The Torneträsk System - A basis for predicting future subarctic ecosystems

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2022

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The Torneträsk System - A basis for predicting future subarctic ecosystems

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DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on Friday 25th November 2022 at 13.00 in Världen, Department of Physical Geography and Ecosystem Science, Sölvegatan 12, 223 62 Lund, Sweden

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Organization LUND UNIVERSITY Department of Physical Geography and Ecosystem Science **Author:** Didac Pascual Descarrega	**Document name** DOCTORAL THESIS **Date of issue** 25th November 2022 Sponsoring organization

Title and subtitle
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Abstract

Arctic and subarctic areas have experienced rapid warming and substantial increases in precipitation in recent decades. The frequency and intensity of some extreme events, such as fires, winter warming events, extreme rainfall, and droughts, have also increased. These climatic changes and other anthropogenic factors have caused profound changes in arctic and subarctic ecosystems with important implications for the local residents and for the global population, which are likely to exacerbate under the predicted climate change scenarios. Thus, a better understanding of potential future ecosystem changes is paramount for defining climate change mitigation goals and adaptation strategies.

Dynamic ecosystem models are powerful tools to study the influences of climatic and other drivers on ecosystem processes. Nevertheless, predictions of ecosystem changes still hold large uncertainties, arising mostly from insufficient observational data, lack of process understanding, difficulties in quantifying the effects of different ecosystem processes and their interactions, and/or model limitations in representing these interacting processes.

The Torneträsk area, in the Swedish subarctic, has an unrivalled history of environmental observations spanning over 100 years and is one of the most studied sites in the Arctic. The area has undergone substantial climatic and ecosystem changes. By studying its rapidly-transforming ecosystems we can obtain critically important information needed to improve our understanding and predictions of future ecosystem changes at a larger scale.

This thesis summarized and ranked the direct and indirect drivers of ecosystem change in the Torneträsk area, and proposed research priorities to improve predictions of ecosystem change. Winter warming events (WWEs) were the top-ranked research priority. Hence, this thesis further examined the impacts of WWEs on subarctic ecosystems using monitoring data, manipulation experiments and modelling. The monitoring and manipulation data suggest an increasingly strong warming effect of WWEs on permafrost, especially rain on snow events occurring in the presence of thick snowpacks. The modeling experiments in LPJ-GUESS indicated a strong cooling effect of WWEs on ground temperature, driven mostly by changes in snow insulation, which resulted in profound changes in the biogeochemical fluxes of magnitudes comparable to long-term climatic changes. We identified several modeling gaps that may explain the mismatch between the model- and the observational-based impacts of WWEs on ground temperatures, including 1) the lack of surface energy balance in LPJ-GUESS, the model's daily timestep that neglects sub-daily freeze-thaw cycles within the snowpack, and 3) the model's simplistic water retention scheme that minimizes the amount of water retained in the snowpack and hence the amount of latent heat release upon freezing. Addressing these issues is paramount for accurately estimating future ecosystem changes and their implications for the arctic's carbon balance.

Climate change, including long-term changes and short-lasting events such as WWEs, affected lowland permafrost sites in the Torneträsk area differently, depending on the site-specific climatic and environmental conditions. This resulted in permafrost thaw rates decreasing eastwards. This thesis revealed, through metagenomic sequencing and greenhouse gas measurements in three peatlands across this thaw gradient, that different rates and stages of permafrost degradation influence greenhouse gas exchange through an altered taxonomic structure and function of the microbial communities. This highlights the need for expanding the monitoring of peatland fluxes and microbial dynamics that is currently based on very few sites.

Key words climate change, ecosystem change, impacts, snow, permafrost, winter warming events, rain on snow, modelling, climate projections, carbon fluxes, CH_4

Classification system and/or index terms (if any)

Supplementary bibliographical information	**Language** English
ISSN and key title	**ISBN** 978-91-89187-15-3 (print) 978-91-89187-16-0 (electronic)

Recipient's notes	**Number of pages: 56**	Price
	Security classification	

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Cover photo by Didac Pascual Descarrega

Faculty of Science
Department of Physical Geography and Ecosystem Science

ISBN 978-91-89187-15-3
ISBN (digital) 978-91-89187-16-0

Printed in Sweden by Media-Tryck, Lund University
Lund 2022

Media-Tryck is a Nordic Swan Ecolabel certified provider of printed material. Read more about our environmental work at www.mediatryck.lu.se

MADE IN SWEDEN

NORDIC SWAN ECOLABEL Printed matter 3041 0903

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Acknowledgements

First and foremost, I would like to express my deepest gratitude to my main supervisor, Margareta Johansson, for taking me on this journey. Thank you for your great guidance, advice, and support throughout this thesis. And thanks for your positivity, happiness, and joy, which made these four years a very pleasant experience. You are truly an inspiration and a role model.

I'm extremely grateful to my co-supervisor Jing Tang for all your valuable input, and for your endless support these four years.

I am also very grateful to my co-supervisors Andreas Persson and Thomas Holst, and to Lars Eklundh, for comments, feedbacks, and discussions of great value.

I am grateful to my department representative Petter Pilesjö for ensuring the quality of my research and for your valuable advice.

I am indebt to my former supervisor Peter Kuhry for providing me with so many good opportunities, and for sharing your endless knowledge and passion for science.

Special thanks to Terry Callaghan for your altruistic help, and for your wise advice. I hope we can meet in person soon.

Thanks to all my friends at the Department, in Sweden, and all around the world, for making life beautiful.

Thanks to all my colleagues and staff at the Department for all your support.

Thanks to the Abisko Scientific Research Station for great hospitality during the field campaigns.

My loving family, especially my parents, Santi and Pilar, my siblings Teia, Claudia, and Aleix, my brother-in-law Sergi, and the newborn Lia: you were always there to support me when I needed it.

Special thanks to my grandpa, "Lo iaio Rafel", my role model and the person who ignited my passion for natural sciences.

Last, but not least, I want to thank my partner, my lover, my friend, and my mentor: Chiara, this endeavor would not have been the same without you. Thank you for everything you have done for me during these four years. Your beautiful spirit, your creative ideas, and your support (motivational, and technical!), have certainly been key in successfully submitting this thesis.

List of Papers

I. **Pascual, D.,** Åkerman, J., Becher, M., Callaghan, T.V., Christenssen, T.R., Dorrepaal, E., Emmanuelsson, U., Giesler, R., Hammarlund, D., Hanna, E., Hofgaard, A., Jin, Hongxiao, Johansson, C., Jonasson, C., Klaminder, J., Karlsson, J., Lundin, E., Michelsen, A., Olefeldt, D., Persson, A., Phoenix, G.K., Raczkowska, Z., Rinnan, R., Ström, L., Tang, J., Varner, R.K, Wookey, P., Johansson, M. 2020. The missing pieces for better future predictions in subarctic ecosystems: A Torneträsk case study. *Ambio*, 50, 375–392.

II. **Pascual, D.,** Johansson, M. 2022. Increasing impacts of extreme winter warming events on permafrost, *Weather and Climate Extremes, 36*, 100450.

III. **Pascual, D.,** Johansson, M. Pongrácz, A., Tang, J. Modelling ecosystem impacts of future enhanced winter warming events using LPJ-GUESS. *Submitted to Geophysical Research Letters.*

IV. White, J., **Pascual, D.,** Lakomiec, P., Johansson, M., Ahrén, D., Ström, L., Parmentier, F.J. Three peatlands under different stages of permafrost thaw; a metagenomic approach to investigate carbon exchanges from thawing peatlands in the sub-arctic. *Manuscript*

Author Contributions

Paper I: DP conceived and designed the study with MJ, conducted the analysis of the expert assessment provided by co-authors, interpreted the results, and wrote the manuscript with reviewing and editing support by co-authors.

Paper II: DP conceived and designed the study, conducted the analysis, interpreted the results with MJ, and wrote the manuscript, with reviewing and editing support by MJ.

Paper III: DP conceived the study with JT and MJ, contributed to the model set-up led by JT, designed and prepared the climate scenarios, performed the model simulations and data analysis, interpreted the results with co-authors, and led the writing of the manuscript, with reviewing and editing support from co-authors.

Paper IV: DP contributed to the design of the study, was involved in the data collection, contributed to the analysis of the environmental data, carbon and nitrogen content, and greenhouse gas fluxes, interpreted the results with co-authors, and contributed to writing, reviewing, and editing the manuscript.

List of abbreviations

AL	Active Layer
AMAP	Arctic Monitoring and Assessment Program
ANS	Abisko Scientific Research Station
CALM	Circumpolar Active Layer Monitoring program
CMIP	Coupled Model Intercomparison Project
DGVM	Dynamic Global Vegetation Model
GCM	General Circulation Model/Global Climate Model
GPP	Gross Primary Production
GT	Ground Temperature
GWC	Ground Water Content
IPCC	Intergovernmental Panel on Climate Change
NEE	Net Ecosystem Exchange
NPP	Net Primary Production
PFT	Plant Functional Type
RCP	Representative Concentration Pathway
ROS	Rain On Snow
R_a	Autotrophic respiration
R_{eco}	Ecosystem respiration
R_h	Heterotrophic respiration
SMHI	Swedish Meteorological and Hydrological Institute
SSP	Shared Socioeconomic Pathway
SWIPA	Snow, Water, Ice and Permafrost in the Arctic
TDD	Thawing Degree Days
WWE	Winter Warming Events

Abstract

Arctic and subarctic areas have experienced rapid warming and substantial increases in precipitation in recent decades. The frequency and intensity of some extreme events, such as fires, winter warming events, extreme rainfall, and droughts, have also increased. These climatic changes and other anthropogenic factors have caused profound changes in arctic and subarctic ecosystems with important implications for the local residents and for the global population, which are likely to exacerbate under the predicted climate change scenarios. Thus, a better understanding of potential future ecosystem changes is paramount for defining climate change mitigation goals and adaptation strategies.

Dynamic ecosystem models are powerful tools to study the influences of climatic and other drivers on ecosystem processes. Nevertheless, predictions of ecosystem changes still hold large uncertainties, arising mostly from insufficient observational data, lack of process understanding, difficulties in quantifying the effects of different ecosystem processes and their interactions, and/or model limitations in representing these interacting processes.

The Torneträsk area, in the Swedish subarctic, has an unrivalled history of environmental observations spanning over 100 years and is one of the most studied sites in the Arctic. The area has undergone substantial climatic and ecosystem changes. By studying its rapidly transforming ecosystems, we can obtain critically important information needed to improve our understanding and predictions of future ecosystem changes at a larger scale.

