Long-Lasting Ecological Legacies of Reindeer on Tundra Vegetation

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“Alla de rara örter jag för sedt och fägnat mig af, gafvos här såsom uti mignateur. Ja des utan så många att jag sielf fasade, och tycktes mig få mehr än jag bestyra kunne.”

“All those dear forbs that I had seen before and fascinated me, were present here but in miniature. Yes there were so many that I became frightened, and thought I would get more than I could take care of.”

Carolus Linnaeus, upon arrival in the Swedish mountains, 6 July 1732
in: Iter Lapponicum, Lappländská resan 1732
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This thesis is based on the following four studies, which are referred to in the text by their respective Roman numerals:

I. Dagmar Egelkraut, Hélène Barthelemy and Johan Olofsson
   Reindeer trampling causes vegetation changes in tundra heathlands: results from a simulation experiment.
   Manuscript

II. Dagmar Egelkraut, Kjell-Åke Aronsson, Anna Allard, Marianne Åkerholm, Sari Stark and Johan Olofsson
    Multiple feedbacks contribute to a centennial legacy of reindeer on tundra vegetation.
    In review

III. Dagmar Egelkraut, Paul Kardol, Jonathan R. De Long and Johan Olofsson
     The role of plant-soil feedbacks in stabilizing a reindeer-induced vegetation shift in subarctic tundra.
     In review

IV. Sari Stark, Dagmar Egelkraut, Kjell-Åke Aronsson and Johan Olofsson
   Do alternative stable states diverge in soil carbon sequestration? Evidence from historical vegetation transitions in tundra.
   Manuscript
Author contributions

Chapter I
HB and JO conceived the ideas and designed methodology; HB and DE collected the field data. DE analyzed the data and wrote the manuscript, with contribution from all co-authors.

Chapter II
JO, KA and DE designed the study; DE collected the field data; MÅ and AA performed the analysis of aerial photographs; SS was responsible for the soil analyses; DE analyzed the data and wrote the manuscript, with comments from all co-authors.

Chapter III
DE, JO, PK and JDL designed the study; DE and JDL collected the data; DE analyzed the data and wrote the manuscript with substantial contributions from all co-authors.

Chapter IV
DE, SS, and JO designed the study and collected the data in the field; SS did all the soil analyses and wrote the manuscript with substantial contributions of all co-authors.

Author abbreviations
Abstract

Reindeer can have strong effects on the plant species composition and functioning of tundra ecosystems, and often promote a transition towards a graminoid-dominated vegetation type. As a result, they influence many ecological processes, such as nutrient dynamics, soil biotic composition and functioning, and carbon storage. Several studies suggest that the effect of reindeer on vegetation may follow predictable patterns and could induce an alternative stable vegetation state. However, little empirical data on the long-term stability of reindeer effects on vegetation exist, as it is inherently challenging to study these ecological processes experimentally on a sufficiently long timescale. The main objective of this thesis was therefore to gain a better understanding of the long-term ecological processes following reindeer-induced vegetation shifts.

In order to gain a more mechanistic insight in what initially drives this transition, I used a field-based grazing simulation experiment in which I separated defoliation, trampling, moss removal and the addition of feces. This allowed me to test the relative contribution of reindeer-related activities to initiating the shift from moss and heath-dominated tundra towards a graminoid-dominated vegetation state. Additionally, I studied the long-term ecological stability following such a vegetation shift. I did this by addressing historical milking grounds (HMGs): sites where high reindeer concentrations associated with historical traditional reindeer herding practices induced a vegetation transition from shrubs towards graminoids several centuries earlier, but which were abandoned a century ago. Studying HMGs allowed me to address: 1. The potential stability of reindeer-induced vegetation shifts; 2. The ecological mechanisms contributing to the long-term stability of these vegetation shifts; and 3. How such long-lasting vegetation changes influence soil carbon- and nutrient cycling.

I found that trampling by reindeer is an important mechanism by which reindeer cause vegetation change. Addressing HMGs further revealed that this vegetation change can be highly persistent, as the studied HMGs showed only a low encroachment at the surrounding borders in the last 50 years. The vegetation in the core areas of all studied HMGs had remained strikingly stable, and were hardly invaded by surrounding shrubs. Interestingly, soil nutrient concentrations and microbial activities were still different from the surrounding area as well, and even comparable to actively grazed areas. Even after many centuries of changed vegetation composition and soil processes, there was no difference in total carbon sequestration. This suggests that the environmental conditions for microbial decomposition were more important than vegetation composition for the soil carbon stocks, in our study site.

After studying the contemporary habitat use of HMGs by reindeer and other herbivores, investigating the potential plant-soil feedbacks mechanisms and detailed soil analyses, I concluded that several ecological mechanisms contribute to the long-term stability of HMGs: first, the altered soil biotic and abiotic conditions appear to have a stronger advantage for HMG vegetation than for the surrounding tundra vegetation. Furthermore, I found a clear browsing preference of small rodents on single shrubs proliferating in
HMGs, causing a strong limitation on shrub expansion. Moreover, the dense established sward of graminoids likely poses a strong direct competition for space and nutrients, hindering seedling establishment. Finally, I conclude that HMGs are highly stable on relevant ecological timescales, and propose how the concepts of historical contingency and ASS can be applied to understand stability of these reindeer-induced vegetation transitions.
Introduction

1. Herbivores mediate many ecological processes.

Herbivores are present in almost all ecosystems (Moles et al. 2011); by consuming plants, interacting with their environment and being prey for predators, they are a vital link in food chains and thereby mediate top-down and bottom-up processes (Prins & van der Jeugd 1993; Schmitz 2008; Estes et al. 2011). This is true also in the Arctic; herbivores are present across the circumpolar tundra (Barrio et al. 2017), and influence the abundance and composition of the vegetation, although the strength of the interaction varies in time and space (Olofsson, Tømmervik & Callaghan 2012). Reindeer (Rangifer tarandus, caribou in North America) is the only large herbivore with a truly wide distribution in the Arctic, and either domesticated or wild reindeer is found in most tundra ecosystems in varying densities (Uboni et al. 2016).

Herbivory can exert a strong influence on the functioning and structure of plant communities (Schmitz 2008; Borer et al. 2014). By a combination of activities, herbivores benefit some plant species and harm others, which ultimately changes the competitive balance in a plant community. For example, herbivores remove photosynthetically active plant tissue (i.e., defoliation), which in most cases reduces plant growth (Crawley 1997). This process is always to some degree selective, because herbivores prefer certain plant species and plant parts to others, based on palatability and nutrient content (Mattson 1980; Bryant et al. 1983). Trampling is another important process, which unlike defoliation exerts an unselective physical impact on all plants in the trampled area (Cumming & Cumming 2003). Moreover, herbivores alter nutrient cycling rates by removing nutrients through feeding and depositing plant-available nutrients in the form of feces and urine (Pastor, Cohen & Thompson Hobbs 2006; Barthelemy 2016). Plant growth is limited by nutrient availability in many ecosystems, and adding nutrients therefore generally increases plant growth (Aerts & Chapin 1999).

