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THE RESILIENCE OF UNDERSTOREY VEGETATION AND SOIL TO INCREASING NITROGEN AND DISTURBANCES IN BOREAL FORESTS AND THE SUBARCTIC ECOSYSTEM
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Abstract
Climate change and its warming effects on vegetation and soils are a widely recognized phenomenon. In addition to warming, the understorey vegetation in northern environments has been subjected to several environmental changes, such as increasing nitrogen (N) and other disturbances. This thesis examines the effects of N-fertilization and disturbances on the vegetation biomass and abundance, plant community composition and plant, soil and microbial N and C pools. Seedling establishment of the most common dwarf shrubs (deciduous Vaccinium myrtillus, evergreens V. vitis-idaea and Empetrum nigrum ssp. hermaphroditum) was investigated after artificial disturbance treatments (vegetation and soil removal). These studies were conducted in the boreal and subarctic ecosystems and in the forest-tundra ecotone in northern Finland.

N-fertilization and disturbances enhanced the amount of graminoids in plant communities, and the recovery ability of graminoids was enhanced after N-fertilization, which homogenized the vegetation and resulted in a new stable state in the plant community. The recovery ability of evergreen dwarf shrubs was low after disturbances. Disturbances created habitats for seed germination, but the seedling establishment of dwarf shrubs studied was still limited by seed availability. N-fertilization had no effect on microbial biomass. Instead, microbial biomass decreased with disturbance treatment in the boreal forest. However, the concentration of N increased in above-ground vegetation, both after N-fertilization and disturbance without any indication of N immobilization, suggesting that plant species captured the available N effectively for their recovery.

The study shows that the likely outcome of N enrichment, when combined with disturbances, is the enhanced growth of graminoids. The seedling establishment does not compensate for the reduction of the vegetative recovery of evergreen dwarf shrubs, which makes evergreen dwarf shrubs sensitive to environmental changes. As the understorey is more resilient to perturbations in the boreal forest than in the subarctic ecosystem, these results emphasize the sensitivity of the vegetation to simultaneous environmental changes in the northernmost ecosystems. Moreover, microbial properties are more resilient to environmental changes than is above-ground vegetation.

Keywords: compensation, Empetrum, fertilization, microbial biomass, nitrogen immobilization, plant functional types, sexual reproduction, simulated herbivory, soil removal, Vaccinium, vegetative recovery
Manninen, Outi, Aluskasvillisuuden ja maaperän palautuvuus typen lisääntymisen ja häiriön jälkeen boreaalissä havumetsissä ja subarktisessa ekosysteemissä.

Tiivistelmä

Ilmaston muutos ja siitä aiheutuvan lämpenemisen vaikutus kasvillisuuteen ja maaperään on laajasti tunnustettu ilmiö. Lämpenemisen lisäksi pohjoisten alueiden aluskasvillisuuteen kohdistuu useita muutospainoita, kuten lisääntyneen typpipitoisuuden nousu ja kasvillisuutta muokkaavat häiriöt. Tässä tutkimuksessa mitattiin lisääntyneen typpipitoisuuden ja häiriöiden vaikutus kasvillisuuden biomassaan ja runsauteen sekä yhteisöraakenteeseen, sekä kasvilajeihin, maaperään ja mikrobibiomassaan sitoutuneen typen ja hiilen määrään. Lisäksi tutkittiin yleisimpien varpukasvien (lehtensä pudottava mustikka, ikivihreät puolukka ja variksenmarja) siemenellistä lisääntymistä kokeellisen häiriön (kasvillisuuden tai maaperän poisto) jälkeen. Tutkimukset tehtiin boreaalissä ja subarctisessa ekosysteemeissä sekä metsänrajaympäristössä Pohjois-Suomessa.


Asiakirjat: Empetrum, kasvien funktionaaliset tyypit, kasvullinen palautuminen kompensaatio, lannoitus, maaperän poisto, mikrobibiomassa, siemenen lisääntyminen, simuloitu laidunnus, typen sitoutuminen, Vaccinium
To My Family
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List of original papers

This thesis is based on the following papers, which are referred throughout the text by their Roman numerals as follows:


Author’s contributions:

I and II: A Tolvanen was responsible for the study idea and study design. OH Manninen contributed to the field work with S Stark, who was responsible for the soil sampling and soil analysis. OH Manninen processed the data, performed the statistical analysis, and interpreted the results. OH Manninen had the major responsibility during the writing process, while A Tolvanen, S Stark and M-M Kytöviita commented and contributed.

III and IV: A Tolvanen, together with OH Manninen, were responsible for the study idea and the study design. OH Manninen was responsible for the field work, processed the data, performed the statistical analysis and interpreted the results. OH Manninen had the main responsibility for the writing process, while A. Tolvanen commented and contributed.
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1 Introduction

Human-induced emissions of reactive nitrogen (Nr) have increased considerably worldwide since the beginning of the industrial revolution (Galloway et al. 2008). The emissions of N originate mostly from the combustion of fossil fuels, N usage in agriculture and industry and in large part from the inefficiency in their use (Galloway et al. 2008). Increased N concentration in the atmosphere alters the biogeochemistry and biodiversity of several aquatic and terrestrial ecosystems through deposition. Concurrently with N deposition, changing climate indirectly enhances soil mineralization processes, which then increases the availability of N for plants and soil microorganisms (Rustad et al. 2001, Dieleman et al. 2012).

In addition to increasing nutrient availability, human induced and naturally occurring disturbances are the principal elements that modify ecosystem processes (Sousa 1984). Disturbance is defined by Grime (1977) as events that causes “partial or total destruction of plant biomass” or more widely by Pickett & White (1985) as “…any event in time that breaks the structure or physical environment of ecosystem, community and population, and changes the amount and availability of resources.”

Resilience is defined as the capacity of a system to absorb perturbation and reorganize while undergoing changes to retain essentially the same function, structure, identity, and feedbacks (Walker et al. 2004). The ecosystems are not equally sensitive to perturbations concerning any increasing N and disturbances (Bobbink et al. 2010), which indicates that the resilience also varies among different ecosystems. The vegetation in boreal and arctic ecosystems is characterized by a strong nitrogen (N) limitation (Tamm 1991, Shaver et al. 2001), cold climate, short growing season and the dominance of slow-growing clonal plant species (Van Cleve & Alexander 1981) that are associated with high ecosystem sensitivity and low resilience. Since warming has been, and is predicted to be the most pronounced in the northern regions, vegetation is expected to face more changes further north than in the ecosystems further south (IPCC 2013, Wookey 2009).

