

Reindeer grazing lands under pressure

Navigating climate and land-use changes in the mountain tundra

Marianne Stoessel



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Abstract

Reindeer herding has a long history in northern Norway, Sweden and Finland, where it has contributed to shaping the Fennoscandian mountain landscape. Through extensive grazing, semi-domestic reindeer influence vegetation structure and composition, and can partly mitigate climate change effects on vegetation. However, northern pastoralism is increasingly challenged by cumulative pressures stemming from land-use changes, climate warming and predator pressure. These pressures act at different spatial and temporal scales, complicating our understanding of how multiple, interacting pressures affect reindeer grazing behaviour. Since reindeer grazing is both an ecological driver of tundra plant communities and is shaped by many factors, disentangling the relative importance of these relationships is therefore critical to better anticipate future ecosystem change in the mountain tundra.

In this thesis, I investigated how climate and land-use changes, in interaction with other factors, influence reindeer grazing patterns in northern Fennoscandia, and may subsequently affect the tundra vegetation. I specifically assessed the spatial exposure to multiple pressures, quantified reindeer grazing behaviour in space and time, and examined how shifts in grazing patterns may cascade through tundra plant communities in the Swedish mountain tundra. To do so, I combined spatial analyses of cumulative pressures, long-term climate data, GPS tracking with accelerometer-based behavioural data, and vegetation surveys.

Over the whole Fennoscandian herding region, I show that the vast majority of the grazing lands is exposed to one or multiple land-use pressures, often co-occurring with predator presence (Paper I). In that same study, I estimated a regional warming of 1.5–2°C over the past sixty years. Such warming in summer implies shifts in grazing patterns, that was further analysed in Paper II. This study showed that reindeer grazing was strongly limited spatially and temporally by warm summer temperatures in the mountain tundra. Such constraining effect of heat is becoming more common with warming summers, likely diminishing herbivory pressure (Paper II). At a local scale, grazing patterns were also shaped by abiotic conditions. Soil wetness emerged as a key predictor of where reindeer grazed, with wetter sites being significantly less grazed, enhancing distinct plant communities (Paper III). Additionally, human presence in the mountains was generally associated with a reduced reindeer occurrence and grazing activity (Paper IV). Although, if it offered protection from predators, reindeer would tolerate human disturbance, yet usually at the cost of grazing less.

Taken together, these results show that cumulative pressures constrain reindeer grazing both spatially and temporally, leading to a fragmented use of summer pastures. Areas that are consistently under-grazed or avoided, particularly near human infrastructures and in warm and wet habitats, are likely to experience a weakened top-down control on vegetation. By demonstrating how anthropogenic activities, environment and predators jointly may alter reindeer behaviour and its ecological functions, this work emphasizes the need to consider cumulative and interacting pressures when predicting future ecosystem change in northern mountain landscapes.

Keywords: *accelerometry, Arctic and subarctic ecosystems, bio-logging, bottom-up versus top-down drivers, climate-land-use interactions, cumulative pressures, extensive grazing system, global warming, habitat selection analysis, land-use changes, mountain tundra, plant community composition, predator presence, reindeer grazing behaviour, reindeer herding, soil moisture regime, tundra plant diversity.*

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“Industrial pollution emits quantities of chemicals of all sorts, among others vast amounts of carbon dioxide. This spreads into the atmosphere and could act like a greenhouse. It could create an overall warming of 2-3°C of the atmospheric temperature, which would melt the ice, in the North and South poles, as well as in the mountains. An average of 2 to 3°C is enough you know. [...] Industries are probably currently creating disorders on great natural cycles as we know them.”

Excerpt from a 1979 TV interview of the volcanologist Haroun Tazieff (translated from French).

Je dédie ce travail à ma famille:

Tout d’abord à mes parents qui m’ont toujours soutenue dans mes choix de vie,
Mais également à mon partenaire dans la vie, qui a été mon rock ces dernières années,
Et à mes enfants, qui m’ont insufflé une énergie créative et insoupçonnée depuis que je suis maman.

Abstract

Reindeer herding has a long history in northern Norway, Sweden and Finland, where it has contributed to shaping the Fennoscandian mountain landscape. Through extensive grazing, semi-domestic reindeer influence vegetation structure and composition, and can partly mitigate climate change effects on vegetation. However, northern pastoralism is increasingly challenged by cumulative pressures stemming from land-use changes, climate warming and predator pressure. These pressures act at different spatial and temporal scales, complicating our understanding of how multiple, interacting pressures affect reindeer grazing behaviour. Since reindeer grazing is both an ecological driver of tundra plant communities and is shaped by many factors, disentangling the relative importance of these relationships is therefore critical to better anticipate future ecosystem change in the mountain tundra.

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Taken together, these results show that cumulative pressures constrain reindeer grazing both spatially and temporally, leading to a fragmented use of summer pastures. Areas that are consistently under-grazed or avoided, particularly near human infrastructures and in warm and wet habitats, are likely to experience a weakened top-down control on vegetation. By demonstrating how anthropogenic activities, environment and predators jointly may alter reindeer behaviour and its ecological functions, this work emphasizes the need to consider cumulative and interacting pressures when predicting future ecosystem change in northern mountain landscapes.

Keywords: accelerometry, Arctic and subarctic ecosystems, bio-logging, bottom-up versus top-down drivers, climate-land-use interactions, cumulative pressures, extensive grazing system, global warming, habitat selection analysis, land-use changes, mountain tundra, plant community composition, predator presence, *reindeer grazing behaviour*, *reindeer herding*, *soil moisture regime*, *tundra plant diversity*

Sammanfattning

Renskötsel har en lång historia i norra Norge, Sverige och Finland, där den har bidragit till att forma det Fennoskandiska fjällandskapet. Genom extensiv betesdrift påverkar renar vegetationens struktur och sammansättning och kan delvis motverka klimatförändringarnas effekter på vegetationen. Ett hot mot renskötseln är ökandet av kumulativa negativa effekter så som förändrad markanvändning, global uppvärmning och närvaro av rovdjur. Dessa faktorer verkar på olika rumsliga och tidsmässiga skalor, vilket komplicerar vår förståelse av hur flera, eventuellt interagerande faktorer påverkar renarnas betesbeteende. Eftersom renbete både är en ekologisk drivkraft för tundrans vegetation som dessutom påverkas av många olika faktorer, är det viktigt att förstå den relativa betydelsen av och sambanden mellan dessa faktorer för att kunna förutse framtida förändringar i fjälleksystemen.

I denna avhandling har jag undersökt hur klimat- och markanvändningsförändringar, i samspel med andra faktorer, påverkar renarnas betesmönster i norra Fennoskandia och därmed potentiell påverkan på tundravegetationen. Specifikt har jag analyserat den rumsliga exponeringen för olika faktorer, kvantifierat renarnas betesbeteende, specifikt var och hur mycket tid de spenderar på bete, samt undersökt hur förändringar i betesmönster kan få kaskadeffekter på tundravegetationen i de svenska fjällen. För att göra detta, har jag kombinerat rumsliga analyser av kumulativa effekter, långsiktiga klimatdata, GPS-spårning med accelerometerbaserade beteendedata och vegetationsundersökningar.

Min avhandling visar att en majoritet av betesmarkerna i Fennoskandia är påverkade av en eller flera typer av markanvändning, ofta i kombination med förekomsten av rovdjur (Artikel I). I samma studie visade jag att det skett en regional uppvärmning på 1,5-2°C under de senaste sextio åren. En sådan uppvärmning under sommaren kan innebära förändringar i betesmönstren, vilket analyserades vidare i Artikel II. Här var det tydligt att renbetet var starkt begränsat både rumsligt och tidsmässigt av varma sommartemperaturer. Värmeeffekter av denna typ förväntas bli allt vanligare med varmare somrar, vilket sannolikt minskar trycket från växtätare generellt (Artikel II). På lokal nivå påverkades betesmönstren dessutom ytterligare av abiotiska faktorer. Jordfuktigheten visade sig vara en viktig faktor som styrde var renarna betade, där fuktigare platser betades betydligt mindre och även hyste distinkta växtgrupper (Artikel III). Dessutom var människors närvaro i fjällen i allmänhet förknippad med en minskad förekomst av renar och betesaktivitet (Artikel IV). I denna studie observerades också att renar till viss del tolererar mänsklig störning, om det samtidigt erbjöds skydd mot rovdjur, vilket indikerar en kontextberoende mänsklig skyddseffekt.

Sammantaget visar dessa resultat att kumulativa effekter förändrar renarnas betesmönster, vilket kan leda till en fragmenterad användning av sommarbetesmarkerna. Områden som konsekvent är mindre betade eller undviks, särskilt nära mänsklig infrastruktur och i varma och fuktiga livsmiljöer, kommer sannolikt att betas mindre frekvent vilket ger minskat betetryck och förändrad vegetation som följd. Genom att visa hur mänsklig aktivitet, miljö och rovdjur tillsammans kan förändra renarnas beteende och deras ekologiska funktioner, pekar detta arbete på behovet av att även inkludera kumulativa och interagerande effekter om man vill förutsäga framtida ekosystemförändringar i fjällen.

List of papers

This doctoral thesis consists of a synthesis chapter, and of four papers listed below, referred as Roman numerals in the text (I-IV):

- I** **Stoessel, M.**, Moen, J., Lindborg, R. 2022. Mapping cumulative pressures on the grazing lands of northern Fennoscandia. *Scientific Reports* 12: 16044. <https://doi.org/10.1038/s41598-022-20095-w>
- II** **Stoessel, M.**, Kato, A., Lindborg, R. Warming summers limit reindeer grazing, weakening herbivory pressure in the mountain tundra. *Early view in Ecography*. <https://doi.org/10.1002/ecog.08209>
- III** Gemal E. L., **Stoessel, M.**, Lindborg, R. 2025 Reindeer grazing and soil wetness interact to drive tundra plant community structure in northern Sweden. *Journal of Vegetation Science* 36: e70073. <https://doi.org/10.1111/jvs.70073>
- IV** **Stoessel, M.**, Wikinger F., Lindborg, R. Balancing forage and fear: How people, environment and predators shape reindeer grazing in the Fennoscandian tundra. *Accepted in People and Nature upon revisions*.

Author contributions

- I** **MS, JM** and **RL** all participated in conceiving and designing the study. **MS** compiled and synthesized the data, she conducted the analysis, results visualization, and was main responsible for writing the paper. **RL** led the study and provided supervision. **RL** and **JM** contributed to the analysis, discussion, and writing the paper.
- II** **MS** and **RL** designed and planned the study. **MS** and **RL** collected the data in collaboration the reindeer herders. **MS** led the analysis assisted by **AK**. **MS** was the lead writer of the paper, helped by **AK** and **RL** who critically commented, edited and reviewed the manuscript to its final version.
- III** **MS** conceptualised the study, based on which **ELG** designed the study, supervised by both **MS** and **RL**. **MS** collected the reindeer data, while **ELG** collected the vegetation data. **ELG** was the lead author, assisted by **MS** for some of the analyses and figures. The revisions were led by **RL** and **MS**, with all co-authors editing and reviewing the manuscript to its final version.
- IV** **MS** initiated the study, using the same dataset collected in collaboration with reindeer herders as in Paper II. **MS** conducted the analysis assisted by **FW**. **MS** led the writing of the manuscript, including the interpretation of the results, with input from **FW** and **RL**. All co-authors helped improve the manuscript to its final version.

MS: Marianne Stoessel, JM: Jon Moen, RL: Regina Lindborg, AK: Akiko Kato, ELG: Emma L Gemal, FW: Felicia Wikinger

I have also co-authored the following articles, which are not included in this thesis:

Wilkinson C., Vigués J., **Stoessel M.**, Vinka M., Angerbjörn A., Norén K., 2024. Phase-dependent red fox expansion into the tundra - implications for management. *Journal of Wildlife Management* 88: e22569. <https://doi.org/10.1002/jwmg.22569>

Vigués, J., Norén K., Wilkinson C., **Stoessel M.**, Angerbjörn A., Dalerum F., 2022. Abundance, predation, and habitat associations of lemming winter nests in northern Sweden. *Ecosphere* 13: e4140. <https://doi.org/10.1002/ecs2.4140>

Montràs-Janer, T., Knape, J., **Stoessel, M.**, Nilsson, L., Tombre, I., Pärt, T., Månsson, J., 2020. Spatio-temporal patterns of crop damage caused by geese, swans and cranes - Implications for crop damage prevention. *Agriculture, Ecosystems and Environment* 300: 107001. <https://doi.org/10.1016/j.agee.2020.107001>

Erlandsson, R., **Stoessel, M.**, Skånes H., Wennbom M., Angerbjörn A., 2019. An innovative use of orthophotos - Possibilities to assess primary productivity from colour infrared aerial orthophotos. *Remote Sensing in Ecology and Conservation* 5: 291–301. <https://doi.org/10.1002/rse2.108>

Stoessel, M., Elmhagen B., Vinka, M., Hellström, P., Angerbjörn, A., 2019. The fluctuating world of a tundra predator guild: Bottom-up constraints overrule top-down species interactions in winter. *Ecography* 42: 488–499. <https://doi.org/10.1111/ecog.03984>

Note on the use of Artificial Intelligence

Words in this PhD thesis are my own. Since 2024, I used the assistance of conversational AI for helping me code for advanced programming in R and gdal. I also have used AI to proof-read my texts, checking the flow and grammar for English and Swedish writing. I initially used free conversational AI tool ChatGPT, but then turned to a European-based AI free service (Le Chat from Mistral AI), that follows European GDPR regulations. For assisting in my literature searches (done primarily in Web of Science), I also started to use the paper finder AI tool “Asta” since 2025, developed by Semantic Scholar Open Data Platform.

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1. Introduction

1.1 The rise and decline of semi-natural habitats

Over the last century, the intensification of land-use practices worldwide has led to major ecosystem disruptions, global biodiversity loss and puts our societies at risk in terms of food production and health security (IPBES 2018). However, human activity did not always have a degrading effect on ecosystems. Over the last 12,000 years, most of the terrestrial biodiversity appears to have been shaped by a long history of traditional and indigenous land-uses (Ellis et al. 2021). Landscapes that are currently seen as “wild” or “intact” actually often display a long history of anthropogenic low-intensity use, such as transhumance, hunting, plant harvesting and early forms of agriculture (Smith 2011; Marshall et al. 2018; Ellis 2021). Areas that are still under indigenous management today are generally identified as amongst the most species-rich habitats on earth (Garnett et al. 2018; Ellis et al. 2021; O’Byrne et al. 2021).

This is the case of pastoral lands, where, if extensively managed, grasslands can harbour a high biodiversity while still being part of a traditional farming system through livestock grazing (Wilson et al. 2012; Dengler et al. 2014; Bengtsson et al. 2019). A pastoral system can be defined as a land-use where animals are bred for consumption and trade, and where limited foraging opportunities require herders to move their livestock across the landscape (Dong 2016; Holand et al. 2022). Except on the South pole, pastoralism occurs on all continents, especially in environments with strong environmental constraints that limit crop production. Hence, traditional grazing lands used to be widespread, with grasslands covering 30-40% of the land (O’Mara 2012; Dengler et al. 2020). Yet, these extensively used semi-natural habitats are now declining at an alarming rate due to land-use conversion and intensification of agricultural practices (Watson et al. 2016).

