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Trait-based selection and plant communities in high-latitude ecosystems

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Abstract

According to theory, the functional traits of species dictate how environmental selection affects them, and also the functioning of ecosystems that those species form. However, we lack a general understanding about how exactly environmental selection affects the trait composition of communities, and consequently, ecosystem functions.

In this thesis, I study how the effects of environmental selection manifest in the functional composition of field-layer plant communities in the tundra and in boreal forests. My aims are 1) to sharpen our understanding about the effects of trait-based selection on plant communities by accounting for the microenvironment in models of trait composition, 2) to elucidate the effects of that selection on tundra carbon cycling, and 3) to reveal how forestry and reindeer husbandry, two forms of human land use, modulate long-term vegetation changes by favouring certain trait combinations over others. The study areas span four tundra landscapes in Finnish Lapland, Greenland, Svalbard, and the southern Indian Ocean, and hundreds of herb-rich boreal forest patches in Northern Finland. I use linear modelling to study how the results of vegetation surveys, visual, sensor-based and laboratory measurements of traits and the environment, and carbon flux chamber measurements relate to each other.

My results suggest the following. 1) The environment strongly determines the functional composition of plant communities when accounting for microenvironmental conditions. Warm, ungrazed and unshaded conditions favor larger plants. Leaf traits that confer fast returns on invested resources are favoured in conditions of high soil resource availability, in ungrazed areas, and in the shade. 2) In the tundra, communities consisting of larger plants cycle carbon more rapidly and have larger above-ground carbon stocks. Communities with "fast" leaf traits also cycle carbon with higher intensity, but they have lower above-ground carbon stocks than communities with "slow" leaf traits. 3) In boreal forests, forestry modifies the functional composition of understory communities by decreasing the amount of light in the long term. While forestry seems to accelerate vegetation change, reindeer husbandry could be seen to counteract it by inhibiting the growth of average plant size observed in areas without reindeer.

These results show that the functional traits of plants dictate how they are affected by environmental selection pressures. The effects of this selection are consistent at the community level across locations up to 15000 km apart. Furthermore, human land use is an important control of the functional composition of communities alongside natural environmental variation. This information will be useful in predicting which species will suffer and which benefit from global change, and what will be the consequences for ecosystem functioning.

Yhteenveto

Lajeja on miljoonia, ja jokainen niistä elää rajallisella alueella. Tutkijat tarvitsevat keinoja yleistää yksittäisiä lajeja koskevat tiedot käyttökelpoisiksi muiden lajien tutkimiseen. Yleistää voi esimerkiksi eliöiden mitattavien ominaisuuksien pohjalta. Voidaan esimerkiksi kysyä, onko jokin elinympäristö yhtä hyvä suurille ja pienille lajeille. Väitöskirjassani tutkin, voidaanko kasvilajien ominaisuuksia käyttää ennustamaan niiden suosimia elinympäristöjä ja vaikutusta ekosysteemitoimintoihin.

Väitöskirjani tutkimusalueet ovat neljä tundramaisemaa Lapissa, Grönlannissa, Huippuvuorilla ja eteläisellä Intian valtamerellä, sekä lehtolaikuissa Pohjois-Suomen metsissä. Ilmastonmuutos ja ihmisen maankäyttö aiheuttavat nopeita ympäristömuutoksia näillä alueilla. Jos ymmärtäisimme, millaisia lajeja muuttuneet ympäristöt suosivat, voisimme ennustaa nykyistä paremmin tulevaisuuden kasvillisuuden koostumuksen.

Tutkimukseni osoittavat, että kokoakseli ja lehtitalousspektri säätelevät lajeille suotuisia elinympäristöjä niin tundralla kuin metsissäkin. Lämpimät, valoisat ja laiduntamattomat ympäristöt ovat hyviä suuriksi kasvaville lajeille. Rehevät, varjoisat ja laiduntamattomat ympäristöt taas suosivat “sijoittajalajeja”, eli lajeja jotka laittavat kaikki resurssinsa peliin nopeiden voittojen toivossa. Tätä lajien ominaisuuksien säätelemää lajiston valikoitumista voidaan käyttää ennustamaan ekosysteemien muutosta. Ihmisen aiheuttamat ilmaston ja maankäytön muutokset ovat jo vaikuttaneet tundran ja boreaalisten metsien kasvillisuuteen ja ekosysteemitoimintoihin, ja muutokset tulevat jatkumaan. Lämpimämmissä olosuhteissa suuret kasvit syrjäyttävät pienemmät. Ihmisen muokkaamat rehevät metsät ovat varjoisempia kuin luonnontilaiset, mikä suosii sijoittajalajeja säästäjien kustannuksella. Toisaalta kasvaneet porotiheydet poronhoitoalueella saattavat hidastaa kasvillisuusmuutoksia viemällä suurilta kasveilta niiden valintaedun.

Lajien ominaisuuksia voidaan siis käyttää ennustamaan niiden ympäristövaatimuksia ja vaikutusta ekosysteemitoimintoihin. Ominaisuudet ovat yhteisiä suureita, joiden avulla yksittäisten lajien vuorovaikutussuhteet ympäristönsä kanssa voidaan tehdä vertailukelpoisiksi. Tämä tieto on mielenkiintoista itsessään, mutta on myös hyödyksi lajien suojelun suunnittelussa sekä globaalimuutoksen seurausten ennustamisessa ekosysteemien toiminnalle.

Acknowledgements

I was still in comprehensive school when I came to the realization that I never wanted to get a real job, you know, a job where someone tells you what to do and you do it with the skills you learned during your education. First, I never wanted to stop learning new things. Second, I have always had a problem with authorities. After considering my options, I decided that immersing myself in scholarship would be the perfect plan for evading a boring, ordinary job. And it has been!

I am an immensely lucky individual for getting to do what I love for a living. There is a large number of individuals and collectives without whom I would not be here, writing these words of thanks in the preface to my doctoral dissertation.

First of all, I want to thank the people who fund this kind of nonsense. Thank you to all the people who pay taxes, all the citizens who vote for people that continue to fund fundamental research, and all the members of the parliament in Finland and the European Union who have allocated funds to studying foundational questions about how the world works. At a more local level, I'm very grateful to the board of the Doctoral Program in Wildlife Biology in the University of Helsinki who believed in me and funded my PhD research for four years.

I want to thank my supervisors Miska, Juha, and Otso for giving me support when I needed and asked for it, and letting me do my thing when I thought I knew what I was doing.

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Thank you friends, especially Anna, Joel, Julia, Lauralotta, and Tuija. There is nothing that helps during slumps to the valley of shit and moments of frustration about the archaic ways of academia like peer support.

Let's change the system.

I'm grateful for the support of my family, without which I would not have managed. Eeva, Ulla, Kimmo, Annina and Enni, thank you for everything. And thank you Kaisa.

Kiitos Kerttu ja Inkeri. Rakastan teitä hirmuisesti.

Helsinki, May 2020
Konsta Happonen

Articles and contributions

I Happonen, Konsta, Juha Aalto, Julia Kemppinen, Pekka Niittynen, Anna-Maria Virkkala, and Miska Luoto (2019). “Snow is an important control of plant community functional composition in oroarctic tundra.” https://doi.org/10.1007/s00442-019-04508-8. *Oecologia* 191. 601–8.

II Kemppinen, Julia, Pekka Niittynen, Peter le Roux, Mia Momberg, Konsta Happonen, Juha Aalto, Helena Rautakoski, Brian Enquist, Vigdis Vandvik, Aud Halbritter, Brian Maitner, Miska Luoto (2020). “Consistent trait-environment relationships within and across tundra plant communities.” *Under review.*

III Happonen, Konsta, Anna-Maria Virkkala, Julia Kemppinen, Pekka Niittynen, Miska Luoto (2020). “Plant community functional composition and diversity drive fine-scale variability in carbon cycling in the tundra.” https://doi.org/10.1101/865899. *Under review.*

IV Happonen, Konsta, Lauralotta Muurinen, Risto Virtanen, Eero Kaakinen, John-Arvid Grytnes, Elina Kaarlejärvi, Philippe Parisot, Matias Wolff, Tuija Maliniemi (2020). “Trait-based responses to forestry and animal husbandry modify long-term changes in forest understories.” https://doi.org/10.1101/2020.04.30.069708 *Under review.*

Contributions of the author using the CRediT taxonomy (Allen, O’Connell, and Kiermer 2019, https://casrai.org/credit/))

	I	II	III	IV
Conceptualization	x	x	x	x
Data curation	x		x	x
Formal analysis	x	x	x	x
Funding acquisition	x		x	x
Investigation	x		x	x
Methodology	x	x	x	x
Project administration	x		x	x
Visualization	x		x	x
Writing - original draft	x		x	x
Writing - review and editing	x	x	x	x

Contents

1 Introduction

Robert MacArthur famously wrote that to do science is to search for repeated patterns, not simply to accumulate facts (MacArthur 1972). Such an endeavour might seem hopeless to some in the face of biological diversity, every species, every habitat being seemingly different from the next in the most wonderfully unique way. Perhaps it is because of appreciation for the beauty in details that the majority of ecological research still focuses on single species (Carmel et al. 2013). However, I must slightly disagree with MacArthur, as I feel that gathering fundamental knowledge about the ecology of single species is still a worthwhile scientific endeavour, a feeling that is shared with many in the research community, and materialized as an increased push for acknowledging data collectors (Data Citation Synthesis Group 2014). For how are we to generalize without data? Nonetheless, I share MacArthur's enthusiasm for uncovering patterns that apply beyond the scope of single species and geographic locations. Much of the present work tries to achieve just that, with the caveat that it deals exclusively with vascular land plants.

There are several paths to uncovering generality in ecology; here, I have adopted two of them. First, this work is done in the context of community ecology (sensu Vellend 2016), which is the study of species assemblages of one trophic level sharing the same space. By focusing on emergent properties of communities, such as diversity and composition, I am able to abstract away the species, and extract signals from their collective responses. Vellend argues that communities are formed by four high-level processes: Speciation, Dispersal, Ecological drift, and Selection (Vellend 2010; Vellend 2016), which mirrors the more traditional view of local communities resulting from the removal of species from the regional species pool by a hierarchical set of filters (Zobel 1997). In the present work, I focus exclusively on the effects of selection on communities, and more precisely, the consequences of external variables changing the relative fitness differences of constituent species.

However, merely focusing on community properties is not enough to uncover general ecological patterns, as the composition of every local community is contingent on a unique history of speciation and dispersal. How does one compare two sets of communities if they share none of the same species?

Fortunately, species are not unique. There are many reasonable comparisons that can be made between apples (*Malus domestica*) and oranges (*Citrus* x *sinensis*), for example. They both have woody stems, which allow them to reach a height of several meters, and both produce fleshy fruits, an adaptation for endozoochorous seed dispersal. Furthermore, the spectral qualities of their fruits are very similar (Sandford 1995). They differ in several characteristics too: the apple has deciduous leaves, an adaptation to surviving unfavorable periods such as winters, whereas the orange has broad evergreen leaves. Just as unique species can be compared based on their non-unique traits, so too can the species composition of two distinct communities be compared based on the average trait values of the resident species (Garnier et al. 2004). This allows the researcher to transcend the constraints of unique species pools and search for general rules governed by the traits that unify species. The traits that are important for the growth, survival, and reproduction of individuals, and thus the niches of species are called functional traits (Violle et al. 2007), and the line of ecological research based on such traits functional ecology (Keddy 1992; McGill et al. 2006). This is the other way I will try to achieve generality, the scope of this thesis is thus being functional plant community ecology.

Central questions on the agenda of functional community ecology include the identification of axes of trait covariation, and how those trait axes govern the fundamental and realized niches (McGill et al. 2006). The aboveground traits of land plants have been found to vary primarily along two independent axes: the leaf economics spectrum (Wright et al. 2004), and the size-structural axis, which together form the global spectrum of plant form and function (Díaz et al. 2016, Fig. 1). The leaf economics spectrum describes trade-offs between traits that are adapted for fast acquisition of resources, and traits that promote survival in low-resource conditions. On the 'fast' end of the spectrum, species tend to have leaves with high nutrient concentrations, low dry matter content, low C:N ratios, and short lifespans. An example of such a species would be the woodland cranesbill, Geranium sylvaticum. 'Slow' species have the opposite traits, a prime example being the crowberry Empetrum nigrum with its evergreen, needle-like leaves. The size-structural axis describes plant height, but also other traits that necessarily vary with it, such as stem specific density. These axes apply not just to variation between species, but between plant communities as well (Bruelheide et al. 2018).

