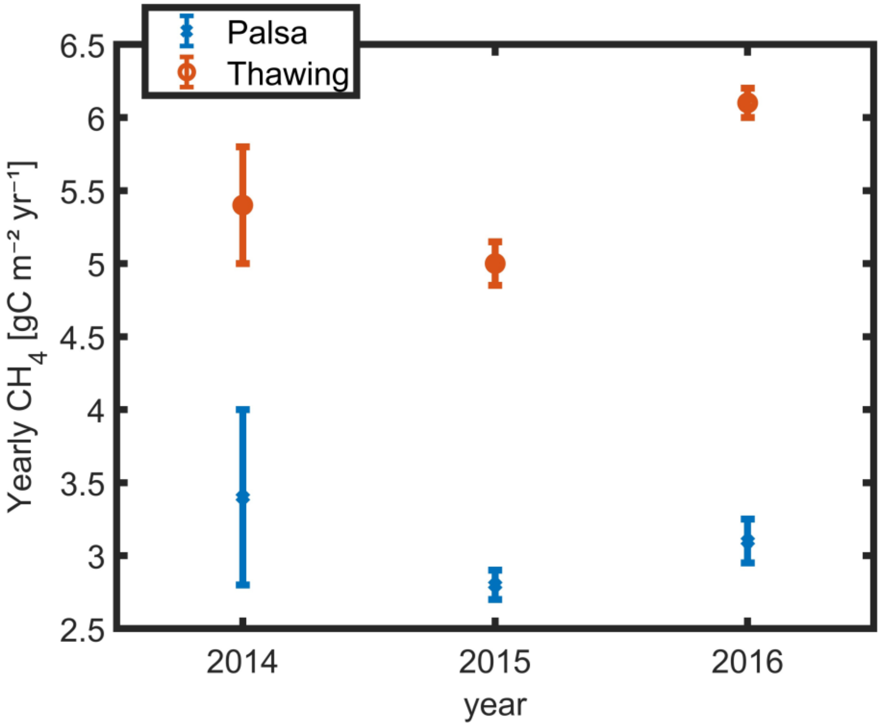

Figure11. Yearly CH_4 emission for Palsa and Thawing sector. Presented values are mean value among three different gap-filling method, ANN, GLM and Jena-algorithm.

Similar spatial patterns have been observed through the discontinuous permafrost zone in northern Sweden, Alaska and Canada (Turetsky et al., 2020; Loisel et al., 2021; McNicol et al., 2023, Delwiche et al., 2025). A permafrost thaw increases soil moisture and creates deeper layer of anaerobic conditions for methanogenesis and reducing CH_4 oxidation zone (Perryman et al., 2020; Loisel et al., 2021; Perryman et al., 2022; McNicol et al., 2023). The transition from palsa to fen vegetation promotes the expansion of sedges which efficiently transport CH_4 directly from saturated soils to the atmosphere, bypassing aerobic oxidation zones (Johansson et al., 2006; Ge et al., 2025), so relatively small changes in hydrological conditions may produce large increases in CH_4 emissions compared with changes in CO_2 exchange.

Part II: Influence of Growing Season Length on Carbon Fluxes (Paper I and Paper II)

The multi-year observations demonstrate that growing season length was an important control of CO_2 exchange across the Stordalen Mire ecosystems. Variations in the timing of snowmelt and the duration of the snow-free period strongly influenced ecosystem productivity, resulting in interannual differences in NEE, GPP and Reco. It was observed in 2016, when an exceptionally early snowmelt prolonged the growing season and produced the highest annual CO_2 uptake in both the palsa plateau and the thawing bog. Enhanced light-saturated NEE, increased GPP, and higher NDVI during this year show that the extended growing season stimulated vegetation development (Figure12).