In Western Europe, the majority of the traditional grazing lands have been replaced by more intensive agriculture and forestry, resulting in a drastic loss of ancient grasslands and the disappearance of associated traditional land-uses (Strijker 2005; Dengler et al. 2014; Queiroz et al. 2014). Today, pastoralism is now confined to a few, marginal, often mountainous areas (Dong et al. 2011).

1.2 Cold environments imperilled by climate change

Besides the intensification of human activities, climate change is the other main anthropogenic driver, impacting species distributions and expected to cause global ecosystem disruptions (Montoya and Raffaelli 2010). Cold environments are among the most vulnerable to climate change, with the Arctic warming much faster than the global average (Post et al. 2019; Rantanen et al. 2022). As a consequence, glaciers are retreating, the sea ice is melting, snowfall and snow cover are altered and permafrost is gradually thawing (Forbes et al. 2016; Niittynen et al. 2018; Biskaborn et al. 2019; Bosson et al. 2023). These shifts not only threaten the physical structure of ecosystems, but are also likely to disrupt ecosystem functioning, by affecting hydrological and nutrient cycles, and the availability of

critical resources for the biota (Ims et al. 2013; Meredith et al. 2019; Post et al. 2019).

Due to cold temperatures, nutrient scarcity, and a short growing season, the terrestrial Arctic and subarctic regions are typically shaped by strong biophysical constraints (Ims et al. 2013). With climate change, theory predicts a conversion of these ecosystems into a more productive land, with a longer growing season. Species that were previously constrained by harsh abiotic conditions can expand their distribution northwards or in altitude, potentially threatening current northern biodiversity (Post et al. 2009). Cold-adapted specialists, having evolved under limited competition and strong abiotic pressures, appear particularly vulnerable when interacting with invading boreal species (Callaghan et al. 2004).

Among plants, woody shrubs appear to benefit most from climate warming, expanding their range into the open tundra and increasing in height (Myers-Smith et al. 2015; Myers-Smith and Hik 2018). The greening of the Arctic and shrubification hence emerge as among the most visible responses to climate change on earth (Myers-Smith et al. 2020; Frost et al. 2025). Yet, these changes are not occurring uniformly across the Arctic (Berner et al. 2020). While many areas exhibit greening trends, declines in productivity called “browning” have also been documented (Phoenix and Bjerke 2016). Similarly, the pace of shrub expansion varies across the tundra biome, highlighting a strong context dependency (Myers-Smith et al. 2020). This spatial heterogeneity appears to be driven by local conditions, such as the soil moisture, orographic and edaphic conditions, microclimate, topography and interspecific interactions (Bjorkman et al. 2018; Myers-Smith et al. 2019; García Criado et al. 2025b). These complex trends are further influenced by winter conditions, which are often overlooked in favour of summer dynamics but also play a critical role in tundra functioning (Ims and Fuglei 2005). For example, a reduced snow cover, more frequent freeze-thaw cycles and rain-on-snow events can cause plant damages, soil instability and browning in some regions (Phoenix and Bjerke 2016; Bjerke et al. 2017). Overall, global studies suggest a more complex response than a simple northward “borealisation”, where local factors appear to prevent a unidirectional shift due to climate change (Bjorkman et al. 2018; García Criado et al. 2025a).

Similar complexity is also observed in animal communities, where climate and land-use changes interact in ways that are difficult to disentangle (Elmhagen et al. 2015; Antão et al. 2022). Nonetheless, one of the clearest community shifts appears to be at high latitude with boreal species expanding northwards, driven by warmer temperatures (Antão et al. 2022). Such re-structuring of species communities is altering ecosystem functioning through new interference competition and an increased predation pressure (Post et al. 2009; Legagneux et al. 2014; Barrio et al. 2016a). While such top-down effects are well documented at higher trophic levels, they still remain rarely addressed in global studies focusing on plant community responses to climate change (Myers-Smith et al. 2020). Yet, species interactions, both within plant communities and between plants and herbivores, are central to northern ecosystem dynamics and add complexity to the ecological response to climate change (Ims et al. 2013).

1.3 The importance of herbivory in the tundra

Herbivory can be defined as the consumption of plants by animals and can be broadly categorised as grazing (feeding on grass and low vegetation) and browsing (feeding on woody plants, leaves, shoots and fruits, Christie et al. 2015). It is a fundamental interaction that can shape vegetation structure and composition, in other words plant diversity. The selective defoliation by herbivores in an environment with strong biophysical constraints represents a long-term disturbance from which plant recovery and growth can be compromised in the short growing season (Crawley 2009). Herbivory can therefore hold a strong top-down control on tundra plant communities, where selective feeding can create space for less competitive species to persist, and consequently promote local community diversity (Kaarlejärvi et al. 2017; Post et al. 2022). Through these plant community changes, herbivores can also influence primary productivity, litter decomposition and nutrient cycling, hereby driving vegetation-soil feedbacks (Tuomi et al. 2019; Koltz et al. 2022). Amid climate change, such top-down effects can be critical in a system where woody plants are likely to encroach, threatening northern plant communities (Post and Pedersen 2008). Depending on plant palatability and its resistance to herbivory, herbivores can counteract shrub encroachment into the tundra, and maintain open landscapes (Olofsson et al. 2009; Christie et al. 2015; Bråthen et al. 2017; Vowles et al. 2017b).

Beyond plant consumption, herbivores interact with the ecosystem through non-selective means by trampling, but also transporting seeds (zoochory) and producing dung and urine (Crawley 2009). These interactions are especially significant in nutrient-limited soils (van der Waal et al. 2011; Koltz et al. 2022). Overall, northern herbivores appear to act as ecosystem engineers, influencing plant diversity, productivity levels, but also nutrient and carbon cycling in the long run (Väisänen et al. 2014; Egelkraut et al. 2018; Sundqvist et al. 2019).

In northern latitudes, herbivores range from large mammals, in particular reindeer (*Rangifer tarandus*) and muskox (*Ovibos moschatus*) to smaller species such as rodents (lemmings and voles), mountain hare (*Lepus timidus*), but also avian herbivores (mainly ptarmigan and geese) and insects (Barrio et al. 2016a). Each of these taxa play a distinct role in shaping northern ecosystems (Barbero-Palacios et al. 2024). Rodents, for instance, display cyclical population dynamics that act as an ‘ecosystem pacemaker’ influencing all trophic levels through these fluctuations in abundance (Ims and Fuglei 2005). At population peak, rodents can cause intense, localised pulses of herbivory that affect vegetation structure and productivity (Olofsson et al. 2012; Tuomi et al. 2019). Similarly, insects can defoliate large areas of deciduous shrubs during outbreaks (Lund et al. 2017). Yet the overall effects of insect herbivory in the tundra, including at low population levels, is much less studied than vertebrate herbivory (Soininen et al. 2021; Barbero-Palacios et al. 2024). Ultimately, herbivory will translate into a significant pressure onto the ecosystem depending on the herbivores’ population numbers, as it is a density-dependent effect (Christie et al. 2015). It is therefore essential to track local herbivore population fluctuations, as they are highly characteristic of the functioning of the tundra biome, and will influence the ecosystem structure and dynamics (Ims and Fuglei 2005; Møller et al. 2013).

Herbivory effects on tundra vegetation is predominantly represented by studies focusing on grazing by *Rangifer* (reindeer and caribou; Soininen et al. 2021). While this reveals a taxonomic bias in Arctic herbivory research, it also emphasizes the ecological importance of reindeer in Arctic and subarctic ecosystems. Given that reindeer is the only large herbivore in many parts of the Arctic, fluctuations in reindeer population densities have the potential to trigger significant shifts in the vegetation (Olofsson and Post 2018; Andruko et al. 2020). For example, changes in reindeer abundance negatively affect lichen abundance (Bernes et al. 2015), and also appear to shift vegetation composition from shrub-dominated to graminoid-dominated tundra, with a higher grazing intensity linked to a decreased height and growth of deciduous shrubs (Spiegel et al. 2023; Villoslada et al. 2023). Multiple experimental studies removing reindeer with exclosures have demonstrated similar trends, with the long-term absence of reindeer leading to an increase in deciduous shrub abundance and productivity (Olofsson et al. 2009; Vowles et al. 2017b; Sundqvist et al. 2019). It appears that shrubs are kept in a browsing-trap when they are small and scattered across the landscape (Villoslada et al. 2023) and if reindeer exhibit a local density of minimum five animals per km² (Bråthen et al. 2017). Reindeer effectiveness at suppressing shrubs will therefore depend on its numbers, but also on its habitat-use, that is not favouring tall shrubs, but rather low stature ones that are more prevalent on wind exposed areas (Skarin et al. 2020).

Rangifer is the most widespread herbivore at northern latitudes, but it does not occur wild in all parts of its range (Huntington et al. 2013). Of all the studies inventoried on the effects of herbivory on Arctic vegetation, about 40% of them are conducted in areas where reindeer are semi-domestic, hence herded under a traditional pastoral system (data from Soininen et al. 2021). While reindeer grazing, and its herbivory pressure are often viewed as part of a natural system, this important trophic interaction can also be embedded within a pastoral system. In northern Europe, specifically northern Norway, Finland, Sweden and large parts of Russia, semi-domestic reindeer usually roam freely in the mountain tundra within their herding districts and they belong to herders (Huntington et al. 2013; Holand et al. 2022). Such herding systems highlight a tight linkage between biodiversity, herbivory and traditional land-use in northern ecosystems.

1.4 The mountain tundra as pastoral land

With reindeer husbandry occurring across large parts of the Arctic and subarctic tundra (Huntington et al. 2013), it is important to contextualize the pastoral effects this land-use system has on landscapes and plant communities (Figure 1). Pastoralism is highly weather dependent and therefore requires an adaptative use of the land, relying on its spatial heterogeneity (Horstkotte et al. 2017). Reindeer herding therefore involves a wide range of activities that takes place in different parts of the landscape at different times of the year (Skarin et al. 2022). As a result, herding relies on multi-purpose landscapes designated for example for dwelling, milking, and grazing, hence creating multi-functional mosaics that can be detected in the plant community composition (Tømmervik et al. 2010; Egelkraut et al. 2018; Lezama-Núñez et al. 2018).

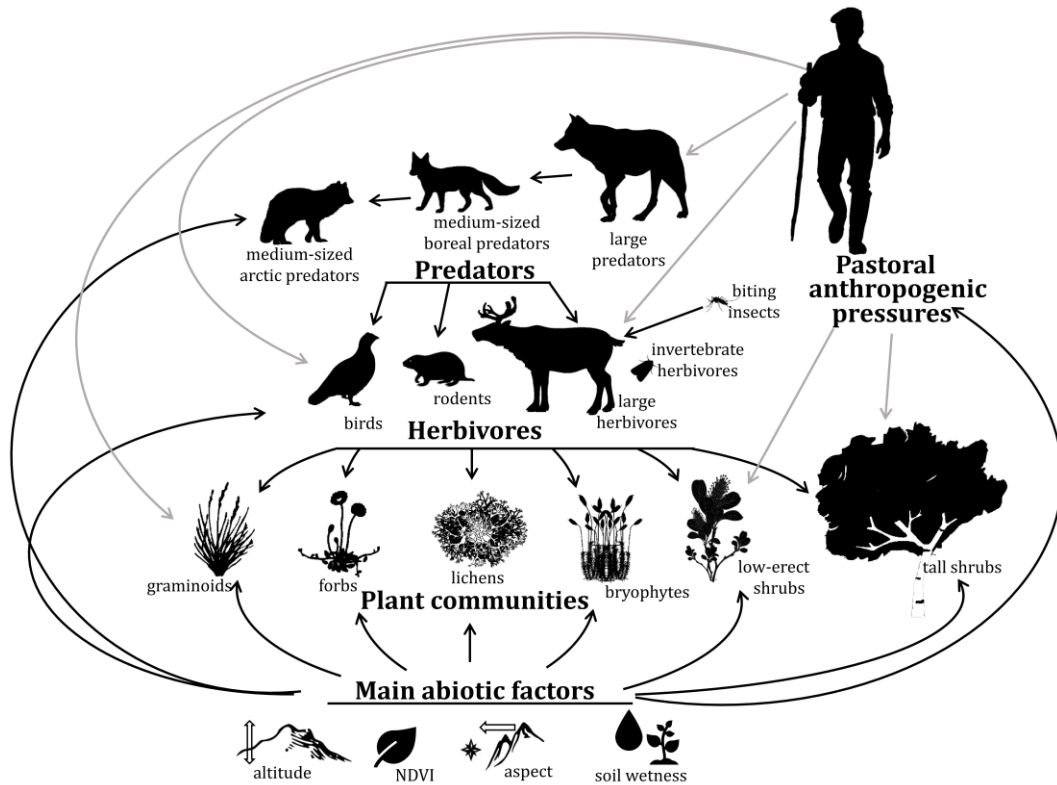


Figure 1. Conceptual model illustrating the tundra trophic network, including pastoral effects. NDVI stands for Normalised Difference Vegetation Index. Note that, for visual clarity, not all species interactions (such as pollination) are represented in this figure, neither are the feedback affecting northern pastoralism (such as predator pressure, biting insects or moth outbreaks)

The main ecological effect of reindeer herding stems from the concentration of herbivory in specific areas of the landscape throughout the seasons (Normand et al. 2017). For example, herding corrals will show soil erosion and local disappearance of plants due to a high number of reindeer gathered in a relatively small area (less than 1 km², Normand et al. 2017). In less intensive settings, where reindeer traditionally graze in summer, the tundra appears to transition from shrub-dominated vegetation to graminoid-dominated communities (Olofsson 2006; Forbes et al. 2009), and interestingly this transition also appears where herders gather, at camping sites, or following off-road vehicle tracks (Forbes et al. 2009; Kumpula et al. 2012). Overall, these spatially and temporally concentrated herding impacts could be summarised as a “pastoral niche”, which extends beyond activities directly associated with reindeer and includes other traditional practices at herding sites (Normand et al. 2017; Lezama-Núñez et al. 2018).

Historically, activities extracting resources, such as hunting, and the collection of firewood, bark, berries, and medicinal plants have also likely shaped northern ecosystems (Axelsson Linkowski 2017; Horstkotte et al. 2017). However, many of these practices, particularly wood harvest at the mountain tundra ecotone, have declined (Tømmervik et al. 2019). Intertwined with climate change, the abandonment of these land-uses likely accelerates the advancement of the treeline in the open tundra (Horstkotte et al. 2017; Tømmervik et al. 2019). Additionally, northern pastoralism historically extended beyond reindeer herding. Archaeological evidence shows that some Sámi groups also herded sheep and goats (Seitsonen and

Viljanmaa 2021; Salmi 2023). Besides, summer farming based on the transhumance of sheep and cattle was practiced in northern Fennoscandia since the late Middle Ages (Dýrmondsson 2006; Larsson 2012). Yet, summer farming heavily declined over the last century, which is suggested to have further contributed to treeline shifts in northern Fennoscandia (Bryn 2008; Potthoff 2017; Tømmervik et al. 2019).

