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Gaia Francini

Plant-Soil Interactions in Cold Climate

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ABSTRACT

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Soil characteristics such as pH, nutrient availability and organic matter content are often the determinants of soil biota composition, ecosystem functioning and vegetation composition. On the other side, above-ground, herbivory exerts as well a strong effect on soil and its inhabitants. Plants are the interface between these two worlds, and the dynamics connecting soil and plants are strictly interwoven. The aim of this thesis is to investigate in first instance how soil characteristics relate with soil microbial community and arbuscular mycorrhizal fungal community. Then I investigate the effect of reindeer grazing on plant community, soil community, arbuscular mycorrhizal fungi and nutrient cycling in two low Arctic meadows. As grazing is composed of a sum of different mechanisms, namely trampling, fertilization and defoliation, I also tested whether defoliation rather than fertilization is the main determinant of changes in the arbuscular mycorrhizal fungal abundance in plant roots. Soil characteristics played a central role in shaping arbuscular mycorrhizal community. This observation confirms that arbuscular mycorrhizal fungi show a certain degree of ecological specificity and adaptation to different environmental conditions. Soil characteristics played also a very important role in determining the ecosystem response to grazing. Plant and microarthropod community had a parallel response to grazing relief, which was observed only in the site characterized by the highest nutrient availability. Grazing relief was responsible of an increase in nutrient cycling, which again was observed only in the nutrient rich site. These findings suggest that the speed of the recovery process from grazing is favored when nutrients are more abundant. I also demonstrated that the different components of grazing have different importance on the variables under investigation. In particular I showed that fertilization and not defoliation caused a reduction in arbuscular mycorrhizal colonization in the grass *Deschampsia flexuosa*.

Keywords: Above-ground; below-ground; *Deschampsia flexuosa*; grazing; arbuscular mycorrhizal (AM) fungi; microarthropod; soil microbial community.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV.

I Francini G., Liiri M., Männistö M., Stark S. and Kytöviita M-M. Recovery from reindeer grazing depends on soil characteristics in a low arctic meadow ecosystem. Submitted manuscript.

II Francini G. and Kytöviita M-M. Reindeer grazing does not promote nutrient cycling and reduces AM colonization in low arctic meadow ecosystem. Manuscript.

III Francini G. and Kytöviita M-M. AM colonization in *Deschampsia flexuosa* responds to fertilization more strongly than to defoliation. Manuscript.

IV Francini G., Männistö M., Alaoja V. and Kytöviita M-M. Arbuscular mycorrhizal fungal community divergence within common host plant in two different successional stages in the subarctic. Submitted manuscript.

The table shows the contributions to the original papers.

	I	II	III	IV
Original Idea	MMK, GF	MMK, GF	MMK, GF	MMK, GF
Data	MMK, MM, SS, GF	GF, MMK	GF, MMK	MMK, MM, VA, GF
Analyses	ML, MM, SS, GF	GF	GF	VA, MM, GF
Statistics	GF	GF	GF	GF
Writing	GF, MM, SS, MMK	GF, MMK	GF, MMK	GF, MM, MMK

GF= Gaia Francini, MMK= Minna-Maarit Kytöviita, MM= Minna Männistö, ML= Mira Liiri, SS=Sari Stark, VA= Vilhelmiina Alaoja

1 INTRODUCTION

1.1 Prelude

Everything that happens above-ground has its roots in the soil as well as soil processes are largely determined by above-ground dynamics. In nature everything is connected and it is impossible to study terrestrial ecosystems without accounting for the below-ground part. Soil hosts a great diversity of life forms: microbes, fungi, algae, protozoa, invertebrates and the food webs that they form are complex and poorly known. Their interactions -and reactions- with and to above-ground processes have huge implications in nutrients cycling, organic matter accumulation, carbon storage and ultimately in ecosystem structure and processes. The heterogeneity and complexity of the soil matrix does not facilitate the investigation and the extrapolation of general mechanisms and rules. Therefore soil science strongly relies on a combined approach of field and greenhouse experiments. Field experiments try to catch the functioning of natural dynamics *in situ*, avoiding oversimplification. Greenhouse experiments help the scientists disentangling the complexity faced in the field and clarifying the fundamental mechanisms of ecosystem functioning. However, field investigation can be extremely challenging due to the high number of variables present. Arctic ecosystems are notably species poor compared to temperate or tropical ecosystem. This characheristic render Arctic ecosystems the perfect natural laboratory to explore and investigate ecosystem functioning and dynamics.

Even though the main focus of this work lies under the ground it cannot be disconnected from the plants and above-ground processes. Plants represent the interface between soil and surface processes and plants link these two components. Soil and plant dynamics are strictly interwoven, thus they must both be taken in account. In this thesis I investigated mainly two aspects of soil, plant and Arctic ecology. In the first two manuscripts I describe the effect of reindeer grazing on plant, (I) soil community, (II) nutrient cycling and root fungal symbionts; in the III manuscripts I present an experiment of simulated grazing in controlled conditions on root fungal symbionts; finally in the IV manuscript I explore the relationship among soil characteristics, soil microbial and plant root fungal community. The overall picture that emerges from this work sees the soil as the main factor shaping plant, fauna and microbial community and their responses to biotic factors. After four years of work more questions than answers opened up. Soil ecology remains a challenging and exciting field of investigation, and it does not matter how deep you go, I still feel I have just scratched the surface.

1.2 The Arctic biome

Arctic can be referred to those areas lying beyond the climatic limit of the boreal treeline (Bliss 2000). Arctic biome can be further divided in the low Arctic, on which this thesis focuses, and high Arctic. The low Arctic is characterized by treeless vegetation known also as tundra. Arctic tundra (from the Russian тундра, tūndâr in Sami and tunturi in Finnish) stands for "treeless mountain tract". Tundra is characterized by a mosaic of vegetation. Acidic soils host a heath vegetation characterized by low diversity and productivity, while calcareous sites are characterized by more productive and diverse graminoid dominated meadows (Gough *et al.* 2000). The low Arctic climate is characterized by very low average temperature and short growing season comprised between three and four months (Bliss 2000). The low temperatures affect also soil biotic activity in the tundra and decomposition processes are slow. Consequently, nutrient availability in the Arctic is usually low, and nitrogen is often a limiting nutrient (Chapin and Shaver 1985). Arctic ecosystems are also characterized by extreme fluctuations in water availability. Water can cause floods during spring, at the snowmelt, while precipitation can be rather scarce during the summer (Autio and Heikkinen 2002). Compared to other high latitude ecosystems, Arctic tundra is fairly productive and its soil hosts a wide variety of species (Jeffery *et al.* 2010). Arctic tundra soil supports more than 700 acari species, 400 species of collembolans, 500 nematode species and 70 species of enchytraeids and earthworms (Jeffery *et al.* 2010). Species number estimates for Arctic soil are not exceptionally low, even when compared with tropical biomes. For example tropical Brazilian soil hosts in average 2800 nematodes species 1500 different species of acari 200 collembolan species and 100 enchytraeids species (Jeffrey *et al.* 2010). All these organisms constitute a complex food web and their activity determines soil quality, functioning and nutrient cycling. Decomposer activity and in particular microbial activity in the rhizosphere strongly influences nutrient availability for the plants. Nutrient availability for plants is not dependent only on the activity of free living decomposers, but also on their symbionts, such as arbuscular mycorrhizal (AM) fungi, which will be treated more thoroughly in the next session.

1.3 Arbuscular mycorrhizal fungi in the Arctic

AM fungi are present in roughly 80% of vascular plants and they are obligate symbionts hosted in plant roots (Smith and Read 2008). The AM symbiosis is based on the interchange of nutrients between the plant and the fungus, where the plant usually gains phosphorus and nitrogen in return for carbon (Smith and Read 2008). AM fungi, in addition to the improvement of plant mineral nutrition (Ames et al. 1983), can also provide relief from drought stress (Allen et al. 1989; Cui and Nobel 2006) and protection from pathogens (Newsham et al. 1995). The benefits gained by the plants do not always outweigh the cost paid to AM fungal symbionts and the association is often described to range from mutualism to parasitism (Johnson et al. 1997). AM fungi affect plant fitness and they also mediate ecosystem dynamics by shaping competitive interactions among plants (Hall 1978; Hartnett and Wilson 1999) and plant productivity and plant diversity (Klironomos *et al.* 2000; van der Heijden *et al.* 1998; van der Heijden and Sanders 2002). Therefore, changes involving the relationship between AM fungi and plant hosts are likely to have an impact at the whole ecosystem level. AM fungi are less common in Arctic ecosystems compared to temperate and tropical ones. Arctic floras are dominated by non-AM plants, probably as a result of the reduction in host size, host life cycle and the parallel evolution of storage organs as well extensive root system (reviewed in: Kytöviita 2005). However, even if AM associations are infrequent in the high Arctic, they are quite common at lower latitudes, in low Arctic and alpine ecosystem (reviewed in: Newsham *et al.* 2009). AM fungi are in particular common in low Arctic meadows, where the vegetation is mainly formed by grasses and forbs (Kytöviita 2005). Arctic ecosystems are generally nitrogen limited, and most of the nitrogen is in the organic form (Chapin and Shaver 1985). In this kind of ecosystems AM fungi can improve access to both inorganic (Govindarajulu *et al.* 2005) and organic formS of nitrogen (Hodge *et al.* 2001, Whiteside *et al.* 2012), thus exerting a pivotal role in plant nutrition and ecosystem dynamics.

1.4 Relationship between soil characteristics and soil biota and plants

Soil abiotic characteristics, such as nutrient availability, carbon availability, moisture and pH are widely recognized as the main factors shaping microbial (Högberg *et al.* 2007, Männistö *et al.* 2007, Lauber *et al.* 2009), plant (Gough *et al.* 2000) and microarthropods communities (Makkonen *et al.* 2011, Bokhorst *et al.* 2012). In particular pH has been shown to shape plant (Gough *et al.* 2000) and microbial (e.g. Lauber *et al.* 2009) communities, while microarthropods are more sensitive to moisture and temperature (e.g. Bokhorst *et al.* 2012). Whereas the effects of different soil parameters on plant, soil animal and microbial community have been widely investigated much less is known on the factors determining the structure of AM fungal communities *in planta*. For a long time it has been assumed that AM fungi were highly generalist as the number of AM species is extremely low compared to the richness present in the plant kingdom. However, more recent studies highlighted that AM fungal communities show clear distinct patterns and ecological specificity (McGonigle and Fitter 1990, Helgason *et al.* 2002). As soil characteristics and plant community change so does the AM fungal community associated with plant roots (Allen 1991, Cázares *et al.* 2005, Sikes *et al.* 2012). Soil type (Lekberg *et al.* 2007), land use (Jansa *et al.* 2002, Oehl *et al.* 2004) and latitude (Öpik *et al.* 2013) emerged as important factors shaping the AM fungal communities.

