

Forest Floor Vegetation in Sweden

Impacts of Intensified Forestry, Nutrient Addition and
Changes in Forest Structure

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Cover: Hemiboreal mixed coniferous forest with abundant undergrowth of bilberry (*Vaccinium myrtillus*) (photo: O. Runfors)

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Abstract

In boreal forests, dwarf-shrubs (*Vaccinium* spp.) often dominate the forest floor and are key-stone species in ecosystems due to their importance for nutrient cycling and as a major food source for herbivores. Forestry affects the vegetation both directly through management and indirectly by altering the forest structure. Forest fertilization with N at the end of the rotation period is a common practice in Swedish boreal forests. Even higher timber production can be achieved if fertilization with multi-nutrient fertilizer is applied early in the rotation period, but the effects on forest floor vegetation have not been studied. The objectives of this thesis were to increase knowledge regarding how 1) intensive fertilization in young forest affects forest floor vegetation; 2) background deposition of N influences the effects of N addition; and 3) to relate observed changes in common species abundances to changes in forest structure. Fertilization decreased the abundance of many common forest plant species while only few species increased (I). Surprisingly, also species known as nitrophilous decreased in abundance. Paper I shows that the decrease in availability of light induced by fertilization is a crucial factor behind this change. Consequently, fertilization reduced both species richness, species diversity and the between site (β) diversity (II). In areas where the background N deposition was low ($4 \text{ kg ha}^{-1} \text{ yr}^{-1}$), the effects of N addition were larger than in areas with intermediate ($16 \text{ kg ha}^{-1} \text{ yr}^{-1}$) deposition (III). Key-stone species among the forest floor vegetation of boreal Sweden (e.g. *Vaccinium myrtillus*) were found to decrease in abundance (IV). These species are strongly dependent on aspects of forest structure, such as forest density and age, and likewise, temporal changes in species abundance coincided with corresponding changes in forest structure (IV). In conclusion, in large parts of Sweden the prevailing forest management is incompatible with a productive forest floor vegetation possessing a high diversity of plant species, and this situation will only be exacerbated by more intensive use of fertilization regimes. To avoid associated cascading effects from the decreased abundance of key-stone species, forestry intensity needs to be relaxed on the landscape level which would likely result in a considerable loss of timber production. Compensation for this loss through intensified forestry on other areas would indicate the need for altered forest zoning.

Keywords: bryophyte, *Deschampsia flexuosa*, eutrophication, forest understory, forest undergrowth, herbaceous layer, lichen, *Picea abies*, vascular plant

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Dedication

To those who are gone, and to those who are still here

An expert is a person who has made all the mistakes that can be made in a very narrow field.

Niels Bohr

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List of Papers

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I. Hedwall, P.-O., Nordin, A., Brunet, J. and Bergh, J. (2010). Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilisation. *Forest Ecology and Management*, 259, pp. 2418-2425.
- II. Hedwall, P.-O., Brunet, J., Nordin, A. and Bergh, J. (2011). Decreased variation of forest understory vegetation is an effect of fertilisation in young stands of *Picea abies*. *Scandinavian Journal of Forest Research*, 26 (S11), pp. 46-55.
- III. Hedwall, P.-O., Nordin, A., Brunet, J., Strengbom, J. and Olsson, B. Does N deposition affect the response of boreal forest floor vegetation to N addition? (submitted manuscript).
- IV. Hedwall, P.-O., Brunet, J., Nordin, A. and Bergh, J. (2012). Changes in the abundance of keystone forest-floor species in response to changes of forest structure. *Journal of Vegetation Science*, published online August 1 2012, [http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1654-1103/earlyview](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1654-1103/earlyview)

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The contribution of Pär-Ola Hedvall to the papers included in this thesis was as follows:

- I Participated in the development of the methodology, conducted the field-work and statistical analyses, and led the writing of the manuscript.
- II Participated in the development of the methodology, conducted the field-work and statistical analyses, and led the writing of the manuscript.
- III Formulated the idea, participated in the field-work, conducted the statistical analyses and led the writing of the manuscript.
- IV Formulated the idea, conducted the statistical analyses and led the writing of the manuscript.

Abbreviations

GAM	Generalized Additive Model
N	Nitrogen
NFI	National Forest Inventory
NMS	Non-Metric Multidimensional Scaling
NPMANOVA	Non-Parametric Multivariate Analysis of Variance
PERMDISP	Permutational test of multivariate dispersion
RDA	Redundancy Analysis
SIMPER	Similarity Percentage

1 Introduction

Large parts of the world's forests are continuously reshaped to produce the goods and services needed by society (Foley et al. 2005). After decades or even centuries during which the planet's growing stock was decreasing by deforestation, growing stocks are now increasing in many parts of the world, including Scandinavia (Anonymous 2009; Rautiainen et al. 2011). The demand from the growing global population and increasing awareness of the potential for replacing fossil fuels with alternatives derived from forest biomass has driven interest in new silvicultural approaches for enhancing forest production (Canadell and Raupach 2008; Malmshheimer et al. 2008).

Swedish forestry is currently heavily reliant on silvicultural practices such as clear-cutting, soil scarification, the planting of coniferous tree species in monocultures and rotation periods that are considerably shorter than the trees' biological life-spans. Clear-cutting of forests with replanting generates stands that are more homogeneous in terms of tree species, age and structure than natural disturbance regimes or the selective cuttings that were practiced in earlier times (Kuuluvainen et al. 2012). Two other factors that had profound effects on forest structure in earlier times are grazing by domestic cattle and forest fires, both of which have become rare (Linder et al. 1997; Linder and Östlund 1998). In conjunction with harvest levels below the increment, this has led to a continuous increase in the growing stock during the last hundred years (Anonymous 2011). In Sweden there is a north-south gradient in forest productivity, with the increment decreasing when moving northwards. This implies that there are differences in canopy closure between the temperate south and the boreal north. While forests in the temperate zone normally develop a full canopy cover, forests in the north remain relatively open even when managed for timber production. Likewise is there a north-south gradient in length of land-use with the longest history of intensive forestry in the south (Angelstam 1997).

