

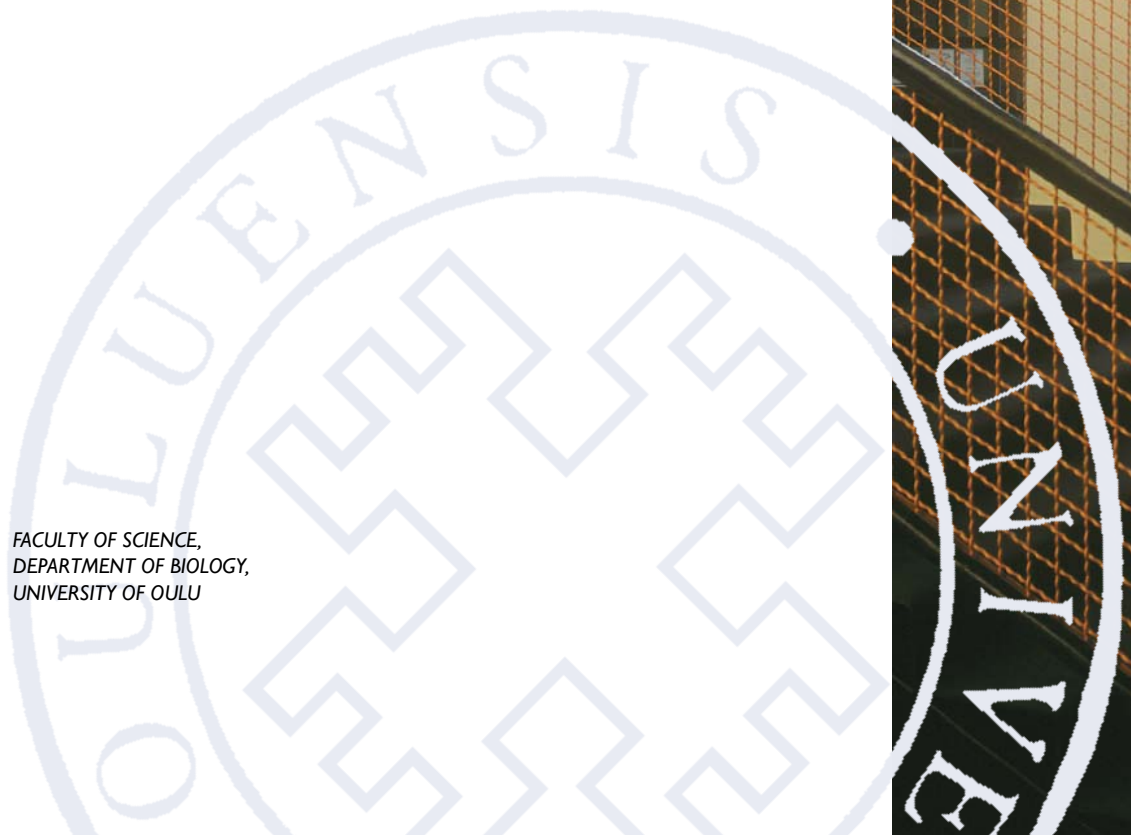
*Anu Eskelinen*

PLANT COMMUNITY DYNAMICS  
IN TUNDRA: PROPAGULE  
AVAILABILITY, BIOTIC AND  
ENVIRONMENTAL CONTROL

FACULTY OF SCIENCE,  
DEPARTMENT OF BIOLOGY,  
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*ANU ESKELINEN*

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**Eskelinen, Anu, Plant community dynamics in tundra: propagule availability, biotic and environmental control.**

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*Abstract*

Plant community composition and diversity are determined by the balance between rates of immigration and extinction. Processes of immigration to a local community, i.e. propagule availability and dispersal of propagules between and within habitats, set the upper limit for the pool of species potentially capable of coexisting in a community, while local biotic interactions, i.e., competition, facilitation, herbivory and interactions with below-ground ecosystem components, and environmental factors control colonisation and establishment, and determine the persistence and dynamics of already existing species.

In this thesis, I studied (1) the interactions between propagule availability, biotic and environmental constraints on colonisation, and (2) the interdependence between biotic and environmental factors regulating community processes in already established resident vegetation. First, I found that both propagule availability and competition with adult plants limited the rates of colonisation and total community diversity in a relatively low-productive tundra ecosystem. Long-term exclusion of mammalian herbivores and alleviation of nutrient limitation by fertilization increased the intensity of competition with established vegetation, and diminished immigration rates. In addition, I also found that community openness to colonization depended on the initial community properties, i.e., the functional composition and the traits of dominant plants in resident vegetation, which mediate the effects of nutrient addition and biomass removal on immigration rates. Second, adult plants in the resident vegetation experienced an increased extent of neighbourhood competition and herbivory in nutrient enriched conditions and in naturally more fertile habitats. However, the effects were also species-specific. On a community level, release from heavy grazing favoured lichens over graminoids and increased species richness. Furthermore, I also showed that plant community composition was strongly linked with soil organic matter quality and microbial community composition, and that these vegetation-soil-microbe interactions varied along a gradient of soil pH.

Overall, my results emphasise that propagule availability, biotic and environmental control over community processes are strongly interconnected in tundra ecosystems. Especially, my findings highlight the role of plant competition and herbivory and their dependence on soil nutrient availability in governing colonisation and resident community dynamics. My results also indicate that plant functional composition and traits of dominant plants are of great importance in channelling community responses to external alterations and dictating plant-soil interactions.

*Keywords:* colonisation, competition, disturbance, diversity, facilitation, herbivory, initial community properties, microsite limitation, plant community composition, plant functional traits, plant-soil interactions, reindeer, soil fertility, tundra



*To the magnificent Nature of tundra*





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Oulu, October 2009

Anu Eskelinen



## List of original articles

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Eskelinen A & Virtanen R (2005) Local and regional processes in low-productive mountain plant communities: the roles of seed and microsite limitation in relation to grazing. *Oikos* 110: 360–368.
- II Eskelinen A (2009) Initial community properties mediate the impacts of nutrient enrichment and neighbor removal on plant immigration rates. Manuscript.
- III Eskelinen A (2008) Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology* 96: 155–165.
- IV Eskelinen A & Oksanen J (2006) Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *Journal of Vegetation Science* 17: 245–254.
- V Eskelinen A, Stark S & Männistö M (2009) Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. *Oecologia* 161: 113–123.



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# 1 Introduction

Plant community composition and diversity are determined by the balance between rates of immigration and extinction (MacArthur & Wilson 1967, Tilman 1994, Leipold *et al.* 2004). Regional influences, *i.e.* evolutionary history, geologic age, time for speciation, migration and dispersal between suitable regions and habitats in a landscape, determine the pool of species potentially capable of coexisting locally (Ricklefs 1987, 2004, Cornell & Lawton 1992, Zobel 1992, Eriksson 1993, Harrison *et al.* 2006, Harrison & Cornell 2008). Local influences such as neighbourhood interactions, disturbance, resource availability and abiotic environmental conditions filter the arriving species and govern local community dynamics together with feedbacks with the soil system, ultimately determining community composition and diversity (Grime 1973, Huston 1979, Tilman 1982, Grace & Tilman 1990, Bertness & Callaway 1994, Wardle 2002, Bardgett 2005, Callaway 2007). The relative importance of species pool, propagule availability and local biotic and abiotic factors in community organisation and dynamics is predicted to show divergent patterns along environmental gradients, and between various habitats and ecosystems.

## 1.1 Immigration and local community dynamics

The roles of abiotic environment and biotic interactions in determining rates of extinctions and constraining local assemblage dynamics are widely recognised. More recently, constraints on immigration to a local community, *i.e.* the limited availability and dispersal of propagules and local obstacles impeding colonisations have been shown to play important roles in determining community composition and diversity (*e.g.* Tilman 1993, Tilman 1997, Zobel *et al.* 2000, Turnbull *et al.* 2000, Foster & Tilman 2003, Foster *et al.* 2004, Stevens *et al.* 2004, Housemann & Gross 2006, Clark *et al.* 2007, Klanderud & Totland 2007, Dickson & Foster 2008). The relative importance of propagule availability and local biotic control on plant immigrations and community dynamics may vary along the successional (Turnbull *et al.* 2000), disturbance and productivity gradients (Grime 1979, Foster *et al.* 2004). The ‘Shifting limitations hypothesis’ (Huston 1999, Zobel *et al.* 2000, Foster *et al.* 2004) predicts a shift from the prevalence of limited propagule availability (*i.e.* seed limitation) to the prevalence of local biotic interactions (*i.e.* microsite limitation, competition with adult plants) when moving from relatively low or moderate productivity to high productivity.