A common way to study contrasting soils that are closely located is to utilize chronosequences. Chronosequences are created by local disturbance such a fire, glacier retrocession, volcanic eruption, wind erosion and grazing. Chronosequences can be related to succession, where space is used instead of time, and where soils with contrasting conditions are subjected to the same climatic conditions.

Local disturbance such as ungulate grazing can also cause deep changes in soil physical and chemical characteristics; presence of ungulates can result in a significant increase in soil bulk density coupled with a decrease in total soil organic carbon and nitrogen concentrations (Steffens *et al.* 2008). As soil characteristics change in response to grazing so does the plant and the soil communities. Vice versa, the response to grazing is highly context-specific and probably driven by underlying soil and site specific characteristics. Local characteristics are strong determinants of the final outcome of grazing: nutrient availability (Proulx and Mazumder 1998) and soil structure (Schrama *et al.* 2012) are pivotal factors in determining the response to grazing of plant communities (Proulx and Mazumder 1998) and the nutrient cycling dynamics (Schrama *et al.* 2012), as well as nutrient availability is probably one of the most important factors in determining the recovery rate after grazing exclusion (Ravolainen *et al.* 2011).

1.5 Ungulate grazing: mechanisms and implications

1.5.1 Reindeer grazing in Northern Finland

Human activities have always exerted a deep influence on ecosystem functioning and structure. Hunting and herding are at the base of the survival and development of human settlings, especially at the northern latitudes, where agriculture is not a feasible option. Not surprisingly, reindeer herding is also nowadays one of the most important economic and cultural activity in all northern Lapland. Reindeer (*Rangifer tarandus*) grazing has been present in northern Lapland since the end of the last ice age (Skogland 1984). In the past, winter food availability and natural diseases were regulating the reindeer stock density (Helle and Aspi 1983). Nowadays, thanks to the introduction of modern herding techniques, veterinary practice, and the supply of extra forage during the winter, the population of semi domesticated reindeer has been growing reaching densities that are far above the natural carrying capacity of the ecosystem (Kojola and Helle 1993, Suominen and Olofsson 2000). Moreover, the pressure of summer grazing on the Finnish pastures has been aggravated by the closure of the borders between Finland and Norway (1852), and later on between Finland and Sweden (1889) with the consequent disruption of the migratory routes between summer pastures, located on the coast, and winter pastures, located inland (Aarseth 1989, Oksanen and Virtanen 1995, Väre *et al.* 1996).

Grazing can be seen as the sum of three different components: (i) defoliation, (ii) fertilization due to urine and faeces deposition and (iii) mechanical disturbance and soil compression following the trampling activity. These three mechanisms interact and have both direct and indirect effects on plant and soil communities. In this thesis I am focusing on grazing *sensu stricto*, rather than browsing. Browsing is characterized by a keen selection of the consumed plants by the herbivores, and is mainly present in forest ecosystem where the production of toxic compounds by the plant is a common strategy in response to herbivory. On the contrary, grazing concerns a more generalized consumption of plants. I first will present the effects of each single grazing component on plants, AM fungi, soil micro- and mesobiota. Then I will present what happens when these components are combined and which are their effects on natural ecosystems, in particular in relationship with Arctic ecosystems.

1.5.2 Defoliation

Defoliation effects are not restricted to the individual plant, but they rebound on the entire ecosystem. There are horizontal effects since defoliation alters competitive relationships among plants, and vertical effects since root dynamics are affected in terms of growth and exudation patterns. Depending on plant characteristics, adaptation to grazing, grazing history and frequency of defoliation, plant and ecosystem effects can vary. According to Belsky (1986), plants respond to clipping either with avoiding strategy, such as escape in time or production of chemical or mechanical defences, or with compensatory regrowth strategy. The latter strategy is mainly present in graminoids or forbs, which usually do not produce toxic chemicals and do not have mechanical defences in response to herbivory. In particular graminoids often show signs of compensatory, or even overcompensatory responses to clipping, meaning that traits connected with fitness (such as the relative growth rate, or seed production) are increased by grazing (Paige and Whitham 1987, Paige 1992, Lennartsson *et al.* 1998, Olejniczak 2011). Yet graminoids do not always show a compensatory response to grazing and neutral and negative effects of defoliation are often observed as well (Milchunas and Lauenroth 1993). A meta-analysis conducted by Ferraro *et al.* (2002) showed for instance that the responses of grasses to defoliation is in general negative, both in term of shoot and root production. However, defoliation has been shown to increase root (Green and Detling 200) and shoot (Ruess *et al.* 1983, McNaughton and Chapin 1985, Jaramillo and Detling 1988) nitrogen content, even though negative effects on shoot nitrogen content have been observed as well (Jaramillo and Detling 1988). Arctic graminoids have been reported to tolerate multiple, intense and frequent defoliation (Archer and Tieszen 1983), and their responses are similar to the one present in other ecosystems. Arctic graminoids respond to defoliation increasing nutrient absorption and respiration rates, while under extremely intense defoliation increased root mortality is also observed (Chapin 1980).

Different plants withstand defoliation better than others and defoliation has a deep influence in shaping the plant community structure since it regulates the competitive dynamics among plants. Defoliation does not alter only plants competitive dynamics directly, but by removing foliage from the preferred plant species it affects also light competition dynamics among plants (Huisman and Olff 1998). Following a defoliation event plant photosynthetic capacity is temporarily impaired and the carbon balance of the plant is altered (Richards 1993). As leaf tissue must be replaced other plant organs and structures can experience a lower carbon supply. In particular AM fungi can experience a dramatic reduction of the carbon flux directed towards them due to the necessity of the plants to direct carbon preferentially to regrowth (Gehring and Whitham 2002). Consequently, negative effect on AM fungal hyphae frequency is observed (Klironomos *et al.* 2004), even though positive (Bayne *et al.* 1984) and variable (Allsopp 1998, Saito *et al.* 2004) responses are also common. The variability of these responses may be dependent on several factors such as intensity of grazing, nutrient availability (Gehring and Whitham 2002) and differences in AM fungal life history traits (IJdo *et al.* 2010). A rearrangement of the carbon flux within the plant has also other important implications. Following a defoliation event plants tend to alter the quantity and the quality of roots exudates. Root exudates are of paramount importance for bacterial activity (Bais *et al.* 2006) and thus they are a key factor when considering changes in decomposition activity following defoliation and grazing events. Defoliation often leads to short term increases in root exudation (Paterson and Sim 2000), which in turn may stimulate microbial carbon use efficiency (Bardgett *et al.* 1998a, Hamilton and Frank 2001) and nutrient cycling (Hamilton and Frank 2001). However, in the long term defoliation has been shown to exert the opposite effect decreasing the activity and the abundance of soil decomposer in systems characterized by a low productivity (Holt 1997, Johnson and Matchett 2001, Sankaran and Augustine 2004). In particular, it has been shown that in the Arctic defoliation causes a decrease in the nitrogen cycling rate (Sørensen *et al.* 2008). Mikola *et al. (*2001b) suggested that, while in the short term defoliation can increase the production of carbon rich exudates by plant roots, which in turn stimulate microbial growth, in the long term plant root exudation can decline. The attenuation of carbon release by plant in strongly defoliated system can in turn lead to a decrease in microbial biomass and activity. In other systems defoliation can also enhance soil microbial activity

(Mawdsley and Bardgett 1997) and this may be related with the fact that under carbon limitation microbes may just expel the NH_4^+ in excess, rendering nitrogen more available for plants (Medina-Roldán and Bardgett 2011). However, this is less likely to happen in nitrogen limited system as the Arctic (Chapin and Shaver 1985). The effects that defoliation has on plant architecture, resource allocation pattern and bacterial abundance rebound also on higher trophic levels. For instance, it has been shown that defoliation can affect nematode density and community structure (Stanton 1983, Mikola *et al.* 2001a), however, most of the studies focus on the overall effects of grazing on soil biota rather than just defoliation.

1.5.3 Fertilization

Ungulate grazing is able to increase the nutrient availability (in particular nitrogen) for plants and microbes through direct and indirect mechanisms. Directly trough urine and faeces deposition, and indirectly stimulating bacterial activity (Bardgett *et al.* 1998a) and mineralization processes (Molvar *et al.* 1993, McNaughton *et al.* 1997). Fertilization can promote an increase in the mineralization rate also by stimulating the activity of extracellular enzymes such as phosphates and proteases, although the effect on enzymatic activity and soil organic matter decomposition are highly context dependent (Keeler *et al.* 2009). The effects of fertilization are also highly context dependent and the positive effects of fertilization on decomposition rates are connected with the plant community composition and ecosystem characteristics: positive effects are mainly present in systems which are characterized by plants producing a high quality litter (rich in nitrogen and poor in phenolic compounds and lignin) and where atmospheric nitrogen deposition is low (Knorr *et al.* 2005). Enhanced soil fertility increases nutrient contents in plants leaves, and consequently improves the quality of the litter. High litter quality in turn will promote decomposition and mineralization processes establishing a positive loop between fertilization and higher decomposition rates (Wardle *et al.* 2004). Fertilization has an important role also in structuring bacterial community where high nitrogen availability selects for copiotrophic (r-selected) bacterial groups over oligotrophic (K-selected) bacterial groups (Ramirez *et al.* 2010).

Increased nutrient availability affects plant architecture and the relative biomass investment in roots and shoots, where the root:shoot ratio decreases under nutrient addition (Olff *et al.* 1990). As a lower investment in root production is needed under high nutrient availability, a lower investment towards AM fungal partner is also often observed, so that fertilized plants frequently have lower AM fungal colonization (Treseder 2004). Nitrogen addition can alter the trade balance between AM fungi and plant hosts. If other nutrients, such as phosphorus, and water are not limiting a reduction of carbon allocation to AM fungi is expected (Johnson *et al.* 2003).

Plant below- and above-ground competitive interactions (Grime 1973, Cahill Jr 1999), plant species diversity and productivity (Grime 1973, Shaver and Chapin 1980, Tilman 1984, Goldberg and Miller 1990, Wilson and Tilman

1991, Hooper *et al.* 2005) are also affected by fertilization. The debate whether productivity is related or not with species diversity remains quite heated and there is not a shared agreement (see for instance: di Tommaso and Aarssen 1989, Adler *et al.* 2011, Maron *et al.* 2011). It has also been suggested that the initial species composition of a plant community is a key factor in determining the response to higher nutrient availability (Johnson *et al.* 1992, Tilman 1993, Gough *et al.* 2000). Litter accumulation, resulting from higher productivity, can also inhibit seedling emergence (Foster and Gross 1998), but this effect is negligible in the presence of herbivores that reduce litter accumulation (Gough and Grace 1998).