Forest fertilization is common in the boreal parts of the country since the 1960s (Lindkvist et al. 2011). Fertilizer is usually applied between once and three times towards the end of the rotation period with about 150 kg N ha⁻¹ at each application. It has been shown recently that wood production can be increased substantially by applying fertilizer at an early point in the rotation period and then applying subsequent treatments of multi-nutrient fertilizer based on foliar analysis (Bergh et al. 1999, 2008; Högberg et al. 2006; Brockley 2010). This implies that rotation periods for coniferous tree species, which normally are between 60 and 120 years depending on site productivity, could be shortened to half (Bergh et al. 2008). This method has not yet been widely adopted in the boreal biome but is presently under consideration in Sweden (Larsson et al. 2009). However, concerns have been raised about the environmental impact of this forest management technique (Gustafsson et al. 2009; Strengbom et al. 2011).

While the management of Swedish forests in recent years has been successful in silvicultural terms, this has been accompanied by a loss of structures that are common in natural forests and are essential for the maintenance of forest biodiversity (Esseen et al. 1997; Linder and Östlund 1998). There has therefore been a growing emphasis on conservation issues and Sweden has adopted a multi-scaled approach to the conservation of biodiversity. Selected measures are applied on a variety of levels, from trees to landscapes, and should be included in the management of all stands (Gustafsson and Perhans 2010). In terms of practical forestry, this has resulted in the creation of coarse woody debris and green tree retention as well as the protection of key woodland habitats. Sweden currently has >2 000 red-listed species that rely on forest or tree habitats (Gärdenfors et al. 2010), and efforts aimed at conserving biodiversity within Swedish forests have focused heavily on these rare and red-listed species. Consequently, the role of common species in ecosystem functions is less well understood.

Forest floor vegetation is an important constituent of forest biodiversity (Gilliam 2007), and plays an important role in the carbon- and nutrient cycles (Nilsson and Wardle 2005; Kolari et al. 2006). A relatively limited number of abundant forest floor species account for a considerable fraction of the forest's total photosynthetic production and can be regarded as keystone species, i.e. species whose presence is important for many other species as well as for ecosystem processes.

Two of the most abundant plant species in Eurasian boreal forests are the ericoid dwarf-shrubs *Vaccinium myrtillus* L. (bilberry) and *V. vitis-idaea* L. (cowberry). *Vaccinium myrtillus*, in particular, can dominate the vegetation and can be considered as a keystone species due to its influence on the population

dynamics of bank voles (*Myodes glareolus*), the capercaillie (*Tetrao urogallus*) and moose (*Alces alces*) (Selås 2001; Selås et al. 2011). Processes such as eutrophication due to the deposition of anthropogenic nitrogen (Nordin et al. 2005, 2006) and forestry practices such as clear-cutting of the forest (Atlegrim and Sjöberg 1996; Hannerz and Hånell 1997; Bergstedt et al. 2008) and forest fertilization (Mäkipää 1994; Olsson and Kellner 2006; Strengbom and Nordin 2008, 2012) have been demonstrated to have negative effects on *V. myrtillus*. Another species with similar site requirements to those of *V. myrtillus* is *Deschampsia flexuosa* (L.) Trin. (wavy hair-grass) (Ellenberg et al. 2001; Grime et al. 2007), a common species that benefits from increased nitrogen availability (Nordin et al. 2009) and flourishes on clear-cuts and in young open forests (Hannerz and Hånell 1997; Bergstedt and Milberg 2001; Bergstedt et al. 2008).

The retention of dead wood and green trees in managed forests has been shown to be beneficial to many species (e.g. Rosenvald and Löhmus 2008). However, one might reasonably expect that the retention of single trees would be less helpful to species from the forest floor vegetation that are negatively affected by clear-cutting and scarification (Rosenvald and Löhmus 2008). Additionally, little is known about the extent to which retaining trees in groups or forest patches has a positive long-term effect on forest floor species (however, see Halpern et al. 2005). In addition, it would be expected that there would be non-linear relationships between the abundances of species on different trophic levels (e.g. species-habitat interactions) and that these relationships would exhibit threshold patterns (Fahrig 2003). Although forest patch retention might be sufficient to conserve late successional species *in situ*, these patches may not be sufficiently large to avoid cascade effects resulting from reduced population sizes on the stand- and landscape levels.

An important way to determine the long-term effects of changes in forest management or retention measures on species abundance is to analyse survey data covering sufficiently long periods of time. To date, there have been relatively few such studies conducted in Sweden (see, however Odell and Ståhl 1998; Anonymous 2011) and none that have dealt with the causality of the observed changes in detail.

1.1 Objectives

1.1.1 Paper I & II

The objectives of paper I and II were to increase our knowledge about the impacts of intensive fertilization on forest floor vegetation in young *Picea abies* (L.) H. Karst. stands. Although a substantial amount of work had been

done on the effects of fertilization, few studies have examined fertilization regimes in which nutrients are applied early in the rotation period. The basic idea was to apply fertilization in young forests where competition for light from the tree layer would initially be low but would increase over time due to the tree growth promoted by the fertilizer. I therefore expected to obtain different results from those achieved under conventional fertilization regimes, in which nutrients are typically applied late in the rotation period.

1.1.2 Paper III

It has been reported that in some cases, the addition of N has no clear effect on forest floor vegetation (Verheyen et al. 2012). This was attributed to confounding factors and two hypotheses have been proposed to explain these findings: 1) that N effects are constrained by competition from the tree layer (Verheyen et al. 2012), and 2) that N effects are confounded by background N deposition (Hurd et al. 1998; Gilliam 2006; Gilliam et al. 2006). In paper III I tested the second of these hypotheses. To avoid interference due to competition from the tree layer, these investigations were conducted on plots that were being used for N addition experiments and in which the forest had been harvested prior to vegetation analysis.