Plant species differ in their tolerance to physical damage caused by defoliation and trampling, and in the extent to which they can benefit from added mineral nutrients. Plants need to balance tolerance to and avoidance of defoliation, meaning that fast growing, palatable species are generally better at tolerating defoliation compared to slow growing ones, or species that are better defended (Herms & Mattson 2010). The ability to resist or be resilient to trampling is primarily determined by vegetation stature, growth form, and location of growth and storage organs (Cole 1995a; b). Further, the extent to which a plant benefits from added nutrients depends on a plant’s ability to take up those nutrients, which to a large extent is governed by root depth, architecture, or associations with mycorrhizal fungi (Aerts & Chapin 1999; Mulder 1999), and on the strategy of allocating these nutrients in terms of growth or storage (Lambers & Poorter 2004). These differences in survival strategies, growth and competitive ability among plant species are important in determining how herbivores ultimately influence the plant community composition (Strauss & Agrawal 1999; Herms & Mattson 2010). Herbivores can, at least in the long-term, increase the abundance of palatable species like graminoids, because
they are well-adapted to tolerating grazing damage and benefitting from added nutrients (Augustine & McNaughton 1998; Del-Val & Crawley 2005).

In addition to changing community composition through altering species interactions and nutrient availability, the removal of aboveground biomass by defoliation or trampling by herbivores can change soil physical properties. For example, it may lead to a change in soil temperature through reducing the density and thus insulating effect of vegetation (Gornall et al. 2007). Lower aboveground biomass may also result in decreased soil moisture because of higher water loss at the soil surface (Srivastava & Jefferies 1996), or alternatively, increased soil moisture through reduced plant biomass production and therefore reduced evapotranspiration (Schrama et al. 2013). Such abiotic changes in soils because of herbivores influence plant performance as well as the activity of soil-dwelling decomposers. Trampling can also directly affect soil physical properties by compacting the soil (Hamza & Anderson 2005). Changes in soil density (i.e., pore size) alter water holding capacity and oxygen available in the soil which can have cascading effects on soil temperature, plant growth, decomposer communities, and moisture (Mulder 1999; Schrama et al. 2013; Veldhuis et al. 2014). Given that, fine-grained soils are known to be more prone to such effects than coarse or organic soils (Schrama et al. 2013).

Herbivores can also indirectly mediate plant-soil processes, by influencing plant composition (Bardgett & Wardle 2003). An altered plant community composition can influence soil biota and soil processes, which may in turn influence plant performance; such two-step interactions are called plant-soil feedbacks (Bardgett & Wardle 2003). Vegetation productivity is often mediated by changes in the soil biotic community (Sørensen et al. 2008; Kardol et al. 2014), such as increased abundances of root-feeding nematodes or pathogens, which can negatively influence plant growth (Chung & Rudgers 2016) or altered communities of rhizosphere microbes and mycorrhizas (Gehring & Whitham 1994). Together, these changes in biotic community can have negative or positive effects on plant growth, and can promote and help sustain the current vegetation composition (Bever 2003; Barto & Rillig 2010; Mangan et al. 2010).

The overall effect of large herbivores on soil fertility can range from positive to negative depending on the type of herbivore, initial productivity of a system, and many other environmental conditions (Bardgett & Wardle 2003; Bakker et al. 2006). For example, browsing by moose can result in a higher abundance of evergreen, non-palatable species which results in reduced nutrient cycling rates (Pastor & Naiman 1992). On the other hand, when promoting a more palatable and nutrient-rich plant community, herbivores can increase nutrient cycling rates (Hobbie 1992), which in return favors fast growing plants (Chapin et al. 1996). This process may also result in the attraction of other herbivores to that place, leading to another positive feedback that maintains the vegetation in a grazed state (Seabloom & Richards 2003); which is one on the main mechanisms behind grazing lawn formation (McNaughton 1984).

The effects of herbivory on carbon (C) cycling and sequestration are complex and less understood than the effects on N cycling. In the short term, defoliation reduces photosynthetic activity and thus gross primary production (GPP) (Metcalfe & Olofsson 2015). However, the long-term effects of herbivory on total C stocks are highly variable.
and dependent on how they specifically affect plant communities, root exudation and turnover, as well as soil microbial respiration (Tanentzap & Coomes 2012). Carbon cycling is mediated by the decomposability of plant litter, which influences carbon storage in the soil through respiration, leaching or immobilization and can thus be enhanced when herbivores promote a more palatable plant community (Cornelissen & Thompson 1997; De Deyn, Cornelissen & Bardgett 2008). On the other hand, graminoids, which are often promoted under grazing, build up a large amount of recalcitrant root biomass, which can contribute to carbon storage in grazed soils (Väisänen et al. 2014).

In conclusion, herbivores can have strong effects on vegetation and ecosystem functioning. Their presence can cause dramatic vegetation shifts that might lead to either less (Srivastava & Jefferies 1996; Côté et al. 2004), or more (McNaughton 1984; Zimov et al. 1995; Augustine & McNaughton 1998) productive vegetation states, and may be persistent over long time scales (van der Waal et al. 2011; Freschet et al. 2014; Valls Fox et al. 2015). One example of such a vegetation shift is the transition from heath- or shrub-dominated tundra to a graminoid-dominated vegetation type, induced by reindeer (*Rangifer tarandus*, caribou in North America) (Olofsson et al. 2001; Olofsson & Oksanen 2002). Reindeer grazing often promotes the development of more productive graminoid-dominated vegetation types through the combined effects of trampling, defoliation, nutrient addition and reduction of the dense moss layer; together enhancing nutrient cycling and soil microbial activity (Olofsson, Stark & Oksanen 2004). Interestingly, such reindeer-induced vegetation changes have been suggested to represent an alternative stable state of tundra vegetation that follow predictable, stepwise transitions in productivity and species composition (van der Wal 2006).

2. **Alternative stable states in ecology and the role of herbivory.**

Sometimes, seemingly stable ecosystems are abruptly changing to a very different state in terms of species distribution, interactions and even abiotic factors. These changes are hard to reverse, often despite intense management practices. The rapid desertification of the Sahara desert (Foley et al. 2003), or loss of coral reefs (Knowlton 1992) can be viewed as examples of such a dramatic shift in biological regimes. Alternative stable state theory is used to understand such dramatic and long-lasting changes in ecosystem composition and functioning. First developed using mathematical models (Lewontin 1969; Holling 1973; Noy-Meir 1975), and later applied to real-life ecosystems (May 1977; McNaughton 1984; Scheffer 1990; Van De Koppel et al. 2001; Persson et al. 2007), the questions addressed are whether more than one stable community could exist in the same habitat, and how small gradual changes in a controlling variable can result in dramatic, often irreversible changes in natural communities.