In very low productivity, species colonisations should be mainly controlled by severe abiotic conditions (Grime 1973, Zobel *et al.* 2000). This model also predicts that disturbance would counteract the competitive exclusion of arriving species in productive habitats. A few existing experimental studies have demonstrated that the relative importance of propagule availability decreases and microsite limitation increases along natural productivity gradient (Foster 2001, Foster *et al.* 2004) and in fertilised conditions (Stevens *et al.* 2004, Dickson & Foster 2008). Disturbance has also been found to alleviate microsite limitation (Foster 2001, Foster *et al.* 2004, Dickson & Foster 2008). Since grazing by mammalian herbivores limits the accumulation of plant above-ground biomass (*e.g.* Virtanen *et al.* 1997), it could impose a similar influence on the relative importance of recruitment limitation vs. local biotic control.

The biotic properties of local communities can also regulate species immigration. For example, species-rich plant communities may be more resistant to invasions of new species (Elton 1958) either due to complementary use of resources, or because of a higher probability to include a highly competitive species in the species assemblage. In experimental studies, successful colonisation has been shown to depend on species richness (Van Ruijven *et al.* 2003, Fargione & Tilman 2005), community dominance, the traits of the dominant species (Smith *et al.* 2004, Emery & Gross 2006, Emery & Gross 2007) and the functional composition of the resident community (Fargione *et al.* 2003).

Some recent studies highlight the role of initial community properties (*e.g.* dominance, functional composition) in determining community responses to environmental and biotic alterations, and thereby potentially affecting species losses and gains (Clark *et al.* 2007, Elmendorf & Moore 2007, Hillebrand *et al.* 2007, Liancourt *et al.* 2009). The susceptibility of the target community to species loss after nitrogen enrichment may be contingent upon environmental conditions (*e.g.* potential for soil acidification, initial N concentrations) and production responsiveness of the community (Clark *et al.* 2007). Dominance relationships in a community have also been emphasised as an important determinant of vegetation change under fertilization and herbivory (Hillebrand *et al.* 2007). These findings suggest that species immigration rates in response to nutrient enrichment, herbivory and other biotic and environmental alterations may similarly depend on initial community properties.

## 1.2 Competition and facilitation in relation to environment

At present, there are divergent views about the intensity of competition and the relative importance of competition and facilitation as structuring forces of plant communities along gradients of productivity and environmental harshness. Grime (1973, 1979) suggested that plant competition is less intense in unproductive and harsh environments, while the intensity of competition increases with increasing productivity and in benign environments. According to this hypothesis, plant species richness should peak at intermediate levels of productivity where resource levels are sufficient to support plant growth and promote species' colonisations. At high productivity, diminished colonisation rates and enhanced extinction rates due to intensified competitive interactions reduce species richness, while at low productivity, resource deficiency and harsh abiotic conditions limit the number of surviving and coexisting species. A contrasting view of the intensity of competitive interactions in low-productive environments is provided by Tilman's resource competition model (1982, 1988). It predicts that competition is equally intense in unproductive and productive environments, but the nature of competition changes from competition for soil resources to light competition, respectively.

More recently, facilitation between plants has been emphasised to influence plant performance, species distributions and community composition, and species richness of communities especially in environmentally severe habitats (*e.g.* Bertness & Callaway 1994, Brooker & Callaghan 1998, Michalet *et al.* 2006, Kikvidze *et al.* 2005, Brooker *et al.* 2008). Plant responses to neighbours may be positive or negative depending on the relative strength of habitat amelioration and resource competition, and species-specific tolerance limits. Net positive responses to neighbours have been proposed to prevail near gradient ends and the distributional limits of the target plants (Choler *et al.* 2001, Liancourt *et al.* 2005).

## 1.3 Herbivores and plant community dynamics

Herbivores modify plant community composition and diversity through their direct influence on plant growth, recruitment, colonisation and extinctions, which alter interactions among individual plants (Louda *et al.* 1990, Huntly 1991, Pacala & Crawley 1992, Olff & Richie 1998, Mulder 1999, Maron & Crone 2006), and favour certain plant growth forms and functional types. For instance, heavy grazing is expected to favour graminoids over other plant groups (*e.g.* shrubs,

forbs, lichens, mosses). In general, graminoids are able to rapidly regrow after a loss of above-ground biomass due to their basal meristems (Kotanen & Jefferies 1987, Mulder 1999) and can effectively utilise nutrients (Grellman 2002, Bret-Harte *et al.* 2004, Van der Wal *et al.* 2004) that are released from grazer faeces and urine. Grazer-induced changes in the relative abundance of different plant groups in a community can extend to landscape- and ecosystem levels. Zimov *et al.* (1995) and Van der Wal & Brooker (2004) suggested that grazing, trampling and fertilization by large mammal herbivores in the arctic tundra stimulates soil nutrient cycling and can change unproductive lichen, moss and shrub-rich tundra into a graminoid-dominated productive grassland.

By the removal of the biomass of superior light competitors, grazing can favour inferior competitors and species coexistence. The removal of vegetation biomass also creates competition-free sites for plant recruitment and likely increases the rates of plant colonisations (Huntly 1991, Olf and Richie 1998). According to the 'Intermediate disturbance hypothesis' (Grime 1973, Connell 1978, Huston 1979) plant species richness should peak at intermediate levels of disturbance where the growth of competitively superior dominants is suppressed allowing inferior competitors to exist. At high levels of disturbance species are lost because intensive and frequent perturbations pose extinctions and prevent new colonisations.

Disturbance (*e.g.* herbivory) effects on plant species richness have also been predicted to depend on soil nutrient availability (Huston 1979, Kondoh 2001). The model by Kondoh (2001) predicts a unimodal disturbance-diversity relationship, however, the level of disturbance maximising diversity should shift towards higher levels of disturbance with increasing productivity. In other words, positive disturbance-diversity relationships should be found in high productivity while negative relationships should prevail in low productivity. There are few recent studies that support these predictions (*e.g.* Proulx & Mazumder 1998, Bakker *et al.* 2006, Olofsson & Shams 2007, Hillebrand *et al.* 2007). In an ecosystem-level review, Proulx & Mazumder (1998) reported an opposite impact of grazers on plant species richness in nutrient-rich vs. nutrient-poor ecosystems, and Bakker *et al.* (2006) showed that experimental exclusion of large mammal herbivores had a positive effect on species richness in high productivity whereas the effect was negative in low productivity. Hillebrand *et al.* (2007) applied meta-analytical statistics to cross-ecosystem data and found that increased producer richness under herbivory was confined to high productivity habitats which also exhibited the strongest reduction in richness with fertilization. Thus far, only the

net effects of herbivory on diversity have been examined, while the separate roles of colonisation and extinction have not yet been investigated.

Herbivores can modify plant competitive interactions by reducing the biomass of neighbouring vegetation which can potentially lead to either increased (e.g. Mulder & Ruess 1998, Van der Wal *et al.* 2000) or decreased plant growth (Brooker *et al.* 2006) depending on whether neighbours compete for shared resources or protect each other against unfavourable abiotic conditions. Herbivore effects on plant-plant interactions should be especially pronounced in ecosystems and habitats where productivity is strongly constrained by nutrient availability (Louda *et al.* 1990). The 'Ecosystem Exploitation Hypothesis' (EEH) by Oksanen *et al.* (1981) and Oksanen & Oksanen (2000, [see also Aunapuu *et al.* 2008]) predicts that plant interspecific competition is reduced in ecosystems of relatively low or intermediate productivity because mammalian herbivores maintain plant above-ground biomass at a low level. In such grazer-controlled systems, enhanced plant production in response to nutrient enrichment should lead to increased consumption by herbivores (and increased herbivore biomass) while plant biomass should remain unaltered.

#### **1.4 Vegetation-soil interactions and abiotic environment**

The dynamics of above-ground plant communities is predicted to be interlinked and to operate in concert with the dynamics of the below-ground soil system (Wardle 2002, Eviner & Chapin 2001, Reynolds *et al.* 2003, Wardle *et al.* 2004, Bardgett 2005, Van der Heijden *et al.* 2008). Plant communities showing distinct species and functional type compositions are likely to produce litter and organic matter of different compositions and chemical qualities (Hobbie 1996), which act as substrates for soil microbes and may therefore influence the composition of soil microbial communities (Kourtev *et al.* 2002, Zak & Kling 2006) and soil nutrient cycling. Because different microbial groups possess varying capabilities to degrade labile and recalcitrant organic substances, microbial community composition also influences decomposition and soil nutrient availability, and may thereby favour certain plant functional groups over others. Litter poor in C and phenolics and rich in N formed by fast-growing herbaceous plants (Pérez-Harguindeguy *et al.* 2000, Shaw & Harte 2001, Questad *et al.* 2003, Dorrepaal *et al.* 2005) has been suggested to result in high-quality, easily decomposable organic matter rich in labile compounds, and a prevalence of bacteria in soil microbial communities (Wardle *et al.* 2004). In contrast, slow-growing evergreen

shrubs producing litter rich in C and phenolics (Hobbie 1996, Pérez-Harguindeguy *et al.* 2000, Shaw & Harte 2001, Dorrepaal *et al.* 2005) should be connected to recalcitrant organic matter rich in lignin and other polyphenolic substances, and a dominance of fungi in microbial communities (Wardle *et al.* 2004, Van der Heijden *et al.* 2008).