1.1.3 Paper IV

Many stand-scale studies have shown that common forestry practices can have a considerable impact on forest floor vegetation. However, there have been very few investigations into the effects of common forest management techniques on the resulting large-scale trends in species abundance in the Swedish forest. Additionally, there is a lack of information on the relationship between forest structure and species abundance. To address these issues, the investigations described in paper IV were conducted in order to: 1) identify current changes in forest structure and in the abundance of common forest floor species, and 2) model the relationships between forest floor species and forest structure.

2 Materials and Methods

This section provides a brief overview of the methodology used in each paper of this thesis. For more detailed information on the methods used, see the corresponding papers.

2.1 Papers I & II

2.1.1 Experimental setup

Papers I and II are based on a series of experiments that were originally set up to investigate the effects of different fertilization intervals on wood production in young *P. abies* forests. The fertilization experiments began in 2002 in what were then 11-19 year old forests located at five sites distributed over the southern half of Sweden (Figure 1). A mixture of nutrients including N, P, K, Ca, Mg, S, Mn, Zn, B and Cu was applied every year, every second year or every third year in 40*40 or 50*50 m plots. The plots were laid out according to a complete randomized block design with three blocks at each site.

2.1.2 Vegetation analysis

Forest floor vegetation was analyzed in 2008, in 20 systematically distributed 1*1 m squares per plot. The presence/absence of all species was recorded, along with cover estimates for the species *D. flexuosa*, *V. myrtillus* and *V. vitis-idaea*. In addition, the aggregate coverage of all vascular plants with a potential height of less than 0.7 m (corresponding to the field-layer) and of all epigeous bryophytes and lichens (bottom-layer) was recorded. The mean cover and relative frequency ($n/20$) was calculated for each species on the plot level for use in further analyses.

2.2 Paper III

Data on forest floor vegetation from N addition experiments conducted during previously published studies were analyzed together with data from experiments inventoried in 2009 as a part of this study. These experiments were conducted at sites that were located along a gradient of N deposition in Sweden ranging from 4 to 16 kg N ha⁻¹ yr⁻¹ (Figure 1) and the forests in all of the experimental plots had been clear-cut prior to the analyses. Due to different inventory methods used in the various experiments, each experimental dataset was standardized before performing any statistical analyses.

2.3 Paper IV

Data from the Swedish National Forest Inventory (NFI) collected between 1994 and 2010 were analyzed to identify trends in forest floor species cover and variables relating to forest structure such as the density and age of the forest. In addition, NFI data on species abundance collected between 2000 and 2009 were used in conjunction with data on tree species, forest densities and site conditions to model species-environment relationships.

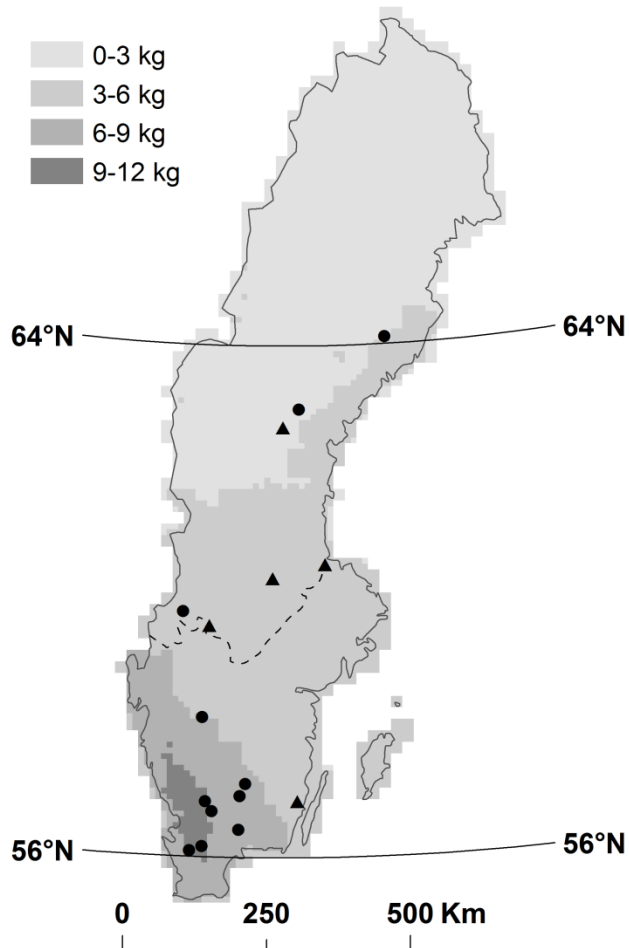


Figure 1. Map of Sweden showing the N deposition gradient and locations of experimental sites for papers I and II (triangles) and paper III (circles). Deposition is shown in terms of the average yearly (1995-2005) wet deposition of NH_x and NO_x in kg ha^{-1} . The dashed line represents the border between the boreal (north) and temperate (south) zones used in the analyses in paper IV.