The alternative stable state theory describes how the state of an ecosystem may have multiple attractors, i.e., can be stable in more than one state. An ecosystem is by definition a combination of many ecosystem variables and environmental parameters that determine its state (e.g., species composition). The state of an ecosystem can shift when certain drivers are changed (e.g., the addition of nutrients), and may respond gradually with a change in such a controlling driver, or remain resistant to change until a
certain threshold is reached and then rapidly shift to an alternative state (Scheffer et al. 2001). Such dramatic shifts can be stable, and show a delayed (hysteresis) response to alteration of the initial driver. For example, when the addition of nutrients is the driver, even when the level of nutrients is brought back to levels equivalent to the levels before the state shift, the species composition would remain in its alternative state. A shift back to the original state therefore usually requires a much stronger reduction of the driving variable, or a different type of disturbance to the system (perturbation), or a combination of the two. An ecosystem can thus be in either of the two alternative states under the exact same environmental conditions.

To simplify this concept, the state of an ecosystem can be imagined as a ball representing the ecosystem state, in a landscape where valleys represent ecosystem equilibria (Scheffer 1990). The ball (ecosystem state) consists of a set of ecosystem-specific variables, whilst the landscape represents the environmental parameters that interact with the ecosystem variables. In the ecological literature, there are two main ways of describing how an ecosystem state shift is initiated (Beisner, Haydon & Cuddington 2003); in other words, how the ball is moved from one valley to the other. One approach, the ‘community perspective’, describes a state shift as a result of a direct impact on a state variable that causes the ball to move in a landscape of unchanged environmental parameters (e.g., Lewontin 1969; Sutherland 1974, Fig. 1). The other approach, the ‘ecosystem perspective’, describes how the state of an ecosystem is altered by a change in the landscape, hence a change in an environmental parameter, which causes the state to land in a different stable point (e.g., May 1977; Scheffer et al. 2001, Fig. 1). Importantly, both these approaches can be a valid way of describing ecosystem processes, and differences are mostly dependent on whether a driver is described as a variable or as a parameter (Beisner et al. 2003).

**Figure 1**: Two approaches of describing an ecosystem state shift: in the ‘community perspective’, a state shift is initiated by a direct impact on the state variables (left); whereas the ‘ecosystem perspective’ describes a state shift as induced by a change in environmental parameters, causing the ball to land at a different location in the landscape. This is analogous to the critical transition point in equilibrium curves. Adapted from Beisner, Haydon & Cuddington (2003) and Scheffer et al. (2001).
Even though there are many studies addressing state shifts in natural systems (McNaughton 1984; Holmgren & Scheffer 2001; Staver, Archibald & Levin 2011; Ratajczak, Nippert & Ocheltree 2014), the question as to which ecological drivers maintain the stability of an alternative state after such a shift occurred, is rarely studied in natural systems. Experimental studies of alternative stable states in natural systems could give insight to such questions. Peterson (1984) listed four criteria that an experiment should meet for it to be an indicator of alternative stable states: 1) The experiment should be performed in one single environment; 2) The experimental site must be shown to be able to be occupied by two communities; 3) The resulting communities should be stable and self-replicable; 4) The experimental perturbation that is supposed to initiate a switch from one stable state to another, should be a pulse perturbation that is representative of the ecosystem and its natural history in terms of intensity, spatial extent and duration. Due to practical limitations, all these criteria are rarely met (but see Persson et al. 2007).

Further, the concept of historical contingency may give a more mechanistic explanation to the long-term stability of state shifts (Fukami 2015). Historical contingency is defined as how the order and timing of species arrival after a disturbance influences further community assembly. Based on which species arrive first, and how they interact with other species or ecosystem processes, these priority effects can lead to different pathways of community assembly and thereby theoretically result in alternative stable states with an altered community structure and functioning. For example, any given set of plant species to first arrive after a disturbance will interact with their environment through a number of ecological interactions (e.g., competitive ability, the quality of litter produced, herbivore attraction, association with soil biota). Each of these interactions may either contribute to the maintenance of the current vegetation type (positive feedback), or may facilitate other species to establish instead (negative feedback) (Kardol et al. 2007). When there is a net negative feedback, other species will be able to establish, and the system is in a transient state. However, when there is a net positive feedback, current vegetation type should be stabilized, i.e., result in a stable state.

Dramatic vegetation shifts induced by herbivores may represent alternative stable states (Brown & Heske 1990; Zimov et al. 1995; Bråthen et al. 2017). By initiating positive (i.e., reinforcing or self-sustaining) ecological feedbacks, it has been suggested that they can drive catastrophic vegetation shifts leading to reduced productivity and habitat degradation (Srivastava & Jefferies 1996; Côté et al. 2004), or to a predictable increase in productivity, by which herbivores maintain their own food source (McNaughton 1984; Seabloom & Richards 2003; van der Wal 2006).

Whether herbivore-induced vegetation state shifts are maintained by active grazing (e.g., Bråthen et al. 2017) or can be maintained even after the grazing pressure is reduced (hysteresis), poses a fundamental difference in interpreting ecosystem stability (Beisner, Haydon & Cuddington 2003), and thus in our understanding of long-term effects of herbivores. Experimental evidence of the stability of herbivore-induced vegetation shifts on a landscape scale is scarce (but see Seabloom & Richards 2003), since it is inherently difficult to study such vegetation shifts in an experimental setting on appropriate temporal scales. In this thesis, I studied the long-term stability of a reindeer-induced
vegetation shift on a centennial time scale, by assessing historical milking grounds (HMGs): graminoid-dominated patches in heath- or shrub-dominated tundra that are formed by high reindeer concentrations in the past.

3. **A brief history of reindeer herding in Northern Sweden.**

In this thesis, I utilize a landscape shaped by traditional historical land use to test ecological theory. It is thus important to briefly introduce the history of land use in the study area. As long as humans have been present in the northernmost areas of the world, reindeer have formed an important part of their livelihood. Hunting was, and in some parts still is, the major form of subsistence, but was gradually replaced by the domestication of reindeer in Eurasia (Ingold 1980). In Fennoscandia, the earliest records of domestication stem from Norwegian tradesmen travelling to England in 890 AD, reporting to the English king Alfred the Great about owning 600 ‘unsold’ reindeer and 6 tame reindeer (Bjørklund 2013). It is, however, possible that domestication originated much earlier when small numbers of reindeer were kept for transportational means, and even used as a decoy attracting wild reindeer to facilitate hunting (Ruong 1969). As any other type of land use, different levels of intensity can be practiced. In reindeer husbandry, intensity is commonly defined as the closeness of the reindeer-man relationship, a product of time and space (Beach 1981). Since the domestication of reindeer, herding practices have ranged between the most extensive to the most intensive forms. The most intensive forms are associated with a high degree of closeness between herders and their reindeer, both in time and space. At the other side of the spectrum is the most extensive form, which to some extent is similar to a hunting system, with the mere difference that reindeer are owned by a herding family or village. Ownership of a reindeer is designated by ear marks with the herder’s signature cut in the reindeer’s ear. The preferred, or most appropriate degree of herding intensity is variable over time and between herders, and dependent on factors concerning social interactions, the amount of reindeer owned, the type of landscape, climate, and/or economy (Ruong 1969).

