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Arctic vegetation, snow and the global change

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Arctic vegetation, snow and the global change

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Abstract

The Arctic is warming two to three times faster than the global average. However, climate change is proceeding at different pace between seasons and the warming has been most prominent in winter. For most of the year, majority of the arctic organisms are covered by insulating snowpack. Snow protects arctic plants, bryophytes and lichens from weather events in the free atmosphere and may provide relatively warm and stable overwintering conditions. The importance of snow has been widely acknowledged, but snow information is rather rarely utilized in climate change impact models that predict the future state of the arctic vegetation. This is largely due to missing wintertime datasets and harsh winter conditions that limit field work efforts in the Arctic. Therefore, there has remained a largely unanswered question: what is the role of snow conditions in spatial redistribution of arctic species and vegetation under rapidly warming climate?

In this thesis, I address these gaps in knowledge and methodology. I utilise extensive plot-scale vegetation datasets and link these data to detailed microclimatic measurements covering both summer and winter conditions and to satellite-born snow information at fine spatial scales. I use a suite of statistical modelling methods to explore the snow-vegetation relationships in species pools consisting several hundreds of arctic, alpine and boreal vascular plant, bryophyte and lichen species in northern Fennoscandia, Svalbard and western Greenland. These models are further used to predict patterns in species distributions, community and functional trait compositions and biodiversity in space and time, to test the sensitivity of these vegetation properties to concurrent and separate changes in snow conditions and temperatures.

I found that snow and winter conditions have a fundamental role in arctic ecosystems by mediating the effects of climate change at local and regional scales. Snow information improves the accuracy of the models of arctic vegetation and reveals possible future trajectories otherwise hidden from climate change impact models if the effects of snow are not quantified. Heterogeneous snow accumulation is one of the main drivers of taxonomic and functional diversity in tundra, and losing the late melting snowbed environments may lead to homogenisation of the tundra and regional extinctions among snow specialist species. It is evident that ignoring the effects of snow can produce biased projections of the future status of arctic vegetation. Given the high ecological importance of snow in the Arctic, it is alarming that the uncertainties in snow projections for the second half of the century are so high. In the upcoming years, the scientific community should pay more attention to plant-snow relationships and interactions and improve the predictions of future snow conditions at fine spatial and temporal scales.

Abstract in Finnish

Arktiset alueet lämpenevät kaksi, jopa kolme kertaa nopeammin kuin maapallo keskimäärin. Lämpeneminen etenee kuitenkin epätasaisesti vuodenaikojen välillä ja talvet ovat lämmenneet kaikista nopeimmin. Lumipeite suojaa arktisia eliöitä suurimman osan vuodesta. Se eristää lumen alla talvehtivat kasvit ja jäkälät vapaan ilmakehän sääilmiöiltä ja voi luoda verraten lämpimät ja vakaat talviolot. Lumen suuri merkitys pohjoisissa ekosysteemeissä tunnustetaan laajalti, mutta se silti usein sivuutetaan ilmastonmuuttoksen vaikutuksia tutkittaessa ja ennustettaessa. Suurin syy tähän on sopivien talvea ja lunta kuvaavien aineistojen puute. Siksi on laajalti tutkimatta, kuinka muuttuvat lumiolot tulevat vaikuttamaan arktisten lajien levinneisyyksiin ja runsauksiin tulevassa ilmastossa.

Tässä työssä tilkitsen näitä aukkoja tiedoissamme. Tutkimusryhmämme on kerännyt kasvillisuusaineistoja pohjoisessa Fennoskandiassa, Huippuvuorilla ja Grönlannissa. Väitöskirjassani linkitän nämä kasvillisuustiedot tarkkoihin mittauksiin niin kesän kuin talven pienilmastosta sekä toistuvista satelliittikuvista irrotettuun lumi-informaatioon. Käytän tilastollisia malleja selvittämään, kuinka nämä ympäristötekijät vaikuttavat satojen pohjoisten putkilokasvi-, sammal- ja jäkälälajien esiintymiseen ja arktisen luonnon monimuotoisuuden alueelliseen jakautumiseen. Tutkin ja mallinnan, kuinka herkkä arktinen kasvillisuus on muutoksille lumipeitteessä erottamalla lumen vaikutukset suorista lämpötilannousun seurauksista.

Sain selville, että talvi- ja lumiolosuhteet määräävät ratkaisevalla tavalla, kuinka ilmastonmuutoksen vaikutukset tulevat ilmenemään pohjoisessa luonnossa paikallisilla ja alueellisilla mittakaavatasoilla. Tiedot lumipeitteestä tai talvisesta pienilmastosta parantavat arktisten lajien levinneisyysmalleja ja voivat paljastaa tulevaisuudenkuvia, jotka jäisivät ennustamatta, jos talven olosuhteet jätetään huomiotta. Lumen vaihteleva kasautuminen ja sulaminen avoimella tundralla on yksi tärkeimmistä pohjoisen luonnon monimuotoisuutta ylläpitävistä tekijöistä. Erityisesti myöhään sulavien lumenviipymien katoaminen hävittäisi samalla suuren joukon tähän habitaattiin erikoistuneita lajeja ja yksipuolistaisi tunturimaisemia ja niiden eliöstöä. Näyttää selvältä, että lumen vaikutusten unohtaminen voi tuottaa harhaisia ennusteita pohjoisen luonnon tulevaisuudesta ja siksi tarvitsemme myös aiempaa tarkemman käsityksen siitä, kuinka lumiolot tulevat kehittymään kuluvan vuosisadan aikana.

Acknowledgements

```
> ########################################
> # an R code to all my loved ones
>
> to_thank <- c(“Family”,
+                “Friends”,
+                “Colleagues”)
>
> thank <- function(x){
+
+   out <- paste0(“Dear “,
+                 if(length(x) > 1){
+                   paste0(paste(x[-length(x)],
+                         collapse = “, “),
+                         “ & “,
+                         x[length(x)])
+                 } else {
+                 x
+                 }, “, You Are Best!!!”
+                 )
+
+    out <- toupper(out)
+    return(out)
+ }
>
> thanks <- thank(to_thank)
>
> thanks
[1] “DEAR FAMILY, FRIENDS & COLLEAGUES, YOU ARE BEST!!!”
```

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List of original publications

This thesis is based on the following articles, which are cited in the text according to their Roman numerals. The articles II, III and IV are reprinted with the retained author copyrights.

I. Niittynen P., Heikkinen R., Aalto J., Guisan A., Kemppinen J. & Luoto M. Fine-scale tundra vegetation patterns are strongly related to winter thermal conditions. Accepted manuscript.
II. Niittynen P. & Luoto M. (2018). The importance of snow in species distribution models of Arctic vegetation. Ecography, 41: 1024-1037. doi:10.1111/ecog.03348
III. Niittynen P., Heikkinen R. & Luoto M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. Nature Climate Change, 8: 997-1001. doi:10.1038/s41558-018-0311-x
IV. Niittynen P., Heikkinen R. & Luoto M. (2020). Decreasing snow cover alters functional composition and diversity of Arctic tundra. Proceedings of the National Academy of Sciences. In Press. doi:10.1073/pnas.2001254117

Author’s contributions to the publications

Pekka Niittynen is fully responsible for the summary of the thesis.

I. P.N. participated in the original planning of the study design, collected a large part of the field data, gathered the environmental data, conducted all analyses and modelling, and was main responsible in writing the article. P.N. is the corresponding author.

II. P.N. participated in the original planning of the study design, collected a large part of the field data, gathered the environmental data, conducted all analyses and modelling, and was main responsible in writing the article. P.N. is the corresponding author.

III. P.N. participated in the original planning of the study design, collected a large part of the field data, gathered the environmental data, conducted all analyses and modelling, and was main responsible in writing the article. P.N. is the corresponding author.

IV. P.N. participated in the original planning of the study design, collected a large part of the field data, gathered the environmental data, conducted all analyses and modelling, and was main responsible in writing the article. P.N. is the corresponding author.

Abbreviations

BIEN	Botanical Information and Ecological Network
FDD	Freezing degree days
GAM	Generalized additive models
GBM	Generalized boosted models
GDD	Growing degree days
GLM	Generalized linear models
LDMC	Leaf dry matter content
LiDAR	Light detection and ranging
MODIS	Moderate resolution imaging spectroradiometer
RF	Random forests
SCD	Snow cover duration
SDM	Species distribution model
SLA	Specific leaf area
TDD	Thawing degree days
TRY	The TRY Plant Trait Database
TTT	Tundra Trait Team
TWI	Topographic wetness index

1 Introduction

Cryosphere is a fundamental component of high-latitude and high-altitude ecosystems (AMAP 2017, Box et al. 2019). It comprises the frozen elements of the Arctic and high mountains such as seasonal and permanent snow, sea ice, glaciers, and permafrost. These are the foundations that have formed the arctic tundra as we know it: treeless, open biome with long winters and various geomorphological formations. Especially the effects of snow cover and its properties – for instance duration and thickness – on tundra vegetation have interested ecologists and phytosociologists at least for a century (Gjaerevoll 1956). As a legacy of this long tradition, the importance of snow for the flora and fauna of the tundra biome is widely acknowledged (Gjaerevoll 1956, Billings and Bliss 1959, Walker et al. 1993). Nevertheless, fundamental research gaps still exist in how to incorporate the effects of snow and winter conditions systematically into the frameworks of quantitative ecology and models of the future of the arctic and alpine ecosystems. Currently, winter-time processes have attained far less attention than growing season conditions in the ecological research and literature (Williams et al. 2015, Ladwig et al. 2016). This conflict, between the widely known importance of winter ecology and the minor attention it receives, is troublesome.

All living organisms have numerous environmental requirements that are, in principle, equally essential for their existence (Raunkiaer 1934). However, abundance of these elements varies in space and time exposing the organisms for possible limitations and stress. Thus, the effective importance of the essential elements can be, in fact, different. Some of these environmental factors vary so smoothly and over large distances and periods (e.g. tropospheric concentration of CO_2) that they have practically no direct effect on how local species communities have been organized. Whereas, some other factors are extremely variable in time and space, and thus they have potential to be agents in driving spatio-temporal patterns and complexity of life. One of these factors is snow that controls the availability of multiple elements important for organisms (Li et al. 2016, Song et al. 2017).