It has been shown that many of the traits that constitute these axes are relevant for species vital rates, and consequently, niches. For example, wood density seems to predict the sensitivity of populations to changes in survival, whereas leaf nitrogen content is a better correlate of sensitivity of responses to changes in fecundity (Adler et al. 2014). However, we are still only beginning to understand how these relationships map into community

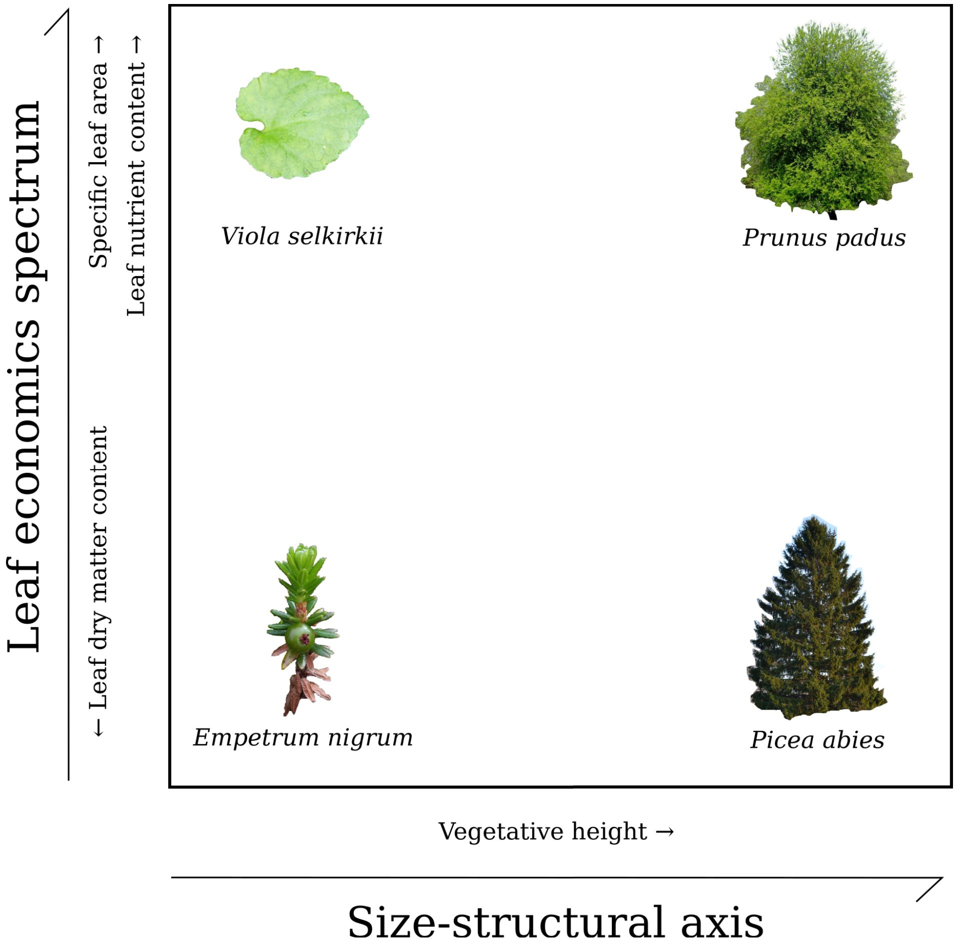

Figure 1: The axes of above-ground trait variation between vascular plant species and communities (Díaz et al. 2016; Bruelheide et al. 2018). Small text next to the axes lists traits used in this thesis to represent these axes. Images highlight boreal and tundra species with different trait combinations. As this thesis deals primarily with field-layer vegetation, the focus of individual studies lies with species on the left side of the figure. Image copyrights (CC-BY-SA): P. abies- Ivar Leidus, P. padus - Udo Schröter

properties in the context of the abiotic environment and the biotic interaction landscape (McGill et al. 2006). To phrase the matter differently, we still need to study how selection that varies with abiotic conditions and species interactions affects the functional composition of communities.

This line of inquiry has relevance beyond being interesting for its own sake. Functional traits are linked to individual performance, and individual performance is, in effect, just a measure of how efficiently said individual diverts matter and energy to increase its fitness. Scaled to the community level, the functional traits of member species can be used to predict how that community affects flows of matter and energy, such as light, carbon, water, and nutrients (Díaz et al. 2004). In addition to controlling species responses to the environment, functional traits thus also predict species effects on ecosystem functions (Lavorel and Garnier 2002). Because human welfare critically depends on plant communities regulating the carbon and water cycles (Díaz et al. 2019), it is imperative that we try to understand how trait-based selection will change the functional composition and diversity of plant communities that are affected by multiple global change drivers.

There is reason to focus much of this attention on high-latitude systems. The boreal and tundra biomes cover 19 and 7.5 million km^2, respectively (Brandt et al. 2013; Callaghan, Velichko, and Borisova 2011), and together make up about 20% of the Earth's ice-free land area (FAO 2011). Because of the polar amplification of climate change, high-latitudes, especially in the northern hemisphere, are warming much faster than the planet as a whole (Serreze and Barry 2011). Arctic tundra, the northernmost biome, could stand to lose the climate needed for its existence in over a third of its current area by the end of the century (Feng et al. 2012). The shrinking of the tundra will come about by the invasion of large plants, which is already detectable in tundra communities around the northern hemisphere (Bjorkman et al. 2018a). Again, while changes in the functional characteristics of high-latitude plant communities are important from a conservation perspective, they are also important from a climate change mitigation perspective. Up to 1700 Pg of carbon is stored in the soils of the tundra and boreal zones (Deluca and Boisvenue 2012), which is equivalent to >150 years of anthropogenic carbon emissions at current rates (IPCC 2018). Warmer temperatures are expected to cause decreases in net carbon storage via increased soil respiration (Xue et al. 2016), but it is as of yet unknown whether they will be partially or even completely offset by changes in plant communities, as results remain mixed (Belshe, Schuur, and Bolker 2013; Schuur et al. 2009). This uncertainty highlights a need to learn more about the responses of high-latitude plant communities to shifting environmental selection (Abbott et al. 2016). Such uncertainties could perhaps be reduced, if study results could be compared using universal metrics such as functional traits.

The transitions of fine-scale plant community functional composition along environmental gradients remain poorly understood (but see Wieczynski et al. 2019 for a coarser scale example). In a global study, Bruelheide et al. (2018) did not find strong correlations between trait averages and variances and coarse-resolution environmental variables for most traits, and note that this points to the importance of local climate, soil properties, disturbance regimes and biotic interactions in structuring those communities. Likewise, Bjorkman et al. (2018a) found coarse-scale environmental variables to explain a very limited amount of variation in functional community properties. Further, they found that temporal predictions of community change based on spatial trait-environment correlations were biased, predicting acceleration of leaf economics when none had occurred. Future research into trait-environment relationships in the functional community ecology research program should thus strive to include environmental predictors at a scale that is relevant for the studied communities. Most plant species are of very limited stature (Kattge et al. 2020), and thus cannot experience environmental conditions further than a few meters away from their point of germination, or the microenvironment. Descriptions of this microenvironment should account for the effects of canopy characteristics, snow conditions, soil effects and local topography, which are known to be important modulators of the microenvironment by decoupling communities from free-air temperatures (Hallinger, Manthey, and Wilmking 2010; Ge and Gong 2010; De Frenne et al. 2019; Niittynen and Luoto 2017; Lembrechts et al. 2020), and by affecting resource availability (Maes et al. 2020; Niittynen and Luoto 2017), among other effects.

Climate change is not the only global change driver affecting plant communities, however. Land use and land-use change still remain the most important drivers of biodiversity decline (Butchart et al. 2010; Díaz et al. 2019). High-latitude ecosystems are widely affected by human management. Only a third of boreal forest remain outside human management, the aim of which is usually wood production (Gauthier et al. 2015). Forest management modifies canopies and understories alike. For example, recent cuttings increase light availability and the cover of light-adapted species in the understory (Tonteri et al. 2016). In addition, humans control the densities of large herbivores, such as reindeer and muskoxen, in both the boreal and tundra biomes. Population sizes are affected by habitat conversion, hunting, and management as domesticated or semi-domesticated livestock, among other drivers (Ripple et al. 2015). As an example, semi-domesticated reindeer are kept as livestock in nine Arctic countries in the tundra and boreal zones, and have been found to buffer tundra communities against invasion by shrubs (Vowles et al. 2017; Sundqvist et al. 2019; Vuorinen et al. 2017), highlighting the importance of understanding the modulating effects of land-use on directional selection driven by climate change. From a conservation perspective, studying the effects of land-use -mediated species filtering in the light of trait-based selection can be informative for management recommendations that are not contingent on species identities and unique locations, but universally measurable properties of species and environments (Keddy 1992).

In this thesis, I provide new evidence on how trait-based selection shapes high-latitude plant communities. Specifically, I have three aims:

1. To sharpen our understanding about the effects of trait-based selection on plant communities by accounting for the microenvironment in models of trait composition, both on local (paper I), regional (IV), and global scales (II).
2. To elucidate the effects of that selection on tundra carbon cycling (III).
3. To reveal how trait-based directional selection caused by land use and land-use change modulates long-term change trajectories in plant communities (IV).

I connect my findings to a causal framework (Fig. 2), to underline how my results fit in the larger context of interacting human land use, environmental filtering and ecosystem functions. This will facilitate generalizing my results beyond the extents of these individual studies, and help in identifying interesting future research questions that still need answering.

2 Materials and methods

2.1 Study areas

These studies were conducted in the tundra and in the boreal zone, the two northernmost biomes warming more rapidly than the rest of the planet (Serreze and Barry 2011). Both biomes are characterized by comparatively low annual temperatures and seasonal snow cover (Eugster et al. 2000). The study sites fall into two Köppen climate classes ET (polar, tundra I–III) and Dfc (cold, no dry season, cold summer, IV), which together cover a large part of the Earth's land surface especially in the northern hemisphere (Fig. 3).

2.1.1 Papers I & III

These studies were conducted above the forest line in Kilpisjärvi, in the northernmost part of the Scandinavian mountain range in northwestern Finnish Lapland (69.05° N, 20.81° E). The area is oroarctic tundra (Virtanen et al. 2016), dominated by ericoid-graminoid heaths and streamside

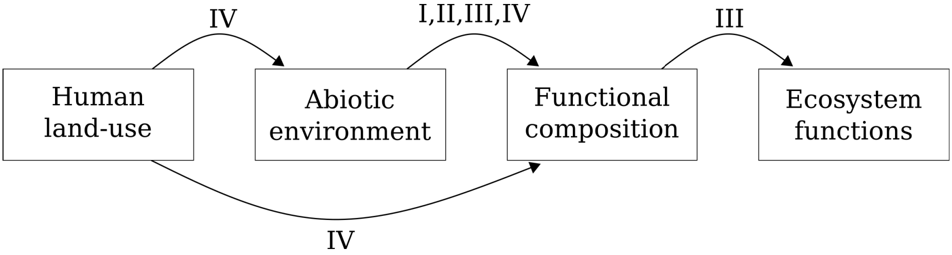

Figure 2: Connections between studied phenomena, and the papers that address them. Studies I–III were conducted in the tundra, and study IV in boreal forests.

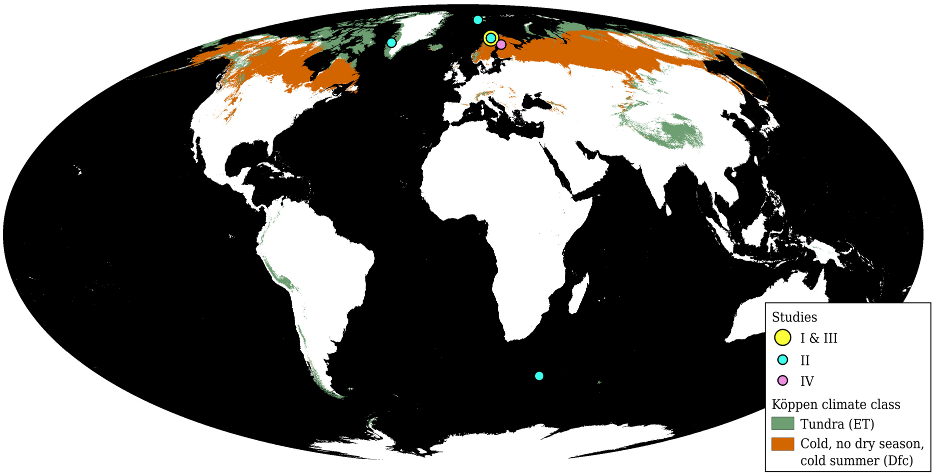

Figure 3: Locations of the study areas and the Köppen climate classes they cover. Climate data from Beck et al. (2018). The projection used is the Mollweide equal-area projection.

meadows. At a nearby weather station (Kilpisjärvi kyläkeskus, 480 m.a.s.l), mean annual temperature is -1.9°C, and annual precipitation is 487 mm (Pirinen et al. 2012). Some abundant species include the dwarf shrubs *Empetrum nigrum* and *Betula nana*, the graminoids *Deschampsia flexuosa* and *Carex bigelowii*, and the herbs *Viola biflora* and *Polygonum viviparum.*

2.1.2 Paper II

This study was conducted in four climatically distinct sites: high-Arctic, low-Arctic, sub-Arctic and sub-Antarctic. The sub-Arctic site is Kilpisjärvi and is described above.

The high-Arctic site is in the valleys of Adventdalen and Endalen (78.20° N, 15.73° E). Mean annual temperature is -5.9°C and annual precipitation is 196 mm, measured at Svalbard airport (28 m.a.s.l) ca. 8 km from the study sites (Norwegian Centre for Climate Services 2019). Dominant species include the dwarf shrubs *Dryas octopetala*, *Salix polaris*, and *Cassiope tetragona*, the graminoids *Festuca rubra* and *Poa pratensis*, and the herb *Bistorta vivipara.*

The low-Arctic site is in western Greenland, in the Ammalortup Nunaa highland (66.95° N, -50.72° W). Mean annual temperature is -4.9°C and annual precipitation is 252 mm, as measured at Kangerlussuaq airport (50 m.a.s.l) 7 km away from the study site (Danish Meteorological Institute 2019). Dominant species include the dwarf shrubs *Vaccinium uliginosum*, *Betula nana*, *Salix glauca*, *Cassiope tetragona*, *Salix herbacaea*, and *Rhododendron groenlandicum.*

The sub-Antarctic site is on Marion Island, located in the southern Indian Ocean (-46.90° S, 37.73° E). The mean annual maximum temperature is 8.7 °C, the mean annual minimum temperature is 3.2°C, and mean annual precipitation is 1800 mm, measured at a weather station 1 km away from the study site. Dominant species include the fern *Blechnum penna-marina*, the graminoid *Agrostis magellanica*, and the keystone cushion plant *Azorella selago* (Le Roux et al. 2005).