From the late middle ages up until approximately the early 1900s, reindeer herding in our study area was characterized by a transhumance (semi-nomadic) existence (Ingold 1980; Beach 1981; Aronsson 2009). Because the reindeer were gathered and milked daily during the females’ lactation period from early summer to late autumn (Ruong 1969; Beach 1981), this form of herding requires a very high closeness between herder and reindeer. This type of reindeer herding was common between approximately 1600 and 1900 AD, but recent studies based on pollen analyses and archeological excavations indicate that the first milking grounds were formed around 1350 AD (Aronsson 2009; Staland, Salmonsson & Hörnberg 2011; Wallin & Aronsson 2012). Based on analysis of coprophilus fungi in a mire approximately 50 m from a former milking ground close to our study site, an early phase of intensive herding can be dated from around 1350 AD to around 1600 AD. A second phase is dated from 1600 AD to the late 19th century with a profound influence on the vegetation, resulting in reduction of the willow belt and the formation of a vegetation type with more graminoids and forbs (Andersen 2017).
During summer, herders and their reindeer migrated through the mountain landscape between different grazing grounds, following migration routes based on family traditions (Bergstrand & Spik 1998). Herders and reindeer therefore recurrently resided in the same locations each summer and used the same milking grounds over the centuries. As a result of the concentration of reindeer on the same locations during many centuries, the tundra vegetation transitioned from a shrub- to a graminoid-dominated state, resulting in small, often oval shaped, meadow-like features in the landscape (Fig. 2). Families would stay at one milking ground for several days up to several weeks; until grazing resources ran out, and to prevent the soil from becoming too disturbed and possibly harbouring diseases. Scandinavian mountain environments can be notoriously dominated by mosquitos, pester ing reindeer and human alike. A suitable location for milking grounds was therefore considered to be on a small hill or ridge, where stronger wind reduced discomfort from mosquitos, and at the same time offering a better view of the surrounding. During these summer months, herders stayed in a kåta (goahti), which was typically set up at one end of the milking ground, and simply taken along to the next one when it was time to move. Milk and cheese were an important product of this intensive form of reindeer husbandry, both for domestic consumption as well as for trade (Ruon 1969). Requiring smaller herds of rather tame animals, this form of husbandry may be characterized by a ‘personalized relationship’ (Bjørklund 2013) between reindeer and herder, and starkly contrasted the more extensive husbandry practices that were practiced further north, with a more pronounced focus on meat production (Bjørklund 2013).

Figure 2: ‘Spikalapporna mjölkas sina renar, Sarek, 1902’. Historical reindeer herding in Sarek, the same region as our study site: Sami milking and herding reindeer in a milking ground. Especially noteworthy are the closeness of the herd, and the dense graminoid-dominated vegetation even during active use of the milking ground. Photo taken by Axel Hamberg (Axel Hambergsamlingen, Uppsala university library).
North Sweden, summer 1732. Young Botanist Carl Linné sets out to the scientific journey through northern Sweden that will strongly shape his understanding of botany, and the natural environment in general. Along his way, which leads also through Padjelanta, he describes everything of interest to him in his diary, whether it be natural phenomena, or social encounters with the local people; the Sami. Amongst other things, Linné describes the daily gathering of reindeer for milking, the specific milking process, and even includes several recipes for the processing of milk into different products (Linné 1732):

“[Rubus chamaemorus] is mashed and mixed with reindeermilk, them turning it into a fine tasting dish...”

Sarek, 1895 – 1931. Axel Hamberg is a professor at Uppsala University whose broad research interests range from geography, geology, meteorology and physics. Much of his field studies are conducted in Sarek, a mountainous area just east of Padjelanta. During his travels, he is often accompanied by local Sami who can guide him through the landscape and aid in transportation, using reindeer. In his journal, Axel Hamberg makes note of the herders of the Spik family (‘Spikalapporna’), milking their reindeer, which he also takes photographs of (Fig. 2), and whose milk he buys later that day (Hamberg 1902).

Figure 3. ‘Lager vid Pesaure, Sarek, 1904’, showing Axel Hamberg’s scientific company and field guides. Photo: Axel Hamberg (Axel Hambergsamlingen, Uppsala University library).
At the end of the 19th century, the borders in the northern part of Fennoscandia were closed for seasonal reindeer migration following a series of geopolitical conflicts. Ultimately, these border closures with their devastating effects on Sámi herding practices necessitated a large, partly forced, partly voluntaly relocation of Sami families from the northernmost part southwards along the Scandic mountain chain (Aarseth 1989). This caused a rather abrupt change in herding practices in our study area, because the incoming people had a different herding culture that could not co-exist with the local intensive form of herding (Park 1924). At the same time economy developed substantially, and people turned to the use of higher yielding goats and cattle for milk. Nowadays, reindeer herding is practiced in an extensive form in our study area (and most of Fennoscandia), meaning that reindeer still occupy the landscape, but roam freely and are not actively gathered in milking grounds. Interestingly, a number of historical milking grounds can still be clearly recognized in the landscape as oval-shaped graminoid-dominated patches, with clear borders towards the surrounding vegetation; even a century after their active use ceased.

**Objectives**

The overall objective of this thesis was to understand the long-term legacies of reindeer induced vegetation shifts, and place these in the context of alternative stable state theory. More specifically, I addressed the following questions:

1. Through which activities do reindeer induce a shift from heath and moss-dominated tundra to graminoid-dominated tundra? (I)
2. How stable are such vegetation shifts? (II, IV)
3. Which ecological mechanisms contribute to the long-term stability of these vegetation shifts? (II, III and IV).
4. How do long-lasting vegetation changes influence soil carbon- and nutrient cycling? (IV)
Figure 4: A mountain landscape as can be found in our study site in Padjelanta. The drawing shows a typical shrub type- (left) and heath type- (right) HMG. Drawing: Erik-Jan Bijleveld.
Materials and methods

1. Field sites

The fieldwork for this thesis was carried out in two different locations in northern Fennoscandia (Fig. 5). The first chapter (I) is based on fieldwork conducted in Nordreisa in Troms, northern Norway (69°31’ N, 21°19’ E; altitude 600 m a.s.l.). The climate is suboceanic with average yearly temperatures of 0.2°C during our study, and mean an annual rainfall of 935 mm (Norwegian Water Resources and Energy Directorate, www.senorge.no). The study area is above the local treeline and reindeer husbandry is a common form of land use in this region. A reindeer management fence established in the 1960s characterizes the site. On the one side of the fence, reindeer abundance is very low, and the vegetation on this side is dominated by heath tundra vegetation (with the most common species Betula nana and Empetrum nigrum ssp. hermaphroditum). The other side of the fence is actively grazed during late summer (mostly the second half of August). Here, high concentrations of reindeer have caused a vegetation transition to a graminoid-dominated state, accompanied by increased nutrient availability and soil temperatures (Olofsson et al. 2001, 2004; Stark & Väisänen 2014; te Beest et al. 2016). Using the dramatic vegetation changes alongside the fence provides an excellent opportunity to study the effects of high reindeer abundance on vegetation in a field environment, using the lightly grazed side as a control.

