Oona Leppiniemi is a physical geographer specializing in subarctic environments and permafrost. She completed her PhD at the University of Oulu's Geography Research Unit, focusing on palsas—permafrost landforms highly sensitive to climate change that contribute to the abiotic and biotic diversity of northern peatlands and store significant organic carbon. She uses statistical modelling to examine the environmental drivers of palsa mire occurrence and morpho-ecological state, and to predict their responses to future climate conditions. Her thesis reveals the distribution and degradation of palsa mires across the Northern Hemisphere, forecasts a dramatic loss of suitable environments by century's end, and shows strong degradation of Finnish palsas over the past 50 years. By working at spatial scales from local to circumpolar, she highlights how key drivers vary geographically, deepening understanding of permafrost dynamics under global change.

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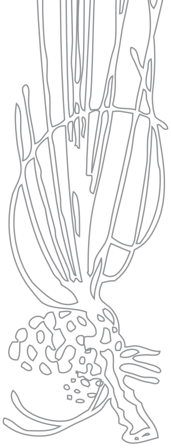

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Contents

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Abstract

Palsas are unique permafrost landforms that are found in the peatlands of discontinuous and sporadic permafrost regions across the Northern Hemisphere. Palsa mounds create diverse microhabitats for both plant and animal species, making them important features that support the biodiversity of periglacial environments. In addition to their ecological importance, palsa mires also are linked to the global carbon cycle and greenhouse gas emissions through permafrost degradation. Future thawing of permafrost is projected to release large amounts of greenhouse gases from northern peatlands, which can further accelerate global climate warming. Therefore, the changing permafrost dynamics make palsa mires an interesting and critical research topic, one that can help us to better recognize and understand the ongoing and future changes in periglacial environments.

The main objective of this thesis is to provide a comprehensive understanding of the environmental factors influencing the occurrence and morpho-ecological state of palsa mires, and to predict future changes in palsa distribution. To achieve this, the thesis employs a multi-scale approach, integrating remote sensing data and statistical modelling across spatial scales ranging from circumpolar to local. First, the environmental characteristics of palsa mires in different parts of the Northern Hemisphere are examined by regional comparisons. Second, circumpolar changes in the suitable environments for palsas are predicted under three different future trajectories of greenhouse gas concentrations. Finally, the morpho-ecological state and degradation of palsa mires at the local scale are investigated in northern Finland.

The results show that palsa mires occur in narrow but regionally varying environmental settings, with climatic factors and soil moisture conditions playing a key role in defining suitable environments for the landforms. Without effective climate change mitigation, environments suitable for palsas are projected to almost completely disappear in the northern permafrost region by the end of the century. This projection is consistent with observations showing the overall poor morpho-ecological state of Finnish palsa mires and their significant degradation over the past 50 years. The results also highlight the scale-dependent influence of environmental factors for the occurrence and state of palsa mires. While climatic factors were consistently important across spatial scales, the influence of seasonal freeze-thaw dynamics and soil moisture varied between larger-scale and smaller-scale studies.

This thesis highlights the urgent need to understand the impacts of climate change on permafrost landscapes. The predicted dramatic loss of suitable environments for palsa mires underscores their vulnerability and the potential ecological consequences of their degradation. By integrating spatial modelling across different spatial scales, this thesis provides novel insights into the complex interplay between climatic and environmental factors governing the distribution and state of palsas. The results improve our understanding of the ongoing changes in the northern permafrost regions and provide valuable information to support policymakers in planning conservation efforts and in making sustainable decisions regarding permafrost regions and peatlands.

Keywords: palsa, peat plateau, permafrost peatlands, permafrost degradation, climate change, statistical modelling

Tiivistelmä (abstract in Finnish)

Palsat ovat ainutlaatuisia ikiroutamuodostumia, joita esiintyy pohjoisella pallonpuoliskolla epäjatkuvan ja sporadisen ikirouta-alueen soilla. Palsakummut luovat suolle vaihtelevia mikrohabitaatteja eri kasvi- ja eläinlajeille, ja siten ne korostavat periglasiaalisten ympäristöjen monimuotoisuutta. Paikallisemman ekologisen merkityksensä lisäksi palsasoilla on merkitystä myös globaalilla mittakaavalla tarkastellessa, sillä ikiroutasuot ovat merkittäviä orgaanisen hiilen varastoja. Ikiroudan sulaessa palsasoilta ilmastonmuutoksen seurauksena niihin varastoitunut hiili pääsee vapautumaan ilmakehään, mikä voi entisestään kiihdyttää ilmaston lämpenemistä. Juuri ikiroudan dynamiikassa tapahtuvat muutokset tekevät palsasoista mielenkiintoisen ja ajankohtaisen tutkimuskohteen. Tutkimalla palsasoita pystymme paremmin tunnistamaan ja ymmärtämään laajemminkin pohjoisissa ympäristöissä tapahtuvia muutoksia nyt ja tulevaisuudessa.

Tämän väitöskirjan päätavoitteena on syventää ymmärrystämme palsasoiden esiintymiseen ja morfoekologiseen tilaan vaikuttavista ympäristötekijöistä, sekä ennustaa tulevia muutoksia palsasoiden esiintymisessä pohjoisella pallonpuoliskolla. Väitöskirjassa teemoja tarkastellaan eri mittakaavoilla aina sirkumpolaarisesta paikalliseen tasoon saakka hyödyntäen kaukokartoitusaineistoja ja tilastollisen mallintamisen menetelmiä. Ensimmäisessä osatyössä vertaillaan alueellisesti palsasoiden ympäristöolosuhteita eri puolilla pohjoista pallonpuoliskoa. Toisessa osatyössä ennustetaan kolmen eri tulevaisuusskenaarion avulla palsoille sopivien ympäristöjen esiintymisessä tapahtuvia muutoksia pohjoisella ikirouta-alueella. Viimeisessä osatyössä syvennytään palsasoiden morfoekologiseen tilaan ja palsojen sulamistrendejä tutkitaan paikallisella tasolla Pohjois-Suomessa.

Väitöskirjan tulokset osoittavat, että palsasuot esiintyvät pohjoisella pallonpuoliskolla kapeissa, mutta alueellisesti vaihtelevissa ympäristöolosuhteissa. Ilmastolliset tekijät ja maaperän kosteus ovat tulosten mukaan keskeisessä roolissa suotuisten ympäristöjen määrittämisessä näille uhanalaisille ikiroutamuodostumille. Ilman tehokasta kasvihuonekaasupäästöjen leikkaamista suotuisten ympäristöolosuhteiden kuitenkin ennustetaan katoavan pohjoiselta ikirouta-alueelta lähes kokonaan jo tämän vuosisadan loppuun mennessä. Tehdyt ennusteet ovat linjassa väitöskirjan kolmannessa osatyössä havaitun Suomen palsasoiden yleisen heikon morfoekologisen tilan sekä viimeisten 50 vuoden aikana tapahtuneen voimakkaan sulamisen kanssa. Väitöskirjan tulokset osoittavat myös, että käytetty tarkastelutaso vaikuttaa eri muuttujien tärkeyteen palsasoiden esiintymistä ja tilaa tutkittaessa. Vaikka ilmastolliset tekijät ovat tärkeitä palsasoille kaikilla tarkastelutasoilla, havaittiin jäätymis- ja sulamiskauden olosuhteiden sekä maaperän kosteuden merkityksen vaihtelevan eri tarkastelutasojen välillä.

Tässä väitöskirjassa saadut tulokset osoittavat ilmastonmuutoksella olevan kriittisiä vaikutuksia pohjoisen pallonpuoliskon ikirouta-alueille, sillä palsasoille sopivien ympäristöolosuhteiden ennustettu katoaminen korostaa niiden ilmastoherkkyyttä. Palsojen sulaminen voi keskeisesti vaikuttaa pohjoisen luonnon monimuotoisuuteen ja ekosysteemien toimintaan. Hyödyntämällä eri mittakaavoja tämä väitöskirja tuo esille uusia näkökulmia erilaisten ympäristötekijöiden merkityksestä palsoille ja auttaa ymmärtämään paremmin palsasoiden esiintymistä ja morfoekologista tilaa. Lisäksi väitöskirja syventää ymmärrystämme ikirouta-alueella ja -soilla meneillään olevista muutoksista ja tarjoaa siten arvokasta taustatietoa päätöksentekijöille erilaisten suojelutoimien kohdentamiseen ja kestävien ratkaisujen tekemiseen.

Avainsanat: palsa, turvelaakio, ikiroutasuot, ikiroudan sulaminen, ilmastonmuutos, tilastollinen mallintaminen

List of original publications and author contributions

Please see the list of original publications with author contributions below. In this thesis, the original papers are referred by their Roman numerals thorough the text:

I Leppiniemi O, Karjalainen O, Aalto J, Luoto M, and Hjort J (2025). Environmental drivers of palsa and peat plateau occurrences: a regional comparison across the Northern Hemisphere. *Permafrost and Periglacial Processe*s 36:37–50. https://doi.org/10.1002/ppp.2253

II Leppiniemi O, Karjalainen O, Aalto J, Luoto M, and Hjort J (2023). Environmental spaces for palsas and peat plateaus are disappearing at a circumpolar scale. *The Cryosphere* 17: 3157–3176. https://doi.org/10.5194/tc-17-3157-2023

In Papers I–II, Leppiniemi developed the original research ideas and study designs together with Karjalainen and Hjort. Leppiniemi collected the response data. Leppiniemi, Karjalainen and Aalto compiled the environmental data and performed the processing of the data. Statistical and geospatial analyses were performed by Leppiniemi with contributions from Karjalainen and Hjort. Leppiniemi wrote the original manuscripts, which were reviewed by all authors. Leppiniemi was responsible for the data visualizations.

III Leppiniemi O, Karjalainen O, Aalto J, Yletyinen E, Luoto M, and Hjort J (Manuscript). The morpho-ecological state of palsa mires: insights from high-resolution spatial modelling.

In Paper III, the research was designed by Leppiniemi, Karjalainen and Hjort. The research data were compiled by Leppiniemi, Yletyinen, Aalto, Karjalainen and Hjort. Data processing was carried out by Leppiniemi. Statistical and geospatial analyses were performed by Leppiniemi with contributions from Karjalainen, Hjort, Aalto, and Luoto. Leppiniemi wrote the original manuscript which was reviewed by all authors. Leppiniemi was responsible for the data visualization.

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Growing up as a researcher is much more joyful when you are surrounded with bright-minded and wonderful people. Thus, I want to thank all the members of the Geography Research Unit for your camaraderie and all the inspiration you gave me during these years. I want to thank especially the members of the Physical Geography Lab for all the stimulating discussions, collaborations, and the innovative ideas. Your peer support has been priceless. Furthermore, sincere thanks go to Tuija, Petteri, Marjo, and Henriikka. Beside my supervisors, you were the people who supported, helped, and encouraged me the most when I needed it, laughed with me, and gave me a sense of belonging in our working community. I am also grateful for Maija, Marjo, Marika, and Niina for all the supportive discussions and joint writing sessions while finishing this thesis. It was a privilege to work together and share all the emotions, problems, and thoughts with you at the different stages of the writing process.

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Overall, I want to express my deepest gratitude to my parents and extended family members for their loving upbringing, keen interest in my work and support throughout my life. I have always enjoyed studying and questioning everything between earth and sky, sometimes to the point of annoyance, and I would like to thank you for encouraging me to continue doing so. Finally, to my husband Karri, your everlasting faith in me and in this PhD journey, even when I doubted myself, has been a constant source of inspiration and motivation for me to keep going. There are so many words to say to you, but above all I want to thank you for sharing these years with ups and downs with me, for bringing me chocolate and strawberries way too often, and for reminding me to relax as well.

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Glossary

Area under the curve (AUC): A performance metric for classification models, representing the ability of a model to distinguish between classes. AUC is the area under the receiver operating characteristic (ROC) curve, where 1 indicates perfect classification.

Akaike information criterion (AIC): A measure used in model comparison that evaluates the goodness of fit of a statistical model while penalizing for the number of parameters. Smaller AIC values indicate better models.

Freezing degree days (FDD): A measure of cumulative freezing conditions, calculated by summing the average temperature below freezing (<0°C) for each day during the freezing season. It reflects the intensity and duration of cold periods.

Coupled model intercomparison project (CMIP): A collaborative framework for climate modelling that coordinates simulations from multiple research groups worldwide to understand past, present, and future climate changes under standardized scenarios and experiments.

Generalized additive model (GAM): A modelling technique that combines multiple smooth functions of predictor variables to capture nonlinear relationships between variables.

Generalized boosted method (GBM): A machine learning algorithm that builds models incrementally by combining decision trees to create a stronger predictive model.

Generalized linear model (GLM): An extension of linear regression model that allows for response variables to have error distributions other than normal. Often used for count, binary, or other non-normally distributed data.

Mean annual air temperature (MAAT): The average air temperature over a year, calculated by averaging daily temperatures over a year.

Mean annual precipitation (MAP): The average total precipitation (rainfall and snowfall) over a year.

Maximum entropy (MaxEnt): A machine learning method used to predict distributions by estimating the most uniform (maximum entropy) distribution constrained by environmental data. MaxEnt is so-called presence-only method.

Non-metric multidimensional scaling (NMDS): An ordination method used to visualize the similarity or dissimilarity of data points in a reduced number of dimensions, commonly applied in ecological data analysis.

Representative concentration pathways (RCPs): Scenarios used in climate modelling that describe different trajectories of greenhouse gas concentrations, such as RCP2.6, RCP4.5, and RCP8.5, representing different levels of future climate forcing.

Random forest (RF): An ensemble machine learning algorithm that builds and merges multiple classification trees using random sampling of predictors and training data to improve predictive accuracy and control overfitting.

Shared socioeconomic pathways (SSPs): Scenarios used in climate research that describe alternative trajectories of global socioeconomic development, including population growth, economic trends, and energy use, influencing future greenhouse gas emissions and climate outcomes.

Soil organic carbon (SOC): The carbon content of organic compounds found in the soil. SOC plays a critical role in soil fertility and carbon sequestration.

Thawing degree day (TDD): A measure of cumulative thawing conditions, calculated by summing the average temperatures above freezing (>0 °C) for each day during the thawing season. It indicates the intensity and duration of warm periods.

True skill statistic (TSS): A measure used to evaluate the accuracy of a binary classification model, with values ranging from −1 to 1, where 1 indicates a perfect model.

Topographical wetness index (TWI): A measure of the spatial distribution of soil moisture, calculated based on the slope and upstream contributing area, proxying areas that are likely to be wetter or drier.

1 Introduction

Northern environments hold profound significance for people and for natural diversity. The unique environments of the North are deeply intertwined with the cultural heritage, traditional livelihoods, and identities of the people who inhabit the region (Larsen & Fondahl 2015; Ward Jones *et al.* 2024). These landscapes also serve as critical habitats that support biodiversity adapted to subarctic and Arctic conditions (Arctic Council 2013) and play essential roles in global systems such as the carbon cycle (Miner *et al.* 2022; Olefeldt *et al.* 2016). Among the distinctive features of these environments are palsas, which are peat-covered mounds with ice-rich permafrost cores (Seppälä 1988). Palsa mounds form under permafrost conditions in northern peatlands where the mean annual air temperature (MAAT) is below 0 °C (Washburn 1980). Palsas exhibit notable morphological diversity, with heights ranging typically from 0.5 to 10 meters and widths varying from a couple of meters to areas spanning over 1 km² (Åhman 1977). While locally valued as unique habitats and indicators of permafrost stability, palsa mires also hold global importance as frozen carbon stores (Hugelius *et al.* 2020; Luoto *et al.* 2004b; Sollid & Sørbel 1998).

Palsa mires are highly climate sensitive and are usually located in the southernmost permafrost regions (Aalto *et al.* 2017a; Fronzek *et al.* 2006; Seppälä 1988). Due to climate change, the permafrost is warming rapidly (Biskaborn *et al.* 2019) and the persistence of permafrost landforms, including palsas, is threatened. Indeed, studies have reported strong degradation of palsas across the Northern Hemisphere (e.g. Borge *et al.* 2017; Jones *et al.* 2016; Wang *et al.* 2023) and in 2016 the European Union listed palsa mires as critically endangered habitats in Europe (Janssen *et al.* 2016). The disappearance of palsa mounds reduces the geodiversity of northern peatlands and can trigger cascading effects on associated biodiversity though the loss of important microhabitats (Luoto *et al.* 2004b). The thawing and collapse of palsa mounds can lead to shifts in plant species assemblages and the release of significant amounts of greenhouse gases such as methane (Bosiö *et al.* 2012; Errington *et al.* 2024; Hugelius *et al.* 2020). Emissions from thawing permafrost peatlands are projected to accelerate climate warming, before the succession of peatlands allows them to function as carbon sinks again (Hugelius *et al.* 2020). Understanding the processes governing these fragile landforms and their responses to climate change is therefore critical. Advancing this knowledge is essential for devising sustainable policies that address both climate change mitigation and biodiversity loss.

Palsa mires have been of keen interest to researchers for over 100 years. During the history of palsa research, the focus has shifted from the description, definition, and formation of the landforms (e.g. Fries & Bergström 1910; Kershaw & Gill 1979; Oksanen *et al.* 2001; Seppälä 1972, 1982; Washburn 1983; Zoltai 1972; Zoltai & Tarnocai 1975) to the examination of observed and predicted changes in palsa mire distribution, biodiversity and the greenhouse gas exchange of the thawing mires (e.g. Aalto & Luoto 2014; Bosiö *et al.* 2012; Errington *et al.* 2024; Fewster *et al.* 2022; Luoto *et al.* 2004b; Verdonen *et al.* 2024). Palsa research can be roughly divided into two categories: local-scale studies and broader-scale studies. Local-scale approaches are often conducted in specific mires or even on individual palsa mounds, using different field methods. These studies have focused, for example, on the formation history, internal structure, and dating of palsas (Kuhry 2008; Oksanen 2008; Saemundsson *et al.* 2012), the seasonal heave, subsidence, and thaw depth of palsas (Renette *et al.* 2024; Verdonen *et al.* 2023, 2024), and on the associated vegetation cover and its influence on palsas (Errington *et al.* 2024; Higgins & Garon-Labrecque 2018; Jean & Payette 2014a). In contrast, other studies approach the topic at a broader scale, utilizing remote sensing and spatial modelling methods, and mainly focus on the historical, current, and future distribution of palsa mires in different parts of the Northern Hemisphere (e.g. Aalto *et al.* 2014, 2017a; Fewster *et al.* 2020, 2022; Fronzek *et al.* 2006; Luoto & Seppälä 2002). Both approaches have made important contributions to our understanding of these unique and endangered landforms.