Arctic tundra is characterized by low availability of nutrients (Chapin and Shaver 1985) and especially nitrogen rather than phosphorus is the limiting nutrient (Nadelhoffer *et al.* 1992). Therefore, nitrogen, which is the main component of urine, exerts a strong effect on tundra ecosystem. Recently it has been shown that in Arctic and Alpine tundra there is a unimodal response to fertilization, with a decline in species richness at higher nitrogen availability (Virtanen *et al.* 2012). Moreover, long term fertilization (20 years) experiments in Arctic tundra, which include addition of nitrogen, phosphorus and potassium, showed that higher nutrient availability leads to an increase in graminoid abundance, while shrub abundance decreases (Campioli *et al.* 2012).

Nitrogen addition has been shown to affect nematodes. For instance, when nitrogen addition increases the bacterial biomass it can promote the presence of bacterial feeding nematodes over the fungal feeding ones (Bååth *et al.* 1978, Bååth *et al.* 1981). It has also been shown that in Arctic and Alpine ecosystems, the effects of nitrogen addition are dependent on soil type and probably observable only at high level of deposition (Lokupitiya *et al.* 2000). Effects of fertilization on soil microarthropods are less studied, but long term experiments report both changes in microarthropod density (Lohm *et al.* 1977) or changes in community composition (Lindberg and Persson 2004).

Not only urine deposition, but also faeces addition has important ecosystem effects. Faeces are rich in carbon and can increase microbial biomass, microbial activity and the number of nematodes (Bardgett *et al.* 1998b). The effects of dung deposition on nitrogen cycling are instead controversial and both positive effects, such as enhanced nitrogen mineralization (Ruess and McNaughton 1987) and negative effects, such as increased nitrogen immobilization (Bardgett *et al.* 1998b), have been observed.

1.5.4 Trampling

Trampling by large ungulates exerts a strong mechanical stress on soil. The pressure and the shear stress applied change the soil matrix and disrupt the soil structure (Proffitt *et al.* 1995, Peth *et al.* 2010, Hiltbrunner *et al.* 2012). Depending on soil characteristics, trampling does not only reduce soil porosity (Pietola *et al.* 2005), but it reduces water and nutrient availability and oxygen diffusion (Rasiah and Kay 1998). Effects of trampling are particularly marked in clay soils: in sandier soils trampling is less likely to reduce soil porosity and alter soil structure (Schrama *et al.* 2012).

Trampling often exerts a direct negative effect on soil microbes and fauna. The effects of trampling on microbial communities vary depending on the system studied and the intensity of grazing. When trampling is associated with soil erosion a decline in microbial abundance (especially in fungi) has been observed (Hiltbrunner *et al.* 2012); otherwise often the observed effect of trampling on microbial community composition and activity was negligible (Busse *et al.* 2006). However, in the Arctic trampling can exert a positive effect on soil microbial fauna and decomposition processes due to the compaction of the moss layer, with consequent positive effects on soil temperature (van der Wal and Brooker 2004, Olofsson 2009, Sørensen *et al.* 2009). Nevertheless, it has been observed that trampling does not always cause an increase in the nutrient cycling rate and trampling has no effect on the primary productivity (Olofsson 2009). The reduction of mosses caused by trampling is associated with other changes in vegetation, but these changes are also mediated by the interaction of trampling with fertilization and defoliation (Sørensen *et al.* 2008). Trampling and soil disturbance have detrimental effects also on soil AM fungi, especially on the extraradical mycelium which can be heavily damaged and disrupted (Mårtensson and Olsson 2012).

It has been shown that cattle trampling reduces abundance and diversity of acari and collembola (Wardle *et al.* 2001, Cole *et al.* 2008). Sørensen *et al.* (2009) showed in a simulated trampling experiment in an Arctic meadow ecosystem that enchytraeids responded negatively to mechanical stress. The reduction of faunal activity deriving from both the mechanical stress and the lower oxygen availability can in turn result in a reduction in the nitrogen mineralization rate (Breland and Hansen 1996). Lower oxygen diffusion can also promote the formation of an anaerobic environment that promotes higher rates of denitrification, depleting nitrogen from the system (Le Roux *et al.* 2003, Menneer *et al.* 2005).

1.5.5 Effects of ungulate grazing in the field

One of the first conceptual frameworks describing the effect of grazing on plant community is the one proposed by Dyksterhuis (1949), which rests on Clements theory of succession. In his range succession model, Dyksterhuis (1949) describes grazing as a retrogressive force that prevents the succession to reach its climax (i.e. forest). According to this model, grazing would favor the dominance of herbaceous plants typical of earlier successional stages or even cause a complete regression to the bare soil stage. In this framework, the transition among the different stages was seen as continuous, reversible and modulated by the intensity of grazing. However, even if this model has been widely applied, it lacked predictive power and many studies showed that not all the systems behave in a continuous way. Forty years later two new models provided conceptual framework that replaced the range succession model: the state-and –transition (S-T) model (Laycock 1967, Milchunas *et al.* 1988, Westoby *et al.* 1989) and the MSL model (from the authors: Milchunas, Sala and Lauenroth 1988). The S-T model provided a conceptual framework that incorporates systems that do not behave continuously, i.e. where the transition between two alternate stages is separated by a threshold. The MSL model instead predicts the outcome of grazing in terms of plant community structure in relation with grazing intensity, grazing history and climate. More recently, Cingolani *et al.* (2005) tried to integrate the two models. They equalized climate with productivity and included scenarios where discontinuous, divergent and irreversible responses are allowed. According to the model by Cingolani *et al. (*2005) in Arctic systems (low-productive and with a long history of grazing) grazing should not lead to big differences in terms of plant diversity, even though changes in plant species composition are expected. Irreversible changes may occur when grazing leads to soil erosion and structural changes of the system. However, Olff *et al.* (1998) suggested that in infertile soils with non-limiting precipitation grazing can lead to a dramatic increase in plant species diversity, even though these effects are strictly dependent on the combination of environmental factors such as water and nutrient availability. Nevertheless, changes in species composition and diversity are strictly dependent on availability of propagules, which may be a critical point in extreme ecosystems such as the Arctic ones. Losses of species or increases in diversity are important when considering grazing, especially in extreme ecosystem such as the Arctic, which is highly vulnerable to disturbance. Diversity is a key determinant of ecosystem processes (Loreau *et al.* 2001, Hooper *et al.* 2005, Balvanera *et al.* 2006, Cardinale *et al.* 2006, Cardinale *et al.* 2011) and ecosystem services depend upon the coexistence of different plant species, where also rare species may exert a strong control on ecosystem functioning (Isbell *et al.* 2011).

A substantial contribution in describing how grazing changes ecosystem function was provided by McNaughton studies on Serengeti savannah (McNaughton 1979, McNaughton 1985). The grazing optimization hypothesis, which draws inspiration from Eggeling (1947), Watt (1947) and Tansley (1949) (but see also: Wilkinson, 1999) predicts an increase in productivity at intermediate intensity of grazing. The increase in productivity results from the increase in nutrient cycling rate and nutrient availability promoted by grazing. The importance of grazers in regulating ecosystem processes was especially emphasized by Zimov (1995) who ascribed the transition from high productive steppe to low productive tundra to the disappearance of the large herbivore megafauna. Mc Naughton (1979) and Zimov (1995) hypotheses, together with the experimental evidence offered by e.g. Oloffson *et al.* (2004), laid the ground for van der Wal (2006) hypothesis, which suggested that reindeer grazing would promote again a transition from the low productive tundra to the high productive steppe, promoting the establishment of graminoids. Van der Wal (2006) proposed that reindeer grazing would be able to manipulate their own food source by pushing the plant succession from the low productive moss dominated stage towards the highly productive graminoid dominated stage. Positive effects of reindeer grazing on graminoids and nutrient cycling have been often reported (Olofsson *et al.* 2001, Olofsson *et al.* 2004, van der Wal and

Brooker 2004) as well as negative effects on shrubs (Oksanen and Moen 1994, den Herder *et al.* 2004, den Herder *et al.* 2008). On the other hand, the transition time between the different stages is asymmetric, and recovery from grazing can take decades (Olofsson 2006).

Most of the earlier ecological studies focused only on the effect of grazing on the vegetation, but recently the effects on below-ground processes in relationship with grazing have received growing attention. As Bardgett *et al.* (1998a) and Wardle *et al.* (2004) clearly showed, grazing promotes, through the mechanisms described in the previous chapters, changes in soil community and processes, and these changes affect also the plant community. Two different scenarios are pictured: one for nutrient poor environments where mainly browsing is present and one for productive ecosystems, where grazing is the main form of herbivory. Briefly, in nutrient poor environment plants present more often a defensive strategy to grazing. The production of phenolic compounds, which are unpalatable for grazers, result in a low quality litter, which is recalcitrant to decomposition. This slows down the entire nutrient cycling, promotes the presence of fungi and fungivorous fauna over bacteria and negatively affects plant productivity. In productive ecosystem (i.e. grasslands) plants tend to present compensative response to grazing. The presence of easily decomposable litter and dung deposition favors microbial activity, promotes the presence of bacterial feeding fauna, and stimulates the nutrient cycling. This two contrasting systems are often referred as the fungal dominated “slow energy channel” and bacterial dominated “fast energy channel”. The effect of grazing in the Arctic on nutrient cycling and microbial biomass are quite controversial, and positive and negative responses are observed (negative: Pastor *et al.* 1993; positive: Stark *et al.* 2000, Olofsson *et al.* 2004; positive and negative: Stark *et al.* 2003). The reason behind this idiosyncrasy still remains unclear. It has been suggested that soil structure may affect the response of nutrient cycling to grazing and a recent study show that grazing tends to reduce nitrogen cycling rate mainly in clay soils, which are most likely to suffer more from compaction deriving from trampling (Schrama *et al.* 2012).

While few studies on the effects of separate components of grazing (trampling, defoliation, fertilization) on soil biota have been conducted, the effects of grazing in the field are even more seldom investigated. Since grazing has a deep influence on plant community composition, as well as on plant exudate production and microbial activity and abundance it is very likely to exert deep effects also on soil biota. Grazing can have positive effects on nematodes, especially on the root- and bacteria-feeders (Davidson and Hackler 1994). However, it has also been observed that grazing has a negligible effect on nematode community structure as well as negative effects on nematode density (Zolda 2006). A study conducted in north American steppe showed that grazing led to changes in arthropod community composition (Milchunas *et al.* 1988). Since very little is still known about the ecological role of many of the microarthropod and nematode species in the Arctic, it remains very difficult to draw solid conclusion about the ecological significance of changes occurring in response to grazing.