3 Results

3.1 Paper I & II

Fertilization induced significant changes in the composition and abundance of the forest floor vegetation. Most of the investigated species declined, with especially large negative effects being observed for common forest bryophytes such as the epigeous feathermosses *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt., and the dwarf-shrubs *V. myrtillus* and *V. vitis-idaea*. Unexpectedly, decreases were also observed for *D. flexuosa*. However, this latter decrease was only statistically significant in terms of the number of times this species occurred. Only a few species increased in abundance following fertilization. The most pronounced increases were observed for the herb *Oxalis acetosella* L. and bryophytes from the genera *Brachythecium* and *Plagiothecium*. A test of the species composition of the community (NPMANOVA) revealed significant differences between the control plots and the most intensively fertilized plots. Multiple statistical analyses of the data were conducted, including an RDA ordination using Ellenberg's indicator values as supplementary explanatory variables, Spearman's correlation analysis, and a test of mean indicator values within treatments. All of these tests indicated that the decrease in light availability due to fertilization was the most important factor in driving the observed changes in species composition/abundance. However, this did not hold for the total cover of the bottom layer, which decreased strongly following the application of fertilizer but was insensitive to increases in the density of the forest. The species richness, Shannon's diversity index and the multivariate variance were significantly lower in the most intensively fertilized plots than in the control plots. Similarly, both an NMS ordination and a PERMDISP test showed a larger variance within the control sample than within the fertilized samples. This indicates that despite the considerable initial between-site variation due to

the sites' distribution across the country, fertilization increased the homogeneity of the vegetation.

3.2 Paper III

N deposition had a confounding effect on the vegetation response to N addition. The higher the N deposition, the smaller was the effect of fertilization on the composition of the forest floor vegetation. Additionally, interactions between N addition and deposition were observed for four individual species or groups of species: *Brachythecium* spp., *D. flexuosa*, *H. splendens* and *V. myrtillus*. While the effects of N addition on *H. splendens* increased with increasing N deposition, they became less pronounced with increasing N deposition for the remaining three species. The amount of time that had passed since the last major disturbance (clear-cutting) had a significant effect on the relationship between N addition and the cover for *D. flexuosa* and *H. splendens* and for the total coverage of the bottom layer. In the case of *D. flexuosa*, longer undisturbed periods increased the strength of the relationship between cover and N deposition whereas the opposite was true for *H. splendens* and total bottom layer cover.

3.3 Paper IV

Analyses of the NFI time-series revealed significant negative trends over time for narrow-leaved grasses (mainly *D. flexuosa*, in paper IV the synonym *Avenella flexuosa* (L.) Drejer was used), total cover of vascular plants, *V. myrtillus*, and forest age. Positive trends were observed for the number of tree stems per hectare, the volume of broadleaved tree species, the volume of pine species and the total volume of all tree species. There was no significant trend for the volume of *P. abies*. There were significant interactions between time and geographical region for total cover of vascular plants, *V. myrtillus*, the age of the forest and the number of stems per hectare. In all cases the trends were stronger in the northern parts of the country. The models (GAMs) of the relationship between the forest floor vegetation components mentioned above (plus *V. vitis-idaea*) and forest structure explained between 25 and 45 % of the species/species group abundances. While *P. abies* volume was the most important factor in determining the overall extent of forest floor vegetation cover, site productivity (measured in terms of the site index) was the most important explanatory variable for narrow-leaved grasses, *V. myrtillus* and *V. vitis-idaea*. The relationship between site index and species abundance was unimodal for all species and species groups studied, with optimum abundances

at increasing site indices in the following order: *V. vitis-idaea* < *V. myrtillus* < narrow-leaved grasses. There were negative correlations between the abundance of all species/species groups and both tree volume and stem density. Narrow-leaved grasses were negatively associated with forest age: their abundance decreased steeply during the first 50 years of the forest's rotation period. Conversely, the abundance of *V. myrtillus* increased up to a forest age of about 80-100 years.

4 Discussion

4.1 Scientific contribution and implications for policy

Although the effects of nutrient addition on forest ecosystems in general and especially on forest floor vegetation had been studied extensively prior to the present work, few studies had focused exclusively on the application of fertilizer in young stands. The results reported in papers I and II show that the effects of nutrient addition in early successional phases differ significantly from those observed in later phases due to the strong effect of fertilization on the light regime in the stand. This implies that going from conventional to intensive fertilization does not simply increase the magnitude of established effects on vegetation.

It has been proposed that previous failures to observe effects on forest floor vegetation following N addition in fertilization experiments were due to elevated N availability stemming from background deposition. Paper III shows that there is a clear relationship between the magnitude of the change in vegetation cover induced by N addition and N deposition, with the most pronounced effects being observed in areas with low deposition. These results imply that background deposition must be considered when evaluating the results of N addition experiments. An understanding of the interactions between anthropogenic N deposition and forest fertilization is essential for the development of efficient policies for increasing forest productivity and conservation of forest floor vegetation. Today's governmental policies for forest fertilization in Sweden prohibit fertilization in areas with high deposition while the largest fertilizer doses are allowed for in parts where the deposition is low. Paper III shows that adding N to forests that already experience enhanced N deposition has only modest effects on the forest floor vegetation. On the other hand are there indications that the long-term effects of N addition on

forest ecosystems with low ambient deposition can be substantial (Strengbom et al. 2001).

Although many studies have shown experimentally that forest management affects forest floor vegetation in numerous ways, little work has been done to date on long-term trends in vegetation composition on a large geographical scale. Paper IV shows that the abundance of important keystone species in the forest floor vegetation has decreased in boreal Sweden. This paper also provides a detailed model of the dynamic relationship between the abundance of the forest floor vegetation and forest structural parameters such as tree age and forest density. The negative relationship between forest density and the abundance of forest floor vegetation established here implies that there is a considerable trade-off between high timber yields and the conservation of forest floor vegetation.

4.2 Temporal development of forest floor vegetation under different management regimes – a conceptual model

The narrow-leaved grass *D. flexuosa* (Df) and the ericoid dwarf-shrub *V. myrtillus* (Vm) are similar in their site requirements (Ellenberg et al. 2001; Grime et al. 2007) and the competitive balance between these species is mediated by disturbance (e.g. Strengbom et al. 2004). The results presented in paper IV showed that Df is most abundant in young forests while Vm is most abundant in old forests. This overall pattern has been reported in previous stand-scale studies, where Df abundance was shown to increase following disturbances such as tree harvesting (Hannerz and Hånell 1997; Bergstedt and Milberg 2001; Bergstedt et al. 2008), which caused Vm abundance to decrease (Atleglim and Sjöberg 1996; Hannerz and Hånell 1997; Bergstedt et al. 2008). Based on these results, a conceptual model of the dynamics of these two key species during a rotation period in a *P. abies* forest of intermediate site productivity was developed (Figure 2).

