



UMEÅ UNIVERSITY

Circumpolar impacts of herbivores on Arctic tundra vegetation

Elin Lindén

Department of Ecology and Environmental Science
Umeå 2022

This work is protected by the Swedish Copyright Legislation (Act 1960:729)
Dissertation for PhD
© Elin Lindén, 2022
ISBN: 978-91-7855-795-0 (print)
ISBN: 978-91-7855-796-7 (pdf)
Cover design: Tobias 'Tobbe Pysslare' Johansson
Electronic version available at: <http://umu.diva-portal.org/>
Printed by: Cityprint i Norr AB
Umeå, Sweden 2022

Till mormor

Contents

List of papers.....	ii
Author contributions	iv
Abstract.....	v
Arctic vegetation, climate and herbivores	1
Objectives	5
Methodology	6
Study areas	6
Plant defence - Sampling and sample processing.....	7
Herbivore impacts on vegetation and the use of exclosures..	8
Data analysis	10
Key findings and discussion.....	11
Concluding remarks.....	15
References.....	16
Tack!.....	21

List of papers

This thesis is based on the following four papers, which are referred to in the text by their respective Roman numerals and some which are reprinted with kind permission of the publisher:

- I. *Circum-Arctic distribution of chemical anti-herbivore compounds suggests biome-wide trade-off in defence strategies in arctic shrubs*
E. Lindén, M. t. Beest, I. Aubreu, M. K. Sundqvist...*et al.*¹...J. Olofsson (2022)
In review in *Ecography*
- II. *Large herbivores alter vegetation structure and plant community composition across the Arctic tundra biome*
E. Lindén, M. K. Sundqvist, M. t. Beest, ...*et al.*¹...J. Olofsson (2022)
Manuscript
- III. *Plant species dominance but not light availability drives herbivore effects on species richness in the Arctic*
E. Lindén, M. K. Sundqvist, M. t. Beest, J. Olofsson (2022)
Manuscript
- IV. *Large and small herbivores have strong effects on tundra vegetation in Scandinavia and Alaska*
E. Lindén, Laura Gough, J. Olofsson (2021)
Ecology and Evolution, 00:1-12

¹ Full author list available in attached chapter

Additional published co-authorships not included in the thesis:

Background invertebrate herbivory on dwarf birch (Betula glandulosa-nana complex) increases with temperature and precipitation across the tundra biome

Barrio, Isabel C.; **Lindén, Elin**; Te Beest, Mariska, et al. (2017)

Polar Biology, Vol. 40, (11): 2265-2278

Proportion of fine roots, but not plant biomass allocation below ground, increases with elevation in arctic tundra

Blume-Werry, Gesche; **Lindén, Elin**; Andresen, Lisa et al. (2018)

Journal of Vegetation Science, Vol. 29, (2): 226-235

Responses of tundra plant community carbon flux to experimental warming, dominant species removal and elevation

Sundqvist, Maja K.; Sanders, Nathan J.; Dorrepaal, Ellen; **Lindén, Elin**;

Metcalf, Daniel B.; Newman, Gregory S.; Olofsson, Johan; Wardle, David A.;

Classen, Aimée, T. (2020)

Functional Ecology, Vol. 34, (7): 1497-1506

Author contributions

Chapter I

JO and MtB planned the study and developed the sampling design. The vast majority of co-authors contributed to the field sampling of birch shrubs in different locations, **EL** processed all samples and IA performed the targeted metabolite profiling. **EL** analysed the data and wrote the manuscript with contributions from all co-authors.

Chapter II

EL, JO and MKS planned the study and developed the methodology. As responsible for the field sites, RvdW, BF, TK, EP, ÅØP, LG, RV, OS, HR, RV, NMS, PG and RB contributed substantially in the planning of field work and information about the study sites. Field data was collected by **EL** (Arctic+Fennoscandia) and MKS and JO (Fennoscandia), **EL** performed data analyses and wrote the manuscript with contributions from all co-authors.

Chapter III

EL and JO planned the study, Field data was collected by **EL** (Arctic+Fennoscandia) and MKS and JO (Fennoscandia), **EL** performed data analyses and wrote the manuscript with contributions from JO, MKS and MtB.

Chapter IV

EL and JO planned the study, **EL** collected the field data, performed data analyses and wrote the manuscript with contributions from LG and JO.

Name abbreviations

EL: Elin Lindén, **JO**: Johan Olofsson, **MtB**: Mariska te Beest, **MKS**: Maja K. Sundqvist, **RvdW**: René van der Waal, **BF**: Bruce Forbes, **TK**: Timo Kumpula, **EP**: Eric Post, **ÅØP**: Åshild Ønvik Pedersen, **LG**: Laura Gough, **RV**: Risto Virtanen, **OS**: Otso Suominen, **HR**: Heikki Roininen, **NMS**: Niels-Martin Schmidt, **PG**: Paul Grogan, **RB**: Robert Björk

Abstract

Arctic tundra vegetation provides many ecological services that have implications for the global climate. However, the tundra biome is currently changing in response to increasing temperatures. Herbivores may mitigate some of these responses to warming through their impact on Arctic vegetation. Understanding plant-herbivore interactions is therefore crucial to make better predictions of future Arctic vegetation changes and possible ecological consequences. Most current knowledge on plant-herbivore-interactions in the Arctic comes from local studies that do not allow for large-scale generalisations due to non-comparable methods. Also, existing large-scale studies of herbivory do not cover the tundra biome in a representative way. In this thesis, I used standardised methodology in biome-wide sampling across the Arctic tundra, to uncover how plant-herbivore interactions shape circumpolar vegetation patterns.

I have identified clear biogeographic patterns in plant chemical defence against herbivores that could influence the capacity of herbivores to control warming-driven increases of birch shrubs. I also found that herbivores counteract many effects of climate change on tundra vegetation by reducing vegetation greenness (NDVI), Leaf Area Index (LAI), vegetation density and shrub abundance and thereby mitigate vegetation responses to climate warming. Herbivores also increase species richness across the Arctic by suppressing dominant species but not by increasing light availability. In a detailed study, I show that the effects of large and small herbivores are similar between continents although they vary with habitat type. This thesis advances our understanding of top-down control of herbivores on tundra vegetation and provides important tools to better predict future Arctic vegetation changes.

Keywords

herbivores, grazing, Arctic, circumpolar, tundra, vegetation, plant defence, secondary metabolites, shrub birch, exclosures, vegetation, species diversity

Arctic vegetation, climate and herbivores

Arctic plants are tough. Having adapted to keep up with cold temperatures, short growing seasons, low light-levels and low nutrient availability (Chapin, 1983) they live on the margin to what many of us might think is possible. But the true challenge for arctic plants originates from elsewhere. Arctic vegetation is also exposed to an ongoing climate warming that is more pronounced and occur more rapidly in the Arctic compared to other parts of the world (Post et al., 2019). The increasing temperatures prolong the growing season and promote plant growth (Zhu et al., 2016). This drives Arctic ‘greening’ which can have large impacts on important ecosystem functions (Kimball et al., 2007) and amplify current climate warming (Zhang et al., 2018). Many arctic plant species are limited in their ability to disperse and/or adapt to the new environmental conditions fast enough, which can have different consequences. For example, shrubs are becoming more abundant (Myers-Smith et al., 2011) while species diversity is predicted to decline in the future (Sala et al., 2000), with potentially huge implications for ecosystem function and resilience (Callaghan et al., 2004; Hooper et al., 2005). Additionally, some vegetation responses to climate change could be negative for socioeconomical and cultural values, since the biodiversity and unique characteristics of tundra landscapes are the basis for reindeer management and tourism practices in many northern societies (Horstkotte et al., 2017).