With many of these traditional activities having disappeared, documentation of such multi-functional northern pastoral systems is scarce, possibly limiting our understanding of the full ecological effect of the northern pastoral niche. Evidence, however, indicates that their influence on plant communities persists for decades or even centuries after abandonment (Normand et al. 2017; Egelkraut et al. 2018). This long-term stability, in particular of the graminoid-dominated swards, appears to stem from competitive interactions between graminoids and shrubs, but also the pivotal presence of rodents, that preferentially browse shrubs within these swards (Egelkraut 2017).

Traditional land-use practices can leave enduring legacies on ecosystem structure and function, with consequences for biodiversity, carbon storage, and resilience to climate change. For example, when there is a long history of grazing, it has been shown that the tundra can still act as a carbon sink under warming (Väisänen et al. 2014). Grazing history therefore appears to mediate ecosystem response to climate change. In parallel, grazing history together with local conditions, appears important in explaining the herbivore effects on plant communities and diversity. By excluding mammalian herbivores in grasslands in a worldwide experiment, grazing history emerged as the primary driver of plant diversity, in interaction with precipitation (Price et al. 2022). Similarly, a systematic review concluded that reindeer impacts on tundra plant communities are mainly influenced by primary productivity and grazing history (Bernes et al. 2015). Such findings underscore that grazing legacies and local conditions are critical for predicting biodiversity patterns and ecosystem responses to both climate change and land-use shifts.

Another aspect of northern pastoralism, yet hardly addressed when focusing on plant communities, implies a control on the predators of livestock (Pape and Löffler 2012; Kuijper et al. 2016). Excluding top predator pressure can cause a trophic cascade, where herbivory pressure (wild or domestic) can be significantly increased, hence impacting plant recruitment (Hebblewhite et al. 2005; Estes et al. 2011). Top predators can also indirectly benefit small herbivores by exerting a top-down control on medium-sized predators, but if absent, this can cause a “mesopredator release”, therefore likely to have cascading effects on plants through a top-down pressure on the small prey (Elmhagen et al. 2010). The main medium-sized predator species that is characteristic of the subarctic and Arctic tundra is the arctic fox (*Vulpes lagopus*) that, when introduced on a subarctic island, has been shown to provoke a trophic cascade by converting grasslands into a shrub-dominated vegetation (Croll et al. 2005). Such cascading effect highlights the importance of predator management in northern ecosystems, although their broader impacts on tundra plant communities remain understudied.

To summarise, northern pastoralism taking place in the mountain tundra upholds many ecological effects (Figure 1), with several of them viewed as ecosystem services. This is why Nordic governments, in particular in Sweden and Norway, value reindeer husbandry and traditional grazing as a way to preserve the mountain

landscape in its current state. Both countries have even set it as a national environmental goal (Swedish Ministry of Environment 1998; Norwegian Ministry of Environment 2011). However, despite being of high ecological, cultural and economic importance, the viability of northern pastoralism is being increasingly undermined by several, cumulative pressures stemming from climate change, but also land-use changes expanding northwards.

1.5 Northern pastoralism under pressure

The pressures on northern pastoralism can be categorised into three classes: those directly affecting livestock fitness and productivity (primary pressures), those triggering ecosystem responses that indirectly affect reindeer (secondary pressures), and those affecting herding practices and management (tertiary pressures, Rasmus et al. 2022). In this section, I aim at giving a broad overview of these pressures, with an emphasis on the ones within the field of ecology.

In Fennoscandia, around 40% of Norway, Sweden and Finland is allocated for traditional grazing by reindeer but much of this land is facing intensifying competition from other land-uses (Tyler et al. 2007; Moen 2008). Estimating the spatial extent of land-use encroachment remains challenging, because many different human activities are operating at distinct spatio-temporal scales, therefore affecting northern pastoralism in various, possibly cumulative, and dynamic ways (Wolfe et al. 2000; Pape and Löffler 2012; Skarin and Åhman 2014).

Winter conditions are the harshest and directly influence reindeer survival, making disturbances during this season particularly impactful (Skarin et al. 2022). Traditionally, reindeer rely on lichen-dominated forests for winter forage, but these resources have declined dramatically, partly driven by intensive forestry (Kivinen et al. 2010; Sandström et al. 2016; Horstkotte and Moen 2019). Besides forestry, other extractive industries are expanding northwards, such as mining, or oil and gas extraction in the Russian Arctic (Forbes et al. 2009; Eftestøl et al. 2019; Fohringer et al. 2021; Loginov et al. 2022). The impacts of an industrial site extend beyond its spatial footprint and can persist even after closing the site (Kivinen et al. 2018). Similarly, yet less intensive, power lines, land-based wind turbines, and recreational infrastructures, have also been shown to affect reindeer habitat use (Vistnes and Nellemann 2001; Vistnes and Nellemann 2008; Anttonen et al. 2011; Skarin and Alam 2017; Skarin et al. 2018). Overall, reindeer are disturbed by many types of human infrastructure, creating “zones of influence” (ZOI) avoided by reindeer, that can range from 1.5 km to 14 km in the case of mines (Boulanger et al. 2012; Eftestøl et al. 2019). Additionally, industrial development spurs further infrastructure expansion, such as logging roads, fragmenting habitats and reducing pasture functional availability (Kivinen 2015; Fohringer et al. 2021; Ring et al. 2024). By reducing pasture quality and availability, the spatial accumulation of anthropogenic activities then decreases the pastoral adaptive capacity to face stochastic events, by limiting the possibility to move reindeer to alternative or safer pastures during adverse conditions (Horstkotte et al. 2017; Axelsson-Linkowski et al. 2020; Uboni et al. 2020). This reduced flexibility is particularly critical during weather events such as rain-on-snow and thaw-and-freeze events (Rasmus et al. 2018). These events, increasingly more common with warming winters, lock the access of lichens

by creating an icy layer on top of the vegetation and can put entire herds at risk (Forbes et al. 2016; Rosqvist et al. 2021).

While winter is most critical for reindeer herding, conditions during other seasons are also important for reindeer survival and productivity (Paoli et al. 2020; Rasmus et al. 2022). With global warming, growing degree days are overall increasing, and reindeer can thus benefit from an extended snow-free season, which may help recovery from the arduous cold season (Turunen et al. 2009; Tveraa et al. 2013). Yet, these changes are not exclusively positive (Rasmus et al. 2022). Warm temperatures in summer also increase the likelihood of insect harassment, which disrupts reindeer grazing activities and pushes them towards higher altitude and wind exposed areas where insect activity is reduced (Hagemoen and Reimers 2002; Skarin et al. 2008; Skarin et al. 2010). The summer season is the period during which reindeer need to gain body mass and accumulate energy reserves by grazing high nutritional fodder (Åhman and White 2018). By disrupting summer grazing, insect harassment is therefore suspected to affect reindeer fitness, although this causal effect remains difficult to demonstrate (Weladji et al. 2003; Joly et al. 2020).

In addition to warming, precipitation patterns at northern latitudes remain variable, with yet an overall increase projected to occur (Rasmus et al. 2022). Warmer and wetter conditions appear to promote exposure to toxins and diseases throughout the year (van Oort et al. 2020; Riseth et al. 2020; Kumpula et al. 2024). The transmission of parasitic and pathogenic infections is predicted to increase with climate change (Tryland et al. 2022). A clear example of this climate change effect is the increasing risk of deadly Anthrax (*Bacillus anthracis*) outbreak following permafrost thaw (Stella et al. 2020).

Aside from infections, predation is the most obvious species interaction that can affect northern pastoralism. Reindeer herding co-occurs with wolves (*Canis lupus*), lynx (*Lynx lynx*), wolverines (*Gulo gulo*), brown bears (*Ursus arctos*) and golden eagles (*Aquila chrysaetos*, Kaczensky et al. 2024). Each species differs in their predation strategies, with the wolf representing the greatest threat to herd survival (Sikku and Torp 2008). Beyond direct losses, the presence of predators disturbs reindeer grazing patterns and can limit access to good foraging areas (Rivrud et al. 2018), further reducing pasture use. Together with climate or land-use changes, there can also be interactive effects detrimental to reindeer. For example, forestry appears to increase the predation risk of bear on reindeer calves (Sivertsen et al. 2016), while harsh winter conditions, in particular deep snow, push reindeer into forested areas where predation risk is higher (Tablado et al. 2014).

1.6 Knowledge gaps and methodological challenges

On the one hand, the ecological value of extensive grazing by semi-domestic livestock, particularly in the tundra, is widely recognised and has been the subject of substantial high-quality research (Stark et al. 2023). On the other hand, reindeer herding is increasingly undermined by multiple cumulative pressures, a topic that has also received growing research attention (Holand et al. 2024). Although challenging, linking these two perspectives is particularly important, as the pressures affecting reindeer herding, and grazing patterns, are likely to modulate reindeer's ecological effects. In the context of climate change, this integration is

timely, as a recent paper identifying Arctic herbivory research priorities highlighted the question “How will climate change affect herbivores and their ecological role in Arctic ecosystems?” for its high scientific and management relevance (Barrio et al. 2025).

Research on reindeer grazing and herding has in the past been described as “functionally isolated within disciplines” (Pape and Löffler 2012). To get a more updated view of this research, I examined the research trends on reindeer grazing and herding over the period 2014-2024 (Figure 2). This analysis revealed a predominant focus on pressures affecting reindeer herding (Figure 2a), a trend aligning with the findings of Holand et al. (2024) who identified this research theme as the fastest-growing research topic over the past decade. Most of these studies addressed a single type of pressure, and only a small fraction examines the combined effects of multiple pressures, such as climate change, land use, and predators, still signalling a lack of interdisciplinarity in the field (Holand et al. 2024).

Climate change remains an expanding research topic, particularly when examined as a pressure on reindeer herding (Figure 2b). When focusing on the ecological impacts of reindeer grazing, most of the studies integrated climate change into their research questions, with a strong emphasis on the growing season, and comparatively less attention to other seasons (Barrio et al. 2025).

Studies that explicitly integrated both perspectives - for instance, by examining how external pressures affect reindeer while also considering the ecological impacts of reindeer grazing or herding - remain marginal (a total of 18 studies out of 310, Figure 2). Nearly half of these studies (8 of 18) include climate change as a research focus, whereas only three consider land-use pressures, specifically forestry. While integrating both perspectives is challenging and may explain this limited representation, this pattern also highlights a research bias: only a minority of studies that examine the ecological effects of reindeer grazing explicitly consider how reindeer themselves are affected by other pressures. Many studies investigating the ecological effects of reindeer grazing have relied on grazing exclusion experiments, or fencing between pastures, thereby comparing ecosystem responses between treatments such as grazed versus ungrazed areas, or year-round versus winter grazing (e.g. Olofsson et al. 2009; Sundqvist et al. 2019; Yläanne et al. 2021). While this experimental approach is effective for isolating treatment effects, it simplifies the study system by not considering the past and present land-uses co-occurring at larger spatial scale, as well as the potential influence of other wild species present in the area (Stark et al. 2023). Moreover, reindeer grazing itself is treated as a fixed pressure rather than as a gradient characterised by varying grazing intensities, despite the need for a better understanding of how different levels of grazing pressure influence ecosystem responses (Bråthen et al. 2017; Barrio et al. 2025).

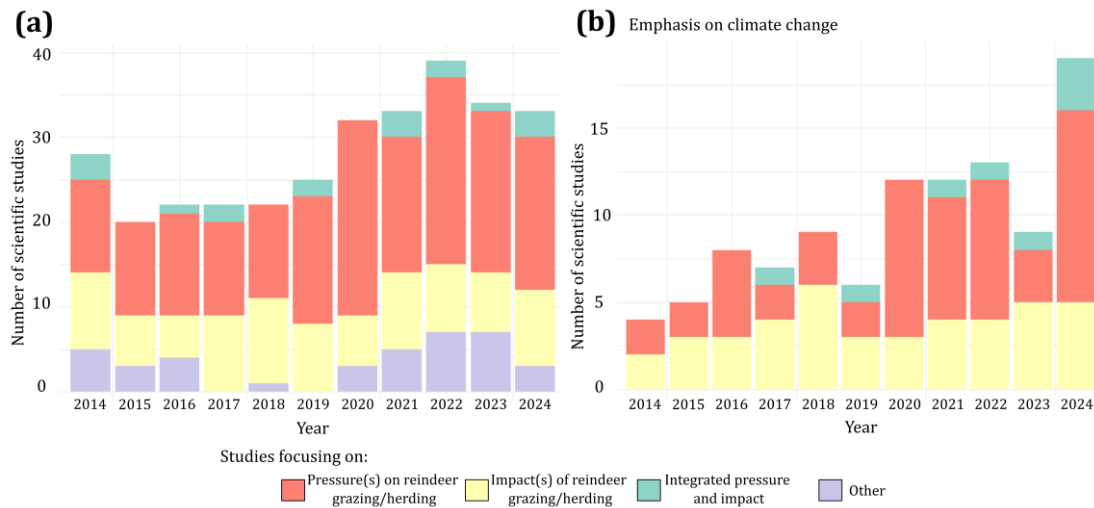


Figure 2. Research focus on reindeer grazing, or herding for the period 2014-2024. Based on Web-of-Science searches done on 17-11-2023 and 23-10-2025. It first yielded a total of 690 scientific papers. After selection for only English written articles within environmental sciences and directly related to the semi-domestic reindeer system, the final sample consisted of 310 studies. The category "Other" includes for example methodological, historical, or behavioural studies without a specific emphasis on pressures, nor impacts.

Effectively quantifying grazing pressure in northern latitudes remains a research priority (Barrio et al. 2025), as it is challenging to infer landscape-scale responses from herbivore-plant interactions that operate at local scales, particularly in an environment characterised by strong abiotic constraints. High context-dependency has been documented when both studying climate change effects on tundra vegetation (e.g. Bjorkman et al. 2020; Myers-Smith et al. 2020) and the impacts of reindeer grazing on plant communities (Bernes et al. 2015). Interestingly, a similar pattern applies to studies of human pressures on reindeer behaviour, where effects are typically detected only in regional-scale analyses spanning one or more herding districts (Skarin and Åhman 2014). This strong context dependency limits the generalisation of results across regions and time periods and has encouraged the development of coordinated, long-term international research protocols to better assess vegetation change and herbivory effects, such as the International Tundra Experiment and the Herbivory Network (Barrio et al. 2016b; Henry et al. 2022). As for studying what affects reindeer grazing and herding, the methods used vary greatly, likely due to pressures differing between local contexts. Many herding districts now use Global Positioning Systems (GPS) to monitor their livestock, and this data can then be used to estimate ZOI, which is becoming a common approach (e.g. Skarin et al. 2018; Eftestøl et al. 2019; Niebuhr et al. 2023). Collaboration with herders and local stakeholders, such as participatory mapping, surveys, and the integration of traditional ecological knowledge, is also increasingly recognised as essential (e.g. Vuojala-Magga and Turunen 2015; Callaghan et al. 2020; Risvoll et al. 2022; Turunen et al. 2024). Additionally, it should be noted that most studies address the effects of cumulative pressures at regional scale, or district scale, and relatively few at broader, international, spatial scales (e.g. Kivinen 2015; Fohringer et al. 2021; Rasmus et al. 2021).