Owing to anthropogenic emissions, previously smoothly fluctuated atmospheric CO_2 concentration has now rocketed inducing contemporary warming of planet Earth (Myhre et al. 2013). In recent decades, climate change has been especially pronounced in the arctic regions and on high mountains (Wang et al. 2016, AMAP 2017, Box et al. 2019). These climatic trends have had and will have impacts on the vegetation of the Arctic (Barrett et al. 2015, Myers-Smith et al. 2015, Hedenas et al. 2016, Bjorkman et al. 2018a, Stewart et al. 2018). Rapid climate change in the Arctic exposes plants to novel environmental conditions, enables more southern species to establish and overall changes the surrounding conditions plants have adapted to (Steinbauer et al. 2018, Niskanen et al. 2019). Predicting the possible changes in patterns of biodiversity and species distributions well in advance is a fundamental task for ecologists and biogeographers of this century.

1.1 The ecological importance of snow and winter

Snow plays an important role in shaping climate and regulating terrestrial hydrology and soil processes (Blanc-Betes et al. 2016, Bring et al. 2016, Bernard et al. 2019). In terms of extent, snow is the largest single component of the global cryosphere (Chen et al. 2016, AMAP 2017). Seasonal snow cover is concentrated in the Northern Hemisphere, where the maximum snow coverage is reached typically in January when snow covers approximately half of the land area of the Northern Hemisphere (Dery and Brown 2007). When present, snow largely controls the radiative balance of the earth surface and heat transfer between ground and atmosphere as well as functions as a massive storage of fresh water fundamental for societies (Barnett et al. 2005, Chen et al. 2016).

Nevertheless, the importance of snow is pronounced in cold ecosystems where temperatures stay below 0 °C for most of the year (Kreyling 2010, Cooper 2014, Bjerke et al. 2015, Bokhorst et al. 2016). Such ecosystems are found in the Arctic and on the highest mountains. There each organism is affected by the snow cover in one way or another (Bokhorst et al. 2016) and snow truly is a multifaceted driver of the physical conditions and biota with both direct and indirect effects (Callaghan et al. 2011a, Callaghan et al. 2011b, Bjerke et al. 2015, Winkler et al. 2018).

Snow has unique physical properties of high albedo and low thermal conductivity. High albedo means high reflectivity, and thus, majority of the incoming solar radiation is reflected back to the atmosphere from snow surfaces (Chen et al. 2016). Low thermal conductivity means that the subnivium (that is, the seasonal microenvironment beneath the snow) is effectively insulated from the temperatures in the freely moving air above the snow (Zhang 2005, Pauli et al. 2013). If the snowpack is thick (e.g. > 100 cm) and is settled early in the autumn, soil temperatures may never decrease much below 0 °C, especially in the area without permafrost (Aalto et al. 2018). This provides relatively warm and stable overwintering conditions for low-growing plants, insects and small mammals living in the subnivium (Pauli et al. 2013, Petty et al. 2015, Zuckerberg and Pauli 2018). Nevertheless, thick snowpack takes time and energy to melt, and therefore, snow can notable shorten the length of the growing season (Musselman et al. 2017, Kankaanpää et al. 2018, Winkler et al. 2018). Thus, on one hand, snow is protecting the biota from harsh winter conditions and extreme weather events, desiccating winds and abrasion by drifting ice crystals, but on the other hand, snow can drastically limit the amount of incoming energy and the length of the most productive season (Pauli et al. 2013, Petty et al. 2015, Zuckerberg and Pauli 2018).

Tundra is a treeless and open ecosystem where snow is freely redistributed by wind (Liston and Sturm 1998, Winstral et al. 2002). Drifting snow is blown away from ridges and hilltops and is accumulated in sheltered slopes and depressions (Billings and Mooney 1968, Aalto et al. 2018). This creates a mosaic of highly diverging habitats across rugged arctic landscapes. Windblown heaths have very limited (sometimes lacking) snow cover, and thus, low winter temperatures, deep frost penetration and a high risk of spring frost but also an extended growing season (Heegaard 2002, Litaor et al. 2008, Wipf et al. 2009, Arnold et al. 2014, Wheeler et al. 2014). On the other end of the snow accumulation gradient, snowbed habitats experience contrasting environmental conditions. These habitats have relatively warm and stable winter temperatures, low risk of frost and an excessive amount of melt water, but the length of the growing season can endure only few weeks (Heegaard 2002, Sieg and Daniels 2005, Bjork and Molau 2007).

For most of the arctic biota, winter and snow denote the season of dormancy and their overwintering success is highly dependent on the prevailing snow conditions (Bale and Hayward 2010, Kreyling 2010, Pauli et al. 2013, Williams et al. 2015). However, several biogeochemical processes can stay active below, in and on the snow, and due to the prolonged snow season in the Arctic, these processes can have significant impacts on the annual budgets of the cycles of matter (Mastepanov et al. 2008, Semenchuk et

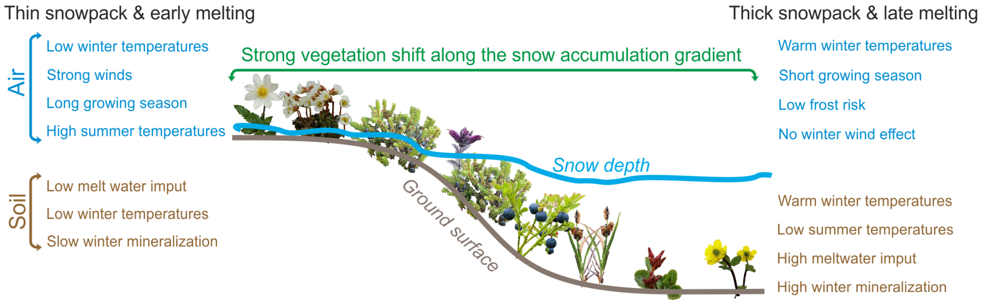

Figure 1. The effects of uneven snow accumulation on abiotic conditions above and below the soil surface that are known to be important for plants. Habitats with thick and thin snowpacks have contrasting microclimatic conditions and differing species and communities.

al. 2015, Li et al. 2016, Semenchuk et al. 2016). Bacterial and algal life is present in the snow and some evergreen vascular plants can be active and photosynthesize under snow cover (Starr and Oberbauer 2003, Kalberer et al. 2006, Saarinen et al. 2011, Solanki et al. 2019).

1.2 Changing climate of arctic winters

In the course of the last decades, climate of the Arctic has warmed two to three time faster than the global average (Gobiet et al. 2014, Pepin et al. 2015, Wang et al. 2016, AMAP 2017, Box et al. 2019). This spatial pattern in global warming is referred as *Arctic amplification* and is partly caused by feedbacks related to the disappearance of snow and ice in the North (Screen and Simmonds 2010, Serreze and Barry 2011, Pithan and Mauritsen 2014, Screen 2014). All key climatic and ecosystem attributes reviewed by Box et al. (Box et al. 2019) indicate that the Arctic is trending away from its 20th Century conditions into a novel ecosystem state. The warming trend has been especially prominent during the winter months with strong consequences to the cryosphere by intensifying the cycle of water between its liquid and frozen phases (Bintanja and van der Linden 2013, Bintanja and Andry 2017).

Snow cover is sensitive to changes in temperatures, but it is also dependent on precipitation and its timing. Winter-time precipitation has increased in many arctic regions (Vincent et al. 2015), which has resulted in rise of snowfall and maximum snow depth in some areas, but also increased the frequency of rain-on-snow events (Bulygina et al. 2011, Harpold et al. 2017, Merkouriadi et al. 2017). Nevertheless, the general trend is that warming temperatures overcome the effects of increases in winter precipitation on snow depth leading to a decrease in yearly ratio of precipitation falling as snow (Bintanja and Andry 2017, Box et al. 2019, Luomaranta et al. 2019). Especially snow cover duration has been decreasing across the arctic and alpine regions (Kim et al. 2015, Klein et al. 2016). Coarse-scale satellite observations have shown that snow extent has been rapidly shrinking in the Northern Hemisphere especially during spring and summer, and snowmelt timing has been advancing with a rate of two days per decade during 1982-2013 (Chen et al. 2016). Meteorological observations largely affirm these trends (Bulygina et al. 2009, Klein et al. 2016, Luomaranta et al. 2019).

1.3 Arctic vegetation

The Arctic is an ecosystem with pronounced seasonality: from total darkness to twenty-four hours of daylight; from extreme cold to relatively warm summers; from period of solid precipitation to excess of melt waters and then to possible late summer droughts. Arctic plant species have had to adapt to these fluctuations by their unique lifeforms and strategies (Raunkiaer 1934, Billings and Mooney 1968, Billings 1973, 1974). In this thesis, I consider arctic vegetation in its very broad sense including vascular plants, bryophytes and lichens. In bryophytes I focus mostly on mosses (*Bryopsida*) and in both mosses and lichens on species growing on soil or similar substrates excluding saxicolous (rock dwelling) and epiphytic (living on the surfaces of trees and shrubs) species. The overall number of plant and lichen species in the Arctic is low on the global scale, however local species richness can be higher than in most of the biomes: a single 1-m^2 area can sustain a community of dozens of vascular plant, bryophyte and lichen species mainly because of their small size (Gough et al. 2000, Wilson et al. 2012, Kemppinen et al. 2019).

The vegetation of the arctic tundra is characterized by low-growing and long-living species (Billings and Mooney 1968, Billings 1974, Sonesson and Callaghan 1991). The species avoid extending their overwintering shoots above the snow surface, and thus, even the woody plants creep along the ground and form a functional group called dwarf shrubs (Myers-Smith et al. 2011, Vowles and Bjork 2019). Tall species are completely lacking in the tundra, but many individuals may grow relatively large due to their lateral growth and long life. Dwarf shrubs comprise the most abundant species group especially in the Sub- and Low-Arctic, whereas forbs and graminoids are the dominant vascular plant groups in the High-Arctic (Walker 1995, Virtanen et al. 2006, Virtanen et al. 2016, Bjorkman et al. 2018a).

The ecological importance and abundance of bryophytes and lichens are pronounced in cold and often waterlogged ecosystems such as the arctic tundra (Sonesson and Callaghan 1991, Cornelissen et al. 2007, Mateo et al. 2016). Bryophytes are abundant in wetlands and snowbeds, whereas lichens often dominate the driest and coldest habitats, such as wind-swept ridges. These groups are different from vascular plants by their evolutionary history, but also by their ecology. Neither bryophytes nor lichens have true roots or tissues specialized to transport water and nutrients, that is, they are called *poikilohydric* (Desamore et al. 2012, Mateo et al. 2016). Thus, bryophytes and lichens are less dependent on processes and resources deep in the soil compared to vascular plants, which invest into their rhizosphere, particularly in the Arctic (Iversen et al. 2015). Bryophytes and lichens also champion surviving over unfavourable periods, and many species can tolerate, for instance, complete drying and deep freezing (Furness and Grime 1982, Sonesson and Callaghan 1991, Schlensog et al. 2004, Cornelissen et al. 2007, Bjerke et al. 2011).