1.1 Sources of increasing N in the ecosystems

The main reasons for increased N in the northern ecosystems are human induced emissions, accelerated below- and above-ground litter and soil organic matter decomposition and N mineralization rates due to climate change, and forest
fertilization in managed boreal forests. N deposition in Europe is delivered mainly from animal husbandry and farming, while N as a by-product of fossil fuel combustion is slightly smaller in magnitude (Holland et al. 2005). N deposition is both wet and dry deposition that include both organic and inorganic forms of N (nitrate, $\text{NH}_4^+$ and ammonium, $\text{NH}_3$), the bulk of which and the throughfall deposition of inorganic N is most commonly measured (Waldner et al. 2012). The northernmost ecosystems in Europe are remote and distanced from the main N emission sources, and consequently, they are subjected to low N depositions. In Finland, the annual total N bulk deposition ranges from approximately 3.5 in southern Finland to 1.5 kg ha$^{-1}$ in northern Finland (Lindroos et al. 2007), of which approximately 3.1 and 1.3 kg ha$^{-1}$, respectively, are inorganic N (Lindroos et al. 2013).

Climatic factors, such as low temperature and moisture, limit the decomposition process in the northern ecosystems, and a high amount of the nutrient pool is accumulated in soil organic matter (SOM) (Jonasson et al. 1999). Litter and soil organic matter decomposition and N mineralization rates are expected to increase if sufficient moisture content is achieved in a warming climate, leading to increased N amounts in the soil (Nadelhoffer 1991, Chapin et al. 1995, Rustad et al. 2001, Schmidt et al. 2002, Aerts et al. 2006, Dieleman et al. 2012, Natali et al. 2012, Sistla et al. 2013). Warming-induced N mineralization varies greatly between sites; however, net N mineralization has increased about 46% in a meta-analysis of experimental warming of 2.4 °C, including 32 study sites in several biomes ranging from tundra to grassland (Rustad et al. 2001) and further about 70% in short-term warming experiments conducted in the northern tundra ecosystem (Aerts et al. 2006).

1.1.1 Understorey vegetation and increasing N

The effects of increasing N in the ecosystems depend first on the total amount, duration and form of N inputted into the ecosystem, secondly, on the sensitivity of existing plant species to N in the ecosystem, and third, on the abiotic conditions found in the ecosystem (Bobbink et al. 2010). Several factors, such as intrinsic soil nutrient availability and the N-immobilization rate, as well as present and past land use and management, are also important (Strengbom & Nordin 2008, Bobbink et al. 2010, Hedwall et al. 2013). Consequently, different ecosystems show a high variation in their sensitivity to increasing N.
N has detrimental effects on vegetation and soil (Aber et al. 1998, Bobbink et al. 2010), but it also increases the growth of vegetation in N deficient ecosystems (van Wijk et al. 2004). Moreover, increasing N may change the plant community composition and structure due to the replacement of N-sensitive species by N-tolerant species, and due to new species introduced to the ecosystems (Strengbom & Nordin 2008, Pardo et al. 2011, Dirnböck et al. 2014).

Plant fertilization studies carried out in boreal forests show that both NPK- and N-fertilization commonly increase the abundance of graminoids and/or deciduous species and decrease the abundance of mosses and lichens (Nams et al. 1993, Hallbäcken & Zhang 1998, Smolander et al. 2000, Skrindo & Ökland 2002, Turkington et al. 2002) and in subarctic and arctic areas (van Wijk et al. 2004, Campioli et al. 2012, Gough et al. 2008, 2012, Alatalo et al. 2015, Veen et al. 2015). In subarctic and arctic ecosystems, however, high regional variability has been observed in the responses of plant functional types to a nutrient increase (van Wijk et al. 2004). In the northern Scandinavian treeless heath ecosystems, fertilization has led to an increase in all plant functional types, whereas in the tussock tundra in northern Alaska, fertilization has led to a strong increase of one specific deciduous shrub, *Betula nana* L., and the decrease of evergreen species (van Wijk et al. 2004, Zamin et al. 2014). Therefore it seems that environmental changes may have different implications in the subarctic and arctic ecosystems in Scandinavia and Alaska.

### 1.2 Disturbances in the boreal and subarctic environments

Vegetation in the boreal and subarctic ecosystems is subjected to several types of natural disturbances, such as storms and windthrows (Ulanova 2000), forest fires (Nilsson & Wardle 2005), insect outbreaks (Karlsen et al. 2013), and herbivory by small rodents (Olofsson et al. 2012) and large ungulates (Tømmervik et al. 2004). Moreover, these ecosystems are affected by human activities, including tourism, recreational use, and forest management (Kangas et al. 2009, Törn et al. 2009, Tonteri et al. 2013), which are gradually replacing natural disturbances in the northern ecosystems in terms of their impacts (Esseen et al. 1997).

Natural and anthropogenic disturbances share common features, as both damage or remove plant tissue, whole plants, and/or soil organic layers. Some of these disturbances, such as herbivory, remove plant tissue selectively and may thus differ in their effects from unselective disturbances. For example, selective herbivory of more palatable species may promote the dominance of those less
palatable evergreen shrubs (Yläne et al. 2015), which are otherwise sensitive to unselective disturbances such as trampling (Tybirk et al. 2000).

1.2.1 Plant vegetative recovery and sexual reproduction after disturbance

The tolerance to disturbance (i.e., the ability to recover or reproduce after disturbance; Strauss & Agrawal 1999) varies among plant species (Speed et al. 2010) and functional types (Chapin et al. 1996, Lavorel et al. 1997). Traits, such as a high photosynthetic and growth rate, belowground nutrient storages (Chapin 1980, Bryant et al. 1983), a high number of dormant buds (Tolvanen & Laine 1997) and their lateral location (Hawkes & Sullivan 2001) are beneficial for vegetative recovery after disturbances. Consequently, the vegetative recovery of graminoids and deciduous dwarf shrubs is generally higher than that of evergreen dwarf shrubs (Archer & Tieszen 1980, Chapin 1980, Karlsson 1985, Haukioja & Koricheva 2000, Hawkes & Sullivan 2001). Variances in the disturbance tolerance of plant species and functional types can lead to changes in plant community, resulting in alleviated resilience (Folke et al. 2004).