Fieldwork for the remaining three chapters (II, III, IV) was conducted in Padjealta national park in northern Sweden (67°18’ N, 16°42’ E). The average yearly temperature is 0.5°C with an average annual precipitation of 968 mm. Soils in the study area are quite heterogenic, but common soil types are glacial tills and sorted fluvial deposits. Only weak podzolic profiles have developed as is common in arctic soils, and there are signs of cryogenic activity in some of the sites. The area is mostly above the local treeline and the dominant vegetation types are heath and shrub-dominated tundra. Heath tundra is dominated by dwarf shrubs like B. nana and E. nigrum (Fig. 6b), whilst shrub tundra is dominated by taller shrubs (mostly Salix lapponum and/or Salix glauca), with an understory composed of graminoids and short and tall forbs like Cirsium helenoides and Geranium sylvaticum (Fig. 6c). This area has a long history of reindeer herding. Currently, the common form of reindeer herding is mostly extensive, meaning that reindeer are present in the area but at rather low densities and in free walking groups, roaming the landscape. For several centuries up until about a century ago, reindeer herding was practiced in a more intense way in this area. Herders would travel with their reindeer through the landscape in summer, and remain on one location for several days up to
several weeks, and the same sites were used repeatedly for this purpose over the centuries. Because milking of the reindeer was a common practice in this type of herding, such places are called historical milking grounds (HMGs). The repeated high concentrations of reindeer during many centuries have resulted in oval-shaped patches where the vegetation has transitioned to a graminoid-dominated state (Aronsson & Israelsson 2008; Aronsson 2009; Andersen 2017). Interestingly, these HMGs are still clearly recognized in the landscape today, even though the active use ceased approximately 100 years ago, and they occur both in heath and in shrub tundra (Fig. 6).

2. **Historical milking grounds: site selection in Padjelanta**

All HMGs studied were originally identified by the Ájtte Museum during a field survey supported by the Swedish National Heritage Board in 2008 (Aronsson & Israelsson 2008). We selected 14 HMGs in the area between the cabins Stáloluokta and Stáddajåhkå. Seven of these were located in a heath-dominant vegetation type, and seven in a shrub vegetation type (fig. 6a). HMGs were selected based on the criteria that they needed to be large enough to accommodate a 5 m × 10 m inventory plot in the center. Moreover, there needed to be a suitable paired control plot close by. To ensure that all differences in vegetation and the soil organic properties between HMGs and controls are caused by the difference in land use history (*i.e.*, whether or not they were used as milking grounds), we chose a paired control plot close to each HMG (on average 50 m away) where each

![Map of historical milking grounds](image1)

**Figure 6**: Position of the 14 historical milking grounds (HMGs) included in our studies (a). Heath sites (n=7) are indicated by green circles and shrub sites (n=7) by red squares. All sites were included in (II and IV), whereas we selected five heath- and five shrub-type HMGs for (III), which are indicated with a black dot. Examples of a typical heath (b) and shrub type HMG (c), respectively, and a closer view on the vegetation types. The location of the control site is indicated in figure b and c using 'C'. Photos: Dagmar Egelkraut.
control and HMG plot had a comparable topography with respect to aspect, hydrology, sediment and elevation.

3. Field recordings

Vegetation surveys

All vegetation inventories were carried out by point frequency recording, using a 10-pin point frame (pin diameter: 2.5 mm, distance between pins: 5.5 cm). For the vegetation surveys in Reisadalen (I), we placed this frame in a 50 cm × 50 cm subplot at 10 evenly spaced intervals, resulting in a grid of 100 points per plot. For the vegetation surveys in HMGs in Padjelanta (data used in II, III, IV), we placed the point frame in an evenly spaced grid at 40 locations within each 5 m × 10 m plot, resulting in 400 points per plot. Every living leaf or stem touched by a pin was identified to species level. Ground cover was recorded as moss (to genus level), lichen (to genus level) and/or bare soil, rock or litter. Here, we counted only one hit per species, but more than one moss or lichen species could be recorded.

Soil moisture and temperature recordings

Soil moisture was measured in the field using a ML3-ThetaProbe soil moisture sensor connected to a HH2 moisture meter (I). The ThetaProbe sensor measures volumetric soil moisture content in the topsoil. We measured soil temperatures in the field (I, II) using a hand-held thermometer with a HI-765BL probe with a resolution of 0.1°C (Hanna Instruments) that measured soil temperatures at 12 cm depth.

Soil sampling

We collected soil samples using a soil corer (diameter: 2.5 cm), (II, III, IV). For (II) and (III), only the organic layer (A+O horizon) was sampled, and for (IV) the top 5 cm of the mineral soil was sampled as well. After collection, soil samples were stored in airtight bags and kept cool at soil temperature (approximately 10°C) until they could be frozen, maximum one week after sampling.

Herbivore recordings

We measured herbivore presence in HMGs and control plots using trampling indicators and dung counts (II). Trampling indicators are nails that we placed, point down, in the soil in a grid of 25 cm × 25 cm. The nails were pushed down in the soil and then pulled up 1 cm, so trampling intensity could be recorded in the subsequent year as the percentage of nails pushed down in the soil. This method has been used by Olofsson, Stark & Oksanen (2004) and Sitters et al. (2017), and has been shown to provide a robust estimate of trampling intensity. Dung counts in HMGs and control sites were carried out by clearing square meter plots of all dung and revisiting those in subsequent years, counting the number of droppings from reindeer, moose, ptarmigan and rodents.

In addition to herbivore presence we recorded vertebrate and invertebrate browsing damage on shrubs in control plots, along stable borders, and on individual shrubs growing
in HMGs. We did this by randomly selecting a number of shrubs (B. nana in heath sites and Salix spp. in shrub sites) on which we recorded damage caused by invertebrates (on leaves) using a protocol developed by the Herbivory Network (Barrio et al. 2015), reindeer (damaged top shoots) and rodents (top shoots that were cut off and bark damage, both showing clear rodent tooth marks).

4. Grazing simulation experiment

We carried out a field experiment in which the main activities of reindeer were simulated, on the lightly grazed side of the fence in our field site in Reisadalen (I). We selected five blocks of homogenous heath tundra, in which we set up seven square meter plots. We applied the following treatments, that aimed to mimic the heavy grazing intensities at the actively grazed side of the fence: control (C), defoliation (D), feces addition (F), trampling (T), moss removal (M), F+D+T (FDT) and F+D+T+M (FDTM). In moss removal plots, we removed as much of the top layer of bryophytes as possible. In the defoliation plots, we cut all graminoids and forbs down to 3 cm, and removed 50% of leaves from deciduous dwarf shrubs. In the feces addition treatment, we added 500 grams of fresh reindeer pellets, spread evenly over the plot. We simulated trampling by dropping a 5 kg pointed wooden pole 100 times from knee height on the plot. In combined F and T plots, we dropped the pole 80-90 times, then added feces and applied the remaining hits. We recorded vegetation composition, soil moisture and soil temperature in 50 cm × 50 cm subplots to avoid edge effects, just before the treatments were applied to the whole square meter plots. This experiment was run for six consecutive years (2011-2016).