Winter ecologists commonly use terms *chionophilous* and *chionophobous* referring to species that accordingly prefer or avoid habitats with thick, long-lasting snowpack (Gjaerevoll 1956). Local species communities are often organized along a so-called mesotopographical gradient, where chionophilous species inhabit the depressions with high snow accumulation and chionophobous species the other extreme where snow cover is minimal thorough the winter (**Figure 1**) (Gjaerevoll 1956, Billings and Mooney 1968). Nevertheless, most of the tundra plant species must balance between a long growing season and harsh winter conditions or a short summer and relatively warm overwintering conditions (Bruun et al. 2006, Litaor et al. 2008, Opedal et al. 2015).

All species have adapted to survive and reproduce in certain environmental conditions over time. These adaptive modifications are observable in organisms' size, structure, phenology and biochemistry (Anderson and Gezon 2015, Dudley et al. 2019). In turn, these features – called

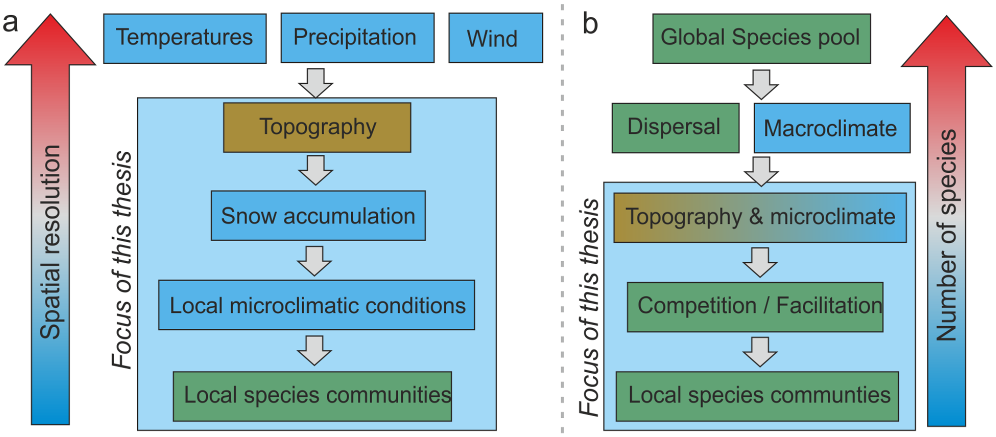

Figure 2. The hierarchy of climate-vegetation relationships across spatial scales (a). The filters that form the local species communities from the global species pool (b).

functional traits –affect how a given species interacts with its environment and modifies functions of the ecosystem (Diaz and Cabido 2001, Asplund and Wardle 2017, Myers-Smith et al. 2019). In practice, functional traits are measurable properties of plant individuals reflecting the size and resource use of the plant (Diaz et al. 2004).

The importance of biotic interactions is often considered low in energy-limited ecosystems such as the arctic tundra compared to ecosystems in the tropics (Hooper et al. 2005, Mitchell et al. 2009). Nevertheless, competition within and between vascular plants, bryophytes and lichens can be notable and competitive exclusion can be one of the major causes why small-stature cryptogams and small forbs are occurring and dominating mainly in the most extreme habitats (Cornelissen et al. 2001, Alatalo et al. 2017). Moreover, herbivory, trampling and nutrient transport and relocation by larger animals can be at least of local importance (Aunapuu et al. 2008, Pajunen et al. 2012, Tommervik et al. 2012, Gauthier et al. 2013). The main herbivores in the northern tundra are reindeers, muskoxen, geese, lemmings and moth caterpillars (Post and Forchhammer 2008, le Roux et al. 2013, Legagneux et al. 2014, Vowles et al. 2017). In addition, even in the High-Arctic many flowering plants are dependent on insect pollination (*Diptera* is the most important pollinator insect group), although asexual reproduction is also common (Billings 1987, Jonsdottir 2011, Tiusanen et al. 2016).

1.4 Climate change and arctic vegetation

Anthropogenic climate change is expected to cause rapid range shifts in species distributions (Parmesan et al. 1999, Chen et al. 2011). These shifts are likely to be non-random and unidirectional towards higher latitudes and altitudes as species ‘track’ their thermal niches, which are shifting along the warming climate (Lenoir et al. 2008, Lenoir and Svenning 2015). These shifts have already been documented in arctic and alpine areas: shrubs have increased in the arctic tundra (Myers-Smith et al. 2011) and alpine mountain summits are gaining more species from lower altitudes (Steinbauer et al. 2018).

Climate change can be fatal for arctic species for several reasons: first, there are no further areas where to escape; secondly, arctic species are poor competitors; and thirdly, the Arctic is warming rapidly, and many changes in the ecosystem can happen abruptly. First issue raises from the geography of the Arctic. The shape of the Arctic tundra biome is mainly a narrow stripe between the boreal forests and the Arctic Ocean (Walker 1995, Higgins et al. 2016, Walker et al. 2018). If the biomes of the Earth shift towards the poles there are simply no new habitable terrestrial areas for arctic species to migrate or the dispersal barriers (e.g. Arctic Ocean) are too wide (Walker 1995, Weider and Hobaek 2000, Wookey 2007, Niskanen et al. 2019).

Secondly, living under harsh arctic conditions favours relatively conservative resource use strategy, slow growing rate and small size, which makes the species poor competitors under more favourable conditions (Oksanen and Ranta 1992, Callaway and Walker 1997, Rajaniemi 2003, Kikvidze 2011, Mod et al. 2016b). Low-stature plants that desperately need all solar radiation they can emit during the short growing seasons are rapidly displaced if the habitat is colonised by taller and more competitive plants (Myers-Smith et al. 2011, Mod et al. 2016a, Vowles and Bjork 2019). This competitive exclusion can be especially strong among bryophytes and lichens (Cornelissen et al. 2001, Walker et al. 2006, Joly et al. 2009). Some tundra species – especially woody plants – may also grow taller in the warmer future climates (Myers-Smith et al. 2011), but this intraspecific variation and adaptations may be too small compared to the size of the southern plants to give them any adequate advantages (Happonen et al. 2019, Tonin et al. 2019).

Thirdly, even if the warming trend in the Arctic is smooth, there is noteworthy potential for drastic state shifts and tipping points in the local growing conditions of the tundra (Wadhams 2012, Clark et al. 2013) and the between-years variability in the arctic climate is high (Schmidt et al. 2019). There is evidence that abrupt changes in tundra ecosystems and vegetation may occur due to several mechanisms: melting permafrost collapses and changes the local hydrology at once (Christensen et al. 2004, Riordan et al. 2006), rain-on-snow events damage and kill vegetation severely across large areas (Bokhorst et al. 2009, Bjerke et al. 2014, Bjerke et al. 2015), or shrubs and the treeline advance to the tundra and transform the local abiotic and biotic conditions rapidly to a novel state (Myers-Smith et al. 2011).

1.5 Understanding biodiversity patterns with species distribution models

There is little doubt these days that the current rate of species extinctions has led to a global biodiversity crisis that has damaging impacts on ecosystem functioning and human societies (Steffen et al. 2015, Pecl et al. 2017). Thus, there is urgent need for models that are able to predict the biodiversity patterns in current and future climates as reliably as possible (Bellard et al. 2012, Travis et al. 2013, Pacifici et al. 2015).

Species distribution modelling (SDM; also known as *habitat modelling* or *niche modelling*) has been an emerging field in biogeography in the last decades and one of the main tools to understand and predict patterns in biodiversity (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Austin 2007, Guisan et al. 2017). SDMs relate species occurrences (and absences) statistically to the environmental conditions at the corresponding locations and enable inference of strength and directions of the species-environment relationships and predictions of species distributions in space and time (Guisan and Thuiller 2005, Guisan et al. 2017). It depends on the modelling method (e.g. models based on linear regression or decision trees) how the data are numerically treated, but the aim is to find the most likely environmental conditions in which a given species is present (Franklin 2009).

Niche is a fundamental concept in predictive ecology and has been presented already in 1917 by Joseph Grinnell (Grinnell 1917) and then further developed by G. Evelyn Hutchinson in his seminal essay in 1957 (Hutchinson 1957). The concept of ecological niche can be further divided to fundamental niche and realized niche (Guisan and Zimmermann 2000). The first is a function of physiological constraints of a species, e.g. a minimum and maximum temperature, in which the species can survive and perform (i.e. where the species can theoretically be found). The second includes additional constrains, e.g. biotic interactions and competitive exclusion, which may limit (or extend) the species' actual realized niche (i.e. where the species is actually found).

Consequently, to set up a correlative species distribution model, two types of datasets are needed: records of species occurrences (and preferably locations where the species is absent as well) and data on the corresponding environmental conditions (Guisan et al. 2017). The amount of both data has been rocketed in the 21st century (Franklin et al. 2017). Global Biodiversity Information Facility is the largest data portal of open biodiversity information and has currently 1 582 638 344 occurrence records openly available (https://www.gbif.org/, visited 9.8.2020). Also open climatological and satellite data products are widely available and routinely used in fitting SDMs and predicting species distributions in space and time (Randin et al. 2020).

Nevertheless, big datasets have their own shortcomings and do not solve some of the main problems regarding data quality and requirements (Franklin et al. 2017, Araujo et al. 2019). Majority of the SDMs runs with binary data, that are data that include both presences and absences of the species (Guisan et al. 2017). However, usually only presences are available if no targeted data collecting has been performed (Jarnevich et al. 2015). Many SDM protocols and algorithms try to tackle this problem by creating random or semi-random pseudo-absences, which is in strictly speaking artificial data (Guisan et al. 2017). This may result in a reasonable outcome but if the occurrence data are severely biased either in the geographical or environmental space, also the end result may be flawed (Wisz and Guisan 2009, Stokland et al. 2011, Jarnevich et al. 2015). Indeed, the global occurrence data are severely biased and are aggregated mostly in Europe and North-America (Sporbert et al. 2019).

1.6 Remote sensing in ecological research

The environmental data used in many of the SDM studies are commonly at coarse spatial scales (typically at a resolution of ~ 1 km^2). Moreover, ecologically important environmental factors in driving species distributions at the fine-scale (e.g. snow and soil moisture) are poorly covered by ready-to-use data products, and thus, in many case, these factors are ignored in studies (Potter et al. 2013, Mod et al. 2016c). However, remote sensing has potential to solve some of these problems (Zellweger et al. 2019, Randin et al. 2020).