Abiotic environmental conditions, which can have a huge influence on the individual components of ecosystems, may function as important initial drivers of plant-vegetation-soil interactions (Reynolds *et al.* 2003, Wardle *et al.* 2004, Bezemer *et al.* 2006). One major environmental factor, soil pH, has for long been connected to high plant diversity (Grime 1979, Gough *et al.* 2000, Pärtel 2002, Virtanen *et al.* 2003, Crawley *et al.* 2005, Virtanen *et al.* 2006), and has also been proposed to promote distinct plant community compositions due to changing nutrient availability along pH gradient (Peet *et al.* 2003, Nordin *et al.* 2004). More recently, pH has also been found to exhibit a strong influence on microbial community composition and diversity (Bååth & Anderson 2003, Fierer & Jackson 2006, Männistö *et al.* 2007, Fierer *et al.* 2007). If soil pH imposes parallel patterns in both above- and below-ground communities, it is likely to drive important ecosystem processes and functioning.

## **1.5 Tundra as a research environment**

In high latitude and altitude ecosystems, harsh abiotic conditions are traditionally considered to limit plant performance and distributions (Billings & Mooney 1968). Tundra ecosystems are also generally regarded as nutrient-limited owing to low nutrient mineralization rates at low temperature, which strongly limits plant growth (Shaver & Chapin 1980). Within these ecosystems, however, drastic variation in local environmental conditions, i.e. in soil nutrient availability and pH, can be found depending on the underlying bedrock material, resulting in distinct soil fertility, habitat productivity, plant community composition and species richness between non-acidic and acidic habitat types (Nordhagen 1943, Gough *et al.* 2000, Virtanen *et al.* 2003, Nordin *et al.* 2004, Virtanen *et al.* 2006). Acidic habitats are characterised by low productivity and strong dominance by a few dwarf shrub species, whereas non-acidic heaths are characterised by relatively high productivity and species-rich forb- and graminoid-rich vegetation. Given this drastic variation in soil abiotic conditions and the composition and diversity of above-ground vegetation, strong parallel linkages between above- and below-ground systems could be expected in such tundra systems. The relative

importance of biotic and environmental constraints controlling plant performance and community dynamics should also vary depending on the initial habitat properties (e.g. soil fertility).

In many tundra areas plants encounter intensive grazing by mammalian herbivores (e.g. Oksanen & Virtanen 1995, Mulder 1999, Olofsson *et al.* 2004). Grazing by semi-domesticated reindeer in northern Europe and by caribou in North America is considered to have a substantial impact on vegetation and ecosystem processes (e.g. Manseau *et al.* 1996, Mulder 1999, Virtanen 2000, Stark & Grellmann 2002, Stark *et al.* 2002, Olofsson 2006, Van der Wal 2006, Bråthen *et al.* 2007, Gough *et al.* 2007, Stark *et al.* 2007, Aunapuu *et al.* 2008, Pajunen *et al.* 2008). In addition to large mammalian herbivores, small grazers such as lemmings and voles, have a profound influence on above-ground vegetation in tundra areas (Virtanen *et al.* 1997, 2002, Olofsson *et al.* 2004, Oksanen *et al.* 2008).

Being tightly coupled with plant-herbivore dynamics and environmental severity, and with pronounced environmental gradients of soil fertility and productivity, tundra ecosystems are ideal for studying mainstream theories in community ecology. These include the relative importance of propagule availability and local biotic control on plant community dynamics, the interdependence of biotic (competition, facilitation, herbivory) and abiotic factors (resource availability, soil acidity) in governing individual plant performance, community composition and diversity, and the links between components of vegetation and the below-ground soil system along environmental gradients.

## **1.6 Aims of the study**

The general aim of my thesis is to elucidate the interdependence between immigration of species to a local community (*i.e.*, dispersal limitation and constraints on colonisation), local biotic (competition, facilitation, herbivory) and environmental factors (soil nutrient availability, pH), and their roles in regulating plant community dynamics in tundra ecosystems. The thesis also aims to disentangle interconnections between vegetation, soil and microbial communities. The thesis is composed of five articles in which I have used both observational (studies IV, V) and experimental (studies I – III) approaches to address the specific objectives and questions outlined below (see also Table 1).

In the first two studies (I, II), I examined the role of processes of species immigration in regulating local community dynamics. In the first study (I), I

experimentally tested the extent of dependence of plant colonization rates and community richness on limited availability of plant propagules (*i.e.* seed limitation) and suitable sites for colonisation (microsite limitation), and how these are related to grazing by mammalian herbivores in a relatively low-productive mountain environment. In the second study (II), I experimentally investigated the roles of biotic (grazing, competition) and environmental (soil fertility and habitat productivity) constraints on plant colonisation rates. I replicated the treatments (herbivore exclusion, biomass removal of established vegetation, fertilization, liming) in two different habitat types, non-acidic and acidic heaths that differed in plant community composition, dominance and nutrient availability, and I was therefore able to assess the influence of the initial community properties and environmental conditions on the response of plant colonisation rates to the treatments.

In the following studies (III – V), I focused on resident community dynamics, *i.e.*, the factors that control the performance of individual plant species, community composition and species richness, and interactions between vegetation and soil in already established vegetation. In the third study (III), I experimentally tested the roles of biotic factors (plant-plant interactions, herbivory by mammalian grazers) and abiotic environmental factors (soil fertility and habitat productivity) on the growth, flowering and survival of three target species that were transplanted to experimental plots. As in the second study (II), the treatments (neighbour removal, herbivore exclusion, fertilization, liming) were replicated in nutrient-rich non-acidic and nutrient-poor acidic heath sites, thereby enabling the examination of the interplay between the treatments and a natural soil fertility gradient. In the fourth study (IV), I explored how a change in the level of summer grazing by reindeer affects the abundance, composition and species richness of mountain plant communities. In this study, permanent plots established at seven sites differing in their original grazing pressure and investigated in 1990 were resampled *ca.* ten years later after a considerable decline in the number of reindeer. This allowed me to follow the recovery of the vegetation, *i.e.*, the effects of reduced grazing pressure. Finally, in the fifth study (V), I collected vegetation and soil data from non-acidic and acidic mountain tundra and investigated the relationships between plant community composition, soil organic matter quality and soil microbial community composition in relation to environmental variation in soil pH.



**Table 1. Summary of the study topics and the main background predictions involved in each study.**

Study Topic	Main predictions based on previous empirical and theoretical work
<p>I Immigration and local community dynamics</p> <p>Seed and microsite limitation in relation to grazing</p>	<p>Seed limitation should be particularly important and microsite limitation less important in relatively low-productive environments</p> <p>Increasing extent of microsite limitation with increasing vegetation biomass due to absence of mammalian herbivores</p>
<p>II Immigration and local community dynamics</p> <p>Interactive effects of herbivory, competition with established vegetation and productivity on plant colonisation rates</p> <p>The interactive impact of initial community properties and the treatments on colonisation rates</p>	<p>In the absence of herbivores and in fertilized conditions, competition with established vegetation should have an especially pronounced negative impact on colonisation rates</p> <p>Community openness to colonisation should depend on interactions between herbivore exclusion, biomass removal, fertilization and initial community properties</p>
<p>III Resident community dynamics</p> <p>Interactive effects of herbivory, neighbour presence and soil fertility on plant performance</p>	<p>Total competition increases with increasing productivity or is equally important in low and high productivity</p> <p>Facilitation should be especially important in environmentally harsh habitats and near the distributional limits of a target plant</p> <p>Plant biomass in response to increased soil fertility should be controlled by grazers, the absence of grazers should lead to intensified plant competition</p>
<p>IV Resident community dynamics</p> <p>Grazer effects on community composition and species richness</p>	<p>Intensive grazing should favour graminoids and decrease species richness</p>
<p>V Resident community dynamics</p> <p>Links between plant community composition, soil organic matter quality and microbial community composition along soil pH gradient</p>	<p>Forb-rich vegetation should be linked to organic matter rich in N and labile compounds, and dominance of bacteria in microbial communities, while ericoid shrub-dominated vegetation should be connected to recalcitrant organic matter rich in phenolics and C, and to dominance of fungi in microbial communities</p>