Next to climate, herbivores are important regulators of arctic vegetation. They are present in almost all vegetated areas in the Arctic (Barrio et al., 2016), and can interfere with or even counteract warming-driven vegetation shifts (Bråthen et al., 2017; Christie et al., 2015), greening trends (Yu et al., 2017) and biodiversity loss (Kaarlejärvi et al., 2017).

Shrubs, large herbivores and plant chemical defence

Some recent changes in tundra vegetation, such as increased shrub abundance (‘shrubification’) can have large consequences for important ecosystem functions. Increased shrub cover can lead to a decreased albedo (Sturm, 2005; te Beest et al., 2016), cause altered nutrient cycling and carbon balance in arctic soils (Natali et al., 2011; Weintraub & Schimel, 2005) and change the dynamics of greenhouse gas fluxes (Chapin et al., 2005; Zhang et al., 2018). Large herbivores are, in contrast to Arctic warming, able to suppress shrubs (Sundqvist et al., 2019). At high densities they keep the tundra in a so-called ‘browsing trap’ (Bråthen et al., 2017), meaning that they can inhibit warming-driven shrub expansions. How efficient herbivores suppress shrub abundance is also likely to depend on shrub palatability (Olofsson & Post, 2018).

Although heavily influenced by herbivores, arctic shrubs are not defenceless. In fact, almost all woody vegetation produces chemical anti-herbivore defences (hereafter called chemical defence) with direct deterrent or even toxic effects on herbivores (Bryant et al., 1991). This chemical defence is generally composed of a variety of plant secondary metabolites (PSMs), compounds that, rather than contributing to growth, are produced by plants to survive in their environment (Fraenkel, 1959). Triterpenes and phenolic compounds, such as tannins, are carbon-based PSMs known to protect plants against herbivores and pathogens by decreasing plant palatability (Forbey et al., 2011; McLean et al., 2009; Reichardt et al., 1984).

In tundra ecosystems, shrub birches are widely abundant and divided into two functional groups (resinous and non-resinous) based on differences in their chemical defences. Resinous birches produce a triterpene-based defence and are often considered to be better defended and less sensitive to grazing compared to non-resinous birches which are predominantly defended by condensed tannins (Fig. 1) (Bryant et al. 2014; Graglia et al. 2001). These ‘less well defended shrub’ birches, which dominate Fennoscandia, Iceland and Greenland, are subject to the strongest effect of herbivores (e.g. den Herder & Niemelä, 2003; Olofsson et al., 2009; Post & Pedersen, 2008; Speed et al., 2010). In contrast, herbivore effects are typically lower or absent in areas with ‘better protected’ resinous shrub birches in Canada, Alaska and East Siberia (Crête & Doucet, 1998; Tremblay et al., 2012). This circumpolar variation in shrub response to grazing has been proposed to depend on the variation in defence strategies between non-resinous and resinous birches (Bryant et al., 2014). However, due to lack of solid large-scale data, the variation of plant chemical defence at this spatial scale remains unknown. In **study I** I therefore measured and mapped plant defence composition in tundra birch shrubs across the Arctic tundra.

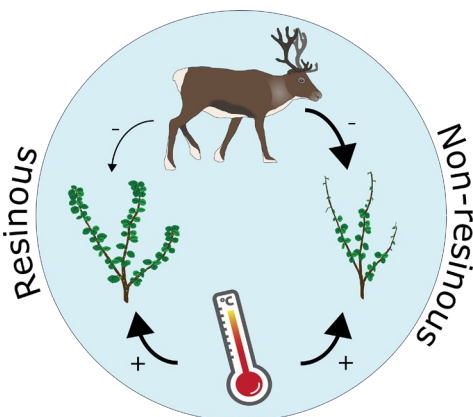


Figure 1. The herbivore control of warming-induced shrub expansion is proposed to vary due to variations in chemical defence strategies. Resinous birches having a stronger defence than non-resinous birch shrubs.

Arctic 'greening'

Increasing shrub abundance is a key change in vegetation that contributes to Arctic 'greening' (Myers-Smith et al., 2011). This process is often studied using satellite-derived spectral measurements translated to vegetation indices such as Normalized Difference Vegetation Index (NDVI), a measure of vegetation greenness which is often used as a proxy for vegetation productivity (Pettorelli et al., 2005). Additionally, Leaf Area Index (LAI), a measure that relates to vegetation density and gives an indication of light availability (Wilhelm et al., 2000) is also commonly used. Both large and small herbivores have been found to affect Arctic 'greening' trends in terrestrial ecosystem models (Yu et al., 2017), in studies comparing NDVI fluctuations with rodent population peaks (Olofsson et al., 2012) and in field experiments (Sundqvist et al., 2019). However, the explanatory power of these vegetation indices and what vegetation changes and properties they link to is currently discussed (Myers-Smith et al., 2020). Also, relating satellite data to vegetation changes at plot level is difficult, if not impossible, due to the substantial miss-match in spatial resolution. In **study II** and **IV**, I therefore examined the circumpolar effects of herbivores on these vegetation properties at plot level, using ground truthed measurements, and connected them to changes in plant community composition.

Large herbivores and plant community composition

In addition to regulating plant biomass and productivity, large herbivores also influence plant community composition (Bernes et al., 2015). This does not only depend on plant palatability as even high-quality, palatable forage plants can be promoted in a grazed vegetation, so long as they are highly tolerant to grazing (Strauss & Agrawal, 1999). Further, herbivores do not only influence the composition of tundra plant communities by selective feeding but also through physical disturbance like destructive trampling (Egelkraut et al. 2020; Tuomi et al. 2020). In addition to their suppression of shrubs (Christie et al., 2015), herbivores typically promote grazing tolerant graminoids at the expense of trampling sensitive mosses and lichens (Gough et al., 2008; van der Wal & Brooker, 2004). Some herbivore-induced vegetation shifts can persist even centuries after the previous grazing pressure has vanished (Egelkraut et al. 2018).

Plant-herbivore interactions in the Arctic are studied at local scale in numerous sites and, typically, effects on several plant functional groups are found (e.g. van der Wal & Brooker, 2004; Gough et al., 2008; Post & Pedersen, 2008; Olofsson et al., 2009). However, when these studies were combined in a systematic meta-analysis, few general herbivore effects could be supported at the circumpolar scale due to methodological differences among studies (Bernes et al., 2015). Currently, the most extensive field study covers 56 exclosure sites across the

Fennoscandian mountains and detected that reindeer presence leads to decreased lichen cover and deciduous shrub abundance, as well as increased nitrogen availability at regional scales (Sundqvist et al., 2019). To better determine the role of herbivore-climate interactions on arctic plant communities and ecosystems, we need to extend this knowledge to obtain a better understanding of herbivore effects on tundra vegetation at the circumpolar level. In study (II), I therefore surveyed experimental herbivore exclosures across the Arctic, using standardized protocols, to explore the large-scale effects of herbivores on Arctic plant communities.

Large herbivores and plant species diversity

Where herbivores graze, they create gaps in the vegetation where new species can establish. By reducing climate-driven increases in vegetation density, grazing animals have the potential to prevent plant species loss, promote rare species occurrence and maintain species diversity (Kaarlejärvi et al., 2017; Post et al., 2022). Species richness is an important vegetation property since a more diverse plant community will typically also contain a larger collection of traits and thus functional diversity (Chapin et al., 2000). Diverse vegetation communities therefore are more resilient to disturbance and environmental changes (Hooper et al., 2005). Tundra plant communities might be especially sensitive to species diversity loss given their limited species pool (Arctic Biodiversity Assessment, 2013), with few functionally substituting species, as well as the strong negative effects from climate change (Sala et al., 2000).