2.1.3 Paper IV

This study was conducted in Northern Finland. The study area is bounded between 64.02–68.25° N and 23.81–29.70° E, from Kajaani in the south to Kittilä in the North, Oulu in the west to Kuusamo in the East. Mean annual temperatures in Kajaani and Kittilä are 2.0°C and -1.3°C, and mean annual precipitations are 556 mm and 547 mm, respectively (Kittilä Pokka and Kajaani airport weather stations, Pirinen et al. 2012). The study subject was the understory vegetation of boreal herb-rich forests. Compared to the surrounding boreal forest matrix, their soils are mould or mould-podzol transitions instead of pure podzol, they have higher species richness, and higher abundance of herbaceous species in the field layer and deciduous species in the tree layer. The spatial distribution of these forests becomes patchier the further north one goes, and correlates with calcareous bedrock and soils (Maliniemi, Happonen, and Virtanen 2019). The vegetation type is of conservation importance, as about half of threatened forest species in Finland use herb-rich forests as their primary habitat ((Hyvärinen et al. 2019). The tree-layer is dominated by *Picea abies*, *Alnus incana*, and *Betula pubescens.* Some dominant field-layer species include the herbs *Geranium sylvaticum* and *Filipendula ulmaria*, the ferns *Gymnocarpium dryopteris* and *Athyrium filix-femina*, the graminoids *Milium effusum* and *Elymus caninus*, and occasionally even dwarf-shrubs such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea.*

2.2 Environmental measurements

In all papers, I used locally measured environmental variables to predict the functional composition of communities. Information about the variables studied in each paper are summarized in Table 1.

2.2.1 Papers I & III

Our research group has set up an environmental monitoring network between the fells Saana and Korkea-Jehkas. The network consists of 220 locations. Most of these are laid evenly on a 1.5 km × 2 km grid, but a few of the locations were manually chosen to capture extreme values of temperature, snow depth, and soil moisture. Monitoring has been going on since 2016. Each monitoring location consists of a central plot, and 4 additional plots 5 metres away, one in each cardinal direction.

Of the 220 locations, 114 have loggers in their central plots that record air temperatures 10 cm above ground and soil temperatures 10 cm below ground with 2–4 h intervals (Thermochron iButton DS1921G and DS1922L) throughout the year. In these papers, I used mean daily air temperatures in July and mean daily soil temperature in February as temperature variables, as they are the warmest and coldest months in the area, respectively.

All 220 locations have manual soil moisture monitoring during the growing season. The locations are measured at least three times during each growing season, each measurement campaign taking place at least 24h after

Table 1: Details on studied variables and study scales for each paper. LDMC: leaf dry matter content, SLA: specific leaf area, TTT: Tundra trait team database, TRY: TRY plant trait database, BIEN: Botanical information and ecology network database.

Paper	Community data	Scale	Traits	Trait sources	Environmental data	Land-use variables	Ecosystem functions
I	Point-intercept frequency Circular 314 cm^2 frames	Local One tundra landscape in Finnish Lapland	Vegetative height LDMC SLA	Measurments TTT	Summer air temperature Soil resources Maximum snow depth		
II	Visual percent cover 1 m x 1 m quadrats arranged in grids of 160 plots	Global Four sites spanning 15000 km	Vegetative height LDMC SLA Seed mass Leaf N% Leaf P%	TTT TRY BIEN Literature	Annual soil temperature Soil moisture Soil pH Potential solar radiation		
III	Point-intercept frequency Circular 314 cm^2 frames	Local One tundra landscape in Finnish Lapland	Vegetative height LDMC	Measurements	Summer air temperature Winter soil temperature Soil resources		Above-ground carbon Soil organic carbon Photosynthesis Ecosystem respiration Soil respiration Peak-season carbon budget
IV	Visual percent cover 5 m x 5 m quadrats	Regional Study area spans 500 km of Finnish boreal forest	Vegetative height LDMC SLA	TRY LEDA	Canopy cover Canopy SLA	Forest management intensity Reindeer herding area	

any rainfall event. The central and additional plots are both monitored. During a measurement campaign, each plot is measured three times with a hand-held time-domain reflectometry sensor (FieldScout TDR 300; Spectrum Technologies Inc., Plainfield, IL, USA), and these measurements are averaged (Kemppinen et al. 2018).

All 220 have manual snow depth monitoring during winter. In April, which is the time of maximum snow depth in Kilpisjärvi, each plot is measured for snow depth with an aluminium probe. Snow was measured because it affects vegetation by providing protection from extreme cold temperatures, frost, and abrasion by wind-blown ice particles, as well as by providing water sometimes long into the summer, and by limiting the length of the growing season (Braun-Blanquet, Conard, and Fuller 1932; Niittynen, Heikkinen, and Luoto 2018).

I used random effects modelling with the R package *lme4* (Bates et al. 2015) to predict average environmental conditions in each location for the years 2016–2018. Random effects modelling allows borrowing information from other plots and reduces the influence of measurement error on calculated averages. I modelled July air temperatures and February soil temperatures using location and year as random effects (y~(1|location+year)). Since they were only measured in the central plot, including plot as a predictor was not necessary. Snow depth and soil moisture, however, I modelled using plot nested in location, and year as random effects (y~(1|location/plot+year)). I log-transformed soil moisture before modelling. Finally, I predicted the values of the environmental variables for the central plot, averaging out the random effects. I back-transformed soil moisture before further analyses.

We collected samples of the soil organic layer from 200 locations to measure soil pH. Low soil pH ($pH < 5$) typical in tundra soils is indicative of reduced nutrient mineralization (Sumner and Yamada 2002). The samples were taken ca. 2 m away from the central plot of each location to avoid perturbing long-term monitoring in these plots. Measurements were performed in the laboratory of the University of Helsinki following ISO standard 10390.

Soil pH and soil moisture were highly correlated with each other ($\rho > 0.8$). I thus reduced them to their first principal component. The resulting variable I shall refer to as soil resources. Thus to characterize the microenvironment of the studied plant communities, I had information on July air temperatures, February soil temperatures, maximum snow depth, and soil resources.

2.2.2 Paper II

The environmental and plant community data in this study were collected in a hierarchical manner. Several study grids were founded in each study site, and each study grid consisted of 160 study plots of 1 m^2. There were 42 grids in total: six in the high-Arctic, six in the low-Arctic, 21 in the sub-arctic, and nine in the sub-Antarctic. The high-Arctic and low-Arctic sites were surveyed in 2018, the sub-Arctic site in 2013, and the sub-Antarctic site in 2017. Grids were placed within each site in such a way as to maximize between- and within-grid variation in mesotopography and community composition. The sub-Arctic grids have been used to study patterns of plant community properties along environmental gradients (Roux, Aalto, and Luoto 2013; Kemppinen et al. 2019).

Soil moisture was measured as volumetric water content (VWC) in each plot using a hand-held time-domain reflectometry sensor (FieldScout TDR 300; Spectrum Technologies, Plainfield, IL, USA). Measurements were taken from a depth of 10 cm in the low-Arctic site and 7.5 cm in the others. Soil moisture measurement campaigns were performed during the growing season. During each measurement campaign, three measurements were taken from each plot, and the average value was used as the value for that plot. Only one measurement campaign was done in the high-Arctic and low-Arctic sites, but soil moisture in the sub-Arctic and sub-Antarctic sites is represented as the average of three and five campaigns, respectively. All measurements were done during daytime, when at least 24 h had passed without precipitation.

Miniature sensors were used to record soil temperature (Thermochron iButton DS1921G and DS1922L). Loggers were installed 5–10 cm below ground and left to measure temperature with 2–4 h intervals for a year. In total, data was obtained from 69 loggers from the high-Arctic, 72 from the low-Arctic, 322 from the sub-Arctic, and 52 from the sub-Antarctic. Each grid had measurements from 3–18 loggers. Mean annual temperature was calculated for each logger. These values were subsequently bilinearly interpolated to each plot in the grid, with the additional constraint that the values had to stay between the minimum and maximum of the measured mean annual temperatures in each grid.

Soil pH was measured from soil samples taken from a subset of the grids. In the high-Arctic and low-Arctic sites samples were collected from 12 plots per grid, in the sub-Arctic 18 plots per grid, and in the sub-Antarctic 16–39 plots per grid. Soil pH was bilinearly interpolated for remaining plots, with the additional constraint that the values had to stay between the minimum and maximum of the measured mean annual temperatures in each grid.

In the three Arctic sites, soil pH was determined from air-dried soil samples using distilled water as a solution liquid following the International Organization for Standardization 10390:1994 (E) protocol, with the exception that the high-Arctic and low-Arctic samples were oven-dried, and the sub-Arctic samples were freeze dried. Soil pH in the sub-Antarctic site was determined from air-dried soil samples and measured in calcium chloride solution (0.01 M). Soil pH values measured in calcium chloride solutions can be lower compared to measurements made in water (Miller and Kissel 2010), which is a potential source of error in this study.

Incident radiation was calculated as the maximum potential solar radiation per plot using field-quantified slope and aspect values (McCune and Keon 2002; McCune 2007).

2.2.3 Paper IV

This paper uses vegetation resurvey data. In the years 1968–1975, Eero Kaakinen surveyed boreal herb rich forests in northern Finland (Kaakinen 1971; Kaakinen 1974, Kaakinen, unpublished). In 2013–2019, we located and revisited 254 of the original sites. Relocation was based on the help of the original surveyor, and field notes that included information on slope, aspect, elevation, and nearby landmarks. The study setting is thus based on semi-permanent plots (Kapfer, Hédl, Jurasinski, et al. 2017). The original surveyor visually estimated canopy variables from a 10 m x 10 m plot. These variables were the relative covers of all tree species, and total tree cover on a three-point ordinal scale (0–30%, 31–70%, 71–100%). These measurements were repeated with the same methodology in 2013–2019.

Data on reindeer densities was provided by Jouko Kumpula from the Natural Resources Institute Finland. Management intensity was estimated based on the protocol used for the assessment of threatened habitats in Finland (Kouki et al. 2018, p. 180). The original protocol assigns sites on an ordinal scale of pristineness ranging from zero to four. We omitted deforested sites and inverted the scale to arrive at a four-level ordinal variable describing management impact (Table 2). Management intensity was only assessed in 2013–2019. However, since the purpose of the original surveys was phytosociological description of typical herb-rich vegetation, they were not conducted in very disturbed forests.

Table 2: The one-out-all-out criteria for inclusion in a management intensity class.

	1: Natural sites	2: Semi natural sites	3: Managed sites	4: Heavily managed sites
Management intensity	Not managed	Light management	Intensive management, but no ditching or mounding	Very intensive management e.g. ditching or fertilization
Soil	Undisturbed	Disturbed, but enables persistence of herb-rich forest species	Disturbed, declined conditions for herb-rich forest species	Severely disturbed, soil may have dried up or topsoil eroded, prevalence of herb-rich forest species endangered
Vegetation layers	All layers present	Layer variability declined	Layer variability clearly declined	Layers missing
Stand structure	Natural variation and gap dynamics	Variability declined, impacts of management visible in gap dynamics	Pronounced decline in variability	Even-aged stand, plantation
Deadwood	Varying in age and size	Impacts of management visible in the amount of decaying wood	Scarce or homogenous in age in size	Scarce or missing

2.3 Plant community data

2.3.1 Paper I & III

I measured species composition in 143 locations with the point-intercept method, using a circular frame with a diameter of 20 cm, and 20 evenly spaced pinholes. The frame was placed as close to the central plot of each location, without perturbing the long-term measurements (average distance was 2.9 m). I quantified the abundance of each vascular plant species as the total number of times each species touched any of the 20 pins lowered into the vegetation through the frame.

2.3.2 Paper II

The absolute cover of each vascular plant species was estimated visually in each plot.

2.3.3 Paper IV

During both survey times, the absolute cover of each vascular plant species in the field layer was estimated visually from a 5 m x 5 m plot nested in the 10 m x 10m plot used to estimate canopy characteristics. I calculated species richness, Shannon diversity, and species evenness for each plot during both sampling times. I used effective numbers of species as the expression of species diversity as per the true diversity framework (Jost 2006). Species evenness I expressed as Pielou's J, or the ratio of log-transformed Shannon diversity and log-transformed species richness, which is a measure of relative evenness ranging from infinitesimal (complete dominance by one species) to one (uniform relative abundance distribution, Jost 2010). I calculated plot-specific turnover rates using the R package vegan (Oksanen et al. 2019), using the version of Jaccard distance that takes into account species relative abundances.

2.4 Functional traits

2.4.1 Paper I & III

I measured vegetative height, specific leaf area (SLA), and leaf dry matter content (LDMC) for all observed species in all 143 plots with plant community data, thus taking into account intraspecific variation. These traits align well with the community-level size-structural and leaf economic trait axes identified by Bruelheide et al. (2018). Trait sampling in each community was done within the boundaries of the point-intercept frame.

I measured vegetative height as the height of the highest leaf for two random ramets of each observed species within a plot. Leaf traits were measured from leaf samples. One mature leaf was sampled from two random ramets and put in a resealable plastic bag with a moist piece of paper towel. Samples were stored in 4℃ for up to 3 days and processed in batches. Each leaf was weighed for fresh mass, scanned with a tabletop scanner, oven-dried at 70℃ for at least 48 h, and weighed for dry mass. Weighing was done with a precision scale with a resolution of 0.001 g. I measured leaf area from the scanned images using the Fiji distribution of the software ImageJ (Schindelin et al. 2012; Rueden et al. 2017). I calculated leaf dry matter content as the ratio of fresh mass to dry mass (unitless), and specific leaf area as the ratio of leaf area to dry mass ($\mathrm{mm}^2\mathrm{mg}^{-1}$). For each species in each plot, I took the average of two trait measurements to represent its traits in that location.

I calculated abundance-weighted or community-weighted means (CWMs) for height, SLA and LDMC. If environmental selection acts via filtering species with unsuitable traits, these values should change along environmental gradients (Vellend 2016). They have been shown to be good summaries of trait effects on ecosystem functions, as well (Garnier et al. 2004; Díaz et al. 2004).