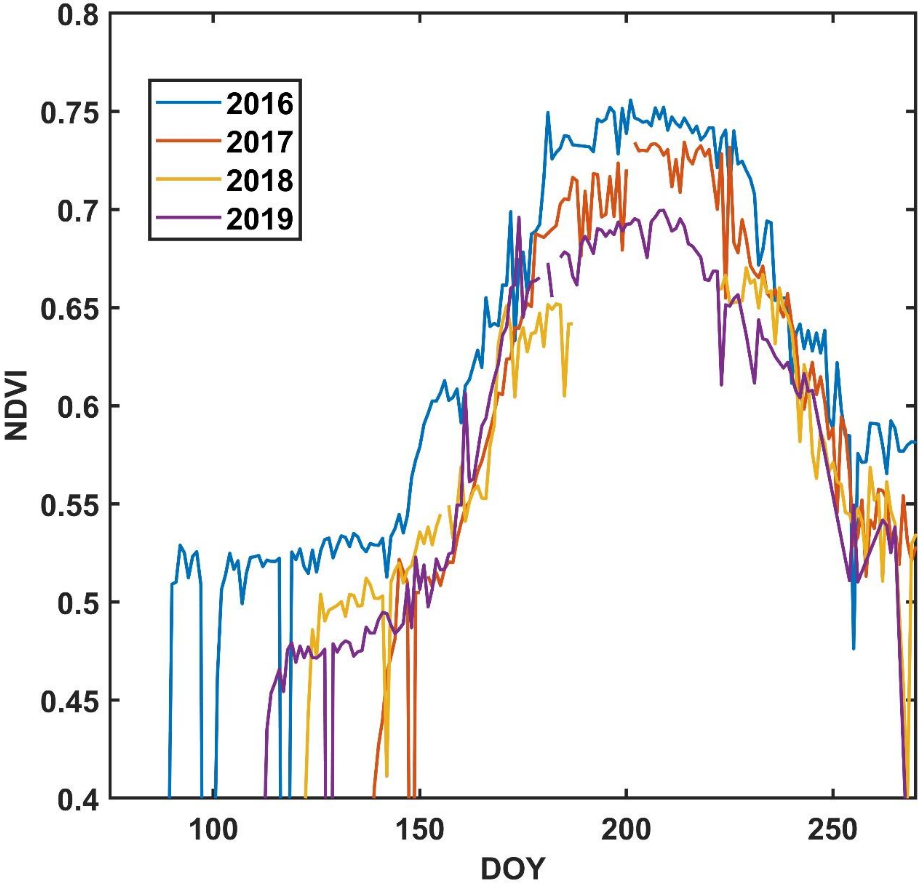

Figure12. NDVI measured for the years 2016-2019 at the Abisko-Stordalen site. It shows the difference in the growing season lenght.

Data shows that growing season length did not change the relative differences between the palsa plateau and the thawing sector. Average annual GPP 195 ± 36 and 192 ± 30 g C m^{-2} yr^{-1}, for palsa and thawing sector respectively. Reco 146 ± 33 and 146 ± 35 g C m^{-2} yr^{-1}, for palsa and thawing sector respectively was similar between the two ecosystems. No changes in the relative differences are consistent with the widely recognised coupling between photosynthesis and respiration in northern peatlands, where enhanced plant growth increases autotrophic and heterotrophic respiration (Lasslop et al., 2010; El-Madany et al., 2020). Similar responses have been observed in Zackenberg, Siikaneva and other Arctic wetlands, where longer growing seasons increased both carbon uptake and respiration, resulting in changes in annual NEE (Rinne et al., 2018; López-Blanco et al., 2020; Lundin et al., 2016).

The higher carbon uptake observed during the longer growing season of 2016 was driven by vegetation dynamics rather than by meteorological forcing alone. The increased NDVI reported for that year suggests greater photosynthetic biomass. Arctic greening enhances seasonal GPP through increased leaf area, vascular plant abundance and canopy development (Callaghan et al., 2010). Earlier snow melt extends the period available for photosynthesis and promotes rapid development of sedges and dwarf shrubs, particularly in permafrost peatlands where low temperatures normally limited plant growth (Aurela et al., 2004; Malmer et al., 2005). Zona et al. 2022 demonstrated that earlier snowmelt enhanced GPP and net CO_2 uptake during June and July but reduced carbon sequestration later in August, suggesting that the benefits of a longer growing season may be lower as the season progresses because of phenological limitations rather than water stress.