Clonal plants recover after disturbance principally through vegetative growth from the surrounding intact vegetation in boreal forests (Hautala et al. 2001, 2007) and in the subarctic mountain birch ecotone (Olofsson et al. 2005). However, the growing body of evidence on the high potential for sexual reproduction in terms of seed rain (Molau & Larsson 2000), soil seed bank (Cooper et al. 2004, Welling et al. 2004), germination rate (Vera 1997) and seedling recruitment (Welling & Laine 2000, Forbis 2003) challenge the traditional view of the rarity of sexual reproduction in the northern ecosystems.

Successful seedling establishment includes both the availability of appropriate propagules and the existence of suitable habitats for seed germination (Salemaa & Uotila 2001, Cooper et al. 2004, Gough 2006, Klanderud & Totland 2007). In northern poor plant communities dominated by clonal dwarf shrubs, seed availability is inherently lower than in the more fertile plant communities (Welling & Laine 2000, 2002, Welling et al. 2004, Forbis 2003, Milbau et al. 2013) and is to a great extent dependent on the year-to-year variation of environmental conditions (Selás 2000, Turtiainen et al. 2011).

Disturbances have a great impact on the availability of suitable habitats for seedling establishment, as they provide essential soil contact for seed germination (Bret-Harte et al. 2004, Graae et al. 2011, Eckstein et al. 2011, Soudzilovskaia et
al. 2011). Disturbance is, therefore, essential for the success of sexual reproduction in several northern ecosystems, where seedling establishment greatly depends on gap formation within the existing vegetation (Eriksson & Fröborg 1996, Hautala et al. 2001, Graae et al. 2011).

According to the “Shifting limitations hypothesis” (SLH; Huston 1999, Zobel et al. 2000, Foster et al. 2004) the relative importance of the limitations of seed availability and suitable microhabitats on seedling establishment varies by environmental gradients. The seedling establishment is suggested to be limited by low seed availability especially at low-productive sites, whereas the availability of microhabitats may limit the seedling establishment at the more productive sites (Eskelinen & Virtanen 2005, Foster et al. 2004, Gough 2006, Mayer & Erschbamer 2011).

### 1.3 Relations of N and disturbances on soil microbial biomass

The impact of N on soil microbial biomass seems to be largely a result of the duration and the amount of N load to the soil (Rinnan et al. 2007, Treseder 2008). N input may have a direct toxic effect of N on microbial biomass (Fog 1988, Treseder 2008) or, in the long term, decrease microbial biomass and change the microbial community composition by suppressing fungal relative to bacterial biomass, as revealed in the boreal forests (Nohrstedt et al. 1989, Smolander et al. 2000, Wallenstein et al. 2006, Högberg et al. 2007, Demoling et al. 2008). However, N addition has also been found to increase microbial biomass in the (sub)arctic (Rinnan et al. 2007, Sistla et al. 2012).

The positive short-term effect of disturbances on the nutrient availability for soil microbes is the result of reduced plant biomass and hence lower plant resource uptake (Jonasson 1992, Bret-Harte et al. 2004, 2008), and an alleviated competition for available resources between plants and soil microbes. More importantly, disturbance affects soil microbial processes through plant-soil interactions by either increasing or decreasing plant-delivered C for microbe growth and maintenance. Moderate disturbance, such as herbivory, which results in biomass loss, increases the exudation of C in the rhizosphere. Increased exudation of C stimulates the growth and activity of the microbes in the short term (Bardgett et al. 1998), which then increases microbial nutrient immobilization and limits the N available for plants. On the other hand, continuous disturbance that reduces the photosynthetic plant biomass may result in decreased C-flux and the decreased C-exudation of roots, thus decreasing
microbial biomass and hence nutrient immobilization as well, leading to a higher amount of N for plants (Sankaran & Augustine 2004).

In addition to the short-term effect of root exudates, C-flux to microbial biomass is greatly affected by the below- and above-ground litter inputs to soil (Leppälammi-Kujansuu et al. 2014). Both N-fertilization and the disturbances often lead to changes in the quantity and quality of both below- and aboveground litter and the plant community composition. These changes may affect soil N and C pools and have substantial feedback effects on plant growth over a long timescale (Wardle et al. 2004).

1.4 Interactions between N, plant recovery, and microbial biomass

The “Compensatory continuum hypothesis” (CCH; Maschinski & Whitham 1989) predicts that the recovery ability of a plant species after biomass loss caused by disturbances, such as herbivory, increases with increasing resource levels. However, in the meta-analysis performed by Hawkes & Sullivan (2001), the recovery ability of species was related to the low location of reproductive meristems that were protected from damage rather than to resource availability. Taken together, the same characteristics that enable plant species to respond to the single effect of N-fertilization and disturbances enhance recovery ability. Consequently, as both N-fertilization and disturbance have positive effects on the growth of fast-growing deciduous dwarf shrubs and graminoids, their combined effects on these species should be stronger than either one alone.

Biotic homogenization has traditionally been defined as the establishment of novel species and the decline in the abundance of native ones (McKinney & Lockwood 1999). Despite the general definition of biotic homogenization and the new species introduced in the plant communities, biotic homogenization may occur via an increased abundance of the fast-growing species (Nielsen et al. 2011) that are already common in the vegetation (Wiegmann & Waller 2006). Several mechanisms, such as N enrichment (Reinecke et al. 2014) and the disturbances (Wiegmann & Waller 2006) may trigger the homogenization of vegetation. If the combined effect of N-fertilization and disturbances on fast-growing species is stronger than their single effects, as could be expected, then the positive interaction between N-fertilization and the disturbance should potentially reinforce the homogenization of the vegetation.

The classical theories predict increasing plant biomass after N-fertilization (Tamm 1991); on the other hand, the plant biomass will be reduced after severe
disturbance (Grime 1973). In addition to the direct effects of N and disturbance on plant biomass, they both indirectly influence soil microbes due to their effects on resource availability for microbial growth. The interconnection between plants and soil microbes is well recognized (Wardle 2002, Jonasson et al. 2006), as microbial biomass can immobilize part of the available N, potentially affecting plant N uptake (Jonasson et al. 1996, Melle et al. 2015) and the recovery ability of the plant species.