1.6 The use of natural abundance of stable isotopes in ecology

All elements present in nature are composed by a mixture of isotopes, which are characterized by a different atomic weight. Since the isotopes differ in their weight it is common to refer to them as light and heavy isotopes; for instance nitrogen exists in the light form ^{14}N and the heavy one ^{15}N, while carbon light isotope is ^{12}C and the heavy one is ^{13}C. Usually the difference in the amount of the different isotopes is very small, so isotopic composition is reported relative to an internationally accepted standard and expressed as (Eq. 1):

$$\delta(‰) = \left(\frac{Rsample}{Rstandard} - 1\right) \times 1000 \qquad (1)$$

where R stands for the ratio between heavy and light isotopes, with R_{sample} being the ratio in the sample and $R_{standard}$ being the ratio in the standard. The study of natural abundance of stable isotopes such as ^{15}N and ^{13}C is a very useful tool to explore biogeochemical processes and plant ecophysiology. Changes in plant and soil $\delta^{15}N$ reflect nitrogen cycle dynamics (Nadelhoffer and Fry 1994, Högberg 1997, Robinson 2001). The biogeochemical processes involved in the decomposition and transformation of organic nitrogen in soil tend to discriminate against ^{15}N, meaning that the products are ^{15}N depleted compared to the substrate, which is enriched. When the products of these transformations, nitrate or gaseous form of nitrogen (N_2 and N_2O), leave the soil system, either via leaching or via evaporation, the soil becomes enriched. So the faster the nitrogen cycle, the higher is the amount of nitrogen that leaches or evaporates, the higher will be the soil $\delta^{15}N$ signature (Nadelhoffer and Fry 1994, Frank *et al.* 2000). Soil and plant $\delta^{15}N$ signatures are usually linearly correlated (Frank and Evans 1997, Kahmen *et al.* 2008), therefore plant $\delta^{15}N$ signature can be used as a proxy of soil $\delta^{15}N$ values (Kahmen *et al.* 2008). However, other factors have to be taken into account, such as the fact that $\delta^{15}N$ values in soil vary also with depth (Hobbie and Ouimette 2009) and thus changes in foliar $\delta^{15}N$ signature can reflect changes in rooting depth rather that changes in soil nutrient cycling. Other factors can also affect foliar $\delta^{15}N$ signature such as the mycorrhizal status of the plant (Handley and Raven 1992, Hobbie and Colpaert 2002, Hobbie *et al.* 2005, Craine *et al.* 2009), the presence of root symbiotic nitrogen fixers (Shearer and Kohl 1978, Delwiche *et al.* 1979, Virginia and Delwiche 1982) and the nitrogen pool utilized by the plant (Yano *et al.* 2010). The nitrogen that is supplied to plant through the symbiotic interface is ^{15}N depleted compared to the source (e.g. Delwiche *et al.* 1979, Craine *et al.* 2009) and organic N sources, such as amino acids, have lower $\delta^{15}N$ values compared to NH_4^+ (Yano *et al.* 2010). This is particularly relevant when considering Arctic plants which are known to commonly utilize organic forms of nitrogen (Näsholm *et al.* 1998).

Carbon stable isotopic signature ($\delta^{13}C$) is also a useful tool in assessing plant water stress and differences related with availability of water for plants (Farquhar *et al.* 1989), with the advantage of being a time integrated signal. Plants that are constantly water limited present in fact a higher $\delta^{13}C$ signal. CO_2 fixation reactions discriminate against ^{13}C when the substrate is not limiting (i.e. when stomata are open). Water limitation reduces stomatal opening, forcing the plant to use relatively more of the CO_2 available, thus utilizing also the heavy ^{13}C isotope (Farquhar *et al.* 1989).

1.7 Aims of the study

In this thesis I investigated in first instance how grazing affects Arctic meadow ecosystems. The studies (I) and (II) comprise observations of the whole ecosystem in presence and absence of grazers. Both above-ground and below-ground components of the ecosystems were taken in account. Following van der Wal (2006) hypothesis I tested whether it is true that grazing at high latitudes promotes nutrient cycling and increases plant diversity and vice versa, if grazing exclusion leads to a decline in diversity, a slowdown of nutrient cycling (II) and a reduction of graminoids in favor of mosses and shrubs (I). I predicted that changes in nutrient cycling rate would be accompanied by changes in the bacterial community structure and that in the grazed area the fast bacterial energy channel would dominate over the slow fungal one (I). I expected also changes in the microarthropods community (I), due to the direct effects of grazing on soil, and due to the changes in plant community structure caused by grazing. In accordance with Gehring and Whitham (2002) and Treseder (2004) I expected a decline in AM colonization in plant roots, as a consequence of the reduced allocation of carbon to the fungal symbionts. This was tested by recording the colonization frequency in plant roots, in grazed and ungrazed areas (II). The target plants were two forbs, *Solidago virgaurea* and *Potentilla crantzii,* and one grass *Deschampsia flexuosa.* The forb *S. virgaurea* (Bråthen and Oksanen 2001) and the grass (Gaare and Skogland 1975) were among the most palatable plants for reindeer. The paper describing the experiment II, where I recorded the effect of grazing on AM fungal colonization frequency, is followed by a greenhouse experiment (III) where I addressed the question whether in *D. flexuosa*, the dominant grass in the study sites, it is mainly defoliation rather than fertilization that caused the decline in AM colonization frequency.

In the (IV) study I investigate the changes in terms of AM fungal community that occur in two different, but closely located soils. These observations were made in the early and late stage of a chronosequence, which both harbored the common plant species *D. flexuosa*. Considering that AM fungal community was investigated in the same plant species I predicted that if AM fungi are generalist and if AM fungi do not show preferences towards different soil characteristics the AM fungal communities should be similar in both stages. On the contrary, if different AM fungal taxa show a certain degree of specificity towards different soil the AM fungal communities should diverge between the early and late stage.

2 MATERIALS AND METHODS

2.1 The field experiments: study areas

2.1.1 Kilpisjärvi

In Finland, the reindeer grazing area extends roughly from just below the polar circle up the northern most part of Finland and it is divided in 57 reindeer herding districts "paliskunta". For each district the government indicates the maximum number of animals that are allowed to graze. The total number of adult individual censed in 2010 was 195500 (Anon. 2010). The area where I conducted the reindeer grazing experiments (I and II) was located in the Käsivarsi district. In this district a maximum number of 11000 adult reindeer is allowed for a density of 2.3 reindeers per km^2. However, this does not consider the fact that in summer these densities can double due to the presence of calves. As the impact of grazing is not only dependent on the biomass consumed, but also on the effect of trampling of reindeer the total density is particularly relevant. In the year 2008-2009 the total number of reindeer in our experimental area was 17968 (11375 adults and 6539 calves for a total area of 4286 km^2), for a total density of 4.2 reindeers/km^2 (Anon. 2010). These numbers give an indication of the grazing pressure present in our study area, and it highlights the fact that the current situation does not reflect the natural occurrence of grazing in Northern Finland. The studies I and II were carried out in two low Arctic meadow sites located in the Kilpisjärvi area, Northern Scandinavia (Fig. 1). The soil in the Kilpisjärvi area is classified as a Leptosol (Jones *et al.* 2010). The meadows are situated around 600 m a.s.l. respectively in Saana (69°03′ N, 20° 50′ E) and Jehkas (69°05′N, 20°47 E) and both have a southern exposure. The meadows are characterized by the predominance of the grass *Deschampsia flexuosa*. Other graminoids such as *Deschampsia cespitosa*, *Carex* sp., *Festuca ovina*, forbs such as *Solidago virgaurea*, *Potentilla crantzii*, *Bistorta vivipara, Trollius europaeus*, small woody plants (*Betula nana, Vaccinium* spp.) and mosses are also common. The length of the growing season is *c.* 90 days, and the mean annual temperature and precipitation measured at Kilpisjärvi meteorological station, which is situated at 483 m a.s.l, are -1.9°C (1979-2009) and 489 mm/year (1979-2009), respectively (data from Finnish Meteorological Institute). The average soil temperature between years 2000 and 2007 at 3-5 cm depth during the warmest months, July and August, was +10.5°C (Kytöviita, unpublished data).

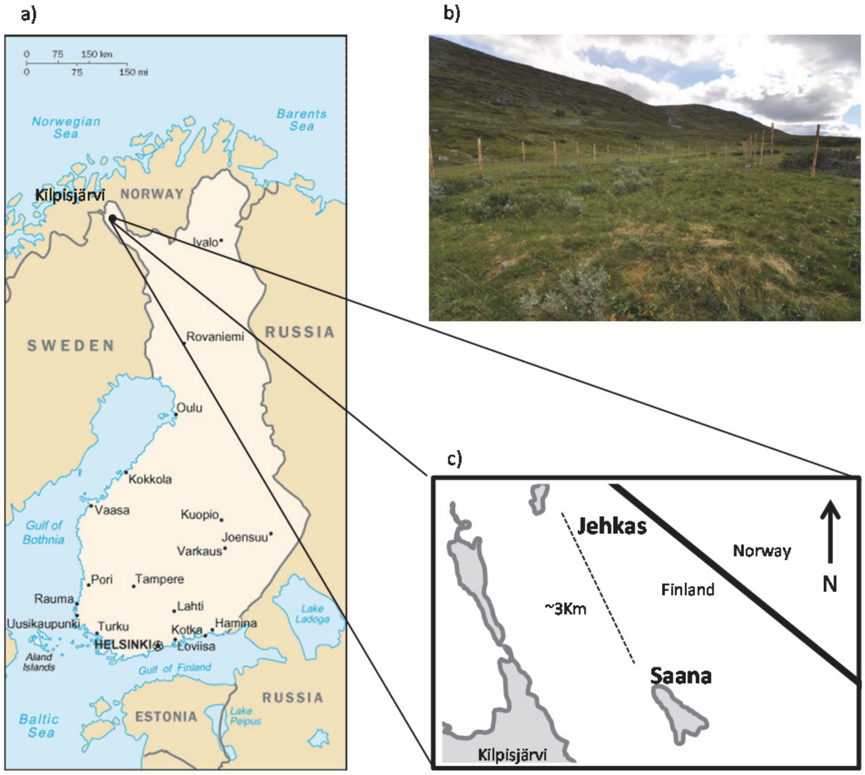

FIGURE 1 a) Finnish map and location of the study areas of the experiments (I) and (II) b) view of one of the experimental grazing exclosures located in Kilpisjärvi, Jehkas c) Location of the two study areas, Jehkas and Saana, in Kilpisjärvi (picture courtesy of Joel Rahkonen).