This thesis summarized and ranked the direct and indirect drivers of ecosystem change in the Torneträsk area, and proposed research priorities to improve predictions of ecosystem change. Winter warming events (WWEs) were the top-ranked research priority. Hence, this thesis further examined the impacts of WWEs on subarctic ecosystems using monitoring data, manipulation experiments and modelling. The monitoring and manipulation data suggest an increasingly strong warming effect of WWEs on permafrost, especially rain on snow events occurring in the presence of thick snowpacks. The modeling experiments in LPJ-GUESS indicated a strong cooling effect of WWEs on ground temperature, driven mostly by changes in snow insulation, which resulted in profound changes in the biogeochemical fluxes of magnitudes comparable to long-term climatic changes. We identified several modeling gaps that may explain the mismatch between the

model- and the observational-based impacts of WWEs on ground temperatures, including 1) the lack of surface energy balance in LPJ-GUESS, the model's daily timestep that neglects sub-daily freeze-thaw cycles within the snowpack, and 3) the model's simplistic water retention scheme that minimizes the amount of water retained in the snowpack and hence the amount of latent heat release upon freezing. Addressing these issues is paramount for accurately estimating future ecosystem changes and their implications for the arctic's carbon balance.

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Popular summary

The Arctic and the Subarctic extend over vast areas in high latitudes of the northern hemisphere. The terrestrial ecosystems in these large territories are very rich in natural resources that benefit the local populations, providing them with food, freshwater, biomass, etc. At the same time, the processes that occur in these ecosystems are very important for the global population. For example, arctic areas regulate the temperature of the Earth, as the snow/ice covered (white) surface of the arctic reflects most of the solar radiation back to space. Also, arctic ecosystems reduce the greenhouse gas effect by removing part of the carbon dioxide from the atmosphere and storing it in plants and its frozen soils. For these reasons, any changes in arctic ecosystems have important implications for the local residents and for the global population.

Human activity has increased the concentration of carbon dioxide and other greenhouse gases in the atmosphere, and this has caused a rise in air temperatures and a change in rainfall patterns all around the world. In the Arctic, precipitation has increased in general, and the rise in air temperature has occurred three times faster than the global average, mostly because the snow and ice surfaces are melting earlier in the spring and forming later in the autumn, and this reduces the amount of solar radiation reflected by the surface. At the same time, extreme events such as fires, droughts, extreme rainfall, heat waves, and anomalously warm episodes during wintertime, have become more frequent and more severe. Altogether, these changes are having severe impacts on arctic ecosystems with important implications for local residents and for the global society. Global warming will likely continue in the coming decades as humans keep emitting carbon dioxide into the atmosphere, and therefore arctic ecosystems will continue to change.

In order to adapt to climate change, and to design mitigation strategies such as, for example, fulfilling the goals of the Paris agreement, it is very important to know how arctic ecosystems will change, and what implications this will have for the Earth. To predict future changes in ecosystems, scientists use ecosystem models, which are simplified mathematical representations of the ecosystems which are used to understand the real system. The predictions from these ecosystem models are improving year after year but they still have large uncertainties, because the real ecosystems are very complex, arctic areas are difficult to access and measure, and we still miss a deeper understanding of many processes and their interactions.

In this thesis, we study the diverse and rapidly-transforming ecosystems in the Torneträsk area, in northern Sweden, to obtain important information that can be used to improve the ecosystem models and therefore can help improve the predictions of future ecosystem changes in other arctic areas.

First, we summarized and ranked the different causes of ecosystem change in the Torneträsk area, and identified the research priorities, i.e. those causes that are not well understood and need to be urgently investigated to improve predictions of ecosystem change. We found that anomalously warm episodes in wintertime, known as winter warming events, were the top-ranked research priority. Hence, this thesis further studied the impacts of winter warming events on arctic ecosystems using field measurements, field manipulation experiments, and experiments using a widely used ecosystem model.

An important and new result of these studies was that we observed that these winter warming events cause warming of the ground not only in winter but also in summer. However, the ecosystem model that we used is not yet complex enough to account for the effects of these events and this directly causes inaccuracies in the model's estimates of the future changes in vegetation and the activity of microbes, which strongly affects the exchanges of carbon dioxide between the atmosphere and ecosystems. We identified the processes that are missing in the model and need to be implemented to estimate with greater accuracy the future ecosystem changes and their implications for the arctic's carbon balance.

Finally, we investigated the composition and the activity of microbes, and the greenhouse gases that these microbes emit, from three wetlands affected by permafrost (perennially frozen ground). These sites are located close to each other but their frozen ground has been degrading at different rates, from very fast to very slow. The results from each of these three sites were very different from one another. This is an important finding because until now, the measurements from very few wetlands were extrapolated to very large areas, but this study emphasizes that the behaviour of the microbes and the greenhouse gases that they emit change can be very different even from wetlands located close to each other, and therefore the measurements need to be done in many more sites before extrapolating the results to larger areas.

1. Introduction

1.1. The importance of arctic terrestrial ecosystems for society and the global environment

Arctic terrestrial ecosystems cover over 7 million km^2 in areas north of the Arctic Circle (66°32' N; AMAP). The subarctic, in turn, includes areas extending from the southernmost parts of the Arctic to the northernmost areas of the temperate zones, between 50°N and 70°N latitude, depending on the local climate. Arctic and subarctic ecosystems contain rich biotic and abiotic resources and provide multiple services with local and global societal and environmental benefits. Biotic and abiotic resources of the Arctic support local residents by providing provisioning services such as food, freshwater, and biomass. In addition, biotic and abiotic processes occurring in arctic and subarctic ecosystems provide the global population with regulatory services, for example by contributing to the global energy balance through the high albedo of its vast snow and ice-covered surfaces, and by contributing to the global carbon (C) cycle through the sequestration of large amounts of atmospheric C and its storage in vegetation and its frozen soils. Any changes in arctic and subarctic ecosystems are therefore likely to have local, regional, and global societal and environmental impacts.

Arctic and subarctic ecosystems are strongly dependent on, and adapted to, the local climatic and environmental conditions. Climate change and other anthropogenic factors are therefore causing changes in ecosystems across the Arctic with impacts on the ecosystem services they provide. In subarctic areas, located at the boundaries between the Arctic and the temperate regions, even small climatic changes are likely to cause particularly large responses in their biotic organisms (such as plants, animals. and microorganisms) and abiotic components and processes (such as permafrost and hydrologic systems) that are at the edge of their climatic range, and therefore are particularly sensitive to climatic and environmental changes.

1.2. Climate change and other drivers of change in arctic ecosystems

Increasing concentrations of greenhouse gases in the atmosphere have resulted in a general increase in air temperature all across the Earth (IPCC 2021). In the Arctic, the initial greenhouse gas radiative forcing has triggered a suite of changes in its cryospheric, hydrospheric, and biospheric components that have further altered the arctic's net radiation balance, resulting in an air temperature increase of 0.6º C per decade over the last 50 years, three times faster than the global average (AMAP 2021).

This greater temperature increase in the Arctic relative to the rest of the planet, known as "Arctic amplification", which is focused in winter but evident throughout the year, is likely to continue throughout the 21st Century (IPCC 2021). The most prominent causes of Arctic amplification are related to changes in the surface energy balance: the decline in Arctic sea ice extent (Walsh et al. 2014) and snow cover duration (Brown et al. 2017) reduce the surface albedo substantially and lead to rapid warming. Other coincident processes triggered by the initial warming, such as increasing atmospheric water vapor and cloud cover, further alter the amount of longwave radiation flux emitted back to the Earth's surface (Serreze and Francis, 2006). On longer timescales, the warming-induced latitudinal and altitudinal expansion of forests and shrublands reduces surface albedo and increases the atmospheric water vapor (greenhouse gas with a radiative forcing of 0.07 W m-2, Forster et al. 2007) content via evapotranspiration, causing further warming. By contrast, the increasing tree density, and expansion of forests and shrublands, may counteract the initial warming both in the short term, by increasing evapotranspiration and thus the latent heat absorbed, and in the long term, by sequestering atmospheric CO_2 (but see papers by Mykleby et al. 2017 and Veldman 2019).

In addition to the observed warming, a general (although uneven) increase in precipitation has been observed in the last 50 years (>9% over the Arctic), mostly as rain (24%) although increases in maximum snow accumulation occurred in some areas, despite the overall substantial decline in snow cover duration (AMAP, 2021). These trends are projected to continue throughout the 21st century (IPCC, 2021).

These climatic changes observed over arctic and subarctic areas are causing substantial impacts on its biotic (e.g. vegetation and the C cycle) and abiotic (e.g. permafrost, hydrology, and local climate) components. For example, the Arctic has experienced a greening trend over most of the satellite's record 33 years history (i.e. an increase in plant biomass and productivity; Phoenix and Bjerke, 2016). Permafrost has been thawing in the last decades at accelerating rates (Biskaborn et al., 2019), and large amounts of organic C (50% of the global soil C, twice as much as the current atmospheric C content) that have been protected for millennia in the cold and water-saturated soils are being exposed to microbial decomposition and the subsequent release into the atmosphere as greenhouse gases (Turetsky et al. 2020). Permafrost degradation is causing surface subsidence and wetland expansion, with the resulting shifts in vegetation composition (e.g. Malmer et al. 2005). Snow cover in May and June has been reduced substantially (SWIPA 2017) and this has caused profound hydrological regime shifts (e.g., Bokhorst et al. 2016). Aquatic systems' activity has increased due to longer ice-free seasons (e.g. Callaghan et al. 2010). These and other ecosystem changes have obvious consequences on the arctic's and the global C and energy balance, which may exacerbate under the predicted scenarios of enhanced climate change (IPCC 2021).

Apart from the observed long-term climatic changes, extreme events in the Arctic are changing in frequency and intensity. The occurrence of extreme cold spells is decreasing, while winter warm spells (hereafter referred to as winter warming events, or WWEs), extreme warm spells, extreme precipitation events, fires, droughts, and insect outbreaks, are becoming more frequent and intense (e.g. Soja et al. 2007; Kivinen et al. 2017; AMAP 2021). Despite their short duration, these extreme events have already caused strong impacts on ecosystems. For example, Phoenix and Bjerke (2016) attributed the overall decline in arctic greenness in 2011-2014 to several extreme events including extreme winter warming, rain on snow (ROS), fires, and insect outbreaks. Sokolov et al. (2016) attributed massive reindeer die-offs to the occurrence of ROS events in Siberia. In Svalbard, extreme ROS events in 2012 induced increases in permafrost temperatures of up to 7 °C near the surface for over one month (Hansen et al. 2014), but some modeling studies suggest an overall permafrost cooling response to WWEs due to the associated reduction in snow depth and thus its insulation capacity (e.g., Beer et al. 2018). Their stochastic nature and short duration make it difficult to predict their occurrence, whilst the simultaneous occurrence of multiple extreme events and other long-term changes make it challenging to estimate their impacts. These impacts are also likely to increase in the coming decades under the predicted scenarios of increased frequency and intensity of many types of extreme events (e.g. Vikhamar-Schuler et al. 2016; Kirchmeier-Young et al. 2017; AMAP 2021).