## 2 Material and methods

### 2.1 Study area and sites

All studies were carried out in Kilpisjärvi in north-western Finland. The mean annual precipitation in the area is 420 mm and the mean annual temperature is  $-2.6\text{ }^{\circ}\text{C}$  (Järvinen 1987). The treeline of mountain birch (*Betula pubescens* ssp. *czerepanowii*) lies at an altitude of ca. 600 – 700 m *a.s.l.* The study site for the experiment investigating seed and microsite limitation in relation to grazing (I) is located on the eastern slope of Mt. Jehkats ( $69^{\circ}01'\text{N}$ ,  $20^{\circ}50'\text{E}$ ) at an altitude of 820 m *a.s.l.* At this site, the snow cover remains till late June, and the vegetation is composed of heath-like *Salix herbacea* – *Cassiope hypnoides* and graminoid-rich *Carex bigelowii* snowbed vegetation (Oksanen and Virtanen 1995). All other studies (II – V) were conducted on Mt. Saana ( $69^{\circ}03'\text{N}$ ,  $20^{\circ}50'\text{E}$ ) at altitudes ranging from 700 to 850 m *a.s.l.* On Mt. Saana, bedrock consists partly of dolomitic rocks resulting in fertile, non-acid soils dominated by graminoid- and forb-rich *Dryas*-heaths, and partly of siliceous rocks resulting in infertile acid soils where dwarf shrub-dominated *Empetrum*-heaths prevail. The underlying bedrock material alternate within short distances (few tens of meters) which results in a mosaic of non-acidic and acidic heath vegetation patches. Ten such heath patches (five non-acidic and five acidic, hereafter called sites) on north-east and south-west slopes of Mt. Saana and interspersed among each other within an area of 50 m  $\times$  5 km were used either as sample collection sites for investigating vegetation – soil interactions (V) or as experimental sites for studies II and III. In the study exploring vegetation – grazer interactions (IV), seven sites located on the south-west slope of Mt. Saana and with contrasting grazing pressures were used. Three of these sites were situated in the middle of boulder fields, and were thus nearly inaccessible to grazers, and four of the sites were normally accessible to grazers.

The main mammal herbivores in the study area are semi-domesticated reindeer (*Rangifer tarandus* L.), microtine rodents such as grey-sided voles (*Clethrionomus rufocanus* Sund.) and Norwegian lemming (*Lemmus lemmus* L.), and mountain hares (*Lepus timidus* L.), which are encountered occasionally. Norwegian lemmings are especially abundant in Mt. Jehkats site (I) from which long-term trapping data are available (Virtanen 1997). In both Mt. Jehkats and Mt. Saana, reindeer grazing is confined to summer (Heikkinen et al. 2005).



Fig. 1. Study area, Kilpisjärvi (marked with open square), in north-western Finland. All studies were conducted in the same area.

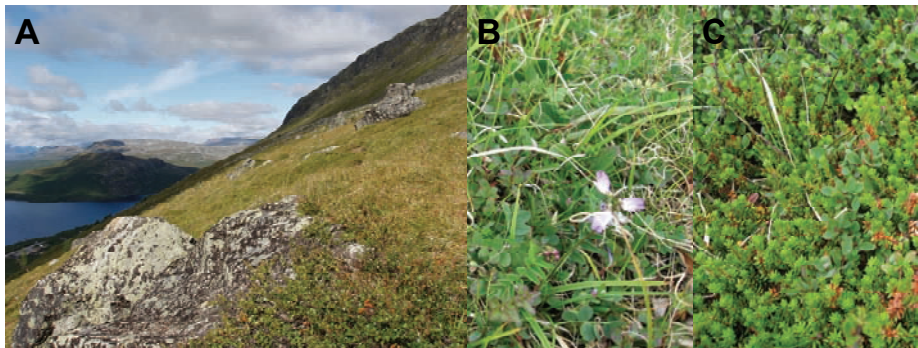


Fig. 2. View from the south-west slope of Mt. Saana (A), where most of the studies (II-V) were carried out. Forb- and graminoid-rich vegetation typical in non-acidic habitats (B) and ericoid shrub-rich vegetation dominated by *Empetrum nigrum* ssp. *hermaphroditum* typical in acidic habitats (C).

## **2.2 Immigration to a local community: propagule availability, biotic and environmental control**

### **2.2.1 Seed and microsite limitation in relation to grazing (I)**

To investigate the relative importance of propagule availability and local biotic processes in relation to grazing, a factorial experiment of disturbance and sowing was established inside and outside twelve-year-old grazer exclosures. At the beginning of the seed sowing experiment in 2001, the biomass of vegetation was significantly higher inside than outside the old exclosures (data not shown). Plots of 25 × 25 cm were marked inside and outside the exclosures, and these were further divided into four subplots (12.5 × 12.5 cm) to which the treatments were allotted. Disturbance treatment was implemented by clipping the above-ground biomass of vegetation to the ground level. The seed mixture for the sowing treatment consisted of seeds of 14 species representing different growth forms and species either abundant, rare or not present at the study site. The subplots were investigated in late July 2002 and 2003. All seedlings were counted and identified to species.

The effects of disturbance, sowing and herbivore exclusion on seedling richness and number and total species richness (seedlings plus adult plants) were analysed using generalized linear mixed effects models (GLMM, Venables & Ripley 2002) with quasi-Poisson error distribution and a logarithmic link function. In the models, the plot was used as a random variable. Generalized linear models (GLM, McCullagh & Nelder 1989) with Poisson error distribution and a logarithmic link function were used to test the impact of the initial community biomass (vascular plants, bryophytes, litter) and species richness (vascular plants, bryophytes) on seedlings richness and number. A subset of data including only plots receiving sowing but no disturbance treatment was used for these analyses.

### **2.2.2 Species colonisation in relation to biotic and environmental factors (II)**

Species immigration rates in relation to biotic and environmental factors were investigated by performing a factorial seed sowing experiment with biomass removal, herbivore exclusion, fertilization and liming as treatments. These treatments were replicated in five fertile non-acidic and five infertile acidic heath sites. In 2004, eight plots of 50 × 25 cm were established at each of the ten sites.

Each plot was further divided into two subplots of 25 × 25 cm and one of these was randomly assigned to the biomass removal treatment. Sowings were later applied to these subplots. The main plots were randomly assigned to herbivore exclusion, fertilization and liming treatments. The biomass removal treatment was accomplished by removing all above-ground biomass of the established vegetation (including also bryophytes and lichens) twice per growing season. For the grazer exclusion treatment, 80 – 100 cm high vole- and reindeer-proof exclosures were established on half of the main plots. Commercial NPK fertilizer and dolomite lime (CaMg(CO<sub>3</sub>)<sub>2</sub>) were applied to fertilization (60 g/m<sup>2</sup> per year) and liming (300 g/m<sup>2</sup> per year) treatment plots, respectively, twice per growing season. Repeated sowings of multi-species seed mixtures were performed in spring 2005, late autumn 2005 and late autumn 2006. All subplots received a mixture of seeds of 16 species, half of which preferred non-acidic habitats and half acidic habitats. Seedlings were counted and identified to species in late July 2008.

The treatment and habitat effects on the number of seedlings and seedling richness were analysed using hierarchical linear mixed effects models (LME, Pinheiro & Bates 2000), where the biomass removal treatment was nested within the main plots which were nested within sites. The interactive influence of the initial habitat conditions (*i.e.* before the application of the treatments) and those experimental manipulations that appeared significant in the first overall analysis was analysed with additional linear mixed effects models. Variables depicting initial habitat properties included community dominance, forb:shrub ratio and soil NH<sub>4</sub> concentration.

## **2.3 Dynamics of resident communities**

### **2.3.1 *Plant-plant and plant-herbivore interactions along environmental gradients (III)***

To test the roles of plant-plant and plant-herbivore interactions in relation to different environmental conditions, a factorial transplant experiment with neighbour removal, herbivore exclusion, fertilization and liming as treatments was conducted, and these treatments were replicated in five fertile non-acidic and five infertile acidic heath sites. The experimental design and manipulations were exactly the same as in study II, except for the sowing which was replaced with

transplantations. In spring 2005, transplants of three target species, *Solidago virgaurea*, *Erigeron uniflorus* and *Saussurea alpina*, were planted into the subplots (25 × 25 cm in size). One transplant of *Saussurea* and two transplants of *Solidago* and *Erigeron* were planted into each subplot. The above-ground biomass of the three transplanted species was harvested in 2006 at the end of the growing season, and the number of surviving and flowering individuals was recorded.

The treatment and the habitat effects on the biomass of the transplants were analysed using similar linear mixed effects models than when analysing the treatment and habitat effects on the seedling richness and number in study II. Generalized linear models (GLM, McCullagh & Nelder 1989) with binomial error and a logit link function were used to analyse treatment effects on the proportion of surviving transplants. The treatment effects on the number of flowering transplants were analysed using chi-square tests.