However, few conceptual approaches (Wardle et al. 2004) have been developed to model how changes in above-ground plant biomass affect soil microbes. Further, the theories for predicting the responses of N and the disturbance in microbial biomass are still being developed. If the classical theories of plant biomass are applied to the soil microbial biomass, changes in these two biomasses are parallel. However, based on earlier studies, N-fertilization and the disturbances may either increase or decrease the soil microbial biomass (Bardgett et al. 1998, Smolander et al. 2000, Sankaran & Augustine 2004, Rinnan et al. 2007, Treseder 2008) and differ from those predicted in the plant biomass (Grime 1973, Tamm 1991) which then reveals a high complexity when linking the theories that predict plant biomass to soil microbes.

1.5 Significance of the study

A changing climate and especially its warming effects on vegetation and soils is a widely accepted phenomenon, and the implications are recognized as being most obvious in northern environments (IPCC 2013). Although several studies do reveal significant changes in vegetation and soil properties in a warming climate, there is still much uncertainty as to which direction vegetation is heading in the future. In addition to warming, the understorey vegetation in northern environments has been subjected to several other environmental changes, such as increasing N (deposition, enhanced mineralization), and continuous disturbances (herbivory, tourism, and forestry practices).

Although the effects of the increasing N and the disturbances in the understorey vegetation are predictable, the knowledge of their interactive role in the ongoing vegetation change in northern areas is still largely unknown. It can be expected that N-fertilization and disturbances have parallel effects on understorey vegetation by increasing the fast-growing species, and consequently, that their interactive effect is stronger than either one alone (Fig. 1). The positive
interaction may potentially reinforce the homogenization of understorey vegetation through increased abundances of graminoids and/or deciduous dwarf shrubs already present in the vegetation (Wiegmann & Waller 2006), leading to the formation of a new stable state in the plant community (see Fig. 1). Moreover,

Fig. 1. The conceptual framework of this study regarding the effects of N-fertilization and disturbance on the plant community. If both N-fertilization and disturbance increase the abundance of fast-growing graminoids and deciduous dwarf shrubs, then their interactive effects may be stronger than either one alone. Thereby the positive interaction between N-fertilization and disturbance may reinforce the homogenization of the vegetation and lead to a new stable state in the plant community in the long term.

predictions of the effects of N-fertilization and disturbance on soil microbial biomass and its feedback effect on plant species recovery ability seem to be complicated based on earlier studies: N-fertilization may decrease microbial biomass as found especially in the boreal forest (Smolander et al. 2000, Wallenstein et al. 2006, Högberg et al. 2007, Demoling et al. 2008), but potentially increase it in the (sub)arctic (Rinnan et al. 2007, Sistla et al. 2012). Moderate disturbance may also enhance, while severe retarding, the growth of microbial biomass (see i.e. Bardgett et al. 1998, Sankaran & Augustine 2004) (Fig. 2). This discrepancy in the expectations of the response of microbial biomass to N-fertilization and disturbances confounds the building of general theory on the item. However, if the classical theories of plant biomass are applied
to soil microbial biomass, then the microbial biomass should increase after N-fertilization and decrease after disturbance, resulting in a higher N immobilization in the former and a lower one in the latter (Fig. 2). After the disturbances, clonal plant species recover mainly by vegetative growth (Hautala et al. 2001, Olofsson et al. 2005). However, the sexual reproduction of clonal species may be enhanced in disturbed environments, as the amount of suitable habitats for seed germination increase.

Fig. 2. The conceptual framework of this study on the effects of N-fertilization and disturbance on the microbial biomass. Both N-fertilization and disturbance may either decrease or increase the microbial biomass. Decreasing of the microbial biomass is linked to boreal forest environments or severe disturbances, and an increasing of microbial biomass to (sub)arctic or moderate disturbances. If microbial biomass decreases after N-fertilization or disturbances, the N immobilization should decrease, while the reverse should be noted in the case of an increase in the microbial biomass.

By producing new results for the effects of understorey vegetation and soils to increasing N and disturbances, this study improves the general knowledge of the implications of environmental changes in the northern ecosystems.
1.6 Aims of the study

The main aim of this study is to investigate the resilience of understorey vegetation and soils to increasing N in combination with experimental disturbances (vegetation and/or soil removal) in boreal and subarctic environments. Experimental disturbances were considered as severe at plant species and community levels. The following research questions and hypotheses were thus offered:

1. Question: What are the effects of N-fertilization and disturbance on plant functional types in the understorey plant community (papers I, II, III)?
   Hypothesis: N-fertilization increases total vascular plant abundance. Both N-fertilization and disturbance increase the abundance of fast-growing graminoids and deciduous dwarf shrubs at the expense of slow-growing evergreen dwarf shrubs in understorey vegetation.

2. Question: Does N-fertilization affect the recovery ability of vegetation after disturbance (papers I, II, III)?
   Hypothesis: N-fertilization enhances the recovery ability of vegetation, which should be identified by significant positive interaction between N-fertilization and disturbance. N-fertilization should especially enhance the recovery of fast-growing species, such as graminoids and deciduous dwarf shrubs.

3. Question: What are the impacts of N-fertilization and disturbance on soil microbial biomass and N and C pools, and how are these changes reflected in plant recovery ability after disturbance (papers I, II)?
   Hypothesis: N-fertilization decreases soil microbial biomass C, especially in the boreal forest, but increases it in the subarctic. Disturbances decrease soil microbial biomass C. The decrease of microbial biomass decreases the potential of microbes to immobilize N. As a result of decreased microbial N immobilization, the availability of N in the soil for plant recovery increases.