However, the ecosystem changes occurring in the arctic and subarctic areas are not only caused by climate change, but by the combined effect of climatic and other anthropogenic drivers such as herding, land use changes, and pollution (ACIA 2005). The total magnitude of the ecosystem changes results from the multiple interactions between the different drivers. Field measurements mostly address overall responses to some changing drivers, rather than the effect of specific drivers and the different interactions between them. To date, a comprehensive assessment of the drivers (including their direct and indirect effects) of different changes and the magnitude of their impact on arctic and subarctic ecosystems is missing.

1.3. Predicting future changes in arctic ecosystems

Given the local and global societal and environmental implications of changes in arctic and subarctic ecosystems, it is of utmost importance to improve our understanding and predictions of future ecosystem changes. This would allow us to define adequate mitigation goals and adaptation strategies.

To predict how climatic and other changing drivers influence the future vegetation dynamics and biogeochemical fluxes (and vice versa), data gathered through monitoring of specific parameters and the process understanding gained through manipulation experiments are combined in dynamic global vegetation models (DGVMs). The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) (Smith et al. 2014) is a DGVM that includes individual-level representations of vegetation dynamics and competition for resources. LPJ-GUESS has been widely applied to simulate regional and global C fluxes, vegetation dynamics, and water fluxes (e.g., Gerten et al. 2004; Ahlström et al. 2012; Miller and Smith, 2012). However, predictions of future ecosystem change still hold large uncertainties, arising mostly from insufficient observational data for parameterization and evaluation, lack of process understanding, difficulties in quantifying the effects of different ecosystem processes and their interactions, and/or model limitations in representing these interacting ecosystem processes. In addition, regional and global studies of ecosystem changes often operate at spatial and temporal resolutions too coarse to explicitly account for some types of extreme events that occur at finer temporal and spatial scales. This further contributes to the uncertainties in regional and global C and energy budget estimates, given the notable impacts that extreme events can cause on ecosystems across the Arctic (e.g., Hansen et al. 2014; Phoenix and Bjerke, 2016; Sokolov et al. 2016).

1.4. From local to global: the Torneträsk area, a microcosm of the subarctic

Local knowledge is key to understanding ecosystem functioning and future changes at a circumpolar scale (Callaghan et al. 2013). This thesis focused on the Torneträsk area, in the Swedish subarctic, which has over a century-long history of environmental observations (Callaghan et al. 2010; Jonasson et al. 2012), and features in about 12% of all published papers and 19% of all study citations across the Arctic (Metcalfe et al. 2018). The relatively small size of the Torneträsk area, its great biological and geomorphological diversity, and its unique datasets present a well-curated microcosm of the Subarctic. Data from the nearby Abisko Station reveals that climate has undergone substantial changes since the measurements began in the area in 1913 (Callaghan et al. 2010), which together with other anthropogenic drivers have caused profound ecosystem changes (Callaghan et al 2013). By studying its rapidly-transforming ecosystems we can obtain critically important information needed to improve our understanding of the ongoing processes and future ecosystem changes at a larger scale. This understanding, in turn, will be key for designing future mitigation and adaptation plans needed in a changing climate.

In this thesis, the drivers of ecosystem change in the Torneträsk area were first summarized and ranked, and subsequently, the current research priorities were identified, by Expert Assessment, to improve predictions of ecosystem changes in the area. Based on this study, we used measurements, manipulation experiments, and modelling, to investigate the potential ecosystem impacts of some of the top-ranked drivers and to identify knowledge gaps that need to be addressed urgently to reduce uncertainties in the predictions of ecosystem change in high latitudes.

2. Aims

The principal aim of this thesis is to improve the overall understanding and future predictions of ecosystem change in the Subarctic. To accomplish this objective, this thesis focuses on the diverse and rapidly-transforming subarctic ecosystems in the Torneträsk area, in northernmost Sweden, and aims to:

- Summarize and rank the direct and indirect drivers of ecosystem change, and propose research priorities identified to improve predictions of ecosystem change. (Paper I)

Based on the results of this study, and using manipulation experiment (Paper II), modelling (Paper III), and measurements (Paper IV), this thesis aims to:

- Assess the impacts of WWEs (top-ranked research priority in Paper I) on lowland permafrost under different snow conditions in the Torneträsk area. (Paper II)
- Evaluate potential future impacts of WWEs on subarctic ecosystems, and identify key model limitations and potential improvements. (Paper III)
- Investigate how different permafrost degradation rates and stages affect microbial dynamics and greenhouse gas emissions from peatlands. (Paper IV)

3. Study area and data

3.1. The Torneträsk area

The study area includes the northwest part of the Lake Torneträsk catchment and was delineated to include the climatic, altitudinal, and vegetation gradients occurring in the area. The Expert Assessment of ecosystem change conducted in Paper I focussed on this whole area (Figure 1).

The region has a highly varied topography, with altitudes ranging between 342 and 1900 m a.s.l. (Andersson et al. 1996). The Torneträsk area extends across a strong northwest-southeast oceanic-continental gradient, with precipitation and winter temperature progressively declining eastwards due to the increasing distance from the Atlantic Ocean and the rain shadow effect caused by the Scandes Mountains. In recent years, the area has experienced rapid warming and a substantial increase in precipitation. At the Abisko Scientific Research Station (ANS; 385 m a.s.l.), the mean annual air temperature increased by 2.5 °C over the period 1913–2006 (Callaghan et al. 2010) and is currently 0.4 °C (ANS 2020). Total annual precipitation in the study area ranges from >1000 mm in the northwestern areas to ~300 mm in the central and southeastern areas. At the ANS, the mean annual precipitation was 357 mm in 2010–2019, 19% higher than the 301 mm in 1961–1990 (ANS 2020). The more maritime climate in the western parts of the Torneträsk area results in much thicker mean winter snowpacks (c. 80 cm in Katterjokk Station, 1972-2019; SMHI), compared to areas affected by the more continental climate in the central and southeastern parts (c. 10 cm at Storflaket mire, 6 km east of the ANS; Johansson et al. 2013). Mean winter snow depth at the ANS doubled over the 20th century to ~40 cm in 2010-2019 (ANS 2020).

Vegetation in the Torneträsk area varies following its climatic and altitudinal gradients and is also dependent on hydrology. Birch (*Betula pubescens var pumila* L.)-dominated deciduous forests occur below an altitudinal limit of c. 600 and 800 m.a.s.l in the western and eastern parts of the Torneträsk area, respectively (Wielgolaski et al. 2005), and have expanded their altitudinal and latitudinal ranges during recent decades (Callaghan et al. 2013 and references therein). In the lowlands, birch forests alternate with peat plateaus underlain by permafrost, mostly composed of shrubs (e.g. *Vaccinium uliginosum* L.), mosses (e.g. *Sphagnum fuscum* (Schimp.)), and lichens (e.g. *Cetraria cucullata*) (Johansson et al. 2013), and non-permafrost fens dominated by graminoids (e.g. *Eriophorum vaginatum* L.) and mosses, which are expanding in areas of permafrost degradation (e.g. Christensen et al. 2004). Above the tree line, the tundra vegetation is dominated by dwarf shrub heathland (e.g. *Empetrum hermaphroditum*, and *Vaccinium species*), and meadows composed of sedges, herbs, and graminoids (e.g. Hedenås et al. 2012; Sundqvist et al. 2013), while the occurrence of snowbed communities is becoming more sporadic mostly due to the loss of suitable habitats (Björk et al. 2007). Vegetation cover becomes more scarce as elevation increases and where bedrock is exposed or small-sized glaciers occur. These four dominant vegetated ecosystem types were included in the modeling experiment in Paper III (Figure 1a).

The climatic changes that occurred in recent decades have contributed to permafrost degradation and the Torneträsk area is now more characteristic of the sporadic rather than the discontinuous permafrost zone (Åkerman and Johansson, 2008). Permafrost is widespread in the mountains above ~850 m .a.s.l on the North- and East-facing slopes, and above ~1100 m a.s.l. on slopes facing South (Ridefelt et al. 2008). In the lowlands, permafrost only occurs in peat mires (Johansson et al. 2006). The lowland permafrost dynamics follow the strong climatic gradient that characterises the Torneträsk area; permafrost thickness increases Eastwards as annual precipitation, winter snow depth, and winter air temperatures decrease (Åkerman and Johansson, 2008). Permafrost thaw rates also tend to decrease Eastwards, according the to long-term monitoring of AL thickness in the Torneträsk area (Circumpolar Active Layer Monitoring program (CALM), Brown et al. 2000; Åkerman and Johansson, 2008; Strandh et al, 2020). Permafrost responses to WWEs were investigated in seven CALM sites in Paper II (Figure 1a). Furthermore, three of these CALM sites, which have been degrading at different rates, were studied in Paper IV to investigate how the different permafrost thaw rates and stages affect microbial dynamics and greenhouse gas emissions in peatlands.