It was also clear that a mismatch in research emphasis emerged both in space and time. First, by combining maps from syntheses reviewing the study locations on the

ecological impacts of reindeer grazing on tundra vegetation (Bernes et al. 2015; Soininen et al. 2021) with maps of reindeer husbandry in northern Fennoscandia (Pape and Löffler 2012; Holand et al. 2022), it appears that a high concentration of studies is carried out in areas with high reindeer density (approximately 5-12 reindeer per km²), and in the northernmost parts of the peninsula. More research attention to southern herding regions would therefore be relevant, as these areas host lower local reindeer densities and potentially experience stronger cumulative pressures.

Second, studies examining pressures on reindeer grazing and herding tend to focus predominantly on winter conditions, whereas research on the ecological impacts of reindeer grazing mainly addresses the summer season (Barrio et al. 2025). These seasonal processes are of course interconnected, as harsh winter conditions can cause population declines that subsequently would reduce grazing pressure in the summer. However, pressures acting during the summer may also be significant enough to influence reindeer grazing dynamics in the mountain tundra. While insect harassment is known to substantially affect reindeer grazing patterns, less research is about how climate-driven changes, such as warmer summers, influence herbivory itself, especially in combination with other potential pressures.

1.7 Objectives of this thesis

This thesis aims to identify and quantify the pressures affecting reindeer grazing in the mountain tundra of northern Fennoscandia (southern extension of the Arctic tundra, Virtanen et al. 2016), and to assess how these pressures indirectly influence tundra plant communities. By recognizing reindeer grazing as both an essential top-down driver of tundra plant biodiversity and a process shaped by many environmental and anthropogenic factors, this work seeks to bridge these two perspectives. Specifically, my thesis objectives are:

- Unravelling the drivers of reindeer grazing in the summer, with a particular emphasis on climate change and human disturbances (Paper I).
- Understanding the spatial dynamics of the reindeer-tundra plant interaction by capturing how grazing patterns vary across the landscape (Papers II and IV).
- Exploring how shifts in grazing behaviour may cascade through tundra vegetation communities (Paper III).

The objectives of this thesis, with emphasis on the specific focus covered by each paper, are outlined in Figure 3. The thesis is broadly structured in two steps:

Spatial overview of the different pressures, collecting spatially-explicit open data. Paper I addresses the first objective of this thesis by compiling public spatial information on land-uses co-occurring with reindeer herding in northern Sweden, Norway and Finland. This paper is the result of an extensive mapping project and includes the spatial extent of anthropogenic activities, predator presence, and the rate of climate warming across the region.

Where do reindeer graze? Empirical studies. Papers II-IV address the second and third main objectives of this thesis through field investigations where reindeer were monitored with bio-loggers to estimate their grazing activities in space and time. With an emphasis on the second objective of this thesis, Paper II focuses solely on the effects of climate change, in particular regarding the warming of summers, on reindeer grazing activity. Paper III specifically analyses the link between environmental factors, reindeer grazing and tundra plant community structure, in line with the third thesis objective. While Paper IV also includes the environmental drivers of reindeer grazing, its emphasis is on the anthropogenic disturbances and their potential interactions with predator presence, particularly whether human presence can also have a significant effect on where reindeer choose to graze (second objective of this PhD thesis).

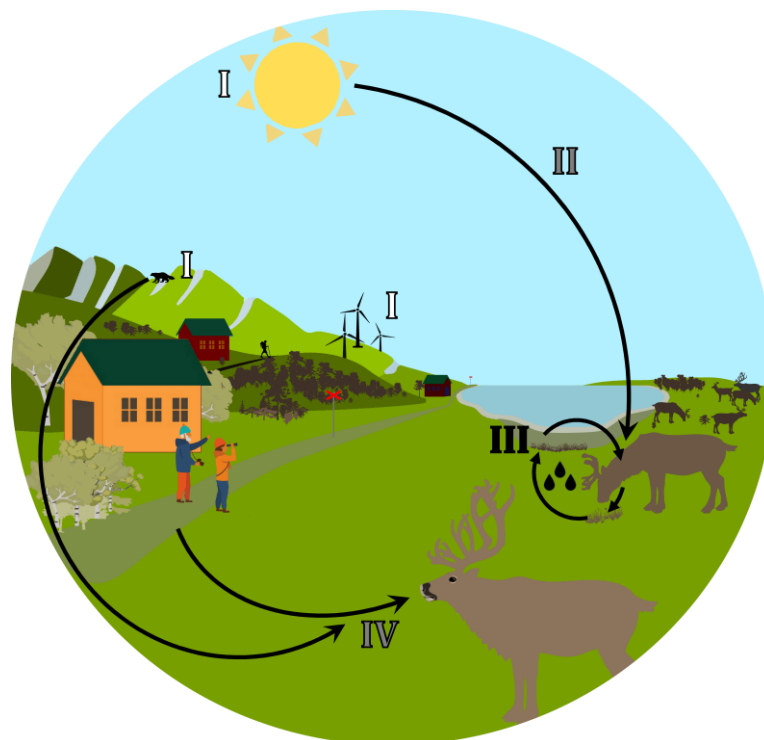


Figure 3. Graphical abstract illustrating the objectives of this thesis, colour-coded with white: 1st, grey: 2nd and black: 3rd thesis objective, and each paper referenced by its Roman numeral.

2. Methodology

2.1 Study system and overview of the study area

This thesis focuses on northern Fennoscandia, a region spanning the northern halves of Finland, Sweden, and Norway, where reindeer husbandry takes place (Figure 4, Tyler et al. 2007; Moen 2008).

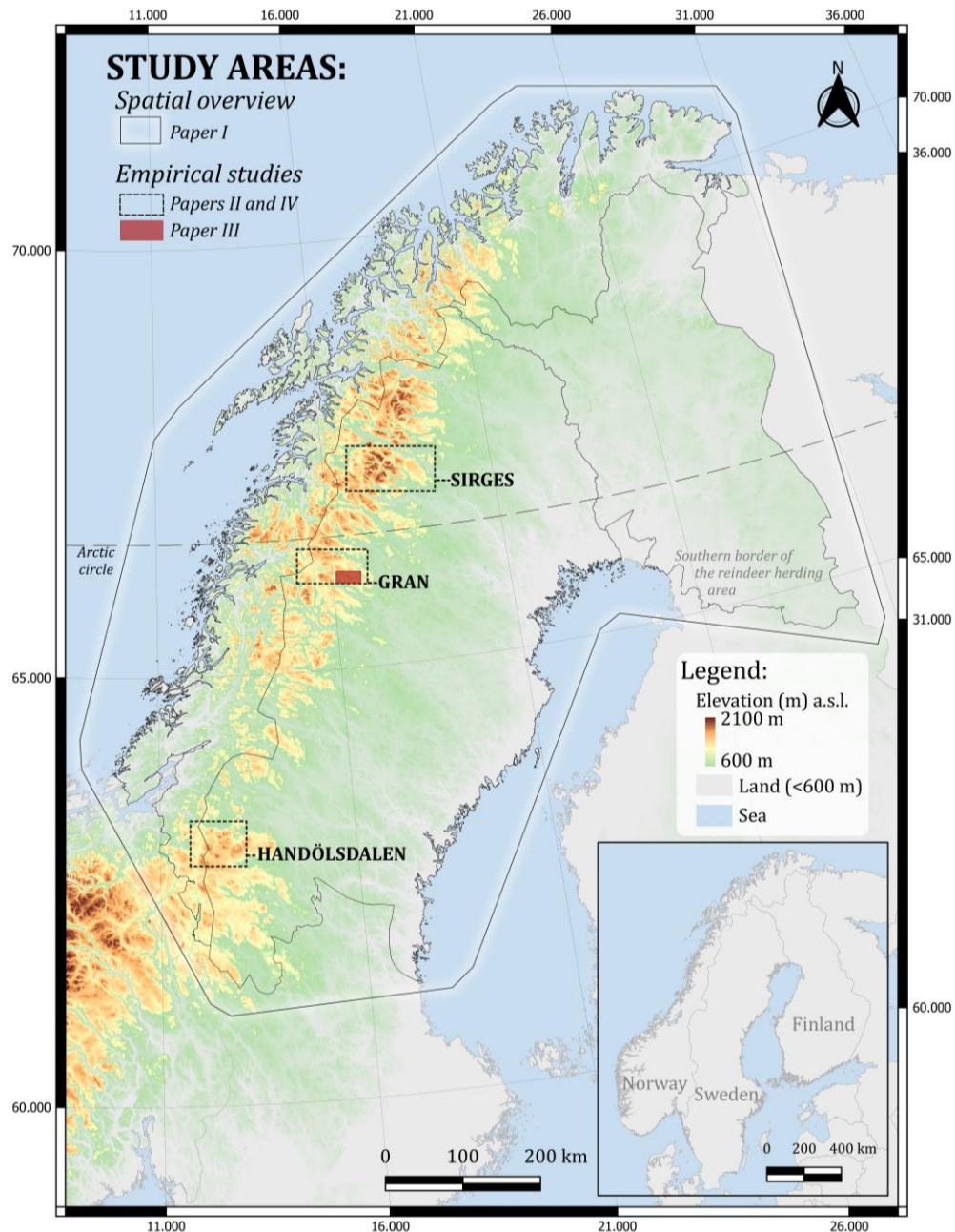


Figure 4. Map of the study sites covered in this thesis. Handölsdalen, Gran and Sirges are the names of the reindeer herding districts that were collaborators in this project. Their summer pastures are shown as dotted rectangles (studied in Papers II and IV). The study area of Paper III is located within the summer pastures of Gran (outlined in red) and partly overlaps with Vindelfjällen nature reserve. The country borders are from ©Eurostat. Projected coordinate system: ETRS89-extended / Lambert Azimuthal Equal Area Europe (EPSG:3035).

This region encompasses several bioclimatic zones, primarily mountain tundra and boreal forest (Ahti et al. 1968), and is characterized by a long history of reindeer herding, with practices that vary between regions and ethnic groups: in Norway and most of Sweden, migratory herding takes place between coastal and mountain areas, while year-round grazing occurs in Finland and some parts of Sweden (Holand et al. 2022). Also, mountain farming with mostly sheep, that used to be historically widespread, has declined drastically, but still remains significant in Norway (Vatn 2009; Larsson 2012). The specific study areas of this PhD thesis are shown in Figure 4, while Table 1 presents a synthesis of the main topics covered by every study, as well as their spatial and temporal scales.

The spatial overview (Paper I) examines the entire Fennoscandian reindeer herding region, analysing land-use pressures, predator presence, and climate trends.

The empirical studies (Papers II-IV) focus on the summer pastures of three specific Swedish herding districts: Sirges, Gran, and Handölsdalen, located in the Scandinavian mountains. These districts represent a gradient of human activity and environmental conditions, from a highly touristic area (Handölsdalen) to remote protected areas (Gran and Sirges) studied in Papers II and IV. On a more local scale, Paper III is located in Vindelfjällen, Sweden’s largest nature reserve, in an area overlapping with the summer pastures of Gran herding district.

Given the high context-dependency of my research, whether examining reindeer response to anthropogenic pressures, herbivory effects on plants, or the plant response to climate change, one of my aims of this PhD was to work on larger landscape scales (Table 1). Of all the studies, only Paper III is conducted at a local scale to be able to examine the relation between the measured reindeer grazing activities and the plant community structure at a fine spatial scale.

Table 1. Summary of the topics and scales covered in this thesis

	<i>Spatial overview</i>	<i>Empirical studies</i>		
	Paper I	Paper II	Paper III	Paper IV
Land-use	✓			✓
Predators	✓			✓
Climate change	✓	✓		
Link with the plants		✓ <i>indirect</i>	✓	
Spatial scale	International	Regional	Local	Regional
	> 500,000 km ²	average of 2,500 km ²	60 km ²	average of 2,500 km ²
Temporal scale <i>main response</i>	2-5 years	2 years	2-4 years	2 years
<i>climate analysis</i>	60 years	35 years		

2.2 Collaborating with reindeer herders

A large part of this thesis relies on data monitoring reindeer movement and grazing activity, collected using GPS tags and accelerometers (*Empirical studies*, Papers II–IV). This research would not have been possible without the collaboration of the three Swedish reindeer herding districts Handölsdalen (in Jämtland), Gran (in Västerbotten) and Sirges (in Norrbotten). All three districts were invited to participate in the project, with the initial plan to equip ten female reindeer in each district with a GPS and an accelerometer, for two consecutive summers (2019 and 2020). After discussions with the herders regarding the study design, we agreed on the GPS brands (which varied by district) and a standardised setup for mounting the accelerometers on the collars (positioned on top of the reindeer’s neck). The deployment of the collars on the reindeer followed the Swedish ethical regulations (The Swedish Board of Agriculture 2019). Reindeer were equipped with the collars by the herders at calf-marking (typically around mid-July) and retrieved in autumn, when the herders gather their reindeer for slaughter.

A total of 30 collars was therefore deployed (10 per district), with a return of 9 in Handölsdalen, 10 in Gran and 5 in Sirges in summer 2019. These 24 collars were then redeployed in summer 2020, yielding returns of 8 in Handölsdalen, 10 in Gran and 3 in Sirges. Unfortunately, additional accelerometer data was lost due to malfunctions, resulting in a final sample size of 31 reindeer monitored with both GPS and accelerometers (13 in Handölsdalen, 12 in Gran and 6 in Sirges).

After completing my analyses using this dataset (in particular for Papers II and IV), I then shared my research results with the reindeer herders. This was done in spring 2025 through a seminar with each district (except Sirges, which was unavailable), where I aimed to present my key findings in an applied perspective for their interest. The seminars ended in an informal discussion, inviting reflections from their part on the project.

2.3 In the field

Two main field campaigns were conducted during my PhD, in summer 2019 and 2022.

In 2019, I collaborated with the reindeer herders during calf-marking and assisted in deploying the GPS and accelerometer collars. Additionally, reindeer were filmed in Handölsdalen to calibrate the acceleration signals with their behaviour. Filming was limited to this district due to logistical constraints. In 2020, COVID-19 restrictions prevented in-person participation, so the collars were delivered to the herders ahead of calf-marking, with the loggers ready for deployment on the reindeer.

In summer 2022, a field campaign was conducted in the summer pastures of Gran by the Masters student Emma L. Gemal (Vindelfjällen, Figure 4). Following a gradient of grazing intensity derived from the reindeer logger data (2019–2020), she collected data on plant species richness from 34 sites, divided between north- and south-facing slopes, within an elevation range of 890 ± 20 m above sea level.

2.4 By the computer

2.4.1 Spatial and climate data compilation

To investigate the effects of competing land-uses, predator presence and climate change on the reindeer grazing lands, spatial data was collected from multiple sources. Additional environmental and non-spatial climatic data were also integrated into the analyses, all detailed in Table 2. The data involving bio-logging and remote sensing analyses are presented in the next section. The compilation of spatial data involving vectors was primarily done using QGIS (version 3.34), while raster processing was partly done using OSGEO4W (version 2023), but also using R (version 4.0 and onward, R Core Team 2023), with the help of the packages ‘terra’, ‘sf’, ‘dplyr’ and ‘SpatialEco’ (Evans et al. 2021; Pebesma and Bivand 2023; Wickham et al. 2023; Hijmans 2025). Even if the same spatial data was used for different studies, its extent varied across studies (Figure 4).