4. Question: Does disturbance enhance the seedling establishment of dominant understorey clonal plant species (*Vaccinium myrtillus* L., *V. vitis-idaea* L. and *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher) in a forest-tundra ecotone (paper IV)?
   Hypothesis: Disturbance creates suitable habitats for seedling establishment of plant species, but seedling emergence is restricted by seed availability after disturbance.
2 Material and methods

2.1 N-fertilization and vegetation removal experiments (I, II)

2.1.1 Study sites

These studies were conducted in two dense, 80–100 year old boreal coniferous forests (Oulu, Kuusamo) and in a subarctic mountain birch forest (Kilpisjärvi) in northern Finland. The locations and the characteristics of the study sites are shown in Table 1. and Fig. 2. The forests chosen for the studies represent an intermediate forest site type between moderately dry and a mesic heath forest. The dominant understorey species in these forests are deciduous dwarf shrub *V. myrtillus* and evergreen dwarf shrub *V. vitis-idaea*. The evergreen dwarf shrub *E. nigrum ssp. hermaphroditum* is also common in Kilpisjärvi. The ground layer is dominated by bryophytes, such as *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp. and *Dicranum* Hedw. sp. The dominant tree species varies between the sites due to climate and pedological differences. The dominant tree species is *Pinus sylvestris* (L.) in Kuusamo, *Picea abies* (L.) H. Karst in Oulu and *Betula pubescens* ssp. *czerepanovii* (N. I. Orlova) Hämet-Ahti in Kilpisjärvi.

<table>
<thead>
<tr>
<th>Location</th>
<th>Oulu</th>
<th>Kuusamo</th>
<th>Kilpisjärvi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vegetation zone</td>
<td>Middle boreal</td>
<td>Northern boreal</td>
<td>Subarctic</td>
</tr>
<tr>
<td>Annual mean temperature*</td>
<td>2.9 °C</td>
<td>0.1 °C</td>
<td>-1.9 °C</td>
</tr>
<tr>
<td>Duration of growing season*</td>
<td>151 days</td>
<td>144 days</td>
<td>109 days</td>
</tr>
<tr>
<td>Annual mean precipitation*</td>
<td>510 mm</td>
<td>584 mm</td>
<td>527 mm</td>
</tr>
</tbody>
</table>

*Finnish Meteorological Institute, 1998-2002

2.1.2 Experimental design and measurements

To investigate the effects of N-fertilization and vegetation removal on understorey and soil microbes, 32 study plots (2 m x 2m) were established in 1998 at each study site. The study plots were assigned to the unfertilized control and the
fertilization treatments: 20, 40 and 80 kg N ha⁻¹ year⁻¹. N was added as an urea solution during 1998–2002.

The understorey vegetation was clipped to the level of the moss layer in June-July in 2000–2002 from 0.5 m x 0.5 m subplots established in each study plot. The clipped biomass was taken to the laboratory, sorted into species and weighed for dry biomass. The concentration of N and C was analysed from the new shoots of *V. myrtillus*, *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum*, and from the aerial shoots of *D. flexuosa*. To detect the effect of N-fertilization on the recovery of understorey plants, additional biomass samples, 0.25 m x 0.25 m in size, were collected from the unclipped vegetation at each study plot in 2002.

**Fig. 3. Location of the study sites.**

Soil samples were collected in 2001 from the clipped subplots and from beneath the undisturbed vegetation to detect the effects of N-fertilization and clipping on
the concentration of ammonium (NH$_4^+$), microbial N and C, and soil dissolved organic N (DON) and C (DOC).

### 2.1.3 Statistical analysis

The biomass data collected in 2002 were used in the analysis. The species biomasses were pooled into four plant functional types, namely, deciduous shrubs, evergreen shrubs, graminoids, and herbs. The relative biomass of these functional types was then calculated as a percentage from the total above-ground vascular plant biomass.

The data were split into two sections before the analysis due to ecological differences between the study sites. In paper I, the effects of N-fertilization and clipping were tested for the boreal forests (Oulu and Kuusamo), and in paper II, the treatment effects for the subarctic mountain birch forest (Kilpisjärvi) were analysed. A repeated measures ANOVA was used to test the effects of N-fertilization and clipping on the total above-ground vascular biomass, relative biomass of plant functional types, concentrations of N and C in the most abundant vascular plant species, and soil and microbial parameters.

In paper I, clipping treatment (not clipped, clipped) was used as a within-subject factor, and the site (Oulu and Kuusamo) and N-fertilization (unfertilized control and 20, 40 and 80 kg N ha$^{-1}$year$^{-1}$) were use as between-subject factors in the repeated measures ANOVA. In paper II, clipping treatment was used as a within-subject factor and N-fertilization as a between-subject factor in the repeated measure ANOVA.

Levine’s test was used to examine the homogeneity of variances prior to the analysis, and logarithmic and arcsine- transformations were used when the data did not fulfill the requirements of normality and homogeneity of variances. Multiple comparisons were made using the Tukey’s post hoc test ($P < 0.05$). These tests were performed using SPSS 15.0 for Windows (SPPS Inc., Chicago, IL, USA, 2000).
2.2 N-fertilization and soil removal experiment (III, IV)

2.2.1 Study site

The study site was located in a forest-tundra ecotone in northern Finland (Ounastunturi Fjell region in Hetta, 68°14’N, 23°45’E). At the study site, the timber line of coniferous forest was located at 420 a.s.l., the subalpine mountain birch forest zone reaches up to 455 a.s.l. and turns into treeless tundra heath. The tops of the Ounastunturi mountains lie approximately at 720 a.s.l. The understorey is dominated by the deciduous dwarf shrub *V. myrtillus* and the evergreen dwarf shrubs *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum*. Mean annual temperature and precipitation were –1.8 °C and 473 mm yr⁻¹, respectively, during the years 1980–2005 (Venäläinen *et al.* 2005).

2.2.2 Experimental design and measurements

The experiment was conducted in 2002–2005. The experiment had a factorial design with five factors: Year (four levels: 2002–2005); site (three levels: coniferous forest, subalpine mountain birch forest and tundra heath); N-fertilization (two levels: unfertilized, fertilized); soil removal (two factors: not removed, removed); and seed sowing (two level: unsown, sown). Each treatment combination had seven replicates applied on the 0.5 m x 0.5 m study plots. Soil removal treatment was applied by cutting the existing understorey vegetation and soil organic layers from the study plots. N-fertilization treatment was applied annually as urea and corresponded to 40 kg N ha⁻¹ year⁻¹.

The initial difference in the plant community composition between the sites was detected from the removed biomass in the soil removal treatments. Berries of *V. myrtillus*, *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum* were collected at the study sites in 2002. From the berries, mature seeds were separated from aborted seeds and unfertilized ovules and then counted. A total of 150 mature seeds of each species was sown on the soil removal treatment plots in 2002.