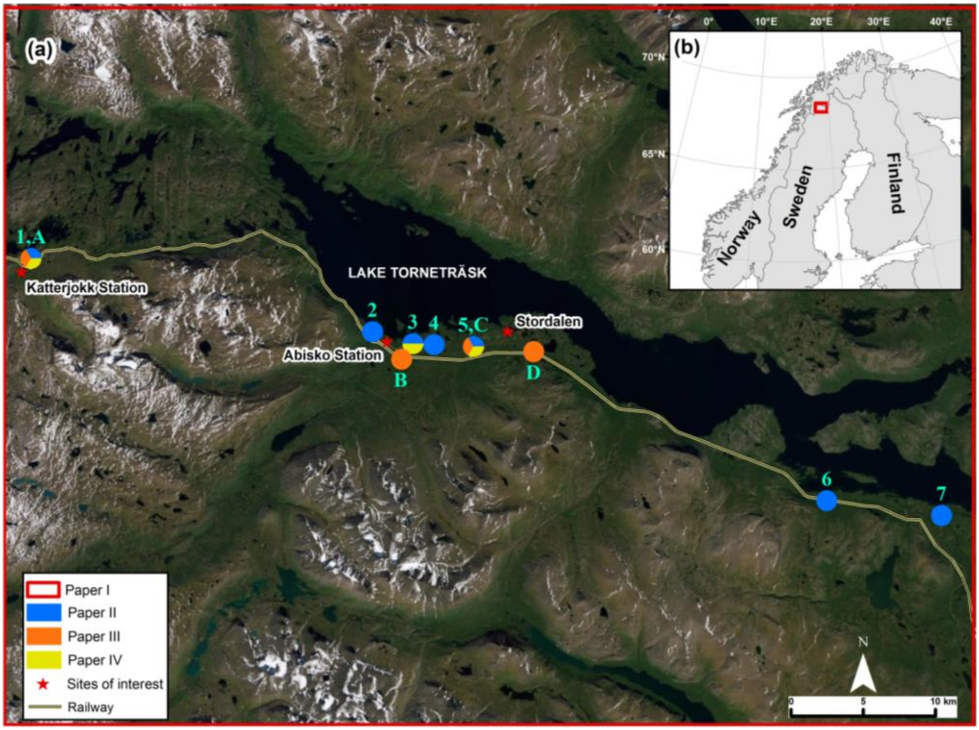

Figure 1. (a) The Torneträsk area delimitation used in Paper I (red line) and the location of the study sites in Papers II-IV. Numbers 1 to 7 correspond to seven CALM sites investigated in Paper II (blue) and three of them in Paper IV (sites 1, 3, and 5; yellow): (1) Katterjokk; (2) Heliport; (3) Kursflaket; (4) Mellanflaket; (5) Storflaket; (6) Torneträsk; (7) Narkervare. Letters A-D refer to the fen (A), tundra (B), peat plateau (C), and birch forest (D) sites investigated in Paper III (orange). The location of additional sites of interest is indicated with red stars. (b) Geographical overview of the study area. Source: Esri; Michael Bauer Research GmbH(B).

3.2. Permafrost monitoring and manipulation data

Permafrost monitoring data

In Paper II, we used permafrost monitoring data consisting of annual maximum AL thickness data derived from gridded AL measurements made in seven CALM lowland permafrost sites, located along the West-East climatic gradient in the Torneträsk region (Akerman and Johansson, 2008) (Figure 1). Measurements were made every year in late September and are therefore interpreted as the annual maximum thaw depth. Before averaging the annual measurements made at each site, data were examined individually to detect and correct any potential flaws. Hence, rapidly expanding pond areas were excluded, as the thermal dynamics in these unstable, inundated areas may have been strongly influenced by factors other than climatic. Data presenting serious anomalies was excluded. In some recent years, the length of the measuring probe (1.5 m) was not sufficient to reach the permafrost table. When this occurred for two consecutive years, the AL thickness of the second year was adjusted by adding the trend observed in the sampling points presenting AL < 1.5 m during the two years concerned

In Paper IV, the AL thickness data from 2019 corresponding to Katterjåkk, Kursflaket, and Storflaket sites was used to upscale plot-level greenhouse gas fluxes to the landscape scale.

Permafrost manipulation data

In Paper II we also used permafrost manipulation data including maximum AL thickness and mean monthly ground temperatures (15 cm depth), measured in six control (ambient) and six manipulated plots at the Storflaket mire (site 5 in Figure 1) since September 2005 (Johansson et al. 2013). In the manipulated plots, snow depth was more than doubled by erecting snow fences perpendicularly to the prevailing East-West wind from September to June. Data issues caused by the insufficient length of the rod were adjusted using the method described above.

3.3. Climate monitoring data and other model input data

Daily measurements of air temperature and precipitation have been made at the Abisko Station since 1913 (ANS 2020), and at Katterjokk Station since 1973 (SMHI) (Figure 1). Additionally, air temperatures have been measured at Storflaket mire since 2005 (M. Johansson, not published). Short-wave radiation has been measured at Abisko Station since 1984.

In Paper III, LPJ-GUESS was run from 1913 to 2018 for the four dominant vegetated ecosystem types in the Torneträsk area (i.e. birch forest, tundra, peat plateau, and fen; Figure 1) using the daily air temperature and precipitation data from the ANS and Katterjokk Station, together with daily short-wave radiation (1913-1984, Sheffield et al. 2006; 1984-2018, ANS), and annual CO_2 concentrations

(McGuire et al. 2001, and TRENDS, https://cdiac.ess-dive.lbl.gov/trends/co2/contents). Given their vicinity and similar elevation (altitudinal range <100 m), the birch forest, peat plateau, and tundra sites were run with climate data from the ANS (1913-2018; ANS 2020), whereas the fen site used data from Katterjokk Station (1973-2018; SMHI) and bias-corrected daily data (1913-1972) from the ANS. Soil property data was extracted from the WISE5min, V1.2 Soil Property Database (Batjes 2005).

To calculate the indices of WWE frequency and intensity in the Toneträsk area (section 4.2), we used the mean daily air temperature and daily precipitation data from the ANS and Katterjokk Station (Papers II and III), and mean daily air temperature from the Storflaket mire (Paper II). This data was also used to calculate other climatic variables relevant to permafrost thermal dynamics used in Paper II. In Paper II, annual climate data refers to the permafrost year (October year 1 to September year 2). The summer season corresponds to the meteorological summer (June–August), while the winter season refers to November to March, which corresponds to the period in which current mean monthly air temperatures in the area lie below 0 °C, the climatological definition of winter (Birkeland 1936, p. 25).

3.4. Evaluation data

In Paper III, a wide range of observational data from the Torneträsk area was used to evaluate the model's performance (Paper III, Appendix E). The data included abiotic parameters such as snow depth and ground temperatures, and biotic parameters including NEE, GPP, R_{eco}, and CH_4 (from both chamber measurements and Eddy covariance towers) from all four study sites (A-D in Figure 1), when available.

3.5. CMIP6 climate data

To generate the different WWE manipulation experiments used in Paper III, we used climate scenarios in the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al., 2016). We selected climate scenarios from two general circulation models (GCMs) with different climate sensitivities, i.e., CanESM5 and GFDL-ESM4, and three shared socioeconomic pathways that represent three levels of varying greenhouse gas emissions projections (SSP119, SSP270, and SSP585). The SSPs describe how global society, demographics, and economics could develop in the future, and whether and how different greenhouse gas concentration scenarios (Representative Concentration Pathways, or RCPs) can be reached under these narratives (Riahi et al., 2017). The scenario names result from the combination of the SSP narratives and the RCP radiative forcings and include a range of scenarios in which mitigation and adaptation challenges vary from low to very high (SSP119: SSP1 and SSP585: SSP5, with the radiative forcing reaching 1.9 and 8.5 W m^2 respectively at the end of this century).

For each scenario (n=6), daily air temperature and precipitation data (1950-2100) for the grid cell near the Torneträsk area was cut out and then bias-corrected at a daily scale against the observed meteorological data during 1985-2014 using the methodology by Hawkins et al., (2013). Precipitation events below a certain threshold (1.5 mm and 1 mm for the ANS and Katterjokk Station data, respectively) were removed to better match the observed wet-day frequency at each site.

4. Methods

4.1. Identifying research priorities by Expert Assessment

In Paper I, the most important research priorities to improve predictions of the ecosystem changes in the Torneträsk area were identified, focusing on five ecosystem components including local climate, permafrost, hydrology, vegetation, and the C cycle. The process involved several steps, including literature review, Expert Assessment, data analysis, and identification of research priorities.

The literature review examined long- and short-term field and laboratory studies, modeling papers, and synthesis of multiple studies conducted in the Torneträsk area. It aimed to (1) identify the drivers causing changes in each of the five ecosystem components above, and (2) the underlying processes, or causal pathways, by which a driver could affect a specific ecosystem component, directly or indirectly. In total, 30 drivers and over 700 processes were identified (Pascual et al. 2020, Appendix S1).

The Expert Assessment involved 27 leading scientists, selected based on their expertise in at least one of the five ecosystem components investigated, and their previous work in the study area (> 5 and up to > 50 years). The Expert Assessment consisted of an online survey, which was composed of three questions for each of the 30 drivers of interest that each expert had to answer concerning the ecosystem component they had expertise in. Question 1 asked them to rank (1–9) the importance of a given driver on the ecosystem component concerned, for the periods 2020–2040 (Question 1A) and 2040–2100 (Question 1B). Question 2 asked them to rank (1–9) how well studied are the potential future impacts of each driver on the ecosystem component concerned. Question 3 allowed the experts to provide self-reported expertise (1–5) for each particular driver. The experts had the option to suggest important studies that they believe need to be conducted in the future. The participants were provided with (i) general instructions; (ii) the findings of the literature review, and iii) a detailed example of how to answer the survey (Paper I, Appendix S1).

The responses were gathered according to each group of experts and analysed using the same methodology (Paper I, Appendix S2). Even though the experts were explicitly asked in Question 1 to assign the highest (9) and lowest (1) possible ranks to the most and least important drivers, respectively, a few responses were not given accordingly. To correct for this and make responses among experts comparable, we normalized them on a 0-10 scale. The scores for Question 2 were inverted to convert awareness into novelty, which indicates how new, or understudied, the ecosystem impacts of a given driver are. Then, the scores were normalized on a 0-10 scale so the variables importance and novelty could be compared. All the normalized scores for each variable (importance and novelty) were averaged. Responses with self-rated expertise of 1 (not familiar) were excluded to ensure that all estimates were provided by experts with expertise in each specific driver. In this study, the drivers considered research priorities were those that obtained high importance (>6) and high novelty (>5) scores.

4.2. Indices of frequency and intensity of WWEs

The frequency and intensity of WWEs was quantified through four indices, calculated using the observational daily air temperature and precipitation data described in section 3.3 (for Papers II and III) and the GCM daily output described in section 3.5 (for Paper III). The indices were derived from Vikhamar-Schuler et al. (2016), and are defined as follows:

- Index 1 refers to the number of melt days (MD) in a specific period, i.e, the number of days with air temperature > 0 °C.
- Index 2, the positive degree-day sum (PDD), is the sum of temperature values above the 0 °C threshold in a specific period and is a measure of the intensity of warm events.
- Index 3, the number of melt and precipitation days (MPD), counts the number of days with both positive air temperature and precipitation > 0 mm (1 mm in Paper III).
- Index 4 accumulates the total winter precipitation amounts (MPDsum) for the MPD and is a measure of the intensity of (potential) ROS events.