5. Plant-soil feedback experiment

The third chapter (III) is based on a greenhouse experiment in which we analyzed the growth of two phytometer species; a typical HMG forb (Potentilla crantzii) and a typical control shrub species (B. nana), on HMG- and control soils. We collected samples (approximately 2 liters) of the organic soil layer from five heath-type HMGs and paired control plots, and five shrub-type HMGs and control plots in 2015. A subsample of each of these soils was used untreated (‘live soils’) and another subsample was sterilized using γ-radiation (≥ 25.0 kGy) at Synergy Health Ede B.V., location Etten-Leur, the Netherlands. Each sterilized soil sample was then divided in half, one part receiving an inoculum of HMG live soil, and the other part an inoculum of control live soil (10% of mass; ‘inoculated soils’). This allowed us to separate the relative importance of soil abiotic and biotic factors on plant growth. For the plants used in this experiment, we collected seeds of B. nana in Padjelanta in 2014 and we retrieved seeds of P. crantzii through a specialized seed company (Pratensis A.B.) in northern Sweden. The seeds were reared to seedlings in a climate chamber on sterilized sand and then transplanted into the prepared soils. The pots with soils and seedlings were placed in a climate chamber set to mimic a growing season in Padjelanta in terms of temperatures and daylight duration. We allowed the plants to grow for just under three months, before harvesting, drying and weighing the above- and belowground biomass.
Finally, we analyzed roots of the plants for mycorrhizal colonization as a proxy for the effect of soil biota. Roots of *B. nana* are commonly associated with ectomycorrhizal fungi, which we analyzed using a 10-12.5 × magnification and counting the percentage of root tips infected with mycorrhizas (Brundrett et al. 1996). The roots of *P. crantzii* are usually associated with endomycorrhizas, which we analyzed by clearing the root tissue using a 2.5% KOH solution, and then using a trypan blue stain that binds stronger to mycorrhizas than to plant cell walls (Koske & Gemma 1989). We then counted the number of hyphae protruding into the plant roots using the gridline intersection method (McGonigle et al. 1990).

6. **Aerial photograph analysis**

To study how stable the HMGs are over time (II), we analyzed high resolution aerial photographs of the study area (1964 and 2008, © Lantmäteriet [I2014/00764]). They were interpreted in a stereo environment, by outlining the HMG shape in the aerial photos from 1964, which was then copied onto the 2008 image. When clear deviations in vegetation were noted, the outline was altered (Fig 7b). This was carried out using ArcGIS and Summit Evolution, on a Planar screen for interpreting in stereo. We could then calculate the total area of each HMG, as well as the percentage of surface change over time. Additionally, we calculated the inward advance of the border in cm per year over the period 1964–2008, by selecting 32 evenly distributed points along each 1964 border and measuring the shortest distance to the 2008 border (Fig. 7c). We were also able to identify reinvaded parts of HMGs (transition zones), where the heath or shrub edge had encroached into the HMG during the last 44 years.

**Figure 7**: Example of the aerial photograph analysis of a heath type HMG (a). The outlines of the HMG in 1964 were copied onto the 2008 image and altered when a deviation in shrub abundance was noted (b). Using the combined outlines, we measured the (mostly inward) expanse of the border along 32 evenly distributed points (c). Note that some parts of the border were stable whilst others moved. This was the case in all analyzed HMGs.
7. Soil analyses

Microbial, soluble organic and mineral N and P (II, III, IV) were analyzed as follows: In (II), extractable inorganic N and P (NO$_3$-N, NH$_4$-N, PO$_4$-P) were measured by shaking 2-3 g fresh soil in 50 ml 0.5M K$_2$SO$_4$ solution (2 hours) before filtering. The extract was then analyzed colorimetrically (Bremner 1965) using automated flow injection (FIA star 5000, FOSS Analytical, Denmark). All extractable N and P in the extract was then oxidized to NO$_3$ and PO$_4$ (Williams et al. 1995) and then analyzed as described above, to retrieve total extractable N and P concentrations. For microbial N and P, soil samples were fumigated (chloroform, 18 hours) prior to extraction and N and P analysis conducted as described above (Brookes et al. 1985). We then calculated the microbial biomass N and P by subtracting the total extractable inorganic N and P from the extractable N and P of the fumigated samples. Following Brookes et al. (1985), we used a correction factor, dividing by 0.54 to account for incomplete fumigation. In (III), mineral N and P were analyzed from soil subsamples that were extracted in 1 M KCl. The extracts were analyzed for mineral N (NH$_4$-N and NO$_3$-N, using wavelengths 660 nm and 520 nm), and mineral P (PO$_4$-P, wavelength 880 nm) by spectrophotometry using an AutoAnalyzer 3 Spectrophotometer (Omniprocess, Solna, Sweden). In (IV), we determined the concentrations of NH$_4$-N (SFS 3032, Shimadzu UV-1700 spectrophotometer), NO$_3$-N (SFS-EN ISO 13395, CFA Seal Analytical AA3) and PO$_4$-P (Murphy & Riley 1962; Shimadzu UV-1700 spectrophotometer) from the soil extracts according to standard protocols.

For total C and N content, samples were dried at 70°C for 18 hours and milled using a ball mill. They were then converted to CO$_2$ and N$_2$ by combustion using an Elemental Analyzer (Flash EA 2000, Thermo Fisher Scientific, Bremen, Germany). All values obtained (C, N and P) were recalculated to g m$^{-2}$. We used the information on the soil layer thickness, bulk density and OMC% to calculate the total N stock in the organic soil layer (II) and total soil C stock in both the soil organic and the top mineral soil layers on an area basis in (IV).

Soil pH (II) was measured by extracting 2 g fresh soil in 50 ml 1M KCl solution, shaking for 2 hours and leaving to settle overnight before measuring pH using a Corning Model 220 pH meter. Moisture content (II, IV) was analyzed as gravimetric weight loss after drying the soils overnight (12 hours) at 105 °C, and organic matter concentration (OMC%) was determined by loss on ignition (475°C, 4 h).

To quantify microbial activity for soil carbon decomposition and N and P mineralization (IV), we measured extracellular enzyme activities (EEAs) after incubations with selected substrates using a microplate method (Allison, Czimczik & Treseder 2008). EEAs provide a tool to understand which resources soil microorganisms derive from soil organic matter degradation based on whether the enzymes catalyze the degradation of organic compounds that contain only carbon (e.g. β-glucosidase; (BG)) or compounds that contain both carbon and nutrients (e.g., N-acetyl-glucosamidase, (NAG); acid-phosphatase, (AP); Sinsabaugh et al. 2008, Wallenstein et al. 2009). Extinction coefficients for calculating EEAs were obtained based on standard curves for paranitrophenol and results calculated as µmol h$^{-1}$ g$^{-1}$ SOM. The Q10 values for EEAs (Q10BG, Q10NAG, Q10AP) were calculated by plotting the natural logarithm of activities against temperature and using the slope (k) of the linear regression, Q10=e(10*)
To analyze the total CO₂ release (microbial respiration) from the soils, a sub-sample of ~3 g soil was incubated in field moisture in 120 ml glass vials. After 48 h pre-incubation, the CO₂ concentrations in the headspace were analyzed every other week for 12 weeks using a gas chromatograph (HP 6890; Stark et al. 2015).