The effects of N-fertilization and soil removal on plant abundances were estimated using the point frequency method in 2002–2005. Due to the vertical growth and multilayer structure of vascular plants in the field layer, all interceptions on each plant were recorded, corresponding roughly to their biomass (Jonasson 1988). Emerged seedlings were identified into species, tagged, and counted in the field in 2003–2005.
2.2.3 Statistical analysis

The data were split into two sections: In paper III, the goal was to study the effect of N-fertilization on the vegetative recovery of plant species after soil removal. In paper IV, sexual reproduction of plant species after soil removal was studied.

In paper III, a mixed linear model was applied to detect the treatment effects on plant abundances between the study years. Models were applied on the most abundant plant species and pooled abundances of graminoids and herbs and the relative proportion of plant functional types. Logarithm- and square root transformations were used when necessary to fulfil the requirements for normality and the homogeneity of variances. Site, year, soil removal, and N-fertilization were included as a fixed effect in the analysis. Statistical analyses in paper III were performed using SPSS 15.0 for Windows (SPSS Inc., Chicago, II., USA, 2000).

In paper IV, to assess possible differences in the seedling number of *V. myrtillus*, *V. vitis-idaea* and *E. nigrum* ssp. *hermaphroditum* between the treatments and sites, a zero-inflated generalized linear-mixed model (ZIGLMM) fitted with the “glmmadmb” function in the “glmmADMB” package (Fournier *et al.* 2012) with a negative binomial error structure “NB1” was used. Statistical analyses in paper IV were performed by software R, Version 3.0.2 (R Core Team, 2013).
3 Results and discussion

3.1 N-fertilization and disturbance increase graminoids in the boreal forest and subarctic environments

The total vascular plant biomass remained constant after N-fertilization in the boreal forest (paper I, Table 2) which was not in line with our expectations and the general assumption of the N-limitation of boreal forests (Tamm 1991). However, similar results were reported earlier in the boreal coniferous forest (Mäkipää 1994, Nohrstedt 1998, Nordin et al. 1998, Skrindo & Økland 2002) suggesting that other factors, such as light (Vitousek & Reiners 1975, Gilliam 2006, Strengbom & Nordin 2012, Verheyen et al. 2012, Hedwall et al. 2013, Reinecke et al. 2014) concomitantly with N may limit the growth of understorey vegetation. The dense cover of coniferous tree canopies, although not investigated, probably also affected both light availability and vascular plant growth in the boreal forest in this study. Alternatively, N-fertilization may have species- or functional type specific responses that then lead to changes in plant community composition without implications at the total vascular plant level (Dormann & Woodin 2002, Gough & Hobbie 2003, Pennings et al. 2005, Bret-Harte et al. 2008, Strengbom & Nordin 2008). Instead, the total vascular plant biomass increased after N-fertilization in the subarctic mountain birch forest and forest-tundra ecotone, as has also been found in other fertilization studies conducted in the subarctic and arctic environments (Dormann & Woodin 2002, van Wijk et al. 2004, Bret-Harte et al. 2008, DeMarco et al. 2014), thus indicating the nutrient limitation of these environments.

The relative proportion of graminoids generally increased in the understorey, both after N-fertilization and disturbance as expected (papers I, II, III, Table 2). Graminoid species have a high recovery capacity from basal meristems after disturbances (Hawkes & Sullivan 2001), which together with other plant characteristics related to the graminoid functional type, such as high photosynthetic rate and water-use efficiency, and effective N uptake (Bowman et al. 1995, Nordin et al. 2006) will enable graminoids to respond rapidly to perturbations.

N-fertilization had no effects on the other functional types than on the graminoids in the boreal forest (paper I, Table 2). Instead, N-fertilization had a contrasting effect on the relative proportion of deciduous dwarf shrubs, as they
increased in the subarctic mountain birch forest and decreased in the forest-tundra ecotone (papers II, III, Table 2). Similarly to graminoids, deciduous dwarf shrubs relate to high rates of photosynthesis and growth, and also to higher competitive ability compared to, for example, evergreen species (Cornelissen et al. 1996, Campioli et al. 2012). Enhanced growth of deciduous dwarf shrubs under high nutrient conditions was reported in tussock tundra in Alaska (van Wijk et al. 2004) and the tundra ecosystem in Scandinavia (Nilsson et al. 2002). However, in this study, the relative proportion of deciduous dwarf shrubs decreased concomitantly with the increasing graminoids after N-fertilization in the mountain birch forest (paper II). Similar results were reported in the studies conducted in the subarctic forest (Veen et al. 2015) and heath ecosystems in Scandinavia (Alatalo et al. 2015) and Alaska (Gough et al. 2008, 2012, Campioli et al. 2012), suggesting that graminoids are most probably able to overgrow other plant functional types at nutrient poor growing sites under high nutrient availability over the long term.

The relative proportion of evergreen dwarf shrubs decreased after N-fertilization in the forest tundra and generally decreased concomitantly with increasing amounts of graminoids after disturbance (papers I, II, III, Table 2). This occurred in accordance with our expectation and the general assumption of low recovery ability of evergreen dwarf shrubs due to slow growth, lower belowground biomass, and fewer resources stored in belowground organs when compared to many graminoid and deciduous species (Archer & Tieszen 1980, Chapin 1980, Karlsson 1985, Tolvanen & Laine 1997). Reduced recovery of evergreen dwarf shrubs has been previously reported both after human-induced disturbances, such as trampling (Törn et al. 2006), and in experiments’ mimicking natural events that cause above-ground biomass loss (Olofsson et al. 2005, Aerts 2010). However, disturbances that cause damages in belowground meristems may be less harmful to the recovery of evergreens than the recovery of deciduous dwarf shrubs (Tolvanen 1994). For example, the evergreen dwarf shrub *V. vitis-idaea* recovers faster than the deciduous *V. myrtillus* after clear-cutting in boreal forests (Tonteri et al. 2013).