After a decline in abundance associated with clear-cutting of the forest, Vm abundance increases with forest age before reaching a plateau at approximately 80-100 years (Kardell 1980; paper IV). Conversely, Df abundance declines rapidly with increasing forest age, reaching a minimum at 40-50 years. Small-scale disturbances such as windfall and thinning can disrupt negative trends in undergrowth abundance (Hart and Chen 2006). However, standard forest management practices aim to minimize the incidence of small-scale natural disturbances such as windfall and those caused by pests while also maintaining a low thinning intensity to maximize wood production. My model assumes that small-scale disturbances and thinnings are insufficient to restore the abundance

of Df and that its growth is restrained by the increased competition from Vm. When the forest is clear-cut, the cycle is reset and starts again (Figure 2).

Typical forest fertilization regimes in Fennoscandian forestry involve one or two applications of fertilizer (150 kg N ha^{-1}) towards the end of the rotation period. The effects of this fertilization on the forest floor vegetation have been shown to depend on site productivity (Gerhardt and Kellner 1986; Kellner 1993; Mäkipää 1994). On mesic sites, such fertilization is expected to increase Df abundance and to cause a corresponding decrease in Vm abundance. The effects on both species are assumed to be relatively small and reversible, which is consistent with the findings of Strengbom and Nordin (2012), although some authors have reported more persistent effects of N fertilization (Quist et al. 1999; Olsson and Kellner 2006). In the latter two studies, however, the amount of N added was greater than that usually applied in practical forestry. Strengbom and Nordin (2012) showed that although it is not possible to detect any residual effects of fertilization in the mature forest, an interaction with the disturbance induced by clear-cutting of the forest should be expected. In principle, this should change the vegetational composition of the forest floor, increasing the abundance of nitrophilous species (Figure 2). It remains to be determined whether or not this change in vegetation will persist.

Under management regimes involving intensive fertilization at an early stage in the rotation period, fertilizer is first applied when the forest is still relatively open and the effects of the preceding clear-cutting are still clearly visible. In other words, fertilization starts when the abundance of Df is at its greatest and that of Vm is at a minimum during the rotation period (paper IV). Df abundance can potentially increase in the immediate aftermath of the first fertilization due to the increased availability of nutrients and minimal light restrictions. Soon, however, the Df abundance decreases as an effect of increasing competition from the tree layer (paper I). Simultaneously, the abundance of Vm decreases (Figure 2). The subsequent development of the forest floor vegetation in these stands will depend heavily on whether the forest is thinned or not. However, it is most likely that stands treated with this fertilization regime will be subjected to short rotations without thinning. In such cases, a recovery of the vegetation is unlikely (Hedwall, unpublished data). When the forest is clear-cut after a rotation period approximately half of that used in conventional forestry, interactions between the previous fertilization and the more recent disturbance would be expected. The magnitudes of these interactions would be (at the very least) comparable to those observed under conventional fertilization.

Very little work has been done on legacy effects of former forest management practices on boreal forest floor vegetation (see however Halpern

and Franklin 1990). Both Df and Vm are gregarious and undergo rapid and efficient vegetative regeneration; seedlings of Vm are rare in undisturbed conditions (Grime et al. 2007). It can be assumed that the increased performance of Df after the clear-cutting of fertilized forest could further inhibit the growth of Vm and that these effects may be cumulative over forest generations.

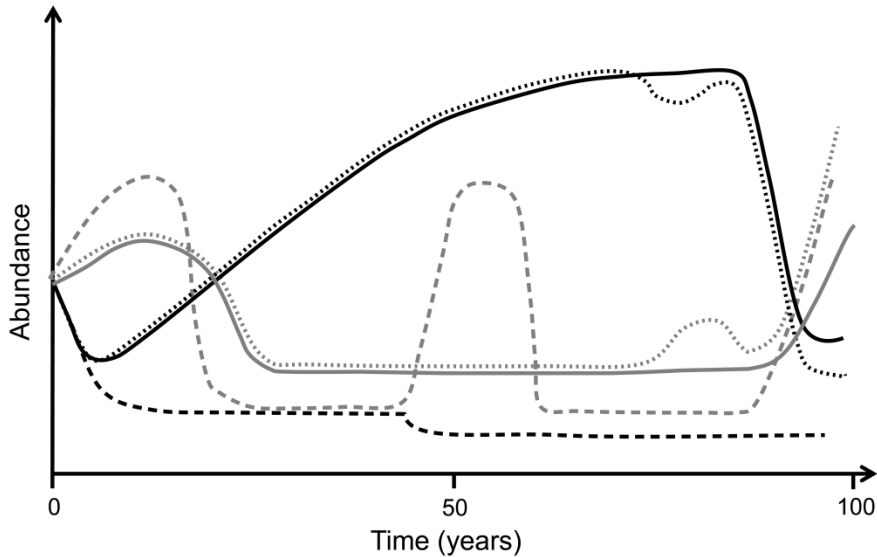


Figure 2. Conceptual model for the growth of *Dechampsia flexuosa* (grey lines) and *Vaccinium myrtillus* (black lines) over 100 years in a *Picea abies* forest of intermediate site productivity with low deposition of anthropogenic N. Three scenarios are compared: 1) conventional forest management with a rotation period of 90 years (solid lines), 2) intensive fertilization starting early in the rotation period (yr 15) with the final harvesting of the forest occurring at 45 years age (dashed lines), and 3) extensive fertilization with one application of fertilizer late in the rotation period (yr 80) and final harvest at 90 years (dotted lines).