8. Statistical analyses

We analyzed vegetation composition per treatment using the NMDS function (metaMDS function, Oksanen et al. 2017) in the statistical package R (R Core Team 2013) based on the point frequency species counts in each plot (I, II). In some cases, we merged species to collective taxa, to remove inconsistencies in species identification among years. We also grouped the plant species in functional groups following Chapin et al. (1996), but added bryophytes, in order to get more insight in differences between plant communities. In (I), we analyzed the abundance of species in these functional groups over time by calculating the percent change of abundance compared to the first (baseline) year, using the following formula:

\[
\text{\% change} = \left( \frac{\text{count}_{2011} - \text{count}_{20xx}}{\text{count}_{2011}} \right) \times 100\%
\]

We used paired t-tests to test for differences in abundance per plant functional type between control and HMG (II).

We used ANOVAs to test for differences between treatments in functional type percentages in 2016 and soil moisture and temperature data (repeated measures ANOVA) (I); to test for differences between heath- and shrub type HMG and control plots in soil properties, herbivore visitation data and browsing damage (II); to test for differences between soil origin and inoculum for biomass, root:shoot ratios, mycorrhizal colonization and soil properties (III); and for differences between heath- and shrub type HMG and control plots (IV). When appropriate (p<0.05), outcomes were further analyzed using post-hoc testing. Datasets were adjusted using log- or square root transformations where needed, to avoid heteroscedasticity.

Lastly, we used a multiple linear regression to test the relative shrub encroachment (% surface decrease) in relation to mineral N availability, border unevenness, area and HMG vegetation density (II), and to test correlations between the soil carbon stock and environmental variables (IV). Statistical tests (I, II, III) were performed using the statistical package R (R Core Team 2013), and using IBM SPSS 22 Statistical Software in (IV).
Figure 8a: Schematic characterization of ecosystem components and a simplified nitrogen cycle in heath tundra (left) and HMG (right). The width of the black arrows indicates the relative strength of the nutrient flow. The height of the grey bars schematically depict measured pool sizes of soil compounds (mineral N and P, total N and C).

Figure 8b: Schematic characterization of ecosystem components and a simplified nitrogen cycle in shrub tundra (left) and HMG (right). The width of the black arrows indicates the relative strength of the nutrient flow. The height of the grey bars schematically depict measured pool sizes of soil compounds (mineral N and P, total N and C).
Results and Discussion

1. **Trampling is an important mechanism by which reindeer induce vegetation shifts.**

Reindeer can cause dramatic vegetation shifts, but little is known about the relative contributions of isolated grazer activities to initiating such a change. I studied the separate effects of trampling, defoliation, feces addition and moss removal using an experimental field study, and monitored the vegetation response during 5 years (I). I found that trampling was the main mechanism altering vegetation composition, causing a dramatic reduction in the abundance of evergreen and deciduous dwarf shrubs (Fig. 3, I), which is probably explained by their rather high sensitivity to mechanical damage (Jonasson & Callaghan 1992; Cole 1995a; b). Even though many studies show that reindeer grazing increases graminoid abundance (Thing 1984; Olofsson et al. 2001; van der Wal 2006), and given the fact that this can happen within comparable timescales in our study site (Olofsson 2006; Ylänne et al. 2017), graminoids were surprisingly slow to increase in abundance under any of our treatments. I attributed this delayed response to a low initial abundance of graminoids in our experimental plots, and to a slow uptake of nutrients from the feces addition treatments. Nutrient release might have been enhanced in a more humid environment aiding the decomposition of fecal pellets (van der Wal et al. 2004; Skarin 2008), and/or with the addition of urea, simulating an important source of plant-available nitrogen from reindeer urine (Hobbs 1996; Barthelemy et al. 2017). I concluded that the strong effect of reindeer trampling on vegetation composition is an important factor to consider when predicting the effects of reindeer on tundra vegetation, especially because reindeer are migratory (Skarin et al. 2010) and much of their habitat is dominated by trampling-sensitive shrub species (Manseau, Huot & Crete 1996; Moen, Boogerd & Skarin 2009).

2. **Reindeer-induced vegetation shifts can be stable on centennial timescales.**

Aerial photographs and vegetation surveys showed that HMGs exhibit a strikingly stable vegetation of turf-forming graminoids and forbs that remained uninvaded by shrub species during a century since the active use ceased (II). I found no difference in community composition between HMGs, regardless of whether they had been formed in heath vegetation or in shrub vegetation (Fig. 3, II). Only at the borders of the HMGs, the heath and shrub vegetation showed a slow vegetative encroachment at a rate of on average 5 cm year\(^{-1}\) during the last 50 years. This vegetative encroachment was never evenly distributed along borders, as in each HMG some parts remained stable while other parts showed encroachment. There was no difference in the rate of invasion between heath- or shrub type HMGs (II).

Maybe even more astonishing than the HMG vegetation remaining in a different state for a century after active use, is that the soil nutrient concentrations and microbial activities still were different as well. Mineral N concentrations (\(\text{NH}_4^+\) and NO\(_3^-\)) were still up to 10
times higher in the HMGs in the heath habitat, even though there was no difference in the total N pool (Fig. 5, II). This clearly indicates that HMGs remain to be characterized by a more open N cycle maintained by different biotic feedbacks, even a century after the active use ceased (Fig. 8a and b). I also found direct indications that soil microbial activities still are different in the HMGs, especially regarding soil enzymatic N:P stoichiometry (IV). Although we do not know to which extent these processes are different now, compared to the era when the HMGs were actively used, it is noteworthy that the detected differences in mineral nitrogen concentrations and extracellular enzyme activities between controls and HMGs were not any weaker than those found in similar vegetation transitions with existing grazing (Stark & Väisänen 2014). Detailed analyses in the transition zones where heath and shrub vegetation had been invading the graminoid dominated vegetation during the last 50 years, suggests that soil microbial activity for carbon degradation (BG) responds slower to vegetation changes than microbial activity related to N acquisition (NAG) and phosphorous acquisition (AP) (IV). These findings reveal, for the first time, that the strength of a historical legacy on soil functioning varies among processes.

Common definitions for an ecologically stable community include: 1. resistance to invasion by species in the species pool that had multiple opportunities to colonize; and 2. having undergone population dynamics over multiple generations within the community since initiation (i.e., being self-replicable) (Peterson 1984; Fukami 2015). Based on our findings in (II and IV), we conclude that indeed, vegetation shifts induced by high reindeer concentrations can be highly stable, as illustrated by HMGs. There are no signs of successful seedling establishment of the surrounding vegetation into the HMG vegetation, even though countless opportunities must have passed, and there should be no limitation of seed availability on the spatial scale considered here. Depending on definition of an individual plant, clonal plants can be very long-lived even if their aboveground production is renewed annually (De Witte & Stöcklin 2010). The second assumption could therefore be debated in terms of plant community stability; however, I also found strong differences in microbial processes, and microbes have a much shorter generation time. Moreover, if a century resisting invasion is insufficient to be categorized as an alternative stable state, the practical value of the concept will be limited, at least in terrestrial systems with long-lived plants.