Irrespective of the changes in the plant community structure, the order of the relative proportions of plant functional types changed only in the mountain birch forest. The dominance of evergreen dwarf shrubs was replaced by the dominance of graminoids, deciduous, and forbs after disturbance (paper II). This is probably a result form breaking the strong dominance of one specific evergreen dwarf shrub, *E. nigrum* ssp. *hermaphroditum*, by disturbance. Once established, *E.*
*nigrum* ssp. *hermaphroditum* can out-compete other species due to the effective resource acquisition and chemical interference (Tybirk et al. 2000). However, *E. nigrum* ssp. *hermaphroditum* recovers ineffectively from severe disturbance, after which subordinate species are able to increase in the understory, and significant changes in the order of relative proportion of plant functional types can occur (Olofsson et al. 2005, Aerts 2010). Taken together, although fertilization may change the order of the relative proportion of plant functional types by increasing deciduous (van Wijk et al. 2004) or graminoid species (Alatalo et al. 2015), in this study the significant change occurred after disturbance, but not after N-fertilization, suggesting that disturbance is more important in shaping the community composition than increased N is.

Table 2. Summary of the most important main effects of N-fertilization and disturbance on plant community composition in different ecosystems. Roman numerals after the ecosystem type refer to the original papers listed on page 11. N-fert = N-fertilization, Dist = disturbance, ↓ = decreasing, ↑ = increasing.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Boreal forest I</th>
<th>Mountain birch forest II</th>
<th>Forest-tundra ecotone III</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vascular plant biomass/</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>abundance</td>
<td>↓</td>
<td>↑</td>
<td>↓</td>
</tr>
<tr>
<td>Graminoids</td>
<td>↑</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td>Deciduous</td>
<td>↓</td>
<td>↑</td>
<td>↑</td>
</tr>
<tr>
<td>Evergreens</td>
<td>↓</td>
<td>↓</td>
<td>↓</td>
</tr>
</tbody>
</table>

1Disturbance type = vegetation removal, 2Disturbance type = soil removal

### 3.2 N-fertilization enhances the recovery of graminoids in the subarctic ecosystem and the forest-tundra ecotone

Significant synergic interaction between N-fertilization and disturbances was detected in the relative proportion of graminoids from the vascular plant biomass in the subarctic mountain birch forest (paper II) and in the abundance of graminoid species in the forest-tundra ecotone (paper III). This synergic interaction reveals that N-fertilization enhanced the post-disturbance recovery rate of graminoids in these environments. Graminoids are most likely to exhibit overcompensation after biomass loss at a high resource level (Bryant *et al.* 1983, Hawkes & Sullivan 2001), supporting the “Compensatory Continuum Hypothesis” by Maschinski & Whitham (1989).
The synergic interaction between N-fertilization and disturbances led to the homogenization of vegetation by the strong increase of graminoids, which resulted in a new stable state in the plant community in the subarctic ecosystem. Graminoids are susceptible to causing homogenization of vegetation (Wiegmann & Waller 2006, Nielsen et al. 2011) if they are already present in vegetation (Wiegmann & Waller 2006), thus emphasizing that in combination, N-fertilization and disturbance may reinforce vegetation change.

It is an interesting question, namely, why the positive interactive effect of N-fertilization and disturbance on graminoids was not detected in the boreal forest (paper I). To answer this question, a closer inspection of species-level responses to N enrichment and disturbance might be enlightening. Graminoid *D. flexuosa*, which constituted almost all of the graminoids, is commonly found in the understorey in boreal coniferous and mountain birch forests. The dominance of this species is mediated by disturbances like clear-cutting that relax the above-ground competition for light and enable *D. flexuosa* to gain a competitive advantage over other species (Strengbom et al. 2004, Tonteri et al. 2013). Given that the light transmission is weaker to the understorey in closed coniferous forests compared to deciduous forests (Canham et al. 1994, Messier et al. 1998), it seems possible that light availability hindered the maximal growth of *D. flexuosa* in the boreal forest, thus preventing any significant positive interaction between N-fertilization and disturbance from occurring.

### 3.3 Microbial biomass does not limit the recovery ability of vegetation

N-fertilization had no effect on microbial biomass C in the boreal coniferous or in the subarctic mountain birch forest (papers I, II, Table 3). These results contradict our hypothesis and also the earlier studies conducted in boreal forests (Fog 1988, Nohrstedt et al. 1989, Smolander et al. 1994, Wallenstein et al. 2006, Högberg et al. 2007, Demoling et al. 2008, Mayor et al. 2015) and (sub)arctic tundra (Stark & Grellmann 2002, Rinnan et al. 2007, Sistla et al. 2012).

Microbial biomass C decreased in disturbance treatment in the boreal coniferous forest (paper I, Table 3), as reported after natural herbivory in the boreal forest (Väre et al. 1996, Stark et al. 2000) and (sub)arctic tundra (Stark & Grellmann 2002, but see Stark et al. 2002). Decreasing microbial C after disturbance suggests that cutting the above-ground photosynthetic biomass reduced the C-flux to the soil microbes and caused a C deficiency for the
microbial growth. However, even though microbial biomass C was reduced, the potential for microbial N immobilization was unaffected (papers I, II, Table 3). The lack of response in N immobilization was not in line with the general assumption of high microbial N immobilization capacity, which exists especially in cold climate soils (Nadelhoffer et al. 1991, Jonasson et al. 1996, 1999, Schmidt et al. 1997, Schimel et al. 2004, Melle et al. 2015). Further, the results of the effects of N-fertilization and disturbance on microbial biomass are not fully compatible with the classical theories on the vegetation responses to increasing N and disturbances. However, decreasing the microbial biomass after disturbance in the boreal forest underpins the close connection between the above-ground plant biomass and soil microbes.

N concentration increased in above-ground vegetation after N-fertilization and disturbance without any indication of N immobilization, which suggests that plant species were able to capture effectively available N for their recovery, as reported earlier from the subarctic (Pietikäinen et al. 2005, Stark & Kytöviita 2006). This is supported by the tendency toward a decreasing concentration of NH$_4^+$ and a decreasing concentration of DON in the soil after disturbance in the subarctic mountain birch forest (paper II, Table 3). DON is an important source of N for several organisms, as plants (Chapin et al. 1993, Kielland 1994), mycorrhizal fungi (Näsholm et al. 1998) and other microbes (Nordin et al. 2004) can access this N pool.