A longer snow-free period enhances CO_2 and CH_4 fluxes. Recent syntheses of northern peatlands consistently show that permafrost thaw and increases in soil saturation are one of the strongest drivers of elevated CH_4 emissions. Fully thawed fens show higher fluxes than thawing bogs or palsa plateaus (McNicol et al., 2023; Saunois et al., 2024). Longer growing seasons may further enhance CH_4 fluxes by extending the period during which soils remain biologically active and stimulating microbial CH_4 production (Mander et al. 2025). The expansion and increased productivity of sedges can promote plant-mediated transport of CH_4, allowing CH_4 to bypass aerobic surface layers and reducing opportunities for oxidation before reaching the atmosphere (Pangala et al., 2017). These mechanisms are consistent with observations from the Stordalen Mire, where CH_4 emissions increased along the permafrost thaw gradient with no difference in CO_2 exchange between the palsa plateau and the thawing bog.

The observed sensitivity of carbon fluxes to growing season length agrees with broader evidence that snowmelt timing has become one of the principal controls of Arctic carbon cycling under climate warming (Zona et al., 2022; McNicol et al., 2023). Earlier snow disappearance has accelerated by approximately four to six days per decade across many Arctic regions, contributing to widespread Arctic greening and increasing vegetation productivity (Callaghan et al., 2010; Biskaborn et al., 2019).

Part III: The Importance of Multiple Gap-Filling Approaches (Paper I and Paper II)

In our studies three independent gap-filling approaches were compared —Artificial Neural Networks (ANN), Generalized Linear Models (GLM), and the Jena partitioning algorithm (Jammet et al., 2017, Rinne et al. 2018, D′Acunha et al. 2019)—to evaluate their influence on annual CO_2 flux estimates across the palsa plateau, thawing bog, and fen ecosystems. All three methods produced similar estimates of annual NEE, shows that annual carbon budgets were robust. These findings suggest that interannual variability in ecosystem carbon exchange was primarily controlled by environmental conditions rather than methodological uncertainty. Three methods were tested due to longer gaps caused by data portioned

Artificial Neural Networks reproduced short-term variability more effectively because they captured complex nonlinear interactions among radiation, temperature, vapour pressure deficit, and seasonal development (Tramontana et al., 2020). In contrast, the GLM and Jena approaches relied on predefined functional relationships that may not fully represent abrupt ecosystem responses during transitional periods such as snowmelt or peak summer productivity. These short-term discrepancies largely compensated over annual timescales, producing nearly identical cumulative carbon balances. Similar findings have been reported by Moffat et al. (2007), who compared fifteen gap-filling techniques using FLUXNET benchmark datasets and demonstrated that differences among algorithms are generally much smaller for annual carbon budgets than for half-hourly flux estimates.

The close agreement observed in the present study increases confidence that the reported differences among years reflect ecosystem responses rather than artefacts introduced during data processing. Similar conclusions have been reached in previous methodological studies demonstrating that annual carbon budgets are robust when multiple independent gap-filling approaches were used (Irvin et al., 2021, Wang et al., 2024).

The annual CO_2 budgets obtained using ANN, GLM and Jena gap filling also supports the interpretation of the exceptional carbon uptake observed during 2016. All three methods identified 2016 as the year with higher net CO_2 uptake (Figure13).