In paper I, I also calculated CWMs with coarser trait measurement resolutions to study if intraspecific trait variation (ITV) is important for trait-based selection in this landscape. If ITV is important for trait-based selection, using coarser-scale trait measurements should decrease the strength of observed trait-environment relationships. I calculated landscape-resolution CWMs by using landscape-level averages of each trait for each species instead of plot-specific averages. Further, I calculated global-resolution CMWs by setting species trait values to averages from the Tundra Trait Team database (Bjorkman et al. 2018b). Communities where less than 80% of total species cover had trait values were excluded from analyses.

In paper III, I also calculated functional diversity for height and LDMC as abundance-weighted coefficients of variation (CV). I chose this metric, because many traits are log-normally distributed (Bjorkman et al. 2018b), and using diversity metrics that depend on standard deviations or correlate strongly with it introduces statistical dependency between functional composition and diversity. CV, on the other hand, avoids this codependence because it normalizes the standard deviation with the mean.

2.4.2 Paper II

Species trait values for plant height, specific leaf area, seed mass, leaf dry mass content, leaf area, leaf nitrogen content, and leaf phosphorus content were extracted from the Tundra Trait Team database (Bjorkman et al. 2018b), when possible. Median values were calculated for species with at least five trait observations. Such values were available for 73% of total plant cover. For missing species-specific traits, values were supplemented with trait observations from the TRY (Kattge et al. 2011), and BIEN databases (Maitner et al. 2018), and with measurements made at the sub-Antarctic site (Rossouw 2014; Louw 2016; Mazibuko 2019). This increased total trait coverage to 97.8–99.6% of total plant cover. For the few remaining species with no trait information, trait values were calculated as the mean of the genus or family, preferably from the Tundra Trait Team database. These were then refined to plot-specific community-weighted means. Ferns were omitted from seed mass analyses, because they do not have seeds.

2.4.3 Paper IV

For field layer communities, I calculated CWMs for vegetative height, LDMC, and SLA, using traits from the databases TRY (version 5, Kattge et al. 2011; Kattge et al. 2020) and LEDA (Kleyer et al. 2008). These databases were supplemented with our own measurements for a few species. Communities where less than 80% of total species cover had trait values were excluded from analyses. I also calculated a CWM for tree-layer SLA, using the same databases. All trait observations were log-transformed before CWM calculations, because most traits follow a log-normal distribution ((Bjorkman et al. 2018b).

2.5 Carbon cycling

In paper III, the carbon cycling variables were measured as follows. Carbon fluxes were measured with the chamber method (Livingston and Hutchinson 1995), using a transparent, 25 cm high cylindrical acrylic measurement chamber with a diameter of 20 cm (Vaisala, Vantaa, Finland). The chamber was used to measure CO_2 concentration, air temperature, and relative humidity at 5-s intervals for 90 s. The CO_2 measurements were done in the exact same spot where community composition and traits were measured, before trait sampling. Photosynthetically active radiation was measured manually during the same time with 10-s intervals, using a quantum sensor (Light Quantum Sensor 3668I, Spectrum Technologies, Inc., USA). Steel collars (diameter 21 cm, height 6–7 cm), in which the chamber was mounted, were inserted in the soil $>=$24 h before CO_2 measurements to avoid CO_2 flush from soil disturbance. The edges of the collar were sealed with inert quartz sand. The collar was ventilated before each measurement series.

In each plot, measurement series were taken in different lighting conditions. Light levels were progressively decreased from clear-sky conditions to ca. 80%, 50%, and 30% by shading the chamber with several layers of mosquito net. In addition, CO_2 concentration and its development was also measured in total darkness by wrapping the chamber in a space blanket. Measurement series in each lighting condition were repeated at least twice. These measurements were used to parametrize light response curves and derive estimates of photosynthesis and ecosystem respiration for each plot, described in more detail in the modelling section. In addition, soil respiration was measured by clipping above-ground vascular plant vegetation $>=$24 h prior to measurements, and by performing three additional measurement series in dark conditions.

Above-ground carbon stocks were measured by drying the clipped vascular plant biomass at 70°C for 48 h, weighing, and multiplying the mass by 0.475, because the carbon content of biomass is 45–50% (Schlesinger 1991).

Soil organic carbon stocks were estimated by combining information on the depths and carbon contents of the soil organic and mineral layers. Depth of the organic and mineral layers were measured in three different locations in the central measurement plot using a metal probe, and consequently averaged. Soil carbon contents were estimated by collecting samples of roughly 1 dl from the soil organic and mineral layers with metal soil core cylinders (4–6 cm diameter, 5–7 cm height). The organic samples were collected from the top soil, and mineral samples directly below the organic layer. Samples were freeze-dried before analyses. Bulk density (kg m^{-3}) was estimated by dividing the dry weight by the sample volume. Total carbon content (C%) was analyzed using a Vario Elementar -analyzer (Elementar Analysensysteme GmbH, Germany), or derived with a loss of ignition method in the laboratory of the University of Helsinki. Before C% analysis, mineral samples were sieved through a 2 mm plastic sieve. Organic samples were homogenized by hammering the material into smaller pieces. Total soil organic stocks were calculated by multiplying relative carbon content with soil bulk density and layer depth for both layers, and adding the stocks of the two layers together.

2.6 Modelling

2.6.1 Paper I

CWMs were log-transformed before analyses. I used the method of Lepš et al. (2011) to decompose trait variation between communities to contributions from species turnover and intraspecific trait variation. The method is based on regressing local-resolution CWMs against landscape-resolution CWMs and ITV (the difference between landscape- and local-resolution CWMs). I did this with the varpart function of the R (R Core Team 2019) package *vegan* (Oksanen et al. 2019).

To study the relationship between environmental gradients and functional community composition, I used generalized additive models as implemented in the R package *mgcv* (Wood 2011). I regressed community-level height, SLA and LDMC against July mean temperature, soil resources, and snow depth. Each environmental variable was added to the model as a thin-plate spline with the basis dimension set to three to avoid overfitting.

To assess the relative importance of each environmental variable for explaining each community-level trait, I calculated the unique contribution of each environmental variable to multiple R^2 by subtracting its smooth term from the fitted values while keeping the other smooth terms constant. The resulting increase in error variance is the unique contribution of that smooth term to the explained variation. To facilitate cross-trait comparisons, I standardized the values to total 1 for each trait.

2.6.2 Paper II

Community-level trait-environment relationships were modelled using hierarchical generalized additive models (HGAMs, Pedersen et al. 2019). HGAMs are an extension of the generalized additive model framework in the same way that linear mixed models are an extension of linear models. HGAMs can be used to study whether the relationship between responses and predictors has the same functional form in different levels of a grouping variable. Here, HGAMs were used to test whether plant community functional composition responds similarly to environmental gradients across the four study sites, or whether there are site-specific deviations from this relationship.

Separate HGAMs were fitted for all seven CWMs, and the CWMs of plant height, specific leaf area, seed mass, and leaf area were log-transformed before analyses. Soil moisture, mean annual temperature, soil pH, and radiation were used as predictors. The global effect of each predictor variable was added to the model as a thin plate spline with the basis dimension set to 20. Site-specific deviations from this global relationship were added as factor-smooth interactions with the same basis dimension as the global effect. To avoid overfitting, the smoothing parameters of each environmental response spline were set to have a minimum value of 1, based on visual inspection of preliminary models. Higher values of the smoothing parameter correspond with less wiggly splines. In addition to the environmental splines, a random intercept was included for each site-grid -interaction. A separate random effect was not added for each site, because the number of sites was less than five, and thus the variance estimate for the random effect would have been unreliable (Bolker et al. 2020). The models were fitted with the package *mgcv* (Wood 2011), using restricted maximum likelihood estimation.

The fitted values of these HGAM models are the sum of the global splines, the site-specific factor-smooth interactions, the random intercept and the global intercept. The relative importance of the global trait-environment relationship in relation to site-specific deviations was assessed by first subtracting the site-specific splines from the fitted values and noting the decrease in the squared correlation between fitted and observed values (r^2). After this, the global splines were further subtracted, and the decrease in r^2 recorded. The sum of these decreases can be interpreted as the amount of variation in a CWM explained by the environment. The relative magnitudes of the amounts of r^2 accounted for by global splines and deviations from it were compared for each site-trait combination to infer whether plant community functional composition can be explained by trait-environment relationships that hold across geographical locations.

2.6.3 Paper III

All models in this paper were built with *brms* (Bürkner 2018), an R (R Core Team 2019) interface to the bayesian modelling platform Stan (Carpenter et al. 2017).

2.6.3.1 Light response model and flux normalization

Each CO_2 concentration measurement series was converted to net ecosystem exchange of CO_2 (NEE, µmol $m^{-2}s^{-1}$) following Kulmala et al. (2010), after omitting the first and last 5 s of measurements from each series. In this paper, positive NEE corresponds to carbon influx in the system. I built a non-linear hierarchical light-response model to predict temperature- and PAR-normalized photosynthesis and ecosystem respiration for each study plot. I used the Michaelis-Menten equation as the functional form of the relationship between PAR and NEE (Eqn 1), offset by an intercept term (dark respiration, ER). The Michaelis-Menten equation additionally has parameters for maximum gross primary productivity (GPP_{max}) and the half-saturation constant (K). Furher, the model also contained an exponential relationship between ER and chamber air temperature (Eqn 2). Equations 2–4 and 6–8 describe the hierarchical parts of the model, i.e. all k plot-specific GPP_{max}, K, and ER are assumed to come from a common distribution. Equation 5 is the global error variance.

$$NEE_{ij} = -ER_{ij} + \frac{GPP_{max\,j}\,PAR_i}{K_j + PAR_i} + e_{ij}$$

$$(i = 1 \ldots n, j = 1 \ldots k) \qquad \text{(Eqn 1)}$$

$$log(ER_{ij}) = Intercept_{ER} + T_{ij}\beta_{temperature} + u_{ER\,j} \qquad \text{(Eqn 2)}$$

$$GPP_{max\,j} = Intercept_{GPP} + u_{GPP\,j} \qquad \text{(Eqn 3)}$$

$$log(K) = Intercept_K + u_{K\,j} \qquad \text{(Eqn 4)}$$

$$e \sim \mathcal{N}(0, \sigma_{NEE}) \qquad \text{(Eqn 5)}$$

$$u_{ER} \sim \mathcal{N}(0, \sigma_{ER}) \qquad \text{(Eqn 6)}$$

$$u_{GPP} \sim \mathcal{N}(0, \sigma_{GPP}) \qquad \text{(Eqn 7)}$$

$$u_K \sim \mathcal{N}(0, \sigma_K) \qquad \text{(Eqn 8)}$$

The Michaelis-Menten parameters GPP_{max} and half-saturation constant K sometimes identify weakly, so that the data would be consistent with infinitely increasing photosynthesis. This is especially true when CO_2 fluxes are small, which is frequently the case in tundra ecosystems. To counter this, I set weakly informative priors on the plot-specific intercept terms based on visual inspection of the scale of variation in our data and typical parameter values reported in Williams et al. 2006a (Eqns 9–11). I also set a weakly informative prior for the temperature effect on respiration $\beta_{temperature}$ (Eqn 12). I left the priors for the variance parameters as the weakly informative *brms* defaults (Eqn 13).

$$Intercept_{ER} \sim \mathcal{N}(1, 2) \tag{Eqn 9}$$

$$Intercept_{GPP} \sim \mathcal{N}(10, 10) \tag{Eqn 10}$$

$$Intercept_{K} \sim \mathcal{N}(6.2, 0.3) \tag{Eqn 11}$$

$$\beta_{temperature} \sim \mathcal{N}(0, 1) \tag{Eqn 12}$$

$$\sigma_{ER}, \sigma_{GPP}, \sigma_{K}, \sigma_{NEE} \sim student - t^{+}(3, 10) \tag{Eqn 13}$$

I fit the model with 4 Hamiltonian Monte Carlo chains, which were run for 2000 iterations each. The first 1000 iterations were discarded as warmup, leaving a total of 4000 samples of each parameter.

I used this model to predict NEE at 0 and 600 PAR and at at 20°C which will be called ecosystem respiration (ER) and photosynthesis (GPP), respectively.

I also used this model with PAR and temperature logger data to simulate changes in carbon stocks during the peak growing season (30-day period between 2017-07-08 and 2017-08-07). For this purpose, I interpolated the temperature time-series from 2–4 h to 10 min resolution. The sum of these predicted 10-minute resolution changes in carbon stocks I call the peak-season carbon budget.

I used a hierarchical linear regression to model the relationship between temperature and soil respiration. I added plot as a group-level (random) intercept, and chamber air temperature as a population-level (fixed) effect. Priors were left as the *brms* defaults. I used this model to predict soil respiration at 20°C (henceforth called SR).

2.6.3.2 Hierarchical model of tundra carbon cycling

I used bayesian linear regression models to relate environmental conditions (July mean air temperature, soil resources, February soil temperature) to community trait composition (log-transformed CWMs of height and LDMC) and diversity (CVs of height and LDMC, submodel 1), community functional properties to CO_2 fluxes (log-transformed GPP,ER, and SR, submodel 2) and carbon stocks above- and belowground (log-transformed AGC and SOC, submodels 3 and 4), and GPP and ER to peak-season carbon budget (submodel 5). Each submodel included residual correlations between responses, if there were more than one. Priors were left as the *brms* defaults. I fitted each submodel using four HMC chains which I ran for 2000 iterations. I then discarded the first 1000 iterations as warmup, leaving a total of 4000 posterior samples of each parameter.

I then coupled the above-described submodels together to simulate the effects of warmer summer air and winter soil temperatures on carbon-cycling. I first calculated median values for all environmental variables, and used 500 posterior draws from submodel 1 to derive fitted values for community functional composition and diversity. I then used these 500 fitted values as inputs for submodels 2–4, derived fitted values using 500 posterior draws from said submodels, and thinned the 500^2 fitted values to 500 by taking the diagonal of the matrix of fitted values. I then repeated the procedure for submodel 5. None of the fitted values took into account residual uncertainty.