C concentration decreased in all plant tissues after disturbance in the boreal forest (paper I, Table 3). In clonal plant species below-ground resources may be redistributed within the clone (Tolvanen 1994). This decreased C in plants suggests that large amounts of resources were used for recovery and also that the recovery was probably limited by C availability. Similar results on C limitation in the recovery of understorey species after severe disturbance have been reported for V. myrtillus (Tolvanen & Laine 1997, Strengbom et al. 2003). Contrary to Vaccinium-species, the lack of a negative effect of disturbance on the biomass of D. flexuosa suggests that D. flexuosa was able to compensate for the biomass loss, irrespective of the reduced C in its tissue. Graminoid growth form included characteristics (Bowman et al. 1995) that resulted in high C reserves to invest for growth.
Table 3. Summary of the most important results of the effects of N-fertilization and disturbance on soil properties and the nutrient concentrations of plant species in the boreal forests and subarctic mountain birch forest. The Roman numerals refer to the original papers listed on page 11. N-fert = N-fertilization, Dist = Disturbance, ↓ = decreasing, ↑ = increasing, na = not available

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Boreal forest I</th>
<th>Mountain birch forest II</th>
</tr>
</thead>
<tbody>
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<td></td>
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<td>Dist&lt;sup&gt;1&lt;/sup&gt;</td>
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<tr>
<td>Soil properties</td>
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<td></td>
</tr>
<tr>
<td>Microbial C</td>
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<tr>
<td>Microbial N</td>
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<td></td>
</tr>
<tr>
<td>NH₄⁺</td>
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</tr>
<tr>
<td>Dissolved organic N</td>
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<tr>
<td>Dissolved organic C</td>
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<td></td>
</tr>
<tr>
<td>Nutrient concentrations in plants</td>
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<td>↑</td>
</tr>
<tr>
<td>N concentration</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C concentration</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>1</sup>Disturbance type = vegetation removal

3.4 Seed availability limits seedling establishment after disturbance in the forest-tundra

The seedling numbers of the three major dwarf shrubs increased the most with the combined treatment of disturbance and sowing (paper IV). Disturbance without sowing increased the seedling number of *V. myrtillus* and *E. nigrum* ssp. *hermaphroditum* marginally, whereas no impact on the seedling number was found for *V. vitis-idaea*. This result is in accordance with the hypothesis in that disturbance creates habitats for seed germination, but the seed availability seems to be a stronger constraint than microsite availability on the seedling establishment of the species in the forest-tundra. This result also supports the “Shifting limitations hypothesis” (SLH; Huston 1999, Zobel et al. 2000, Foster et al. 2004), which predicts the seed limitation in poor habitats. Seed limitation for *V. myrtillus* and *V. vitis-idaea* was reported from boreal and subalpine forests and alpine tundra (Hautala et al. 2001, Eriksson 2002, Lindgren et al. 2007). In the previous studies, as opposed to this study, the seeds of *E. nigrum* ssp. *hermaphroditum* have been found to germinate in low numbers in the subalpine birch forest and alpine heath, but the seed limitation of this species has not been confirmed (Lindgren et al. 2007).
4 Conclusion: the resilience of understorey vegetation and soils

The results of this research suggest that graminoid species are the main benefactors from environmental changes in northern ecosystems. The enhanced post-disturbance recovery ability of graminoids after N enrichment homogenizes the vegetation and results in a new stable state in the plant community. This result may have important outcomes for the resilience of the ecosystem, if the system shifts to a more productive state.

The recovery ability of evergreen dwarf shrubs is generally slow after disturbances, which together with the low potential for sexual reproduction, implies low resilience to disturbances. The amount of graminoid species generally increases after a decrease in the amount of evergreen dwarf shrubs when disturbed.

To summarize the results of N-fertilization and disturbances on understorey vegetation in terms of the resilience of the ecosystem, the scenario shown by the most important results of this thesis is shown in Fig. 4. Taken together, a likely outcome of N enrichment combined with disturbances is a new more productive state of the ecosystem. This finding is supported by 1) the homogenization of vegetation in the combined treatment of N-fertilization and disturbance, and 2) the low resilience of evergreen dwarf shrubs to disturbances, both of which increase the amount of graminoids and may push the system over the critical threshold and lead to a new more productive state for the ecosystem. Although N-fertilization has a clear positive effect on the amount of graminoids, its effect on plant community structure is weaker than the effect of disturbances alone or when disturbances are combined with N-fertilization.

Based on this study then, this scenario is more likely to happen in the subarctic ecosystem, where the homogenization of vegetation has occurred. However, the scenario presented in Fig. 4 relies only on the findings of this singular study and does not take into account all aspects of the expected changes in the future. For example, if the density of the shrub layer is increased due to a warming climate in (sub)arctic as suggested in earlier studies, it may suppress the growth of graminoids through shadowing in the long term. Moreover, graminoids are preferred forage species and susceptible to selective herbivory. If the consumption of graminoids by selective herbivory increases along with environmental changes, it may contribute to the resilience of the ecosystem by returning the system to a lower productive state. Compared to the subarctic
ecosystem, the vegetation was less responsive to perturbations studied in the boreal forest, indicating that the understorey vegetation of boreal forests is more resilient to environmental changes.

The microbial biomass seems to be resilient regarding N-fertilization. Instead, disturbance decreased the microbial biomass in the boreal forest, which underpins a close connection between above-ground plant biomass and soil microbes. However, the most obvious changes after N-fertilization and the disturbances were found in the understorey vegetation in this study. That suggests that microbial properties are more resilient to environmental changes than is above-ground vegetation.

Fig. 4. The possible outcome of N-fertilization and disturbances based on the most important results of this study in terms of resilience of the ecosystem. Graminoids are increasing in the understorey, due both to the homogenization of vegetation after N-fertilization combined with disturbances and the low resilience of evergreen species to disturbances. Increasing graminoids may push the system over the critical threshold and lead to a new more productive state for the ecosystem. Although N-fertilization has a clear consistent positive effect on the amount of graminoids, its single effect is weak on the plant community structure and thus the threshold of ecosystem resilience is not exceeded.
References


Original articles


Reprinted with permission from John Wiley and Sons (I, II) and Springer (III).

Original publications are not included in the electronic version of the dissertation.
657. Lappalainen, Katja (2015) Modification of native and waste starch by depolymerization and cationization: utilization of modified starch in binding of heavy metal ions from an aqueous solution


663. Pakanen, Minna (2015) Visual design examples in the evaluation of anticipated user experience at the early phases of research and development

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THE RESILIENCE OF UNDERSTOREY VEGETATION AND SOIL TO INCREASING NITROGEN AND DISTURBANCES IN BOREAL FORESTS AND THE SUBARCTIC ECOSYSTEM