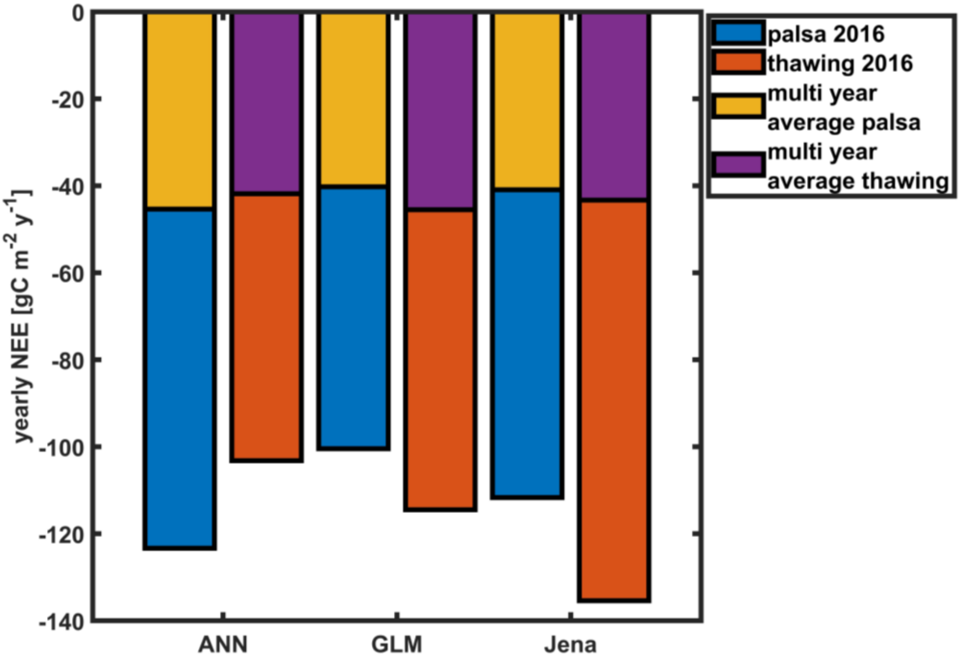

Figure13. Annual NEE estimates for the palsa and thawing sectors obtained using the ANN, GLM, and Jena algorithms. Blue indicates the palsa sector in 2016, orange the thawing sector in 2016, yellow the palsa sector during 2014–2021 (excluding 2016 and 2020), and purple the thawing sector during the same period.

This agreement suggests that the increased carbon sequestration resulted from the early snowmelt and longer growing season rather than methodological artefacts related to individual algorithms. Similar conclusions have been reported for Arctic peatlands where early snow disappearance enhanced annual carbon uptake despite of the partitioning or gap-filling procedure used (Aurela et al., 2004; Lundin et al., 2016; Zona et al., 2022).

Recent FLUXNET-CH_4 analyses have highlighted that CH_4 gap filling is even more challenging than CO_2 because CH_4 has stronger temporal variability, episodic ebullition events and nonlinear responses to hydrological drivers (Irvin et al., 2021). ANN and decision-tree algorithms have become increasingly important for reconstructing continuous CH_4 time series (Irvin et al., 2021).

Recent EC studies recommend combining multiple gap-filling approaches rather than relying on a single algorithm (Lucas-Moffat et al., 2022, Zhu et al., 2022). Large international initiatives such as ICOS and FLUXNET suggest uncertainty quantification based on ensembles of statistical models because methodological uncertainty represents an important component of ecosystem carbon-budget estimates (Heiskanen et al., 2022; Friedlingstein et al., 2023). Similarly, the FLUXNET-CH_4 synthesis demonstrated that comparing several independent machine-learning algorithms significantly improves confidence in annual CH_4 budgets while providing realistic uncertainty estimates for long-term monitoring networks (Irvin et al., 2021).

Individual half-hourly flux estimates differed among algorithms, annual carbon budgets remained highly consistent, confirming that the observed interannual variability relate to ecosystem responses to changing environmental conditions rather than methodological bias. The application of multiple independent gap-filling techniques represents an important quality-control procedure that increases confidence in long-term carbon-budget estimation and improves comparability among EC studies.

Part IV: The Necessity of Long-Term Observations (Paper I, Paper II and Paper IV)

Papers I, II and IV demonstrate that long-term ecosystem observations are essential for understanding GHG dynamics in northern peatlands. Long observational records are required to separate long-term trends from short-term climatic variability (Jackson et al., 2024; Kuhn et al., 2025).

The importance of long-term measurements is shown by the exceptional growing season of 2016 (Figure12, Figure13). The strongest net annual CO_2 uptake was observed during this year, while fluxes on other years inside this measurement period were relative stable. The same difference is not visible in CH_4 fluxes. If our analysis has been limited to this single year, we would have concluded that these ecosystems function as stronger carbon sinks than the long-term data suggest. It shows that individual years rarely represent long-term ecosystem behaviour (Jackson et al., 2024).

Long-term observations are equally important for understanding the effects of climatic extremes. In **Paper IV**, we investigated the impact of the 2018 European drought on GHG exchange across five northern mire ecosystems. The drought lowered water-table depth, reduced both CO_2 uptake and CH_4 emissions, and caused three of the five peatlands to shift temporarily from net CO_2 sinks to net CO_2 sources. Reduced CH_4 emissions generated a short-term cooling effect. Reduction in CO_2 sequestration dominated over longer timescales. These findings demonstrate that individual climatic extremes can temporarily change the typical functioning of peatland ecosystems, from CO_2 sink to source. Increasing climatic variability, including more frequent droughts and heat extremes, is expected to amplify temporal variability in peatland GHG exchange (Page & Baird, 2016; Mander et al., 2025). Long-term monitoring is important for detecting ecosystem responses to climate change (Kuhn et al., 2025).