I then repeated the above-described procedure, but with datasets that had +1°C warmer mean July air temperatures, +1°C warmer mean February soil temperatures, or both. For the simulations with augmented July air temperatures, I ran the simulations with and without direct temperature effects on summer respiration. I took direct temperature effects into account by multiplying fitted ER by the exponential of the temperature sensitivity parameter from the previously fitted light-response model ($\beta_{temperature}$, Eqn 2).

Data and scripts used in this study have been deposited to Zenodo (Happonen et al. 2020a).

2.6.4 Paper IV

All models were fitted using *brms*, the R (R Core Team 2019) package for bayesian modelling (Bürkner 2018), using default priors and four Hamiltonian Monte Carlo chains of 2000 draws. In each chain, the first 1000 draws were discarded as warmup, leaving a total of 4000 draws of each parameter.

To study temporal differences in community composition and diversity, I subtracted values of species richness, Shannon diversity, species evenness, community-level height, LDMC and SLA during the original survey from those during the resurvey. These observed differences, along with logit-transformed temporal turnover, are the response variables in the following models, unless otherwise stated.

To study average plot-level changes, I fitted an intercept-only model with residual correlations and gaussian errors. Length of the sampling interval was originally included in the model, but was dropped because of its statistical insignificance.

To study the effects of canopy changes and reindeer herbivory on vegetation changes, I first calculated the temporal difference in Canopy SLA in the same way as I did with the field layer variables. I also transformed the ordinal canopy cover variable into a categorical measure of canopy cover change with three levels: canopy cover decrease, stasis, and increase. I then regressed the community changes against changes in canopy SLA, canopy cover, and residence inside the reindeer herding area, to see how biotic interactions might modulate changes in plant communities.

The number and distribution of reindeer are under complete human control, but canopy layer properties are also affected by natural processes. To see how forest management influenced canopy-layer changes, I made two models. First, I modelled canopy SLA using a hierarchical model with normally distributed errors. Plot was added as a group-level (random) effect, and management intensity, sampling time, and their interaction as population-level effects. Second, I modelled canopy cover with the same explanatory variables, but using hierarchical ordinal regression with a cumulative logit-link (Bürkner and Vuorre 2019).

I used these two canopy models to study the indirect effects of management intensity on community diversity and composition via changes in canopy characteristics. I took 4000 draws from the posterior distributions of the model parameters, and used them to acquire fitted values of canopy cover and canopy SLA in each management intensity class during original sampling and resampling. For the ordinal model, this was the probability of each of the canopy cover classes. I then used these fitted values to calculate the posterior probability of canopy cover transitions (canopy cover decreased, canopy cover stayed the same, canopy cover increased), and the posterior probability distribution of canopy SLA changes. Further, I used these posterior distributions of canopy changes as predictors in the model of community change described above to infer the indirect effects of forest management intensity on community properties via effects on canopy characteristics.

To study the direct effects of management intensity on community characteristics, I looked at the distribution of residuals in different management intensity classes. I calculated average residual bias for each response-management intensity -combination, and standardized these values with the standard deviations of the responses during the original sampling, or in the case of turnover, their total standard deviation.

Finally, to quantify spatial correlations in community properties, I used a hierarchical model explaining community diversity and functional composition with plot as a group-level (random) effect, time as a population-level (fixed) effect, and modelled residual correlations in the response variables. The model had gaussian errors. I then compared these spatial correlations to temporal correlations to see whether temporal covariations in community properties reproduce covariations observed spatially.

Data and scripts used in this study have been deposited to Zenodo (Happonen et al. 2020b).

3 Results and Discussion

Identified connections between land-use, abiotic conditions, functional community composition, and ecosystem functions are summarized in Table 3. I have omitted results that are not directly related to selection in the context of the global spectrum of plant form and function, most noteworthily all results that do not consider the traits listed in Fig. 1. These are discussed in more detail in the constituent papers. In the following section, I go through how these results attend to the aims of this thesis: to gain insight about trait-based microenvironmental selection, to understand its consequences for tundra carbon cycling, and to connect land-use -modulated vegetation changes to a context of trait-based selection.

3.1 Trait-based responses to the microenvironment are strong and consistent across scales

Our results suggest stronger environmental control of plot-scale community functional composition than found in previous global analyses at local (I), regional (IV), and global scales (II). While it is perhaps not surprising that explaining functional community composition in one landscape is easier than at pan-Arctic scales (paper I), our results in papers II and IV show that the effects of microenvironmental selection are strong and consistent between locations that lie up to 15000 km apart.

Table 3: Connections between land-use (blue), abiotic conditions (cyan), functional composition (green) and ecosystem functioning (yellow). Roman numerals in parentheses refer to papers in this thesis in which the connections were identified. Canopy cover, although a biotic variable, is included in abiotic conditions because it represents lack of light. Connections from paper III that were identical with connections from paper I were omitted, because they were based on the same data.

System	Predictor	Response	Effect
Boreal	Management intensity	Canopy cover	Positive (IV)
		Height	Positive (IV)
	Reindeer husbandry	Height	Negative (IV)
		SLA	Negative (IV)
	Canopy cover	Height	Negative (IV)
		LDMC	Negative (IV)
		SLA	Positive (IV)
Tundra	Summer temperature	Height	Positive (I)
	Soil resources	Height	Negative (I)
		LDMC	Negative (I)
		SLA	Positive (I)
	Maximum snow depth	LDMC	Negative saturating (I)
		SLA	Unimodal or positive saturating (I)
	Annual soil temperature	Height	Positive or saturating (II)
		LDMC	Negative (II)
		Leaf N	Positive or saturating (II)
		Leaf P	Positive or saturating (II)
		SLA	Positive or saturating (II)
	Soil pH	Height	Negative (II)
		LDMC	Negative (II)
		Leaf N	Positive (II)
		Leaf P	Positive (II)
		SLA	Positive (II)
	Soil moisture	Leaf N	Positive (II)
		Leaf P	Positive or saturating (II)
		SLA	Positive (II)
	Potential solar radiation	Height	Positive (II)
	Winter soil temperature	Height	Positive (III)
		LDMC	Negative (III)
	Height	Photosynthesis	Positive (III)
		Ecosystem respiration	Positive (III)
		Soil respiration	Positive (III)
		Above-ground carbon	Positive (III)
	LDMC	Photosynthesis	Negative (III)
		Soil respiration	Negative (III)
		Above-ground carbon	Positive (III)

At the local scale, summer temperature, snow depth and soil resources explained 20%, 35% and 50% of variance in average plant height, SLA and LDMC, respectively (Paper I). These figures are about 10, 15 and 20 times larger than what was achieved by explaining functional composition with univariate regression against remote-sensing based climate products across the pan-Arctic (Bjorkman et al. 2018a), and 2, 9 and 6 times larger than when the same type of analysis was applied to global vegetation plot data (Bruelheide et al. 2018). This highlights the importance of within-landscape variation in micro-environmental selection for trait-based community assembly.

Most explained variation in vegetation height was accounted for by a positive response to summer air temperatures, variation in LDMC by a negative response to soil resources, and variation in SLA by a positive saturating or hump-shaped response to snow depth. The directions of these effects were further consistent with results from studies that have treated corresponding variables in isolation (Bruelheide et al. 2018; Choler 2005; Pérez-Ramos et al. 2012). Averaged across the traits, snow depth was responsible for the most explained variation. As in the tundra as a whole, variation of plant height in this landscape is severely limited by temperature, whereas variation in leaf economic traits covers a large fraction of the global spectrum of possibilities (Thomas et al. 2020; Bjorkman et al. 2018b). The strongest responses of leaf economic traits were related to factors that can have very large variation at local to landscape scales, namely, snow depth and soil resources. This might explain why it can be hard to explain functional composition in these traits with coarse-resolution predictors. The results in this paper agree with other recent work that raise awareness on the importance of winter conditions for ecological research performed in environments with seasonal snow cover. Among other effects, snow decouples plant-experienced temperatures from the free-air temperatures that most temperature products describe (Lembrechts et al. 2020), which is one explanation for why snow has been observed to be very important for plant distributions in the tundra (Niittynen and Luoto 2017), while coarse-scale winter temperatures often show weak predictive power (Bjorkman et al. 2018a; Bruelheide et al. 2018).

Nevertheless, results from one location cannot necessarily be generalized to others, as the community ecological literature is ripe with results contingent on geography (Simberloff 2004). In paper II, we showed that vegetation height and leaf economic traits have strong and consistent responses to mean annual soil temperature and soil pH across tundra sites located up to 15000 km apart from each other. Furthermore, the responses of height, LDMC and SLA to temperature and soil pH were consistent with those of paper I, if one takes into account that deeper snow correlates with higher winter temperatures, and pH is a component of the soil resource variable in paper I. An important issue to consider is that much of the variation in mean annual soil temperatures was caused by variation in snow cover. The distributions of soil temperatures in the Arctic sites with topographically varying snow cover were wide and overlapping, whereas the snow-free hyperoceanic sub-Antarctic site had a narrow distribution of soil temperatures, again highlighting the importance of accounting for microclimate that can be decoupled from free-air temperatures. Taken together, papers I and II thus show that higher plant-experienced temperatures strongly select for taller plants with faster leaf economic traits, while soil resource availability selects for fast leaf economic traits, at least in the tundra. These effects have been reported before in the literature (Bruelheide et al. 2018; Garnier et al. 2004; Spasojevic and Suding 2012; Pérez-Ramos et al. 2012; Bjorkman et al. 2018a), here I show that they are strong and consistent across the tundra biome. The global spectrum of plant form and function (Díaz et al. 2016) thus seems like an excellent set of traits for monitoring tundra plant communities and the effects caused on them by global change factors such as climate warming and eutrophication.

Moving away from the tundra, in paper IV I investigated the effects of canopy cover changes on 40–50 year trends in the height, SLA and LDMC of boreal forest understories. Canopy cover had increased across the study area. Deepening shade correlated positively with SLA, while the correlation with LDMC was negative. SLA has been previously identified as a key trait predicting understory species responses to succession, i.e. lower light availability, because high SLA maximizes light-capturing area in relation to leaf carbon construction costs (Dahlgren et al. 2006). While LDMC has not been directly identified as such a trait, it correlates negatively with SLA as part of the leaf economic spectrum (Bruelheide et al. 2018). In addition, decreased canopy cover had an uncertain positive effect on vegetation height, and increased cover an uncertain negative effect, leading to reasonable certainty that decreases and increases in canopy cover had affected vegetation height differently. Decreasing height in response to shade is an expected response if light is a limiting resource, as is the case in forest understories (Blondeel et al. 2020), especially among herbaceous plants that cannot annually increment their heights. To sum up, the direct selection pressure of increased shading thus pushed understory composition towards trait values adapted to shadier conditions: faster leaf economics and decreased size, again highlighting how fundamental these trait axes are in explaining species environmental responses. Since climate warming and other factors are increasing the total leaf area of trees and, consequently, the shading of understories globally (Zhu et al. 2016), the trait-based responses identified here and in earlier literature will be important in predicting and explaining understory composition and its changes. A key finding of my research is thus that climate change will likely have additional indirect selection effects on understory plants and their communities via changes in light availability due to increased forest density.

3.2 Plant community functional composition mediates environmental effects on tundra carbon cycling

Returning to the tundra, in paper III I found the functional composition and diversity of plant communities to be strong predictors for both carbon fluxes and carbon stocks. Furthermore, as already identified in paper I, functional composition had strong spatial relationships with environmental conditions. Directional shifts in the composition of plant communities in response to trait-based environmental selection thus has important consequences for tundra carbon cycling.

The strongest connections between carbon cycling and the functional characteristics of communities involved vegetation height. Communities composed of larger plants had larger above-ground carbon stocks, and larger CO_2 influxes and effluxes. More is thus more, even in plant communities. In addition, regression coefficients in the log-log model between vegetation height and CO_2 fluxes had values smaller than unity, leading to diminishing absolute rates of flux increase with plant size, agreeing with previous research on the allometric scaling of productivity (Niklas and Enquist 2001). This is a logical consequence, since a greater fraction of the biomass of large plants needs to be allocated to metabolically inactive structural tissues (Niklas et al. 2007).

Community-level LDMC, the leaf economic trait studied here, affected CO_2 fluxes negatively, but above-ground carbon storage positively. Slow leaf economic trait composition thus led to slower metabolic activity, manifesting as smaller CO_2 fluxes, which is a well-documented relationship (Williams et al. 2006b; Street et al. 2007; Shaver et al. 2007). The positive effect of LDMC on above-ground carbon storage is perhaps due to species with slower strategies having more long-lived above-ground structures. Slower leaf economic traits are found in low soil resource conditions (Paper I), where slower turnover of leaves is favored due to nitrogen-use efficiency:

plants try to minimize inevitable nitrogen losses caused by leaf senescence (Hikosaka 2005). Longer leaf longevity then mandates higher investments in structural carbon compounds, which manifest as higher LDMC. Perhaps such a strategy applies to stems as well, as the stems of species with faster leaf economics in the area are green and ephemeral, and building such stems results in inevitable carbon and nutrient losses after each growing season.

Functional diversity also affected carbon cycling, and the effects could be partitioned between the diversity in size and in LDMC. Size diversity increased carbon stocks above ground, indicating that vegetation layeredness minimizes empty space and increases the amount of carbon stored in the ecosystem. LDMC diversity correlated with increased carbon fluxes and below-ground carbon stocks. This points to the conclusion that increases in the diversity of leaf economic traits but not size-structural traits lead to a more efficient partitioning of resources in this landscape. Across the landscape, the most important functional diversity measure was typically as or more important than average LDMC for the various carbon cycling variables, measured as standardized regression coefficients. However, the diversity measures were only weakly connected to environmental conditions, suggesting that at this fine resolution environmental change is not very consequential for diversity-driven changes in carbon cycling.