Remote sensing is an umbrella term for methods detecting the physical features of a target location by measuring its reflected and emitted radiation at a distance. Remote sensing is a valuable tool for ecologists as it provides spatially continuous and repeated information about land surface conditions and vegetation (Randin et al. 2020). Remote sensing techniques (passive and active) has been used in various applications, for example, to track mass migrations of flying insects and birds in the atmosphere (Chapman et al. 2003, Stepanian et al. 2016), measure vegetation volume and biomass (Riihimaki et al. 2017), characterize meso- and microclimate (Zellweger et al. 2019), monitor human impact and land use (Hansen et al. 2013), track surface water dynamics (Higgens et al. 2019) and predict and detect soil moisture patterns (AghaKouchak et al. 2015, Ozerdem et al. 2017, Kemppinen et al. 2018).

In the Arctic, satellite imagery is mostly used to monitor climate change induced effects in vegetation dynamics (Beck and Goetz 2011, Bhatt et al. 2013, Raynolds et al. 2013, Edwards and Treitz 2017) and changes in the cryosphere, i.e. snow cover and sea ice (Frei et al. 2012, Bhardwaj et al. 2016, Chen et al. 2016, Selkowitz and Forster 2016). However, most of the studies have used satellite imagery with large pixel sizes (satellite instruments such as AVHRR or MODIS) disabling the detection of small, but ecologically important, snow patches and their evolution within and between years.

The Landsat satellite mission is one of the major satellite-born data sources in ecological research (Cohen and Goward 2004, Kennedy et al. 2014, Roy et al. 2014). The first Landsat satellite that was equipped with a sensor comparable with the currently operating Landsats was launched in 1984, and since then, multiple Landsat satellites and sensors have provided openly available earth observation data with a 30-m spatial resolution and a maximum revisiting time of 16 days (Cohen and Goward 2004, Roy et al. 2014, USGS 2017). Landsat satellite images constitute an important source of snow information with a global coverage, but that information is still rather rarely utilized in SDMs or other biogeographical studies (Macander et al. 2015, Selkowitz and Forster 2016, Wayand et al. 2018).

2 Objectives and framework

The main aim of this thesis is to examine the role of snow and winter conditions in shaping the spatial patterns of arctic vegetation properties in current and future climates. I target to fill an evident research gap in how to incorporate snow conditions and winter microclimate into climate change impact models of arctic vegetation. Since the beginning of the project, I have paid special attention to the high quality of the vegetation data and the ecologically relevant spatial scale at which we have collected the datasets. Thus, my focus is particularly in developing methodology and best practices in gathering reliable information on snow and winter microclimate and how to incorporate this data into modelling frameworks. Only then, it is possible to predict how snow conditions and their evolution in the warming climate may affect individual species, biotic communities and the whole tundra ecosystem, and consequently, how this may modify our perspectives on the future of the Arctic.

More specifically, this thesis seeks answers to these four questions:

- How are snow and winter microclimate distributed across arctic landscapes and wide climatic gradients? (**Chapters I & II**)
- What are the relative roles of summer and winter temperatures in driving fine scale patterns of tundra vegetation? (**Chapter I**)
- Can we improve the accuracy of species distribution models of tundra species by incorporating snow information into the models? (**Chapter II**)
- What is the contribution of changing snow cover duration in the future trends of plant functional trait compositions and biodiversity? (**Chapters III & IV**)

3 Material and methods

Me, my co-authors and other members of the BioGeoClimate Modelling Lab at University of Helsinki have collected most of the data I have used in the analyses of this thesis.

3.1 Study area

The studies presented in this thesis were conducted in Fennoscandia, Svalbard and Greenland (**Figure 3**). More specifically, at four research areas: 1) Rastigaisa in northern Norway (**Chapters II, III & IV**), 2) Kilpisjärvi in northwestern Finland (**Chapter I**), 3) Kangerlussuaq in western Greenland (**Chapter I**), and 4) Adventdalen in Svalbard, Norway (**Chapter I**).

All four research areas represent mountainous tundra with strong both local and regional gradients in environmental conditions. Together the study areas represent the whole main arctic climatological gradient from Sub-Arctic to High-Arctic. See the main climatological statistics in **Table 1**.

Rastigaisa in Finnmark, northern Norway is a mountainous tundra area (195 km^2) at the margin of the Arctic (Virtanen et al. 2016). The geology of the area consists mostly acidic base rocks, but the highest peaks are fringed by more base-rich shales (Ryvarden 1969). The altitude spans from 120 to 1064 m a.s.l. and the tree line reaches the altitudes of 250–350 m a.s.l. depending on the slope aspect. Snowbed habitats are numerous above the tree line, but the main vegetation type is dwarf shrub tundra dominated by *Empetrum nigrum*, *Betula nana* and *Vaccinium* sp.. The flora of northern Fennoscandia is a mix of boreal, alpine and arctic species (Virtanen et al. 2016). The permafrost in the area is mainly sporadic or discontinuous and the active layer is thick (~10 m (Gisnas et al. 2017)). Reindeer graze the area mainly in winter.

Kilpisjärvi area is located in the northwesternmost corner of Finland in Enontekiö commune. The area can be classified as part of the Sub-Arctic or Oro-Arctic tundra biome (Virtanen et al. 2016). The study sites lie on the slopes of Mt. Saana that reaches the altitude of 1029 m a.s.l., while the elevation of the Lake Kilpisjärvi near Mt. Saana is 473 m a.s.l.. Here, the tree line reaches the altitude of 600 m a.s.l. in the most favourable locations of the southwest facing slopes. The geology of the northern Fennoscandia is mostly old and acidic but the mountainous areas with recent orogenic activity have also base rich rock types creating favourable conditions for many plant species that require calcareous substrate (Odland 2014). Because of the dolomitic rocks in the area of Kilpisjärvi, the region is one of the hotspots of arctic-alpine biodiversity in Fennoscandia (Kauhanen 2013). Reindeer is the main herbivore but in contrast to Rastigaisa area, here the reindeers are present and numerous also in summer (Pajunen et al. 2012).

The study area in Kangerlussuaq, western Greenland represents the Low-Arctic tundra and have clear floral elements of North America. It is situated along the arctic bioclimate subzone E characterized by thick moss layers, abundant dwarf shrubs and occasionally by low-shrub layers up to 80 cm tall (Walker et al. 2018). Kangerlussuaq is situated close to the Greenlandic ice

Table 1. The key climatological statistics for the study areas from the nearest weather stations, or in case of Rastigaisa from a gridded climatological dataset. The data are from (Pirinen et al. 2012, Aalto et al. 2017, Bilt et al. 2019) and https://www.dmi.dk/vejrarkiv/normaler-groenland/. Because of the various data sources, the climatological periods differ between areas. T = temperature (°C); Precip. = Precipitation (mm). Winter = December + January + February; Summer = June + July + August.

Study area	Annual mean T	Winter mean T	Summer mean T	Annual Precip.	Winter Precip.	Summer Precip.
Rastigaisa	-3.4	-13.9	8.6	568	126	201
Kilpisjärvi	-1.9	-12.6	9.5	487	129	162
Kangerlussuaq	-5.6	-19.2	9.2	150	16	72
Longyearbyen	-5.9	-13.9	4.5	196	41	52

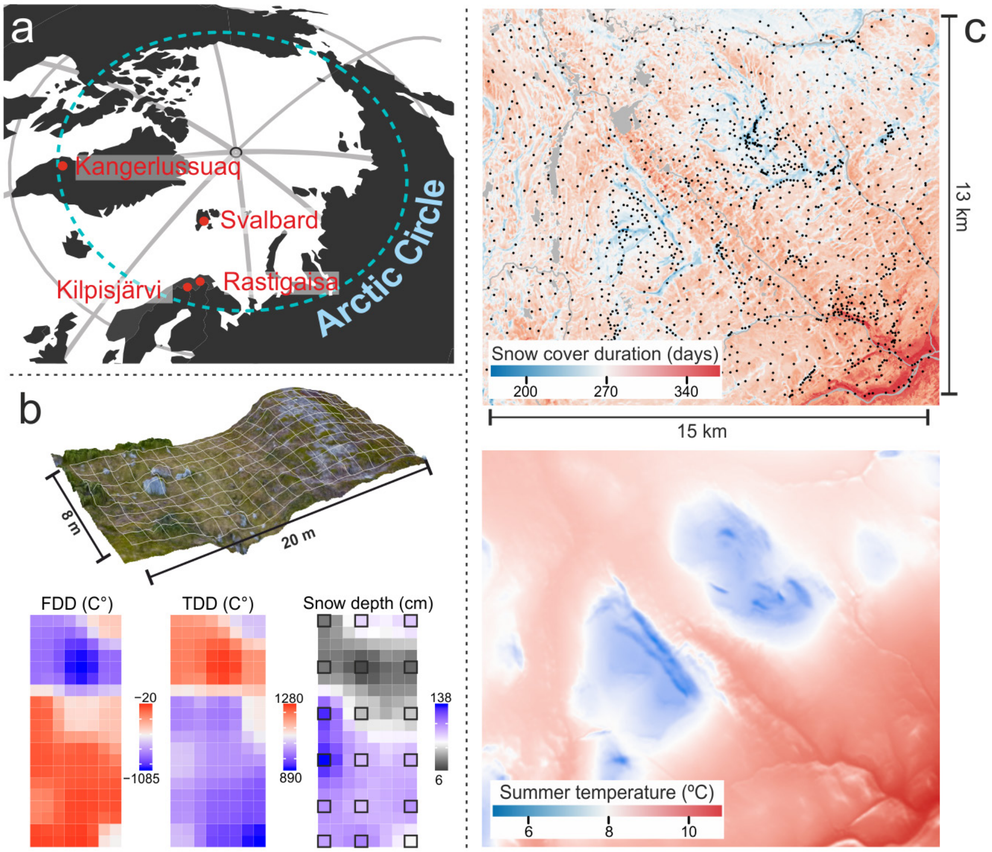

Figure 3. The locations of the four study areas (a). Example grid from data used in Chapter I (the grid is from Kilpisjärvi). The black rectangles represent the intensively studied plots within the grids, that were used in the analyses (b). Locations of the 1325 study sites (black dots) in the Rastigaisa area used in Chapters II, III & IV (c). The sites are displayed over a snow cover duration map (c). Below the summer temperatures for Rastigaisa that are driven mostly by altitude and slope aspect.

sheet in the end of a long and narrow fjord, but the open sea is far away, and thus, the climate of the area is rather continental and dry (partly due to the rain shadow effect from the ice sheet) (Higgens et al. 2019). Kangerlussuaq is situated at the southern margin of the zone of continuous permafrost, but the relatively warm summers maintain a thick active layer. Muskox and caribou are the main herbivores in the area. The gently sloping mountains consist mainly of Precambrian gneiss (Ozols and Broll 2005).