### **2.3.2 Vegetation-grazer interactions (IV)**

The effect of changed grazing pressure on the abundance, composition and species richness of plant communities was studied comparing vegetation changes during *ca.* a ten-year time scale at sites that had never been heavily grazed (located inside boulder fields, initially lightly grazed sites) and at sites normally accessible to grazers (initially heavily grazed sites). The number of reindeer had declined considerably from 1980's to 1990's and the recovery of vegetation was followed by investigating vegetation in permanent plots that had been established in 1990. The second sampling was done partly in 1999 and partly in 2001. At each seven sites, two to twelve blocks consisting of five randomly chosen quadrats were studied using the point intercept method (Levy & Madden 1933) where only the first contacts with each plant species were recorded at every point.

The responses of individual species, species groups and species richness to reduced grazing pressure in initially heavily and lightly grazed sites were analysed using linear mixed effects models (LME, Pinheiro & Bates 2000) with a repeated measures structure (the block as a conditioning variable).

### **2.3.3 Vegetation-soil interactions (V)**

To explore vegetation-soil interactions, data on plant functional group composition, soil organic matter quality and microbial community composition were collected from five non-acidic and five acidic heath sites. At each site, eight

plots of 25 × 25 cm were randomly selected (but avoiding stones and reindeer paths), the above-ground vegetation was harvested and later sorted into five groups (graminoids, forbs, shrubs, bryophytes, lichens), and composite soil samples consisting of four soil cores were taken. Homogenised soil samples were analysed for basic soil chemical and microbial variables (*e.g.* total C and N of soil organic matter, soil pH, NH<sub>4</sub> concentration). The sequential fractionation method was used to investigate the chemical composition of soil organic matter (Ryan *et al.* 1990). In this method, soil organic matter is fractionated into four fractions: non-polar extractives (NPE, *e.g.* fatty acids and lipids), water-soluble extractives (WSE, *e.g.* sugars and soluble phenolics), the acid soluble fraction (AS, *e.g.* cellulose and hemicellulose), and the acid-insoluble fraction (AIR, *e.g.* cutin, surface waxes, suberin, tannins, lignin). In order to study soil microbial community composition, soil phospholipid fatty acid (PLFA) patterns were analysed from the soil samples (Ruess *et al.* 2005, Männistö & Häggblom 2006). The fungal to bacterial ratios were used to indicate major variation in soil microbial community composition.

Linear mixed effect models (LME, Pinheiro & Bates 2000) with a hierarchical structure (the site as a random variable) were used to assess how the habitat types differed with respect to the abundance of different plant functional groups, soil nutrient availability and pH, abundance of different organic matter fractions and soil C:N ratio, and fungi to bacteria ratios. The direct relationships between major variation in plant community composition (*i.e.* forb:shrub ratio), organic matter composition (C:N ratio, soluble N:soluble phenols ratio, individual fractions), microbial community composition (fungi:bacteria ratio) and soil pH were also analysed using LME with similar hierarchical structure as in the previous models.



**Table 2. Summary of the study designs and the main findings of each study.**

Study	Design	Main findings
I	Factorial experiment with long-term herbivore exclusion (twelve years), sowing and clipping as treatments Mountain snowbed as a study site	Both seed and microsite limitation important in relatively low-productive mountain snowbed Long-term exclusion of grazers increases intensity of competition with adult plants, and thereby, diminishes immigration rates
II	Factorial seed sowing experiment with short-term herbivore exclusion (four years), biomass removal of adult plants, fertilization and liming as treatments Treatments replicated in non-acidic and acidic habitats	Increased intensity of competition with adult plants in nutrient enriched conditions No interactive effect of herbivory, competition and fertilization on colonisation rates The effects of fertilization and biomass removal of adult plants on immigration rates depend on the functional composition of the resident vegetation
III	Factorial transplant experiment with herbivore exclusion, biomass removal of neighbouring plants, fertilization and liming as treatments Treatments replicated in non-acidic and acidic habitats Three target species	Small plants and arctic-alpine specialists experience increased extent of neighbourhood competition in nutrient enriched conditions and in fertile habitats Facilitation in extreme gradient ends The performance of grazer-preferred tall plants is limited by consumption by mammalian herbivores in nutrient enriched conditions and in fertile habitats No interactive effect of competition, herbivory and productivity
IV	Observational study where the impact of reduced grazing pressure on vegetation was followed in permanent plots in ca. ten years time scale	Release from heavy grazing favours lichens over graminoids and increases total species richness
V	Observational study where plant and soil material collected from non-acidic and acidic habitats were analysed for various parameters	High proportion of forbs in vegetation is associated with low C:N ratio and high soluble N:phenols ratio in soil OM and a high proportion of bacteria in microbial communities Dominance of shrubs is connected to high C:N and low soluble N:phenols ratios in soil OM, and the prevalence of fungi in microbial communities Low soil pH favours high proportion of fungi in microbial communities



## 3 Results and discussion

### 3.1 Constraints on immigration

Number of seedlings, seedling richness and total species richness were all significantly increased by sowing in a low-productive mountain snowbed (study I), indicating that limited seed availability and species dispersal between and within habitats contribute to control species colonisation rates and community species richness in low-productive environments. These findings are consistent with the findings from other studies conducted in intermediately productive southern grasslands where seed additions have led to increased diversity (*e.g.* Tilman 1997, Zobel *et al.* 2000, Foster 2001, Foster & Tilman 2003). More recently, several other studies have drawn similar conclusions about the importance of seed and dispersal limitation in relatively low-productive environments (Klanderud & Totland 2007, Lindgren *et al.* 2007, Stein *et al.* 2008). The shifting limitation hypothesis predicts that the relative role of dispersal versus local biotic and environmental control on community dynamics shifts from the prevalence of environmental control in very low productivity to dispersal limitation in relatively low – intermediate productivity, and to local biotic control in high productivity (Grime 1973, Huston 1999, Zobel *et al.* 2000, Foster 2001, Foster *et al.* 2004). The results from the present and other studies are consistent with the predictions of the shifting limitations hypothesis, and emphasise that seed limitation may be particularly pronounced in relatively low-productive systems.

However, the present study also emphasises that local biotic factors have a strong role constraining successful species establishment to a local community in relatively low-productive ecosystems. The removal of above-ground biomass of the resident vegetation exhibited a strong positive effect on plant colonisation rates (studies I, II) and the colonisation rates were directly and negatively associated with above-ground biomass (study I), indicating that competition with adult plants can effectively prevent the immigration of species. These results concur with findings from other investigations reporting the negative impact of adult plants on seedling emergence and richness both in more productive ecosystems (Xiong *et al.* 2003, Foster *et al.* 2004, Zimmermann *et al.* 2008, Dickson & Foster 2008) and in barren alpine and arctic ecosystems (Gough 2006, Klanderud & Totland 2007, Lindgren *et al.* 2007). It is especially noteworthy that

even in the snowbed community with a mean above-ground biomass of only 108 g m<sup>-2</sup> (study I), competition with adult plants played a significant role for the arriving species. This result clearly contrasts with suggestions that competitive displacement is not important in unproductive environments (*e.g.* Grime 1973, Zobel *et al.* 2000).

Both resource enrichment by fertilization (study II) and long-term exclusion of mammalian herbivores (twelve-year-old exclosures, study I) resulted in diminished immigration rates. Fertilization exerted a strong negative impact on seedling number and richness (study II), and seedling number, richness and total species richness were all clearly higher in unfenced than in fenced plots (I). Furthermore, the biomass removal of resident vegetation interacted with both fertilization (II) and grazer exclusion (I) in such a way that it alleviated the negative effects of these treatments on colonisation rates. These findings imply that increased intensity of competition with established vegetation (*i.e.* increased extent of microsite limitation) impedes species immigration in high soil fertility (see also Stevens *et al.* 2004) and in the long-term absence of herbivores. Fertilization and long-term exclusion of grazers increase the biomass of vegetation, which is generally associated with reduced availabilities of light and space on the ground level and increased litter mass, all of which can hamper seed germination and seedling establishment (Foster & Gross 1998, Emery & Gross 2007), and may therefore pose a considerable obstacle for species immigration. The results from the present study are consistent with findings by Foster *et al.* (2004) that the extent of microsite limitation increased along a natural productivity gradient and experimental disturbance was needed to counteract the negative impact of high productivity. However, in the study by Foster *et al.* (2004) the factors that control the biomass of vegetation were not isolated, and the reasons behind the observed relationship between productivity gradient and microsite limitation were unknown. In the present study, the highest biomasses in the snowbed community (I) were encountered in the long-term herbivore exclosures, which emphasises that grazing can be an important agent depressing vegetation biomass also in relatively low-productive habitats, and thereby, contribute to the relative importance of regional and local control on community processes. Thus, the results from the present study provide evidence that an increase in soil nutrient availability and exclusion of mammalian herbivores can lead to increased above-ground competition and, consequently, decreased immigration rates in tundra plant communities.