In this thesis, palsa mires are studied across the northern permafrost region at scales ranging from circumpolar to local. Methodologically the thesis engages with studies utilizing spatial modelling and the main objective is to improve our understanding of the environmental factors affecting palsa mires as well as their responses to anthropogenic climate warming. The thesis consists of three papers, each approaching the main objective from a different angle. Paper I focuses on regional differences in the environmental characteristics of palsa mires across the Northern Hemisphere. Paper II predicts future changes in palsa mire suitable environments in the circumpolar permafrost region. Paper III uses high-resolution (10 m) spatial datasets to examine factors influencing the morpho-ecological state of Finnish palsas mires at a local scale. In addition, Paper III examines the degradation of Finnish palsa mires. Thus, this thesis positions itself within the broader field of geographical research, exploring regional patterns and analyzing spatial changes. By comparing across local and circumpolar contexts, this study helps us to better understand the variations and spatial dynamics of palsa mires. The research contributes to geomorphological research by examining how climate-induced changes affect landform stability and distribution, while also while also considering the broader implications of palsa degradation for global carbon cycling and ecosystem functioning.

The thesis is structured as follows. First, the reader is introduced to the theoretical background on the morphology, formation, and occurrence of palsa mires (Chapter 2) in order to provide the essential context for understanding the landforms. Second, the impact of climate change on palsa mires is discussed (Chapter 3) and the environmental factors affecting their stability addressed. The ecological role of palsa mires in northern ecosystems is presented next (Chapter 4) to emphasize the importance of palsa mires with respect to the diversity of northern environments. After establishing the theoretical background, the objectives and research questions are presented (Chapter 5) to frame the purpose of the thesis. Next, the research areas are introduced (Chapter 6) and the used materials and methods are presented (Chapter 7) to ensure the transparency of the research process. The main findings of the thesis are presented (Chapter 8), followed by a discussion of their relation to current palsa research (Chapter 9). Finally, the conclusions and implications of the thesis are summarized (Chapter 10) to highlight the academic contributions and potential applications of the research.

2 Palsa mires

Palsa mires are permafrost peatlands found across the Northern Hemisphere characterized by distinctive landforms, palsa mounds (Seppälä 1988). Permafrost itself refers to ground, soil or bedrock that remains at or below 0 °C for at least two consecutive years. It is a key component of periglacial landscapes (French 2017). Permafrost regions are typically classified by the areal coverage of permafrost: continuous (90–100% coverage), discontinuous (50–90%), sporadic (10–50%), and isolated permafrost (<10%; Brown *et al.* 1997). Palsa mires are mainly found in discontinuous and sporadic permafrost regions in North America, Iceland, northern Fennoscandia, and Siberia where peatlands provide suitable conditions for the formation of palsas (e.g. Kirpotin *et al.* 2011; Luoto & Seppälä 2002; Saemundsson *et al.* 2012; Seppälä 1988; Zoltai *et al.* 2000).

A sufficient peat layer is crucial for both the formation and persistence of palsas, as it acts as an insulating layer that regulates ground temperatures (Kujala *et al.* 2008; Seppälä 1986). The peat layer not only supports palsas but also distinguishes them from mineral-cored permafrost features such as lithalsas (so-called mineral palsas; Pissart 2002). Palsas are particularly precarious landscape features because the persistence of their permafrost core depends on a delicate balance between climate and the insulating properties of peat, making them highly sensitive to climatic changes and valuable indicators of environmental change (Aalto *et al.* 2017a; Fronzek *et al.* 2006; Sollid & Sørbel 1998). The influence of palsa mires extends beyond their physical presence; they play an essential role in the biodiversity and hydrology of northern peatlands, supporting a variety of plant and animal species adapted to permafrost conditions (Luoto *et al.* 2004b).

2.1 Morphology of palsas

Palsas are often defined as peaty permafrost mounds with diameters greater than 2 meter and heights ranging from 0.5 to 10 meter (Seppälä 1988; Washburn 1983). However, palsas are morphologically diverse landforms and can be classified into five different types based on their shape and structure (e.g. Åhman 1977; Seppälä 1988). Dome-shaped palsas are typically 10 to 30 meter wide and 0.5 to 10 meter high (Åhman 1977). In contrast, palsa plateaus are extensive, flat formations, usually only 1 to 1.5 meter in height but which can extend over areas greater than 1 km^2. In addition, researchers have identified two elongated types of palsas, known as string-form and ridge-form palsas, as well as a fifth type called a palsa complex (Seppälä 1988). Palsa complexes are morphologically the most diverse type, containing different palsa types at different stages of their cyclic development (Åhman 1977; Figure 1).

In recent literature, palsa plateaus are often referred to as peat plateaus (see e.g. Borge *et al.* 2017; Fewster *et al.* 2020; Martin *et al.* 2019; Sannel & Kuhry 2011; Wang *et al.* 2023) and are in this way distinguished from the dome-shaped palsas. However, for the sake of simplicity, this thesis will refer to the different morphological types collectively as ‘palsas’. When differentiation by landform morphology is necessary, the terms ‘dome-shaped palsa’, ‘peat plateau’, and ‘palsa complex’ will be used.

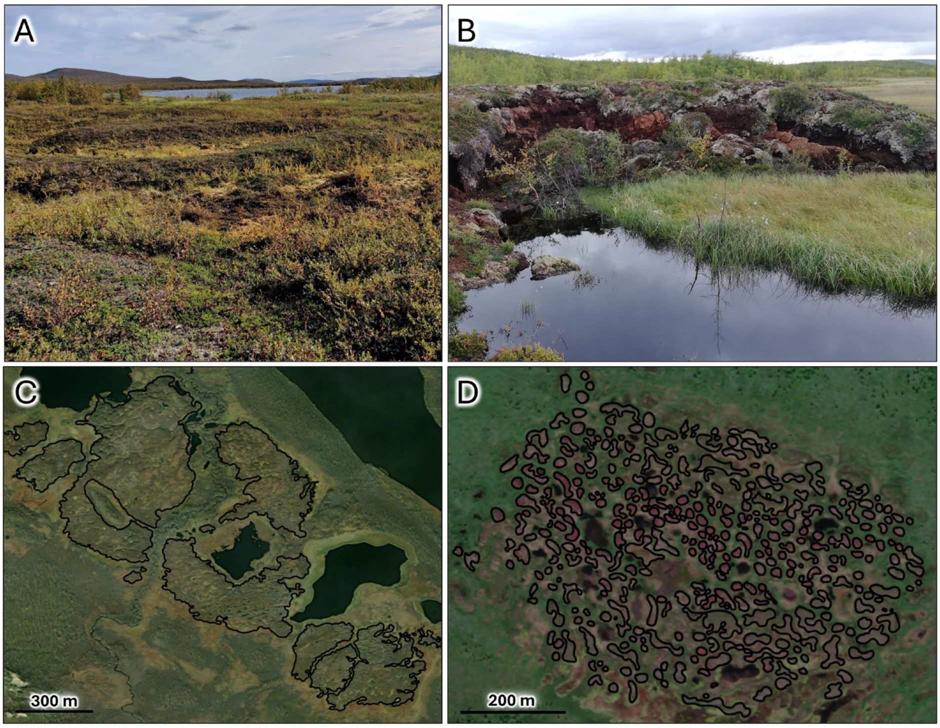


Figure 1. Palsas in Peera, Enontekiö, Finland (A–B), palsa complexes near Saarikoski, Kiruna, Sweden (C), and near Vorkuta, Western Siberia, Russia (D). The satellite imagery in panels C–D is obtained from Esri ArcGIS Pro (version 3.1.0; sources: Esri, Maxar, Earthstar Geographics, GIS User Community: Esri CIS, Esri, TomTom, Garmin, Foursquare, METI/NASA, USGS). Photos: Oona Leppiniemi (A) and Jan Hjort (B).

2.2 Formation and cyclic development of palsas

Several hypotheses have been proposed for the formation of palsas (Gurney 2001). However, the snow hypothesis has gained support among most researchers. The hypothesis was suggested by Fries and Bergström in 1910 but was proved experimentally by Seppälä (1982). According to this theory, the formation of palsas starts when snow is redistributed by wind. Due to the thinner snow cover and reduced insulation, the ground freezes deeper in winter. In such places, the resulting frost does not always thaw completely in the following summer, leading to the formation of the permafrost core of the palsa. Due to the growth of the frozen core, the palsa mound begins to rise above the surface of the mire, which further accelerates the redistribution of snow and the freezing of the ground in subsequent winters (Seppälä 1986). Seppälä (1982) conducted a field experiment based on this hypothesis, removing snow from a 5 by 5 meter study plot in a northern Finnish mire for three consecutive winters (1976–1979). Already after the first winter, the study plot had become slightly elevated (ca. 10 cm) in relation to the surrounding area due to frost heave, and the vegetation had begun to change. At the end of the experiment, a small artificial palsa embryo (ca. 30 cm high) had formed (Seppälä 1982).

Palsas of different ages and at various development stages can be found in the same mire (e.g. Kuhry 2008; Zoltai 1972; Åhman 1977). This diversity of palsas within the same area led to the concept of cyclic development. A model conceptualizing this idea was developed by Seppälä (1982, 1986, 2006) based on his field observations and experiments (e.g. 1982, 1986, 1988). According to this model (Figure 2), palsa development begins in the first thawing season during which the seasonal frost does not thaw completely and therefore the development of the frozen core begins (Figure 2A–B). As a result, the palsa starts to rise above the surface of the mire, allowing the wind to more effectively redistribute snow from the top of the palsa embryo (Figure 2C). This process enhances ground freezing, causing the permafrost core to grow and further elevating the mound (Figure 2D–E). When the core reaches the mineral soil beneath the mire, the degradation of the mature palsa begins. Due to the volumetric expansion of the frozen core, the peat on top of the palsa begins to crack and large blocks of peat may erode from the sides of the mound (Figure 2F). As a result of permafrost degradation, a thermokarst pond also forms around the collapsing palsa. As the degradation progresses, the palsa mound may be completely replaced by a thermokarst pond, where the submerged peat begins to decompose (Figure 2G). After the collapse of the palsa, new peat begins to accumulate, and if

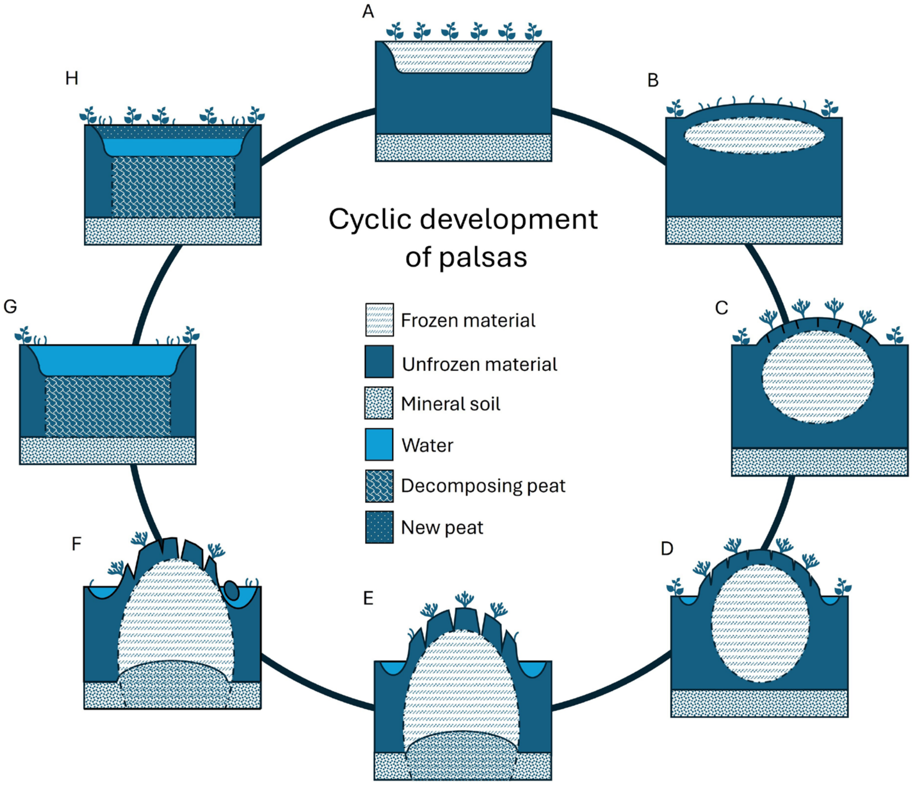


Figure 2. Cyclic development of palsas as proposed by Seppälä (1986, 2006). Situation at the beginning (A) and at the end of (B) the first thawing season. As a result, an embryo palsa has developed (C), and permafrost aggradation leads to the growth of young (D) and later mature (E) palsas. An old palsa begins to collapse and is surrounded by meltwater (F). Eventually, the palsa is completely thawed, a thermokarst pond has formed, and peat begins to decompose (G). New peat begins to accumulate in the thermokarst pond (H). If conditions are favorable, new permafrost can develop, and the cycle can begin again (A).

environmental conditions are favorable, new permafrost may form, restarting the cycle (Figure 2H–A).

As palsas rise from the surrounding mire due to permafrost aggradation, the associated growing conditions change, leading to the replacement of species favoring wet habitats with those adapted to drier and harsher growing conditions, characterized by increased exposure to freezing temperatures and stronger winds (Zuidhoff & Kolstrup 2005). Shifts in the vegetation are reflected in the composition of the peat, which allows the detection of permafrost initiation from the peat stratigraphy (Treat *et al.* 2016). Using peat core samples and radiocarbon dating, the formation and collapse of palsas can be identified and dated. For example, Zoltai (1993) used these methods to study the cyclic development of peat plateaus in northwestern Alberta, Canada. The alternating peat layers revealed the cyclic nature of palsa development, both as part of their natural development and in response to wildfire. Similarly, the permafrost cycles of palsa mires have been studied in northern Norway, as discussed by Vorren (2017).

Various factors and processes influence the formation of the palsas (Gurney 2001; Seppälä 2011; Seppälä & Kujala 2009). However, cryosuction is considered to be the dominant process responsible for the development of icy cores in palsas. Cryosuction is driven by the capillary effect: when sediments and soil moisture freeze, the remaining water is confined to smaller spaces due to the volumetric expansion of the freezing water (French 2017). This process lowers the free energy of the remaining water, causing it to migrate toward the freezing zone. The cryosuction and freezing of in-situ water draws water from the saturated soil materials around the frozen palsa core, contributing to the growth of the permafrost core (Gurney 2001). The buoyancy effect also contributes to the volumetric growth of palsas (Seppälä & Kujala 2009). Because water expands by about 9% when it freezes (French 2017), the density of the frozen core is reduced relative to the surrounding soil material, allowing the palsa to ‘float’ in the unfrozen mire. Ice-rich layers can also form during the winter as the in-situ water beneath the palsa core freezes. With repeated cycles over subsequent winters, these ice-rich layers contribute to the volumetric growth and, together with the buoyancy effect, cause the palsa mounds to rise (Seppälä 2011).

A sufficient peat layer is crucial for the formation of palsas due to the thermal properties of peat (Seppälä 1986). Wet and frozen peat conducts heat efficiently, with a thermal conductivity of approximately 1.49 W/mK, allowing deep freezing during winter. In contrast, during summer, when the unfrozen peat dries, its thermal conductivity decreases to about 0.23–0.28 W/mK, making it an excellent insulator that helps protect permafrost from thawing (Kujala *et al.* 2008). As palsas grow, the peat layer on top of them dries, which increases their resistance to thaw (Kujala *et al.* 2008; Railton & Sparling 1973; Seppälä 1986). In addition, associated vegetation changes, such as the replacement of *Sphagnum* mosses with *Cladonia* lichens, can further preserve the permafrost cores by increasing the surface albedo and decreasing the moisture retention capacity of the vegetation (Higgins & Garon-Labrecque 2018).

2.3 Suitable climate space for palsa mires

Palsa mires are found in specific climate conditions and are restricted to cold and dry environments (Seppälä 1988). According to Washburn (1980), palsas require the upper limit for MAAT be no more than 0 °C. More recent studies have defined region-specific climate envelopes for palsas based on air temperature and precipitation conditions. In northern Fennoscandia, climate envelope models indicate that suitable conditions occur where MAAT is around −2 °C and mean annual precipitation (MAP) ranges between 400–600 mm (Aalto *et al.* 2017a). Several studies have refined these parameters by distinguishing freezing and thawing seasons. For example, optimal winter conditions for palsas in Fennoscandia are characterized by approximately 2000 freezing degree days (FDD) and 200 mm of snowfall, while summer conditions involve around 1000 thawing degree days (TDD) and 250 mm of rainfall (Aalto & Luoto 2014; Luoto *et al.* 2004a; Parviainen & Luoto 2007). Climate envelopes for North American palsa mires show similar patterns to those in Fennoscandia but span broader climatic gradients, with MAAT ranging from −11 to 0 °C (Fewster *et al.* 2020). Studies suggest that palsa mires in Western Siberia typically occupy colder climate envelopes than those in Fennoscandia, while Icelandic palsas are found in regions with higher precipitation (Fewster *et al.* 2022; Saemundsson *et al.* 2012).