Svalbard is a northern, mostly glaciated and mountainous archipelago surrounded by the Arctic Ocean. The warm Gulf Stream keeps the sea south from Svalbard ice-free for most of the year, and thus, the climate is relatively oceanic, although cold. However, Svalbard contains large climatic gradients and especially the inner fjord areas have relatively favourable climatic conditions (Jónsdóttir 2005). Our study area near the town Longyearbyen is classified belonging to the arctic bioclimate subzone C (Jónsdóttir 2005) characterised by extensive moss layers, numerous small herbaceous species and few prostrate and hemi-prostrate dwarf shrubs species (Walker et al. 2018). Permafrost is continuous and cool summers melt a relatively thin layer of soil each summer. Svalbard has its own isolated population of reindeer, while geese are also important herbivores (Descamps et al. 2017).

Table 2. The vegetation properties used in the analyses as response variables.

Variable	Chapter	Unit	Description	Source data
Community composition	Chapters I, II, IV	%	All species and their cover values recorded in a plot. Multidimensional plot-species matrix	Plot-scale field data
Species richness	All chapters	Species count	Number of species recorded in a plot.	Plot-scale field data
Species occurrence	All chapters	0/1	Presence or absence of an individual species.	Plot-scale field data
Species cover	Chapter IV	%	Cover of an individual species.	Plot-scale field data
CWM Height	Chapter IV	cm	Community weighted mean (CWM) of plant vegetative height. Only vascular plants considered.	Plot-scale field data and traits from database
CWM Leaf area	Chapter IV	mm^2	Community weighted mean (CWM) of leaf surface area. Only vascular plants considered.	Plot-scale field data and traits from database
CWM SLA	Chapter IV	mm^2/mg	Community weighted mean (CWM) of specific leaf area (SLA). Only vascular plants considered.	Plot-scale field data and traits from database
CWM LDMC	Chapter IV	g/g	Community weighted mean (CWM) of leaf dry matter content (LDMC). Only vascular plants considered.	Plot-scale field data and traits from database
CWM LeafN	Chapter IV	mg/g	Community weighted mean (CWM) of leaf nitrogen content. Only vascular plants considered.	Plot-scale field data and traits from database
CWM LeafP	Chapter IV	mg/g	Community weighted mean (CWM) of leaf phosphorus content. Only vascular plants considered.	Plot-scale field data and traits from database
CWM Seed mass	Chapter IV	mg	Community weighted mean (CWM) of seed dry mass. Only vascular plants considered.	Plot-scale field data and traits from database
Functional diversity	Chapter IV	unitless	A measure of the distribution, range and evenness of the functional trait in a plant community. Only vascular plants considered. Multiple different indices.	Plot-scale field data and traits from database

3.2 Vegetation data

There are two plot-scale vegetation datasets that I utilized in the analyses of this thesis. All the vegetation properties, which represent response variables, are described in **Table 2**.

The vegetation data used in **Chapter I** consist 463 1-m^2 plots arranged within 33 study grids (size of 8 m x 20 m each). Majority of the grids (21) are in Kilpisjärvi, Finland, but both Greenland and Svalbard have six grids. The second vegetation dataset (**Chapters II, III & IV**) was collected in the Rastigaisa area in Northern Norway. It consists 5300 1-m^2 vegetation plots aggregated within 1325 study sites (at the time of the analyses of the **Chapters II & III** the numbers were 4800 and 1200, respectively).

All vascular plant, and soil-dwelling bryophyte and moss species were identified from the plots and their covers were estimated visually. All species were identified to the species level with few exceptions in the cryptic species groups (such as genus *Taraxacum*). Both datasets cover wide environmental gradients and vegetation types, thus the number of studied species is relatively high in the context of arctic tundra vegetation: 460 species in the data from Rastigaisa and 391 species in the dataset that combines the rest of the study areas. Depending on the analyses the species cover values were used or they were further processed to presence-absence or species richness values.

Plant functional trait measurements in **Chapter IV**, which were used to produce community weighted trait values, were not collected by me. Instead, to obtain a single trait value per trait per vascular plant species, I downloaded trait data from three databases: Tundra Trait Team (TTT) (Bjorkman et al. 2018b), TRY Plant Trait Database (TRY) (Kattge et al. 2011) and the Botanical Information and Ecological Network (BIEN) (Maitner et al. 2018). The trait data constitutes seven widely used plant functional traits: plant vegetative height, leaf area, seed dry mass, leaf dry matter content (LDMC), specific leaf area (leaf area per leaf dry mass; SLA) and leaf nitrogen and phosphorus contents. The first three are measures of plant size and the following four are related to leaf economics and resource use efficiency. The species-specific trait values were combined with the plant community data collected by me and my colleagues to calculate community weighted mean trait values and several functional diversity indices for every vegetation plot (Petchey and Gaston 2002, Botta-Dukat 2005, Laliberte and Legendre 2010, Venn et al. 2011).

3.3 Environmental data

All environmental data used in **Chapter I** are based on direct in-situ measurements or laboratory analyses. We installed miniature temperature loggers in each of the plots and let them record soil temperatures for one full year. All the used predictor variables are described in **Table 3**.

The environmental data used in **Chapters II, III & IV** are more based on proxy-variables (derived from topographical or remotely sensed information) rather than direct field measurements. The snow persistence (melting day of year) and snow cover duration (SCD) variables form the baseline for the last three chapters (**Figure 4**). Melting day and SCD were constructed from multitemporal satellite imagery from Landsat satellites over a period of 1984-2017. The individual cloudless images (dates) were first processed to binary snow maps (snow / no snow) and then passed to binomial regression to determine the melting and new-snow dates for each pixel separately. See short description of the predictor variables in **Table 3**.

Table 3. The environmental variables used in the analyses as predictors.

Variable	Chapter	Unit	Description	Source data	Reference
FDD	**Chapter I**	°C	Freezing degree days; Thermal sum of daily average temperatures below 0 °C	Temperature logger buried in soil	Loffler and Pape 2020
TDD	**Chapter I**	°C	Thawing degree days; Thermal sum of daily average temperatures above 0 °C	Temperature logger buried in soil	Loffler and Pape 2020
Radiation	**Chapters I, II & III**	MJ/cm^2/yr^1	Potential annual incoming solar radiation assuming clear sky conditions	Slope and aspect from digital elevation model or in-situ measurement and latitude	McCune & Keon 2002
Radiation	**Chapter IV**	kWh/m^2/yr^1	Potential annual incoming solar radiation assuming clear sky conditions, sky view factor included	Slope and aspect from digital elevation model and latitude	Böhner & Antonić 2009
Soil moisture	**Chapter I**	VWC%	Soil volumetric water content measured from the top 10 cm soil	Direct measurements	Kemppinen et al. 2018
soil pH	**Chapter I**		Soil pH determined in laboratory from soil samples	Soil sample	Kemppinen et al. 2019
Rock cover	**Chapter I**	%	Cover of rock surface	Visual estimate	
GDD	**Chapter II**	°C	Growing degree days; Thermal sum of daily average temperatures above 3 °C	Digital elevation model, weather station record	Aalto et al. 2017
Tsummer	**Chapters III & IV**	°C	Mean temperature of summer months (June, July, August)	Digital elevation model, weather station record	Aalto et al. 2017
Snow persistence	**Chapter II**	day of year	The average snow melting day of year	125 Landsat images	Macander et al. 2015
Snow cover duration	**Chapters III & IV**	days	The average length of snow season	142 Landsat images	Macander et al. 2015
TWI	**Chapters II, III & IV**	unitless	Topographic wetness index, proxy of soil moisture and water flow, SAGA wetness index algorithm	Digital elevation model	Böhner & Selige 2006
EDAP	**Chapters II, III & IV**	unitless	Edaphic status of the base rock, downhill distance to the base rich rock type	Digital elevation models	
SOILQ	**Chapters II, III & IV**	unitless	Five class interpretation of surface deposit quality	Fine-scale satellite image	
Slope	**Chapter III**	degrees	local slope angle indicating slope stability and processes	Digital elevation models	

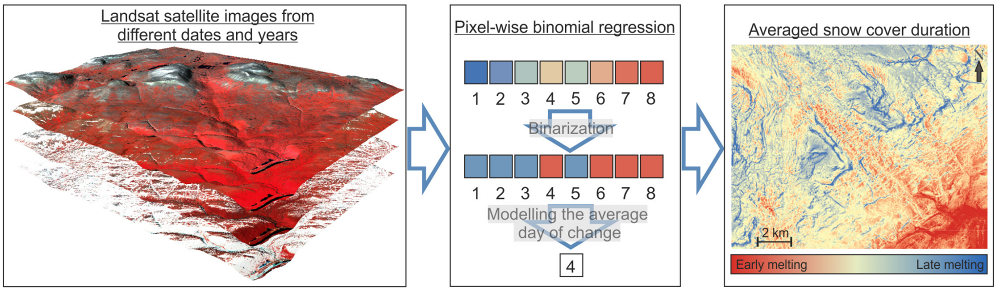

Figure 4. The workflow to construct the snow cover duration variable for the Rastigaisa area from a stack of cloud-free Landsat images to an analyses-ready predictor.

3.4 Data analyses

Species distribution models (SDMs) form the core framework for the statistical analyses used in this thesis (**Figure 5**). SDMs are utilized in all four chapters. More specifically, I used multiple modelling methods, especially generalized linear models (GLM), generalized additive models (GAM), boosted regression trees (BRT) and random forests (RF), although in **Chapter III**, multiple other modelling methods were used as well. In **Chapters I, II & III**, I used binomial models (presence-absence), but in **Chapter IV**, I modelled the continuous cover values of the species instead of their occurrences. Similar modelling methods were used in **Chapter I** to model species richness values with the data assumed to be *Poisson* distributed.

Using multiple modelling methods is recommendable in predictive ecology, because each of the modelling methods treat the data differently and all methods have their unique strengths and weaknesses. Averaging over multiple methods (or multiple species or species groups) may provide more generalizable results, and these summarising ensemble models have become a standard tool in SDM studies (Marmion et al. 2009, Thuiller et al. 2009). Therefore, I mostly report results of the ensemble models instead of single modelling methods.

Ordination analyses are a set of statistical methods to compress multi- or hyperdimensional data (e.g. biotic community data where each species constitutes its own dimension) into just a few dimensions. This enables to correlate variation in environmental variables with the principal components of the species community (ordination axes) to see which variables are related to community level variation. Here, I used non-metric multidimensional scaling (NMDS) which is a commonly used and flexible ordination method (**Chapter I**).