The contrast between the highly productive conditions observed at Abisko-Stordalen in 2016 and the drought conditions analysed in **Paper IV** illustrates the strong sensitivity of northern peatlands to climatic variability. Earlier snowmelt promotes vegetation development, extends the growing season, and enhances carbon uptake (Aurela et al., 2004; Malmer et al., 2005; Callaghan et al., 2010; Johansson et al., 2013), while drought lowers the water table, decrease photosynthesis, and reduces net ecosystem carbon uptake (Helbig et al., 2022). These responses demonstrate that annual carbon budgets reflect the combined influence of multiple interacting environmental drivers rather than temperature alone. The drought investigated in **Paper IV** demonstrated that reductions in water-table depth lower CH_4 emissions across contrasting peatland ecosystems (Abdalla et al., 2016; Evans et al., 2021). These findings suggest that distinguishing long-term ecosystem responses from climatic anomalies requires continuous, multi-year observations that capture the interannual variability in peatland GHG exchange (Lund et al., 2009; Mander et al., 2025).

Finally, long-term monitoring provides an opportunity to evaluate ecosystem resilience and identify gradual changes. Year-to-year variability in other Northern wetlands shows temporary environmental fluctuations rather than shifts from CO_2 sink to source (Aurela et al., 2007; Rinne et al., 2018; Helbig et al., 2022). Repeated climatic extremes combined with ongoing permafrost degradation may eventually lead to irreversible ecosystem transitions, including the expansion of sedge-dominated fen vegetation and associated increases in CH_4 emissions (Christensen et al., 2004; Johansson et al., 2006; Olefeldt et al., 2013; Biskaborn et al., 2019).

Part V: Variability in CH_4 Isotopic Composition (Paper III and Paper V)

Papers IV and V investigated the spatial and temporal variability of the $\delta^{13}C$-CH_4 across northern peatlands using chamber measurements, Keeling plot analyses, continuous isotope observations and atmospheric isotope syntheses. Together, these studies demonstrate that CH_4 emitted from northern peatlands cannot be represented by a single characteristic isotopic signature. Improving isotopic signatures characterisation is important due to increasingly usage of them to for regional and global CH_4 budgets (Nisbet et al., 2019; Lan et al., 2024).

Our measurements demonstrated spatial variability in $\delta^{13}C$-CH_4 over relatively small distances, confirming that local environmental conditions have a stronger influence on CH_4 isotopic composition (Figure14).