Historically the development of suitable spaces for palsa mires is related to the presence of sufficient peat layers and cold climate. Thus, the formation of palsa mires is often associated with cold periods during the Holocene (e.g. Arlen-Pouliot & Bhiry 2005; Fewster *et al.* 2020; Vorren 2017). In some peatlands within present-day continuous permafrost regions permafrost has persisted continuously for at least 6000 years, whereas permafrost in isolated and discontinuous permafrost regions developed after 6000 BP, with aggradation increasing after 3000 BP and peaking around 750 BP (Treat & Jones 2018). In North America, for example, permafrost progressively aggregated into these peatlands around 4300 BP and during the Little Ice Age (ca. 1650–1850) (Arlen-Pouliot & Bhiry 2005; Kuhry 2008; Treat & Jones 2018; Vitt *et al.* 1994). In Iceland, the first permafrost aggregated in peatlands approximately 4000–3000 BP, but the formation of palsas continued even into the 1960s (Emmert & Kneisel 2021; Hirakawa 1986; Kneisel 2010). The formation of the permafrost peatlands in northern Fennoscandia occurred around 2500 BP, but studies show that most of the current palsas in the region were formed during the Little Ice Age (Oksanen 2008; Seppälä 2005; Vorren 2017). The first palsas in the West Siberian lowlands developed between 3100 and 2200 BP, but palsas that are less than 600 years old can be found there as well (Oksanen *et al.* 2001, 2003).

3 Palsas in a changing climate

Climate change is predicted to alter the environmental conditions of northern regions by increasing air temperature and precipitation (IPCC 2021). In fact, Arctic regions are warming almost four times faster compared to the average warming of the globe (Rantanen *et al.* 2022), placing permafrost-related landforms in a vulnerable position. The predicted and already observed changes in climatic conditions threaten palsas for multiple reasons. First, increased summer temperatures promote stronger thawing of permafrost, while warmer and shorter winters limit the deep freezing of the ground (see e.g. Olvmo *et al.* 2020; Sannel *et al.* 2016). Second, increased precipitation can accelerate the degradation of palsas, as wet peat efficiently conducts heat deep into the ground, whereas a dry peat layer acts as an insulator and protects the permafrost core against thawing (Seppälä 1986, 1988). Changes in soil moisture patterns are particularly critical for palsas because the presence of discontinuous and sporadic peatland permafrost depends on the thermal properties of peat (Kujala *et al.* 2008). In these regions, the temperature of permafrost is often already close to 0 °C (Christiansen *et al.* 2010) and thus, even slight warming can lead to degradation. The response of palsas to climate change is further complicated by related changes in snow conditions and vegetation shifts (Errington *et al.* 2024; Higgins & Garon-Labrecque 2018; Olvmo *et al.* 2020).

Although the degradation of palsas is a natural part of their cyclic development, a growing body of research indicates widespread and accelerated degradation of palsas across the Northern Hemisphere (e.g. Borge *et al.* 2017; Mamet *et al.* 2017; Saemundsson *et al.* 2012; Verdonen *et al.* 2023). For example, the most recent documentation of new palsa embryos in Finland is from the early 2000s (Seppälä 2006). The MAAT in northernmost Finnish Lapland has increased by 0.5 °C when comparing the periods 1990–2006 and 2007–2023 (Finnish Meteorological Institute 2024), suggesting that conditions are currently less favorable for palsas in the region. Consequently, it is likely that more palsas are being degraded than formed. Valman *et al.* (2024) argue that climatic conditions since 2000 no longer support the formation of new palsas in certain parts of northern Sweden, and that the conditions for preserving existing palsa mires in Sweden have deteriorated due to climate change.

The overall degradation trend of palsa mires is most likely caused by anthropogenic climate warming (Aalto *et al.* 2017a; Fewster *et al.* 2022). Conversely, the thawing of palsa mires contributes to global greenhouse gas emissions and impacts northern biodiversity by reducing habitat availability (Hugelius *et al.* 2020; Luoto *et al.* 2004b). In addition, permafrost thaw can impact infrastructure (Hjort *et al.* 2022), as seen in northern Finland, where recurring road damage from palsa degradation has necessitated the construction of a dry land bridge over a palsa mire to prevent further disruptions. It is therefore critical to better understand the degradation of palsa mires. In this chapter, I will present shortly the different mechanisms and trends of palsa mire degradation in different parts of the northern permafrost region. This will be followed by a discussion of the morpho-ecological states of palsa mires.

3.1 Degradation of palsas

The degradation of palsas has been studied through by several different methods, including historical orthoimagery, drone imagery, ground motion monitoring, soil temperature logging, and field measurements, involving measurements of the height, width, and active layer thickness of palsas (e.g. Borge *et al.* 2017; Laberge *et al.* 1995;

Renette *et al.* 2024; Saemundsson *et al.* 2012; Verdonen *et al.* 2023, 2024). In addition, statistical modelling has been utilized to spatially predict future changes in the distribution of palsa mires and to estimate the future degradation trends in different regions (Aalto *et al.* 2017a; Fewster *et al.* 2022; Fronzek *et al.* 2006; Leppiniemi *et al.* 2023). Physical signs of the palsa degradation include, for example, peat cracking, peat block erosion, exposed peat surfaces, and thermokarst ponds (Borge *et al.* 2017; Luoto & Seppälä 2003; Seppälä 1988; Figure 3).

Lateral degradation is considered the main mechanism responsible for the degradation of palsas (Borge *et al.* 2017; Martin *et al.* 2021). Palsa edges are particularly susceptible to thawing due to snow accumulation, which provides enhanced insulation against freezing during winter (Olvmo *et al.* 2020). The excess snow also increases the amount of meltwater during spring and summer, which accelerates the thawing and can cause peat block erosion (Olvmo *et al.* 2020). When peat blocks are eroded from the palsa edges, the frozen core is exposed to solar radiation and precipitation, which accelerate thawing. The darker surfaces of the exposed peat also reduce albedo, further contributing to palsa degradation (Figure 3E–F). In addition to lateral degradation,

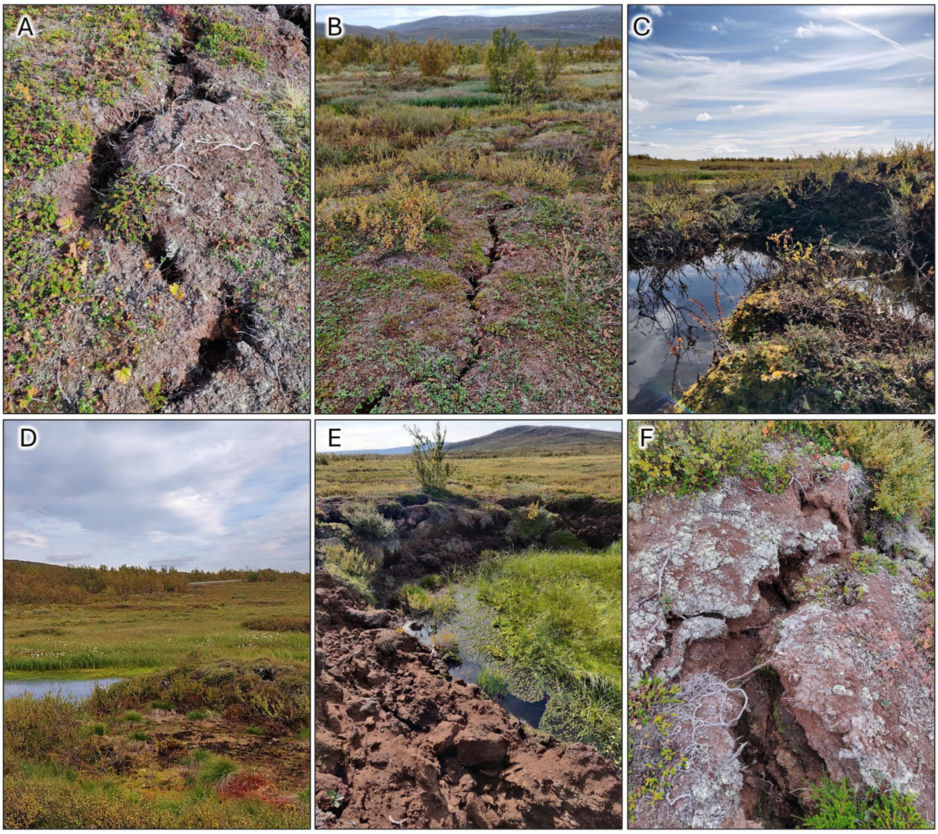


Figure 3. Signs of palsa degradation in Enontekiö, Finland, in August 2024. Expansion of the permafrost core causes the peat covering the palsa to crack. The formation of these cracks (A–B) can lead to the degradation of palsas by allowing rainwater and solar radiation to thaw the permafrost cores more efficiently. As a result of the degradation, thermokarst ponds can form from the meltwater (C–E), and if the degradation is strong, large peat blocks can erode from the sides of the palsa, making its core more vulnerable to thawing (E–F). Photos: Oona Leppiniemi.

palsas can be degraded by thaw subsidence or wind abrasion of the peat layer (Seppälä 2003; Valman *et al.* 2024; Verdonen *et al.* 2023).

Several authors have used orthoimagery and satellite imagery *to estimate* the lateral degradation of palsas across the Northern Hemisphere (e.g. Borge *et al.* 2017; Jones *et al.* 2016; Mamet *et al.* 2017; Wang *et al.* 2023). These studies indicate a strong degradation of palsas but also show spatial and temporal variations in the degradation rates across the Northern Hemisphere (see Table 1). It should be noted that the different calculation methods employed hamper direct comparisons between the studies (see Verdonen *et al.* 2023). However, the results broadly indicate that landform degradation has accelerated in recent decades in some regions, while slowing in others (see e.g. Mamet *et al.* 2017; Payette *et al.* 2004). Degradation trends between palsa mires can vary even within relatively small regions, as shown by Verdonen *et al.* (2023). Studies also suggest that the morphology of palsas may influence their susceptibility to degradation: palsa complexes and dome-shaped palsas are generally more susceptible than peat plateaus (Beer *et al.* 2024; Mamet *et al.* 2017; Ruuhijärvi *et al.* 2022; Verdonen *et al.* 2024; Wang *et al.* 2023).

Table 1. Examples of the areal degradation rates of palsas for different periods across the Northern Hemisphere. Where a range of degradation rates is presented, the rates vary within the region because of differences in the morphology and landscape position of the landforms, for example.

Region	**Mean annual loss rate (% a^{-1})**	**Reference**
South-central Alaska, United States of America	1950–1984: 0.5 1984–1996: 2.6 1996–2010: 2.1 1950–2010: 1.0	Jones *et al.* (2016)
Northwestern Territories, northwestern Canada	1940–1970: 0.5–2.8 2010–2016: 0.6–1.0 1940–2016: 0.8–1.7	Mamet *et al.* (2017)
Hudson Bay region, northeastern Canada	1957–1983: 2.5 1983–1993: 2.8 1993–2003: 5.3	Payette *et al.* (2004)
Coastal Labrador, northeastern Canada	1948–2021: 0.8–1.5	Wang *et al.* (2023)
Central Iceland	1960–2004: 0.3–0.7 2001–2010: 1.6–2.2	Saemundsson *et al.* (2012)
Northern Norway	1956–1982: 0.8 1982–2003: 1.0 2003–2012: 1.8 1956–2012: 0.9	Borge *et al.* (2017)
Northern Sweden	1963–1983: 0.3 1994–2010: 0.9 2010–2016: 0.8 1955–2016: 0.6–1.3	Olvmo *et al.* (2020)
Northwestern Finland	1959–2021: 2.4–3.6 2016–2021: 1.6–3.9	Verdonen *et al.* (2023)

3.2 Morpho-ecological state of palsas

The degree of palsa degradation can be used to classify palsa mires into different morpho-ecological states. For example, Ruuhijärvi *et al.* (2022) applied this approach using orthoimagery and field validation to classify Finnish palsa mires into five different classes based on their degradation state. Each class represents a specific level of degradation, ranging from near pristine palsa mires with minimal signs of degradation to completely collapsed ones. These classes reflect different stages of permafrost thaw and associated ecosystem changes. A degradation-based classification provides a structured method for monitoring the impact of climate change on palsa mires and for quantifying the decline of their morpho-ecological state across landscapes using remote sensing data. In this thesis, the classification approach of Ruuhijärvi *et al.* (2022) is used, with further details provided in Chapter 7.1.

In addition to the degradation-based methods, other methods of classifying palsas based on their morpho-ecological state exist. For example, palsas can be classified according to their developmental stage in the natural cycle, as interpreted through landform morphology and associated species assemblages (Zuidhoff & Kolstrup 2005). In this classification, different plant communities reflect different stages of palsa formation, stabilization, and decline. This approach emphasizes the dynamic role of palsas as habitats for specific plant species and thus provides an ecological perspective for assessing their morpho-ecological state. However, this method typically requires more field validations compared to degradation-based classification methods, since species must be identified on site in order to classify the palsas. The role of palsa mires as habitats for different species is further discussed in the next chapter.

4 Role of palsas in northern ecosystems

Palsa mires contribute to the diversity of northern peatlands and landscapes by creating diverse habitats that support distinct plant and animal communities. However, accelerated degradation has put these communities under threat, and palsa mires are now classified as critically endangered habitats in Europe (Janssen *et al.* 2016). Similar degradation trends have been observed across the Northern Hemisphere (see Chapter 3.1), suggesting that palsa mires could also become endangered elsewhere. In this chapter, I will describe the role of palsa mires in sustaining the geo- and biodiversity of northern peatlands.

4.1 Palsa mires as habitats

Palsa mounds create topographical variation in the peatland landscape, and this variation provides a basis for heterogeneous microhabitats (Figure 4A–B). First, the topographical variation and permafrost alter soil moisture patterns as the palsa mounds provide drier growing conditions compared to the surrounding mire (Luoto *et al.* 2004b). Second, the palsas represent more Arctic microhabitats because the snow cover is thinner due to more effective wind redistribution, which reduces the insulation and cover for species during winters (Seppälä 1988). In addition, the topographical variation creates microhabitats that differ in solar radiation and wind conditions, resulting in habitats that are both more sheltered and more exposed, permitting different species. Finally, nutrient availability varies in palsa mires as palsa mounds are ombrotrophic, relying solely on nutrient inputs from precipitation, while the surrounding mire is

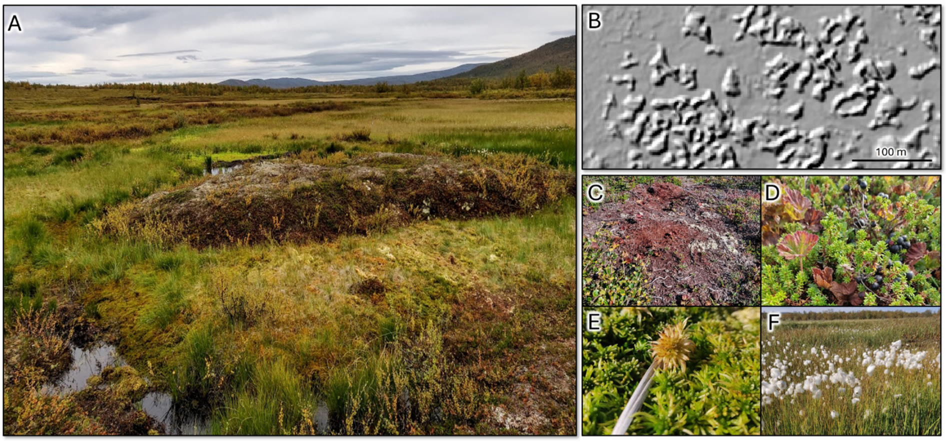


Figure 4. Palsa mires are heterogeneous habitats (A). Palsa mounds create topographical variation in the landscape, as shown in this hillshade image of the Liŋkinjeaggi palsa mire in Utsjoki, Finland (B). Topographic variation creates different microhabitats with varying soil moisture, wind, and solar radiation conditions. Because of these microhabitats, the species assemblage of a palsa differs from that of the surrounding mire (A, C–F). Palsa mounds represent a drier and more Arctic microhabitat, favored by dwarf birch (*Betula nana*), lichens (such as *Cladonia* sp.) (C), crowberry (*Empetrum nigrum*), and cloudberry (*Rubus chamaemorus*) (D). Bare peat can also be found on top of palsas (C). In contrast, the surrounding mire is favored by more hydrophilous species such as *Sphagnum* sp. (E) and hare's-tail cottongrass (*Eriophorum vaginatum*) (F). The hillshade image is from National Land Survey of Finland (2024). Photos: Oona Leppiniemi.

minerotrophic and enriched by nutrients from the groundwater (Luoto *et al.* 2004b). This variation in nutrient availability influences plant species composition. Indeed, the different abiotic conditions support distinct plant assemblages on top of the palsas compared to the surrounding mire (Beilman 2001; Seppä 2002; Zuidhoff & Kolstrup 2005; Figure 4C–F), and studies suggest that abiotic diversity in nature contributes to species richness (e.g. Hjort *et al.* 2015; Salminen *et al.* 2023).

4.2 Biodiversity of palsa mires

Palsas can be divided into non-wooded and wooded palsas based on their vegetation (Jean & Payette 2014a; Zoltai & Tarnocai 1971). In northern Europe, palsas are predominantly non-wooded, with plant communities composed mainly of mosses, lichens, and dwarf shrubs, including species such as *Empetrum nigrum*, *Ledum palustre*, *Betula nana*, *Rubus chamaemorus*, *Sphagnum* mosses, and *Cladonia* lichens (Ruuhijärvi 1983; Seppä 2002; Zuidhoff & Kolstrup 2005). In North America both wooded-palsas and non-wooded palsa mires are found, and the plant species of wooded palsas include trees such as black spruce (*Picea mariana*) and white birch (*Betula papyrifera*) (Zoltai & Tarnocai 1971). The plant communities found in palsa mires resemble those of aapa mires, and no species is known to occur exclusively in palsa mires (Luoto *et al.* 2004b; Ruuhijärvi 1983). However, as discussed above, the distinct species assemblages between palsa mires and the surrounding environment enhance the overall biodiversity of the mire ecosystem (Figure 4). Further, species richness in palsa mires may increase when permafrost begins to thaw, likely due to increased soil moisture heterogeneity such as the formation of thermokarst ponds (Zuidhoff & Kolstrup 2005). However, when palsas completely collapse and disappear, species richness decreases, and the peatland becomes homogenized (Luoto *et al.* 2004b). A recent study from northwestern Canada reported that permafrost degradation in peat plateaus resulted in significant shifts in vegetation from lichens and ericaceous shrubs to mosses and graminoids (Errington *et al.* 2024).