In Paper II, these indices were used to investigate the potential impacts of WWEs on permafrost thermal dynamics. Each WWE index was computed for the entire winter season (from November year 1 to March year 2). WWE indices calculated with the climate data from Katterjokk Station represent the westernmost CALM site of Katterjokk mire, whilst indices calculated with the ANS data represent the remaining six easterly CALM sites. For the permafrost manipulation site at Storflaket mire, the WWE indices and the other climatic variables were calculated for the period 2006-2020 using i) mean daily air temperature data from Storflaket, and ii) daily precipitation data from the ANS, as no *in situ* precipitation data was available.

In Paper III, the four WWE indices were calculated for each of the winter months (November-March). WWE indices calculated for the historical period using Katterjokk Station data represent the fen site, whereas the indices calculated with ANS data represent the birch forest, tundra, and peat plateau sites.

4.3. WWE-permafrost relationships

In Paper II, we examined the relationship between WWEs and permafrost dynamics in the snow manipulation experiment and at the seven CALM sites.

In the manipulation experiment, we examined the strength and direction of the WWE-permafrost relationships over the period 2006–2020 through Pearson's correlation coefficients between each of the WWE indices and i) annual maximum AL thickness, and ii) mean monthly ground temperatures (15 cm depth). The WWE-AL thickness relationships were compared to those observed between AL thickness and other relevant climatic parameters. The influence of the underlying snow conditions was investigated by performing the analyses in the ambient and manipulated plots separately.

For the analysis concerning the seven CALM sites, we examined site-level dynamics over time in the strength and direction of the relationships between maximum AL thickness and i) each WWE index, and ii) other relevant climatic variables, through the calculation of Pearson's correlation coefficients over 17-yr moving windows over the period 1978–2018.

Before these analyses, the permafrost-related variables were detrended to remove the significant trends over time (p-value $\leq$ 0.1) caused by the ongoing climate change and by the altered snowpack conditions in the manipulated plots at Storflaket mire. All climate variables and WWE indices presenting a significant (p-value $\leq$ 0.1) trend over the period concerned were also detrended.

4.4. Modeling ecosystem responses to future WWEs in LPJ-GUESS

In Paper III, we conducted a modeling experiment in LPJ-GUESS, with two main aims. First, we aimed to examine the potential future impacts of WWEs on the four subarctic ecosystem types investigated (Figures 1, 2), including impacts on physical variables such as snow depth and ground temperatures, and biogeochemical variables such as GPP, plant and soil respiration (R_a and R_h), and CH_4 emissions. Then, we aimed to identify key model limitations related to WWEs and potential improvements to better predict future ecosystem change.

Figure 2. Landscape images of the four ecosystem types investigated in Paper III: a) birch forest (photo by M. Johansson); tundra site, with birch forest in the background (photo by A. Michelsen); c) peat plateau at Storflaket (photo by D. Pascual); d) fen area at Katterjokk (photo by D. Pascual).

LPJ-GUESS is a process-based dynamic ecosystem model (Smith et al., 2001; 2014) widely used on regional and global scale studies of vegetation dynamics and biogeochemical fluxes. The model simulates vegetation dynamics (including vegetation establishment, mortality and competition, etc.), water fluxes, C and N cycles, and soil biogeochemistry. This study used the latest version of LPJ-GUESS (version 4.1, Smith et al. 2014), which includes a recently-developed dynamic, intermediate complexity snow scheme that can simulate up to five snow layers, their physical and thermal properties, and their changes throughout the cold season. This model version simulates freeze-thaw processes in snow layers and heat transport through the snowpack between the atmosphere and soil, based on the individual snow layer properties (e.g., temperature, density, thermal conductivity), enabling the representation of ROS events (Pongracz et al. 2021). Permafrost and wetland processes, including peatland hydrology, peatland-specific plant functional types (PFTs), and CH_4 emissions, are also represented in LPJ-GUESS (see Wania et al. 2009a, 2009b, 2010).

The model was run from 1913[1] to 2018 with daily meteorological data and other inputs described in section 3.3. When simulating the peat plateau and fen sites, we enabled high-latitude and wetland-specific PFTs in the simulations to better capture the site-specific conditions (Wania et al. 2009a). The applied PFTs were selected and parameterized following previous studies (e.g., Tang et al. 2015; Gustafson et al. 2021). Additional parameterization followed results from a sensitivity analysis that explored the influence of eight parameters and their interactions on the simulated snow density, snow depth, snow temperature, and ground temperature at each site. The model was evaluated with independent observational data (data not used to calibrate the model) when possible (section 3.4).

In addition to the HISTORICAL runs performed with the observation-based climate inputs described in section 3.3, we generated three WWE manipulation experiments (S1-S3) (Table 1). In these, the future monthly (November to March) anomalies (2071-2100 vs 1985-2014) in the frequency and intensity of melt days (S1), ROS (S2), and both (S3), in the GCM outputs (see section 3.5) were added to the HISTORICAL climate inputs in the period 1985-2018, maintaining the long-term climate means as unchanged as possible. These anomalies were calculated for each of the six CMIP6 scenarios based on the WWE indices described in section 4.2. An additional manipulation experiment (S4) was generated by adding the future winter anomalies (2071-2100 compared to 1984-2014) in monthly air temperature and precipitation to the daily air temperature and precipitation in the historical period 1985-2018. This allowed us to compare the magnitude and direction of the

[1] When climate monitoring started at the ANS.

ecosystem changes induced by altered WWEs to that of altered long-term climatic trends.

The differences in the outputs between the MANIPULATION and the HISTORICAL simulations were interpreted exclusively due to the effect of more frequent and intense WWEs (S1-S3), and of altered future winter climatologies (S4).

Table 1. Description of the HISTORICAL and MANIPULATION runs designed for each of the GCMs (CanESM5 and GFDL-ESM4) and SSPs (SSP119, SSP270, and SSP585) included in this study. Modified from Paper III.

Simulation name	**Description**	**Data**
S0	HISTORICAL scenario	Daily historical dataset (daily observational data 1985-2018)
S1	WWE manipulation experiment of altered frequency and intensity of melt days	Daily historical dataset + future monthly anomalies in the WWE indices 1 & 2 added to the daily historical data
S2	WWE manipulation experiment of altered frequency and intensity of ROS	Daily historical dataset + future monthly anomalies in the WWE indices 3 & 4 added to the daily historical data
S3	WWE manipulation experiment of altered frequency and intensity of both melt days and ROS	Daily historical dataset + future monthly anomalies in the WWE indices 1, 2, 3 & 4 added to the daily historical data
S4	Manipulation experiment of altered winter climatologies	Daily historical dataset + future winter monthly anomalies in air temperature and precipitation

4.5. Metagenomics and C fluxes in degrading permafrost peatlands

In Paper IV, whole metagenomics sequencing of microbial communities, greenhouse gas fluxes, the isotopic signature of emitted CH_4, and C to nitrogen (N) ratios (C:N), were measured in, and compared between, the natural landscape gradients of permafrost thaw in three peatlands that are part of the CALM program (Figure 1). These sites were selected to include the range of permafrost degradation rates and stages occurring in the Torneträsk area: Katterjok, the westernmost site, rapidly degraded and thawed completely around 2010; Kursflaket presents an intermediate degree of degradation and has been thawing at a rate of 1.3 cm y^{-1} since the late 1970s; Storflaket, the easternmost site, is the most stable permafrost site and has been degrading at 1.0 cm y^{-1}.

Measurements were made in 40 plots established across the three sites (Katterjåkk n = 8, Kursflaket n = 16, Storflaket n = 16). Each site was classified as drained, mesic, or wet, based on its AL thickness, vegetation composition, and local geomorphological and hydrological characteristics.

Measurements of CO_2 and CH_4 fluxes were conducted from July to August 2019 using the static chamber technique (Duchemin et al. 1999), in both light and dark conditions to establish Net Ecosystem Exchange (NEE) and Ecosystem Respiration (R_{eco}), which allowed us to calculate the Gross Primary Production (GPP). For site-to-site comparisons, plot level C fluxes were upscaled to the landscape scale based on the permafrost category classifications created for each site, derived from maximum AL thickness measurements performed across 100 x 100-meter grids in September 2019 (CALM 2019).

The $\delta^{13}C$ and δD isotopic signatures of the emitted CH_4 were measured in mesic and wet plots (Roeckmann et al. 2016).

Peat material for genomic and elemental analysis was collected from 34 plots, both at ~10 and ~40 cm (n = 68). All 68 samples were analysed for total C and N content. DNA samples were extracted from a subset of 40 peat samples and analysed for metagenomics sequencing of microbial communities.

To characterise the thermal and hydrological states of the mires, monitoring of ground temperature and peat volumetric water content was initiated in a mesic thaw area at each study site (wet in Katterjokk).

5. Results and Discussion

5.1. Research priorities for improving predictions of ecosystem change in the Torneträsk area (Paper I)

In Paper I, the drivers (including their direct and indirect impacts) of ecosystem change in the Torneträsk area were ranked according to their importance and novelty, which allowed us to identify future research priorities.

The top research priorities, i.e., those identified by at least three groups of experts (out of five; on local climate, permafrost, hydrology, vegetation, and the C cycle), include understanding impacts on ecosystems caused by altered frequency and intensity of winter warming events, evapotranspiration rates, rainfall, duration of snow cover and lake-ice, changed soil moisture, and droughts (Table 2). These research priorities are perceived as the most urgent elements to investigate to improve future predictions of ecosystem changes in the study area.

Table 2 Summary of the top 7 most important drivers (including their direct and indirect effects) (with mean importance estimates, on a 0–10 scale), and research priorities (identified by number of expert groups, on a 0–5 scale) for the time periods 2020-2040 and 2040 to 2100. Modified from Paper I.

Most important drivers (mean importance estimates across all groups)		**Research priorities (identified by number of expert groups)**	
2020 – 2040	**2040 - 2100**	**2020 – 2040**	**2040 – 2100**
Air temperature (8.5)	Air temperature (8.9)	Winter warming events (5)	Winter warming events (5)
Snow cover (7.8)	Snow cover (8.2)	Evapotranspiration (3)	Evapotranspiration (5)
Winter warming events (7.3)	Rainfall (8)	Rainfall (3)	Rainfall (4)
Rainfall (7)	Winter warming events (7.4)	Snow cover (3)	Snow cover (3)
Snow depth (6.8)	Evapotranspiration (6.8)	Lake-ice duration (3)	Lake-ice duration (3)
Evapotranspiration (6.5)	Soil moisture (6.7)	Soil moisture (3)	Soil moisture (3)
Soil moisture (6.4)	Snow depth (6.5)	Droughts (2)	Drought (3)

The only driver of ecosystem change that was identified as a research priority by all expert groups and study periods was winter warming events (WWEs).