Both sites (Saana and Jehkas) are part of reindeer summer grazing area and grazing history can be dated back for at least two centuries. In both study sites, two exclosures prevented a portion (about 10×30 m) of the meadow from reindeer grazing for 10 years.

2.1.2 Kalmakaltio

The study (IV) was carried out in Kalmakaltio (Fig. 2) which is located in the subarctic Northern Fennoscandia (68° 29' 16" N, 24° 42' 13" E). Kalmakaltio has an average annual temperature between -2° and -3°C (Finnish Meteorological Institute).

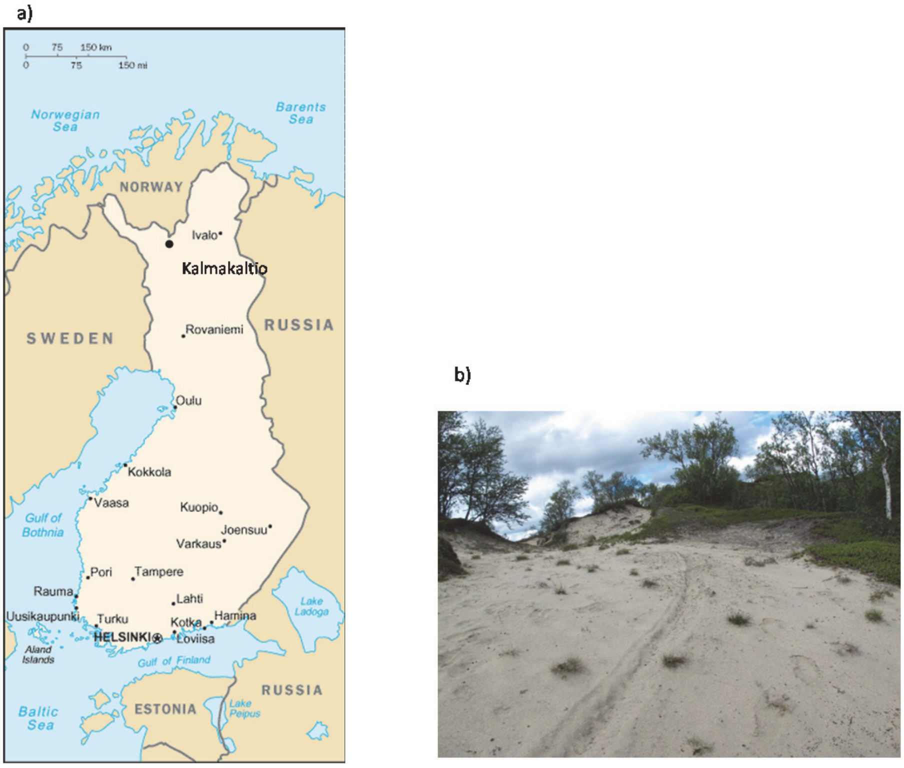

FIGURE 2 a) Finnish map and location of the study area of experiment (IV) b) View of one of the sampling sites of the experiment (IV) in Kalmakaltio. Here it is possible to notice the proximity of the early and the late successional stages with few sparse *Deschampsia flexuosa* tussocks growing in the sand dune. Picture courtesy of Minna-Maarit Kytöviita.

The area is an inland sand dune ecosystem that was vegetated after ice age 9000 years ago (Seppälä 1995). During the last 700 years the sand has been drifting creating deflation areas without vegetation in some places (Seppälä 1995). Forest fires and the presence of reindeer grazing, especially in historical times and wind erosion has partially prevented the reestablishment of a plant cover (Seppälä 1995, Heinonen *et al.* 1996). As a result, the vegetation is patchy with mountain birch forest climax community persisting next to deflation patches with no vegetation cover and to patches representing other successional stages. We studied two successional stages, one representing early successional stage and one representing late successional stage. These two stages present very different vegetation and soil characteristics, but they have one plant species, *Deschampsia flexuosa*, in common.

2.2 The field experiments: the sampling scheme

2.2.1 Kilpisjärvi

We had a specific spatial structure in our sampling scheme: the site, the block within site and the individual samples within blocks. The sites are at 3 km distance from each other. In both sites, the meadow was divided in three adjacent blocks so that each block (about 10×10 m) included the area inside (ungrazed) and outside the exclosure (grazed). For each block, eight samples were taken (four inside and four outside the exclosure), so that for each site there were 24 samples, 12 inside the exclosure and 12 outside the exclosure. Within block, the samples were taken randomly, apart from the fact that samples were collected a few meters from the fence to avoid margin effect and that there was at least one meter distance between replicate samples. The plant community composition was estimated in August 2010 and the soil samples were collected from both grazing treatments and sites July 15th 2009.

2.2.2 Kalmakaltio

For the experiment (IV) we sampled *D. flexuosa* plants (shoots and roots) and associated soil in two different successional stages: in the early successional stage where only *D. flexuosa* was sparsely growing and in the nearby late successional stage which is dominated by the dwarf shrubs with occasional birch trees occurring. Samples were collected from 10 early stage areas and from 10 closely situated late stage areas, so that the total number of samples was 20. The distance between each sampling site ranged between 100 and 500m, while the distance between each sampled pair (early vs. late) was a few meters. *Deschampsia flexuosa* was chosen as the study plant species because it is an abundant species in both successional stages and it is also an AM fungi host plant (Wang and Qiu 2006). Shoots were air-dried. Root systems were carefully mixed and divided into two fractions. One fraction was stored in 50% ethanol while the remaining fraction was air-dried. Twenty soil cores 3 cm in diameter were collected at a depth of 7 cm from the early stage areas and the late stage areas. The soil was immediately sieved (mesh size 4 mm) and frozen.

2.3 The greenhouse experiment

Soil and plant material for the experiment was collected in Kilpisjärvi, in Saana (69 03’N, 20 50’E) in August 2011. The soil was stored over winter in a cold room. Prior to the experiment the soil was sieved through a 4mm mesh. Part of the soil was sterilized at 120°C for 2 hours. To replace the bacterial fauna, excluding any fungal inoculum, the sterile soil was incubated for two weeks with plankton net (20 µm) bags containing an aliquot of non-sterile soil. Ramets of *D. flexuosa* were collected from the same soil. The roots were cut during the collection and the plants deprived of their root system were grown for four months in sterile sand with the addition of a commercial N:P:K fertilizer. Plants were then divided in ramets and used in the experiments. Prior to the experiment plant roots were checked for AM colonization to be sure that there was no AM or dark septate endophytes (DSE) colonization. Natural non sterilized soil containing AM inoculum and re-inoculated sterile (non-AM) soil was placed in 10x10x7cm pots and on the 14/04/2011 we placed one *D. flexuosa* ramet per pot. In each treatment there were 15 plants. The treatments were: sterilized and non-sterilized soil, clipping and fertilization, in a full factorial design, so that the total number of pots was 120. Pots were placed in trays containing 15 pots each, one plant per pot, so that each tray contained the plants representing one treatment combination. Trays were rotated weekly. On the 20/05/2011 plants in the clipped treatment were cut at 5 cm distance from the soil, just above the rhizome. The frequency and the intensity of the clipping simulated the natural occurrence of grazing. We simulated one grazing event since reindeer are feeding once in a place and then they move across the grazing range and since it is generally found that the extent of plant response to clipping is independent of biomass removed (Ferraro and Oesterheld 2002). For each pot subjected to the fertilization treatment we added 10 ml of urea (4.25 g l^{-1}) 4 times between the 20th and the 27th of May 2011 simulating a stock of reindeer urinating activity. For each simulated urination event a total of 0.02 g N pot^{-1} was added. In environment where nitrogen availability is low urea concentration in urine may be far lower than 100 mmol l^{-1} (Maloiy and Scott 1969), which corresponds to a concentration of urea lower than 6 g l^{-1}. The plants were harvested between the 21-27th of July 2011.

2.4 Analyses

2.4.1 Vegetation analyses

Vegetation analysis and biomass estimation were conducted inside and outside the exclosures in both sites in the experiment (I). The vegetation analysis was conducted using the point frequency method with a 50×50 cm frame with 50 contact points (Whitman and Siggeirsson 1954). We recorded data from a total of 60 frames in the experiment. For the biomass estimation, eight vegetation samples (25×25 cm) were harvested in both sites and grazing treatments (grazed and ungrazed). All above-ground biomass and litter were collected and dried at 50°C, sorted to species and weighed (Fig. 3). When plant samples were collected (II, III, IV), roots and shoots were separated. A part of the roots was stored in 50% ethanol, for the microscopical analysis of root endophytes, while another part was dried and stored for the molecular analysis (IV). Shoots were dried for the consequent stable isotope analysis (II, IV).

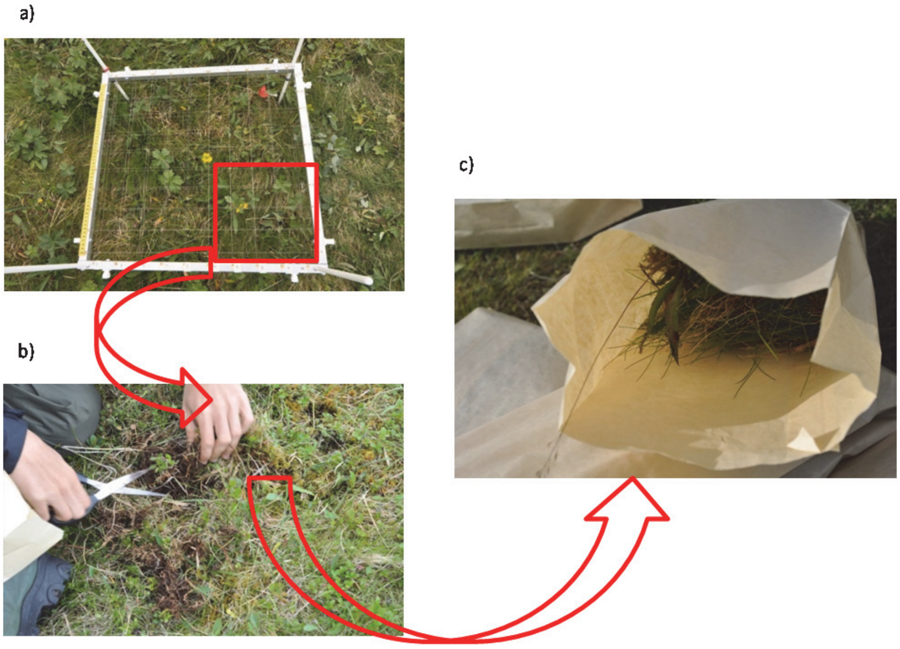

FIGURE 3 a) Point frequency frame used in the vegetation analysis. For the biomass estimation point frequency was recorded in an area corresponding to a quarter (25x25 cm) of the total frame area. b) All standing biomass was collected in the 25x25 cm area. c) Biomass was placed in paper bags and dried (picture courtesy of Joel Rahkonen).