4 Results

4.1 The spatial distribution of snow and winter microclimate

Arctic landscapes are characterized by high variety of snow accumulation and soil thermal regimes. Both summer and winter soil temperatures may vary within 20 meters by a magnitude equivalent to a macroclimatic shift of hundreds of kilometres in north-south direction. However, the spatial heterogeneity is pronounced in winter thermal conditions. It is notable that the correlation between winter and summer soil temperatures was low (r = 0.16) but the relationships within the three study areas in **Chapter I** had different direction and ranged from -0.32 to -0.56. This indicates that the factors that control winter and summer microclimate differ between seasons and across spatial scales. (**Chapter I**)

Spatial heterogeneity was clear also in snow persistence and snow cover duration. In Rastigai-

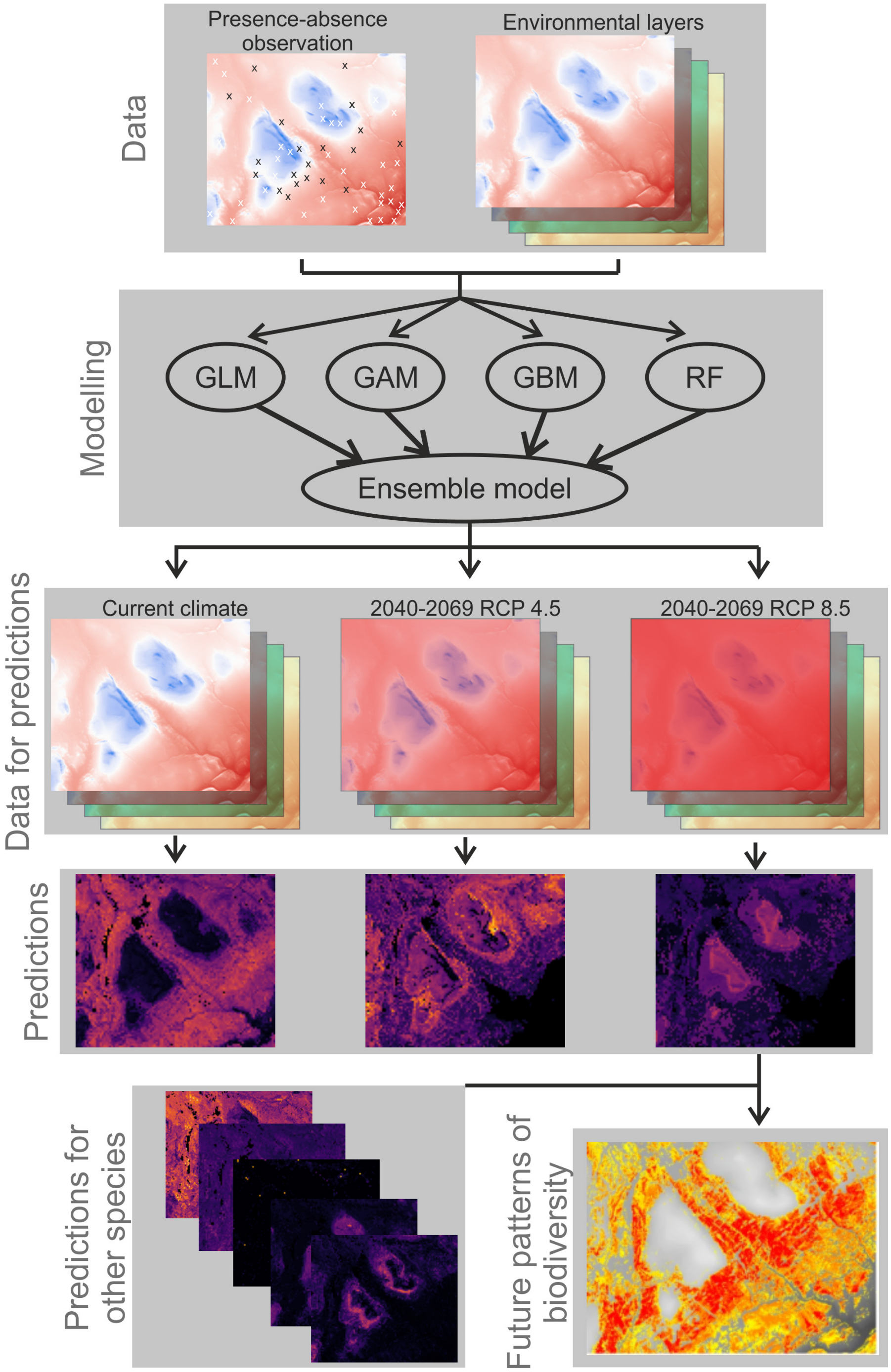

Figure 5. The simplified workflow of the species distribution models used in the analyses. The models relate species observations to environmental data, and these models can be then used to produce spatial predictions under multiple scenarios. In the end, spatial predictions of multiple species can be stacked together to inform about patterns in species richness and community compositions. In addition to the spatial predictions, the same models were also used to calculate variable importance values and shapes of the species-environment relationships.

sa area where elevation spans from 120 to 1065 m a.s.l. and is the main driver of thermal conditions, the two snow variables were only moderately correlated with summer temperatures (r_s = -0.38 and -0.45 respectively). Thus, the local snow conditions cause large thermal deviations from the general trend (altitudinal gradient) and create thermal heterogeneity across the landscape. The earliest areas in Rastigaisa melt in mid-April, on average, and the latest in late September resulting in a remarkable five-month difference in melting date within the 195 km^2 study area. (**Chapters II & III**)

4.2 The importance of summer versus winter temperatures

The results from the three contrasting arctic areas showed that winter soil temperatures are a powerful predictor in explaining local scale patterns in species occurrences, species richness and community composition, and in most cases exceed the importance of summer-time soil temperatures. Winter thermal conditions were the strongest driver especially for vascular plants and lichens, but for bryophytes summer temperatures, radiation, soil moisture and soil pH were just as or even more important. It seems that summer temperatures are more strongly filtering the regional species pools, whereas winter thermal conditions determine which species are present in the local species communities. The relationships between soil thermal conditions and species richness and occurrences were rather consistent between the study areas demonstrating generalisable vegetation-temperature associations across the Arctic. (**Chapter I**)

4.3 Improving species distribution models

The inclusion of snow persistence (average snow melting day) improved significantly the accuracy of species distribution models for 273 arctic, alpine and boreal species in Fennoscandian tundra. The improvement in cross validated predictive accuracy after including snow information in the SDMs was largest for lichens (mean area under curve evaluation metric improved from 0.658 to 0.724) followed by bryophytes (from 0.675 to 0.717) and vascular plants (from 0.729 to 0.763). The improvement was statistically significant for all three taxonomic groups. The improvement was also consistent for species with different niche optima along the snow gradient, indicating that not only SDMs for snowbed species were benefitted from the snow information but the inclusion of snow predictor was valuable for modelling species with variate of snow preferences. In addition to the statistical improvement of the models, the spatial patterns of the predicted species distributions were much more detailed and revealed fine-scale heterogeneity in species communities. (**Chapter II**)

4.4 The importance of snow for the future of tundra biodiversity

The evolution of snow and subnivium conditions has a fundamental role in shaping the future of arctic biodiversity. Shorter snow cover duration and warmer temperatures may increase the local species richness among vascular plants and bryophytes, but at the same time, changing snow conditions may erase a large proportion of species from the regional species pool. The most vulnerable species group was arctic-alpine vascular plants from which 36% of the studied species were threatened with extinction in our study area under the most extreme snow scenario (snow cover durations shortened by 40%). Lichens showed contrasting trends: lichen species richness was projected to decrease especially when warmer temperatures were simulated, but lichen species were less sensitive to decreasing snow cover duration (a maximum of 8% of the lichens species were threatened with extinction).

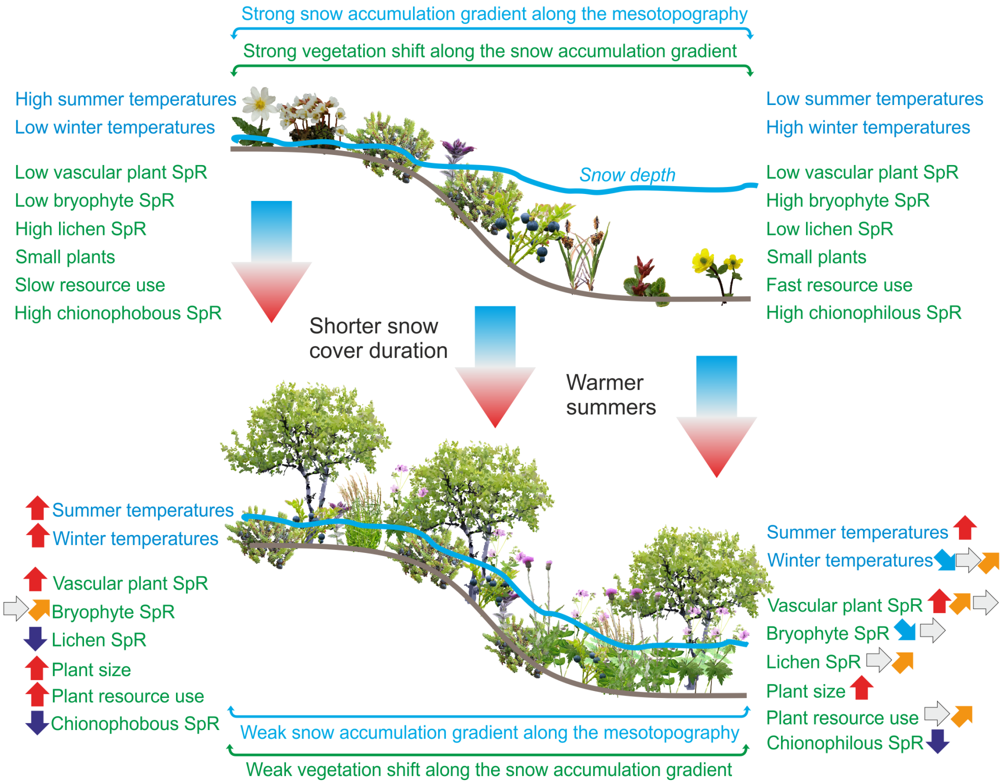

Figure 6. The effects of uneven snow accumulation on microclimate and key vegetation properties in habitats with minimal snow cover (left side) and in snowbeds (right side). Current climate (upper part) and how the microclimate and vegetation properties are expected to change in the future climates (lower part) according to the results presented here. Taller vegetation will inhibit the snowdrift and eliminate the effects of uneven snow accumulation on local conditions and vegetation. SpR = species richness.