There are essentially two common paradigms regarding the mechanisms explaining how herbivory drives species richness globally. The ‘light paradigm’ proposes that herbivores control species richness by reducing light limitation, i.e. increasing species richness via increased light availability caused by biomass removal, which allows also shade-intolerant species to thrive (Borer et al., 2014). Secondly, the ‘dominance paradigm’ proposes that herbivore-induced shifts in plant species dominance is the best predictor for effects on species diversity (Koerner et al., 2018) since herbivores often target dominant plant species that can outcompete surrounding plants for resources such as light, nutrients, water and space (Olf & Ritchie, 1998). However, these paradigms were predominantly developed in temperate grasslands (Borer et al., 2014; Koerner et al., 2018) and may not apply to a harsh and resource-limited environment such as the Arctic tundra (Chapin, 1983). In **study III**, I therefore tested if herbivore-induced shifts in light availability and species dominance might drive herbivore effects on tundra species richness, to assess to what extent these paradigms hold in the Arctic.

Small herbivores and herbivore diversity

The Tundra is not only impacted by large herbivores. Microtine rodents, such as voles and lemmings, are also key species in arctic ecosystems by influencing plant community composition and serving as food for predators (Legagneux et al., 2012). Their multi-year cyclic population dynamics with alternating high (outbreaks) and low population sizes are well-known phenomena throughout the Arctic (Ehrich et al., 2019). During population peaks, their impact on the vegetation is often stronger than the effect of large herbivores (Petit Bon et al., 2020) and can even be detected from space (Olofsson et al., 2012). Compared to large herbivores, rodents often cause a stronger decline in dwarf shrub abundance (Olofsson et al., 2009), as well as declines in moss and lichen biomass (Johnson et al., 2013; Moen et al., 1993). With their smaller guts that fill up more easily, rodents require nutrient-rich forage and are more sensitive to deterrent plant secondary metabolites (Batzli & Jung, 1980) than large herbivores. However, rodents can also reduce biomass of less palatable plants substantially through physical disturbance from building runways (Olofsson et al., 2012). With a herbivore diversity as low as in the Arctic (Barrio et al., 2016), having multiple herbivore types present can strongly affect Arctic vegetation. A more diverse herbivore composition can target a more diverse assembly of plants since different herbivores target different plants (Olofsson & Post, 2018). In order to understand the different roles of different herbivores in shaping plant communities, we need to separate their relative contributions. **Study IV**, was therefore developed as a detailed study on the relative effects of large versus small herbivores, and compared these effects among four vegetation types on two continents (one low and one high productive site on each continent).

Objectives

The overall aim of this thesis is to uncover large-scale impacts of herbivores on arctic tundra vegetation and describe how plant-herbivore interactions shape circumpolar vegetation patterns. By using standardised methods and generating comparable data from many locations across the Arctic tundra biome, I have specifically addressed the following research questions:

1. How does plant chemical defense against herbivores vary across the Arctic tundra? **(I)**
2. What are the general, large-scale effects of large herbivores on key vegetation properties (NDVI, LAI, vegetation density), community composition and species richness across the Arctic? **(II-IV)**
3. What consequences does the diversity of herbivores have for their effects on tundra vegetation? **(IV)**

Methodology

Study areas

My studies cover circumpolar tundra vegetation across the Arctic. **Study I** covers 128 sampling sites in 44 locations at latitudes between 47.3°N and 74.5°N (Fig. 2), that were all selected based on shrub birch presence. Given the wide spatial distribution of sampling sites, the study covers a wide range of environmental conditions. Annual precipitation ranges between 153-1750 mm, mean annual temperature ranges between -15.2-4.1°C, mean mid-growing season temperature (July) ranges between 2.7-16.1°C.

Study II and **III** cover 28 locations across the circumpolar Arctic, from 61°N to 78.9°N in latitude, where exclosures² keep out large herbivores such as reindeer and muskoxen (Fig 2). A total of 95 exclosures and paired grazed controls (i.e. 190 plots) were included. By the time of inventory, the exclosures were between 9-50 years old. The locations cover long gradients in climate and productivity (NDVI 0.552-0.925) and represent common vegetation types in the Arctic tundra. In 10 locations, the vegetation is graminoid and/or forb dominated, two of these locations are wet, one is dry and seven are intermediate or moist. Out of 15

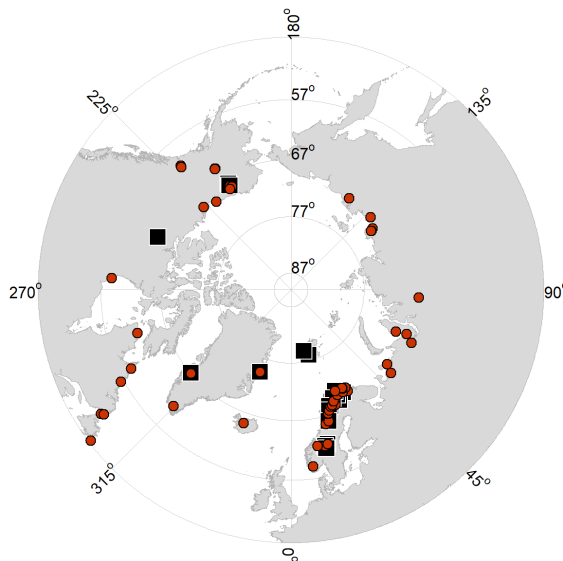


Figure 2. A total of 128 shrub birch samples was used to analyse circumpolar variation in plant chemical defence (**study I**, red circles). 28 exclosure sites were inventoried to study herbivore effects on tundra vegetation (**study II-IV**, black squares).

² The experimental methodology of herbivore exclosures is further explained later in this section

locations dominated by deciduous or evergreen shrubs, one is moist, 10 are dry and four have intermediate moisture levels. Three locations were characterised as dry lichen heath. All inventories of exclosures for this thesis took place in the summers of 2014 and 2017-2019. Data collected in 2014 is a part of previously published study from the Fennoscandian mountains (Sundqvist et al. 2019). I have used the nine tundra sites from Sundqvist et al. (2019) as a basis for our circumpolar database and, using the same field protocol, I extended the database with three additional Fennoscandian sites, six Arctic sites outside of Fennoscandia and updated data from Scandinavian Abisko and Joatka. These studies do not include any exclosure sites in Russia, due to a lack of exclosures of substantial size and/or age. **Study IV** includes two Scandinavian and two Alaskan sites with both large and small herbivore (rodent) exclosures. In both locations I used one low and one high productivity site. The Scandinavian locations represent moist (*Empetrum*) heath and dry lichen heath. The two Alaskan locations represent sedge-dominated moist acidic tundra (tussock tundra) and dry lichen heath.

Main herbivores

The most common large herbivores across all study sites are reindeer or wild caribou (*Rangifer* sp.). The exceptions are Zackenberg in eastern Greenland where muskoxen (*Ovibos moschatus*) are the main herbivores (included in **I-III**) and in Audkuluheidi, Iceland where mainly sheep graze (included in **I**). Muskoxen also occur in other parts of Greenland, North America and Siberia, and moose (*Alces alces*) might occasionally visit some North American and Scandinavian sites. Many sites also accommodate microtine rodents such as grey-sided voles (*Myodes rufocanus*) and Norwegian lemmings (*Lemmus lemmus*) in Fennoscandia and tundra voles (*Microtus oeconomus*) and brown lemmings (*Spermophilus parryi*) in North America. Herbivorous insects are also present in the Arctic although no large outbreaks were recorded at the sites during sampling and their background herbivory is known to be low in the tundra (Barrio et al. 2017).