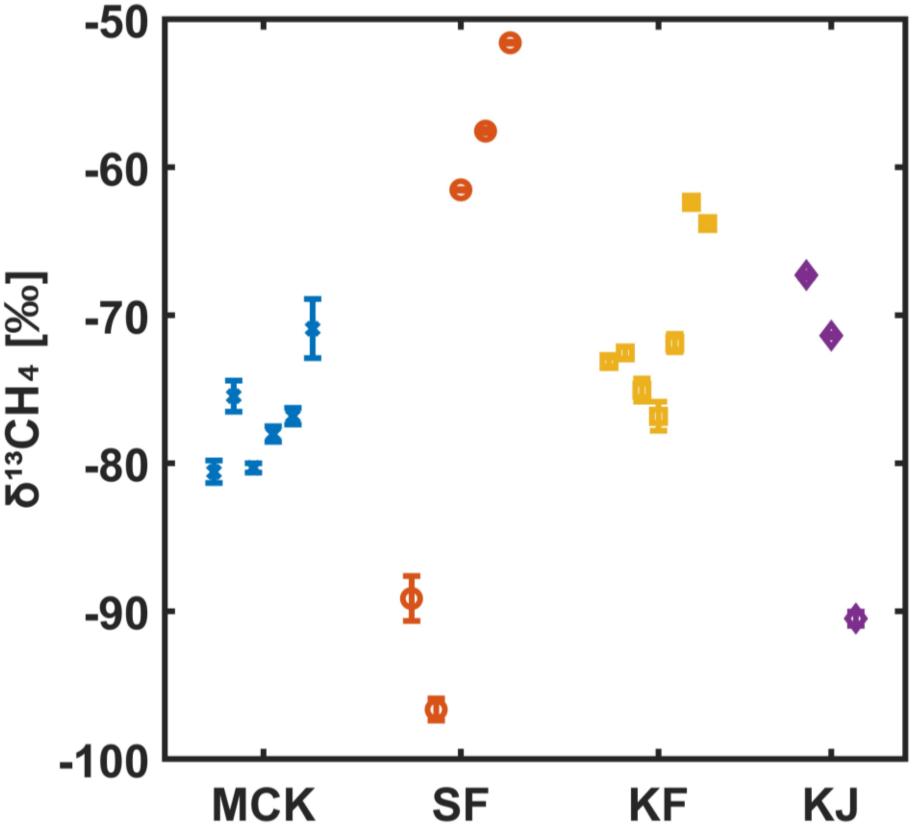

Figure14. Isotopic composition of CH_4 measured at Mycklemossen (MCK, blue), Storflaket (SF, orange), Kursflaket (KF, yellow), and Katterjåkk (KJ, purple). Error bars indicate measurement uncertainty, some are too small to be visible.

Neighbouring microsites experience the same temperature and precipitation. However, peatland microtopography makes differences in vegetation composition, water-table position, substrate availability and microbial activity which caused differences in isotopic signatures. In Paper IV, we observed differences of approximately 15 ‰ among vegetation communities within the same mire, whereas seasonal variability was small. These observations suggest that spatial heterogeneity dominates over temporal variability in controlling CH_4 isotope signatures at the ecosystem scale. Similar conclusions have recently been reported in syntheses demonstrating that local ecosystem characteristics explain much of the variability in wetland CH4 isotopic composition (Kuhn et al., 2024).

Metagenomic analyses performed in Paper IV demonstrated that methanogenic communities have the genetic capacity to use both hydrogenotrophic and acetoclastic pathways, indicating metabolic flexibility. The observed isotopic differences are result from shifts in substrate availability and environmental conditions. This interpretation agrees with previous studies showing that microbial metabolism is changed by environmental conditions rather than by replacing microbial communities entirely (McCalley et al., 2014). More recent studies similarly demonstrate that changes in hydrology and substrate quality strongly regulate CH_4 production pathways across northern peatlands (McCalley et al., 2022). These environmental differences generate contrasting microbial habitats that support different CH_4 production pathways and oxidation rates. Similar relationships between vegetation, hydrology and CH_4 cycling have been reported across Arctic and boreal peatlands (Bridgham et al., 2013; McCalley et al., 2014; Ge et al., 2024).

Papers III and V also demonstrate that the observed spatial variability is observed across different peatlands. Many atmospheric inversion studies have represented wetland CH_4 emissions using a $\delta^{13}C\text{-}CH_4$ source signature of approximately −60‰ to −61‰ (Schwietzke et al., 2016; Oh et al., 2022). Our field observations showed much lighter isotopic signatures, with mire-scale averages approaching −80 ‰ in some vegetation communities. Paper V demonstrated that this difference is not unique to our study site. By combining published isotope measurements from wetlands worldwide, we showed that northern European wetlands are characterized by significantly lighter CH_4 isotopic signatures than the global wetland average. The mean value for European wetlands −73.6 ± 2.3 ‰ was more depleted than the global average −63.3 ± 0.8 ‰ (Fisher et al., 2017, Oh et al., 2022). It suggests that hydrogenotrophic methanogenesis is dominating pathway production in boreal and Arctic peatlands. Global isotope syntheses demonstrate that wetland CH_4 isotopic composition has much greater spatial variability than previously represented in atmospheric models (Lan et al., 2024).

Atmospheric inverse models combine concentration measurements with isotopic observations to distinguish among natural wetlands, fossil fuels, agriculture and biomass burning (Nisbet et al., 2019; Lan et al., 2024). If isotopic signatures assigned to northern wetlands are systematically too enriched, wetland CH_4

emissions may be underestimated while emissions from other sources are overestimated. Recent modelling studies show that more accurate representation of wetland isotope variability, improve CH_4 source characterization (Lan et al., 2024).