Importantly, small changes in snow cover duration did not led into high rates of extinctions, but when decrease in snow cover duration exceeds 20% the number of species predicted to go extinct accelerated rapidly indicating possibility for a tipping-element in the biodiversity-snow relationship. (**Chapter III**)

4.5 The effects of snow in the future trait compositions of tundra vegetation

I found that snow cover duration plays a critical role in the evolution of the local vegetation trait compositions and diversity. Depending on the trait, shorter snow cover duration may either amplify or restrain the impacts of the warmer temperatures on the vegetation trait composition. Shorter snow cover duration and warmer temperatures will lead to communities of taller species with fast and efficient resource use. For example, the community weighted mean height is projected to increase from 10 to 60 cm, and the specific leaf area from 10 to 16 mm^2/mg under the most severe warming and snow loss scenarios. Climate change may increase the plot-scale functional diversity but losing the late snowbeds may homogenize tundra landscapes and lead to biotic communities more alike each other's. (**Chapter IV**).

5 Discussion

This thesis contributes to the current trend in predictive ecology in which a growing number of studies aims to utilize environmental variables which are directly linked to the target organism and are represented at ecologically relevant spatiotemporal scales (Mod et al. 2016c, Stewart et al. 2018, Kemppinen et al. 2019, Zellweger et al. 2019, Randin et al. 2020). Here, those environmental factors were snow cover and winter temperatures measured with remote sensing imagery or in-situ at plot-scale. While I conducted the studies at fine spatial resolutions, I also examined the vegetation-environment relationships across large geographic and environmental gradients and showed that the similar conclusions about the importance of local snow and winter conditions hold in the Arctic irrespective of the macroclimatic conditions.

5.1 The importance of heterogeneity of snow conditions

Snow cover and its interaction with the local topography is possibly the single most influential environmental factor in controlling microclimatic variation in tundra (Aalto et al. 2018). Both, winter temperatures and snow melting date varied from one extreme to another within short distances (**Chapters I & II**). This heterogeneity seems to be a major factor in driving community-level variability and biodiversity in tundra (**Chapters III & IV**) (Nabe-Nielsen et al. 2017). The Arctic is relatively poor in the overall number of species (gamma diversity) but the mosaic-like structure of different communities (i.e. high diversity of habitats; beta diversity) is a characteristic feature of the Arctic tundra biome (Stewart et al. 2018).

The spatial heterogeneity in winter soil thermal conditions was especially strong at the study site in western Greenland but was also present in the other study areas across the Arctic (**Chapter I**). In western Greenland the compact study area with minimal elevational differences showed microclimatic variability that was comparable to the temperature differences between the weather stations from Fennoscandia to Svalbard via western Greenland. This remarkable heterogeneity indicates that even if the climate warms rapidly, there might still remain cold microclimatic pockets for cold-adapted species increasing their probabilities to survive (Keppel et al. 2012, De Frenne et al. 2013, Winkler et al. 2016). Nevertheless, because this large microclimatic variability and the potential refugia imply strong links to snow conditions, the sensitivity of the snowpack to changing climate is critical (Stewart et al. 2018, Vitasse et al. 2018).

5.2 The mechanisms behind the strong snow-plant relationships

In this thesis, I investigated the effects of winter frost sum, melting day of year and snow cover duration on the spatial patterns of tundra vegetation. All these three variables showed distinct importance in the arctic ecosystems. Nevertheless, it is a different question what the actual mechanism is explaining such an importance. The three variables may summarise multiple aspects of winter (and summer) conditions and separating the effects of these likely tightly linked aspects can be challenging (Cooper 2014, Makoto et al. 2014, Williams et al. 2015, Sanders-DeMott and Templer 2017).

One plausible explanation and mechanism is the shortening effect of snow on the growing season length (Galen and Stanton 1993). It is likely that if the growing season length is severely limited by the accumulated snow, prolonged snow cover forms a strong ecological filter eliminating species that cannot maintain their carbon balance or accomplish their lice cycle events in such a short period (Galen and Stanton 1995). Our analyses showed that plants in snowbeds differ in their functional traits compared to the communities in habitats with longer growing seasons. This indicates that snowbed species have specific adaptations (e.g. small size and high phosphorus content) to grow and reproduce fast.

Another possible explanation is related to frost and extreme temperatures (Mondoni et al. 2015, Malyshev et al. 2016, Pardee et al. 2019). Thick snowpack insulates the subnivium effectively from extreme temperatures in the free atmosphere, and additionally, prolonged snowmelt decreases the risk of frost events in spring (Wheeler et al. 2014, Cannone et al. 2016, Pardee et al. 2019). In general, arctic plants are tolerant to freezing temperatures (Janmohammadi et al. 2015, Strimbeck et al. 2015), but they may be much more sensitive to frost in the spring after dormancy with the most sensitive buds predisposed or to icing events that build up anoxic conditions within and under icy layers. (Ogren 1996, Bjerke 2011, Wheeler et al. 2014).

Despite the high frost tolerance among arctic plants indicated by experiments (Rapacz et al. 2014, Strimbeck et al. 2015), my results showed that very few vascular plant and bryophyte species occur in the habitats with minimal snow cover. That indicates that some abiotic aspect in the wind-swept habitats act as a strong environmental filter and the freezing temperatures may not be the only explanation. Species in these habitats experience other extreme conditions as well, e.g. strong radiation when plants are still dormant, ground icing, strong wind and abrasion by snow crystals. Additionally, minimal snow cover provides minimal meltwater pulse, while these habitats are also typically in topographic positions with limited water flow into the system (Stewart et al. 2018, Kemppinen et al. 2019). However, while vascular plants and bryophytes are missing, lichens shall flourish because they are poor competitors but have high tolerance to extreme cold and drought (Cornelissen et al. 2001).

Interspecific competition is possibly one of the main explanations why not all the species inhabit the sites with relatively long summers but with sheltering snow cover as well, which are perhaps the most ‘favourable’ habitats for life in tundra. Although, in general, competition has been considered low in tundra environments, there are multiple studies highlighting that some dominant vascular plants can be strong competitors and alter distributions of subdominant species (le Roux et al. 2012, Mod et al. 2016a). Moreover, multiple tundra experiments and revisiting studies have shown that the decreasing lichen and bryophyte cover and richness are typically a function of increasing vascular plant cover and biomass (Cornelissen et al. 2001, Alatalo et al. 2017, Vuorinen et al. 2017).

Multiple indirect pathways of how winter conditions may affect plant communities via soil processes, are also probable (Semenchuk et al. 2015). Snow manipulation experiments indicate that added snow can significantly enchain the nutrient mineralization processes as a consequence of increased winter temperatures (Hobbie and Chapin 1996, Baptist et al. 2010, Cornelissen and Makoto 2014, Darrouzet-Nardi et al. 2019). Even if these increases can be small and the overall rate of biochemical activity low under the snow, winters are so long in the Arctic that already small changes in mineralization processes may accumulate over the winter resulting in large impacts at the annual level. The winter-time mineralization might be especially crucial for plants because nutrients that are readily available in early summer, when the growing burst is the strongest, are of special importance (Bilbrough et al. 2000).

The results shown here indicate that also the functional trait composition of arctic vegetation is sensitive to snow cover properties. There is

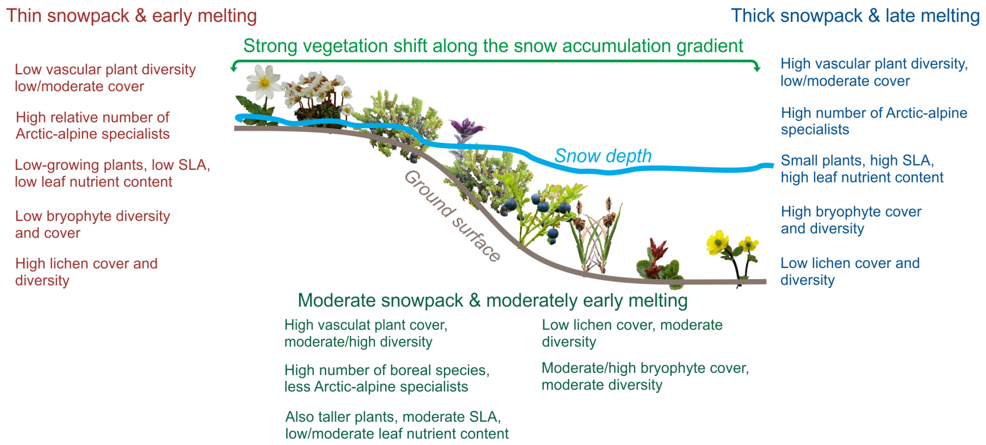

Figure 7. The effects of uneven snow accumulation on vegetation properties in tundra under current climatic conditions. Most of the tundra species have specific niche along the snow accumulation gradient. For instance, *Dryas octopetala* and *Diapensia lapponica* are found in exposed habitats with little or no snow cover and a long growing season (on the left), whereas *Empetrum nigrum*, *Bartsia alpina*, *Vaccinium myrtillus* and *Carex bigelowii* prefer the intermediate conditions. Under the thick snowpack and short growing seasons, in habitats located in the lower parts of the relief (on the right) *Salix herbaceae* and *Ranunculus nivalis* are typical species.

little experimental evidence on the topic (Mark et al. 2015, Semenchuk et al. 2015), but gradient studies agree with my results (Choler 2005, Carlson et al. 2015, Happonen et al. 2019). This gives further strength for the conclusions drawn here because it appears that snow conditions form environmental filters that select species based on their morphological and biochemical properties and that plants show clear adaptations to the local snow conditions. Hence, snow conditions are not only reflected on what species are present but likewise what kind of species (Venn et al. 2011, Tonin et al. 2019).

5.3 Different methodologies, different strengths, consistent conclusions

Snow-plant relationships have been mostly studied either by investigating compositional changes in plant communities along local mesotopographical gradients (Stanton et al. 1994, Kudo et al. 1999, Heegaard 2002, Choler 2005, Bruun et al. 2006, Odland and Munkejord 2008) or by manipulating the snow conditions by delaying or advancing snowmelt and then observing what are the consequences of the treatment in plant communities (Galen and Stanton 1993, Groffman et al. 2001, Wahren et al. 2005, Wipf and Rixen 2010, Bosio et al. 2014, Cooper et al. 2019). Here, I have not performed experimental manipulations and the methodology is closer to the traditional gradient studies. Yet, the study designs here were planned to maximise the number of different habitats, environmental conditions and their combinations in the data, and moreover, to use direct measurements and state-of-the-art multivariate modelling methods to draw conclusions from these complex systems.