In experiment (II), we collected samples (both shoots and roots) of *Deschampsia flexuosa*, a grass, *Solidago virgaurea* and *Potentilla crantzii*, two forbs. Both *D. flexuosa* and *S. virgaurea* are preferred plants by reindeer (Bråthen and Oksanen 2001) and *P. crantzii* is a quite common plant in our study areas. In the experiment (IV), we collected 20 *D. flexuosa* plants, of which 10 were in the early successional stage and 10 were in the late successional stage. In the greenhouse experiment (III) plant root and shoot biomasses were measured as well.

In the stable isotope analyses, dried plant shoots were finely ground and subsamples were placed into pre-weighed tin capsules. Foliar N, δ^{15}N, C and δ^{13}C contents were determined (II and IV). For recording of frequency of AM fungi and DSE fungi in roots, roots were stained (II, III and IV) according to McGonigle *et al.* (1990). AM percent root length colonization (PRLC) was estimated by recording presence/absence of AM hyphae, arbuscules and vesicles. Other fungal structures such as dark septate endophyte (DSE) fungi, yeasts and hyphae of Ascomycota and Basidiomycota were recorded as well, if present.

(AM) fungal communities in *D. flexuosa* in the two different points, the early and the late stage of the successional gradient were characterized by cloning and sequencing small subunit rRNA genes amplified with the AM-specific primers AML1/AML2 (IV). The retrieved sequences were compared to the virtual taxa (VTX) present in the Maarj*AM* database (Öpik *et al.* 2010) and a cutoff level of 97% was used when defining groups. The homologous sequences retrieved were included in the phylogenetic analysis as references while *Corallochytrium limacisporum* (GenBank accession number: L42528.1) was used as an outgroup. Alignment of the sequences and phylogenetic analysis were conducted using MEGA version 5.05. We used a bootstrap test (1000 replicates) and the evolutionary distances were computed using the Maximum Composite Likelihood Method. Sequences were deposited in GenBank under accession numbers KC211907- KC211987.

2.4.2 Soil characteristics

In the soil analysis (I), the samples consisted of soil pooled from six soil cores (6 cm length, 3 cm diameter) taken within 1m distance from each other, while in the experiment (IV) we collected in total 20 soil cores of 3 cm of diameter and 7 cm of length from the early successional and late successional stage. The soil samples were sieved through a 4 mm sieve and half of it was immediately frozen at -20° C and part was stored at +4° C. Frozen soil was used for soil organic matter content (OM) and pH measurements. In the experiment (I) we measured also soil nutrient content (NH_4^+, microbial N, organic N), and soil enzymatic activity (acid-phosphatase, leucine aminopeptidase, β-N-acetylglucosaminidase, β-glucosidase, phenol oxidase). Soil enzymatic activity was measured using the soil stored at +4° C.

2.4.3 Soil biota

In the experiment (I) a survey of the soil biota was carried out. Frozen soil was used for phospholipid fatty acids (PLFAs) and neutral lipids fatty acid (NLFAs) analysis. To measure enchytraeids and nematode community, twelve soil samples were taken from both grazing treatments and sites between the 15th and 18th July 2009. Each sample consisted of soil pooled from six soil cores (9 cm length, 3 cm diameter) taken within 1m distance from each other. The soil was gently mixed by hand and nematodes were extracted from ca. 10 g fresh mass soil sample. Enchytraeids were extracted from 25 cm^3 soil volume using wet funnels (Sohlenius 1979). For microarthropods, twelve samples were taken from both grazing treatments and sites. Each sample consisted of two soil cores (6×6 cm) taken within 50 cm distance of each other. The samples were kept intact with the adhering moss cover and extracted with a modified high-gradient extractor (Macfadyen 1961). Feeding strategies were assigned to species and genera belonging to the order of Acariformes as by (Mulder *et al.* 2008). I did not assign feeding strategy to collembolas as the majority of them are fungivorous.

2.5 Statistical analyses

To investigate the effects of reindeer grazing on plant community, soil community and nutrient cycling different statistical approaches were used. Statistical tests were performed using SPSS Statistics 19 (SPSS Inc.), PC-ORD (McCune and Mefford 1999), PAST (Hammer *et al.* 2001) and R using the MASS (Venables *et al.* 1994) and the Vegan package (Oksanen *et al.* 2007). Before proceeding with any parametric test assumption of normality and homoscedasticity were checked and if they were not met data were transformed. If the data failed to meet these assumptions also after being transformed, alternative statistical approaches were adopted, such as non-parametric test, or general linear model (GLM). In the latter case, residual plots were checked for normality and homoscedasticity.

In the experiment (I) a factorial ANOVA was used to detect significant differences between sites (Jehkas and Saana) and grazed and ungrazed areas in fungal PLFA and bacterial PLFA ratio, soil enzyme activities, soil nutrient concentrations, plant coverage rate, plant biomass and microarthropod abundances (collembola, acari, nematodes). Soil microbial community diversity and dependence on environmental variables were assessed by redundancy analysis (RDA) where all the identified PLFA peaks were used as proxies of different microbial groups.

Differences in plant and microarthropod communities were examined using non-metric multidimensional scaling (NMDS) ordination method. The "autopilot" mode of PC-ORD was used with the Sørensen (Bray Curtis) distance measure. To further explore whether microarthropod and plant communities differed between the sites and grazed and ungrazed areas a two way analysis of similarity (ANOSIM) was performed. Similarity percentage (SIMPER) analysis was performed to determine which species were the major contributors to these differences. A canonical correspondence analysis (CCA) with forward selection for significant environmental variable was performed in order to check which environmental parameters contributed in determining plant and soil animal community structure.

ANOVAs were performed to assess the response of DSE and AM fungi (hyphae, vesicles and arbuscules) to grazing (II), fertilization and clipping (III) and successional stage (IV).

We estimated rarefaction curves for the VTX retrieved after the cloning and the sequencing of the AM fungal SSU present in *D. flexuosa* roots (IV).

3 RESULTS AND DISCUSSION

3.1 Grazing effects on Arctic ecosystems (I, II)

The importance of grazing as the mechanism that is vital in the maintenance of meadow and prairie ecosystems has been widely investigated (i.e.McNaughton 1979, Ruess and McNaughton 1987, McNaughton *et al.* 1997, Augustine and McNaughton 1998, Collins *et al.* 1998, McNaughton *et al.* 1998, Knapp *et al.* 1999) and both historic (Zimov *et al.* 1995) and contemporary (Olofsson *et al.* 2004) evidence suggests that this can be also one of the most important mechanisms promoting the formation of graminoid dominated systems in the Arctic (van der Wal 2006). According to van der Wal (2006) grazing should enhance the activity of decomposers, promote nutrient cycling and increase nutrient availability, thus favoring the presence of grasses. Vice versa, when grazers are removed from a meadow ecosystem the opposite effect should be observed: nutrient cycling and availability should decrease. The lower nutrient availability should in turn push the ecosystem toward a less productive stage, where grasses give way to mosses and lichens. What I observed in the experiments (I) and (II) was against this prediction and only few variables responded directly to grazing. In most cases the response to grazing was strongly mediated by the site and opposite to the expectations. Site itself was responsible for the response of some variables (Table 1).

Nutrient availability was expected to determine plant community structure, but the vegetation was very similar in both sites, despite the fact that Jehkas soil is characterized by a higher amount of nitrogen (NH_4^+) than Saana (I). The similarity of the vegetation in the two sites can depend on the fact that in Arctic tundra the most productive species, *D. flexuosa*, exploits the most abundant nitrogen form, while the other species rely on the other available nitrogen forms (McKane *et al.* 2002). In this case the difference in nitrogen availability will be evened out by the most efficient uptake of *D. flexuosa*. This means that in the two different meadows the nitrogen availability for the other plant species could be reduced to similar levels, which would then support a similar vegetation. However, this does not explain why the coverage and the abundance of *D. flexuosa* was very similar in the two sites, but this may depend on the fact that also other nutrients can be limiting to a similar level in both sites.

Variation in nitrogen availability corresponded to changes in the soil microarthropod community and trophic structure. The higher nutrient availability in Jehkas was accompanied by higher microarthropod species richness and higher diversity when compared to Saana. Overall, the structure of the microarthropod community was correlated with organic nitrogen availability, site and grazing. However, a previous study show that nutrient addition plays a small role in determining the microarthropod community structure, while trampling effects are visible already in the short period (Cole *et al.* 2008). In Jehkas, the nitrogen rich site, the proportion of predatory acari was higher than the proportion of plant-feeding acari, while the opposite trend was observed in Saana (I). This is an indication that the quantity of resources available is a determinant of the structure of the soil trophic chain, probably because higher nitrogen can support higher plant productivity which in turn rebounds on the below-ground compartment. Even though not much is known about the consequences of changes in soil food web structure, different amount of predatory fauna can have important consequences on soil processes such as decomposition and mineralization (Bardgett 2005). For instance, it has been observed that a decrease in predatory acari had a negative effect on decomposition processes due to an increase in bacterial feeding nematodes, which in turn reduced microbial growth (Santos *et al.* 1981). However, the trophic cascades generated by changes in the abundance of predators are difficult to predict, and the effect may be negative (Bouwman *et al.* 1994, Mikola and Setälä 1998) or neutral (Laakso and Setälä 1999). In my work changes in the trophic structure were reflected by the different relative amount of bacteria and fungi, with the latter being more abundant in Jehkas, as showed by the PLFA analysis and the higher relative abundance of fungal feeding acari. This was quite surprising since usually the more nutrient poor the ecosystem, the higher the fungal dominance (e.g. Bardgett and McAlister 1999).