Conclusions and future work

This thesis demonstrates that GHGs dynamics in northern peatlands are controlled by multiple interacting environmental. Methodological factors operating across different spatial and temporal scales have impact on the calculation of their budgets. Both CO_2 and CH_4 are products of ecosystem carbon cycling, they respond differently to environmental change and should not be interpreted as indicators of peatland functioning. While CO_2 exchange was primarily regulated by vegetation productivity, growing season length and atmospheric conditions, CH_4 emissions were controlled peat temperature, vegetation composition and anaerobic microbial activity. Permafrost thaw affected the two GHGs in different ways, increasing CH_4 emissions while producing smaller changes in ecosystem-scale CO_2 exchange.

The multi-year observations further demonstrate that growing season length is an important driver of ecosystem carbon uptake. Earlier snowmelt and a longer snow-free period enhanced vegetation productivity, resulting in greater GPP, ecosystem respiration and net CO_2 uptake. Those conditions did not produce similar responses in CH_4 emissions, highlighting that CH_4 dynamics are regulated primarily by soil temperature and microbial processes rather than by plant productivity alone. These findings demonstrate that evaluating climate feedback in northern peatlands requires both GHGs estimation, as changes in CO_2 exchange alone do not represent ecosystem responses to permafrost degradation.

The methodological analyses presented in this thesis show that uncertainty associated with data processing is an important component of GHG budget estimation. Different gap-filling approaches produced highly comparable annual CO_2 and CH_4 budgets. Differences occurred at shorter temporal scales, particularly during periods of rapid environmental change. Applying several independent gap-filling methods represents an effective strategy for quantifying methodological uncertainty and increasing confidence in long-term ecosystem carbon budgets.

The results presented in this thesis also show the importance of long-term observationsecosystem monitoring. Individual years were strongly influenced by climatic anomalies, including unusually early snowmelt and drought events, demonstrating that short-term studies may not adequately represent ecosystem functioning. Only multi-year observations allow the separation of transient responses from long-term ecosystem change, providing a robust basis for evaluating the effects of ongoing climate warming on peatland carbon cycling.

The isotopic investigations further demonstrate that CH_4 emitted from peatlands cannot be represented by a single characteristic isotopic signature. Instead, $\delta^{13}C$-CH_4 varied over relatively small spatial scales due to differences in hydrology, vegetation, substrate availability and microbial pathways. The combination of detailed field observations with recent isotope syntheses demonstrates that northern peatlands are generally characterized by isotopically lighter CH_4 than assumed in many atmospheric studies. These findings highlight the importance of ecosystem-specific isotope signatures into atmospheric inverse models and CH_4 budget assessments to improve source attribution and reduce uncertainty in estimates of natural CH_4 emissions.

This thesis demonstrates that reliable prediction of future GHG dynamics in northern peatlands requires a combination of long-term ecosystem observations, high-resolution chamber measurements, EC techniques, stable isotope analyses and robust statistical methods. Multidisciplinary approaches are essential for reducing uncertainties in regional and global carbon budgets and for improving predictions of peatland–climate feedback under environmental change.

Future research should continue to investigate the mechanisms controlling CO_2 and CH_4 exchange across peatlands representing different stages of permafrost degradation and hydrological development. Attention should be given to the interactions among vegetation succession, microbial community dynamics, water-table fluctuations and active-layer development.

Long-term observations should remain a priority. Expanding continuous measurements within international monitoring networks such as ICOS and FLUXNET-CH_4 will improve the detection of long-term trends, climatic extremes and ecosystem tipping points connected with ongoing permafrost thaw. Combining EC observations with automated chamber measurements, remote sensing and high-resolution environmental monitoring would further improve the scaling of plot-level observations to landscape and regional scales.

Finally, continuous high-frequency measurements of CH_4 isotopic composition should become an integral component of peatland monitoring. Recent advances in laser spectroscopy now allow in situ isotope measurements at temporal resolutions. Combining these observations with microbial analyses, vegetation mapping and ecosystem-scale flux measurements will improve understanding of CH_4 production, oxidation and transport pathways. At the same time, expanding isotope databases for northern wetlands will strengthen atmospheric inverse modelling and improve source partitioning at regional and global scales.

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