In the Torneträsk area, as in many parts of the Arctic, the frequency and intensity of WWEs has increased in recent decades (e.g., Vikhamar-Schuler et al. 2016). These short-lasting winter episodes of unusually high air temperatures, which sometimes are accompanied with rainfall (rain on snow, or ROS), cause profound changes in the snowpack and the below-ground thermal regime, with major implications for multiple ecosystem processes ranging from microbial activity to permafrost and vegetation dynamics.

A few studies have investigated the effects of WWEs on arctic and subarctic ecosystems. Riseth et al. (2011) observed increasing ice layers in the snowpack after extreme WWEs with negative effects on local grazing conditions. Phoenix and Bjerke (2016) suggested that WWEs, mainly through altering the snow insulating effect and the plant available water in growing seasons, may be a potential driver of the 'browning' of vegetation (declining biomass or productivity) recently observed in some parts of the Arctic. Bokhorst et al. (2009) had already observed a 26% decline in vegetation greenness (NDVI, normalized difference vegetation index) after a severe WWE in 2007 in northern Scandinavia. Other observational and modeling studies suggested substantial permafrost warming after extreme ROS events in the short-term (e.g., Putkonen and Roe, 2003; Hansen et al. 2014) and long-term (Westermann et al. 2011) due to direct heat transfer and, very importantly, through latent heat release from re-freezing rain and meltwater within the snowpack. Contrastingly, a modelling study by Beer et al. (2018) suggested long-term permafrost cooling due to reductions in the insulating capacity of snow and vegetation. These and other impacts are likely to intensify under the predicted scenarios of enhanced WWEs (AMAP 2021). Despite these few studies, the future impacts of the ever more frequent and intense WWEs remain largely uncertain for most of the Arctic.

In Paper I, we highlighted, based on expert knowledge, important interactions among the drivers that have thus far been overlooked in the area, and proposed further studies according to the 3 M concept (Johansson et al. 2012), using monitoring, manipulation, and modelling. Among other relevant questions (Paper I, Appendix D), one important research question posed by the experts concerning WWEs was *''How do different snow conditions and vegetation characteristics influence the impacts of winter warming events on ground temperatures?''*. In this respect, we suggested to *"…(2) perform manipulation studies to investigate impacts of winter warming events on (i) land cover types other than dwarf shrub heathland (which has been covered by e.g. Bokhorst et al. (2010)), and (ii) on the snow thermal conductivity and ground temperatures across a latitudinal gradient, and under* *different snow and vegetation conditions…"* and *"…(4) improve the representation of snow-related processes such as snowmelt, rainwater percolation and refreeze in the snowpack, and the insulating capacity of snow, in ecosystem models".*

Papers II and III in this thesis tackle these aspects by using long-term monitoring and manipulation data (Paper II), and modeling (Paper III).

5.2. Lowland permafrost responses to WWEs (Paper II)

Paper II aimed to examine the impacts of WWEs (top-ranked research priority) on lowland permafrost under different snow conditions in the Torneträsk area.

The findings from the 15-year snow manipulation experiment indicate that WWEs might cause substantial near-surface permafrost warming in winter and that the presence of a relatively thick snowpack might amplify the warming effect of intense ROS events, leading to permafrost warming also in summer (Figure 3), and a greater maximum AL thickness. These results have two major implications for lowland permafrost dynamics. On the one hand, in areas already presenting relatively thick snowpacks, the long-term climate-induced ground warming and AL thickening is and will likely be exacerbated by the effects of the ever more frequent and intense WWEs. On the other hand, this could also occur in areas currently experiencing small snow accumulations where snow depth may increase due to the predicted greater winter precipitation (AMAP, 2021), or/and the preferential accumulation of wind-blown snow in areas experiencing surface subsidence following permafrost thaw. The latter process may become more frequent in permafrost areas where mean annual ground temperatures are close to the freezing point.

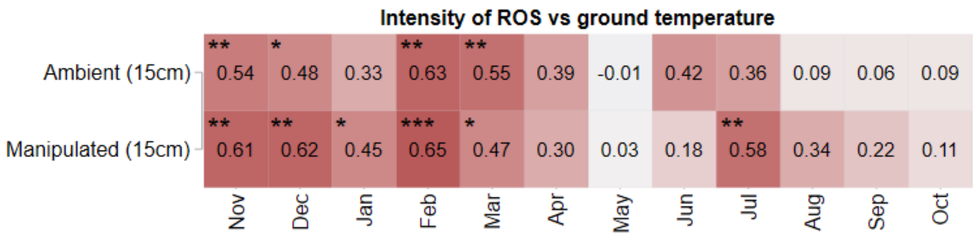

Figure 3. Pearson's correlation coefficients between the intensity of ROS events during the whole winter and mean monthly ground temperature, in ambient and manipulated plots. Significance levels are given by stars: * - 10%, ** - 5%, and *** - 1%. Modified from Paper II.

Over the manipulation experiment period 2006-2020, AL thickness in the manipulated plots was found to be much more strongly correlated with ROS events than with any other climatic variable, including those previously found to exert the largest influence on permafrost thermal dynamics in the Torneträsk area, such as summer air temperature, thawing degree days (TDD), and mean snow depth (Åkerman & Johansson, 2008).

The 40-year record of AL thickness at the seven CALM sites supports the findings from the manipulation experiment: there has been a consistent increase in the influence of WWEs on AL thickness over the period 1978-2018, while the influence of summer air temperature and TDD on AL thickness has decreased over the same period (Figure 4). This suggests that the lowland permafrost thermal dynamics in the Torneträsk area may no longer be dominated by summer climatic variables, as previously found (Åkerman & Johansson, 2008), but by winter climatic processes such as WWEs. The transition from summer-dominated to winter-dominated permafrost thermal regimes in the mid- 1990s coincides temporally with a strong enhancement of WWEs in the area. Winter temperatures and snow depth have also increased substantially in the area in recent decades (e.g., Callaghan et al. 2010), but their influence on AL thickness increased at a much weaker pace compared to WWEs: this would confirm the amplifying effect of WWEs on permafrost warming.

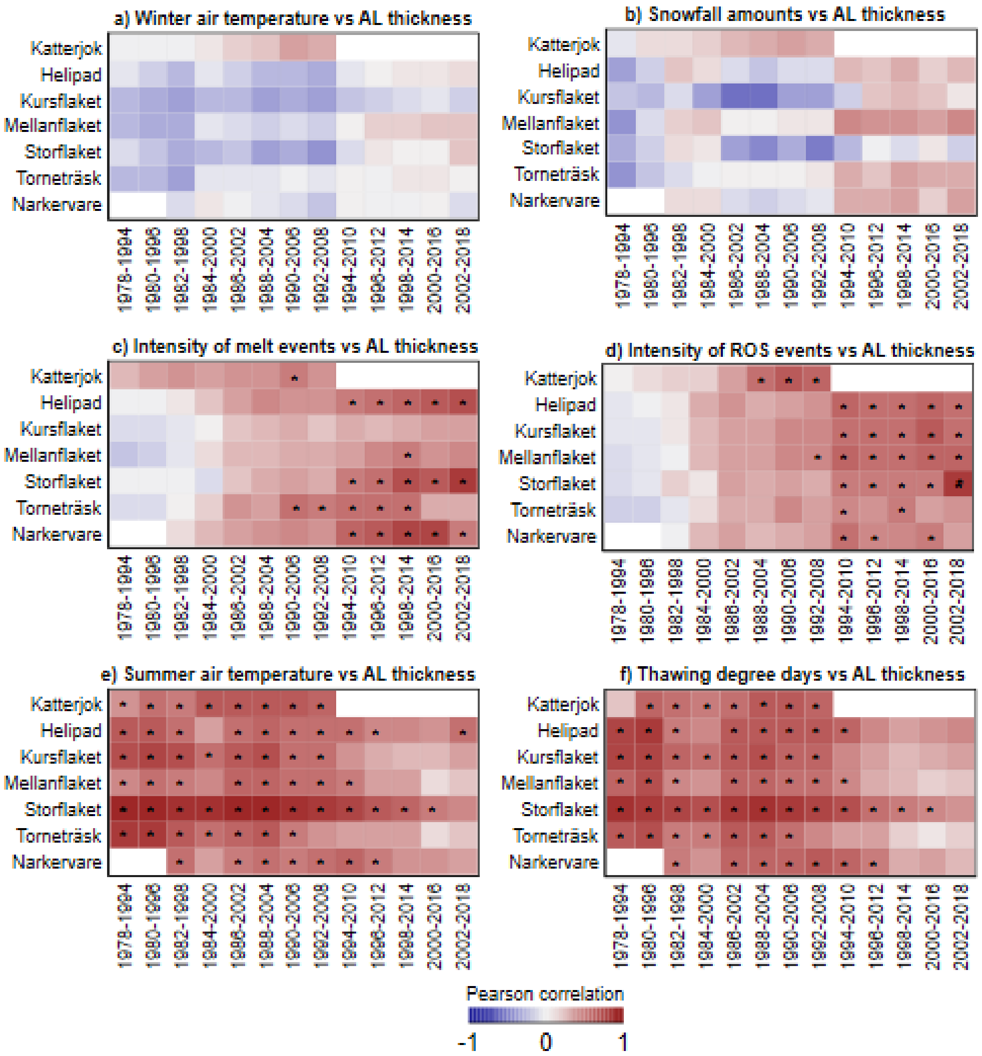

Figure 4. Moving correlation coefficients, calculated over 17-yr windows, between the detrended maximum AL thickness and a) mean winter air temperatures, b) snowfall amounts (precipitation falling when air temperature < 0 °C), c) intensity of melt events, d) intensity of ROS events, e) mean summer air temperatures (JJA), and f) TDD (May–September), in seven CALM sites over the period 1978–2018. The periods with missing data in Narkervare occur due to the late initiation of AL monitoring in this site (since 1984), while in Katterjokk mire this occurs due to permafrost disappearance. The sites are displayed top-down according to their location in the Northwest - Southeast climatic transect. Stars (*) indicate significant correlations ($P < 0.05$). Modified from Paper II.

This study is the first attempt to investigate the short- and long-term effects of WWEs on permafrost thermal dynamics using long-term manipulation and monitoring data. Few studies investigated the short-term effects using observational data and modeling (e.g., Putkonen and Roe, 2003; Hansen et al. 2014), all of which identified a short-term warming effect of WWEs on permafrost. The long-lasting impacts of WWEs on permafrost have only been investigated by a few modeling studies, with contrasting results, from strong and long-lasting permafrost warming (Westermann et al. 2011) to permafrost cooling (Beer et al. 2018). The main reason for this discrepancy may be related to the fact that the latter study did not account for the percolation of rainwater and its subsequent re-freeze in the snowpack, a process in which large quantities of latent heat are deposited at the snowpack and the surface soil layer (Woo and Heron, 1981). This process may exert stronger effects under the presence of thick snowpacks capable of absorbing and holding larger quantities of melt and rainwater until it freezes, which could explain the stronger and more durable effects of ROS events in our manipulated plots.