Grazing, and trampling in particular, is probably one of the main determinants of the decline of enchytraeids in the grazed area (Sørensen *et al.* 2009). A decline in the enchytraeid abundance due to soil compaction may have strong repercussion on the entire ecosystem. At high latitudes, where earthworms and ants are virtually absent, enchytraeids may exert an important function in terms of soil aeration, thus enhancing bacterial activity and decomposition (I). Moreover, trampling *per se* may have important repercussion on soil microbial activity and soil characteristics. In both sites, grazing cessation led to a decrease in soil OM content, which could be caused by higher microbial activity in the ungrazed areas. Higher microbial activity could have been favored by larger soil pore space and aeration. On the contrary, trampling in the grazed area may result in anaerobic conditions (Rasiah and Kay 1998), which are less favorable for decomposition. Anaerobic conditions in the grazed area could have been also caused by increased water retention ability, as the grazed soil was moister than the ungrazed one. However, higher moisture content in the grazed area may be also related with the higher OM content. Probably these two variables are positively correlated: OM can promote soil water retention, and water retention can impair microbial activity. On the other hand, soil moisture may vary in time and $\delta^{13}C$ measurements in plants leaves showed that there were no changes in long term between grazed and ungrazed areas. Grazing led also to a shift between the two collembola *Isotomiella minor* and *Folsomia quadrioculata*. The causes behind this shift are difficult to pinpoint, but it may be related to the different sensitivity of these two species to different sources of environmental stress, since previous studies show similar patterns in response to abiotic disturbance (Tranvik and Eijsackers 1989). Grazing had an important effect on AM fungi, even though the effects were dependent on both plant species and site. While in the grass *D. flexuosa* grazing led to a decline of AM fungal frequency in both sites, the two forbs responded mainly in Saana, the nutrient poor site. The AM decline observed in the two forbs showed a clear similarity with the model proposed by Gehring and Whitham (2002) in which a decrease in AM colonization frequency due to grazing is expected in environments with high grazing intensity and nutrient limitation. In terms of other variables measured, such as enzymatic activity, organic nitrogen, microbial nitrogen, foliar $\delta^{15}N$, plant and microarthropod community structure, a response to grazing relief was observed only in Jehkas. In Jehkas, the coverage of *D. flexuosa* increased by 10% in the ungrazed area, and this was the main determinant of the difference in plant community structure, which otherwise was quite homogenous. Decline of *D. flexuosa* in areas subjected to reindeer grazing has been previously observed, however also in that case *D. flexuosa* was the dominant species in both grazed and ungrazed areas (Bråthen and Oksanen 2001). The microarthropod structure had exactly the same pattern and the ungrazed Jehkas site was substantially different from Saana (grazed and ungrazed) and Jehkas (grazed). Grazing relief in Jehkas caused an increase in the enzymatic activity and $\delta^{15}N$ foliar signature. These facts, together with a decrease in soil OM content and an increase in the microbial biomass in the ungrazed areas, suggested that grazing relief favored decomposition processes and promoted nutrient cycling, especially in Jehkas. Higher $\delta^{15}N$ signature depends on the fact that when nitrogen cycling is faster nitrogen can leave the system via leaching (NO_3^-) or evaporation (NO_2, N_2). It has been shown that losses of N_2O can be also promoted by the presence of grazers (Holst *et al.* 2008). Holst *et al.* (2008) suggested that grazing, reducing plant cover and thus snow insulation, negatively affects soil moisture. This in turns hampers nutrient release in concomitance of freeze-thaw cycling due to a reduction of ice formation in the soil. However, in our study we did not observe major changes in plant community composition and biomass and nutrient cycling acceleration and changes in N_2O losses, if present, may also be dependent on inherent topographic differences between the two sites which interact with the presence of grazers.

Taken together, these results show that there is a strong link between site specific characteristics, which may be related with different nutrient availability, and the outcome of grazing. In particular, nutrient availability may be positively correlated with the temporal scale of the response to grazing relief, with the higher the nutrient availability the shorter the recovery time (Ravolainen *et al.* 2011). This may explain as well why only a few changes are detectable in Saana compared to Jehkas where the response to grazing exclusion is clear and consistent.

TABLE 1 List of variables measured in Kilpisjärvi (I, II) which responded significantly to grazing, site or the interaction between site and grazing (site x grazing).

Site	Soil organic matter content is the highest in Saana. Soil extractable NH_4^+ is the highest in Jehkas. Relative abundance of predatory and fungal feeding acari is the highest in Jehkas.
Grazing	Soil organic matter content is the highest in the grazed area. Soil moisture is the highest in the grazed area (gravimetric measurements). Soil microbial biomass is the lowest in the grazed areas Enchytraeids are the least abundant in the grazed areas *Isotomiella minor* declines in the grazed areas, while *Folsomia quadrioculata* abundance increases. AM colonization in *D. flexuosa* declines.
Site x Grazing	Enzymatic activity of acid-phosphatase, leucine aminopeptidase and phenol oxidase is the lowest in the grazed area in Jehkas. Soil microbial nitrogen and organic nitrogen content is the lowest in the grazed area in Jehkas. *Deschampsia flexuosa* declines in the grazed area in Jehkas. Plant community structure and soil microarthropod community structure are affected by grazing mainly in Jehkas. AM colonization in *P. crantzii* and *S. virgaurea* declines due to grazing in Saana. Nitrogen cycling is reduced by grazing in Jehkas.

3.2 Mechanisms behind the AM reduction due to grazing in *Deschampsia flexuosa* (II, III)

In the previous section I showed that AM fungi in the two forbs, *P. crantzii* and *S. virgaurea* had a different response to grazing compared with *D. flexuosa*. In *D. flexuosa* grazing caused a consistent reduction in AM fungal colonization across sites. This suggests that different mechanisms than the one proposed by Gehring and Whitham (2002) and observed in the two forbs (*P. crantzii* and *S. virgaurea*), caused a reduction of AM fungal colonization in *D. flexuosa*. The causes that explain this difference may lie in the different physiology and adaptation of the three plants to grazing. Changes in the foliar $\delta^{15}N$ signature were not only related with grazing, but were also dependent on plant species. The $\delta^{15}N$ signature of the two forbs was significantly lower than the one of *D. flexuosa*. Different pools of nitrogen have different $\delta^{15}N$ values, organic nitrogen (i.e. amino acid) is ^{15}N depleted when compared to nitrogen contained in urine and NH_4^+ (Yano *et al.* 2010). The ability of many boreal plants to utilize amino acids and organic form of nitrogen as nitrogen source is well recognized (Kielland 1994, Näsholm *et al.* 2009), as well as the fact that *D. flexuosa* has more affinity for NH_4^+ compared with other plant species (Gigon and Rorison 1972). It has been shown that *D. flexuosa* suffers from grazing (Pegtel 1994, Bråthen and Oksanen 2001). These studies show that this plant often declines in grazed area (Bråthen and Oksanen 2001). Changes in AM dependency may also play a role in maintaining the high abundance of *D. flexuosa* in both the grazed and ungrazed area, even though the coverage of this plant was negatively affected by grazing in Jehkas.

In the greenhouse experiment (III) the relationship between AM fungal decline, fertilization and defoliation was investigated. While no significant effect of defoliation was observed, the effect of fertilization was consistent and in line with the decline observed in the field under the natural occurrence of grazing. Nitrogen fertilization has been previously observed to reduce AM colonization in plants, when other nutrients, phosphorus in particular, are not limiting (Treseder and Allen 2002). Arctic environments are usually mainly nitrogen limited, while phosphorus is more available (Nadelhoffer *et al.* 1992). Moreover *D. flexuosa* is characterized by an extremely low demand for phosphorus (Rorison 1968). A low demand for phosphorus may correspond to a higher reliance on AM fungi for nitrogen acquisition, a reliance that would be lowered under the fertilization treatment. The greenhouse experiment confirmed the fact that fertilization plays a major role in determining the reduction of AM colonization frequency in *D. flexuosa*. This supports the fact the different plants may show different response to grazing depending on which mechanisms (defoliation, fertilization) they are more sensitive to. The high affinity of *D. flexuosa* to NH_4^+ that is contained in reindeer urine may enable *D. flexuosa* to exploit the sporadic flushes of resources which follow reindeer urination, lowering at the same time the costs paid to its fungal symbionts.

3.3 Soil characteristics and AM fungal community structure (IV)

Deschampsia flexuosa has a wide holoarctic distribution (Hultén and Fries 1986) and is well adapted to different conditions that range from sand dunes to birch forest understory. In the field, AM fungi can colonize it intensively (up to 60%

colonization rates) and grazing, and in particular fertilization, can result in a decline in AM colonization in this plant. In my (IV) experiment I demonstrated that soil characteristics themselves are an important determinant of plant reliance on AM fungus and AM fungal community. In the Kalmakaltio area, *D. flexuosa* is able to grow both in the early successional stage, characterized by the lack of other vegetation, and the late successional stage, a heat where sparse shrubs are growing together with grasses, forbs and mosses. These two stages have contrasting characteristics in terms of pH, organic matter content, plant and microbial communities. In both stages *D. flexuosa* was colonized by AM fungi, but the frequency was significantly lower in the late successional stage. AM frequency is a good indicator of plant nutrient status (Treseder 2013), thus the higher AM fungal frequency in the early stage might indicate that *D. flexuosa* is more dependent on AM fungi for nutrient acquisition or water balance than in the late stage. The early stage was characterized by 10-folds lower soil OM content than the late stage. This probably was related to a lower water retention capacity in the early stage. Despite this fact, plants in the late stage had a higher $\delta^{13}C$ signature, which is symptomatic of higher water stress. This suggests as well that in the early successional stage AM fungi may improve water access mitigating the harsh condition of the sand dunes. On the other hand, plants growing in the early stage are subjected to a more intense competition, due to the presence of other plant species. Competition, which involves both mineral and water resources, might also explain why plants growing in the late stage present a higher water stress.

The differences between the two stages also affected the structure of the AM fungal community. The molecular analysis of the AM fungal community *in planta* revealed that *D. flexuosa* plants growing in the two different stages shared no common AM fungal virtual taxa, showing two clearly distinct AM fungal communities. This agrees with the finding of Sikes (2012) which shows that the AM spore pool in the soil is completely different between the late and the early point of a successional sequence. In addition to this, I show that the AM fungal community diverges with diverging soil type and plant communities also if the same plant host (*D. flexuosa*) is present. There is a growing body of evidence that shows that soil characteristics play an important role in selecting the AM community (McGonigle and Fitter 1990, Helgason *et al.* 2002, Jansa *et al.* 2002, Lekberg *et al.* 2007). This might have very important ecological implications, since the fitness of the plants is strongly linked not only with the presence of AM fungi, but also the identity of the AM fungal partner. These results are in agreement with a previous study (Johnson *et al.* 2010) that suggest that different soil conditions promote coadapeted complexes of plant, soil microbes and AM fungi, whom fitness (both plant and microbial) is maximized under specific soil conditions.