Short-term exclusion of grazers did not have any influence on the rates of plant colonisation (study II). Obviously, the shorter duration of the exclusion treatment in study II than in study I (four vs. twelve years, respectively) is likely to explain this result. In relatively low-productive tundra ecosystems, where short growing season and low temperatures limit plant growth, a considerably longer time is probably needed for the biomass of vegetation to accumulate to the extent that prevents germination and establishment of the arriving species. It is plausible that the same obstacle explains the lack of interaction between grazer exclusion, biomass removal and fertilization on plant colonisation rates (II) although, competition, productivity and herbivory should interactively determine species extinction and immigration rates (Grime 1973, Kondoh 2001).

Recently, initial community properties and environmental conditions, such as community evenness and initial nitrogen concentrations, have been proposed to exert a potentially important role in determining community responses to external events, and thereby, determining species gains and losses (*e.g.* Clark *et al.* 2007, Hillebrand *et al.* 2007). Indeed, in the present study, the effects of fertilization and biomass removal on plant colonisation rates depended on the prevalence of shrubs vs. forbs in the resident vegetation (II), suggesting that plant functional composition is an important determinant of vegetation responses to biotic and environmental alterations. Fertilization negatively affected plant immigration rates (seedling richness) in communities dominated by forbs while the impact was negligible in shrub-dominated assemblages (II). The dominant shrub of the studied system, evergreen *Empetrum nigrum* ssp. *hermaphroditum* and other ericoid shrubs (*Vaccinium* sp.), have traits that are likely to constrain their growth response to nutrient enrichment, *e.g.*, long-lived tissues, slow growth rates and a capability to tolerate low nutrient concentration (Chapin 1980, see also Chapin & Shaver 1985). By contrast, forbs are likely to exhibit greater biomass increment in response to fertilization due to their rapid growth rates, higher nutrient demands and shorter life spans, and thereby, inhibit immigrations to a greater extent than shrubs. It seems that the potential for productivity increase of the resident vegetation is an important mediator of fertilization effects on plant colonisation rates.

The positive effect of biomass removal on plant colonization success (seedling richness and number) was contingent upon forb prevalence in such a way that biomass removal enhanced plant recruitment more in forb-dominated vegetation, where the overall colonisation rates were highest, than in shrub-dominated vegetation, where the overall colonisation was lowest (II). It therefore

seems that shrub dominance leads to generally low colonisation rates and even the removal of the vegetation itself cannot relax the inhibitory effect of shrubs. The dominant shrub *Empetrum*, which comprises on average 67 % and 40 % of the total shrub biomass and 64 % and 20 % of all plant biomass in acidic and non-acidic heaths of the studied system, respectively, produces phenolic compounds that are highly resistant to decomposition and persistent in the soil (Gallet *et al.* 1999) and can have phytotoxic effects on seed germination (Nilsson & Zackrisson 1992, Zackrisson & Nilsson 1992). The accumulation of these allelopathic substances in the soil may explain the lower colonisation rates in shrub-dominated communities despite the removal of the vegetation itself. This result and the finding that evenness per se had no impact on plant colonisation (see also Emery & Gross 2006, Emery & Gross 2007, Hillebrand *et al.* 2008) emphasise that the presence of certain functional groups and, possibly, the specific traits of dominant plants rather than evenness itself mediate community response to external events and, thus, control colonisation rates.

### **3.2 Competition and facilitation in relation environment**

The growth of two of the studied species, *Erigeron* and *Saussurea*, was negatively affected by neighbour presence in fertilized plots whereas in unfertilized plots neighbouring plants had a neutral or slightly positive effect on plant growth (study III). These findings indicate that arctic-alpine ‘specialists’ *Erigeron* and *Saussurea*, which inhabit a relatively narrow range of conditions (*i.e.* nutrient-rich habitats with relatively low biomass), experience an increased extent of competition in high soil fertility. *Erigeron*, which is the smallest of the studied three species, suffered most from neighbours in nutrient enriched plots (both flowering and growth were affected). Due to its small size it is most easily suppressed by greater biomass of neighbouring vegetation resulting from nutrient addition. In general, these results support the predictions by Grime (1973, 1979) that overall competition becomes more intense in higher productivity. However, the performance of *Solidago*, which is a tall ‘generalist’ species occurring in a wide range of habitat conditions and having a large geographical range, was independent of neighbour presence. Therefore, the results from this study also suggest that competition-productivity relationships depend on individual plant traits (*e.g.* stature relative to neighbours).

In addition, the growth and survival of *Saussurea* showed opposing responses in the two habitats: *Saussurea* survived better with neighbours in acidic heaths

where it rarely occurs but suffered from neighbours in non-acidic heaths where it occurs commonly. This result supports the hypothesis that net positive responses to neighbours are more likely in abiotically severe habitats near the distributional limits of a species while net negative responses to neighbours should prevail in more benign habitats (Choler *et al.* 2001, Kikvidze *et al.* 2005). Overall, the findings from the present study imply that plant responses to neighbours are species-specific and depend on target plant traits, environmental conditions and species-specific tolerance and distributional limits.

### 3.3 Herbivores and plant community dynamics

Grazers exhibited a strong control on individual plant growth, survival and reproductive performance and plant responses to herbivores appeared to be also species-specific and depended on nutrient availability and initial habitat productivity (study III). The flowering and growth of *Solidago* and *Saussurea* and *Saussurea* survival were highly negatively affected by the presence of herbivores. These two species are relatively tall, their flowering stalks reach higher than that of neighbouring vegetation, and they both are preferred forage for reindeer (Bråthen & Oksanen 2001, Virtanen 1998, personal observation). Such suppression of growth and sexual reproduction of grazer-preferred tall forbs has also been reported in other studies (*e.g.* Mulder & Ruess 1998, Virtanen 1998, Van der Wal *et al.* 2000, see also Bråthen *et al.* 2007 for large scale effects). By contrast, *Erigeron*, a low-statured forb with a hairy appearance, was totally independent of grazer presence. These traits of *Erigeron* have traditionally been considered to be selected to cope with harsh environmental conditions, however, they can also affect grazer preference via palatability (McNaughton 1978, Miller *et al.* 2007) and low stature in relation to surrounding vegetation (*e.g.* Mulder & Ruess 1998, Fowler 2002, Brooker *et al.* 2006). Such specific plant traits that reduce plant vulnerability to grazer attacks may have acted as selective forces leading to evolution of low-statured vegetation in intensively grazed ecosystems (Oksanen 1990).

Herbivore effects on the performance of *Solidago* and *Saussurea* were greater in nutrient enriched than in unfertilized plots (III), which implies that greater plant biomass in response to fertilization is actually consumed by mammal herbivores. This result supports the theory by Oksanen *et al.* (1981) and Oksanen & Oksanen (2000) that in relatively unproductive ecosystems an increase in plant productivity leads to increased consumption by herbivores. The grazer-controlled

plant growth along increasing productivity in tundra ecosystems is also supported by recent findings from Alaskan arctic tundra (Gough *et al.* 2007), where herbivores had a greater impact on the performance of graminoids and a deciduous shrub under fertilized conditions. Similar conclusion were drawn by Grellmann (2002), who reported a reduction of plant cover after nutrient enrichment due to reindeer and rodent grazing in the arctic tundra of northern Fennoscandia. Also Bonser & Reader (1995) reported increased herbivory effects on target plant with increasing vegetation biomass. In the present study, grazer effects on the performance of *Solidago* and *Saussurea* were also greater in fertile non-acidic than in barren acidic heaths (III), which emphasises that the influence of herbivores extends from plot level to habitat level being more intense in productive habitats. It seems that in heterogeneous tundra landscapes with habitat patches varying in productivity, grazing is concentrated on nutrient-rich sites, which provide more and better-quality forage, and are consequently grazed to a greater extent. This finding concurs with findings from other ecosystems, *e.g.*, southern savannah ecosystems, where grazing ungulates selectively consume plant biomass in nutrient-rich and productive sites (McNaughton *et al.* 1989, Milchunas & Lauenroth 1993, Augustine *et al.* 2003).

However, exclusion of herbivores did not reinforce plant competition, and even nutrient enrichment together with herbivore exclusion did not encourage intensified neighbourhood competition (III). This result clearly contrasts findings from other studies (*e.g.* Van der Wal *et al.* 2000, Gurevitch *et al.* 2000) and predictions by Oksanen *et al.* (1981). Possibly, short experimental duration may explain this finding, similarly as the lack of seedling response to the same treatment combinations (II, see before).