Palsa mires are known to support rich birdlife (Järvinen & Sammalisto 1976; Luoto *et al.* 2004b). For example, in Europe the species richness and density of birds breeding in peatlands increases with latitude, and especially waders and passerines prefer palsa mires (Järvinen *et al.* 1987; Järvinen & Väisänen 1976). The abundance of birds in palsa mires can be explained by the diversity of habitats and the presence of shallow waters, which provide an excellent food source due to the abundance of insects (Luoto *et al.* 2004b). Compared to birds, the diversity of other fauna in palsa mires is much less studied. However, some studies focusing on invertebrates have been conducted (see e.g. Markkula 2014; Van Steenis & Zuidhoff 2013). For instance, Markkula (2014) found that while the degradation of palsas does not necessarily impact the species richness of oribatid mites (*Acari, Oribatida*), their community composition is strongly influenced by permafrost dynamics. In contrast, the degradation of palsas is a potential risk for the endangered palsa mire hoverfly (*Diptera, Syrphidae*) in Europe (van Steenis 2022).

5 Objectives of the thesis

The main objective of the thesis was to improve our understanding of the environmental factors that affect palsa mires as well as the responses of palsas to changing climatic conditions, filling gaps in the current palsa research. Given the extensive nature of this task, the main objective was divided into more specific objectives (O1–4), each addressed by detailed research questions (RQ1–6).

O1: To explore and compare the environmental characteristics of palsa mires in different parts of the northern permafrost region (Paper I).

The distribution of palsa mires has been relatively well studied, especially in northern Fennoscandia and North America (Backe 2014; Borge *et al.* 2017; Tammilehto *et al.* 2024; Zoltai *et al.* 2000). In addition, palsas are widely distributed in Western Siberia and can also be found in Iceland (Kirpotin *et al.* 2011; Ottósson *et al.* 2016). Although palsa studies have been conducted across different regions of the Northern Hemisphere, differences in the spatial and temporal scales and environmental factors used in the studies make it challenging to compare results across regions. In Paper I, the objective was to facilitate systematical comparisons by using spatially and temporally harmonized datasets. To achieve this, the environmental conditions of palsa mires in the Hudson Bay region of Canada, Iceland, northern Fennoscandia, and Western Siberia were explored. Additionally, spatial modelling was used to examine how various environmental factors influence the probability of palsa occurrence. The following research questions were addressed:

> **RQ1:** How do the environmental characteristics and responses of palsa mires vary in different parts of the Northern Hemisphere?
>
> **RQ2:** Which environmental factors are most important in explaining the occurrence of palsa mires?

O2: To spatially predict the suitable environmental spaces for palsa mires in the Northern Hemisphere, both currently and in the future (Paper II).

The responses of palsa mires to climate change have been modelled since the early 2000s (e.g. Fronzek *et al.* 2006; Luoto *et al.* 2004a). However, even the more recent studies have been conducted only regionally and at relatively coarse spatial resolutions (Fewster *et al.* 2020, 2022). In addition, the vast areas of Central and Eastern Siberia are often neglected in English-language studies on palsa mires. To address gaps in our current knowledge, the suitable environments for palsa mires across the entire circumpolar permafrost region were modelled using high-resolution data for the recent and two future periods. The main objective of Paper II was to estimate future changes in the distribution of suitable environments for palsa mires. Therefore, the following research question was posed:

> **RQ3:** How is the distribution of suitable environmental spaces for palsa mires predicted to change in the Northern Hemisphere under climate change?

O3: To estimate the morpho-ecological state of Finnish palsa mires and their historical degradation (Paper III).

While much research has focused on modelling the distribution of palsa mires and their response to climate change, studies modelling the morpho-ecological state of palsa mires have not been conducted. In Paper III, the main objective was to determine if we can produce a model that can predict the morpho-ecological state of palsa mires in Finland. As palsa mires represent diverse and vulnerable habitats, a better understanding of their state was considered to be crucial in the context of global climate change. Paper III investigates whether the environmental characteristics of palsa mires differ in different morpho-ecological states, and how the morpho-ecological state of palsa mires has changed during the last half century in Finland. In order to study these issues, the following research questions were raised:

> **RQ4:** What is the morpho-ecological state of Finnish palsa mires?
>
> **RQ5:** How has the area of Finnish palsas in good morpho-ecological state changed during the last 50 years?

O4: To explore the role of key environmental factors affecting palsa mires at different spatial scales (Papers I–III).

Since the distribution and environmental characteristics of palsa mires are examined at three different scales in Papers I–III, a fourth objective is set to synthesize the findings. Thus, this thesis explores how the influence of environmental factors varies across scales, from circumpolar to local levels. To address the objective, a final research question was posed:

> **RQ6:** Does the scale at which palsa mires are studied affect the influence of environmental factors?

6 Research areas

This thesis examines the distribution and environmental characteristics of palsa mires at three scales, ranging from the circumpolar permafrost region of the Northern Hemisphere to the regional and local levels (Figure 5). These scales were chosen to better understand whether the environmental factors influencing palsa occurrence and persistence vary depending on the scale of the study (O4).

Paper II examined the current and future distribution of suitable environments for palsas throughout the circumpolar permafrost region of the Northern Hemisphere (O2; Figure 5A). The study focused on land areas north of the 40th latitude and was further restricted to the permafrost regions defined by Ran *et al.* (2022). This vast area encompasses diverse environments, from the continental and dry interior of Siberia to the maritime, milder climate of Iceland (Beck *et al.* 2018), from continuous permafrost regions (e.g. Alaska and Greenland) to more marginal permafrost areas with only discontinuous or sporadic permafrost (e.g. northern Fennoscandia) (Brown *et al.* 2002). To better understand how this diversity influences palsa mires, regional comparisons were made between different parts of this vast area (O1). Consequently, four research areas were selected for Paper I, representing the main distribution areas of palsa mires

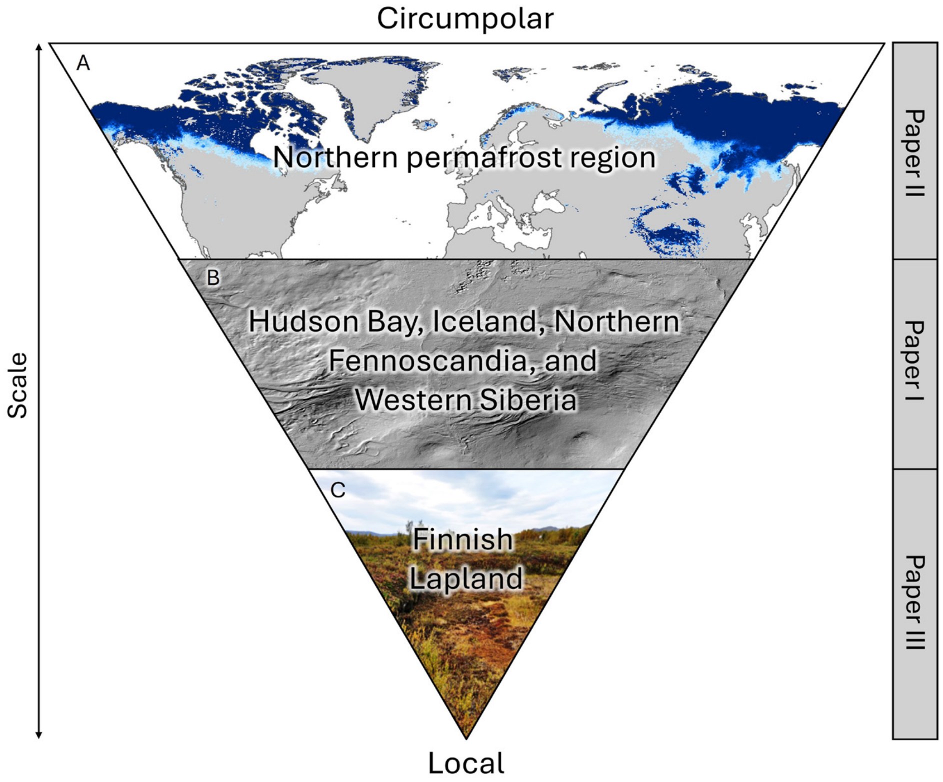


Figure 5. The scale of the research areas of this thesis varies from circumpolar to local (A–C). The background of panel A presents the probability of permafrost (darker shades representing higher probability of permafrost (Ran *et al.* 2022), basemap adapted from geoBoundaries database (Runfola *et al.* 2020)). Panel B shows a hillshade image from Finland (National Land Survey of Finland 2024). Panel C is a palsa mire in Enontekiö, Finland. Photo: Oona Leppiniemi.

(Seppälä 1988). To encompass the environmental gradients in which palsa mires are found, the Hudson Bay region of Canada, Iceland, northern Fennoscandia, and Western Siberia were chosen for the regional comparisons (Figure 5B).

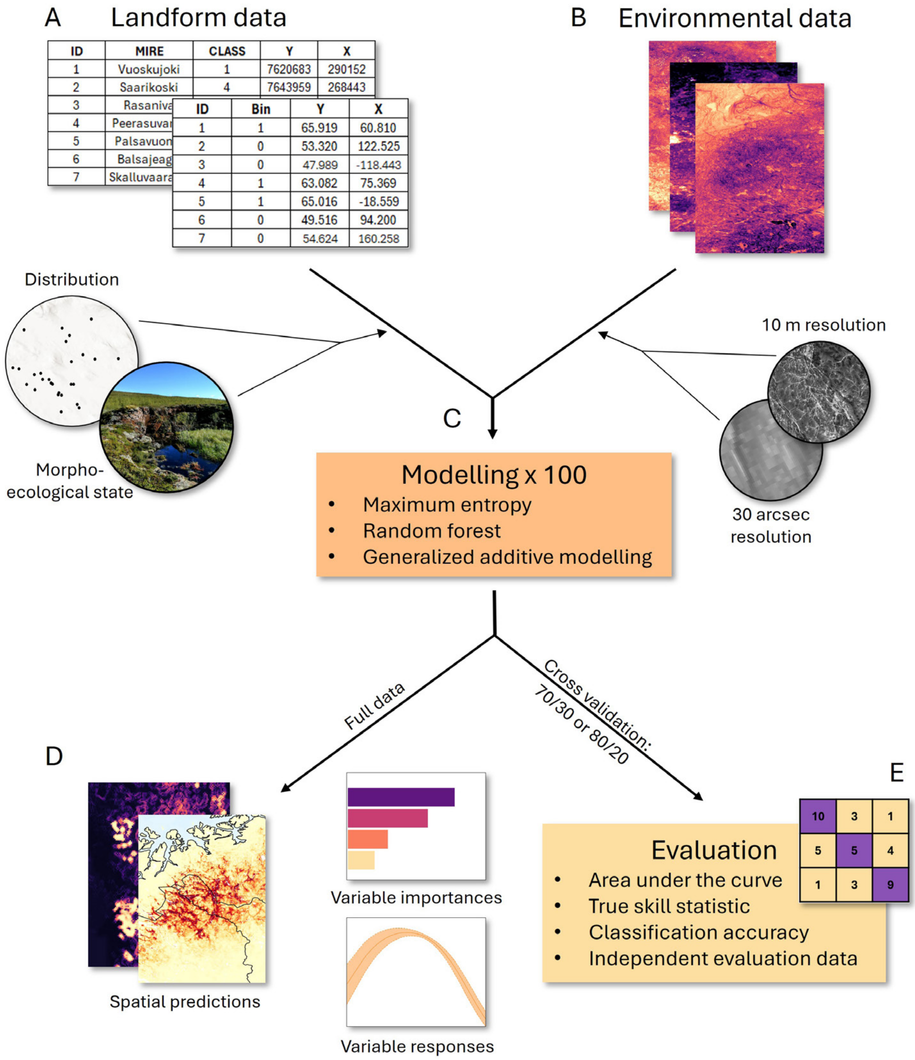
Analyzing the morpho-ecological state of palsa mires (O3) requires accurate, high-resolution datasets, making it necessary to study the topic at a local scale. Due to the availability of suitable datasets, Finnish Lapland was chosen as the research area for Paper III (Figure 5C). The selected research area lies between latitudes 68° 15' N and 70° 5' N and longitudes 20° 50' E and 28° 30' E, where only discontinuous and sporadic permafrost is found (Gisnås *et al.* 2017). Lateral degradation of palsas in the Paistunturi Wilderness Area (ca. 2200 km^2) in northeastern Finland was studied, which represented the most local analysis performed in the thesis.

7 Materials and methods

This chapter describes the materials and methods used in Papers I–III. However, to provide context, I will first briefly introduce statistical modelling as a method and explain the general workflow that was followed throughout the studies. Statistical modelling is a valuable tool in geomorphology, providing a possibility to explore and predict the relationships between landforms, geomorphic processes, and environmental conditions. By integrating spatial environmental data with observations of geomorphic landforms and processes, these models can, for example, identify the environmental drivers behind distribution patterns and predict changes (Hjort & Luoto 2013). In practice, statistical models work by identifying patterns and correlative relationships between a response variable and one or more predictors (Elith & Leathwick 2009; Guisan & Zimmermann 2000). To do this, statistical models use mathematical functions or algorithms to quantify these relationships and analyze how changes in the predictors influence the response variable. The choice of modelling method determines how the data are processed and the complexity of the relationships that can be captured (see Hjort & Luoto 2013).

In this thesis, statistical modelling was employed to compare the environmental characteristics of palsa mires across the Northern Hemisphere (Paper I), to explore the distribution of suitable environmental conditions for palsa mires under current and future climates (Paper II), and to spatially predict the morpho-ecological state of Finnish palsa mires (Paper III). The simplified workflow that was followed is illustrated in Figure 6. First, the response data (e.g. presence/absence of palsa mires and their morpho-ecological state) and predictors (e.g. variables describing climate, topography or soil conditions) were compiled by using open databases, literature and satellite imagery (Figure 6A–B). When selecting the potential predictors for the models, Spearman's correlations were calculated in order to avoid the most highly correlated variable pairs. After the data compilation and reprocessing, the models were run 100 times with the selected modelling methods to allow for the k-fold cross validation of the models (Figure 6C, E). For this purpose, the data were randomly split into calibration and evaluation datasets during each model run. In Papers I–II the calibration datasets consisted of 70% of the palsa observations, and the remaining 30% of the observations were left for model evaluation, while in Paper III an 80/20 split of the data was utilized (see Aalto *et al.* 2017a). Different data splits were applied to account for differences in the number of observations between the utilized datasets and to ensure sufficient data for both model calibration and evaluation. In Paper II, a separate evaluation dataset was also randomly sampled from the original data before model calibration. This provided an additional dataset (n=398) that retained the prevalence of presence and absence observations in the original data and was used for evaluation purposes only, complementing the cross validation performed with the calibration dataset (n=2057).

Based on the results of 100 model runs, the metrics were averaged and standard deviations were calculated to account for the stochasticity inherent in individual random samples. The averaged results were then used to assess variable responses, importances, and model performance (Figure 6D–E). For evaluation purposes, area under the curve (AUC; Papers I–III; Hanley & McNeil 1982), true skill statistic (TSS; Paper II–III; Allouche *et al.* 2006), and classification accuracy (Paper III) were computed separately for the calibration and evaluation datasets. In addition, independent datasets were used to evaluate the accuracy of the spatial predictions of Papers II–III (see Chapters 7.1 and 7.3 for details) (Figure 6E). Spatial predictions were calculated using the full data to take advantage of all the information in the compiled landform observations (Figure 6D).



ID	MIRE	CLASS	Y	X
1	Vuoskujoki	1	7620683	290152
2	Saarikoski	4	7643959	268443
3	Rasaniva			
4	Peerasuvar			
5	Palsavuon			
6	Balsajeag			
7	Skalluvaara			

ID	Bin	Y	X
1	1	65.919	60.810
2	0	53.320	122.525
3	0	47.989	-118.443
4	1	63.082	75.369
5	1	65.016	-18.559
6	0	49.516	94.200
7	0	54.624	160.258

10	3	1
5	5	4
1	3	9

Figure 6. Simplified workflow of the data compilation and analyses. First, the landform data describing the distribution or morpho-ecological state of palsas were collected (A) and environmental data were compiled from available datasets and published studies (at 10 meter and 30 arcsec resolution) (B). These data were then utilized for spatial modelling using different methods and 100 model runs (C). Spatial predictions, variable importances, and responses were calculated from the modelling results using the full data (D). Models were cross validated (with 70/30 or 80/20 data split) using different evaluation methods, such as area under the curve, true skill statistic, classification accuracy, and independent evaluation datasets (E).

All analyses were performed in R (version 4.1.3 was used in Papers I–II and version 4.3.2 was utilized in Paper III; R Core Team 2023).

Next, I will describe the datasets and modelling methods used in Papers I–III. First, I will outline the various palsa datasets that served as response variables in the models, were used for evaluation purposes, or were otherwise utilized in the studies. Second, I will present the environmental datasets that were utilized to compile the set of predictors for the models. Third, the compilation of the absence observations and datasets utilized for independent evaluation of the models are briefly described. Finally, I will present the paper-specific modelling methods and study designs employed in the thesis.

7.1 Palsa data

The first task that I had when I started my research was to collect the circumpolar observational data. The landform observations were mainly compiled from previously published datasets and studies. A literature search was conducted in Scopus and Google Scholar by using the search terms 'palsa', 'peat plateau', and 'permafrost peatland'. The search results were reviewed, and observations that met the palsa criteria and could be located with the information provided (e.g. coordinates, maps, and study site descriptions) were added to the dataset. The landform observations were limited to so-called true palsas and were based on descriptions in the studies. A sufficient layer of peat on top of the landform was required to accept it as a palsa. Thus, landforms described as palsa-like formations or lithalsas (i.e. mineral palsas) were excluded from the data.

In cases where the studied landforms were inadequately described in the original studies, a comprehensive interpretation of the satellite imagery (including an assessment of the size and shape of the landforms, their location, and the surrounding environment) was utilized to interpret whether the criteria for palsa was met. In addition, interpretation of the same satellite imagery available in Google Earth Pro and ESRI's ArcGIS Pro software was used to compile additional observations for the less studied regions, such as central and eastern Siberia. The regions selected for this further analysis were chosen based on several available datasets on peatland distribution (e.g. Hugelius *et al.* 2020; Terentieva *et al.* 2016; Xu *et al.* 2018). After compiling, the palsa observations were all verified using recent satellite imagery to ensure that the landforms had not disappeared since their original documentation. The final dataset consisted of 961 grid cells, each representing an area of approximately 1 km^2 (30 arcsec) with palsas being present. This dataset was used in both Papers I and II (Table 2). All compiled observations are available in the supplementary materials for Paper II, and the subset of the data used for regional comparisons is available in the supplementary materials for Paper I.