3. Altered ecological interactions contribute to the maintenance of HMG vegetation.

Despite the slow vegetative encroachment of parts at the borders, I found no signs of invasion by the surrounding heath or shrub vegetation in the center of the HMGs, showing that establishment success of shrub species via seedlings is low in HMGs although nutrients are abundant and environmental conditions should be suitable. This might indicate that the HMG vegetation has a competitive advantage over the invading shrubs and dwarf shrubs. Although the attempt to measure competitive interactions directly in this study system failed due to high mortality of the phytometer seedlings, I can, based on our findings, identify four mechanisms that contribute to a competitive advantage of
the established herbaceous vegetation and thereby to a positive, stabilizing feedback (Fig. 9).

First, I found a higher mineral N availability in heath type HMGs compared to controls (II, III, IV). Based on our findings in the plant-soil feedback experiment (III), combined with the general theory of fast-growing versus slow-growing plant species and their ability to take up and use nutrients (Lambers & Poorter 2004), I conclude that this enhanced mineral N availability favors the established HMG vegetation more than the heath and shrub vegetation. Second, I showed that in both heath and shrub sites, small rodents (lemmings and voles) have a strong browsing preference on single shrubs establishing in HMGs, compared to control sites or borders (Fig. 6, II). This intense browsing by rodents is expected to have a strong effect on the shrub expansion (Olofsson et al. 2009). Third, herbivore-induced vegetation shifts can alter soil biotic communities, which may result in historical contingency (Kardol et al. 2007), and vegetation stability (Bever 2003; Revilla et al. 2013). By separating biotic from abiotic factors in the plant-soil feedback study (III), I showed that indeed, HMG biota facilitated higher growth rates for HMG vegetation compared to control, in heath type HMG soil (Fig. 4, III). Last, HMGs are characterized by a high dominance of dense, turf-forming graminoid species. I propose that these well-established dense grass swards are hard to invade due to strong competition for light and accessibility to the soil layer. We tried to experimentally test this hypothesis by planting seedlings of an evergreen (V. vitis-idaea) and deciduous (Salix) shrub species in HMG- and control plots, both in undisturbed vegetation and small gaps. Unfortunately, most seedlings died irrespectively of habitat and treatment due to unusually dry and warm weather. Nevertheless, this study still illustrated how demanding it is for seedlings to establish in these habitats.

Figure 9: Conceptual model of the main studied ecological processes contributing to the resistance to shrub establishment in HMGs. The width of the arrows is indicative of the relative strength of the interaction. Grey arrows indicate a neutral effect, and dashed arrows represent processes that were not measured directly, but rather inferred from our general understanding of HMGs.
4. **Insensitivity of carbon pools to long-term grazing and altered vegetation.**

HMGs can be used to study the long-term effects of different ecosystem states on carbon storage. Contrary to what we expected, we found that carbon pools were unaffected by vegetation state (HMG or control). The insensitivity of carbon storage is surprising considering that the sites have had highly contrasting vegetation for centuries, which is expected to result in differences in litter quality and soil biota (especially mycorrhiza) (II, III). I also recorded differences in enzyme activities, and nearly significant differences in microbial respiration (IV), which both are expected to influence carbon sequestration (Tanentzap & Coomes 2012; Väisänen et al. 2014). I proposed that the multi-centennial differences in plant and processes may have coincidentally counteracted each other, resulting in a similar rate of soil carbon sequestration, or that the environmental conditions for microbial decomposition are more important for the soil carbon stocks than vegetation composition. I concluded that despite a long legacy of grazing on the soil processes in tundra, grazer-induced alternative states might not necessarily differ in the ecosystem capacity for storing soil carbon.

5. **Historical milking grounds in the light of alternative stable state theory.**

Historical contingency, i.e., the effect of the order and timing of past events, can influence contemporary community assembly (Fukami 2015). Based on my findings (I, II, III, IV), I argue that this concept can be applied to explain how the effects of reindeer on tundra vegetation can be strikingly long-lasting, as is illustrated by historical milking grounds (HMGs). I reason that an initial disturbance, caused by repeated high concentrations of reindeer during several centuries, resulted in a strong decrease in heath- and shrub-dominated vegetation (I). The high reindeer abundance simultaneously promoted graminoids to become dominant in HMGs. Graminoids are able to withstand high rates of defoliation and rapidly take advantage of increased nutrient availability from feces and urine, which gives them a competitive advantage over other plant functional types and allows them to become dominant in areas that are (heavily) disturbed by reindeer grazing (McNaughton 1984).

My investigations of HMGs (II, III, IV) revealed that this shift in species dominance induced a series of ecological interactions (Fig. 7a and b, II, IV). Some of these processes appear to influence the ability of other species to establish in these sites (priority effect), or in

![Figure 10: Hypothetical model visualizing how HMGs can be interpreted in the context of the alternative stable state theory. Adapted from Beisner, Haydon & Cuddington (2003).](image)
other words, contribute to increased competitive ability of HMG vegetation over the surrounding vegetation in HMGs (i.e., a home advantage). This generates a positive, stabilizing feedback of HMG vegetation (Fig. 9). Importantly, none of these altered processes were dependent on contemporary high intensity reindeer grazing, and not induced by a direct legacy of higher nutrient input from the past.

I here propose a slightly altered way of describing state shifts and stability, by combining both the ecosystem perspective and community perspectives discussed by Beisner, Haydon & Cuddington (2003). The high concentrations of reindeer can be viewed as a change in an environmental parameter acting as a pulse perturbation, and initiating a vegetation shift towards an alternative vegetation state; following the ‘ecosystem perspective’. The subsequent establishment of a dense graminoid mat then resulted in a series of altered biotic interactions, or state variables, that generate a positive feedback maintaining HMG vegetation; following the ‘community perspective’ (Fig. 10). Noteworthy, this state is maintained for centuries after reindeer pressure is reduced dramatically, showing a clear hysteresis effect in response to the initial driver of the vegetation shift.

Concluding remarks and implications

Historical milking grounds are unique landscape features showing legacies of historical herding traditions in an otherwise relatively undisturbed environment. Owing to their cultural value (Aronsson & Israelsson 2008; Aronsson 2009), understanding their ecology is important if conservation of these landscape features is desired. Even though the HMGs studied in this habitat were highly stable, this may not hold true in other environments.

Reindeer grazing has also been proposed to reduce the shrubification of the tundra (Olofsson et al. 2009, Myers-Smith et al. 2011). Reducing the expansion of trees and shrubs in the Swedish mountains in response to a warmer climate, and thus contributing to maintaining the open tundra is considered to be an important ecosystem service that reindeer provide in the Swedish environmental quality goal (Naturvårdsverket 2017). This study contributes to the evidence that reindeer can efficiently reduce shrub encroachment and suggests that these effects can be extremely long-lasting, at least under certain conditions. This indicates that reindeer may be a more important tool than previously believed in conservation of our mountain environments in a changing climate.

Lastly, HMGs allowed me to gain insight in long-term ecological processes. Studying these culturally induced features, increased my understanding of ecosystem stability in a way that could not be achieved by traditional experiments alone.
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