Table 2. Spatial and climate data used in this thesis

Variable category	Description and source*	Temporal & spatial resolution	Part of the PhD thesis
Habitat and vegetation maps	Corine Land-Cover data from Copernicus Land Monitoring Service	2018, 100 m	<i>Spatial overview I</i> <i>Empirical study IV</i>
	National mountain vegetation map from Lantmäteriet** (LM)	2012, mmu*** of 1 km ²	<i>Empirical study II</i>
Terrain data	Digital Elevation Model (DEM) from national mapping authorities. Other topographic variables were derived from the DEM	2016 (Norway) 2018 (Sweden) 2 m	<i>Empirical studies II, III, IV</i>
Other environmental data	Soil wetness from the Swedish University of Agricultural Sciences (SLU)	2020 2 m	<i>Empirical study III</i>
	Soil depth from LM	2017 10 m	<i>Empirical study III</i>
Land-use data <i>Tourism</i>	Locations and bed capacity of tourism accommodations collected from national tourism websites (via ParseHub)	2018-2019	<i>Spatial overview I</i> <i>Empirical study IV</i>
	Locations of private cabins from national mapping authorities	2021	<i>Spatial overview I</i> <i>Empirical study IV</i>
	Hiking trails network from LM	2024	<i>Empirical study IV</i>
Land-use data <i>Infrastructure</i>	All buildings from LM	2024 mmu of 15 m ²	<i>Empirical study IV</i>
	Main road (min. 5 m wide) and railway network from national transport agencies	2019-2021	<i>Spatial overview I</i>
	Locations of active land-based wind turbines from national energy agencies	2018-2019	

Table 2 (continued). Spatial and climate data used in this thesis

Variable category	Description and source*	Temporal & spatial resolution	Part of the PhD thesis
Land-use data <i>Industries</i>	Locations of active mines from the Fennoscandian Mineral Deposits	2019	<i>Spatial overview I</i>
	Locations of land-based industries with permits for environmentally hazardous activities, from national environmental agencies	2019	
	Forests primarily used for wood production, derived from a forest management regime map (Schulze et al. 2019)	2019 1 km	
Predator presence data	Range maps for large mammal predators (bear, lynx, wolf, and wolverine) from Kaczensky et al. (2018, 2024)	2015-2017 10 km	<i>Spatial overview I</i>
		2017-2023 10 km	<i>Empirical study IV</i>
Climate data <i>Spatial data</i>	Monthly surface air temperature and monthly precipitation from the Climate Research Unit (from Harris et al. 2014, updated yearly)	1959-2018 0.5 °	<i>Spatial overview I</i>
Climate data <i>Non-spatial data</i>	Hourly air temperature data from the nearest SMHI**** weather stations to the summer pastures of Handölsdalen, Gran, and Sirges	1988-2022	<i>Empirical study II</i>

*if not specifically indicated, the exact source of the dataset is given in the respective paper;
 Lantmäteriet stands for “the Swedish mapping authority”; *mmu: minimum mapping unit;
 ****SMHI stands for the Swedish Meteorological and Hydrological Institute

For the *Spatial overview*, the data was aggregated using a gridding system in GIS (Geographic Information System) to get a consistent resolution over the different countries covered by the study area, following European guidelines (INSPIRE 2014). The variables of interest were therefore extracted for each grid cell, which had a spatial resolution of 10 x 10 km.

For the *Empirical studies*, the data was extracted at the GPS locations of the reindeer (Paper II), the locations of the field surveys (Paper III), and at the GPS locations of the reindeer, but also at random pseudo-absence points for further habitat selection analysis (Paper IV).

Regarding the tourism spatial data, five types of human infrastructure were studied in Paper IV: large tourist stations, small mountain buildings (e.g., cabins, shelters), all other buildings outside the mountains (i.e. urban edges), large national hiking trails and small local hiking trails. These vector datasets were rasterized where I accounted for the potential spatial cumulative effect of the infrastructures in space by modelling a “zone of influence” with a specific type of decay (threshold, gaussian and exponential), and seven different radii (100 m, 250 m, 500 m, 1 km, 2.5 km, 5 km, 10 km), using the package ‘oneimpact’ (Niebuhr et al. 2023).

2.4.2 Bio-logging and remote sensing data processing

In collaboration with the reindeer herding districts Handölsdalen, Gran and Sirges, a total of 54 reindeer were fitted with GPS and accelerometer collars across the three districts for the summers of 2019 and 2020, with a return of 31 accelerometers and 37 GPS (see 2.2). The accelerometers recorded high-resolution movement data at 10 Hz in 3 dimensions (heave, surge and sway, Figure 5a), while temperature was recorded every 5 minutes (TechnoSmart AB). The GPS units were of different brands per district (Pellego AB for Handölsdalen, TechnoSmart AB for Gran and Findmy AB for Sirges), and were set to record a location every 4 hours in Handölsdalen and Sirges, and every 5 minutes (sometimes extending up to 15 minutes) in Gran. For the Papers II and IV, this temporal frequency was harmonised to 1 GPS fix every 4 hours for all districts.

For all the *Empirical studies*, I classified the reindeer activities by processing the acceleration data as follows:

- I first derived the pitch, that represents the orientation of the reindeer neck (Figure 5b), from static acceleration. The static acceleration was produced by smoothing the raw acceleration with a 5-second running mean (Shepard et al. 2008). A smoothed pitch was also computed using a 1-minute running mean.
- I produced a variable representing the overall activity level, called Minimum Specific Acceleration, (MSA; Simon et al. 2012), corresponding to the sum of all movement in 3D. From the MSA, I then derived a Dominant frequency and Power Spectral Density for every second via a Fast Fourier Transform analysis done over a detrended 5-second rolling window (Fehlmann et al. 2017; Patterson et al. 2019).
- I computed summary statistics for every second on 6 variables (sway, surge, heave, pitch, smoothed pitch, overall activity level). Together with the Dominant frequency and Power Spectrum Density, these were the 8 input variables used for devising the classification algorithm.
- I calibrated the reindeer behaviour with the acceleration signals using the video recordings of the tagged reindeer in Handölsdalen. Using these videos, I trained myself to assign three basic behavioural classes (grazing, static and other activities) to the acceleration data up to the millisecond, using BORIS (version 7.9) and IGOR Pro (version 8.04). I then labelled 3,849 seconds from 8 reindeer (from the three different districts) and used half of the data to train a decision-tree model (Figure 5c), that was then assessed with the other half of the labelled data, giving an overall accuracy of 0.92. As a final step, the unsupervised classification algorithm K-means clustering was used to further refine the behavioural categories (Patterson et al. 2019), and separate moderate (walking) from high-intensity activities (shaking and running, Figure 5c).

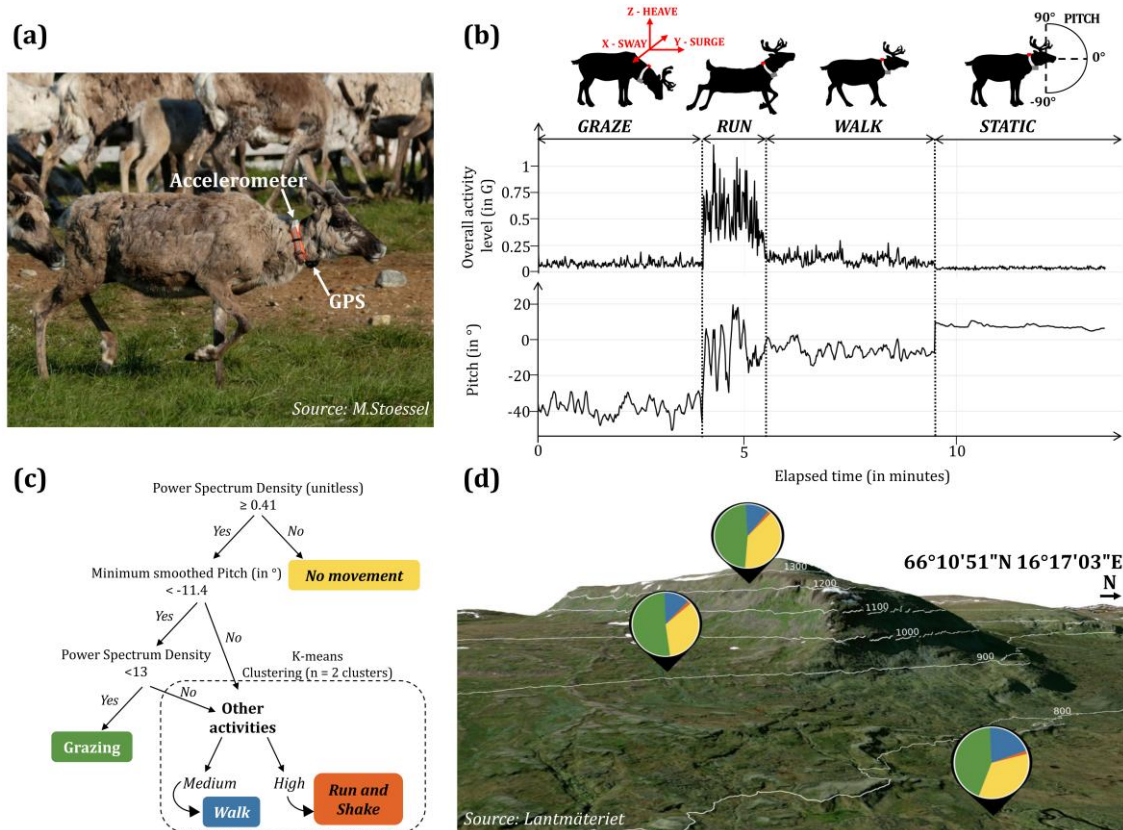


Figure 5. Overview of the bio-logging monitoring set-up with: (a) a photo of a reindeer tagged with an accelerometer (on the top of the neck) and GPS in Handölsdalen; (b) an illustration of the signals that can be derived from the raw acceleration data (expressed in units of standard gravity G), classified with the corresponding reindeer activity; (c) the algorithm used to classify the reindeer activities, based on decision-tree modelling and K-means clustering and (d) the mean duration of these activities over a window of 4 hours at three altitudinal ranges (< 800 m a.s.l., 800-1100 m and > 1100 m). *This figure is based on modified Figure 2 in Paper II, modified Figure S1 in Paper III, and Figure 2 in Paper IV.*

Once classified, the durations of the reindeer activities were summed per 4-hour window (± 2 hours of a GPS fix) in Papers II and IV. In these studies, the temperature (recorded every 5 minutes) was also averaged for the same 4-hour window. In Paper III, the grazing activities were summed between two consecutive GPS points (Figure 5d), and then interpolated across Gran's summer pastures using the Inverse Distance Weighted method. Assuming that repeated grazing can have long-term effects on the tundra vegetation (Egelkraut et al. 2018), the interpolated grazing duration map from summer 2019 was therefore summed with the one from 2020.

For the study focusing directly on plants (Paper III), a remote sensing analysis involving colour infrared aerial orthophotos (called CIR orthophotos) was conducted.

In Paper III, CIR orthophotos from 2021 (with a spatial resolution of 0.16 m) were used to compute the Normalised Difference Vegetation Index (NDVI) formula (Tucker 1979). Since the bands used in the CIR orthophotos are not calibrated to represent the true red and near-infrared reflectance, but still give a highly

representative index of primary productivity (Erlandsson et al. 2019), this value will be hereafter called rel-NDVIortho.

2.4.3 Statistical analyses

Throughout the thesis, I used a variety of statistical tests in R to investigate (1) what affects reindeer grazing in space and time, (2) how the tundra plant communities are affected, and (3) the extent of climate warming in my study areas:

- In the *Spatial overview* (Paper I), climatic trends were analysed using quadratic regressions to assess temperature changes over two 30-year periods.
- Generalized additive mixed models were used in Paper II to test the effects of temperature on reindeer grazing duration and speed, accounting for individual behaviour as random effects. In that same study, generalized linear models (GLMs) were also used to study the summer warming rate in the mountain tundra.
- In Paper III, linear models were applied to assess the influence of environmental factors and grazing on tundra plant species richness and composition, while a GLM was used to study the influence of environmental factors on grazing duration.
- In Paper IV, Habitat Selection Function (HSF) analyses were used to model reindeer presence in space in relation to environmental, predator and anthropogenic variables. Additionally, GLMs were implemented to investigate the reindeer grazing patterns in space, with environmental and anthropogenic factors included in the models. Due to the low spatial resolution of the predator maps (Table 2), only the potential interactions between predator presence and human infrastructures within the mountain areas were tested in the HSF analyses, and not in the GLM analyses. For more details on the model selection process, please see the Method section for Paper IV.

3. Summary of the Papers

3.1 Spatial overview of the cumulative pressures in the reindeer grazing lands (Paper I)

Northern pastoralism in Fennoscandia is increasingly pressured by the expansion of other human activities, predator presence and climate change, yet the spatial extent of these pressures across the region has remained poorly quantified. To estimate this extent, I conducted, to my knowledge, the first spatial analysis of the cover of competing land-uses, predator presence and climate change, over the free-ranging grazing lands of northern Fennoscandia, encompassing northern Sweden, Norway, and Finland. Using a grid-based approach, I mapped five key land-use pressures: outdoor tourism, road and railway networks, forestry, land-based polluting industries, and land-based wind energy facilities, alongside the permanent distribution of four large predators (lynx, wolverine, bear, and wolf). This large-scale GIS analysis showed that a vast majority of the land was exposed to at least one anthropogenic pressure (85%), and that more than half the region (60%) experienced multiple land-use pressures (Figure 6). This resulted in a marginal proportion of the grazing lands left undisturbed, with only 4% of the area free of co-occurring land-uses and predator presence (see Figure 4 in Paper I for more details).

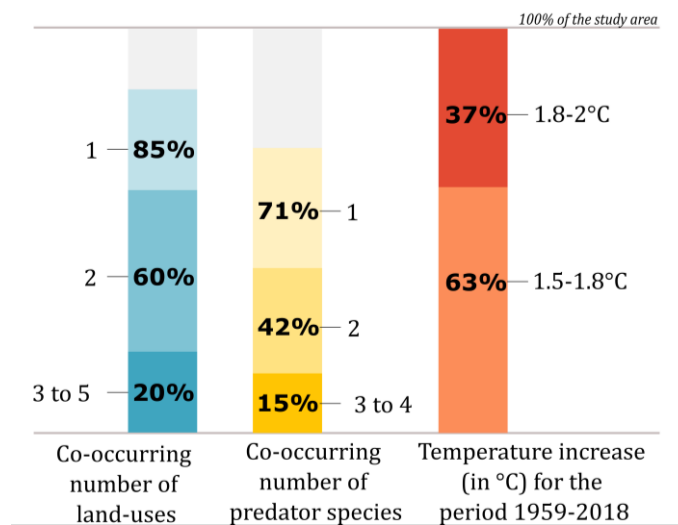


Figure 6. Cumulative proportions of the areas covered by the studied pressures, consisting of competing land-uses, predator presence and climate change, in the Fennoscandian reindeer herding region.