Ruuhijärvi *et al.* (2022) published a dataset classifying 282 Finnish palsa mires into five classes according to their morpho-ecological state. This classification was used to spatially model the state of all Finnish palsa mires (Table 2). The classification was based on the degradation state of palsas, interpreted from orthoimagery and satellite imagery and validated with field observations. The palsa mires were categorized as follows (Ruuhijärvi *et al.* 2022):

1) collapsed mires (100% areal degradation of palsas; n=91)
2) mires with high degradation (degradation >60%; n=100)
3) mires with notable degradation (30–60% degradation; n=61)
4) mires with minor degradation (10–30% degradation; n=23)
5) mires in near pristine condition (degradation <10%; n=7).

In Paper III, this classification was slightly altered: classes 4 and 5 were combined due to the limited number of observations. To extract the environmental characteristics for each palsa mire classified by Ruuhijärvi *et al.* (2022), the data delineating all Finnish palsa mires were used (Tammilehto *et al.* 2024; Table 2). Due to spatial mismatches between the datasets, the final number of classified palsa mires used in Paper III was reduced to n=199. The delineation of Finnish palsa mires (Tammilehto *et al.* 2024) was also used as the baseline for estimating the lateral degradation of Finnish palsas. Digitized palsa mounds in the Paistunturi Wilderness Area from the 1960s and 2014 orthoimages obtained from the National Land Survey of Finland (Yletyinen 2023; Table 2) were used to validate the spatial predictions and estimate the degradation of palsa mires over the last 50 years.

Table 2. Palsa datasets used in Papers I–III.

Description of dataset	**Paper(s)**	**Reference**
Circumpolar distribution of palsas	I–II	Leppiniemi *et al.* (2023, 2025)
Morpho-ecological state of Finnish palsa mires	III	Ruuhijärvi *et al.* (2022)
Delineation of Finnish palsa mires	III	Tammilehto *et al.* (2024)
Digitized palsas in 1960s and 2014	III	Yletyinen (2023)

7.2 Environmental data

Data describing the environmental characteristics of palsa mires across the Northern Hemisphere and at different scales were obtained from available databases at 30 arcsec resolution (ca. 1 km) (Table 3). Climate data were compiled from the WorldClim v1.4 database (Hijmans *et al.* 2005), and seasonal air temperature conditions were derived by calculating the freezing and thawing degree days (FDD and TDD, respectively). In addition, the air temperature data were also used to determine the form of precipitation (snowfall or rainfall). Precipitation was considered as snowfall if the monthly mean temperature was below 0 °C, and as rainfall if the monthly mean temperature was above 0 °C (Aalto *et al.* 2018). Based on this classification of precipitation, seasonal precipitation sums were calculated. The continentality of the climate was accounted for using the bioclimatic variable (Bio7 in WorldClim v1.4), which describes the range of annual air temperatures (calculated by subtracting the minimum temperature of the coldest month from the maximum temperature of the warmest month).

The climate variables for Papers I and II were computed for the period 1950–2000, which corresponded well with the original documentation of the palsa observations and was considered a better representation of the climate conditions suitable for palsas than more recent periods. In Paper II, climate variables were also calculated separately for two future periods (2041–2060 and 2061–2080), and for three different trajectories of greenhouse gas concentrations (representative concentration pathways: RCP2.6, RCP4.5, and RCP8.5; van Vuuren *et al.* 2011). Climate variables were similarly calculated for Finnish Lapland in Paper III using data from Aalto *et al.* (2017b) and Heikkinen *et al.* (2020) (Table 3). The variables were resampled from the original 50-meter resolution to 10-meter resolution by using nearest neighbor interpolation.

In addition to climatic factors, the influence of other environmental characteristics was considered as well (Table 3). The topographical wetness index (TWI) was calculated with SAGA GIS (version 7.8.2; Conrad *et al.* 2015) at two different resolutions (for Papers I–II and III separately) to account for the effect of topography and potential soil moisture conditions. Soil composition and properties were also considered in Papers I–II. Variables describing the soil organic carbon (SOC) and silt content were compiled from the global SoilGrids 2.0 database (Poggio *et al.* 2021). The probability of bedrock within two meters of the ground surface was used to estimate the thickness of the soil layer (Shangguan *et al.* 2017).

Table 3. Environmental data and variables used as predictors in Papers I–III. Abbreviations in the table refer to freezing and thawing degree days (FDD and TDD, respectively), soil organic carbon content (SOC), soil silt content (Silt), probability of bedrock within two meters of the ground surface (Bedrock), global multi-resolution terrain elevation data (GMTED), and topographical wetness index (TWI).

Original dataset	Derived variables	Unit	Paper(s)	Reference
WorldClim v1.4	FDD TDD Continentality Snowfall Rainfall	°C-days °C-days °C mm mm	I–II	Hijmans *et al.* (2015)
Aalto *et al.* (2017)	FDD	°C-days	III	Aalto *et al.* (2017)
Aalto *et al.* (2017) Heikkinen *et al.* (2020)	Snowfall Rainfall	mm mm	III	Aalto *et al.* (2017) Heikkinen *et al.* (2020)
SoilGrids250m 2.0	SOC Silt Bedrock	g kg^{-1} g kg^{-1} %	I–II	Poggio *et al.* (2021) Shangguan *et al.* (2017)
GMTED	TWI	index	I–II	Danielson & Gesch (2011)
Elevation model 10 m	TWI	index	III	National Land Survey of Finland (2024)

7.3 Other datasets

Distribution modelling often requires absence or background data against which the presences (i.e. palsa observations) are reflected. For Papers I–II, these datasets were collected by random sampling to ensure an unbiased representation of the environmental conditions in the study area. In Paper II, the sampled observations were verified against the satellite imagery available in Google Earth Pro to ensure that they represented true absences (n=1496). In contrast, the background data (n=10,000 for each research area) of Paper I did not distinguish between the presence and absence of palsas, as the paper used so-called presence-only modelling method (see the following section). To evaluate the performance of the models, the spatial predictions of Paper II were evaluated by using several independent datasets that describe the occurrence of thermokarst landforms (Olefeldt *et al.* 2016), permafrost peatland coverage (Hugelius *et al.* 2020; Olefeldt *et al.* 2021), peatland distribution (Xu *et al.* 2018), and peat depth (Treat *et al.* 2016).

7.4 Modelling methods

Maximum entropy (MaxEnt) is a distribution modelling method that uses presence-only data and contrasts it against background data (Phillips *et al.* 2017; Phillips & Dudík 2008). The principle of maximum entropy suggests that rare events, such as the presence of palsas, contain more information than common events (Guiasu & Shenitzer 1985). Using this assumption, MaxEnt predicts the distribution of the response variables by identifying the one with the maximum entropy, while meeting constraints based on the environmental conditions of the recorded observations (Elith *et al.* 2011; Phillips *et al.* 2017). MaxEnt is known to perform well with a limited number of observations, which has increased its popularity in distribution modelling studies (see e.g. Elith *et al.* 2006; Støa *et al.* 2019). This was also the reason why MaxEnt was chosen for Paper I, as the number of palsa observations was limited, especially in Iceland (n=57).

In Paper I, MaxEnt (version 3.4.3; Phillips *et al.* 2017) was run in R with the 'dismo' package (version 1.3.5; Hijmans *et al.* 2021). The models were run separately for each research area to enable comparisons between the environmental characteristics of the palsa mires in the four regions (Figure 7A). From the modelling results the variable responses were plotted to examine the effect of each variable on the probability of palsa occurrence (Figure 7C). The variable contributions in the models were calculated to estimate the importance of different environmental factors for palsas in different research areas (Figure 7D). In addition to the modelling results, the environmental characteristics of different palsa regions were also examined by plotting the observed conditions (Figure 7B).

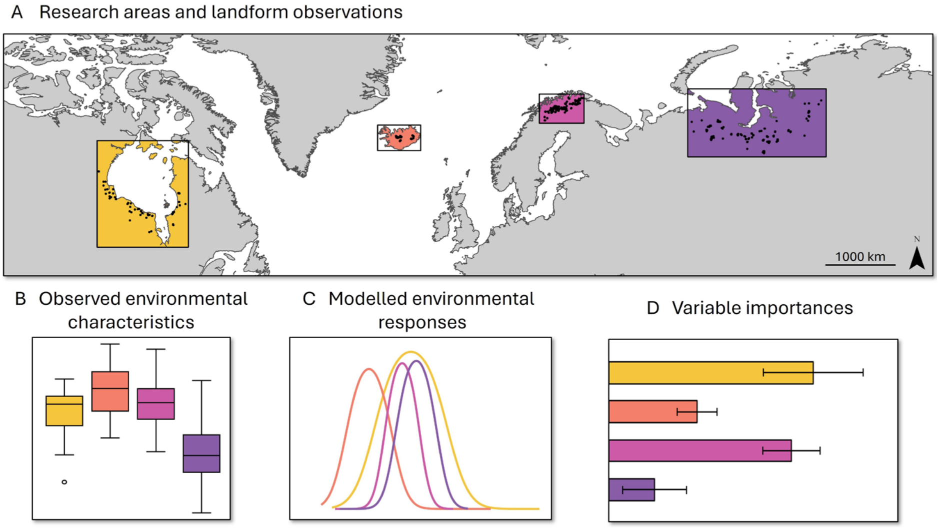


Figure 7. Study design for Paper I. The locations of the four research areas (Hudson Bay, Iceland, northern Fennoscandia, and Western Siberia) are presented in panel A. Observed environmental characteristics were visualized (B), environmental responses modelled (C), and variable importances calculated (D) to facilitate comparisons across the research areas. The basemap in panel A is from the geoBoundaries database (Runfola *et al.* 2020).

In Paper II, five different modelling methods (generalized linear model (GLM), generalized additive model (GAM), generalized boosted method (GBM), random forest (RF), and an ensemble of these four methods) were utilized. The modelling was performed with the biomod2 package (version 3.5.1; Thuiller *et al.* 2021). Of the modelling methods used, RF was chosen for further analysis as it obtained the highest evaluation scores, outperforming the other methods. RF is a machine learning method based on the construction of multiple classification trees, each of which uses a random subset of training data and predictors (Breiman 2001). RF has become a popular method in distribution modelling due to its wide applicability and accuracy (Biau & Scornet 2016). In Paper II, models were run for the baseline period (1950–2000) using historical climate data, and for two future periods (2041–2060 and 2061–2080) using three greenhouse gas concentration trajectories (RCP2.6, RCP4.5, and RCP8.5) to predict changes in the suitable environments for palsas across the Northern Hemisphere (see Figure 8). Similarly to Paper I, environmental responses and variable importance were also calculated.

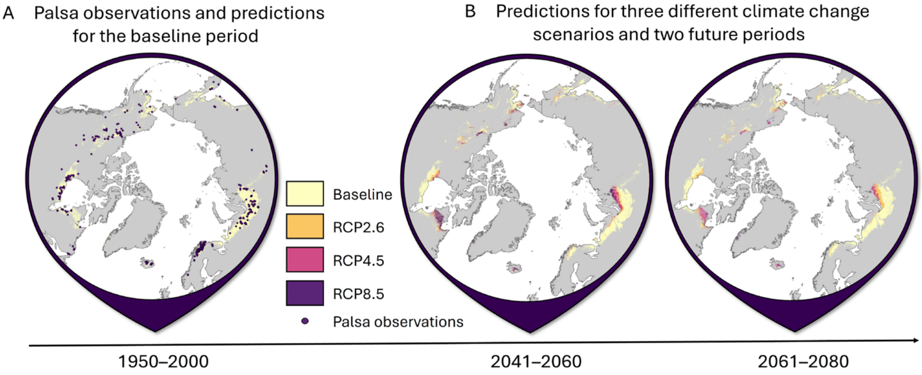


Figure 8. Study design for Paper II. First, circumpolar palsa observations were utilized to spatially model the distribution of the suitable environments for palsas in the baseline period (1950–2000) (A). Second, three different representative concentration pathway scenarios (RCP2.6, RCP4.5, and RCP8.5) were used to predict changes in the distribution of suitable environments in two future periods (2041–2060 and 2061–2080) (B). The basemap used in panels A–B is from the geoBoundaries database (Runfola *et al.* 2020).

GAM (Hastie & Tibshirani 1986) was utilized in Paper III to predict the morpho-ecological state of Finnish palsa mires. GAMs are flexible semi-parametric extensions of GLMs that use smoothing functions and can handle different datatypes (Hastie & Tibshirani 1986). GAMs are especially useful for investigating environmental responses (see Austin *et al.* 2006; Hjort & Luoto 2013). In Paper III, GAMs were run with the ‘mgcv’ package (version 1.9.0; Wood 2011) using collapsed palsa mires as absences and near pristine palsa mires as presence observations (Figure 9A). This approach was chosen for further analysis because the environmental overlap between the four morpho-ecological classes hindered model performance when observations from all classes were used. Using the binarized data and GAM, spatial predictions of the morpho-ecological state of palsa mires were computed (Figure 9C). When the areal degradation of palsas was estimated, a probability of 0.50 was considered as the

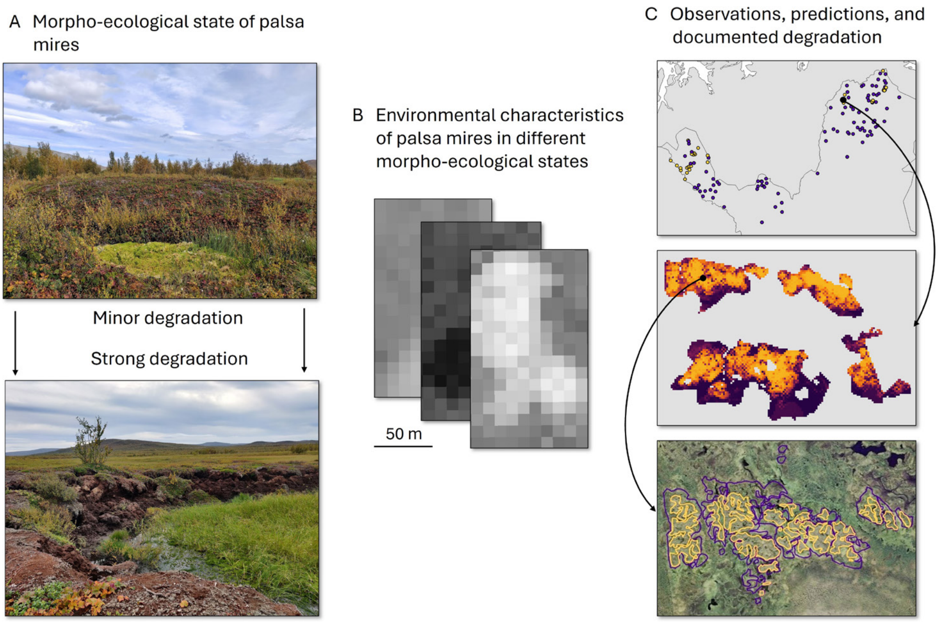


Figure 9. Study design for Paper III. Data classifying Finnish palsa mires into different morpho-ecological states (A) and high-resolution environmental data were used to investigate the environmental characteristics of palsa mires in different states (B). Non-metric multidimensional scaling (NMDS) was used to identify the environmental factors that distinguish palsa mires in different morpho-ecological states (B). Observations of collapsed and near pristine palsa mires were used to compute spatial predictions of the probability of a good morpho-ecological state, and these predictions were compared with the observed degradation of palsa mires (C). The basemap in panel C is from the geoBoundaries database (Runfola *et al.* 2020), and the orthoimage was obtained from the National Land Survey of Finland (2024). Photos: Oona Leppiniemi.

threshold for the occurrence of palsas. Finally, the modelling results were compared against the observed degradation of palsas in the Paistunturi Wilderness Area in NE Finland (Figure 9C).

Similarly to Papers I–II, the variable responses and importances were calculated to explore the effect of different environmental factors on the state of palsa mires. To further examine the role of different environmental factors in differentiating the collapsed and near pristine palsa mires, non-metric multidimensional scaling (NMDS; Borg & Groenen 2005; Kruskal 1964) was performed with the ‘vegan’ package (version 2.6-8; Oksanen *et al.* 2024) (Figure 9B). NMDS is an ordination method which is used to visualize the similarity or dissimilarity between objects (here palsa mires) by reducing the number of dimensions (Borg & Groenen 2005).

8 Results

In this chapter, I will present the main results of Papers I–III to address the research questions outlined in Chapter 5. The results include a regional comparison of the environmental characteristics of palsa mires in different parts of the Northern Hemisphere (Paper I), predicted changes in the circumpolar distribution of suitable environments for palsa mires (Paper II), insights into the morpho-ecological state and degradation trends of Finnish palsa mires (Paper III), and an analysis of the influence of spatial scale in the studies (Papers I–III). Collectively, the results set the stage for Chapter 9, which discusses how the findings of the thesis contribute to current knowledge on palsa mires and permafrost landscapes.

8.1 Regional differences in environmental characteristics of palsa mires (Paper I)

The first research question **(RQ1)** of the thesis was: **How do the environmental characteristics and responses of palsa mires vary in different parts of the Northern Hemisphere?** Comparisons between the observed environmental characteristics of palsa mires across the Northern Hemisphere revealed regional variation between the research areas (Table 4). However, the ranges of TDD, snowfall, TWI, and SOC were comparable in most of the research areas. The observed environmental characteristics of the Icelandic palsa mires differed the most from the other research areas, especially with respect to their climatic conditions. Icelandic palsas were found in lower FDD, TDD, and continentality conditions, while the precipitation (both rainfall and snowfall) was remarkably greater when compared to palsas found in other research areas (Table 4). In general, the environmental gradients of palsa mires were most pronounced in the Hudson Bay region.