Warmer temperatures, both during winter and summer, selected for communities with greater peak-season carbon uptake capacity. Both summer air temperatures and winter soil (i.e. below-snow) temperatures were positively correlated with plant size. Additionally, warmer winter temperatures correlated with faster leaf economics. Increased size and faster leaf economics both increased standardized photosynthesis and ecosystem respiration. According to my simulations, the net consequence of these indirect warming effects was increased CO_2 sequestration during the peak season.

However, our study area in Kilpisjärvi lacked both wetlands with waterlogged peat soil and continuous permafrost, which in some other studies have been shown to be important for CO_2 release (Schuur et al. 2009; Heikkinen, Elsakov, and Martikainen 2002). Additionally, temperature effects on carbon cycling extend beyond the peak growing season. A significant portion of carbon losses might occur in the shoulder seasons (Euskirchen et al. 2017). In addition, microbial respiration continues into winter, even in frozen soils (Heikkinen, Elsakov, and Martikainen 2002; Drotz et al. 2010). Thus, even though warmer summer and winter conditions probably increase the carbon uptake capacity of vegetation, this will not necessarily lead to higher annual net carbon assimilation because of the direct effect of temperature on soil respiration (Bond-Lamberty and Thomson 2010; Mikan, Schimel, and Doyle 2002).

Lastly, increased temperature begins affecting respiration immediately, while the increases in productivity will be delayed. Changes in species composition lag behind environmental changes due to dispersal limitation (Ash, Givnish, and Waller 2017), extinction debts (Bertrand et al. 2011), priority effects and other biotic interactions (HilleRisLambers et al. 2013; Kaarlejärvi, Eskelinen, and Olofsson 2013), and delays caused by ontogenesis, as large plants take time to grow, especially in the tundra (Chapin and Shaver 1996). These lags are very consequential from a climate change mitigation perspective, as I found even the peak-season carbon budget to be two times more sensitive to standardized ecosystem respiration than to standardized photosynthesis, since respiration continues day and night, while photosynthesis follows a diurnal cycle. Thus, while lagged temperature responses are probably good news from a conservation point of view, they also lead to a larger net release of soil carbon to the atmosphere. My results should thus not be interpreted as saying that warming will lead to a higher annual net carbon sink.

To sum up, because average plant size has been shown to increase in communities across the tundra (Bjorkman et al. 2018a), my research shows that warmer temperatures have already caused major shifts in the functioning of tundra ecosystems. Tundra carbon fluxes are accelerating. Since carbon assimilation by plants is intimately linked to the cycles of water and nutrients (Schimel, Braswell, and Parton 1997), increased plant average size across tundra communities has already comprehensively accelerated the cycling of matter and energy in this ecosystem.

3.3 Land use and land-use change cause directional selection on understory functional traits

Moving back to boreal forests, in paper IV I showed how the direct and indirect selective pressures exerted by forestry and reindeer husbandry had shaped vegetation changes during 40–50 years.

I showed that forest management increased canopy cover in the long-term except in recent clearcuts, leading to understory communities composed of species with faster leaf-economic traits. While recent wood harvests have been shown to increase light availability at the forest floor (Tonteri et al. 2016), in paper IV I argue that the long-term effects of forest management can actually be decreased light availability. Forest management in the prevailing periodic cover silviculture replaces natural gap dynamics with temporally and spatially highly concentrated light availability after clearcuts, followed by rapid development of a highly shading canopy whose architecture is designed by humans to fill all gaps in the canopy. This decreased light availability favors species with fast leaf economic traits; the so-called "Oxalis effect" (Wilson, Thompson, and Hodgson 1999).

There was an ambient trend of increasing vegetation height in the absence of canopy changes and reindeer herbivory, consistent with the reported effects of climate warming (Bjorkman et al. 2018a). However, there was considerable spatial variation in this trend. Within the reindeer herding area, communities were actually composed of shorter species than 40–50 years prior, with 88% probability. In addition, SLA remained stable outside but decreased within the reindeer herding area in the absence of canopy changes, with 98% probability.

Larger plants are typically more susceptible to mammalian herbivory than small plants (Carmona, Lajeunesse, and Johnson 2011). Additionally, SLA has been shown to correlate with traits that indicate forage quality for herbivores, such as leaf nitrogen concentration (Díaz et al. 2016). Taking the former into account, and the fact that reindeer density had increased by 40% during the study period, these results suggest that reindeer husbandry is reversing or at least negating the effects of climate change and forest management on the functional composition of boreal herb-rich forest understories. This interpretation is further supported by the fact that forests in the reindeer herding area had 8% lower temporal turnover. Such biotic buffering of climate change effects has been reported before in the tundra (Post and Pedersen 2008; Olofsson et al. 2009; Olofsson and Post 2018). My results suggest that the buffering effects of artificially increased reindeer densities extend spatially to boreal forests.

Functional changes in the understories were also reflected in species diversity measures. Most notably, changes in species richness, species evenness, and Shannon diversity all correlated negatively with changes in species height. Increase in average plant size, assuming plants cannot stretch in only one dimension, leads necessarily to a decrease in the number of plant individuals that can fit in a given area (Oksanen 1996). Consequently, there is a mechanistic link between vegetation height and plot-scale diversity. Thus, the selective pressure towards shorter vegetation exerted by reindeer herbivory was also manifested as increased species evenness and Shannon diversity. Furthermore, these temporal correlations in community properties were also evident spatially, suggesting that their coordination is controlled by more general processes than just incidental covariation.

3.4 Uncertainty and reservations

The studies in this thesis are based on observational data and correlative methods, meaning that they do not provide direct evidence about causal relationships between variables. Rather, their results should be interpreted as exploratory or confirmatory, showing us how natural phenomena actually co-occur, and providing confirmation for predictions based on experimental work and theory (Shipley 1999). In the absence of the latter, observational work can also act as inspiration for new experiments and theoretical synthesis.

The most pervasive problem with observational data is multicollinearity (Graham 2003). Situations where variables of interest vary completely independently from each other and from confounding factors are rare in nature, leading to uncertainty about the true causes of studied phenomena. Uncertainty can sometimes be reduced by including all confounding variables in the models explicitly (Mod et al. 2016), but often this is hard or impossible due to the complexity of natural phenomena. However, basing research on theoretically solid conceptual models reduces the probability of misidentifying causal links between variables (Shipley 1999; Graham 2003). In this work, I have opted for this latter path by studying traits that align well with identified trait axes, by selecting as their predictors environmental variables that are known to constrain plant vital rates in high-latitude ecosystems, and by choosing to study ecosystem functions that could plausibly depend on size-structural and leaf-economic traits. This does not make my analyses impervious to problems arising from multicollinearity, however, and all results should be interpreted in light of other available evidence. For example, in Papers I–III, indicators of soil resource availability (soil moisture, soil pH) correlated negatively with vegetation height, which goes against predictions from theory (Tilman 1988) and reported effects from the literature (e.g. Harpole and Tilman 2007). Most likely this is because water is not only a resource, but can also cause stress and disturbance on vegetation (Kemppinen et al. 2019). Still, most findings in this thesis are as expected based on theory and previous observations about the linkages between studied variables. Conclusive evidence can only be acquired with further experimental work, however.

4 Conclusions and future perspectives

In this thesis, I have shown how the size-structural and leaf economic trait axes modulate the effects of environmental selection on plant communities in the tundra and boreal zones. Large size confers an advantage in warm, ungrazed, unshaded conditions, while fast leaf economic traits are selected for by shade, high soil resource availability, and lack of herbivory. Furthermore, I have shown how the effects of functional composition and diversity on tundra carbon cycling differ between size-structural and leaf economic traits. Carbon dioxide fluxes and above-ground carbon stocks increase along with average plant size. Faster leaf economics similarly result in higher carbon fluxes, but also in lower above-ground stocks. Additionally, size-structural diversity increases carbon stocks above ground, while leaf economic diversity correlates with increased carbon fluxes and below-ground carbon stocks. Lastly, I have shown that these trait axes are able to capture the signal of human economic actions (forestry and livestock grazing) on forest understory communities that are of conservation importance. These findings are summarized in Fig. 4.

The global spectrum of plant form and function (Díaz et al. 2016) thus mediates the effects of different natural and anthropogenic selection pressures on plant communities (Papers I, II & IV), and also how the effects of that selection ripple on to ecosystem functions (Paper III). Functional traits have been proposed as one set of “Essential Biodiversity Variables” for monitoring biodiversity change across the planet (Pereira et al. 2013). Traits that align well with the identified axes of variation, such as height, LDMC and SLA, form a natural set of variables to monitor in plant communities. Given how consistently the location of communities along these trait axes seems to respond to selection across systems, basing trait-based research around this paradigm could allow for meaningful global synthesis. I have summarized some ideas for future research directions in Fig. 5, and discuss them below.

My research suggests that the lack of strong explanatory power of environmental variables in previous global studies of trait composition (Bruelheide et al. 2018; Bjorkman et al. 2018a) is at least in part due to the importance of micro-scale environmental heterogeneity, which remote-sensing products cannot always reliably capture. Studies at the local scale are fortunately beginning to take advantage of the decreasing prices of environmental loggers, and development is underway for global temperature products that take into account the different factors that decouple local temperatures from free-air temperatures (Lembrechts et al. 2020). Improved access to remote-

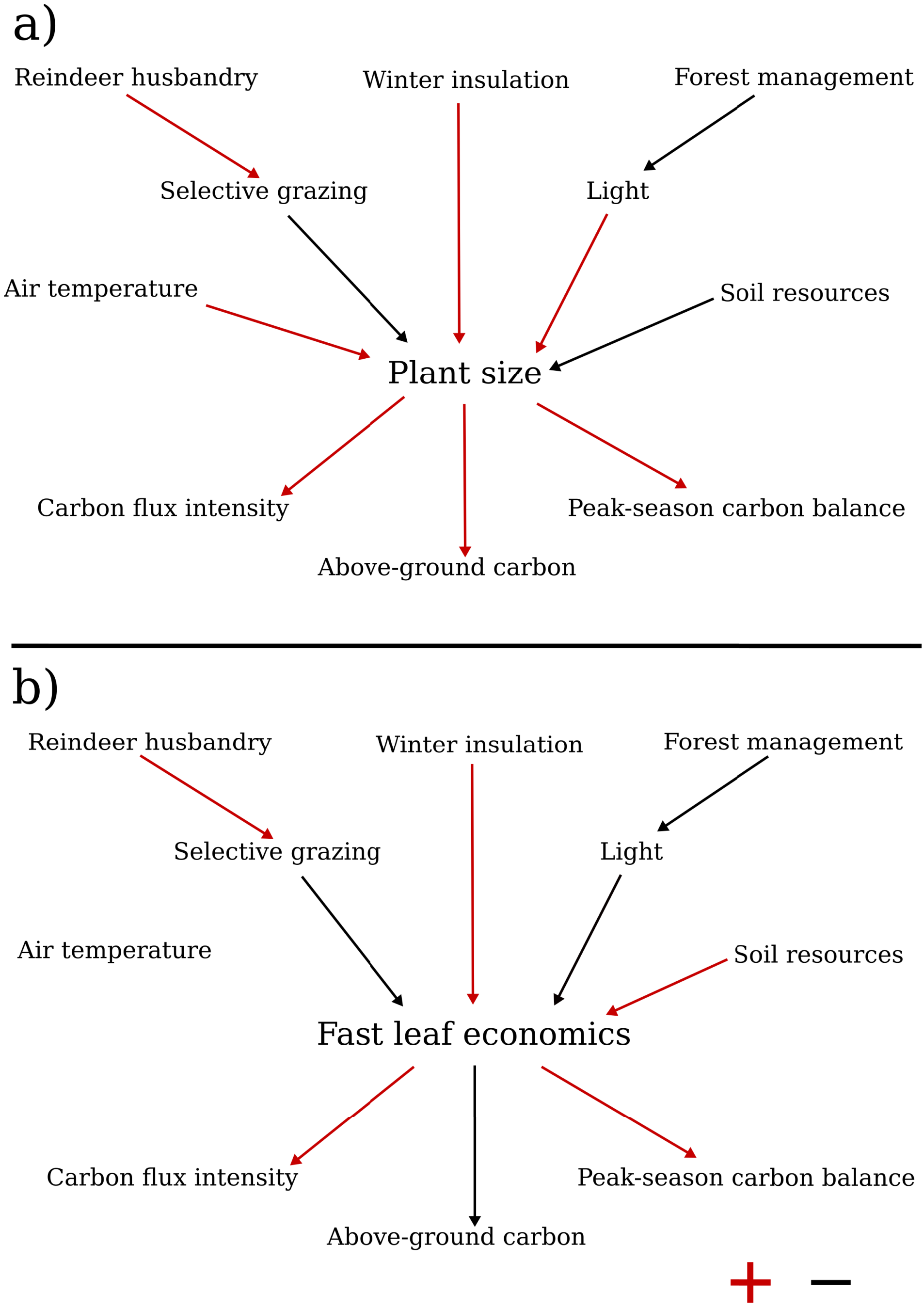

Figure 4: A conceptual summarization of the ways community position on size-structural (a) and leaf economic (b) trait axes is affected by land-use and abiotic conditions, and how these axes modulate carbon cycling. Positive carbon balance equals more carbon sequestered.