Plant defence - Sampling and sample processing

In **study I**, me and my co-authors sampled resinous (*Betula glandulosa*, *Betula nana* ssp. *exilis*) and non-resinous dwarf birch (*Betula nana* ssp. *nana*, *Betula pumila*) across the Arctic. From each of the 128 sites (~10 m radius), 10 random individuals were selected. From these we sampled 50 random short-shoot leaves (leaf rosettes along the stem with leaves of the same age; n=500 per site), and 10 random long-shoots (twigs and leaves representing the current annual growth; n=100 per site). All samples were air-dried in the field and further oven-dried when they arrived to the lab.

Measuring Plant Secondary Metabolites

Modern analytical techniques and refined extraction methodologies make it possible to quantify a vast number of secondary metabolites in a single analysis with substantial resolution and accuracy. In **study I**, we measured metabolites using an untargeted metabolomics analysis by liquid chromatography - mass spectrometry (LC-MS) followed by metabolite identification. We used a targeted approach to process the MS files focusing on secondary metabolite classes previously reported to be involved in plant chemical defence: Triterpenes, condensed tannins, hydrolysable tannins, flavonoids and chlorogenic acid. We also found complex tannins, a group of tannins that consists of condensed and hydrolysable tannin units held together but rarely considered in ecological plant defence studies.

Other plant palatability characteristics measured

To explore if there are plant characteristics that can be used to determine the composition of chemical defence in shrub birch, I measured additional physiological plant properties. I measured the resin gland density on the stems of long shoots, a proxy³ of Specific Leaf Area (leaf thickness) and also leaf nitrogen and carbon content. I also measured the *In-Vitro* digestibility of birch leaves to see how different defence compounds might limit how well herbivores digest the leaves they eat. Here, '*In-Vitro*' means that I studied the digestion process outside of the animal where it usually occurs. A detailed description of the methodology for these measures can be found in chapter **I**.

Herbivore impacts on vegetation and the use of exclosures

To study the effects of herbivores on vegetation, one of the most commonly used methods is, ironically, to build fences to remove the herbivores from the system, known as exclosures (Fig. 3). Since almost all ecosystems, the Arctic included, have been naturally grazed for a long time, it is impossible to find ungrazed vegetation to use as a reference. Instead, we implement a so-called 'removal treatment', where we use the grazed natural condition as our reference and observe what happens if the influence of herbivores is removed. What we measure with this experimental design the recovery effect following removal of herbivores from an already grazed system. This effect is then most often translated into which vegetation properties herbivores *maintain* through their presence (the properties that change when herbivores are removed) and is what we describe as 'the effect of herbivores'.

³ Specific Leaf Area is normally measured as [fresh leaf area/dry weight] but we worked with dried leaf samples and estimated SLA as [dry leaf area/dry weight].

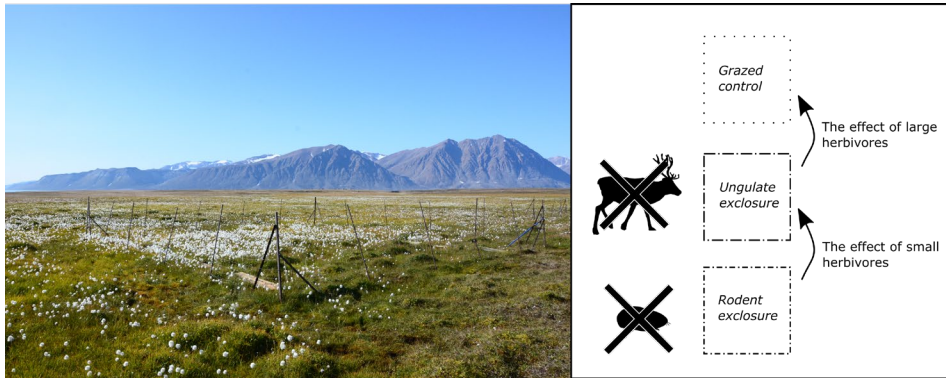


Figure 3. To the left, a large herbivore enclosure in Zackenberg valley, eastern Greenland. To the right, a schematic figure of an experimental setup for enclosure studies.

In experimental setups where the effects of both large and small herbivores are studied (**IV**) there are three treatment levels. Grazed control plots where all herbivores can access the vegetation, large mesh enclosures that keep out large herbivores but allow access for small herbivores and small mesh enclosures that keep all mammalian herbivores away from the vegetation (Fig. 3). The effect of small herbivores is measured as the difference between small and large mesh enclosures. The effect of large herbivores is measured as the difference between large mesh enclosures and grazed controls. It is physically impossible to fence out small herbivores while allowing large herbivores access, so the effect of large herbivores can therefore only be measured as their effect given the presence of other herbivores. This is the case also in experiments where only large herbivore enclosures are used (**II**, **III**). It is however important to remember that these two treatment level experiments (grazed/ungrazed) measure the effect of excluding large herbivores rather than the effect of allowing of small herbivore presence.

Plant community composition

I recorded plant community composition using the point intercept method (Goodall DW, 1952) in all enclosures and controls (**II-IV**). I lowered a total of 50 pins through the vegetation in all subplots (50 cm wide rows of 10 vertical pins every 10 cm) and counted plant-pin intercepts. All hits on field layer plants (forbs, shrubs, graminoids etc.) was recorded, but for ground hits (mosses, lichens, bare soil etc.) we only recorded the uppermost pin-hit.

Other measured and calculated vegetation properties

From the point intercept data, I calculated species dominance and species diversity (**III-IV**). Species dominance was calculated as Berg-Parker dominance index, a dominance measure based on proportional abundance of the most

abundant species (**III**). I calculated species diversity as both species richness, i.e. number of species (**III**), and Simpson diversity index (**IV**). I also used total pin hits on vascular plants as a measure of vegetation density (**II, IV**). In the field, I measured standard vegetation measures such as Normalized Different Vegetation Index (NDVI) (**II, IV**) and Leaf Area Index (LAI) (**II-IV**) in each subplot.

Soil nutrients

I collected soil samples in exclosures and grazed controls using a soil corer with a 2.5 cm diameter (**II**). I collected the organic soil layer and pooled 10 soil samples per plot (exclosure and control). All samples were kept cool until they could be frozen. In lab, the soil samples were thawed and homogenised through a 4 mm sieve. I measured soil nutrients by dissolving 5 gr of fresh soil in 80 ml of 1 M KCl solution, quantified the extractable NH_4^+ , NO_3 and PO_4 by colorimetry and calculated their concentrations as mg/g dry soil weight.

Herbivore density

To estimate herbivore density at each location (**II** and **III**), I counted reindeer/muskoxen pellet groups in 50 m x 1 m (in 2014) or 30 m x 1 m (in 2017-2019) transects outside of each exclosure. The pellets counts were then standardised per square meter (pellets/m²) and used as a herbivore density index. In some moist and more productive sites, transects were established in dry (heath) areas nearby instead, since pellets decompose fast in such habitats (Skarin, 2008).

Data analysis

I analysed most variable relationships using Linear Mixed Effects models (LME's) with random factors and co-variables when needed (**I-IV**). Composition data such as chemical defense composition (**I**) and plant community composition (**IV**) was analysed using Non-metric Multidimensional Scaling ordination methods (NMDS's).