Table 4. Averaged observed environmental characteristics of palsa mires across the four research areas, presented with ±1 standard deviation. The abbreviated variables are freezing and thawing degree-days (FDD and TDD, °C-days), continentality of the climate (Continentality, °C), topographic wetness index (TWI), soil organic carbon content (SOC, g kg^{-1}), soil silt content (Silt, g kg^{-1}), and bedrock probability within two meters of the soil surface (Bedrock, %).

	Hudson Bay	**Iceland**	**Northern Fennoscandia**	**Western Siberia**
FDD	3000 ± 300	600 ± 100	1900 ± 300	3400 ± 400
TDD	1200 ± 200	800 ± 100	1100 ± 100	1200 ± 100
Continentality	47 ± 4	17 ± 8	35 ± 3	48 ± 2
Rainfall	350 ± 80	520 ± 90	260 ± 10	240 ± 30
Snowfall	190 ± 30	670 ± 70	220 ± 30	240 ± 20
TWI	13.2 ± 1.3	12.8 ± 0.8	12.8 ± 1.2	13.4 ± 0.7
SOC	120 ± 80	120 ± 15	90 ± 10	130 ± 20
Silt	340 ± 40	370 ± 40	350 ± 40	260 ± 50
Bedrock	7 ± 5	26 ± 5	11 ± 4	2 ± 2

Overall, the results of Paper I showed that palsa mires occur in relatively narrow TDD ranges, but the winter conditions vary more between the regions (Table 4; Figure 10). Across the research areas, palsa mires showed the most consistent response to TDD. The response of the Icelandic palsas to TDD was similar to other regions; however, the optimal conditions for palsa occurrence in Iceland were found at lower TDD values than elsewhere. In addition, the probability for the occurrence of palsas increased with the continentality of the climate in Iceland while, for example, a unimodal response (northern Fennoscandia) or a decreasing trend (Hudson Bay) was observed elsewhere (Figure 10).

In Hudson Bay, northern Fennoscandia, and Western Siberia, palsa mires were predicted to occur in dry climates with rainfall and snowfall below 300 mm, respectively. Predicted precipitation conditions suggest that Icelandic palsa mires are found in areas

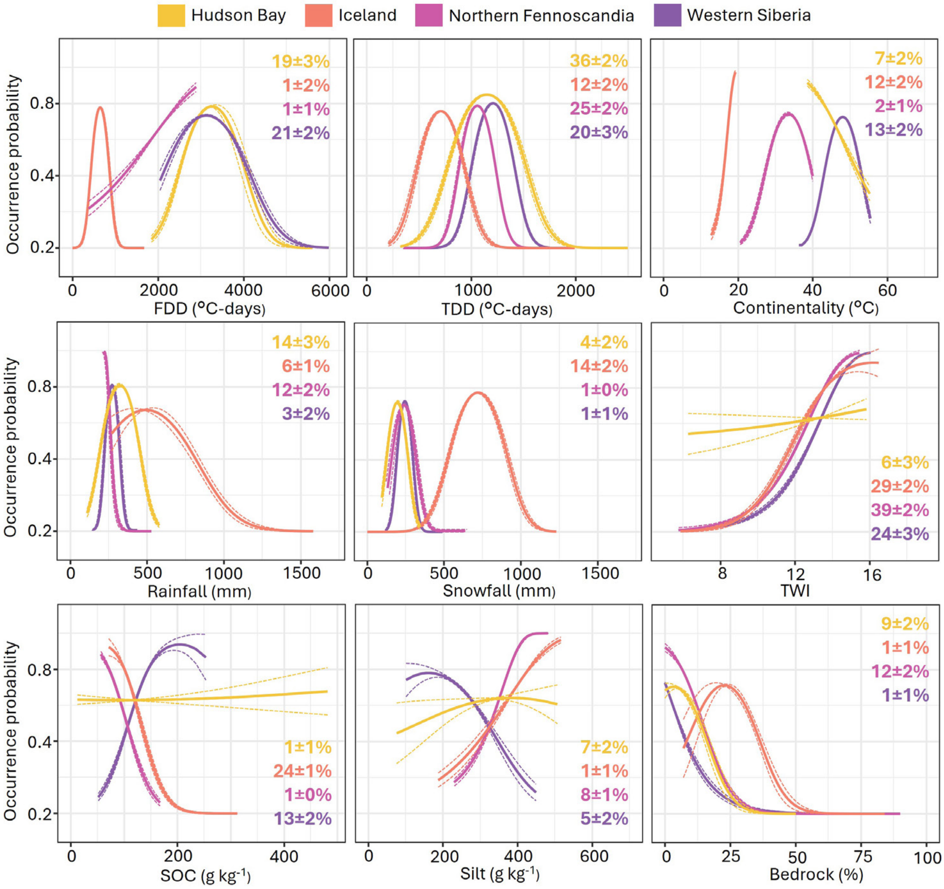


Figure 10. Modelled environmental characteristics and responses of the four research areas. Solid lines represent averaged responses, while dashed lines indicate ±1 standard deviation of prediction. The color-coded percentages in each plot show the relative contribution of each variable, along with ±1 standard deviation, in models fitted for the research area. The results are based on 100 modelling runs. The abbreviated variables are freezing and thawing degree-days (FDD and TDD), climate continentality (Continentality), topographic wetness index (TWI), soil organic carbon content (SOC), silt content (Silt), and bedrock probability within two meters of the soil surface (Bedrock).

with higher rainfall and snowfall compared to the other research regions (Figure 10). The predictions also showed that the occurrence probability of palsa mires increased with higher TWI values. The trend was clear for Iceland, northern Fennoscandia, and Western Siberia, but not so for Hudson Bay. The modelled responses of palsa mires to the soil variables varied more among research areas than did climate variables. The most diverse responses were predicted for SOC and silt content (Figure 10).

The second research question—**(RQ2): Which environmental factors are most important in explaining the occurrence of palsa mires**—was addressed by calculating the relative contributions of the different predictor variables (Figure 10). The results of Paper I showed substantial variation in the importance of the variables between the research areas. However, in general, TDD and TWI followed by FDD were the most influential variables across the research areas. In all regions except Western Siberia, TDD was clearly more important than FDD in explaining the occurrence of palsa mires. Among the precipitation variables, rainfall was more important than snowfall in all research areas except Iceland. The influence of the climate variables (FDD, TDD, continentality, rainfall and snowfall) was most evident in Hudson Bay and Western Siberia, while in Iceland and northern Fennoscandia TWI and the soil variables (SOC, silt and bedrock) contributed more to the occurrence of palsa mires (Figure 10).

Papers II and III also examined the importance of environmental factors for palsa mires. TDD, TWI and SOC were recognized as the most important variables explaining the distribution of suitable environments for palsas at a circumpolar scale (Paper II). At a local scale (Paper III), the utilized variables (i.e. FDD, rainfall, snowfall, and TWI) contributed almost equally to the morpho-ecological state of the palsa mire. However, FDD, snowfall and rainfall were the most effective variables in distinguishing the collapsed palsa mires from the near pristine ones.

8.2 Loss of suitable environments for palsas due to climate change (Paper II)

The third research question **(RQ3)** was: **How is the distribution of suitable environmental spaces for palsa mires predicted to change in the Northern Hemisphere under climate change?** During the baseline period (1950–2000), the suitability of environmental spaces for palsa mires in the circumpolar permafrost region was best characterized by TDD, with optimal ranges falling between 1000 and 1250 °C-days. The largest and most continuous regions suitable for palsas were predicted to occur in Western Siberia, around Hudson Bay and northern Quebec in Canada, and in northern Fennoscandia. In addition, Iceland, the Northwest Territories of Canada, western coastal Alaska, and the Russian Far-East had high probabilities for suitable environments. The total area of the predicted suitable environments during 1950–2000 was approximately 1.58 million km^2.

The area of suitable environments for palsas was predicted to decrease dramatically in all RCP scenarios used. The worst-case scenario (RCP8.5) predicted an areal decrease of about 90% already by 2041–2060 and an almost complete loss (ca. −98%) of suitable environments by 2080 (Figure 11). The greatest degradation was predicted in Siberia, with areal loss of 99%. In contrast, the Nordic countries (including northern Fennoscandia and Iceland) were predicted to experience the least, but still dramatic, loss of suitable environments (ca. −93%) by the end of the century under RCP8.5. More optimistic scenarios (RCP2.6 and RCP4.5) predicted more moderate losses of suitable environments (Figure 11). However, even these scenarios predicted future losses of

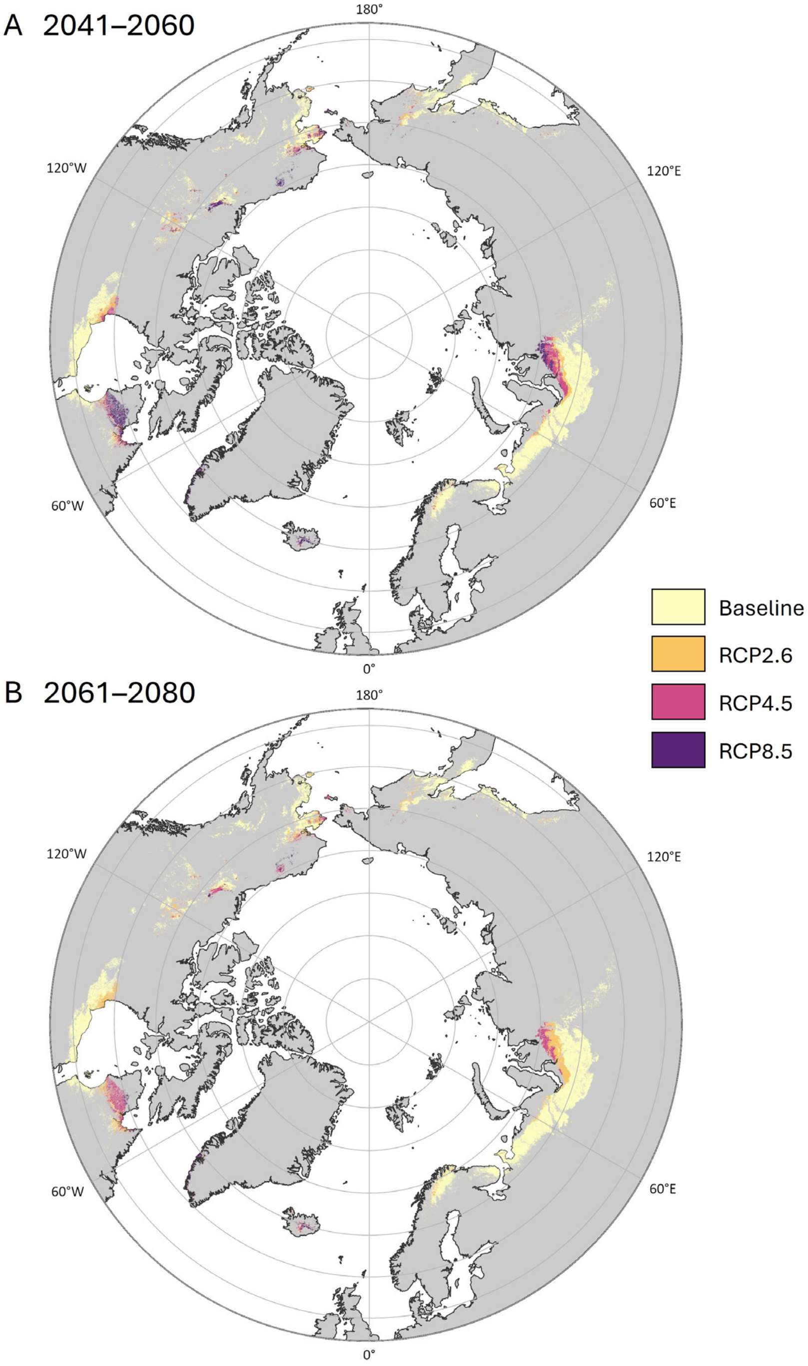


Figure 11. Predicted changes in the circumpolar distribution of suitable environments for palsa mires between the baseline period (1950–2000) and the periods 2041–2060 (A) and 2061–2080 (B), based on three different representative concentration pathway (RCP) scenarios. The basemap is from the geoBoundaries database (Runfola *et al.* 2020).

74–76% (RCP2.6) and 81–89% (RCP4.5) of suitable environments for palsas in the circumpolar area (2060 and 2080, respectively).

According to RCP2.6, suitable environments for palsas would most likely still be found in northern Quebec, the Northwest Territories of Canada, Iceland, northern Fennoscandia, and in Western Siberia in the future. This scenario did not predict major changes in the distribution of suitable environments after 2060. However, in the moderate emissions scenario (RCP4.5), the loss of suitable environments is expected to continue after this period. In RCP4.5, the suitable environments are predicted to shift to the northernmost parts of the regions identified in the RCP2.6 scenario. Under the high emissions scenario (RCP8.5), nearly all suitable environments for palsas are predicted to be lost, leaving only limited areas in Alaska, the Northwest Territories, northern Quebec, Greenland and in Iceland potentially suitable for palsas.

8.3 Morpho-ecological state of Finnish palsa mires (Paper III)

To assess the morpho-ecological state of palsa mires, the fourth research question **(RQ4)** asked: **What is the morpho-ecological state of Finnish palsa mires?** The results showed that most Finnish palsa mires appear to be in poor morpho-ecological condition. Approximately 53% of the palsa mires had a low probability (<0.25) of being in a good morpho-ecological state. In contrast, only 28% of the mires had a high probability (>0.75) of being in good state. The morphology of the landform was found to influence their state: peat plateaus were more likely (ca. 0.65 probability) to be in good condition, whereas dome-shaped palsas had a considerably lower probability (ca. 0.28) of good morpho-ecological state (Figure 12A). The calibrated GAM was able to predict the probability of a good morpho-ecological state with moderate to good accuracy.

The fifth research question of the thesis **(RQ5)** was: **How has the area of Finnish palsas in good morpho-ecological state changed during the last 50 years?** The results of Paper III indicate a decline of over 76% in the area of palsa mires in the

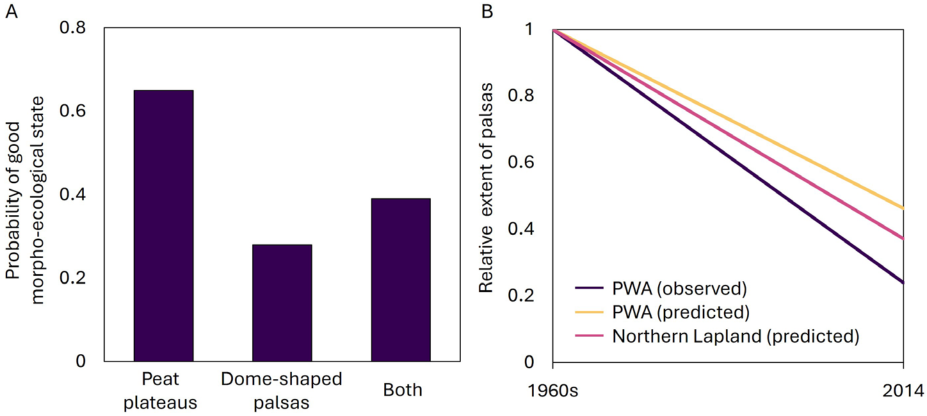


Figure 12. Averaged probabilities of morphologically different palsas being in a good morpho-ecological state across Finland (A). Relative change in the areal extent of palsas in good morpho-ecological state based on observed degradation in the Paistunturi Wilderness Area (PWA), and predicted degradation in both PWA and Northern Lapland between the 1960s and 2014 (B).

Paistunturi Wilderness Area, NE Lapland, between the 1960s and 2014 (Figure 12B). This observed change, based on historical orthoimagery, suggests a degradation rate of approximately −1.5% per year. The models predicted a slightly more moderate but comparable areal decline of palsa mires in good morpho-ecological state in the Paistunturi Wilderness Area (−53.7%; ca. −1.1% a^{-1}) and across Finnish Lapland (−62.8%; ca. −1.3% a^{-1}) (Figure 12B).

8.4 The impact of the spatial scale (Papers I–III)

The studies of palsa mires across different spatial scales in Papers I–III provided a basis for examining the influence of scale in palsa research. Each paper approached the analysis of palsas from distinct perspectives: from the broad circumpolar to the more localized research context. This multi-scale approach allows for a deeper understanding of how environmental factors affect the occurrence and persistence of palsas as well as how these factors may vary depending on the scale at which they are studied. Thus, the final research question of this thesis **(RQ6)** asked: **Does the scale at which palsa mires are studied affect the influence of environmental factors?**

Papers I and II showed that summer conditions (especially TDD and rainfall) had a stronger influence on the models when examining the occurrence of palsa mires and the distribution of suitable palsa environments at regional and circumpolar scales. In contrast, Paper III, conducted at the local spatial scale, indicated that winter conditions had a stronger influence on the morpho-ecological state of palsa mires. The differences in influence of the environmental factors between the different scales were not limited to the climate variables. At the circumpolar and regional scales, the probability of the occurrence of suitable environments and palsas increased with higher TWI values, while the opposite trend was observed for the probability of good morpho-ecological state at the local scale. In Paper III, lower TWI values were more often associated with good morpho-ecological state of palsas. Furthermore, soil variables were included in models at broader scales, but excluded at the local scale, which highlights the varying importance of different environmental factors across the scales.

9 Discussion

The findings of this thesis provide insights into the distribution, morpho-ecological state, and climate-driven change of palsa mires across spatial scales, enhancing our understanding of these unique permafrost landforms in the context of global change. This chapter considers the findings in the context of the recent literature on palsa mires, periglacial environments, and climate change. First, the environmental characteristics of palsa mires are discussed, followed by a discussion on the predicted changes in the distribution of suitable environments and the morpho-ecological state of palsa mires. Next, the chapter discusses the impacts of the used spatial scale, and the potential limitations related to the utilized materials and methods. Finally, some suggestions for future research are presented.