4 CONCLUSIONS

My results emphasize the importance of soil characteristics at two levels. In first instance soil characteristics are strictly linked with microarthoropod, microbial and plants symbiont community structure (I, IV). Secondly soil characteristics determine soil microarthropod, plant community and ecosystem response to grazing (I, II).

My results show that soil characteristics determine AM community *in planta* (IV), in agreement with previous findings. This suggests that different soil conditions can favor the formation of complexes of plant and AM fungi that are coadapted. However, what renders certain AM fungi better adapted to different environmental conditions remains unclear. Therefore, targeted greenhouse experiments are needed in order to investigate, characterize and describe the autoecology of different AM fungi in relationship with different environmental conditions.

Microarthropod community and soil trophic chain was affected by nutrient availability (I). This suggests that nutrient availability, probably by promoting plant productivity, is in turn reflected on soil consumers.

Plant community and soil microarthropod community responded in parallel to grazing relief only in the site with the highest nutrient availability. Differences in soil nutrient availability were probably modulating also the decline in AM fungi in response to grazing. This suggests that nutrient availability is a key factor in determining the overall ecosystem response to grazing. However, this should be further tested including more sites or through a metanalysis including previously published work. My results show that grazing exerted a negative effect on nutrient cycling and relief from grazing caused a shift in soil processes. The increase in the microbial biomass, the depletion of soil OM, and the changes in $\delta^{15}N$ signature all supported the fact that nutrient cycling and decomposition processes where higher in the ungrazed area (I, II). Again, the difference in the intensity of the response to grazing relief between the two sites highlights the fact that inherent soil characteristics play a key role in determining and modulating the outcome of grazing. Besides nutrient availability other factors such as topography or soil physical structure can modify the intensity and type of response to grazing and certainly more experiments are needed in this direction. In particular, what needs to be investigated is how and which soil properties can inhibit or promote the ecosystem responses to biotic disturbance.

This thesis also shows that the different components of grazing have different importance on the variables under investigation. For example, in the experiment III, I showed that fertilization and not defoliation caused a reduction in AM colonization in the grass *D. flexuosa*, a reduction that resembles the one observed in the field (II). This is of particular importance considering that *D. flexuosa* is negatively affected by grazing and the fact that it is still the dominant species in both grazed and ungrazed meadow areas in northern Fennoscandia. These results suggest that the ability of *D. flexuosa* to persist in grazed and ungrazed areas depends on two factors: the well-recognized adaptation to different levels of nutrient availability and the capacity to modulate the resources allocated to the fungal symbionts in response to sporadic nutrient flushes.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Maaperän vuorovaikutussuhteet pohjoisissa ekosysteemeissä.

Maaperässä elää monimuotoinen eliöstökirjo: mikrobeja, sieniä, protistoja , ja selkärangattomia. Maaperän ravintoverkot ovat monimutkaisia ja huonosti tunnettuja. Maaperän eliöiden keskinäiset vuorovaikutukset sekä maanalaiset ja maanpäälliset prosessit vaikuttavat merkittävästi ravinteiden kiertoon, orgaanisen aineksen kertymiseen, hiilen varastoitumiseen ja viime kädessä koko ekosysteemin rakenteeseen ja toimintaan.

Arktisilla alueilla elämään kykeneviä eliölajeja on vähän, sillä arktiset alueet ovat ilmastoltaan ankaria pitkine talvineen, alhaisine lämpötiloineen ja lyhyine kasvukausineen. Vähäisen lajikirjon vuoksi arktiset alueet voivat toimia ekosysteemin toiminnan tutkimisen ”luonnon laboratorioina”. Kronosekvenssien avulla on mahdollista tutkia erilaisia maaperiä samoissa ilmasto-olosuhteissa. Kronosekvessit ovat alueita, joissa on lähekkäin sijaitsevia, eri-ikäisiä maannoksia. Yleensä kronosekvenssit muodostuvat häiriön seurauksena (esimerkiksi tuulieroosion tai laidunnuksen) tai esimerkiksi vetäytyvän jäätikön reuna-alueille.

Toinen tärkeä tekijä ala-arktisilla alueilla ja erityisesti Pohjois-Lapissa on porojen laidunnus. Poronhoidon taloudellisesta merkityksestä seuraa, että porojen määrä on ylittänyt ympäristön kantokyvyn. Suuri porojen määrä vaikuttaa ekosysteemin rakenteeseen ja toimintaan. Laidunnuksen on osoitettu muuttavan kasvillisuutta, maaperän prosesseja, kuten ravinteiden kiertoa ja maaperän eliöyhteisöjen rakennetta.

Väitöskirjassani tutkin arktista ekosysteemiä kahdesta näkökulmasta. Kahdessa ensimmäisessä työssä selvitin poronlaidunnuksen vaikutuksia kasvillisuuteen, maaperän eliöyhteisöihin, ravinteiden kiertoon ja sienijuurisymbioosiin. Kontrolloiduissa olosuhteissa tutkin jäljitellyn kasvinsyönnin vaikutuksia sienijuurisymbioosiin. Väitöskirjani viimeisessä osassa selvitin maaperän ominaisuuksien, maaperämikrobien ja kasvien sienijuurisymbioosin välisiä vuorovaikutussuhteita kahdessa eri sukkession vaiheessa subarktisessa ekosysteemissä.

Ennustin, että porojen laidunnuksen lopetus hidastaisi ravinteiden kiertoa ja muuttaisi kasvien, mikrobien ja niveljalkaisten yhteisörakennetta. Ennustin, että poronlaidunnuksen vaikutus sienijuurisymbioosiin olisi kielteinen, sillä laidunnnus vähentää kasvien yhteyttävän pinta-alan määrää, jolloin kasveilla on vähemmän yhteyttämistuotteita siirrettäväksi maanalaisten osien tarpeisiin. Lehtipinta-alan väheneminen ei kuitenkaan ole ainoa tekijä. joka voi vähentää sienijuuren määrää, sillä myös lannoituksen (virtsan lisäyksen) on osoitettu vaikuttavan kielteisesti sienijuurisymbioosiin. Tutkin kontrolloiduissa olosuhteissa lehtipinta-alan vähentämisen ja lannoituksen vaikutusta metsälauhan (*Deschampsia flexuosa*) sienijuurisymbioosin määrään. Sienijuurisymboosin on usein osoitettu vähenevän häiriön seurauksena. Enenevässä määrin on myös raportoitu arbuskelisienijuurisymbionttien reagoivan määrällisesti ja yhteisörakenteellaan maaperän laatuun. Ennustin, että kahdella lähekkäin sijaitsevalla alueella, jotka eroavat maaperältään, olisi erilainen arbuskelisieniyhteisö.

Tutkin Kilpisjärvellä poronlaidunnuksen vaikutuksia ekosysteemin maanpäällisiin ja maanalaisiin osiin. Kymmenen vuotta sitten rakennetut aitaukset suojasivat osaa kahdesta ala-arktisesta niitystä porojen laidunnukselta. Aitauksien sisäpuolelta ja ulkopuolelta otettiin maanäytteitä ja verso- ja juurinäytteitä heinälauhasta (*Deschampsia flexuosa*), keväthanhikista (*Potentilla crantzii)* ja kultapiiskusta (*Solidago virgaurea*). Maanäytteistä selvitettiin mikrobi- ja niveljalkaisyhteisöt, sukkulamatojen runsaus, entsyymiaktiivisuus ja ravinteiden saatavuus. Kasvinäytteistä mitattiin juuriston symbionttisten sienten määrä ja versosta $\delta^{15}N$. Verson $\delta^{15}N$ korreloi yleensä maaperän $\delta^{15}N$ kanssa, ja sitä voidaan käyttää arvioitaessa ravinteiden kiertoa ekosysteemissä. Sekä aitaamattomilla (jatkuvasti laidunnuspaineen alla) että aidatuilla alueilla (ei laidunnettu kymmeneen vuoteen) selvitettiin myös kasviyhteisön rakenne.

Jäljitellyn kasvinsyönnin vaikutuksia sienijuurisymbioosiin tutkittiin antamalla heinälauhoille lehtien poisto-käsittely, lannoituskäsittely, tai molemmat käsittelyt yhdessä. Viimeisessä tutkimuksessa heinälauhaa kerättiin kahdesta eri sukkession vaiheesta ja arbuskelisienten yhteisörakenne selvitettiin molekyylimenetelmin.

Tämän väitöskirjan päätulos oli, että porojen laidunnuksen estäminen muuttaa kasviyhteisön ja maaperän niveljalkaisyhteisöjen rakennetta sekä maaperän toimintaa riippuen alkuperäisistä maaperän ominaisuuksista. Laidunnuksen estämisellä oli selkeimmät vaikutukset alueella, joka oli ravinteikkaampi. Laidunnus vähensi heinälauhan arbuskelisienijuurisymbioosin määrää todennäköisesti virtsan sisältämän typpilisäyksen vuoksi. Kahden muun tutkimuslajin sienijuurisymbioosin määrää selitti myös alueen maaperän ominaisuudet, jotka olivat tärkeitä tekijöitä myös verrattaessa kahdella eri-ikäisellä maannoksella kasvavien heinälauhojen juuristosymbiontteja. Heinälauhan arbuskelisieniyhteisö oli täysin erilainen eri-ikäisissä maannoksissa.

Tuloksissani korostui maaperätekijöiden merkitys kahdella tasolla. Ensinnäkin maaperän ominaisuudet ovat yhteydessä niveljalkaisten, mikrobien, kasvien ja kasvien sienijuurisymbionttien yhteisörakenteeseen. Toiseksi maaperän ominaisuudet määrittävät miten niveljalkais- ja kasviyhteisöt reagoivat laidunnukseen. Tässä väitöskirjassa osoitin myös, että laidunnuksen eri osa-tekijät vaikuttavat eri tavalla ja lannoitus, mutta ei lehtien poisto vähentää arbuskelisienten määrää heinälauhan juuressa. Tämä tulos on erityisen merkityksellinen siksi, että laidunnus vaikuttaa kielteisesti heinälauhaan, joka silti on kenttäkerroksen vallitseva laji Pohjois-Fennoskandiassa. Näiden tulosten perusteella voidaan päätellä, että heinälauhan menestyminen laidunnetuilla alueilla perustuu kahteen ominaisuuteen: sen tunnustettuun kykyyn sopeutua eri ravinnetasoihin ja kykyyn säädellä sienijuurisymbioosiin allokoituja resursseja ravinnetason mukaan. Tulokseni osoittivat, että maaperän ominaisuudet säätelevät arbuskelisienijuuriyhteisön rakennetta kasveissa.

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