4.3 Mechanisms behind N-induced changes in vegetation – implications of N deposition and tree canopy response

In Sweden there is a gradient of N-deposition ranging from about $15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (wet + dry deposition) in the southwest to near-ambient levels in the north (paper III; Akselsson et al. 2010; Pihl-Karlsson et al. 2011). The model for the abundance dynamics of Df and Vm shown in Figure 2 is dependent on the assumption of low ambient deposition of anthropogenic N. In areas with high deposition, the frequency and abundance of Vm is lower while Df is more abundant (paper IV; Odell and Ståhl 1998; Strengbom et al. 2003). However,

this pattern was not observed for Df in the latter of the three studies cited above, presumably because only forests with relatively high levels of canopy cover were considered. Paper III shows that adding N to forests that are already subject to high levels of deposition will cause only small changes in the composition of the forest floor vegetation. It is thus essential to consider the level of background deposition in any general model aiming to describe the impact of N addition on vegetation. Gilliam (2006) identified six mechanisms that may be responsible for N-induced changes in forest floor vegetation. The conceptual model presented in Figure 3 includes five of these, excluding exotic earthworm activity.

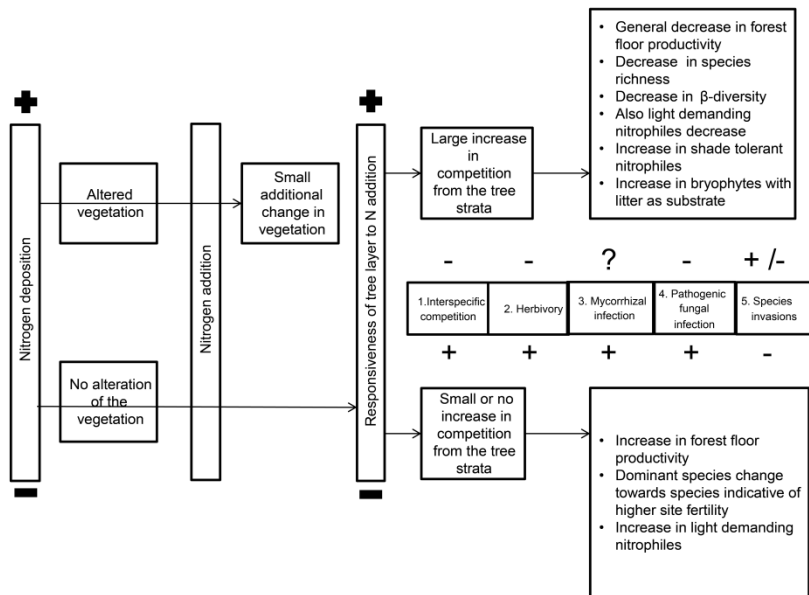


Figure 3. Conceptual model of the interacting effects of N deposition, N addition and N-induced closure of the tree layer on the forest floor vegetation and mechanisms of change. The mechanisms of change (1-5) were taken from Gilliam (2006). The model initially describes the development of the forest floor vegetation under two scenarios involving N addition in low or high deposition environments. It goes on to show the different effects of N addition on the vegetation depending on the N response of the tree strata. Additionally it includes the hypothesis that the relative importance of the different mechanisms changes depending on the responsiveness of the tree strata.

Competition from the tree strata is commonly acknowledged as a major factor controlling the productivity and composition of the forest floor vegetation. This has been attributed to the effects of aboveground competition for light and

belowground competition for nutrients and water. The relative importance of these two factors has been shown to depend on site-specific characteristics such as nutrient and water availability (Coomes and Grubb 2000), with aboveground competition for light becoming more important with increasing soil resource availability. In this work, both factors were pooled under a general term to describe competition from the tree layer, although their relative significance may also depend on artificial productivity gradients. As the competition from the tree layer increases, the importance of other factors may change. There is considerable spatial and temporal variation in the availability of light on the forest floor. As a young forest grows, the canopy closes and light availability decreases. Light heterogeneity increases initially and peaks at intermediate canopy cover levels (Martens et al. 2000). As mentioned above, fertilizer is generally applied only to mature forests under typical Swedish forest fertilization regimes. As such, it does not usually cause a substantial increase in canopy cover or tree growth and the effects of fertilization on canopy cover have seldom been an issue. However, when young forests are treated with multi-nutrient fertilizers, the drastic increase in canopy cover and decline in light availability has important effects on the composition and abundance of the vegetation (paper I; Thomas et al. 1999). Similarly, Verheyen et al. (2012) hypothesized that high tree canopy cover can confound the effects of nitrogen deposition. The effects of N addition on within-strata competition might be expected to become less important as competition from the tree layer increases (Figure 3). However, due to the initial patchiness of light reaching the forest floor after the fertilizer treatment, this relaxing effect may be spatially heterogeneous.

The boreal flora in general is N-limited (Tamm 1991), and so are its herbivores (Gurevitch et al. 2006). Plants in N-enriched environments often have a surplus uptake of N that results in elevated N contents if the increased uptake is not matched by increased growth (paper I; Aber et al. 1989). N enrichment increases palatability and nutritional value for a large variety of herbivores (e.g. Ball et al. 2000; Nordin et al. 2009). Simultaneously, carbon-based chemical defense mechanisms are retarded by increased N availability (Witzell and Shevtsova 2004). Selective foraging by herbivores can shape plant communities (Huntly 1991) and there is some evidence that herbivory can mediate N-induced changes in the composition of forest floor vegetation (Brunsting and Heil 1985; Hartley and Mitchell 2005; Strengbom et al. 2005). Moreover, pathogenic fungi also respond positively to increased N levels in plant tissue and reduced concentrations of defense compounds (e.g. Witzell and Shevtsova 2004). There are interactions between herbivores and pathogenic fungi since each can adversely affect the other's habitat (Nordin et

al. 2009). It is not currently known whether the influence of these factors is affected by N induced increases in forest density. One might speculate that the changes in micro-climate arising from increasing canopy cover would affect the relative importance of organisms such as thermophilic herbivores and hydrophilic fungi. To date, all of the studies that have examined the effects of pathogens on the competitive balance between species in the forest floor vegetation following N enrichment have focused on plant communities where the perceptible species is dominant and a potentially strong competitor is present (e.g. *Vaccinium/Deschampsia*, *Calluna/Molinia*). It is likely that if this balance has already been shifted by factors such as increased competition from the tree layer, the relative importance of herbivory and pathogens would decrease (Figure 3).