9.1 Regional characteristics and drivers of the occurrence of palsa mires

The occurrence of palsa mires has been associated with cold and dry environments and the role of climate in shaping palsa occurrence is well documented (e.g. Aalto *et al.* 2017a; Fewster *et al.* 2020, 2022; Parviainen & Luoto 2007). Papers I–III support these findings, but the comparisons using harmonized datasets in Paper I revealed regional differences regarding the environmental conditions under which palsa mires occur and regarding the relative importance of different factors. The influence of climate was most evident in Hudson Bay and Western Siberia, whereas in the spatially more limited research areas in Iceland and northern Fennoscandia, topography and soil conditions were more influential for the occurrence of palsa mires. This can at least partly be explained by the more limited variation in climate factors in the smaller research areas. Notably, TWI and SOC were also key predictors of the circumpolar distribution of suitable environments for palsas (Leppiniemi *et al.* 2023). This emphasizes that the inclusion of both local and global factors enhances our understanding of palsa mire occurrence and highlights the benefits of incorporating more-local factors into geomorphological distribution models (see e.g. Aalto & Luoto 2014; Phillips 2006).

Interestingly, Iceland emerged as an outlier in several environmental parameters when the different regions were compared. Palsas in Iceland are found in areas with higher precipitation, lower freezing and thawing degree days, and a less continental climate compared to the other regions. They are also more likely to occur in areas where bedrock lies within 2 meters of the soil surface (Leppiniemi *et al.* 2025). However, although their climatic characteristics differ markedly from the other research areas, the uniqueness of Icelandic palsa mires should be interpreted with caution. The thermal balance between winter and summer air temperatures determines the energy budget available for permafrost maintenance (French 2017) and plays a key role in the occurrence and persistence of Icelandic palsas. Therefore, although the mild winter temperatures in Iceland limit deep freezing of peatlands, the cooler summer temperatures are likely to reduce the extent of seasonal thawing compared to regions with higher TDD. In contrast, the cold winters in the Hudson Bay region and Western Siberia enable the persistence of palsas despite higher summer air temperatures. The importance of thermal balance was highlighted by the relatively high contribution of the continentality variable in the models computed for Iceland and Western Siberia (Leppiniemi *et al.* 2025). Strand *et al.* (2021) also found that the continentality of the climate and the seasonality in the climate influence the patterns of the active layer thickening. Continued thickening of the active layer can threaten the persistence of permafrost-related landforms (e.g. Jean & Payette 2014b; Romanovsky *et al.* 2010).

Still an interesting question remains: why do Icelandic palsas persist in regions with high precipitation? Palsas are typically associated with relatively dry climates with mean annual precipitation between 400–600 mm (Aalto *et al.* 2017a; Fewster *et al.* 2020, 2022; Leppiniemi *et al.* 2023, 2025; Luoto *et al.* 2004a). The redistribution of snow by strong winds may explain why palsas can persist in areas with high annual snowfall like Iceland. In Iceland open landscapes such as palsa mires typically have only a thin snow cover (<30 cm) due to snow redistribution by wind (Eythorsson *et al.* 2023). For example, Czekirda *et al.* (2019) observed that the distribution of palsas in Iceland is strongly linked to shallow snow depths, which facilitate sufficient ground freezing even in mild winter conditions due to reduced insulation. Since the snowfall can be high but the snow depth remains shallow because of wind action, high-resolution spatial data on snow depth could significantly improve models of palsa distribution in Iceland and other regions. In fact, the snowfall variable utilized in Papers I–III can only be considered as a proxy for snow depth.

In addition to redistribution of snow, soil composition also may play an important role in the occurrence of Icelandic palsa mires (Leppiniemi *et al.* 2024). Aeolian depositions of tephra and sand reduce the carbon content of soils in Icelandic palsa mires, forming a mineral layer over the peat (Saemundsson *et al.* 2012). Tephra has notable insulating properties and has been shown to promote permafrost aggradation in Iceland (Kellerer-Pirklbauer *et al.* 2007). With its strong insulating properties, tephra layers within and on top of the palsas help insulate and protect permafrost from thawing. Unlike peat, for which the insulating capacity decreases with moisture content (Kujala *et al.* 2008), the thermal conductivity of tephra is more influenced by its silica content, porosity, and texture (Möller *et al.* 2020). This could explain why Icelandic palsas are less affected by higher precipitation than those in other regions.

Understanding how different environmental factors influence the morpho-ecological state of palsa mires provides insights into the resilience and degradation processes of the landforms. The environmental characteristics of Finnish palsa mires in different morpho-ecological states were partially overlapping (probably due to the limited spatial extent of the research area) but contrasting environmental characteristics were also recognized between mires in different states. The probability of good morpho-ecological state was recognized to increase in regions with less precipitation and colder winters (Leppiniemi *et al.* manuscript), which is consistent with previous studies suggesting that a dry and cold climate is required for the occurrence of palsas (Aalto *et al.* 2017a; Fewster *et al.* 2020; Luoto *et al.* 2004a). However, near pristine palsa mires were also found to receive more snowfall than collapsed palsa mires (Leppiniemi *et al.* manuscript). This was interesting because thin snow cover is known to be a crucial factor for the formation and persistence of palsas (Czekirda *et al.* 2019; Sannel 2020; Seppälä 1982). This finding must be interpreted with caution because, as mentioned above, regional snowfall is only a proxy for snow depth and does not consider the redistribution of snow. The calculation of the variable is based on both precipitation and air temperature data, and thus the variable may also reflect the length of the freezing season. Long and cold winters support the persistence of palsas (Olvmo *et al.* 2020) and may therefore also contribute to their better morpho-ecological state.

In northern Europe, palsas are typically non-wooded, whereas in North America, wooded palsas are common (Jean & Payette 2014b; Zoltai 1972; Zuidhoff & Kolstrup 2005). This difference in species composition can affect the environmental characteristics of palsa mires, as vegetation is known to impact palsas in multiple ways (see e.g. Cyr & Payette 2010; Higgins & Garon-Labrecque 2018; Jean & Payette 2014b). For example, Jean and Payette (2014a) found that the vegetation composition of palsas significantly affects their annual and seasonal thermal regimes, particularly due to the snow trapping and shading caused by trees and forest canopy. Unfortunately, due to the lack of harmonized high-resolution data on the vegetation composition of palsa mires, the impact of vegetation on the environmental characteristics of palsa mires across the Northern Hemisphere could not be considered in this thesis. However, climate change is expected to further impact air and permafrost temperatures, snow cover thickness and duration, and species composition (Biskaborn *et al.* 2019; IPCC 2021; Post *et al.* 2009). These changes can affect wooded and non-wooded palsas differently, and it has been suggested that wooded palsas may be more vulnerable to climate change because trees influence snow accumulation and insulation, which in turn affects ground temperatures and permafrost stability (Jean & Payette 2014a; Thibault & Payette 2009). Further studies are needed to better understand the influence of vegetation composition on the morpho-ecological state and degradation of palsas.

Overall, the findings highlight how environmental factors influencing the occurrence and morpho-ecological state of palsa mires can vary substantially across the Northern Hemisphere, driven both by regional climatic conditions and by site-specific characteristics such as soil composition. This variability underscores the importance of integrating local and regional data in future studies to better understand the persistence of palsas under changing environmental conditions. Because they differ in several environmental characteristics from the palsa mires of the other research areas, the study of Icelandic palsa mires would offer valuable insights into the complex interplay of factors that enable palsas to occur under diverse environmental settings.

9.2 Disappearance of the suitable environments for palsas

Paper II produced circumpolar-scale predictions of the potential loss of suitable environments for palsa mires, providing a comprehensive spatial perspective on the fate of these landforms across the Northern Hemisphere. The results highlight the vulnerability of palsa environments and align with previous predictions made for northern Europe and Western Siberia (Aalto *et al.* 2017a; Fewster *et al.* 2022). If the predicted loss of suitable environments materializes, dramatic changes in periglacial landscapes are likely to occur. These include permafrost degradation, which can release substantial amounts of carbon and nitrogen from peatlands to the atmosphere (Hugelius *et al.* 2020). In addition, the formation of thermokarst ponds and shifts in vegetation composition could further amplify methane emissions. For example, Bosiö *et al.* (2012) predicted that a shift from dry hummock vegetation to vegetation better adapted to wetter conditions in palsa mires could result in increased carbon fixation but also a nearly threefold increase in methane efflux. However, significant uncertainties remain regarding the development of soil moisture, hydrology, and vegetation succession in Arctic environments (Andresen *et al.* 2020). These uncertainties make it difficult to predict the timing and intensity of greenhouse gas emissions from thawing permafrost peatlands. While the drying of peatlands could enhance carbon sequestration, it is likely that emissions from thawing peatlands will initially contribute to global warming (Hugelius *et al.* 2020).

In Paper II, a drastic loss of suitable environments for palsas was predicted across the northern permafrost region, with the most dramatic changes anticipated in

Western Siberia, where palsa mires are currently most widely distributed (Kirpotin *et al.* 2011; Leppiniemi *et al.* 2023). The lowlands of Western Siberia represent one of the world's largest carbon pools (Hugelius *et al.* 2020), and therefore, the degradation of permafrost peatlands in this region would contribute substantially to global greenhouse gas emissions (see e.g. Glagolev *et al.* 2011). Furthermore, the degradation of palsas can also have critical regional and local impacts, for example on local communities. Permafrost degradation can damage infrastructure, such as roads and pipelines, while also affecting agricultural activities including reindeer husbandry and berry picking (Hjort *et al.* 2022; Ward Jones *et al.* 2024). In addition, the predicted degradation of palsas will have biological consequences (Luoto *et al.* 2004b), which will be further discussed in the next section (Chapter 9.3). Before proceeding, it is important to discuss some of the methodological choices and potential limitations associated with Paper II.

Although the predictions suggest a dramatic loss of suitable environments already by mid-century and an almost complete loss by the end of the century (Leppiniemi *et al.* 2023), the response of palsa mires to climate change may involve a time lag. In fact, discontinuous permafrost has been shown to warm less than continuous permafrost (Biskaborn *et al.* 2019), which can partly be explained by the zero-curtain effect. The zero-curtain effect refers to the absorption of latent heat during the thawing of permafrost soils near 0 °C. This slows the increase in soil temperature and delays permafrost degradation (Outcalt *et al.* 1990). The soil temperatures in palsa mires are also influenced by the well-known insulating effect of the organic soil layers (e.g. Atchley *et al.* 2016; Johnson *et al.* 2013). Therefore, changes in precipitation will eventually reduce the insulating capacity of peat and may lead to palsa degradation, due to increased precipitation and higher meltwater volumes (Kujala *et al.* 2008; Olvmo *et al.* 2020).

Given the complex interplay between climate and soil factors, the temporal predictions presented in Paper II must be interpreted with caution. However, since these projections represent the loss of suitable environments rather than the disappearance of palsas themselves, they can indicate when the climatic conditions become unsuitable for the persistence of palsas and highlight regions most vulnerable to future degradation. It is noteworthy that several studies report fast degradation of palsas (see Table 1). For example, Borge *et al.* (2017) concluded that if degradation continues at the current pace, palsas are likely to largely disappear from northern Norway during the 21st century, which supports the projections of Paper II. Further potential limitations related to the materials and methods used are discussed later in Chapter 9.5.

9.3 Changes in the morphology and ecology of palsa mires

The majority of palsa mires in Finland were predicted to have a low probability of being in a good morpho-ecological state (Leppiniemi *et al.* manuscript). This aligns with the circumpolar observations of strong degradation of palsas (e.g. Borge *et al.* 2017; Mamet *et al.* 2017; Payette *et al.* 2004; Verdonen *et al.* 2023) and with predictions suggesting almost complete loss of suitable environments for palsas by the end of this century (Aalto *et al.* 2014; Fewster *et al.* 2022; Leppiniemi *et al.* 2023). In the Paistunturi Wilderness Area, the area of palsa mounds was observed to have decreased by more than 76% between the 1960s and 2014 (ca. −1.5% a^{-1}), while the area of Finnish palsa mires in a good morpho-ecological state decreased by about 63% (ca. −1.3% a^{-1}). These degradation rates are comparable to findings from other parts of the Northern Hemisphere (see e.g. Olvmo *et al.* 2020; Wang *et al.* 2023; Table 1) and emphasize the widespread decline of palsa mires and the high probability of them being in a poor morpho-ecological state. However, the degradation rates and trends of palsa mires can vary remarkably even within small geographic areas (Verdonen *et al.* 2023). This spatial and temporal variability may partly explain the discrepancies between the documented and predicted degradation rates of palsa mires.

Discontinuous and sporadic permafrost regions, where palsa mires are found, are located at the southern edge of the permafrost region, where the permafrost temperatures are often close to 0 °C (Christiansen *et al.* 2010; Ran *et al.* 2022). Consequently, even slight warming of the permafrost can lead to palsa degradation. Studies show that the permafrost is warming globally, and for example, the temperature of discontinuous permafrost increased by 0.20±0.10 °C between 2007–2009 and 2016 (e.g. Biskaborn *et al.* 2019; Romanovsky *et al.* 2010). Although permafrost warming poses a threat to palsas, not all palsas are equally threatened by climate change, as their morphology can affect their susceptibility to degradation. The results of Paper III showed that Finnish peat plateaus had a mean probability of being in good morpho-ecological state that was more than twice as high as that of dome-shaped palsas (Leppiniemi *et al.* manuscript). Recent studies support these findings, highlighting similar differences in the degradation patterns of palsas and suggesting that peat plateaus are more resilient to thaw than dome-shaped palsas or palsa complexes (Beer *et al.* 2024; Mamet *et al.* 2017; Verdonen *et al.* 2024; Wang *et al.* 2023).

The greater resilience of peat plateaus has been explained by their higher volumetric ice content and lower degree of fragmentation (Beer *et al.* 2024). Fragmentation increases the area of exposed surfaces, which facilitates lateral energy exchange and accelerates permafrost degradation (Beer *et al.* 2024). In addition, snow often accumulates at the edges of palsas, providing more insulation against freezing during winter. As a result, the more complex morphology of dome-shaped palsas and palsa complexes may accelerate their degradation (Borge *et al.* 2017; Olvmo *et al.* 2020). Indeed, dome-shaped palsas are considered more susceptible to lateral erosion compared to peat plateaus (Mamet *et al.* 2017; Olvmo *et al.* 2020). The differences in the resilience to thawing can explain the predicted differences in the probability of dome-shaped palsas and peat plateaus being in a good morpho-ecological state (Leppiniemi *et al.* manuscript).

Based on the overall poor morpho-ecological state of Finnish palsa mires observed in Paper III, even stronger degradation of palsas can be expected in the future. This degradation will have significant consequences for both the abiotic and biotic diversity of northern peatlands (e.g. Errington *et al.* 2024; Luoto *et al.* 2004b; Seemann & Sannel 2024). The impacts of permafrost degradation on landscape diversity can vary depending on the stage of degradation. Initially, as palsas begin to thaw, their degradation can enhance peatland landscape diversity by forming thermokarst ponds in otherwise relatively dry palsa mires (Seppälä 1988, 2006). This increases the availability of different microhabitats and can thus lead to a temporary peak in local biodiversity (Beilman 2001; Camill 1999; Zuidhoff & Kolstrup 2005). However, as degradation progresses, this pattern is reversed. The collapse of palsas homogenizes peatland topography and soil moisture, and only plant species adapted to wetter growing conditions can persist (Errington *et al.* 2024; Zuidhoff & Kolstrup 2005). Although there are only few species specialized to them (Luoto *et al.* 2004b), the poor morpho-ecological state of palsa mires contributes to habitat loss and may therefore threaten some waders that prefer palsa mires (e.g. *Calidris alpina* and *Limosa lapponica*) (Järvinen *et al.* 1987) or the endangered palsa mire hoverfly (*Diptera*, *Syrphidae*) (van Steenis 2022).

Changing permafrost dynamics can also alter the hydrology of thermokarst ponds, leading to enhanced surface and subsurface connectivity, which can result in pond drainage (Seemann & Sannel 2024). Conversely, the expansion of thermokarst ponds and lakes has also been documented (Sannel & Brown 2010). The complexity of factors and processes driving landscape change in permafrost peatlands highlights the need for further research to better understand the abiotic and biotic consequences of palsa mire degradation. For example, it would be interesting to study whether the poor morpho-ecological state of Finnish palsa mires (Leppiniemi *et al.* manuscript) is currently increasing biodiversity or if the degradation has led to more homogenized landscapes and species assemblages. Although the results of Paper III do not directly address this question, they provide important insights into the historical development and current state of Finnish palsa mires. These findings can serve as a basis for estimating the impact of climate change on the biodiversity of northern peatlands.

9.4 The spatial scale matters

Geographers are often interested in the effect of spatial scale on the studied phenomena (Atkinson & Tate 2000; Lloyd 2014). The multi-scale approach of this thesis demonstrates how the chosen spatial scale influences the role of the predictor variables used. For example, the importance of freeze-thaw conditions differed considerably when palsa mires were studied at circumpolar to regional scales (Papers I–II) compared to the local-scale case study in Finland (Paper III). At the circumpolar to regional scale, thaw season conditions, such as TDD and rainfall, were generally the most influential factors in explaining the distribution of suitable environments and the occurrence of palsas (Leppiniemi *et al.* 2023, 2025). Other studies have also highlighted the role of increased precipitation and a warming climate in destabilizing palsa mires, degrading permafrost, deepening the active layer, and causing the loss of other permafrost landforms (e.g. Karjalainen *et al.* 2020; Mekonnen *et al.* 2021; Sannel & Kuhry 2011). At broader spatial scales, differences in air temperature and precipitation patterns during the thaw season become more pronounced between landform and absence/background observations, helping to define the environmental limits for permafrost formation and persistence. Consequently, factors such as TDD or rainfall may emerge as key limiting conditions for palsa mires. In contrast, in spatially more restricted research areas, the range of thaw season conditions may not be wide enough for models to recognize them as limiting factors which, in turn, can increase the relative importance of other conditions in determining the occurrence of palsa mires.

At a local scale, winter conditions have indeed been suggested to have a great influence on the formation of permafrost, and on the degradation of palsas (see e.g. Olvmo *et al.* 2020; Renette *et al.* 2024; Seppälä 2011; Valman *et al.* 2024; Way & Lewkowicz 2018; Zuidhoff & Kolstrup 2000). In particular, wetter, warmer, and shorter winters have been identified as key factors driving palsa degradation (Olvmo *et al.* 2020). Sannel *et al.* (2016) found that different meteorological variables influence interannual changes in the thaw depth and ground temperatures of palsa mires in Sweden. They suggested that thaw season air temperatures primarily control thaw depth, while snowfall plays a more important role in shaping ground temperature regimes. This highlights that, although the relative importance of climate factors may vary at different spatial scales, summer and winter conditions influence the stability and state of palsa mires through distinct processes.