These and other processes are not accounted for in most land-surface models (e.g., Lawrence et al., 2008; Etzelmüller et al., 2011; Ekici et al. 2015), and therefore it is likely that most of the current estimates of ecosystem change in the Arctic are inaccurate partly because they overlook some of the potentially large impacts of WWEs. This could be addressed by 1) realistically representing in modelling schemes the melt and rainwater infiltration in the snowpack, its subsequent refreeze, and the resulting latent heat release, 2) accounting for the spatially varying surface microtopography of permafrost terrain, and the spatial heterogeneity of snow properties across the Arctic, in modeling schemes, 3) developing more sophisticated downscaling algorithms producing climate datasets at spatial and temporal scales relevant for WWEs, and 4) conducting modeling studies evaluating the effects of enhanced WWEs on permafrost and ecosystem dynamics in the Arctic.

5.3. Ecosystem responses to predicted WWE scenarios (Paper III)

In Paper III, we investigated the responses of four dominant ecosystem types to different WWE frequencies and intensities using the ecosystem model LPJ-GUESS, and identified model gaps in representing these ecosystem responses.

LPJ-GUESS simulated the seasonal snow cover patterns at all sites and the short-term fluctuations in snow depth and GT during WWEs, but had difficulties accurately simulating the snowpack thickness at each site, as well as the magnitudes of the snow depth and GT fluctuations during WWEs.

In response to the WWE manipulation experiments, the model simulated decreases in winter GT in all ecosystem types under the vast majority of WWE experiments (Figure 5a-d). These GT decreases were driven by the modeled reductions in snow insulation, which declines as a combination of 1) the reduction in snow depth (Figure 5i-l), and 2) the change in snow properties (i.e, higher thermal conductivity and lower heat capacity) due to freeze-thaw processes, facilitating the heat exchange between atmosphere and soil. The greater reductions in GT occurred in sites presenting thicker snowpacks where the snow insulating effect is the largest, such as at the fen site (up to 2 °C) compared to the birch forest, peat plateau, and tundra sites, which exhibit shallower snowpacks (up to 1 °C). Noticeably, these modelled ground cooling responses were largely induced by the warmer air temperatures of enhanced melt days (causing snow melt), whilst the effects of enhanced ROS were weak. The modelled cooling effects diminished above a certain WWE magnitude, when further reductions in snow depth had a smaller effect on GT compared to the stronger warming effects of longer and more extreme WWEs.

The modeled winter ground cooling effect of WWEs partially endured till the growing-season (Figure 5e-h), especially at the fen site which experienced the greatest winter GT cooling and the largest reduction in groundwater content (GWC), which in turn reduced the soil thermal conductivity and may have hindered the heat transfer from air deeper into the ground.

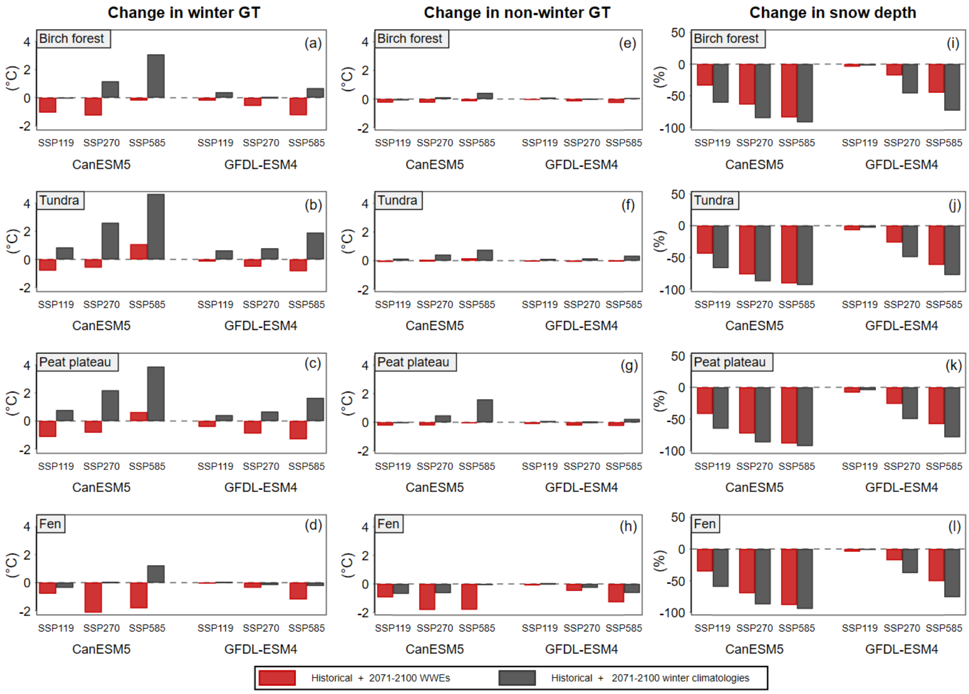

Figure 5. Differences between the model output of the MANIPULATION run (historical data with added future WWEs, or S3, dark red; historical data with added future winter climatologies, or S4, dark grey) and the HISTORICAL runs (S0) for the variables winter GT (°C; left column), non-winter GT (°C; middle column), and winter snow depth (%; right column), at the simulated sites. Modified from Paper I.

The WWE-induced impacts on GT and, to a lesser extent, on GWC, caused substantial changes in biogeochemical processes in all ecosystem types (Figure 6). For example, WWE events caused reductions in net primary production (NPP) ranging between 5% and 20% except in the tundra, where both positive and negative fluctuations (<5%) occurred. Heterotrophic respiration (R_h), highly influenced by GT (Natali et al. 2019), increased or decreased by up to 25% following the GT responses, and CH_4 emissions decreased by up to 50% at the fen site and marginally at the peat plateau. The different changes in biogeochemical fluxes resulted in overall reductions in NEE at all sites ranging between 20% and 50% (i.e. became weaker C sinks), except for the fen site where NEE increased slightly (i.e. became a stronger C sink), due to comparatively larger losses of respired soil C.

As opposed to WWEs, altered winter climatologies caused increases in the modeled winter GT in all sites (up to 4 °C) despite snowpack reductions of >80%, and smaller increases in summer GT. This caused sizable changes in biogeochemical variables, often in the opposite direction as seen in the WWE experiments.

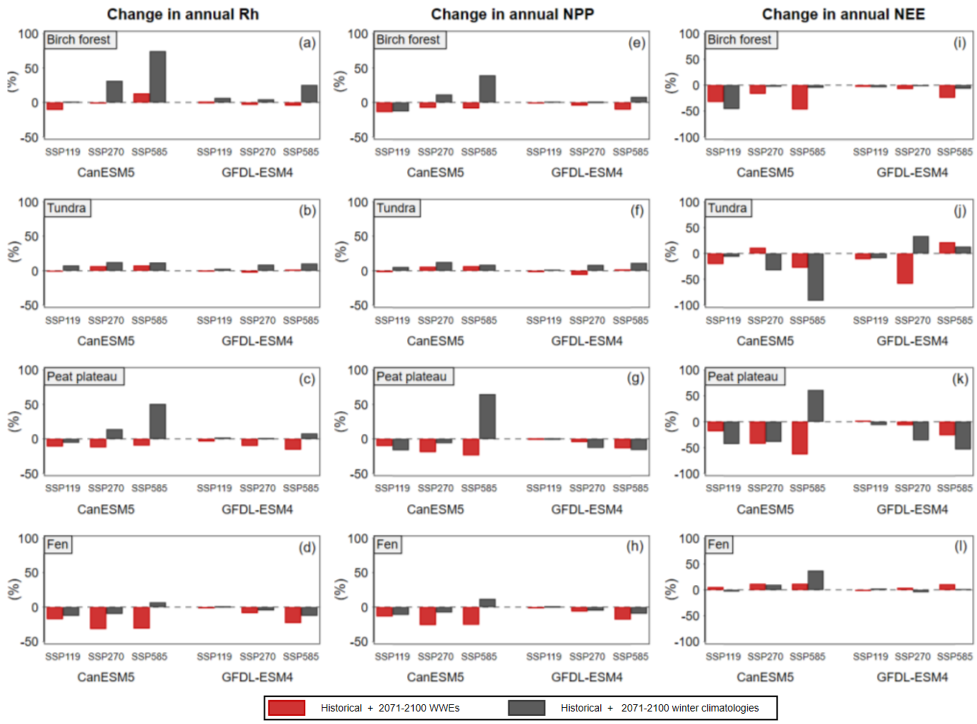

Figure 6. Differences between the model output of the MANIPULATION runs (historical data with added future WWEs, or S3, dark red; historical data with added future winter climatologies, or S4, dark grey) and the HISTORICAL runs (S0), for the variables annual Rh (%; left column), annual net primary production (NPP; %; middle column), and annual NEE (%; right column), at the simulated sites.

The modelled impacts of the WWE experiments were substantial and, often, their magnitudes were comparable to those caused by altered future winter climatologies. This suggests that WWEs, despite their short duration, may induce changes in the high-latitude ecosystems C cycling of magnitudes comparable to changes induced by long-term climatic trends.

This study highlights the urgency of realistically simulating the effects of WWEs on snow properties and GT for improving estimates of future changes in water and C fluxes in high latitudes. For example, winter Rh, which currently offsets as much as ~40% of the measured annual vegetation C uptake at our sites, could change by up to 25% under WWE-induced GT changes of the magnitudes reported in our study, according to recent estimates of the winter Rh response curve to GT (Natali et al. 2019). However, the biogeochemical processes investigated are particularly dependent on GT and GWC. As revealed by the model evaluation, LPJ-GUESS did not accurately capture the observed GT responses to WWEs, and therefore the modeled impacts reported here should not be interpreted as accurate estimates of future impacts of WWEs, but rather as a sensitivity test of the current model's responses to altered frequencies and intensities of WWEs. In addition, there is a mismatch in the direction of the GT responses to WWEs between our modelling results and findings from observations and more sophisticated snow and permafrost models (e.g., Putkonen and Roe, 2003; Westernmann et al 2011; Hansen et al. 2014; Pascual et al. 2022). This suggests that LPJ-GUESS lacks some essential processes and interactions controlling the timing and magnitude of heat exchanges between atmosphere, snowpack, water, and soil. These limitations include:

- The lack of surface energy balance in LPJ-GUESS, which affects the computed snow layer and ground temperatures, and the rate and magnitude of snowmelt events.
- The simplistic water retention scheme applied in LPJ-GUESS, which minimizes the amount of water retained in the snowpack, which in turn 1) limits the amount of latent heat released upon freezing, which makes the model fairly insensitive to extreme melt and ROS events, and 2) prevents the formation of ice layers in the snowpack, which could significantly affect the heat transfer capacity of the snowpack and therefore the simulated GT.
- The model's daily timestep, which may be too coarse to capture the sub-daily freeze-thaw cycles and the related processes within the snowpack.