Invasive species can potentially affect the abundance of native species (Vilà and Weiner 2004) and influence nutrient cycles (Ehrenfeld 2003). It has been suggested that low resource environments best preserve native vegetation against invasive alien plant species (Daehler 2003). Cassidy et al. (2004) found that nitrogen availability was the most important factor regulating the success of an invasive shrub. While Daehler (2003) also suggested that low light availability presented a hindrance to invasive species, Windham (2002) proposed that nitrate deposition creates a low light/high nutrient environment that is favorable to invasive herbs. The addition of N in forests with a reactive (+) tree layer generally creates two windows of opportunity for invasive plant species depending on their species-specific light requirements. First, when the forest density increases, the productivity and abundance of the forest floor vegetation decreases which increases the scope for a low light/high N plant to become established (Figure 3). However, the number of potential invasive species for a fertilized young *P. abies* forest is probably very low due to the strong tendency of this tree species to rapidly reduce forest floor light availability (Johansson 1987; Vandekerckhove and Hermy 2004). Secondly, natural or anthropogenic disturbances in forests with low abundances of native vegetation may facilitate the establishment of light-demanding nitrophilous species (Figure 3). The establishment of invasive species could in turn disturb the succession of forest floor species that would have taken place otherwise.

N-induced competition from the tree layer reduces the positive impact of N addition on forest floor productivity. Substantial decreases in light availability also limit the potential number of species on the forest floor and thus reduce both α - and β -diversity (paper II). The relationship between species diversity and productivity is commonly described as being unimodal, with the highest number of species occurring at intermediate productivity (e.g. Huston 1999, see however: Gross et al. 2000; Pärtel et al 2007; Oberle et al. 2009). The

inconsistency in the relationship between species richness and forest fertilization described in paper II could be due to similar patterns along artificial productivity gradients. However, one might expect the pattern of species richness along a common gradient of increasing productivity and decreasing light availability to differ substantially from one where the influence on the light regime is less pronounced (Figure 3).

4.4 Intensified forestry – implications for the conservation of forest floor vegetation

Plantation forest has been defined by the FAO (Anonymous 2006) as artificially regenerated forest mainly with introduced species, although indigenous species may occur. Additionally, plantation forests are even-aged and contain few species. Although the latter two criteria apply to a considerable share of the Swedish forest, only a small fraction of the Swedish forest is classified as plantations (due to the use of non-native tree species) while the majority is categorized as semi-natural (Anonymous 2006). However, as forestry becomes intensified, the discussion about plantation forestry versus conservation may become increasingly relevant in Sweden. Brockerhoff et al. (2008) highlighted some key questions that should be considered when deciding whether plantation forestry has a positive or negative impact on biodiversity. These questions will be used as a framework for the continued discussion about the impact of intensive forestry on forest floor vegetation (Box 1). However, questions three and five might be more relevant when discussing afforestation measures and where species colonization is to be expected (Brunet 2007), so the following discussion focuses on the other three questions.

Box 1.

Key questions in determining the impact of plantation forestry on biodiversity conservation

1. Whether plantation forestry leads to reduced harvesting and thus improved protection of natural forests, and at what scale,
2. What was the land use or vegetation that preceded the establishment of plantation forest, and how well can the plantation forest provide substitute habitat for species of the former natural land cover (and thus what the appropriate comparison is),
3. How much time has passed since plantation establishment and thus, for example, how long have local species been able to colonise and adapt to the new habitat,
4. Whether the planted area is being managed with conservation goals in mind, whether remnant areas of natural habitat are being protected, and whether conservation goals across the wider landscape are being considered,
5. How plantation forestry compares relative to other alternative land uses that are likely to be practised on a particular piece of land.

From Brockerhoff et al. 2008

To avoid negative effects on forest biodiversity stemming from intensified forestry, it is necessary to increase the number and scale of conservation activities in other areas (Brockerhoff et al. 2008, question 1; Côté et al. 2010;

Strengbom et al. 2011). However, large forest owners and forest owners' associations object to this assertion (Lindkvist et al. 2011). Whether or not any such measures will actually be implemented is a question for policy, as pointed out by Marland and Obersteiner (2008). As such there is a need for governance, which is largely lacking at present concerning this specific issue (Larsson et al. 2009). When estimating the potential gain in biomass production from intensive forestry, it is necessary to bear in mind that there will be some losses in timber production due to the need for more extensive efforts to maintain biodiversity elsewhere. Little work has been done to date on the biological and economic effects of so-called forest zoning in Sweden (see however, Carlsson et al. 1998; Thorell and Götmark 2005; Ranius and Roberge 2011). There is some evidence from Canada to suggest that dividing forest landscapes into separate areas with different management objectives and levels of management intensity can be beneficial for both conservation and forestry (Côté et al. 2010). However, as pointed out by Strengbom et al. (2011), the proportion of the Canadian forest that has been reserved for conservation is far greater than that in Sweden. Additionally, most of the forest in Sweden, in opposite to Canada, is owned by private industrial and non-industrial owners. Thus it remains important to study the effects of this type of landscape management under Swedish conditions. Due to the rapid effects of fertilization on forest production, large industrial owners often chose to realize the expected increase in growth immediately by raising the harvested volume of wood (Thuresson 2002). Since most of the wood harvested in Swedish forestry comes from final cuttings, this could cause changes in the forest's age structure, decreasing the rotation periods of both the fertilized stands and also the age of the forest in the surrounding matrix.