Outdoor tourism emerged as the most widespread pressure, covering 71% of the study area and predominantly overlapping the summer grazing areas, that are mainly located in the Fennoscandian mountain range (Figure 7). Whereas forestry and the road-railway infrastructures (covering 67% and 66% of the region respectively, Figure 7) were more prevalent in winter grazing areas, mostly made of boreal forests. Land-based wind and industrial infrastructures occupied a relatively small area of the region (3 and 5% respectively, Figure 7), yet they also

Climate change constituted yet another layer of pressure, with temperatures estimated to have risen by 1.5–2°C over the past 60 years over the whole study region (Figure 6). Such warming is likely to negatively affect the cold-adapted livestock (Paper II), and to drive shifts in the tundra plant communities (Vuorinen et al. 2017; Maliniemi et al. 2018; Vowles and Björk 2019). Even if reindeer husbandry is recognised in governmental policies as a means to preserve the mountain landscape (Swedish Ministry of Environment 1998; Norwegian Ministry of Environment 2011), livestock grazing is likely to become constrained where competing land-use and predator pressures expand. This suggests that additive or synergistic effects between climate-driven changes and other pressures are likely to occur in areas where multiple pressures overlap (Oliver and Morecroft 2014). Given the high extent of cumulative pressures identified over the study region, together with ongoing climate change, the results hence indicate a substantial risk of future vegetation and landscape change, likely leading to a concentration of grazing in less disturbed areas and encroachment of trees and shrubs in the more disturbed ones (Moen and Danell 2003; Horstkotte et al. 2017).

3.2 Effect of climate change on reindeer grazing (Paper II)

Building on the spatial analysis of Paper I that documented a regional warming of 1.5–2°C across the Fennoscandian reindeer herding region, Paper II examined how such warming translates into summer grazing conditions for reindeer. Specifically, this study addressed how warming summers affect reindeer grazing patterns in space and time, in the Swedish mountain tundra.

By monitoring 31 free-ranging reindeer with bio-loggers, it generated a dataset of 7145 spatially explicit behavioural observations, revealing a range of different effects on reindeer activity. First, warm summer conditions drastically reduced reindeer grazing activity once the body surface temperature (T_R) exceeded 20.3°C, a response most likely linked to insect harassment (Figure 8a, Hagemoen and Reimers 2002; Ehlers et al. 2021). Additionally, at higher temperatures (with $T_R \geq 24^\circ\text{C}$), reindeer speed also declined sharply (Figure 8b), suggesting the onset of heat stress (Sejian et al. 2018). Taken together, these results indicated that heat limits grazing through insect harassment, but also overheating, a mechanism rarely documented for free-ranging reindeer in the subarctic tundra (Trondrud et al. 2023).

Moreover, on days defined as warm spells, i.e. when the daily maximum of air temperature was above 13°C, grazing activity dropped around noon, with no compensatory grazing at other times of the day. This resulted in an estimated daily loss of 1.12 ± 0.15 hours of grazing compared to a cooler day.

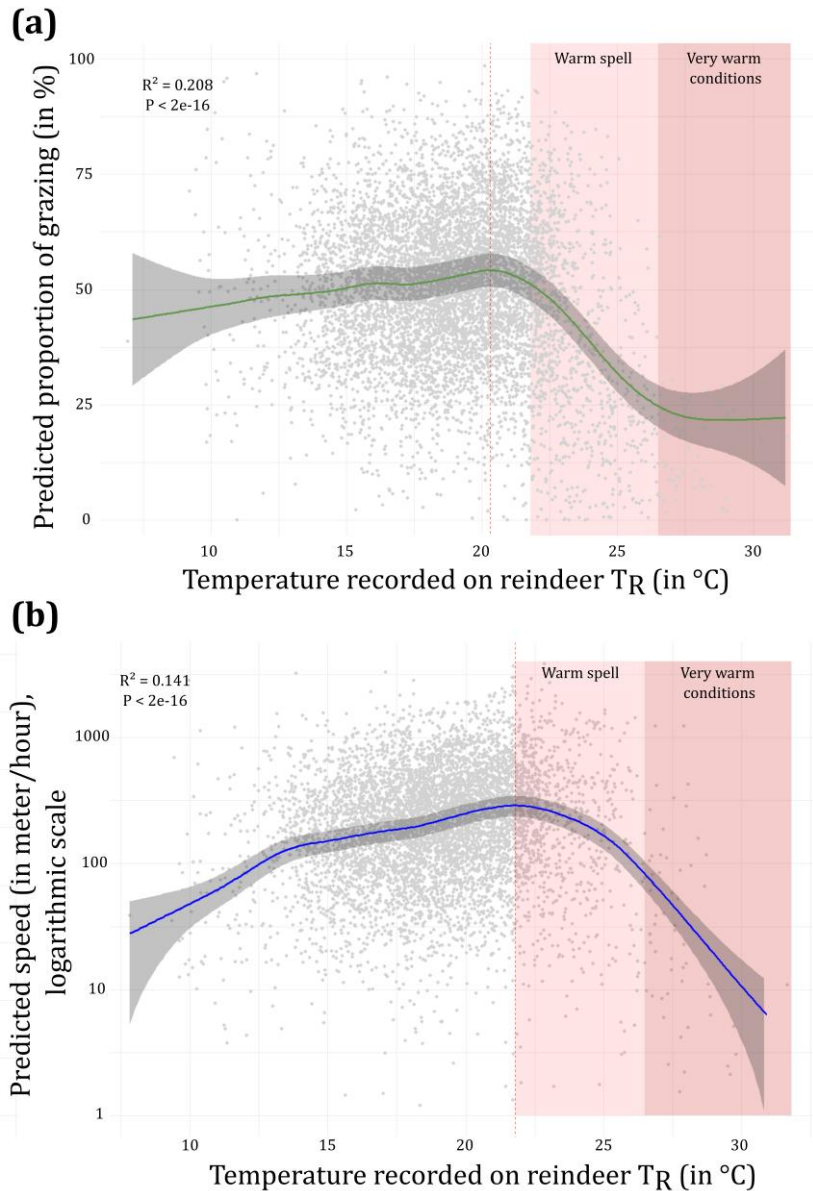


Figure 8. Effect of temperature on reindeer grazing and speed: (a) Predicted response showing the relationship between temperature recorded on reindeer (in °C) and proportion of time reindeer were grazing per 4-hour window (in %); (b) Predicted response showing the relationship between temperature recorded on reindeer (in °C) and reindeer speed (in meter per hour, on a logarithmic scale). The red dotted vertical lines indicate at which temperature the slope of the predicted response becomes negative. The temperature zones were drawn based on a correlation model between air temperatures recorded at the nearest weather station T_A and T_R , with the light-red zone indicating a warm spell (from 13°C T_A corresponding to 21.8°C T_R) and the dark-red zone indicating very warm conditions (equal or above the 90th-percentile of summer T_A for the period 1988-2022, that is 19.3°C T_A corresponding to 26.5°C T_R). Confidence intervals are based on standard errors returned by the prediction of the models. R^2 values are the adjusted R^2 of the models, with the p-values ‘P’ indicating the statistical significance of the relationships ($p \leq 0.001$ indicates highly significant). *This figure is based on part of Figure 3 from Paper II.*

When integrating the reindeer activity data with the GPS locations, the results indicate a heat-driven redistribution of grazing activity across the landscape, coupled with an overall reduction in foraging activity (Figure 9). Reindeer favoured cooler habitats as temperatures rose, which meant that they targeted less productive vegetation types, while also grazing less overall. These spatial shifts observed during warm spells, as well as their associated net foraging loss, imply direct physiological effects on reindeer (Åhman and White 2018). As summer will get warmer, reindeer therefore face greater risks of a reduced fitness (Joly et al. 2020; Ehlers et al. 2021).

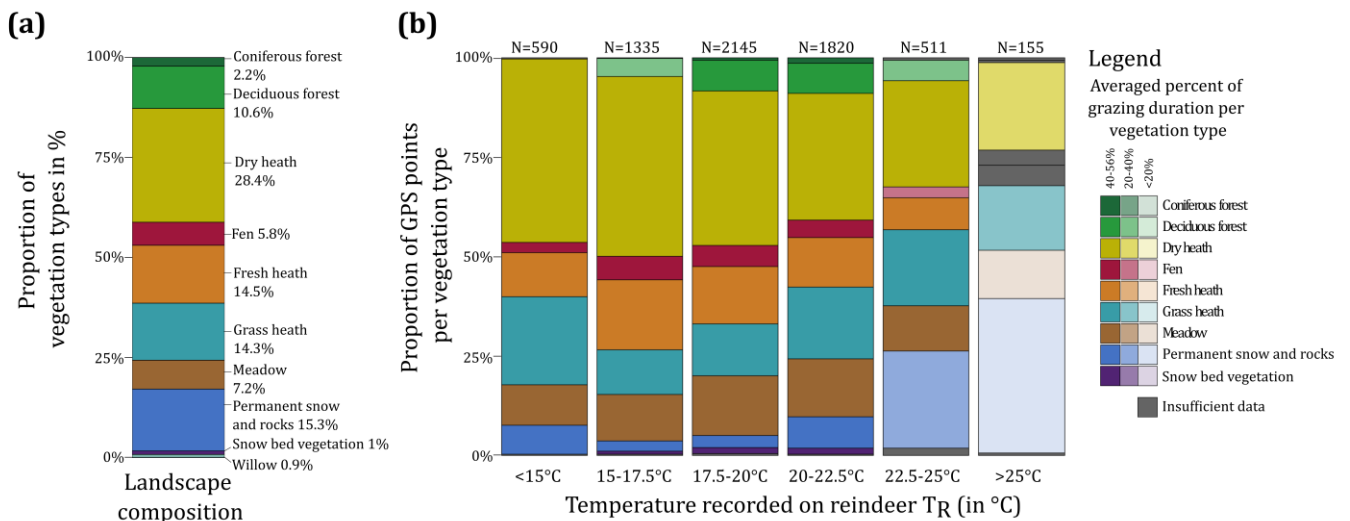


Figure 9. Reindeer spatial partitioning over the vegetation types and temperature: (a) overall landscape composition; (b) proportion of the vegetation types where reindeer graze per temperature class T_R . The GPS sample size is given for each temperature class. For Figure (a), water bodies (which represents 4.36% of the land) and artificial surfaces (corresponding to 0.03% of the land) were excluded. *Figure 5 from Paper II.*

Altogether, this study provides the first empirical evidence of how warm summer temperatures can drastically alter the grazing behaviour of free-ranging reindeer. In our study areas (Figure 4), the frequency of warm spells associated with a reduced grazing activity had increased significantly over the past 35 years, indicating that such disruptions are becoming more common. Consequently, shifts in tundra plant communities may not only be driven by climate change (Myers-Smith et al. 2015), but also by a diminished capacity of cold-adapted key herbivores, such as reindeer, to mitigate vegetation change under warmer summer conditions.

3.3 The interactive effect of reindeer grazing and environmental factors on tundra plant communities (Paper III)

The interplay between biotic and abiotic factors in structuring plant communities is yet to be fully understood, especially in the mountain tundra where plant responses are slow and highly context dependent. While reindeer grazing is known to influence the plant community composition, its effects may be modulated by strong abiotic constraints. Paper III addressed this question by explicitly disentangling the effects of reindeer grazing from those of key abiotic factors on tundra plant

community structure, with the aim of assessing which factor (biotic versus abiotic) prevailed at local scale. To do so, this study uniquely combined accelerometer-based activity data with vegetation surveys, allowing grazing activity to be quantified directly in relation to fine-scale variations in plant community structure and composition.

The analysis revealed that abiotic factors were the primary drivers of the tundra plant community structure, overshadowing the influence of reindeer grazing at local scale (Figure 10). Soil wetness emerged as the strongest predictor of species richness, with wetter conditions favouring higher richness of graminoids and forbs, whereas drier, south-facing slopes supported a greater richness of shrub species (Figure 10).

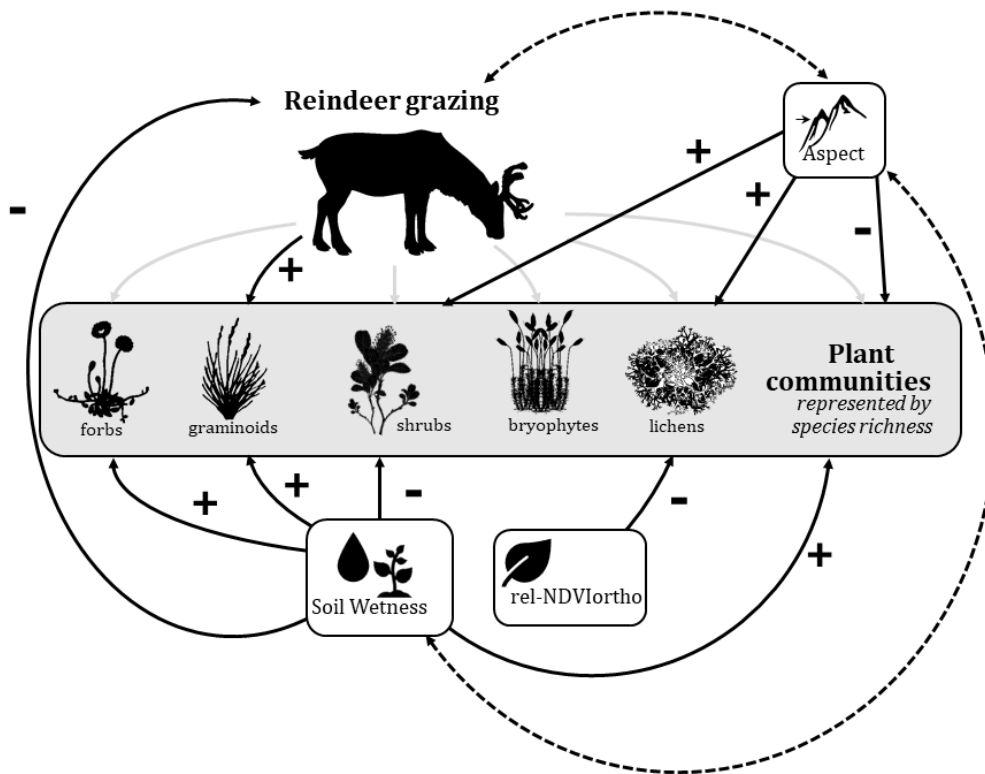


Figure 10. Conceptual workflow of the studied relationships between abiotic factors, reindeer grazing and the tundra plant communities, based on the summary statistics given in Table 3 of Paper III. Significant relationships are shown in bold back arrows, with their estimated directions indicated as +/- . The significant interactions between aspect and other drivers are shown in dotted arrows. Note that the directions of the relationships shown for aspect are only for south-facing slopes, that subsequently includes the relationship between reindeer grazing and graminoids (that is only positive on south-facing slopes). For simplicity, only the non-significant trends between reindeer grazing and tundra plant community species richness are represented in light grey arrows.

Reindeer grazing only had a weak, context-dependent effect on species richness, most notably on south-facing slopes (Figure 10, but see Table 3 in Paper III for more details). Interestingly, a strong negative interaction was also found between soil wetness and reindeer grazing activity, with wetter areas grazed substantially less by reindeer than drier ones (Figure 11).