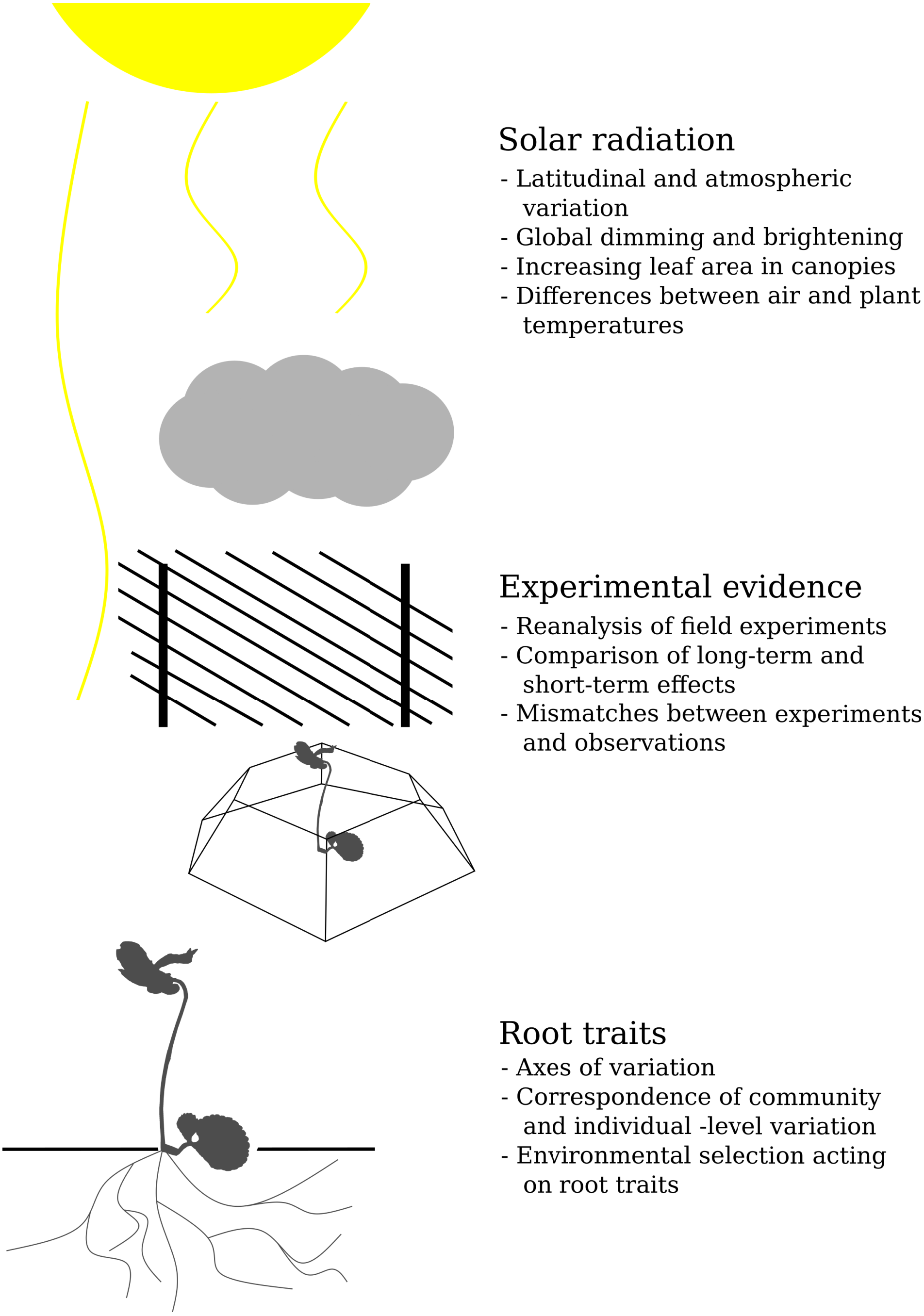

Figure 5: Future directions in the study of trait-based selection on plants and plant communities.

sensing cloud-computing tools such as Google Earth Engine (Gorelick et al. 2017) are also making it easier than ever to include directly observed rather than modelled environmental properties at the resolution of up to 10 m in models of trait composition. Technological advancement is thus opening up possibilities to study trait-environment relationships at extents and resolutions never seen before, paving the way for global syntheses of trait-based microenvironmental selection effects on plant communities. However, as observational work is always subject to confounding factors, a first step to making such a synthesis could be the reanalysis of experimentally induced vegetation changes from a functional trait perspective for experiments where species composition data is available. Such a meta-analysis should already be feasible given how fast the coverage of open species trait databases has grown (Bjorkman et al. 2018b; Kattge et al. 2020; Maitner et al. 2018).

That the microenvironment is important does not mean that regional environmental variation is not. We know that the availability of light is an important selective force structuring plant communities (Paper IV; De Frenne et al. 2015; Dahlgren et al. 2006; Tonteri et al. 2016). Yet very little is known about its effects on community composition beyond local-scale studies, despite light availability varying remarkably along with latitude and climate. Solar radiation displays heterogeneous trends in space and time (Wild 2012), leading to potentially biased inference on the causes of vegetation change in observational studies if changes in light availability are not controlled for. Additionally, productivity in large parts of northern ecosystems, even in the tundra, has been shown to be as or more sensitive to changes in cloud cover than to changes in temperature (Seddon et al. 2016), hinting that changes in light quantity and quality could be important drivers of vegetation change even in treeless ecosystems. Thus, many interesting and important connections between the spatial and temporal availability of light and the functional composition of plant communities probably await discovery.

While the axes of above-ground traits seem a highly useful framework for trait-based plant ecology, they are not a sufficient summary of plant properties. A sizable portion of plant biomass is allocated to below-ground parts (Iversen et al. 2015). While some work suggests that especially chemical fine-root properties vary in concert with above-ground traits as parts of a whole-plant economics spectrum (Freschet et al. 2010; Pérez-Ramos et al. 2012), other analyses have shown that root structural properties such as specific root length are quite free to vary in relation to chemical traits (McCormack and Iversen 2019), highlighting the need for further research on where root traits fit in with the already identified global axes of variation. Identifying below-ground trait axes that are independent from above-ground traits would be a highly useful first step. Progress is hindered by the low coverage of openly available root trait data, although steps are being taken to tackle this (Iversen et al. 2017). Root traits could be thought to be especially important for the storage and cycling of belowground carbon, whose fate under climate change is of utmost importance for human welfare. Taking into account that soil organic carbon was the ecosystem property with the weakest links to above-ground traits (paper III), the functional ecology of roots seems like one of the more timely research priorities in ecology.

I have hopefully demonstrated how trait-based community ecology is one formidable path towards finding repeated patterns in nature, the goal of ecology and science in general as suggested by MacArthur. Understanding how communities react to natural and anthropogenic selection pressures is important in itself, for protecting the intrinsically valuable species with which we share this planet, but also for safeguarding human welfare against unexpected changes in ecosystem functions that we rely on. After more than a century of ecological research, we already know something about how natural systems work, but much remains unexplored. I am in a happy position to be able to follow the advancements made in this field by brilliant researchers around the world, and perhaps also contribute something myself. It took me 3.5 years to write this thesis. I look forward to returning to the questions raised here in another 3.5 years, as I expect many of them to be answered. Nothing is quite as exciting as getting an answer to a long-standing question, except perhaps the process of arriving at the answer yourself.

References

Abbott, B. W. et al. (2016). "Biomass offsets little or none of permafrost carbon release from soils, streams, and wildfire: an expert assessment". *Environ. Res. Lett.* 11, 034014.

Adler, P. B. et al. (2014). "Functional traits explain variation in plant life history strategies". *PNAS* 111, 740–745.

Allen, L., A. O'Connell, and V. Kiermer (2019). "How can we ensure visibility and diversity in research contributions? How the Contributor Role Taxonomy (CRediT) is helping the shift from authorship to contributorship". *Learn. Publ.* 32, 71–74.

Ash, J. D., T. J. Givnish, and D. M. Waller (2017). "Tracking lags in historical plant species' shifts in relation to regional climate change". *Glob. Chang. Biol.* 23, 1305–1315.

Bates, D. et al. (2015). "Fitting Linear Mixed-Effects Models Using lme4". *Journal of Statistical Software, Articles* 67, 1–48.

Beck, H. E. et al. (2018). "Present and future Köppen-Geiger climate classification maps at 1-km resolution". *Sci Data* 5, 180214.

Belshe, E. F., E. a. G. Schuur, and B. M. Bolker (2013). "Tundra ecosystems observed to be CO2 sources due to differential amplification of the carbon cycle". *Ecol. Lett.* 16, 1307–1315.

Bertrand, R. et al. (2011). "Changes in plant community composition lag behind climate warming in lowland forests". *Nature* 479, 517–520.

Bjorkman, A. D. et al. (2018a). "Plant functional trait change across a warming tundra biome". *Nature* 562, 57–62.

Bjorkman, A. D. et al. (2018b). "Tundra Trait Team: A database of plant traits spanning the tundra biome". *Glob. Ecol. Biogeogr.* 27, 1402–1411.

Blondeel, H. et al. (2020). "Light and warming drive forest understorey community development in different environments". *Glob. Chang. Biol.* 26, 1681–1696.

Bolker, B. et al. (2020). *GLMM FAQ*. `https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html`. Accessed: 2020-5-12.

Bond-Lamberty, B. and A. Thomson (2010). “Temperature-associated increases in the global soil respiration record”. *Nature* 464, 579–582.

Brandt, J. P. et al. (2013). “An introduction to Canada’s boreal zone: ecosystem processes, health, sustainability, and environmental issues”. *Environmental Reviews* 21, 207–226.

Braun-Blanquet, J., H. S. Conard, and G. D. Fuller (1932). *Plant sociology; the study of plant communities;* 1st ed. New York and London, McGraw-Hill book company, inc.,

Bruelheide, H. et al. (2018). “Global trait–environment relationships of plant communities”. *Nature Ecology & Evolution* 2, 1906.

Bürkner, P.-C. (2018). “Advanced Bayesian Multilevel Modeling with the R Package brms”. *R J.* 10, 395–411.

Bürkner, P.-C. and M. Vuorre (2019). “Ordinal Regression Models in Psychology: A Tutorial”. *Advances in Methods and Practices in Psychological Science* 2, 77–101.

Butchart, S. H. M. et al. (2010). “Global biodiversity: indicators of recent declines”. *Science* 328, 1164–1168.

Callaghan, T., A. Velichko, and O. Borisova (2011). “Tundra in a changing climate”. *Geography, environment, sustainability* 4, 4–18.

Carmel, Y. et al. (2013). “Trends in Ecological Research during the Last Three Decades – A Systematic Review”. *PLoS One* 8, e59813.

Carmona, D., M. J. Lajeunesse, and M. T. J. Johnson (2011). “Plant traits that predict resistance to herbivores”. *Funct. Ecol.* 25, 358–367.

Carpenter, B. et al. (2017). “Stan: A Probabilistic Programming Language”. *J. Stat. Softw.* 76, 1–32.

Chapin III, F. S. and G. R. Shaver (1996). “Physiological and Growth Responses of Arctic Plants to a Field Experiment Simulating Climatic Change”. *Ecology* 77, 822–840.

Choler, P. (2005). “Consistent Shifts in Alpine Plant Traits along a Mesotopographical Gradient”. *Arct. Antarct. Alp. Res.* 37, 444–453.

Dahlgren, J. P. et al. (2006). “Specific leaf area as a superior predictor of changes in field layer abundance during forest succession”. *J. Veg. Sci.* 17, 577–582.

Danish Meteorological Institute (2019). *Weather observations from Greenland 1958-2018 - Observation data with description.* Tech. rep. Danish Meteorological Institute.

Data Citation Synthesis Group (2014). *Joint declaration of data citation principles.*

De Frenne, P. et al. (2015). “Light accelerates plant responses to warming”. *Nat Plants* 1, 15110.

De Frenne, P. et al. (2019). “Global buffering of temperatures under forest canopies”. *Nat Ecol Evol* 3, 744–749.

Deluca, T. H. and C. Boisvenue (2012). “Boreal forest soil carbon: distribution, function and modelling”. *Forestry* 85, 161–184.

Díaz, S. et al. (2004). “The plant traits that drive ecosystems: Evidence from three continents”. *J. Veg. Sci.* 15, 295–304.

Díaz, S. et al. (2016). “The global spectrum of plant form and function”. *Nature* 529, 167.

Díaz, S. et al. (2019). *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services.* Bonn, Germany: IPBES secretariat.

Drotz, S. H. et al. (2010). “Both catabolic and anabolic heterotrophic microbial activity proceed in frozen soils”. *PNAS* 107, 21046–21051.

Eugster, W. et al. (2000). “Land-atmosphere energy exchange in Arctic tundra and boreal forest: available data and feedbacks to climate”. *Glob. Chang. Biol.* 6, 84–115.

Euskirchen, E. S. et al. (2017). “Long-Term Release of Carbon Dioxide from Arctic Tundra Ecosystems in Alaska”. *Ecosystems* 20, 960–974.

FAO (2011). *The state of the world’s land and water resources for food and agriculture (SOLAW) – Managing systems at risk.* London: Earthscan.

Feng, S. et al. (2012). “Evaluating observed and projected future climate changes for the Arctic using the Köppen-Trewartha climate classification”. *Clim. Dyn.* 38, 1359–1373.

Freschet, G. T. et al. (2010). “Evidence of the ‘plant economics spectrum’ in a subarctic flora”. *J. Ecol.* 98, 362–373.

Garnier, E. et al. (2004). “Plant Functional Markers Capture Ecosystem Properties During Secondary Succession”. *Ecology* 85, 2630–2637.

Gauthier, S. et al. (2015). “Boreal forest health and global change”. *Science* 349, 819–822.

Ge, Y. and G. Gong (2010). “Land surface insulation response to snow depth variability”. *J. Geophys. Res.* 115, 247.

Gorelick, N. et al. (2017). “Google Earth Engine: Planetary-scale geospatial analysis for everyone”. *Remote Sens. Environ.* 202, 18–27.

Graham, M. H. (2003). “Confronting Multicollinearity in ecological multiple regression”. *Ecology* 84, 2809–2815.

Hallinger, M., M. Manthey, and M. Wilmking (2010). “Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia”. *New Phytol.* 186, 890–899.