The land-use preceding plantation establishment is to a large extent deciding the effects of plantation forestry on biodiversity (Brockerhoff et al. 2008, question 2). Forestry in Sweden primarily deals with indigenous conifers: *P. abies* and *Pinus sylvestris* L. together comprise almost 80 % of the standing stock (Anonymous 2011). The reference areas in papers I and II are forests managed in a conventional way with the same species mixture as in the fertilized areas. This indicates that there is no large shift in land-use when forestry is intensified. However, intensive fertilization can double the productivity of the forest (Bergh et al. 1999, 2008). This suggests that the habitat conditions of the forest will change considerably even though there is no great change in land-use patterns or the identity of the main tree species present.

In Sweden there is a north-south gradient in land-use history, with the southern regions having the longest history of human influence (Angelstam

1997). A large proportion of the coniferous forests in southern Sweden were established on former pastures and arable land or on forest land that was previously dominated by broadleaved tree species. Consequently, a huge land-use induced transformation has taken place in southern Sweden during the last centuries, resulting in the dominance of *P. abies* (Björse and Bradshaw 1998; Lindbladh and Bradshaw 1998). Forest land that has been continuously covered by forests might be expected to host a larger number of forest species than seemingly similar first generation forests established on former arable land (Hermy and Verheyen 2007). Consequently, the effects of forestry intensification in the south may be dependent on land-use history. A large number of the threatened species in southern Sweden are associated with broadleaved tree species (Berg et al. 1994) and the negative effects may be reduced by restraining forestry operations to present coniferous forests. Conversely, most secondary forests in northern Sweden were established on former forestlands that were occupied by the same species that constitute the current primary forest. Therefore, the conventional system for managing coniferous forests will have different effects on the forest floor vegetation in the northern parts than in the south. Forests of *P. abies* established on fertile soils in southern Sweden will normally develop very limited field-layer vegetation due to low light availability at the forest floor (paper IV). On the other hand, managed *P. abies* forests in the north normally have more abundant forest floor vegetation resembling that found in natural forests, at least in terms of the total abundance and composition of common species. Additionally, paper III shows that the effects of fertilization on forest floor vegetation are confounded by N deposition and that N addition will have only small additional effects in areas with high background deposition. This implies that the implementation of intensive fertilization may have different effects in different regions. The direct effects on the stand-level will be larger in the north, while the effects on the landscape-level maybe smaller due to the generally higher abundances of species such as dwarf-shrubs (paper IV). While the effects on the stand-level in the south may be smaller, additive landscape-level effects can still present a risk of biodiversity loss due to the intensive management of the southern forests.

The decreasing age of forests under current forest management regimes implies problems for common late successional species (paper IV). There is also evidence that several rare, late successional species have decreased dramatically in the southern Swedish coniferous forest, including *Chimaphila umbellata* (L.) W. P. C. Barton, *Goodyera repens* (L.) R. Br., *Linnaea borealis* L., *Listera cordata* (L.) Rich., *Lycopodium clavatum* L. and *Pyrola chlorantha* Sw. (Tyler et al. 2007). Active conservation measures integrated in forestry

operations has the potential to considerably reduce the negative effects of forestry on biodiversity (Brockerhoff et al. 2008, question 4; Gustafsson and Perhans 2010). A possible conservation measure to improve the conditions for the above mentioned species would be to increase the forest age. However, in terms of forestry, one of the advantages of intensified management is that the length of the rotation periods can be decreased considerably. To maintain late successional habitat, many conservation efforts focus on the retention of single or small groups of living and dead trees. However, this is probably relatively unimportant for ground vegetation (Rosenvald and Löhmus 2008). Forest edges where the forest borders areas with other land-use types and between forest stands may serve as habitat for light-demanding generalist forest species. On the other hand also negative edge effects on late successional forest specialist species may occur. It is likely that maintaining larger areas of vegetation intact, with a relatively high number of remaining trees and low degree of soil disturbance (e.g. soil scarification, covering with logging residues), might be more important for maintaining the diversity and resilience of the vegetation (Halpern et al. 2005). This implies that *in situ* conservation measures may be insufficient for forest floor vegetation unless they are combined with practices that also result in a sufficient amount of old forest on the landscape level and reduce the competition from the tree layer during all stand phases.

Thinning is a standard procedure in Swedish forestry that is performed to promote the growth of the remaining trees and generate income from the forest. However, thinning for production does not generally reduce the competition from the trees to an extent that would be expected to positively affect the abundance of forest floor vegetation (paper IV; Bergstedt and Milberg 2001), but positive effects on species richness have been reported (Widenfalk and Weslien 2009). Although thinnings are performed frequently in Swedish forests, forest density has been increasing continuously with concomitant decreases in the abundance of many forest floor species (paper IV; Odell and Ståhl 1998; Anonymous 2011). A similar trend has been observed in Finland (Reinkainen et al. 2000). Despite the positive effects listed above, thinnings do reduce the total wood production in the stand (Nilsson et al. 2010). Performing more extensive thinnings to promote forest floor vegetation would probably further reduce wood production. The two main measures that have been proposed in paper IV for conserving forest floor vegetation are thinning and increasing the forest's age, both of which conflict with the goal of maximizing production. This incompatibility may be impossible to resolve on the stand-level, requiring solutions that can be implemented on the landscape and regional levels instead. That is, conservation of forest floor vegetation and

associated species requires less intensive forestry on an area large enough to avoid cascade effects. Whether or not this can be compensated for economically by intensified forestry on other areas (forest zoning) is a matter for further investigation.

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