Key findings and discussion

This thesis presents how plant-herbivore interactions shape large-scale vegetation patterns across the Arctic tundra. I show that there are biogeographic patterns in circumpolar chemical defence in tundra birch shrubs. These patterns might affect how herbivores can control Arctic shrubification (**I**). I also show that herbivores reduce key vegetation properties such as vegetation greenness (NDVI), Leaf Area Index (LAI) and vegetation density across the Arctic (**II, IV**). These effects depended on site productivity (**II, IV**) and in some habitats they can be driven by small herbivores (**IV**). Both large and small herbivores increased species diversity by suppressing dominant species or growth forms (**III, IV**) although this was not connected to increased light availability (**III**).

Clear biogeographic patterns exist in circumpolar plant defence...

It is proposed that variations in Arctic shrubification patterns can depend on variation in plant chemical defence towards herbivores (Bryant et al., 2014). I mapped the circumpolar variation of plant defence composition in tundra birch shrubs and found clear biographic patterns (**I**). On average, triperpenes were mainly found in resinous birches and correlated to their high resin gland density, while the tannin concentrations were greater in non-resinous birches, supporting parts of the hypothesis presented by Bryant et al. (2014). This suggests a trade-off between a triterpene-dominated and tannin-dominated defence across the arctic tundra. Such a trade-off has been proposed before in a two-site comparison between Scandinavia and Alaska (Graglia et al., 2001), and I can now show that it applies to the whole tundra biome. I discovered that complex tannins are likely to play an active role in tannin-dominated defences. Little is known of the ecological meaning of complex tannins but they were the only compound group with a negative effect on *In-Vitro* digestibility in this study and are expected to have deterrent effects on herbivores based on their structural similarities to both condensed and hydrolysable tannins.

... but there are limitations to what this can tell us about Arctic shrubification

I found that triterpene and tannin concentrations can vary substantially within both resinous and non-resinous birches (**I**). Despite being densely covered in resin glands, some resinous birches had a tannin-dominated defence comparable to the one of the non-resinous species, *B. pumila*. This means that although chemical defence in birch shrubs can be generalised to a certain extent across the Arctic tundra, there is still variation that crude groupings do not explain. Characteristics other than chemical defence also determine plant palatability and to what extent plants are consumed, such as alternative food resources (Barbosa

et al., 2009) as well as herbivore type (Barbehenn et al., 2011) and density. There are thus limitations in the extent that these groupings can be used to predict future shrubification patterns. However, detailed chemical studies like **study I**, contribute new and important tools for better understanding top-down control of warming-driven shrubification.

Herbivores still shape circumpolar tundra vegetation

There are more physiological characteristics than plant defence that influence how vegetation responds to herbivory. Multiple effects of herbivores on plant community composition have been found in numerous Arctic studies, but few effects hold for broad generalisations across studies and/or sites (Bernes et al., 2015). I generated comparable data from experimental herbivore exclosures across the Arctic tundra and found that herbivores reduce key vegetation properties such as vegetation greenness (NDVI), Leaf Area Index (LAI) and vegetation density across the Arctic (**II**, **IV**). These effects depended on site productivity (**II**, **IV**) and in some habitats they can be driven by small herbivores (**IV**).

I found the strongest reduction of NDVI by herbivores in sites with low productivity, while vegetation density was most strongly reduced in sites with high productivity (Fig. 4; **II**, **IV**). Large herbivores reduced LAI independent of site productivity (Fig 4.; **II**) while I found effects of small herbivores mainly in one of the more productive habitats (**IV**). The reduction of NDVI by herbivores at low productivity sites as well as the general reduction of LAI (**II**, **IV**) were of the same magnitude as observed warming-driven increases of NDVI (Xue et al., 2021) and LAI (Mao et al., 2016). At least for LAI, these changes are considered sufficient to affect the global temperature (Zhang et al., 2018.) suggesting that the effect of herbivores on arctic vegetation might even have global implications. The

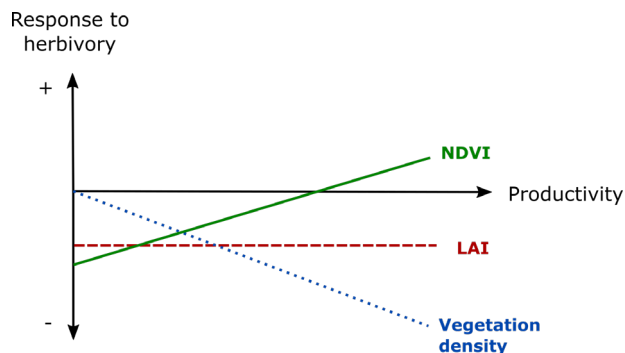


Figure 4. Graphical representation of how NDVI, LAI and vegetation density respond to herbivory along a gradient in productivity.

productivity dependency in the herbivore effects on NDVI, LAI and vegetation density was partly linked to contrasting responses in plant functional group abundance along the productivity gradient.

In productive sites, I found that large herbivores suppressed graminoid and tall deciduous shrub abundance, which reduced vegetation density and LAI (**II**). These vegetation changes were, however, not detected by NDVI. Instead I found that the effect of herbivores on NDVI was weaker at sites with higher productivity. This can at least partly be explained by saturation of NDVI in highly productive plots (Pettorelli et al., 2005). NDVI saturation is a phenomenon that occurs when the vegetation cover is so high that a further increase in vegetation cover does not result in a greener surface. Therefore, I show that NDVI does not detect increased shrub abundance in productive arctic habitats where this vegetation change is most likely to occur (Tape et al., 2012). This adds to the current discussion on limitations in the use of vegetation indices (Myers-Smith et al., 2020). In addition to the productivity dependency, I also found indications that small herbivores cause declines in NDVI, LAI and vegetation density in habitats dominated by plants that are less palatable to large herbivores, such as evergreen shrubs and sedges (**IV**). The reduction of NDVI and vegetation density in my studies does, however, confirm what has been found in local (Post & Pedersen, 2008) and regional studies (Manseau et al 1999; Sundqvist et al., 2019).

Species richness depends on species dominance, but not light availability

I found that herbivores decrease species richness in low productivity sites and increase species richness in high productivity sites. They promote species richness by suppressing species dominance but not by increasing the light availability (Fig. 5; **III**). In contrast to what is found in temperate grasslands across the world (Borer et al., 2014), I found no correlation between increased

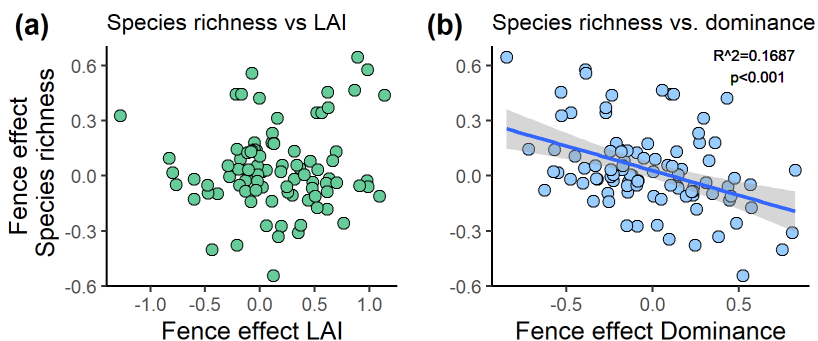


Figure 5. Relationship between the effect of herbivore exclusion on species richness and (a) light availability (LAI) and (b) plant species dominance.

light availability due to herbivory and their impact on species richness (Fig. 5a). In other words, the ‘light paradigm’ does not seem to extend to the Arctic tundra. This might be because arctic plants are already adjusted to low light levels (Chapin, 1983), and therefore less sensitive to light limitation. Alternatively, many arctic vegetation types might not be productive enough to reach light limitation. While the ‘light paradigm’ does not hold for the Arctic, the ‘dominance paradigm’ does. I found that negative herbivore effects on species dominance correlated with positive effects on species richness (Fig. 5b), which is in line with what is found in large-scale studies in temperate systems (Koerner et al. 2018). I also found indications that in some habitats this is probably driven by small rather than large herbivores (**IV**). By reducing species dominance, herbivores also change plant-plant interactions, such as competition, opening up ecological niche space for other, less competitive, species (Grime, 1973). My study covers a wide range of tundra vegetation types and the dominant plant species vary among sites. This suggests that herbivores promote species richness by suppressing species dominance independent of dominant species identity.