Happonen, K. et al. (2020a). *Data and code for “Plant community functional composition and diversity drive fine-scale variability in carbon cycling in the tundra”.*

Happonen, K. et al. (2020b). *Data and code for the paper: Trait-based responses to forestry and grazing modify long-term changes in biodiversity hot-spots of boreal forests.*

Harpole, W. S. and D. Tilman (2007). “Grassland species loss resulting from reduced niche dimension”. *Nature* 446, 791–793.

Heikkinen, J. E. P., V. Elsakov, and P. J. Martikainen (2002). “Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia: CARBON 1999”. *Global Biogeochem. Cycles* 16, 62–1–62–15.

Hikosaka, K. (2005). “Leaf canopy as a dynamic system: ecophysiology and optimality in leaf turnover”. *Ann. Bot.* 95, 521–533.

HilleRisLambers, J. et al. (2013). “How will biotic interactions influence climate change-induced range shifts?” *Ann. N. Y. Acad. Sci.* 1297, 112–125.

Hyvärinen, E. et al. (2019). *The 2019 Red List of Finnish species.* Finnish Ministry of the Environment & Finnish Environment Institute.

IPCC (2018). “Summary for Policymakers”. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty.* Ed. by V. Masson-Delmotte et al. Geneva, Switzerland: World Meteorological Organization.

Iversen, C. M. et al. (2015). “The unseen iceberg: plant roots in arctic tundra”. *New Phytol.* 205, 34–58.

Iversen, C. M. et al. (2017). “A global Fine-Root Ecology Database to address below-ground challenges in plant ecology”. *New Phytol.* 215, 15–26.

Jost, L. (2006). “Entropy and diversity”. *Oikos* 113, 363–375.

– (2010). “The Relation between Evenness and Diversity”. *Diversity* 2, 207–232.

Kaakinen, E. (1971). “Tutkimuksia Kainuun lehtokasvillisuudesta”. MA thesis. Oulu, Finland: University of Oulu.

– (1974). “Kainuun ja Kuusamon lehtokasvillisuudesta”. PhD thesis. Oulu, Finland: University of Oulu.

Kaarlejärvi, E., A. Eskelinen, and J. Olofsson (2013). “Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes”. *Funct. Ecol.* 27, 1244–1253.

Kapfer, J., R. Hédl, G. Jurasinski, et al. (2017). “Resurveying historical vegetation data–opportunities and challenges”. *Appl. Veg. Sci.*

Kattge, J. et al. (2011). “TRY - a global database of plant traits”. *Glob. Chang. Biol.* 17, 2905–2935.

Kattge, J. et al. (2020). “TRY plant trait database - enhanced coverage and open access”. *Glob. Chang. Biol.* 26, 119–188.

Keddy, P. A. (1992). “A Pragmatic Approach to Functional Ecology”. *Funct. Ecol.* 6, 621–626.

Kemppinen, J. et al. (2018). “Modelling soil moisture in a high-latitude landscape using LiDAR and soil data”. *Earth Surf. Processes Landforms* 43, 1019–1031.

Kemppinen, J. et al. (2019). “Water as a resource, stress and disturbance shaping tundra vegetation”. *Oikos* 128, 811–822.

Kleyer, M. et al. (2008). “The LEDA Traitbase: a database of life-history traits of the Northwest European flora”. *J. Ecol.* 96, 1266–1274.

Kouki, J. et al. (2018). “5.5: Metsät”. In: *Suomen luontotyyppien uhanalaisuus 2018 : Luontotyyppien punainen kirja. Osa 1: Tulokset ja arvioinnin perusteet.* Ed. by T. Kontula and A. Raunio. Suomen ympäristö. Helsinki: Ympäristöministeriö, 171–202.

Kulmala, L. et al. (2010). “A novel automatic chamber to measure soil CO2 efflux”. In: *Proceedings of the Finnish Center of Excellence and Graduate School in ’Physics, Chemistry, Biology and Meteorology of Atmospheric Composition and Climate Change’ Annual Workshop 17.-19.5.2010.*

Lavorel, S. and E. Garnier (2002). “Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail”. *Funct. Ecol.* 16, 545–556.

Le Roux, P. C. et al. (2005). “Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species”. *Glob. Chang. Biol.* 11, 1628–1639.

Lembrechts, J. J. et al. (2020). “SoilTemp: a global database of near-surface temperature”. *Glob. Chang. Biol.*

Lepš, J. et al. (2011). “Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects”. *Ecography* 34, 856–863.

Livingston, G. P. and G. L. Hutchinson (1995). “Enclosure-based measurement of trace gas exchange: applications and sources of error”. In: *Biogenic trace gases: Measuring emissions from soil and water.* Ed. by P. A. Matson and R. C. Harriss. Oxford, United Kingdom: Blackwell Science, 14–51.

Louw, A. (2016). “Plant functional types on Marion Island”. PhD thesis. Stellenbosch University.

MacArthur, R. H. (1972). *Geographical Ecology: Patterns in the Distribution of Species.* New York: Harper & Row.

Maes, S. L. et al. (2020). “Plant functional trait response to environmental drivers across European temperate forest understorey communities”. *Plant Biol.* 22, 410–424.

Maitner, B. S. et al. (2018). “The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database”. *Methods Ecol. Evol.* 9. Ed. by S. McMahon, 373–379.

Maliniemi, T., K. Happonen, and R. Virtanen (2019). “Site fertility drives temporal turnover of vegetation at high latitudes”. *Ecol. Evol.* 9, 13255–13266.

Mazibuko, N. (2019). “Does wind dispersal potential constrain plant species range expansion on sub-Antarctic Marion Island?” MA thesis. University of Pretoria, Pretoria.

McCormack, M. L. and C. M. Iversen (2019). “Physical and Functional Constraints on Viable Belowground Acquisition Strategies”. *Front. Plant Sci.* 10.

McCune, B. (2007). *Improved estimates of incident radiation and heat load using non- parametric regression against topographic variables.*

McCune, B. and D. Keon (2002). “Equations for potential annual direct incident radiation and heat load”. *J. Veg. Sci.* 13, 603–606.

McGill, B. J. et al. (2006). “Rebuilding community ecology from functional traits”. *Trends Ecol. Evol.* 21, 178–185.

Mikan, C. J., J. P. Schimel, and A. P. Doyle (2002). “Temperature controls of microbial respiration in arctic tundra soils above and below freezing”. *Soil Biol. Biochem.* 34, 1785–1795.

Miller, R. O. and D. E. Kissel (2010). *Comparison of Soil pH Methods on Soils of North America.*

Mod, H. K. et al. (2016). “What we use is not what we know: environmental predictors in plant distribution models”. *J. Veg. Sci.* 27. Ed. by S. Scheiner, 1308–1322.

Niittynen, P., R. K. Heikkinen, and M. Luoto (2018). “Snow cover is a neglected driver of Arctic biodiversity loss”. *Nat. Clim. Chang.* 8, 997.

Niittynen, P. and M. Luoto (2017). “The importance of snow in species distribution models of Arctic vegetation”. *Ecography.*

Niklas, K. J. and B. J. Enquist (2001). “Invariant scaling relationships for interspecific plant biomass production rates and body size”. *PNAS* 98, 2922–2927.

Niklas, K. J. et al. (2007). "“Diminishing returns” in the scaling of functional leaf traits across and within species groups". *PNAS* 104, 8891–8896.

Norwegian Centre for Climate Services (2019). *Climate in Svalbard 2100 – a knowledge base for climate adaptation.* Tech. rep. NCCS.

Oksanen, J. (1996). "Is the Humped Relationship between species Richness and Biomass an Artefact due to Plot Size?" *J. Ecol.* 84, 293–295.

Oksanen, J. et al. (2019). *vegan: Community Ecology Package.*

Olofsson, J. and E. Post (2018). "Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding". *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 373.

Olofsson, J. et al. (2009). "Herbivores inhibit climate-driven shrub expansion on the tundra". *Glob. Chang. Biol.* 15, 2681–2693.

Pedersen, E. J. et al. (2019). "Hierarchical generalized additive models in ecology: an introduction with mgcv". *PeerJ* 7, e6876.

Pereira, H. M. et al. (2013). "Essential biodiversity variables". *Science* 339, 277–278.

Pérez-Ramos, I. M. et al. (2012). "Evidence for a 'plant community economics spectrum' driven by nutrient and water limitations in a Mediterranean rangeland of southern France". *J. Ecol.* 100. Ed. by R. Aerts, 1315–1327.

Pirinen, P. et al. (2012). "Climatological statistics of Finland 1981–2010". *Finnish Meteorological Institute Reports* 1, 83.

Post, E. and C. Pedersen (2008). "Opposing plant community responses to warming with and without herbivores". *PNAS* 105, 12353–12358.

R Core Team (2019). *R: A Language and Environment for Statistical Computing.* Vienna, Austria.

Ripple, W. J. et al. (2015). "Collapse of the world's largest herbivores". *Sci Adv* 1, e1400103.

Rossouw, M. W. (2014). "Spatial variation in plant nutrient composition on Marion Island". PhD thesis. Stellenbosch: Stellenbosch University.

Roux, P. C. le, J. Aalto, and M. Luoto (2013). "Soil moisture's underestimated role in climate change impact modelling in low-energy systems". *Glob. Chang. Biol.* 19, 2965–2975.

Rueden, C. T. et al. (2017). "ImageJ2: ImageJ for the next generation of scientific image data". *BMC Bioinformatics* 18, 529.

Sandford, S. A. (1995). "Apples and Oranges – A Comparison". *Annals of Improbable Research* 1.

Schimel, D. S., B. H. Braswell, and W. J. Parton (1997). "Equilibration of the terrestrial water, nitrogen, and carbon cycles". *PNAS* 94, 8280–8283.

Schindelin, J. et al. (2012). "Fiji: an open-source platform for biological-image analysis". *Nat. Methods* 9, 676–682.

Schuur, E. A. G. et al. (2009). "The effect of permafrost thaw on old carbon release and net carbon exchange from tundra". *Nature* 459, 556–559.

Seddon, A. W. R. et al. (2016). "Sensitivity of global terrestrial ecosystems to climate variability". *Nature* 531, 229–232.

Serreze, M. C. and R. G. Barry (2011). "Processes and impacts of Arctic amplification: A research synthesis". *Glob. Planet. Change* 77, 85–96.

Shaver, G. R. et al. (2007). "Functional convergence in regulation of net CO2flux in heterogeneous tundra landscapes in Alaska and Sweden". *Journal of Ecology* 95, 802–817.

Shipley, B. (1999). "Testing Causal Explanations in Organismal Biology: Causation, Correlation and Structural Equation Modelling". *Oikos* 86, 374–382.

Simberloff, D. (2004). "Community ecology: is it time to move on? (An American Society of Naturalists presidential address)". *Am. Nat.* 163, 787–799.

Spasojevic, M. J. and K. N. Suding (2012). "Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes". *J. Ecol.* 100, 652–661.

Street, L. E. et al. (2007). "What is the relationship between changes in canopy leaf area and changes in photosynthetic CO2flux in arctic ecosystems?" *Journal of Ecology* 95, 139–150.

Sumner, M. E. and T. Yamada (2002). "Farming with acidity". *Commun. Soil Sci. Plant Anal.* 33, 2467–2496.

Sundqvist, M. K. et al. (2019). "Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale". *J. Ecol.* 107. Ed. by R. Aerts, 2724–2736.

Thomas, H. J. D. et al. (2020). "Global plant trait relationships extend to the climatic extremes of the tundra biome". *Nat. Commun.* 11, 1351.

Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities.* Princeton University Press.

Tonteri, T. et al. (2016). "Forest management regulates temporal change in the cover of boreal plant species". *For. Ecol. Manage.* 381, 115–124.

Vellend, M. (2010). "Conceptual synthesis in community ecology". *Q. Rev. Biol.* 85, 183–206.

– (2016). *The Theory of Ecological Communities.* Vol. 57. Monographs in Population Biology. New Jersey, USA: Princeton University Press.

Violle, C. et al. (2007). "Let the concept of trait be functional!" *Oikos* 116, 882–892.

Virtanen, R. et al. (2016). “Where do the treeless tundra areas of northern highlands fit in the global biome system: toward an ecologically natural subdivision of the tundra biome”. *Ecol. Evol.* 6, 143–158.

Vowles, T. et al. (2017). “Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range”. *J. Ecol.* 105, 1547–1561.

Vuorinen, K. E. M. et al. (2017). “Open tundra persist, but arctic features decline—Vegetation changes in the warming Fennoscandian tundra”. *Glob. Chang. Biol.* 23, 3794–3807.

Wieczynski, D. J. et al. (2019). “Climate shapes and shifts functional biodiversity in forests worldwide”. *PNAS* 116, 587–592.

Wild, M. (2012). “Enlightening Global Dimming and Brightening”. *Bull. Am. Meteorol. Soc.* 93, 27–37.

Williams, M. et al. (2006a). “Identifying Differences in Carbon Exchange among Arctic Ecosystem Types”. *Ecosystems* 9, 288–304.

– (2006b). “Identifying Differences in Carbon Exchange among Arctic Ecosystem Types”. *Ecosystems* 9, 288–304.

Wilson, P. J., K. Thompson, and J. G. Hodgson (1999). “Specific leaf area and leaf dry matter content as alternative predictors of plant strategies”. *New Phytol.* 143, 155–162.

Wood, S. N. (2011). “Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models”. *J. R. Stat. Soc.* 73, 3–36.

Wright, I. J. et al. (2004). “The worldwide leaf economics spectrum”. *Nature* 428, 821.

Xue, K. et al. (2016). “Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming”. *Nat. Clim. Chang.* 6, 595–600.

Zhu, Z. et al. (2016). “Greening of the Earth and its drivers”. *Nat. Clim. Chang.* 6, 791–795.

Zobel, M. (1997). “The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence?” *Trends Ecol. Evol.* 12, 266–269.