In addition to climate factors, the spatial scale also affects the influence of soil moisture conditions. For example, Papers I–III revealed contrasting trends for TWI when studying palsa mires at circumpolar to regional scales compared to a local scale.

At broader spatial scales, TWI effectively identified peatlands within the surrounding landscape, with higher TWI values correlating with an increased probability of palsa occurrence (Leppiniemi *et al.* 2023, 2025). In contrast, at the local scale, peatlands are already the focus of study, so there is no need to distinguish them from the surrounding landscape. This, however, does not mean that TWI is not a useful variable at the local scale as well. TWI has been used to model the hydrology of mires, and particularly high correlations were found in the case of palsa mires (Persson *et al.* 2012). Within peatlands, TWI can distinguish the drier areas, such as palsas, from the wetter areas and thermokarst ponds. Consequently, lower TWI values were associated with a higher probability of palsa mires being in a good morpho-ecological state, suggesting that TWI has potential in future studies as well (Persson *et al.* 2012; Leppiniemi *et al.* manuscript).

At the local scale, TWI has roles beyond simply measuring soil moisture. As a topographical variable, it can also indirectly indicate wind and snow conditions. Snow is more efficiently redistributed from elevated palsa mounds, promoting deeper ground freezing during winter and supporting palsa persistence (Gurney 2001; Outcalt & Nelson 1984; Seppälä 1982). Small-scale topographic variations within the landscape influence snow depth and soil moisture patterns, which significantly affect the thermal conditions and stability of palsas (e.g. Jean & Payette 2014a; Johansson *et al.* 2013; Martin *et al.* 2019; Sannel 2020). Therefore, TWI can provide important insights into the stability and morpho-ecological state of palsas when high-resolution datasets are available.

Aalto and Luoto (2014) presented a theoretical model of the different environmental factors affecting earth surface processes, including the formation and degradation of palsa mires, across spatial scales. They suggested that while climate factors provide a basis for predicting the occurrence of such processes, the inclusion of local factors such as topography, soil, and vegetation can significantly improve the accuracy of the predictions. In this thesis, all these different 'factor levels' were considered. At the circumpolar scale, TDD was clearly the most influential variable, followed by TWI and SOC (Leppiniemi *et al.* 2023). The greater influence of TDD compared to FDD on palsa occurrence may be due to the key role of thaw temperatures in biological processes such as plant growth and peat decomposition. These processes, in turn, affect palsas by influencing shading, insulation, and peat thickness. In contrast, additional winter cooling may have little effect on palsas once the ground is frozen. The primary contribution of FDD is to characterize the length of the freezing season, whereas TDD may play a greater role in shaping the annual heat balance (see e.g. Sannel *et al.* 2016). These findings align with the notion that incorporating more localized factors can enhance model performance (Aalto & Luoto 2014). Climate change has complex effects on vegetation in northern environments (Elmendorf *et al.* 2012; Errington *et al.* 2024; Maliniemi *et al.* 2018; Myers-Smith *et al.* 2015; Post *et al.* 2009). However, because accounting for potential vegetation shifts in future predictions is challenging, vegetation variables were not included in the circumpolar models of Paper II.

In Paper III, vegetation was considered by testing normalized difference vegetation index (NDVI) and shrub cover variables. Interestingly, both vegetation and soil variables were excluded from the final models to optimize model performance during model calibration (Leppiniemi *et al.* manuscript). Vegetation is known to influence palsas by modifying thaw depth through shading and insulation, as well as by altering albedo and snow depth patterns (Higgins & Garon-Labrecque 2018; Jean & Payette 2014a). Therefore, the weak explanatory power and low importance of vegetation variables in the models were unexpected. This finding likely points to the need for higher-resolution datasets on vegetation composition. Especially in wooded palsa mires, the vegetation strongly influences the thermal regime of palsas (Jean & Payette 2014a), and the integration of vegetation variables describing, for example, the canopy cover, could improve model performance in North America, where also wooded palsas are found. At circumpolar and regional scales, soil variables such as SOC, silt content, and thickness of soil can help the models to recognize peatlands and areas with sufficient peat soil layers in the landscape (Leppiniemi *et al*. 2023, 2025). However, if the focus is exclusively on palsa mires at local scales (e.g. Finnish Lapland), this becomes unnecessary. Between palsa mires, variation in soil variables is more limited, reducing their importance in the local models (Leppiniemi *et al*. manuscript). These findings highlight how the relevance of different variables depends on the spatial scale of the study and underscore the importance of tailoring variable selection to the scale of analysis.

9.5 Data and methodological considerations

Statistical modelling, like any research method, has its own uncertainties and limitations. Hjort and Luoto (2013) listed several weaknesses that can hinder the use of statistical modelling in geomorphology, including issues related to data compilation and accuracy, assumptions related to the modelling methods, as well as subjective choices made during the different modelling steps. To address these challenges, a spatially representative dataset of palsa mires was compiled and the accuracy of the landform observations was ensured through critical assessment and verification using satellite imagery. In addition, different modelling methods were tested during the research process to identify the most appropriate methods for addressing the research questions. Subjectivity in model calibration was mitigated by applying widely used techniques such as the Akaike information criterion (AIC; Stoica & Selén 2004) for model calibration, and the 'ENMeval' package (version 2.0.3; Kass *et al*. 2021) to optimize parameters for MaxEnt in Paper I. Despite the efforts to minimize weaknesses in the materials and methods used, certain limitations remain and need to be discussed with respect to assess the results and conclusions of the thesis.

During the compilation of the circumpolar palsa dataset for Paper II, it became evident that there is a lack of research on palsa mires in Central and Eastern Siberia, at least in the English literature (Leppiniemi *et al*. 2023). Some studies have been conducted in the region and published in Russian (see e.g. Vasil'chuk *et al*. 2014, 2013a, 2013b); these were used to locate the landforms when possible. However, the scarcity of landform observations from this area may reduce the accuracy of the spatial predictions, particularly if the relevant environmental gradients are not adequately represented in the compiled dataset. Given the varying environmental conditions of palsa mires in different parts of the Northern Hemisphere (Leppiniemi *et al*. 2025), efforts were made to maximize the number and representativeness of landform observations during model calibration. Consequently, fully independent landform observations were not available for model evaluation; instead, semi-independent evaluations were performed by splitting the dataset into separate calibration and evaluation subsets prior to model calibration and performing 100-fold cross validation on both the evaluation and calibration datasets.

Cross-validation often overestimates model performance compared to evaluation with fully independent data (see e.g. Roberts et al. 2017), and this should be considered when evaluating model performance. Due to the potential overestimation, other evaluation methods were used in addition to cross validation. In Paper III, the spatial predictions were compared with the observed degradation of the Finnish palsa mires, and in Paper II the semi-independent evaluations were complemented by comparisons with independent datasets on the distribution of permafrost peatlands, peat depth and thermokarst landscapes (Hugelius *et al.* 2020; Olefeldt *et al.* 2016, 2021; Treat *et al.* 2016; Xu *et al.* 2018). The comparisons showed, for example, that most of the peatlands in Central Siberia are located in the continuous permafrost region, where environmental conditions may favor the formation of other landforms, such as polygon mires and pingos, rather than palsas (see e.g. Fewster *et al.* 2022; Grosse & Jones 2011). Thus, the comparisons support the finding of Paper II that suitable environments for palsas in the region are limited. However, it should be noted that the independent evaluation datasets utilized also have limitations related to data availability, and for example, the thermokarst landscape dataset produced by Olefeldt *et al.* (2016) is also based on modelling rather than direct observations.

Another important consideration related to Paper II is the choice of climate change scenarios used in the analysis. With advances in climate science and the availability of more comprehensive data, new scenarios for future predictions have been developed. The latest generation of climate change scenarios is produced using the coupled model intercomparison project phase 6 (CMIP6) climate model, which integrates the shared socioeconomic pathways (SSPs; Meinshausen *et al.* 2020) with the representative concentration pathways (RCPs) (Eyring *et al.* 2016; O'Neill *et al.* 2016). However, in Paper II, the chosen RCP scenarios were those used in the WorldClim 1.4 database, which uses the period 1950–2000 as a baseline for historical climate conditions (Hijmans *et al.* 2005). This baseline period corresponds well with the original documentation of the palsa observations used in the thesis. More importantly, it represents colder climate conditions compared to more recent periods, and was therefore considered to better reflect the conditions of the colder climate phases of the Holocene, during which most of the current palsas formed (Fewster *et al.* 2020; Treat & Jones 2018; Vorren 2017). In contrast, it is possible that the baseline period (1970–2000) of WorldClim version 2.1, which does use CMIP6 scenarios (Fick & Hijmans 2017), no longer represents conditions enabling palsa formation, as studies report degradation of palsas since the 1960s across the Northern Hemisphere (Leppiniemi *et al.* manuscript; Mamet *et al.* 2017; Payette *et al.* 2004; Saemundsson *et al.* 2012; Verdonen *et al.* 2023). Although the use of RCPs can be justified, the choice of scenarios used can affect the spatial predictions produced, and I recognize the added value of the newer generation of scenarios for future studies related to the evolution of permafrost landscapes.

The relative importance and responses of different predictor variables should likewise be interpreted with caution, as strong correlations (e.g. >0.70) between predictors can affect the interpretability of the findings (see e.g. Dormann *et al.* 2013; Meloun *et al.* 2002; Smith & Santos 2020). In Paper I, it was not feasible to eliminate all highly correlated variable pairs, as doing so would have required the removal of multiple variables necessary to maintain consistency across research areas. This, in turn, would have compromised the ability to effectively address the research questions and objectives. That said, MaxEnt is considered effective in dealing with multicollinearity by reducing the contribution of highly correlated variables (Elith *et al.* 2011; Feng *et al.* 2019; Phillips & Dudík 2008).

In addition to addressing multicollinearity in the environmental data, the quality and representativeness of the predictors must also be considered. It is possible that the variables used do not fully capture the relevant environmental factors. In the case of palsa mires, new high-resolution and harmonized datasets on snow and peat depth and vegetation composition could especially improve model performance. Such datasets were not available for the Northern Hemisphere, and therefore proxies (e.g. snowfall and SOC) had to be used, especially in Papers I–II, but also in Paper III. The proxies used may not adequately account for all related processes, such as redistribution and trapping of snow, which can reduce their importance in the models and hinder the interpretation of the results. Therefore, the development of new high-resolution datasets could provide valuable insights into the current and future distribution of these landforms.

9.6 Suggestions for future research

While some suggestions for future research have already been discussed in the previous sections, additional research ideas are presented and discussed here. The compilation of the palsa data revealed that the distribution of palsa mires is relatively well documented in North America, northern Europe and Western Siberia, but much less is known about the occurrence of palsa mires in Central and Eastern Siberia (see Chapter 9.5). Future research could benefit from the application of geospatial artificial intelligence (so-called GeoAI) and machine vision tools (see Li & Hsu 2022) to identify palsa mires from satellite imagery. These tools would help expand our knowledge of the distribution of palsa mires, particularly in remote areas, and fill the existing gaps in our understanding. Moreover, such technologies may provide valuable opportunities for monitoring the degradation of palsa mires in the future.

Although remote sensing and GeoAI tools can contribute to future research, traditional monitoring of palsa mires remains essential for a deeper understanding of the ecological impacts of palsa degradation. Future investigations could include field measurements and data collection from palsa mires in different morpho-ecological states, monitoring of ground temperatures, seasonal heave and subsidence of palsas (see Renette *et al.* 2024) as well as documentation of the vegetation succession that has already occurred in degraded palsa mires (see Errington *et al.* 2024). Such studies would not only enhance our ability to monitor the degradation of palsa mires and estimate the associated greenhouse gas emissions, but also provide valuable insights into the effects of palsa degradation on the biodiversity and geodiversity of northern peatlands. For example, measuring greenhouse gas emissions from palsa mires in different morpho-ecological states could improve our understanding of potential future emissions from degrading palsa mires. Furthermore, the impacts of palsa degradation on local communities, such as impacts on livelihoods, infrastructure, and ecosystem services, could be a valuable focus for future research.

Recent studies have observed that several factors, including morphology, fragmentation, and position within the landscape, can influence the degradation and morpho-ecological state of palsa mires (e.g. Beer *et al.* 2024; Mamet *et al.* 2017; Wang *et al.* 2023). While these factors are currently recognized to influence palsa degradation rates, further research is needed to better understand the processes through which these factors affect palsas and their role in the context of accelerated anthropogenic climate warming. In addition to the factors mentioned above, vegetation type strongly influences the thermal regime of palsas and thus may affect the degradation patterns and rates (Higgins & Garon-Labrecque 2018; Jean & Payette 2014a). Therefore, it is important to investigate the role of vegetation composition more thoroughly in future studies.

This thesis provided an opportunity to examine the interplay between the spatial scale of the research and the environmental factors that affect palsa mires. However, since the studies were conducted in different regions and involved different response and predictors, they were not specifically designed to assess the direct impact of spatial scale. Therefore, further research investigating the effects of spatial scale would be valuable and could, for example, help enhance our understanding of the distinct roles of summer and winter conditions for palsa mires. In sum, there are still many opportunities for further research on palsa mires, and the context of climate change makes them a particularly important and timely research topic.

10 Conclusions

In this final chapter, the main conclusions of this thesis are presented, and their implications for academic research and potential applications are briefly discussed. Table 5 provides an overview of the research questions, key findings, and conclusions, offering a structured summary of the thesis. The thesis highlights the variability in environmental characteristics and responses of palsa mires across the Northern Hemisphere, as well as their vulnerability to anthropogenic climate change. In addition, it emphasizes the strong degradation of Finnish palsa mires over recent decades and the critical role of scale in interpreting their ecological and environmental drivers. These findings deepen our understanding of palsa mires and provide valuable insights into broader trends in permafrost dynamics and environmental change in the periglacial domain.

This thesis has implications for further research on palsa mires and, more broadly, on permafrost dynamics. During the preparation of Papers I–II, a comprehensive circumpolar dataset of palsa distribution was compiled, and the landform observations were openly shared, providing researchers with a valuable resource to use and expand upon in advancing our understanding of palsa mires. In addition, the spatial predictions produced in Papers II–III have been made publicly available, facilitating their use in future studies. The findings of this thesis can contribute to the assessment of long-term environmental changes by improving our understanding of historical trends and enabling more accurate future predictions, particularly regarding shifts in discontinuous and sporadic permafrost. The thesis also provides valuable insights into the impact of spatial scale in modelling, emphasizing the importance of selecting appropriate variables and scales to optimize study outcomes. Furthermore, the results of Paper III demonstrate that spatial modelling can be used to predict the morpho-ecological state of palsa mires with relatively good accuracy. This indicated that there is potential for the development of models that predict the morpho-ecological state of palsas in other parts of the Northern Hemisphere as well, and that the approach can be used to model other climate-sensitive landforms.

The findings of this thesis have potential applications beyond academic research as well. Palsa mires are recognized by the EU as critically endangered habitats, and the thesis provides insights that may inform political decision-making. For example, the results can be used to help identify the areas that are most vulnerable to palsa degradation, which could support the prioritization of monitoring efforts and conservation strategies. The research also highlights the broader implications of permafrost thaw for global carbon dynamics, providing a basis for understanding the potential locations of future greenhouse gas sources. However, it is important to acknowledge the uncertainties associated with the materials and methods, particularly at the circumpolar scale, which may limit the direct applicability of the findings. Locally, palsa mires ease reindeer migration across peatlands, while also holding cultural and economic importance as berry-picking areas, making them valuable resources for northern communities. This research can therefore help to identify potential changes in traditional livelihoods, although further studies are needed to refine these assessments.

Table 5. The summary of the main findings and conclusions of this thesis ordered by research question.

Research questions	Main findings	Main conclusions
RQ1: How do the environmental characteristics and responses of palsa mires vary in different parts of the Northern Hemisphere?	• Palsa mires of Hudson Bay region had the most pronounced environmental gradients. • Especially the soil characteristics between regions differed. • Environmental characteristics of Icelandic palsa mires differed most from those of other regions.	• Palsa mires are typically found in cold and dry climates. • However, the range of environmental gradients varies regionally. • Responses to climate factors are more consistent across regions than those of soil factors.
RQ2: Which environmental factors are most important in explaining the occurrence of palsa mires?	• Freezing and thawing degree days, rainfall and topographical wetness index contributed most to the models.	• Climate factors and soil moisture are the most important factors explaining the occurrence of palsa mires at regional scale.
RQ3: How is the distribution of suitable environmental spaces for palsa mires predicted to change in the Northern Hemisphere under climate change?	• Dramatic loss of suitable environments for palsas is predicted to occur by 2041–2060 and almost complete loss by 2061–2080.	• The suitable environments for palsas are critically threatened by climate change.
RQ4: What is the morpho-ecological state of Finnish palsa mires?	• Over half of the Finnish palsa mires had low probability (<0.25) of being in good morpho-ecological state. • Peat plateaus were more likely to be in good morpho-ecological state than dome-shaped palsas.	• Majority of Finnish palsa mires are in poor morpho-ecological state.
RQ5: How has the area of Finnish palsas in good morpho-ecological state changed during the last 50 years?	• Based on interpretation of orthoimagery of Paistunturi Wilderness Area: –76% (ca. –1.5% a^{-1}). • Based on statistical modelling of all Finnish palsa mires: –63% (ca. –1.3% a^{-1}).	• Strong lateral degradation of palsas has occurred.
RQ6: Does the scale at which palsa mires are studied affect the influence of environmental factors?	• At circumpolar to regional scales, thaw season conditions have a greater impact on the occurrence of palsa mires, while winter conditions influence more the morpho-ecological state of palsa mires at local scale. • The influence of soil moisture and composition is affected by the used scale.	• Seasonal climatic conditions and soil factors, exhibit scale-dependent importance, emphasizing the need for scale-specific interpretation of the influence of variables.

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