Large and small herbivores affect tundra vegetation in a similar, yet context-dependent way

Lastly, I compared the effects of large and small herbivores among sites with low- and high-productivity habitats in Scandinavia and Alaska. I found that the general effect of herbivores on the plant communities varied more between contrasting habitats within continents than between continents (**IV**). Suggesting that the effect of herbivores depend more on vegetation type than biogeographical context. I also found that the strength of the herbivore effect and which herbivore type causing these effects differed across habitats (**IV**). Large herbivores, but not small herbivores⁴, reduced plant height to the same magnitude as plant height increase due to climate change (Bjorkman et al. 2018). Further, in these habitats small herbivores increased species diversity, while large herbivores didn’t. A likely explanation is that the studied habitats are dominated by plant species of low palatability, especially for large herbivores (reindeer). The small herbivores instead reduced the abundance of these species through physical disturbance by building burrows and runways. These results provide further support for the importance of herbivore diversity in Arctic ecosystems (Olofsson & Post, 2018) since they affect different aspects of the tundra vegetation.

⁴ This is perhaps not so surprising since there are obvious physiological limitations for rodents to affect plant height.

Concluding remarks

This thesis contributes to understanding of top-down control by herbivores on Arctic tundra vegetation. It shows that effects of herbivores are fairly similar across the entire tundra biome, but also that there are biogeographic patterns in plant chemistry that potentially influences some of these effects. This thesis also brings to light many novel questions about the regulation of Arctic tundra vegetation.

For example, the ecological importance of complex tannins and variations in plant defence, still remain uncertain and need to be addressed. There is also a need for a better understanding of the processes driving variation in plant chemical defence at larger spatial scales. I also think it is important to obtain a more mechanistic understanding of the interaction between herbivores and species dominance, since this relationship seems to be crucial for the fate of Arctic species richness.

In my work, I have found several impacts of herbivores on plant community composition at circumpolar scales that were not detected in previous research. This clearly shows that gathering comparable data using standardised methodology is key in order to understand what drives large-scale vegetation patterns. Broad scientific collaborations and/or joint sampling efforts are crucial in order to achieve this. In the end, me and my co-authors has proven that "Together, we can do it!".

Acknowledgement

I want to give special thanks to Tim Horstkotte and Sam Cook for invaluable feedback in the writing of this thesis summary. I also thank Johan Olofsson, Maja Sundqvist and Mariska te Beest for proofreading. The work in this thesis was mainly supported by the Swedish research council grant #2017-04515 and Swedish Research Council Formas grant #2015-109 to Johan Olofsson. It was also funded by the following grants and stipends to Elin Lindén; INTERACT Transnational Action grant funded by the US National Science Foundation via Toolik Field station and stipends from Gunnar och Ruth Björkmans fond för norrländsk botanisk forskning, J C Kempes Minnes Stipendiefond and Stiftelsen Ymer-80.

References

- Arctic Biodiversity Assessment (2013). Arctic Biodiversity Assessment - Status and trends in Arctic biodiversity. Publ. Conservation of Arctic Flora and Fauna, Audkureyri
- Bakker, E. S., Ritchie, M. E., Olf, H., Milchunas, D. G., & Knops, J. M. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, 9(7), 780–788. <https://doi.org/10.1111/J.1461-0248.2006.00925.X>
- Barbehenn, R.V & Constabel, C.P. (2011) Tannins in plant-herbivore interactions. *Phytochemistry*, 72, 1551-1565. <https://doi.org/10.1016/j.phytochem.2011.01.040>
- Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational Resistance and Associational Susceptibility: Having Right or Wrong Neighbors. *Annual Review of Ecology, Evolution and Systematics*, 40, 1–20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>
- Barrio, I.C., Lindén, E., te Beest, M., Olofsson, J., Rocha, A., Soininen, E.M., *et al.* (2017) Background invertebrate herbivory on dwarf birch (*Betula glandulosa-nana* complex) increases with temperature and precipitation across the tundra biome. *Polar Biology*, 40, 2265-2278. <https://doi.org/10.1007/s00300-017-2139-7>
- Barrio, I. C., Bueno, C. G., Gartzia, M., Soininen, E. M., *et al.* (2016). Biotic interactions mediate patterns of herbivore diversity in the Arctic. *Global Ecology and Biogeography*. <https://doi.org/10.1111/geb.12470>
- Batzli, G. O., & Jung, H.-J. G. (1980). Nutritional Ecology of Microtine Rodents: Resource Utilization near Atkasook, Alaska. *Arctic and Alpine Research*. <https://doi.org/10.2307/1550496>
- Bernes, C., Bråthen, K. A., Forbes, B. C., Speed, J. D. M., & Moen, J. (2015). What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. In *Environmental Evidence*. <https://doi.org/10.1186/s13750-014-0030-3>
- Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., *et al.* (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*. <https://doi.org/10.1038/nature13144>
- Bråthen, K. A., Ravolainen, V. T., Stien, A., Tveraa, T., & Ims, R. A. (2017). Rangifer management controls a climate-sensitive tundra state transition. *Ecological Applications*. <https://doi.org/10.1002/eap.1618>
- Bryant, J. P., Joly, K., Chapin, F. S., DeAngelis, D. L., & Kielland, K. (2014). Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? *Ecography*, 37(3), 204–211.
- Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P., & du Toit, J. T. (1991). Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, 22, 431–446. <https://doi.org/10.1146/annurev.es.22.110191.002243>
- Callaghan, T. v., Björn, L. O., Chernov, Y., Chapin, T., *et al.* (2004). Biodiversity, distributions and adaptations of Arctic species in the context of environmental change. *Ambio*, 33(7), 404–417. <https://doi.org/10.1579/0044-7447-33.7.404>
- Chapin, F. S. (1983). Direct and Indirect Effects of Temperature on Arctic Plants. *Polar Biol*, 2, 47–52.

- Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., *et al.* (2005). Role of land-surface changes in arctic summer warming. *Science*, 310(5748), 657–660. <https://doi.org/10.1126/science.1117368>
- Christie, K. S., Bryant, J. P., Gough, L., Ravolainen, V. T., Ruess, R. W., & Tape, K. D. (2015). The Role of Vertebrate Herbivores in Regulating Shrub Expansion in the Arctic: A Synthesis. *BioScience*, 65(12), 1123–1133. <https://doi.org/10.1093/biosci/biv137>
- Crête, M., & Doucet, G. J. (1998). Persistent suppression in dwarf birch after release from heavy summer browsing by Caribou. *Arctic and Alpine Research*, 30(2), 126–132. <https://doi.org/10.2307/1552127>
- Egelkraut, D. D., Barthelemy, H., Olofsson, J. (2020). Reindeer trampling promotes vegetation changes in tundra heathlands: Results from a simulation experiment. *Journal of Vegetation Science*. 476-486.
- Egelkraut, D.D. (2017). Long-lasting ecological legacies of reindeer on tundra vegetation. Doctoral thesis, Umeå university.
- Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., *et al.* (2019). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*. <https://doi.org/10.1007/s13280-019-01198-7>
- Forbey, J. S., Pu, X., Xu, D., Kielland, K., & Bryant, J. (2011). Inhibition of Snowshoe Hare Succinate Dehydrogenase Activity as a Mechanism of Deterrence for Papyriferic Acid in Birch. *Journal of Chemical Ecology*, 37(12), 1285–1293. <https://doi.org/10.1007/s10886-011-0039-9>
- Fraenkel, G. S. (1959). The Raison d'Être Substances of Secondary Plant. *Science*, 129(3361), 1466–1470.
- Goodall DW. (1952). Some Considerations in the Use of Point Quadrats for the Analysis of Vegetation. *Australian Journal of Biological Sciences*.
- Gough, L., Shrestha, K., Johnson, D. R., & Moon, B. (2008). Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra. *Arctic, Antarctic, and Alpine Research*. [https://doi.org/10.1657/1523-0430\(06-087\)\[GOUGH\]2.o.CO;2](https://doi.org/10.1657/1523-0430(06-087)[GOUGH]2.o.CO;2)
- Graglia, E., Julkunen-Tiitto, R., Shaver, G. R., Schmidt, I. K., Jonasson, S., & Michelsen, A. (2001). Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. *New Phytologist*, 151(1), 227–236.
- Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, 242(5396), 344–347. <https://doi.org/10.1038/242344A0>
- Herder, M. den, & Niemelä, P. (2003). Effects of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow. *Rangifer*, 23(1), 3–12. <https://doi.org/10.7557/2.23.1.308>
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. <https://doi.org/10.1890/04-0922>
- Horstkotte, T., Utsi, T. A., Larsson-Blind, Å., Burgess, P., Johansen, B., Käyhkö, J., ... & Forbes, B. C. (2017). Human–animal agency in reindeer management: Sámi herders’ perspectives on vegetation dynamics under climate change. *Ecosphere*, 8(9), e01931.

- Johnson, D. D. P., Blumstein, D. T., Fowler, J. H., & Haselton, M. G. (2013). The evolution of error: Error management, cognitive constraints, and adaptive decision-making biases. *Trends in Ecology and Evolution*, 28(8), 474–481. <http://dx.doi.org/10.1016/j.tree.2013.05.014>
- Julkunen-Tiitto, R., Rousi, M., Bryant, R. J., Sorsa, S., Keinänen, M., & Sikanen, H. (1996). Chemical diversity of several Betulaceae species: comparison of phenolics and terpenoids in northern birch stems. 16–22.
- Kaarlejärvi, E., Eskelinen, A., & Olofsson, J. (2017). Herbivores rescue diversity in warming tundra by modulating trait-dependent species losses and gains. *Nature Communications*, 8(1). <http://dx.doi.org/10.1038/s41467-017-00554-z>
- Kimball, J. S., Zhao, M., McGuire, A. D., Heinsch, F. A., Clein, J., Calef, M., Jolly, W. M., Kang, S., Euskirchen, S. E., McDonald, K. C., & Running, S. W. (2007). Recent Climate-Driven Increases in Vegetation Productivity for the Western Arctic: Evidence of an Acceleration of the Northern Terrestrial Carbon Cycle. *Earth Interactions*, 11(4), 1–30. <https://doi.org/10.1175/EI180.1>
- Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., Knapp, A. K., Lemoine, N. P., Forrester, E. J., Eby, S., Thompson, D. I., Aguado-Santacruz, G. A., Anderson, J. P., Anderson, T. M., Angassa, A., Bagchi, S., Bakker, E. S., Bastin, G., Baur, L. E., ... Zelikova, T. J. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, 2. <https://doi.org/10.1038/s41559-018-0696-y>
- Legagneux, P., Gauthier, G., Berteaux, D., Bêty, J., Cadieux, M. C., Bilodeau, F., Bolduc, E., Mckinnon, L., Tarroux, A., Therrien, J. F., Morissette, L., & Krebs, C. J. (2012). Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology*. <https://doi.org/10.1890/11-1973.1>
- Mao, J., Ribes, A., Yan, B., Shi, X., Thornton, P. E., Séférian, R., Ciais, P., Myneni, R. B., Douville, H., Piao, S., Zhu, Z., Dickinson, R. E., Dai, Y., Ricciuto, D. M., Jin, M., Hooman, F. M., Wang, B., Huang, M., & Lian, X. (2016). Human-induced greening of the northern extratropical land surface. <https://doi.org/10.1038/NCLIMATE3056>
- McLean, S., Richards, S. M., Cover, S. L., Brandon, S., Davies, N. W., Bryant, J. P., & Clausen, T. P. (2009). Papyriferic acid, an antifeedant triterpene from birch trees, inhibits succinate dehydrogenase from liver mitochondria. *Journal of Chemical Ecology*, 10, 1252–1261. <https://doi.org/10.1007/s10886-009-9702-9>
- Moen, J., Lundberg, P. A., & Oksanen, L. (1993). Lemming grazing on snowbed vegetation during a population peak, northern Norway. *Arctic & Alpine Research*, 25(2), 130–135. <https://doi.org/10.2307/1551549>
- Myers-Smith, I. H., Forbes, B. C., Wilmsking, M., Hallinger, *et al.* (2011). Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters*, 6(4). <https://doi.org/10.1088/1748-9326/6/4/045509>
- Myers-Smith, I. H., Kerby, J. T., Phoenix, G. K., Bjerke, J. W., Epstein, H. E., Assmann, J. J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P. S. A., Berner, L. T., Bhatt, U. S., Bjorkman, A. D., Blok, D., Bryn, A., Christiansen, C. T., Cornelissen, J. H. C., Cunliffe, A. M., Elmendorf, S. C., ... Wipf, S. (2020). Complexity revealed in the greening of the Arctic. In *Nature Climate Change*. <https://doi.org/10.1038/s41558-019-0688-1>
- Natali, S. M., Schuur, E. A. G., Trucco, C., Hicks Pries, C. E., Crummer, K. G., & Baron Lopez, A. F. (2011). Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan

- tundra. *Global Change Biology*, 17(3), 1394–1407. <https://doi.org/10.1111/j.1365-2486.2010.02303.x>
- Olf, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. In *Trends in Ecology and Evolution*. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P. E., Oksanen, T., & Suominen, O. (2009). Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, 15(11), 2681–2693.
- Olofsson, J., & Post, E. (2018). Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. In *Philosophical Transactions of the Royal Society B: Biological Sciences*. <https://doi.org/10.1098/rstb.2017.0437>
- Olofsson, J., Tommervik, H., & Callaghan, T. v. (2012). Vole and lemming activity observed from space. *Nature Climate Change*. <https://doi.org/10.1038/nclimate1537>
- Petit Bon, M., Gunnarsdóttir Inga, K., Jónsdóttir, I. S., Utsi, T. A., Soininen, E. M., & Bråthen, K. A. (2020). Interactions between winter and summer herbivory affect spatial and temporal plant nutrient dynamics in tundra grassland communities. *Oikos*, 129(8), 1229–1242. <https://doi.org/10.1111/oik.07074>
- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology and Evolution*, 20(9), 503–510. <https://doi.org/10.1016/J.TREE.2005.05.011>
- Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., Iler, A., Kerby, J. T., Laidre, K. L., Mann, M. E., Olofsson, J., Stroeve, J. C., Ulmer, F., Virginia, R. A., & Wang, M. (2019). The polar regions in a 2°C warmer world. *Science Advances*, 5(12). <https://doi.org/10.1126/SCIADV.AAW9883/ASSET/3FA8FAD3-21FF-4F94-A5D4-390EB60B9173/ASSETS/GRAPHIC/AAW9883-F7.JPEG>
- Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, 105(34), 12353–12358. <http://www.pnas.org/cgi/doi/10.1073/pnas.0802421105>
- Post, E., Pedersen, C., & Watts, D. A. (2022). Large herbivores facilitate the persistence of rare taxa under tundra warming. *Scientific Reports*, 12(1), 1292. <https://doi.org/10.1038/S41598-022-05388-4>
- Reichardt, P. B., Bryant, J. P., Clausen, T. P., & Wieland, G. D. (1984). Defense of winter-dormant Alaska paper birch against snowshoe hares. *Oecologia*, 65(1), 58–69. <https://doi.org/10.1007/BF00384463>
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., *et al.* (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774. <https://doi.org/10.1126/SCIENCE.287.5459.1770>
- Skarin, A. (2008). Decay rate of reindeer pellet-groups. *Rangifer*, 28(1), 47. <https://doi.org/10.7557/2.28.1.151>
- Speed, J. D. M., Cooper, E. J., Jónsdóttir, I. S., van der Wal, R., & Woodin, S. J. (2010). Plant community properties predict vegetation resilience to herbivore disturbance in the Arctic. *Journal of Ecology*, 98(5), 1002–1013.
- Strauss, S. Y., & Agrawal, A. A. (1999). The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution*, 14(5), 179–185.

- Stuart, F., Iii, C., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., & Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405: 234-242
- Sturm, M. (2005). Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research*, 110(G1). <https://doi.org/10.1029/2005jg000013>
- Sundqvist, M. K., Moen, J., Björk, R. G., Vowles, T., Kytöviita, M. M., Parsons, M. A., & Olofsson, J. (2019). Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.13201>
- Tape, K. D., Hallinger, M., Welker, J. M., & Ruess, R. W. (n.d.). Landscape Heterogeneity of Shrub Expansion in Arctic Alaska. <https://doi.org/10.1007/s10021-012-9540-4>
- Te Beest, M., Sitters, J., Olofsson, J. (2016). Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environmental research letters*, 11: 125013. <http://doi.org/10.1088/1748-9326/aa5128>
- Tremblay, B., Lévesque, E., & Boudreau, S. (2012). Recent expansion of erect shrubs in the Low Arctic: Evidence from Eastern Nunavik. *Environmental Research Letters*, 7. <https://doi.org/10.1088/1748-9326/7/3/035501>
- Tuomi, M., Väisänen, M., Yläne, H., Brearley, F.Q., Barrio, I.C. *et al.* (2020). Stomping in scilence: Conceptualizing trampling effects o soils in polar tundra. *Functional Ecology*. 35:306-317. <https://doi.org/10.1111/1365-2435.13719>
- van der Wal, R., Brooker, R.W. (2004). Mosses mediate grazer impacts on grass abundance in Arctic ecosystems. *Functional Ecology*, 18: 77-86. Stable URL: <https://www.jstor.org/stable/3599008>
- Weintraub, M. N., & Schimel, J. P. (2005). Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *BioScience*, 55(5): 408–415. [https://doi.org/10.1641/0006-3568\(2005\)055\[0408:NCATSO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0408:NCATSO]2.0.CO;2)
- Wilhelm, W. W., Ruwe, K., & Schlemmer, M. R. (2000). Comparison of three leaf area index meters in a corn canopy. *Crop Science*, 40(4), 1179–1183. <https://doi.org/10.2135/CROPSCI2000.4041179X>
- Xue, S. Y., Xu, H. Y., Mu, C. C., Wu, T. H., Li, W. P., Zhang, W. X., Streletskaia, I., Grebenets, V., Sokratov, S., Kizyakov, A., & Wu, X. D. (2021). Changes in different land cover areas and NDVI values in northern latitudes from 1982 to 2015. *Advances in Climate Change Research*, 12(4), 456–465. <https://doi.org/10.1016/J.ACCRE.2021.04.003>
- Yu, Q., Epstein, H., Engstrom, R., & Walker, D. (2017). Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. *Global Change Biology*, 23(9), 3895–3907. <https://doi.org/10.1111/gcb.13632>
- Zhang, W., Miller, P. A., Jansson, C., Samuelsson, P., Mao, J., & Smith, B. (n.d.). Self-Amplifying Feedbacks Accelerate Greening and Warming of the Arctic. <https://doi.org/10.1029/2018GL077830>
- Zhu, Z., Piao, S., Myneni, R. B., Huang, M., Zeng, Z., Canadell, J. G., Ciais, P., Sitch, S., Friedlingstein, P., Arneeth, A., Cao, C., Cheng, L., Kato, E., Koven, C., Li, Y., Lian, X., Liu, Y., Liu, R., Mao, J., ... Zeng, N. (2016). Greening of the Earth and its drivers. *Nature Climate Change*, 6(8), 791–795. <https://doi.org/10.1038/NCLIMATE3004>

Tack!

I can honestly say that I am incredibly proud of all the hard work behind this thesis. My PhD project has taken me on adventures I could never dream of but it would not have been half as fun without all the great people around me.

Johan, you're one of a kind! Your mind is a brilliant, slightly messy, everlasting source of ideas and knowledge and it has been both a privilege and a challenge trying to keep up with you. You have had my back when I needed it and believed in me when I didn't. The last few years, you have not only taught me how to do science, we have been discussing science *together* and I have been extremely proud to finally be able to contribute more to these conversations. Thanks to you, I've become a more independent researcher than I thought I would ever be, and I hope you take some pride in that I do not always agree with you anymore ;).

Maja, one of the coolest researchers I know. Your passion for research is truly inspiring and I have always left our meetings convinced that I actually am a researcher. In fact, you've been telling me that since I was 'just' a student. I can't thank you enough for all your support, pep-talks and conversations on both science and life.

Mariska, I'm so happy you wanted to join my supervisor team! You always contribute with the cleverest of ideas and cheer me on even when you're far away. I know I should have used you more.

To all my fantastic collaborators, this thesis would not have happened without you. You have showed me nothing else than great enthusiasm and taught me that scientific collaborations is a lot of fun. From the bottom of my heart, thank you.

Dagmar, I'm not sure how to express how much you mean to me. I love how we are there for each other when things truly suck and I love all the laughs and good times we've shared. Thanks for being my rock!

Sofia, how lucky am I that I got to figure out how to do a PhD with you? Thanks for all bright ideas, snack times and runs. If it wasn't for you, I would not have made it through corona as well as I have.

Madde, a friendship that begins in a Hilleberg tent lasts forever. You, and your family remind me of what is truly important in life (disco party).

Sarah and Sam, spending time with you is always a blast and never boring. So much laughter, so many discussions, so much support, so many hugs, so much wine.

Old and new EMG PhDs and postdocs, I have had so much fun with you. You're the best!

Gammgänget, you included me in your fantastic gang when I was a new student, and made me feel so much at home. I see it as a personal win that most you have no clue what student generation I belong to. Thanks for all the shenanigans!

Other friends and family, thanks for being you and for keeping me grounded!

Mamma och Pappa, a special thanks to you for always letting me go my own way, trusting I will manage, yet, being there when I haven't.

Lilla mormor i himlen, thanks for loving nature so much it rubbed off on me. I miss you.