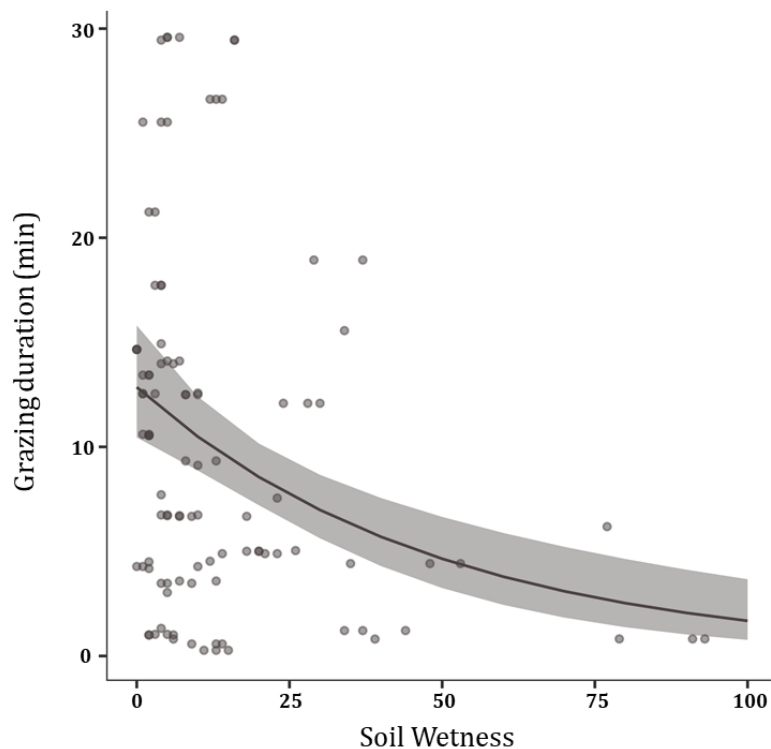


Figure 11. Modelled relationship between soil wetness and reindeer grazing duration (in minutes). The shaded areas represent 95% confidence intervals derived from the standard errors of the model predictions. *Figure 7 from published Paper III.*

Overall, these results highlighted the central role of hydrological conditions in shaping local plant diversity, while also providing insights into the environmental factors influencing the summer grazing patterns of reindeer. As climate change is expected to alter the hydrological regime of the mountain tundra (Winkler et al. 2016), this study delineated a valuable baseline by identifying a triangular relationship between soil wetness, reindeer grazing activity and vegetation composition at local scale. This framework is particularly relevant to better anticipate future shifts in tundra plant communities under changing climatic and land-use conditions.

3.4 The effect of human presence, environment and predators on reindeer grazing patterns (Paper IV)

Reindeer grazing in summer takes place in landscapes that are predominantly overlapped with predator and anthropogenic pressures (as shown in Paper I). Studies examining how reindeer behaviourally respond to the co-occurrence of multiple pressures in space remain scarce, especially in the mountain tundra. Paper IV was designed to address this gap, using the same dataset as in Paper II, consisting of GPS and accelerometer data from 31 semi-domestic reindeer across three Swedish reindeer herding districts (Handölsdalen, Gran and Sirges, Figure 4). In contrast to the climate focus of Paper II, this study examined how environmental conditions, human presence and predator occurrence jointly shaped the summer grazing patterns of reindeer in the mountain tundra.

By combining grazing activity data with habitat selection analyses, the results showed that environmental factors, such as elevation, topographic positioning index and vegetation types, were the primary drivers of reindeer presence and foraging activity (see Tables 2 and 3 of Paper IV, and Figure 12 for an overview). However, human infrastructures and predator presence also played significant roles in shaping reindeer behaviour, often interacting with each other (Figure 12). Reindeer generally avoided areas with high levels of human activity, such as large tourist stations and urban edges, as illustrated for Handölsdalen (Figure 12). By demonstrating that human presence can significantly influence both where reindeer occur and how much they graze, these findings highlight the need to further recognize the human influence on herbivores, even in the remote tundra.

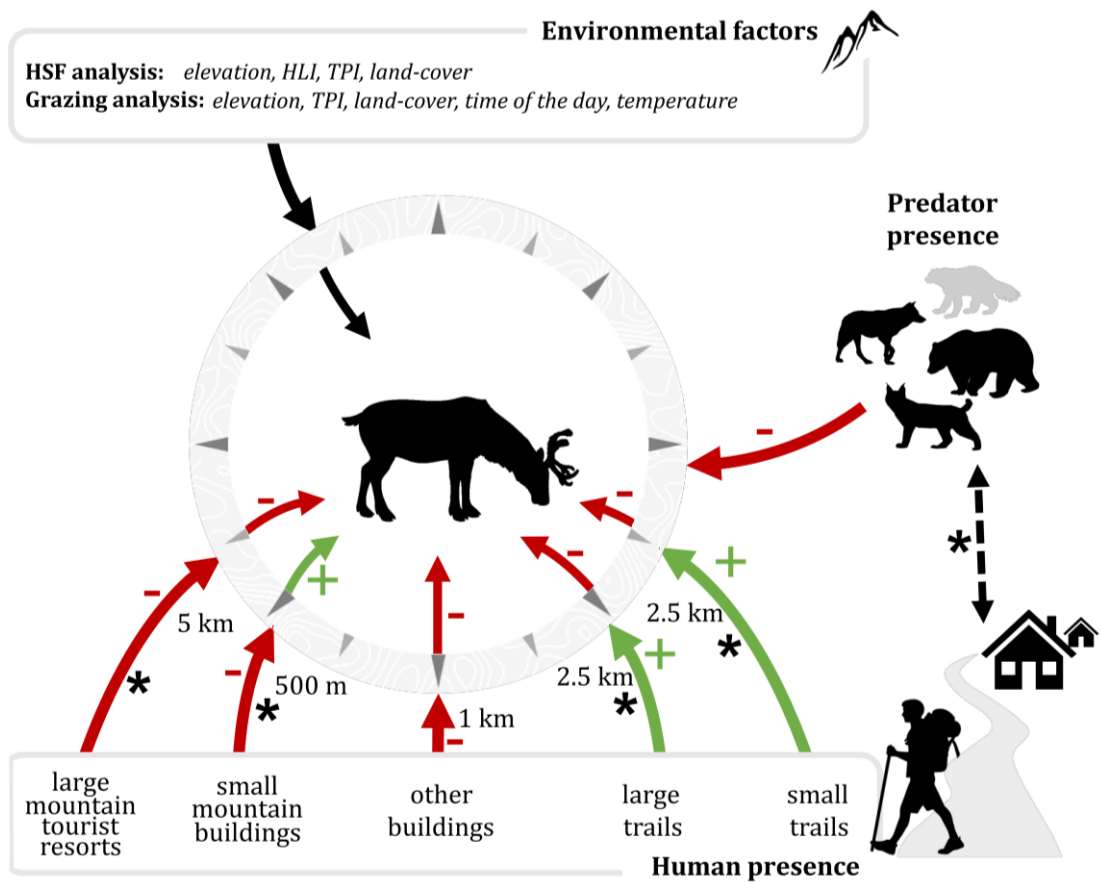


Figure 12. Conceptual model summarizing what drives reindeer grazing in space. For clarity, results are shown for the Handölsdalen district only (see Figure 3 in Paper IV for the other districts). The model includes only significant relationships with the directions of effects shown for human and predator pressures. Arrows outside the compass indicate results from habitat selection function analysis (HSF; focusing on reindeer occurrence), whereas arrows inside the compass represent the results from the generalised linear mixed model (focusing on grazing duration). The distances given for the outer arrows represent the radii of the zones of influence. * denotes the significant interactions between a human infrastructure and predator presence. Wolverine is greyed out because it was present throughout the study area, preventing its effect from being tested. *This figure is based on modified Figure 3a in Paper IV.*

In all districts, reindeer also appeared to use certain human infrastructures as a behavioural refuge from predators, particularly near small mountain buildings or less frequented hiking trails (see Figure 7 in Paper IV). This adaptive behaviour suggests a trade-off whereby reindeer avoided high disturbance areas, but tolerated low intensity human presence when predation risk was high. The identification of significant interaction effects between human and predator presence should also encourage a shift beyond single-driver perspectives when anticipating reindeer responses to cumulative stressors.

An additional key result was that grazing activity itself significantly decreased in the vicinity of most human infrastructures (Figure 12). This pattern indicates that even when reindeer are present near human infrastructures, their foraging behaviour is usually disrupted. Taken together, the results suggest that an increasing human footprint in the tundra may reduce reindeer grazing, likely reinforcing the risk of additive effects between land-use change and climate warming identified in Paper I. In such areas, climate-driven changes may therefore proceed more rapidly in areas that reindeer avoid, or reduce grazing, in response to human presence.

While environmental conditions were the main drivers of reindeer presence and grazing patterns, the effects of human infrastructures and predator presence differed between districts. This context-dependency is consistent with previous research on anthropogenic impacts on reindeer behaviour (Skarin and Åhman 2014), and may reflect differences in reindeer tolerance levels towards human presence depending on the herding district. A strikingly consistent pattern across districts however, was that the predicted areas of prolonged grazing activity were generally larger than areas of high likelihood of reindeer presence, and only partially overlapped (Figure 13). This discrepancy suggests that reindeer restricted their habitat-use despite the large availability of suitable forage across the summer pastures, likely reflecting a combination of perceived predation risk, human disturbances, and additional environmental constraints such as thermal discomfort during warm periods (Valente et al. 2020, Paper II).

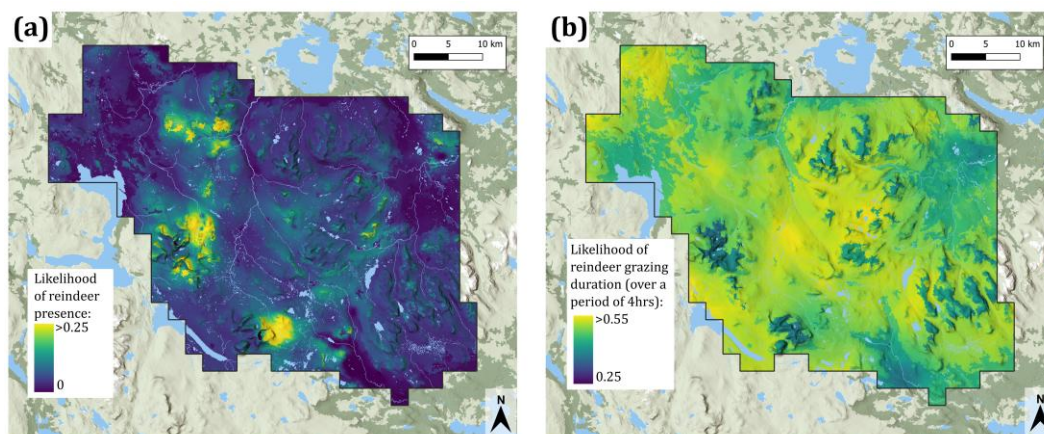


Figure 13. The spatial predictions of (a) reindeer presence (excluding the predator effect due to its coarse spatial resolution); (b) reindeer grazing duration within the study area of Handölsdalen.

4. Discussion and implications for future research

4.1 Potential interactive effects on the reindeer grazing lands

In Paper I, the spatial analysis of the various pressures across Fennoscandia's reindeer herding region showed that the majority of the grazing lands is exposed to multiple overlapping pressures, posing a significant threat to the resilience of traditional northern pastoralism (Horstkotte et al. 2022; Moen et al. 2022). Among these pressures, outdoor tourism emerged as a dominant land-use, particularly in the summer mountain pastures. This type of human presence in the mountain tundra has been shown to influence reindeer habitat selection (Helle et al. 2012; Skarin and Åhman 2014; Gundersen et al. 2020), and Paper IV further demonstrated that although reindeer responses to human activity are context-dependent, both reindeer presence and grazing activity were generally negatively associated with areas of high human activity. Recreational activities in the Scandinavian mountains have a long history, but have intensified over recent decades (Eriksson et al. 2023, Figure 14). Given that semi-domestic reindeer were already reported to avoid tourism buildings in the early 2000s (Skarin et al. 2010), this raises the question of whether reindeer tolerance to anthropogenic disturbances has evolved over time.

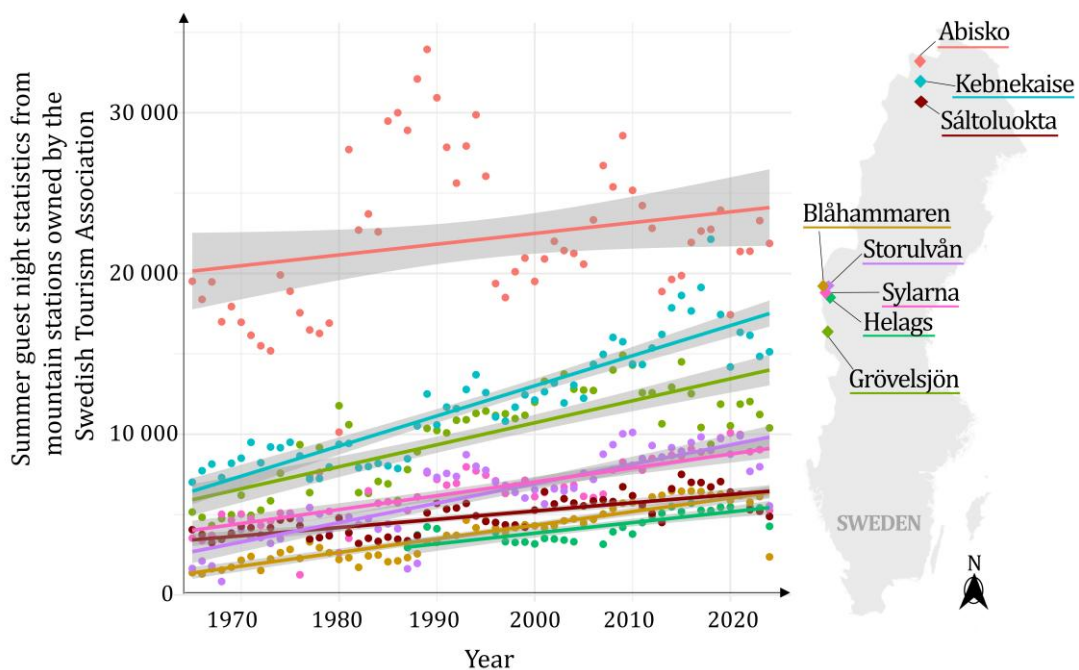


Figure 14. Outdoor tourism trends over time using summer guest nights statistics from the tourist mountain stations owned by the Swedish Tourism Association, for the period 1965-2024 (source: Swedish Tourism Association 2025). The shaded ribbons show 95% confidence intervals around the linear regression trends for each mountain station.

To address this, Wikinger (2024) compared reindeer movement and habitat use in the herding districts of Handölsdalen and Sirges between the summers of 2002–2003 and 2019–2020. The study showed that reindeer exhibited a greater tolerance to tourist infrastructures over time when access to undisturbed pastures was limited, whereas avoidance behaviour persisted where large undisturbed areas were available. These findings are congruent with those of Helle et al. (2012) who observed an increased tolerance of Finnish reindeer towards recreational areas over time, together with some level of avoidance from tourism resorts. Altogether, these findings underscore the need to assess whether ZOI around human infrastructure persist over time (Flydal et al. 2019), and to further investigate the long-term ecological consequences of prolonged avoidance (Barrio et al. 2025). Historical grazing patterns, in particular long-term avoidance of touristic areas by reindeer, and potentially by other wildlife, could unlock climate-driven changes on the tundra ecosystem, that might otherwise be mitigated by herbivory.