To address these limitations, the snow scheme in LPJ-GUESS should be further developed, or existing more complex snow models should be utilized. A recent extension of LPJ-GUESS with detailed land surface processes and surface energy balance, LPJ-GUESS LSMv1.0 (Belda et al. 2022), could be used to assess whether the mismatch between the modelled and the observed impacts of WWEs is reduced.

This paper examined the responses of different ecosystem types to future changes in climate extremes and long-term climatologies, but it is likely that these responses also vary spatially within ecosystem types themselves. In Paper IV, we investigated whether the rate and timing of permafrost thaw affects the microbial dynamics and the exchange of greenhouse gases from degrading permafrost peatlands.

5.4. Microbial dynamics and greenhouse gas emissions from degrading permafrost peatlands (Paper IV)

In paper III, we investigated whether different rates and stages of permafrost degradation in peatlands affect greenhouse gas exchange through an altered microbial taxonomic structure and function.

The taxonomic structure of the microbial communities and the functional potential of methane-producing genes showed high variability across the permafrost thaw gradients within each site, i.e., from drained to mesic and ultimately wet areas, and as hypothesized in Paper IV, also across sites, i.e., when comparing similar thaw categories between the Storflaket, Kursflaket, and Katterjokk sites.

As compared to the drained areas in Storflaket, the drained areas in the more degraded permafrost mire at Kursflaket presented a significantly higher ($p \leq 0.05$) relative abundance of Actinobacteria, Acidobacteria, and Solibacteres, suggesting a higher decomposition potential of previously frozen organic compounds (Zhang et al., 2019) that became exposed to decomposition following the more rapid permafrost thaw at Kursflaket. Mesic areas did not present any significant differences in the taxonomic structure of microbial communities between sites, likely because the microbial groups occurring therein are shifting and adapting to the rapidly changing environmental conditions, which tends to homogenise bacterial community structure (Monteux et al. 2018). In wet areas, we expected the largest variation across sites between the slowly degrading mire at Storflaket and the fully-thawed mire at Katterjokk, but these sites showed no significant differences in the relative abundance of microbial taxa.

Within sites, the composition of microbial taxa in drained areas differed substantially from that in mesic and wet areas, which in turn exhibited a more similar taxonomic structure. Previous studies in nearby permafrost mires had already observed shifts in microbial composition in response to permafrost thaw and the associated hydrological shifts (e.g., Mondav et al. 2017).

The functional potential of methane-producing genes also varied across the thaw gradients in the different sites: the abundance of genes with high functional potential for hydrogenotrophic methanogenesis was lowest in drained areas, increased in mesic areas (significantly in Storflaket; $p \leq 0.05$), and was significantly higher in wet areas compared to drained areas ($p \leq 0.10$). The overall functional potential of methane-producing genes did not vary significantly across sites, although the opposite was true regarding the abundance of specific genes. The dominant methane production pathway during the measurement period in the study sites was hydrogenotrophic, as suggested by both the functional potential of methane-producing genes and the $\delta^{13}C_{CH4}$ isotopic signal.

These differences in microbial community structure and functional potential may have contributed to the substantial differences in the form and rates of emitted greenhouse gases across sites and within them. At both Storflaket and Kursflaket, the net C uptake rates increased with thaw, i.e, from drained to wet areas. Moreover, wet areas in the most degraded mire at Katterjåkk showed a ~2-fold greater C sink capacity compared to wet areas at Storflaket and Kursflaket. At Storflaket and Kursflaket, CH_4 fluxes increased by >50 times from drained to wet areas. However, the CH_4 emission rates decreased across the thaw gradient: Storflaket, the most stable permafrost site, yielded the largest CH_4 emission rates, whilst these were 15% lower at Kursfluket and 34% lower at Katterjåkk. This occurred despite the increase in GT, and the consistent decrease in C:N ratios (generally associated with increases in organic matter quality), observed across the thaw gradient, which are commonly linked to higher CO_2 and CH_4 production (e.g., Hodgkins et al. 2014).

The upscaling of the CO_2 fluxes indicated that Katterjåkk as a whole absorbed >3 times more CO_2 than Storflaket and Kursflaket, although its larger extent of wet areas (100%) resulted in 3-fold greater CH_4 emissions compared to Storflaket (21% wet area), and slightly larger CH_4 emissions than at Kursflaket (>70% wet area) (Figure 7).

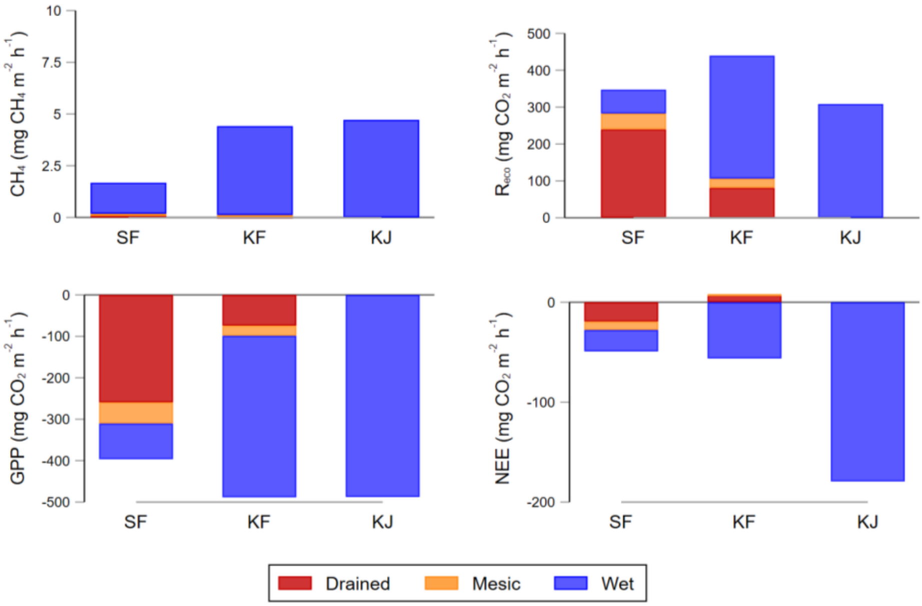

Figure 7. Upscaled CH_4, GPP. R_{eco}, and NEE fluxes, and contribution of each thaw category (drained = red, mesic = orange, wet = blue) at each site.

Our measurements are likely overestimating the potential ecosystem CO_2 uptake and CH_4 release. This is because we sampled the peak of the growing season during day time, when C uptake and CH_4 emissions peak, but these emissions continue at night and during the rest of the growing season (when photosynthesis diminishes) via plant respiration and microbial metabolism, and in the case of microbial metabolism also in winter when photosynthesis ceases (e.g., Natali et al. 2019). Hence, inferring the long-term net carbon budget from these measurements is not possible. Previous studies in similar settings suggest that these ecosystems are not likely to be strong C sinks (e.g., Tang et al. 2015; Lundin et al. 2016). Our flux measurements do not capture the temporal variability, but demonstrate the high spatial variability across sites experiencing different stages of permafrost thaw. This variability in the measured C fluxes do not always follow a clear pattern across the permafrost thaw gradients, which makes it challenging to infer potential future C dynamics from degrading permafrost peatlands. However, the increasing C sink capacity with thaw, and the greater CH_4 emissions in the recently-developed wetland settings (Storflaket, followed by Kursflaket), suggests that, in the long run, the net greenhouse gas balance of permafrost wetlands may be favourable for the climate.

Conclusions

This thesis provides the first comprehensive assessment of the current state of knowledge, and proposes research priorities regarding ecosystem change in a subarctic area in northern Sweden. The most important research priorities identified include studies of the impacts on ecosystems caused by altered frequency and intensity of WWEs, evapotranspiration rates, rainfall, duration of snow cover and lake-ice, changed soil moisture, and droughts.

WWEs were the only driver of ecosystem change identified as a research priority by all expert groups. Hence, this thesis also investigated, through monitoring data, manipulation experiments, and ecosystem modeling, how WWEs affect the permafrost thermal dynamics, and how the WWE impacts on ground temperature and water fluxes influenced biogeochemical fluxes in different ecosystem types. Further, this thesis identified current monitoring, manipulation, and modeling gaps related to WWE that, if addressed, could help perform more accurate predictions of ecosystem change in arctic and subarctic areas.

We found that WWEs might cause substantial near-surface permafrost warming in winter and that the presence of a relatively thick snowpack might amplify the intensity and duration of the warming effect of ROS events. The data also suggest a recent shift from summer- to winter-dominated permafrost thermal regime in the study area.

The modeled ecosystem responses to enhanced WWE were substantial and of magnitudes often comparable to those of altered winter climatologies. These results further emphasized that WWEs, despite their short duration, may cause profound changes in high-latitude ecosystems and that their effects need to be realistically simulated in ecosystem models. The direction of the modeled impacts differed from those found in the majority of the observation-based literature. We identified model limitations contributing to this mismatch, including 1) the lack of surface energy balance, 2) the model’s daily timestep, 3) and the simplistic water retention scheme applied in LPJ-GUESS.

Climate change and extreme events such as WWEs hit the vulnerable lowland permafrost areas in the Torneträsk areas differently, and the underlying snow conditions played an important role in modulating these impacts. This thesis revealed, through metagenomic sequencing and greenhouse gas measurements, that different rates and stages of permafrost degradation result in notable differences in the taxonomic structure and function of the microbial communities within peatlands and between them, resulting in high spatial variability in greenhouse gas emissions. This highlights the need for expanding the monitoring of peatland fluxes and microbial dynamics, currently based on a single or very few sites, to obtain the information needed to predict future changes in peatland at larger catchment and regional scales.

The great biological, meteorological, and geomorphological diversity of the Torneträsk area, its unique datasets, and its rapidly transforming ecosystems, makes the area a microcosm of the subarctic. The understanding obtained in this thesis can therefore help the scientific community understand the ongoing and future ecosystem changes in the Torneträsk area, and contribute to improving predictions of future ecosystem changes at a larger scale.

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