At the community level (study IV), a decade long relaxation from heavy reindeer grazing resulted in increased lichen abundance at initially heavily grazed sites, while at the initially lightly grazed sites lichen abundance decreased. Graminoids showed a consistent decline at all sites, however, this decline seemed greater at initially heavily grazed sites where graminoids were more abundant from the beginning. It appears that these plant groups are most sensitive to summer grazing by reindeer. The increase in lichen abundance in response to relief from heavy grazing coincides with findings from previous studies where winter grazing by reindeer has been shown to decrease lichen abundance (*e.g.* Helle & Aspi 1983, Väre *et al.* 1996, den Herder *et al.* 2003). The decrease in graminoid abundance in response to reduced grazing is consistent with findings by Manseau *et al.* (1996) and Olofsson *et al.* (2001) from comparisons of lightly



and heavily grazed areas and showing greater graminoid abundance in heavily grazed areas. Olofsson *et al.* (2001) also found a lower abundance of lichens in heavily grazed area. The results from all these studies are in line with the hypothesis stating that heavy mammal grazing favours graminoids over mosses and lichens and can shift unproductive barren tundra heath into a productive grassland (Zimov *et al.* 1995, Van der Wal & Brooker 2004, Van der Wal *et al.* 2004). In a recent study, Olofsson (2006) reported that three common graminoid species declined in response to a three-year relief from grazing in arctic-alpine tundra. This result together with the results from the present study suggests that the changes in plant community composition imposed by heavy grazing (Zimov *et al.* 1995, Van der Wal & Brooker 2004, Van der Wal *et al.* 2004) can be reversed under reduced grazing pressure.

Under reduced grazing, total species richness (bryophytes, lichens and vascular plants) increased more at initially heavily grazed sites than at initially lightly grazed sites (IV), indicating that heavy reindeer grazing exhibits a negative effect on diversity in tundra. Although grazing by large mammal herbivores is generally expected to favour species coexistence (*e.g.* Olf & Richie 1998) and the exclusion of grazers can hamper species colonisation (study I), high levels of disturbance (*e.g.* heavy grazing and trampling) may decrease species richness because of increased local extinction rates and decreased colonisation rates (Grime 1973, Connell 1978, Huston 1979). Bryophyte and lichen species, which increased most pronouncedly in response to reduced grazing pressure, may also suffer from the direct influence of reindeer faeces under intensive grazing (Van der Wal *et al.* 2004). Furthermore, given the simultaneous decline in graminoid abundance under reduced grazing, bryophytes and lichens may have been suppressed by light competition with rapidly growing graminoids (see Van der Wal *et al.* 2005) in previously heavily grazed conditions. Similar findings of an inverse relationship between graminoid abundance and lichen/bryophyte richness have been reported by Klanderud & Totland (2005b, see also Van der Wal *et al.* 2004). In tundra ecosystems, bryophyte and lichen species seem to be particularly important indicators of diversity changes in response to biotic and environmental alterations.

### **3.4 Individual plant-soil and vegetation-soil interactions**

Abiotic environmental conditions generally exerted a profound influence on individual plant performance (study III), emphasising the role of the abiotic

environment in governing plant occurrence and distributions in tundra ecosystems. The growth of all three studied species, and the flowering of *Solidago*, showed a strong positive response to nutrient amendment, indicating that growth (and sexual reproduction of *Solidago*) under natural conditions is constrained by limited nutrient availability. This result corresponds to findings from previous studies from tundra areas (e.g. Shaver & Chapin 1980, Klanderud & Totland 2005a, Gough *et al.* 2007). Also, acidic heaths were much less favourable sites for the survival, growth and flowering for all three transplant species (study III), as they were for plant colonisations (study II, both seedling richness and number were significantly lower in acidic habitats), which may partly result from the lower nutrient availability in these habitats (see Results in papers III). Better germination and performance of plants in nutrient-rich non-acidic heaths also likely expands to the greater abundance of forbs at the community level (study V, see also Nordin *et al.* 2004). Forbs that have higher nutrient demands, intrinsic growth rates and foliar nutrient concentrations than shrubs (Chapin 1980, Hobbie & Gough 2002), are likely to benefit from high nitrogen concentrations.

Liming did not have any effect on any of the transplant species, and fertilization led to a much greater biomass increment of all three species in non-acidic than in acidic heaths (III), suggesting that even nutrient addition or liming could not alleviate the unfavourable conditions that transplants encountered in acidic habitats. Soil pH, which remained clearly lower at acidic sites despite liming (see Results in paper III), may directly diminish nutrient supply rates to plants because high soil  $H^+$  concentration leads to displacement of cations from their adsorption sites on soil particles, and inhibits cation uptake by proton pumps in plant roots, thus reducing nutrient availability (Kinzel 1983). Low soil pH also is attributed to enhanced aluminium availability, which together with the effects of pH on nutrient availability, may constrain plants in acidic heaths from responding to short-term nutrient additions. Besides these, scarcity of suitable mycorrhizal symbionts or otherwise disadvantageous soil microbial community composition may constrain germination and performance of forbs in acidic heaths (see below).

Differences in vegetation between non-acidic and acidic heaths, i.e. the prevalence of either forbs or ericoid shrubs, respectively, were associated with divergent composition of soil organic matter and microbial communities, and the variables depicting major variation in each community were also directly linked with each other (study V). Prevalence of forbs in vegetation was positively connected to a low C:N ratio and a high soluble N:phenols ratio in soil organic

matter. This result concurs with previous studies showing that forbs produce N-rich and phenolic-poor litter, while shrubs produce N-poor, phenolic- and C-rich litter (Hobbie 1996, Pérez-Harguindeguy *et al.* 2000, Shaw & Harte 2001, Dorrepaal *et al.* 2005). N-rich organic matter and forb-prevalence were, in turn, associated with a high proportion of bacteria in soil microbial communities, whereas high proportions of phenolics, total C and ericoid shrubs were connected to prevalence of fungi in microbial communities. These findings are consistent with those by Högberg *et al.* (2007) and indicate that a high proportion of phenolics and total C combined with low N concentrations favour fungi in soil microbial communities. Most shrubs in the studied system (*Empetrum*, *Vaccinium* sp.) possess ericoid mycorrhizal symbionts associated with their root system, which probably contributes to the observed fungi-shrub relationship (see also Kourtev *et al.* 2002). Taken together, these findings suggest a strong three-way linkage between plant community composition, soil organic matter quality and microbial community composition, that is predicted by the general framework of Wardle *et al.* (2004) but has not been previously shown.

A surprising result from this study was that the most recalcitrant organic matter fraction, AIR, which in the plant litter consists of lignin and other polyphenolic compounds (Hobbie 1996), was not positively correlated with shrub abundance. This inconsistency between the concentration of AIR in soil organic matter and the abundance of AIR-producing woody shrubs in vegetation may be partly due to inadequate understanding of the exact composition of AIR in organic matter (Lützwow *et al.* 2006) and partly due to differing degradation potential of the microbial communities beneath forb- and shrub-dominated vegetation. Given the high proportion of fungi in microbial communities at ericoid shrub-dominated acidic sites and the capability of saprotrophic and ericoid mycorrhizal fungi to degrade polyphenolic substances (Paul & Clark 1996, Bending & Read 1997, Mutabaruka *et al.* 2007), the microbial community beneath shrubs is probably better adapted to metabolise polyphenols. These factors may lead to convergence in AIR concentration despite divergence in vegetation.

In general, the optimal conditions for the growth of bacteria as a group occur at higher pH than for fungi (Madigan *et al.* 2003), which may explain the positive relationship between soil pH and the proportion of soil bacteria (V). Given that high-pH habitats were also dominated by forbs, high soil pH may simultaneously favour the prevalence of both forbs in vegetation and bacteria in the soil decomposer system. Furthermore, these existing community patterns are probably reinforced by the indirect effect of forbs on soil organic matter which further

benefits bacteria, and feeds back to the dominance of forbs at non-acidic sites. The findings from the present study therefore suggest that soil pH drives important ecosystem processes in tundra through its direct and indirect effects on both plants and microbes.

## 4 Conclusions and future perspectives

### 4.1 The interplay between propagule availability, local biotic and environmental controls over plant community dynamics

Overall, my results demonstrate that propagule availability, biotic and environmental factors work in concert to govern immigration to local communities and resident community dynamics in low-productive tundra ecosystems (main findings are summarised in Table 2). Especially, my results highlight the role of mammalian herbivores in tundra ecosystems, their influence on vegetation encompassing the whole range of community organisation. Herbivore effects on community dynamics extend from (1) the effects on colonisation success from the local species pool (I) to (2) the effects on individual plant survival, reproductive performance and growth (III), and to (3) the effects on abundances of different plant groups and assemblage species richness (IV). Grazing by mammalian herbivores can alleviate microsite limitation (I); however, the consumption of preferred forbs may also lead to recruitment limitation, and may constrain distributions of preferred plants in tundra landscapes (IV). Herbivore effects on plants in relatively low-productive tundra also depend on soil nutrient availability and habitat productivity with increased plant productivity due to greater soil fertility leading to greater losses to herbivores (III), as predicted by Oksanen *et al.* (1981). My results also emphasise the important role of plant interspecific interactions in low-productive tundra ecosystems, their direction and strength depending on soil fertility and habitat conditions. Plant competition operates both via immigration and extinction to control community dynamics, which is demonstrated by the negative effect of the presence and functional composition of resident vegetation on colonisation rates (II) and the negative effect of neighbouring vegetation on adult plant survival, reproduction and growth (III). The findings of increased intensity of competition with increasing soil fertility (II, III) are consistent with the hypothesis of productivity-richness relationship (Grime 1973, Huston 1979) stating that high levels of productivity result in low species richness due to competitive displacement of species. My results emphasise that both increased extinction and decreased immigration rates account for the productivity-richness relationship. I did not detect interactions between plant competition, herbivory and productivity over a short time scale (II, III), and long-term experimental approaches (>10 years) are

still needed to resolve the mutual relationships among these, and to assess how changes in plant immigration and extinction channel these relationships.