To explore this potential cascading effect of human presence in the mountain tundra, I have also analysed vegetation changes, particularly shrub expansion, around six Swedish mountain stations over the past 40 years using historical and contemporary CIR aerial imagery (Stoessel et al. in prep.). Preliminary results reveal a shrub encroachment across all study sites, with an average of $23.4 \pm 2.5\%$ of the current shrub-cover representing new growth that was absent four decades ago (see Figure 15 as an illustration for one study site).

Further, analysis showed that topography was a major driver of shrubification, with elevation, heat load index, slope, and planar curvature showing strong effects. Distance to hiking trails and mountain stations also influenced shrub expansion, although these relationships were non-linear and appeared context-dependent, warranting further investigation. Soil wetness, in interaction with heat load index, was another significant predictor of new shrub establishment. These patterns are consistent with previous research highlighting that temperature, but also soil moisture are important mediators of climate change effects on tundra plants (Bjorkman et al. 2018; Scharn et al. 2021).

Reindeer density data in Sweden are too coarse and outdated to use as a measure of grazing pressure among sites. Hence, it is not possible to test whether differences in the rate of landscape change could be linked to local reindeer density. An alternative approach could be to focus on reindeer habitat use, as it has previously been shown to correlate with the tundra landscape structure (Skarin et al. 2020). Following this line of reasoning, Paper III identified a triangular relationship between soil wetness, reindeer grazing activity, and plant community structure, highlighting the importance of soil wetness in predicting where reindeer choose to graze.

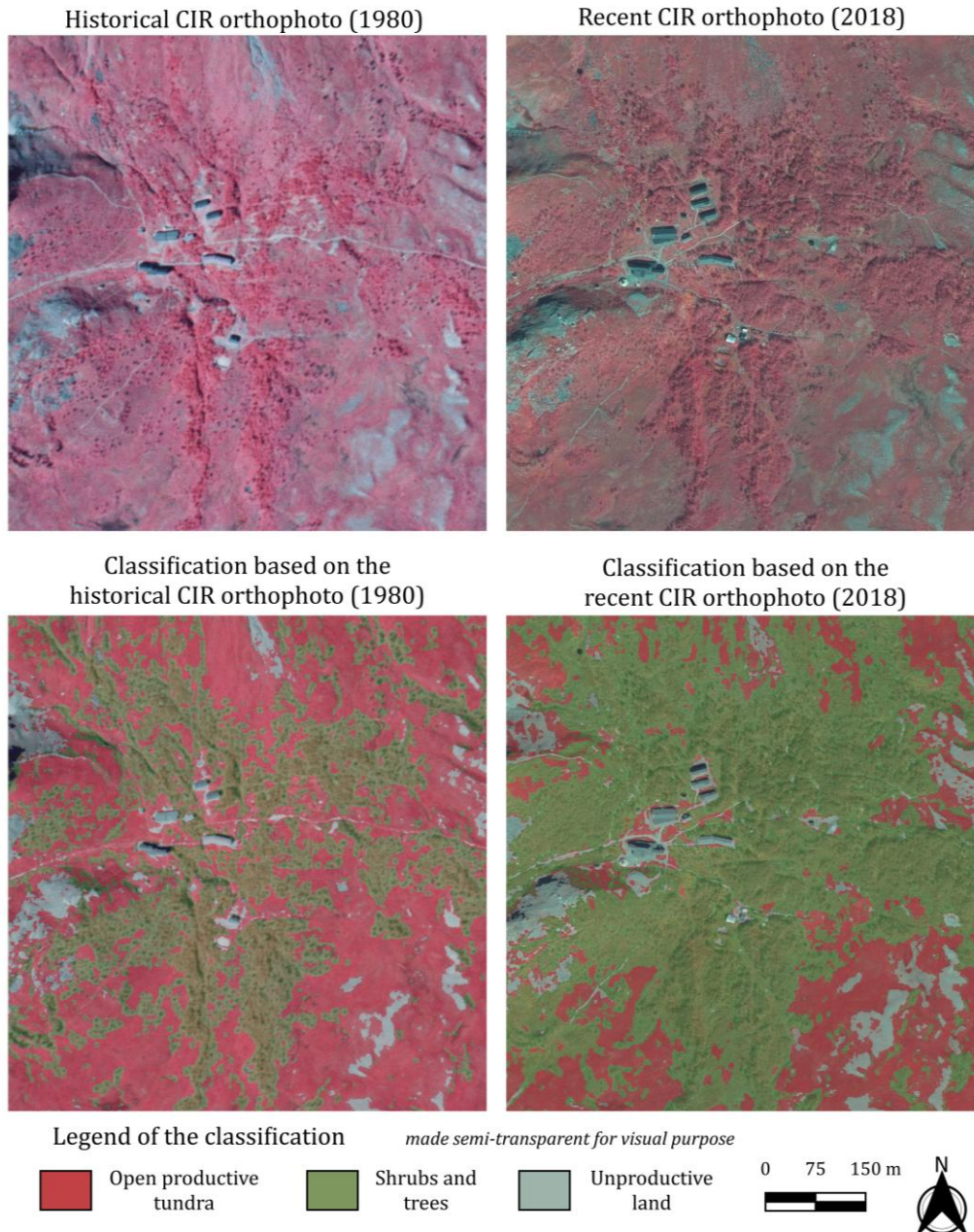


Figure 15. CIR orthophotos and their respective classification result at Kebnekaise mountain station.

The soil moisture regime is an abiotic factor that has received relatively little attention in studies of reindeer habitat use, although it has previously been linked to divergent grazing impacts on tundra plant communities (Saccone et al. 2014; Vowles et al. 2017a). In Paper III, wet sites were grazed much less than dry sites, suggesting that they may offer less attractive forage, likely due to a higher dominance of less palatable evergreen shrubs (Scharn et al. 2021). Wet areas may also host a higher insect abundance and a higher risk of developing diseases (Rasmus et al. 2022; Tryland et al. 2022).

While insect harassment is well known to deter reindeer from low altitude shrubby areas (Moen 2008; Skarin et al. 2008), potentially reinforcing shrub expansion through a reduced grazing pressure (Horstkotte et al. 2017), much less is known

about how pathogen and disease transmission risk might affect reindeer habitat use. Traditionally, herders would prevent the spread of foot rot disease in early summer by relocating their livestock to unused pastures and avoid prolonged use of trampled and wet soils (Riseth et al. 2020). A comparable pattern can be observed in relation to predation risk, as herders would also move their reindeer to safer pastures when predators are known to be present nearby (Sikku and Torp 2008). Fear of predation is a well-known driver of herbivore habitat selection that can trigger cascading effects onto ecosystems (Laundré et al. 2010). By accounting for predation risk, Paper IV revealed an interactive effect between human and predator presence, suggesting that, depending on the predator species in the area, reindeer presence was predicted to increase near tourism infrastructures. This context-dependent response suggests that a human-shield effect can also operate in the mountain tundra, previously documented in other biomes (Berger 2007). These findings hence indicate that predator presence should be considered when delineating zones of influence around human infrastructures and when assessing their potential long-term effects on vegetation. However, it is also important to note that proximity to human infrastructure was still generally associated with a reduced grazing activity.

4.2 Methodological insights from bio-logging technologies

A key insight from the empirical studies (Papers II-IV) is that reindeer grazing cannot be inferred solely from reindeer presence. Instead, how long reindeer forage in different parts of the landscape represents a distinct behavioural dimension from where they select to be. This distinction has received relatively little explicit attention so far, as grazing patterns are usually inferred with spatial movements and distribution ranges of large herbivores (Owen-Smith et al. 2010; Bubnicki et al. 2019; Skarin et al. 2020).

In particular, Paper IV showed a trend where the areas with a high likelihood of reindeer presence were spatially more restricted than the predicted areas with prolonged grazing. This implies that reindeer foraging is constrained within a subset of the summer pastures, and therefore that a high proportion of these pastures upholds a low potential for being grazed, even though large parts of this land are good foraging grounds and appear accessible. Mapping reindeer occurrence thus remains essential for estimating herbivory pressure at the landscape scale, particularly for delineating ZOI and identify areas with a high likelihood of reindeer absence. Ultimately, it is in these areas of reduced pasture use, that prolonged avoidance could lead to pasture abandonment and shrub encroachment, potentially similar to those observed in reindeer exclusion studies. Grazing also causes additional effects on vegetation through trampling and fertilizing (e.g. Barthelemy et al. 2018; Egelkraut et al. 2020). With the rise of bio-logging technologies, accelerometers or incorporated cameras on collars now enable the fine-tuning of herbivory behavioural measurements (Ehlers et al. 2021; Rautiainen et al. 2022). While this thesis focused on grazing activity in broad terms, it would also be possible to separate activities, such as trampling from digging, and browsing from grazing with such bio-logging technologies, which will likely expand our understanding of the specific reindeer herbivory effects on the tundra (Barrio et al. 2025).

Decoupling reindeer presence from grazing activity revealed behavioural responses undetectable through presence data alone, showing that reindeer grazing is more sensitive to biotic and abiotic pressures in the tundra than previously documented, particularly when accounting for heat and soil wetness. Such vulnerability indicates that the ecological impacts of summer pressures may be underestimated. This was particularly evident in relation to the effects of climate warming on reindeer grazing behaviour, demonstrated in Paper II. In northern latitudes, the behavioural impacts of heat on wildlife have received relatively little attention, largely because exposure to high temperatures has historically been rare (Hagemoen and Reimers 2002). Paper II showed that warming summers could trigger not only a strong reduction in grazing activities, but also a net foraging loss over time. With grazing disrupted in space and time, such responses have the potential to disrupt species interactions and weaken top-down control on vegetation in warmer areas, thereby likely accelerating vegetation change under ongoing climate warming. Taken together, these findings highlight the importance of considering not only where herbivores occur, but also how their functional role in ecosystems may be altered by climate-driven constraints on behaviour.

4.3 Climate and land-use effects at a broader scale

Paper I documented a minimum warming of 1.5-2°C over the whole Fennoscandian herding region. Such warming is likely to increase the frequency of warm spells in the subarctic tundra (Paper II) although this effect is likely to vary spatially, with windier coastal areas probably experiencing different thermal conditions than the inland mountain tundra. While Paper II showed that warm spells can disrupt reindeer grazing patterns, much less is known about how other Arctic herbivores respond to heat. Importantly, herbivory pressure in the Arctic is not only determined by the grazing intensity within a single species, but it is also driven by the diversity of the co-existing herbivore species (Olofsson and Post 2018; Barbero-Palacios et al. 2024). Heat may similarly reduce the activity of other cold-adapted herbivores, by resting or seeking thermal refuge (Long et al. 2005). If such responses are widespread, warming summers could progressively reduce herbivory by cold specialists and disrupt key ecosystem processes in the tundra during warm spells. These speculations are consistent with modelling work showing that climate warming is altering the tundra herbivore communities, consequently leading to its borealisation (Speed et al. 2021).

Outdoor tourism was shown to be the dominant competing land-use in the Fennoscandian mountain tundra (Paper I). Areas with high levels of human activity correlated with stronger reindeer avoidance, with the likelihood of human shield being higher when human presence was overall low (Paper IV). As land-uses intensify in the tundra, human activities may force reindeer (or other wildlife) to areas with a higher predation risk, although such effect remains to be studied. Since other tundra regions face more intensive land-uses than tourism (Forbes et al. 2009; Kumpula et al. 2012), synergetic or additive effects between pressures should therefore not be overlooked. For example, in Russia, where land-use changes have been intense (with the expansion of extractive industries) as well as climate change effects (due to rain-on-snow events and anthrax outbreak), this interplay has unexpectedly led to the emergence of arctic fox predation on reindeer calves (Terekhina et al. 2021).

ZOI may also apply more strongly to wild herbivores than to semi-domestic reindeer, given their lack of habituation to human presence (Skarin and Åhman 2014). For example, in Paper IV, I found that semi-domestic reindeer showed a context-dependent avoidance towards human infrastructures, while using the same method for delineating ZOI, wild reindeer actively avoided much larger areas towards similar anthropogenic presence (Niebuhr et al. 2023). While anthropogenic pressures are known to influence the spatial distribution of other tundra herbivores, such as muskox (Cuyler et al. 2020) or geese (Nishizawa et al. 2021), to my knowledge, no studies have yet delineated ZOI for species other than *Rangifer* in the tundra, representing a critical research gap.

Overall, results of this PhD thesis indicate that ongoing climate and land-use changes in the Fennoscandian tundra are likely to constrain herbivory pressure both spatially and temporally. These processes may lead to a fragmented use of summer grazing lands by reindeer, consequently contributing to a negative feedback loop, where shrub encroachment further reduces both the extent and quality of the available grazing pastures (Horstkotte et al. 2017; Horstkotte et al. 2022). While much of the global literature on grazing systems continues to predominantly focus on the risks of overstocking and its degrading effects on vegetation and ecosystems (Anadón and Sala 2026), this thesis points out the ecological significance of where and when herbivory is reduced, drawing attention to areas that are consistently under-grazed or avoided.

From a management perspective, declining pasture quality or accessibility ultimately affects the carrying capacity of the grazing lands. To date, these consequences have been examined primarily through the lens of winter conditions, which are indeed critical for herd survival and productivity (Rasmus et al. 2020; Simmonds et al. 2025). In addition, this thesis emphasizes the importance of cumulative pressures operating during summer, particularly as summer constraints may exacerbate fragmentation and reduce the functional role of herbivory in maintaining open tundra ecosystems. The climate-driven encroachment of evergreen crowberry (*Empetrum nigrum*) in reindeer pastures provides a clear illustration of such processes (Vowles and Björk 2019). Avoided by reindeer, crowberry expansion reduces pasture quality, alters plant community composition, and has been modelled to ultimately affect reindeer herd size if there is no control to its expansion (Nhat et al. 2024; Nhat et al. 2025).

5. Conclusions

This thesis shows that a majority of the grazing lands in northern Fennoscandia is under cumulative pressures, from competitive land-uses, large predators and climate change (Paper I). In the mountain tundra, climate warming was shown to limit reindeer grazing during increasingly frequent warm spells, likely weakening herbivory pressure (Paper II). Where reindeer graze, and more importantly where they consistently avoid grazing, in particular in relation to soil wetness, is modulating the tundra plant community structure (Paper III). Aside from environmental drivers, human presence and predation risk jointly shaped where and how much reindeer grazed in the mountain tundra (Paper IV). Taken together, climate change and land-use changes, alongside other interacting pressures in the Fennoscandian mountains, was shown to constrain reindeer grazing both spatially and temporally despite large areas of suitable forage apparently available. Finally, this thesis highlights the importance of cumulative pressures operating during summer, and encourages for further research on their cascading effects on the tundra ecosystem.

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MERCI



“My childhood tundra”. This wonderful illustration is the first contact I had with the tundra when I was 9 or 10 (it is done by François Desbordes in “Le Livre des animaux sauvages”, edited by Gallimard Jeunesse, 1996). Growing up in a city in the nineties, I was already worried by climate change, and really believed polar bears would become extinct very soon. This is the reason why I wanted to become a scientist. I am now very grateful that I get to study some of the species shown in this illustration, hoping to make a difference.

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