Observational and experimental studies have their unique advantages and shortcomings, but importantly, the results from both kind of studies show no major conflicts: both have indicated the high importance of snow conditions in driving vegetation properties and ecosystem functions in the tundra (Galen and Stanton 1995, Walker et al. 1999, Wipf and Rixen 2010, Semenchuk et al. 2016, Cooper et al. 2019). However, it can be challenging to utilize information from the traditional gradient studies or the snow manipulation experiments in the modelling frameworks to produce numerical predictions in space and time. While experiments are needed to infer causality, quantify short-term sensitivity to disturbance or confirm correlative relationships detected in observational studies, here the special attention was paid to the predictive side of biogeography and ecology.

Extending the observed and inferred snow-plant relationships over large tundra regions and climate-snow scenarios provided further insights how the whole tundra ecosystems may evolve in this century. Including snow information into the species distribution models did not only made them more accurate but changed the spatial patterns in predictions as well: without snow information species occurrence patterns varied rather smoothly, but snow related predictors revealed the fragmented nature of the species occurrence patterns in tundra landscapes (**Chapter II**). Even more importantly, snow information changed considerably the projections of vegetation properties into the future, showing that the same rate of warming may produce highly different future trajectories depending on the contemporary evolution of the snow conditions (**Chapters III & IV**).

5.4 Emerging uncertainties

There are a few methodological and data-related issues that must be considered when evaluating the results presented here. In observatory and correlative studies, separating the effects of covarying environmental predictors can be challenging, even though the correlations between the predictors were relatively small in all my studies presented here. Models of the complex nature are always radical simplifications and one source of uncertainty is related to the projections of species distributions under the future climate scenarios. Even if we can explain and predict the species occurrences accurately in the current climate, it is not guaranteed that the same rules hold in the future (Pearson et al. 2004). Correlations between the environmental factors may change creating non-analogue conditions, and thus, force us to extrapolate our predictions into combinations of environmental conditions that are not present in the original data (Williams and Jackson 2007, Alexander et al. 2018).

Lichens and bryophytes showed lower predictive accuracy across the analyses compared to vascular plants, and thus, the results for these species groups are less certain. These uncertainties may arise from the fact that identification and detection of cryptic and tiny cryptogam species can be challenging and that they might occupy microsites that occur at even finer spatial scales than our 1m^2 plots or the resolution of the environmental predictors (Hespanhol et al. 2011, Potter et al. 2013, Lewis et al. 2017). Another important aspect is that most of our measurements of the vegetation properties or environmental factors are from limited (and often different) periods of time. We might not be able to capture the whole variation in conditions and extreme events that occur more sporadically in time but might still be important for arctic vegetation (Bokhorst et al. 2010, Schmidt et al. 2019).

It is also likely, that I was not able to include every single essential environmental variable important for plant and lichen species into the models, and some lacking variables (e.g. soil nitrogen or phosphorus content, biotic interactions) might have altered (improved) the results (Dubuis et al. 2013, Mod et al. 2016a, Mod et al. 2016c). One shortcoming in the data used in **Chapter I** is that I had microclimatic measurements only from the topsoil, not above the soil. While I think that the soil temperatures measured along the strong local environmental gradients and across multiple arctic regions probably reflect the whole microclimatic realm rather comprehensively, I still was not able to test the effects of air temperatures on the vegetation patterns in the models. Furthermore, many of the environmental variables used in the **Chapters II, III & IV** were more about proxy variables than true measurements (e.g. topographic wetness index as a proxy for soil moisture). Although, all the variables were constructed with state-of-the-art methodology (Böhner and Antonić 2009, Aalto et al. 2017), and I am confident than having true in-situ measured variables (e.g. soil moisture) would generate largely similar results and conclusions.

The **Chapter IV** was the only one where I utilized data from openly available databases. The trait values for species were not measured in our plots or study areas but collected all over the world (Bjorkman et al. 2018b, Kattge et al. 2020). Therefore, we rather linked the prevailing environmental conditions to the global trait averages instead of true local trait compositions, which would be, of course, optimal. Therefore, neither did we consider intraspecific variation that might be important for some traits and species (e.g. height of woody plant species) (Violle et al. 2012, Mitchell et al. 2017, Happonen et al. 2019). These elements should be carefully considered when interpreting the trait-related results of **Chapter IV**.

5.5 implications for climate-smart conservation

The results of this thesis are – hopefully – applicable also outside the purely scientific community. It is evident that the future of arctic biodiversity is highly dependent on how the arctic snow conditions will evolve during this century along the warming climate. The results of this thesis illustrate the importance of snow variability in creating environmental heterogeneity and biological diversity in tundra ecosystems. Especially the late laying snowbed environment is home for variety of specialized arctic-alpine flora, and it seems that these species and habitats are among the first that the warming climate will impact negatively (Sandvik and Odland 2014, Gritsch et al. 2016, Matteodo et al. 2016, Kobiv 2017, Czortek et al. 2018, Sperduto et al. 2018). Unfortunately, monitoring and revisiting studies considering snowbed habitats are largely missing especially in the Arctic, and only limited observational evidence exists on how snowbed communities have already been altered by climate change (Carbognani et al. 2014, Sandvik and Odland 2014, Gritsch et al. 2016, Czortek et al. 2018). However, in order to conserve these species, we must conserve their snowy and late melting habitats. Certainly, this is best done by tackling the warming trend, but the crucial role of local snow conditions may serve possibilities for local-scale conservation acts, for example, by using snow fences to modify the local snow accumulation or reflective blankets to delay the melt of the snowpack.

In this study, I investigated three taxonomic groups that together consist major part of the biomass and diversity in the arctic ecosystems (Chapin et al. 1996, Iversen et al. 2015): vascular plants, bryophytes and lichens. While it is challenging to evaluate how the results would have looked for other organism – such as insects, fungus, bacteria or other soil biota – there is yet a few snow manipulation experiments published that have considered these taxonomic groups (Legault and Weis 2013, Robroek et al. 2013, Morgado et al. 2016, Markkula et al. 2019). According to these studies, it is likely that snow plays a crucial role in shaping biodiversity and community patterns among the other species groups, matching the results represented here.

5.6 Future perspectives

Although the importance of snow in driving patterns and functions of arctic ecosystems is widely acknowledged, fundamental research gaps remain. The reason behind omitting snow and wintertime information from climate change impact models of arctic biota has probably been mostly methodological. Yet, poor availability of fine-scale snow data has been a severe bottleneck in the process to include the effects of snow into the modelling frameworks. Gathering reliable records of snow conditions and winter temperatures should have high priority in the following years to avoid the biased predictions caused by ignoring one of the most effective environmental factors in shaping local abiotic conditions and biotic communities in the terrestrial Arctic. To achieve these goals, more thorough collaboration with ecologists, remote sensing specialists and geoscientists is needed (Wayand et al. 2018, Zellweger et al. 2019, Randin et al. 2020).

In this thesis, I considered a wide range of snow scenarios and their effects on future projections of the arctic tundra ecosystems (**Chapters III and IV**). However, it is challenging to evaluate which one of these snow scenarios is most likely, and the future of local snow conditions is highly uncertain and probably varies between arctic regions and topographic positions (Bokhorst et al. 2016, Vihma et al. 2016, Huss et al. 2017). To tackle these shortcomings, more research effort should be paid for investigating the climate sensitivity of snow accumulation, melting and interactions between snow, topography and vegetation.

I discussed above about some of the possible pathways how the snow and winter conditions are affecting arctic species, communities and ecosystems. We need, however, more studies that aim to detangle the possibly different or even contrasting effects of the aspects of winter and snow conditions to construct mechanistically more accurate understanding of the arctic ecosystems. For example, here, I cannot separate reliably what relationships are caused by snow persistence and what are impacts of the thickness of the snowpack. In our datasets these factors are rather strongly correlated, but it is likely that the snow cover duration and thickness may be partly decoupled in the near future. It is widely acknowledged that snow cover duration is likely to decrease in most of the arctic and alpine areas, whereas snow depth may have more complicated and spatially heterogeneous response to changing climate. This complex snow depth response is mostly caused by the increasing trend in winter precipitation, but may be partly due to the taller shrubs and trees spread to the tundra that change the snow accumulation regimes drastically (Bulygina et al. 2009, Bulygina et al. 2011, Callaghan et al. 2011a, Vowles and Bjork 2019).

Additionally, while I considered mostly long-term averages of snow conditions, the extreme years and events can also be important, and more frequent in the future climates (Bjerke et al. 2014, Bjerke et al. 2015, Schmidt et al. 2019). Arctic species are probably well protected against these extreme years (Kranner et al. 2008, Harrison et al. 2014, Strimbeck et al. 2015), but they might have a significant impact on southern species possibly slowing their establishment in arctic habitats.

Correlative species distribution models have limitations in capturing some of the dynamical elements in ecosystems. The predictions presented here rely on space-for-time substitution, that is, we assume that species will strictly track their environmental niches in space when the climate changes. The models are so called equilibrium models, which exclude processes involved in vegetation dynamics, such as dispersal, population density, succession and disturbance (Neilson et al. 2005, Taylor and Hastings 2005, Frost et al. 2013) or phenotypic plasticity and evolutionary processes. These dynamic processes may cause substantial time lags in the vegetation responses to climate change, and thus, it is likely that many changes projected here may happen slower – or sometimes faster – than indicated by the models

(Epstein et al. 2007, Sinclair et al. 2010). Additionally, the northward/upward movement of species can be limited by geological processes, such as soil formation, and thus, these slow processes may further slowdown the species relocation (Dubuis et al. 2013, Bjorkman et al. 2017). Therefore, there is an urgent need for mechanistic models that can take these dynamic elements and possible feedback loops into account to be used along the correlative, and more traditional, species distribution models.

6 Conclusions

Arctic areas are prone to dramatic ecosystem state shifts in this century, many that are tightly linked to changes in the cryosphere. The results of this thesis highlight uncertainties for the future of arctic plants, bryophytes and lichens. The results indicate that the gaps in our capability to predict the future snow conditions might be more severe shortcoming than previously thought. Snow cover and winter conditions were strongly linked to all vegetation properties and patterns studied in this thesis. By designing frameworks for climate change impact models that investigate the effects of winter and summer climate factors together, there is a chance to develop an improved mechanistic understanding of the ecosystem responses to climate change that would not be evident from examining the effects of either of the seasons alone. Furthermore, these advancements may well lead to more accurate predictions of the future states of the arctic ecosystems and enable better climate-smart conservation and climate change mitigation.

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