The findings from the present study also underscore the role of plant functional groups and the traits of dominant plant groups in governing community dynamics and plant-soil interactions. Environmental control by soil pH on the development of ericoid shrub- or forb-dominated plant assemblages and fungi- or bacteria-based decomposer systems, respectively, appears to drive major ecosystem processes in tundra. Forb-dominated vegetation, which is connected to high N availability, high-quality organic matter rich in labile N and prevalence of bacteria in microbial communities (V), supports high rates of immigration (II), greater plant growth and higher levels of above-ground herbivory (III), and also shows greater potential for productivity increase and competitive exclusion under nutrient enrichment (II, III). By contrast, vegetation dominated by ericoid shrubs (especially *Empetrum*), that produces phenolic- and C-rich organic matter and is associated with fungal dominance in microbial communities (V), shows surprising resistance to immigration even under alleviation of nutrient limitation and removal of the dominant vegetation (II). It also provides a hostile environment for survival and growth of forbs (III). The dominant plant in acidic heaths, *Empetrum*, also exhibits considerable resistance to grazing (Bråthen *et al.* 2007), which together with the results from the present study, emphasise the role of *Empetrum* as a key species exerting potentially major impact on ecosystem processes. Consequences of dominance by such species for species interactions and ecosystem functioning, and the role of their traits in dictating these relationships, should be of high concern in future studies of community and ecosystem ecology (see also Hillebrand *et al.* 2008).

Because my findings concerning vegetation-soil interactions are based on a correlative approach, my future tasks will include experimental inspection of the causal nature of relationships between vegetation, soil organic matter and soil micro-organisms. I also aim at expanding the investigation towards greater understanding of the role of diversity and functional groups of microbes and soil functional attributes (*e.g.* enzyme activities) in vegetation-soil interactions.

#### **4.2 Why are non-acidic tundra habitats so species-rich compared to acidic habitats?**

Plant species richness in temperate grasslands, and arctic and alpine ecosystems has long been related to high soil pH (*e.g.* Nordhagen 1943, Grime 1979, Gough

*et al.* 2000, Peet *et al.* 2003, Virtanen *et al.* 2003, Crawley *et al.* 2005, Virtanen *et al.* 2006) and different factors such as physiological, biotic and evolutionary processes have been proposed to account for this relationship. Pärtel (2002) found that positive richness-pH relationships were more likely in those regions where plants had evolved in high pH habitats whereas negative relationships were probable in regions where plants had evolved in low pH habitats. This implies that species richness-pH relationship is determined by the size of the regional species pool. However, findings by Virtanen *et al.* (2003) suggested that in acidic habitats of European mountain areas there is an upper ecological limit for local species number independent of regional species pool, while in high pH soils higher species number seems to be largely determined by regional species pool. Peet *et al.* (2003) also reported that despite a greater species pool size for acidic habitats in the southern Blue Ridge Mountains in North-America, high pH sites were still much more species-rich, and proposed that greater diversity in base-rich habitats is a consequence of generally more favourable conditions for plant establishment and growth. Similarly, Nordin *et al.* (2004) emphasised the potentially important role of greater nutrient availability in non-acidic habitats in governing diversity patterns and community composition in tundra areas.

My results provide evidence that species-poor acidic tundra heaths develop and remain species-poor because, first, the generally adverse abiotic conditions, i.e. low nutrient availability, negatively affect plant performance and species immigration in these habitats (II, III). Second, the dominant plants inhabiting these barren systems, i.e., ericoid dwarf shrubs such as *Empetrum*, positively feed back on their own performance via producing N-poor and phenolic- and C-rich organic matter that support fungi-based microbial communities and slow nutrient cycling. All these factors benefit ericoid shrubs themselves that possess access to the recalcitrant organic matter via their ericoid mycorrhizal symbionts and can tolerate low nutrient concentrations (*i.e.* are good nutrient competitors according to Tilman [1988] and stress tolerators according to Grime [1979]) (V). Third, the dominant shrubs in acidic heaths possess an inhibitory impact on colonisation from the local species pool, this effect persisting even after the removal of the dominant plant groups and possibly resulting from phytotoxic substances that hamper seed germination (II). Although evolutionary history may have originally been the driving force for the distinct diversity patterns of non-acidic and acidic habitats in tundra, my results suggest that the strong environmental and biotic controls over species immigration, plant performance and soil processes in infertile acidic systems and the resistance of acidic heaths to biotic and

environmental perturbations reinforce the dominance of a few plant groups in acidic systems and amplifies the differences in diversity between acidic and non-acidic habitats. Besides, in high latitude and altitude ecosystems, where plants are strongly constrained by limited nutrient availability (III, Shaver & Chapin 1980), pH-imposed changes in soil resource availability may be of especially great concern for plant survival and growth.

### **4.3 Implications for responses to climate change and reindeer grazing pressure**

Because decomposition and nutrient mineralization in high latitude and altitude ecosystems, and thereby soil nutrient availability, are strongly limited by cold temperatures (*e.g.* Nadelhoffer *et al.* 1991, Hobbie 1996), global warming is predicted to indirectly alter nutrient supply rates to plants via enhancing nutrient mineralization. The findings from the present study portend alarming implications if nutrient supply rates increase under global warming in tundra areas. Productivity increase inflicts intensified competition for light, which hampers colonisation dynamics of the resident species (II). It may also constrain the survival, growth and reproductive performance of arctic-alpine specialists and low-statured forbs (III) leading ultimately to extinctions and population losses. Biomass increment under nutrient enrichment and, therefore, the loss of diversity in tundra, will likely be especially pronounced in forb-dominated non-acidic habitats that currently resemble diversity ‘hotspots’ of tundra areas. On the contrary, barren acidic tundra heaths dominated by a few species of ericoid dwarf shrubs, appear highly resistant to species immigration even under the alleviation of nutrient limitation and removal of dominant vegetation and may change relatively little under anthropogenic nutrient addition. Such persistence of infertile ecosystems in the face of global change has also been suggested by Grime *et al.* (2008).

However, my results also imply that selective foraging by large mammalian herbivores may counteract the influence of increased nutrient availability on preferred forbs under global change because increased plant biomass is lost to grazers (III, see also Gough *et al.* 2007). Since grazers seem to be attracted by nutrient-rich habitats and selectively concentrate foraging in them, grazing may be an especially important counterforce of nutrient enrichment in fertile non-acidic habitats. The assertion of a potentially pronounced role of mammal herbivores in mitigating the impact of global change on tundra vegetation was



recently demonstrated by Post & Pedersen (2008), who discovered that herbivory by muskoxen and caribou counteracted a warming-induced increase in shrub biomass (for similar findings see also Olofsson *et al.* 2009). Clearly, more investigation is needed to untangle how plant immigration and extinction rates are affected by the interplay of soil nutrient availability, warming and herbivory. In general, grazing by large mammal herbivores is an essential aspect shaping tundra ecosystems, and cessation of grazing could have far-reaching consequences on plant community composition, diversity and ecosystem functioning. For instance, in the absence of grazers or at very low levels of grazing, increased biomass of vegetation and intensified plant interspecific competition inhibit species immigration and may lead to isolation of communities from the local species pool, which may decrease diversity (I). On the other hand, my results indicate that heavy reindeer grazing decreases diversity and can convert species-rich tundra vegetation into less species-rich vegetation dominated by graminoids (V). Also, heavy grazing likely results in reduced survival and an increased extent of seed limitation of reindeer-preferred plants (III). In the long-term, this may lead to suppression of forb abundance and distributions in tundra landscapes (see also Bråthen *et al.* 2007).



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## Original papers

The thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Eskelinen A & Virtanen R (2005) Local and regional processes in low-productive mountain plant communities: the roles of seed and microsite limitation in relation to grazing. *Oikos* 110: 360–368.
- II Eskelinen A (2009) Initial community properties mediate the impacts of nutrient enrichment and neighbour removal on plant immigration rates. Manuscript.
- III Eskelinen A (2008) Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology* 96: 155–165.
- IV Eskelinen A & Oksanen J (2006) Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *Journal of Vegetation Science* 17: 245–254.
- V Eskelinen A, Stark S & Männistö M (2009) Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. *Oecologia* 161: 113–123.

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