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Decomposition of Beech and Spruce Litter in Neighbouring Beech and Spruce Forests

Ingrid Kleppenes Verne
Master of Science in Ecology

« We cannot hope to either understand or to manage the carbon in the atmosphere unless we understand and manage the trees and the soil too »

Freeman Dyson (1992)

Preface

This thesis is a part of my Master's degree in Ecology at the Norwegian University of Life Sciences, and is written as a part of the project "From spruce to beech forests – fundamental ecosystem transformation driven by climate change", managed by Line Nybakken. The aim of the project is to advance the understanding climate change induced forest transformation.

The thesis could not have been written without the help and support from several people. First, I am greatly thankful to my supervisor Professor Mikael Ohlson, Doctor Johan Asplund and Professor Line Nybakken, Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU). Thank you for letting me be a part of the project and for all your help with study design, field work, laboratory work, statistical analyses, and valuable input during the writing process.

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Ingrid Kleppenes Verne

Abstract

Climate change is expected to cause a transformation from spruce to beech dominated forests in a large part of southeast Norway. A shift in dominating tree species may have a large effect on the factors controlling the rate of litter decomposition, and consequently the rate of greenhouse gas induced climate change. To better understand how this transformation will influence the carbon balance in these forest ecosystems, we need to understand the factors controlling decomposition. A litter bag experiment was conducted in neighbouring beech and spruce forests in southeast Norway. Litter bags with beech and spruce litter was placed in manipulated litter layer plots in the two forest types. This was done to investigate the relative importance of litter type, forest type, the litter layer, and their interactions as determinants of litter decomposition rate. The litter layer manipulations were: transplanted beech litter, transplanted spruce litter, and removal of litter. Un-manipulated plots served as control. After incubation, litter mass loss and nitrogen release as a function of mass were calculated.

The interaction between litter type and forest type had a significant effect on mass loss. In the spruce forest, spruce litter lost significantly more mass than beech litter, but there were no significant differences between the two litter types when placed in the beech forest. Litter layer transplantations also had significant effects. More mass was lost when litter was placed in the transplanted beech compared to the transplanted spruce and removal plots. Individually, neither the litter type nor the forest type had significant effects on mass loss. This indicates that litter type in the litter layer is more determining for the decomposition rate than forest type. Higher mass loss in plots with beech compared to spruce in the litter layer indicates that a transformation from spruce to beech forests will likely lead to a faster decomposition rate. This may especially be true in the transitional phase when the forests are mixed. The implication of a transformation from spruce to beech dominated forests may thus be a faster release of CO₂ to the atmosphere, contributing to increased global warming.

Keywords: litter decomposition, litter layer manipulation, forest transformation, boreal and temperate forests, litter bag technique, climate change

Sammendrag

Det antas at klimaendringene vil føre til et skifte fra gran- til bøkedominerte skoger i store deler av sørøst-Norge. Et skifte i dominerende treslag kan ha stor innvirkning på faktorene som kontrollerer hastigheten til strønedbrytningen, og dermed hastigheten til fremtidige klimaendringer. For å øke forståelsen av hvordan et slikt skifte vil påvirke karbonbalansen i disse økosystemene, må vi øke kunnskapen om faktorene som kontrollerer nedbrytningshastigheten. Et strøposeeksperiment ble utført i en gran- og en bøkeskog som grenser til hverandre i sørøst-Norge. Strøposer med bøkeløv og grannåler ble plassert i ruter med manipulert strølag i de to skogtypene. Dette ble gjort for å undersøke den relative viktigheten av strøtype, skogtype og strølaget, samt deres interaksjoner som bestemmende for nedbrytningshastigheten. Manipulasjonene i strølaget var: transplantert bøk, transplantert gran og fjerning av strø. Umanipulerte ruter fungerte som kontroll. Tap av masse fra strøet og frigjøring av nitrogen som en funksjon av masse ble beregnet.

Interaksjonen mellom strøtype og skogtype hadde en signifikant effekt på tap av masse. I granskogen var det et signifikant større tap av masse fra granstrøet enn fra bøkestrøet, men det var ingen signifikant forskjell mellom de to strøtypene i bøkeskogen. Strølagstransplantasjon hadde også en signifikant effekt. Mer masse gikk tapt da strøet ble plassert i ruter med transplantert bøk enn i ruter med transplantert gran og ruter der strøet hadde blitt fjernet. Derimot hadde verken strøtype eller skogtype individuell effekt på tap av masse. Dette indikerer at strøtypen i strølaget har større betydning for nedbrytningshastigheten enn skogtypen. Den raskere nedbrytningen i ruter med bøk sammenlignet med gran i strølaget viser at et skifte fra gran- til bøkeskog trolig vil føre til en raskere nedbrytningshastighet, spesielt i blandingsskogene som oppstår i overgangsfasen. Resultatene tyder på at et skifte fra gran- til bøkeskog vil føre til et større utslipp av CO₂ til atmosfæren, som vil bidra til økt global oppvarming.

Nøkkelord: strønedbrytning, manipulasjon av strølaget, treslagsskifte, boreale og tempererte skoger, strøposeforsøk, klimaendringer

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1 Introduction

Global climate change causes shifts in the range of many plant species. A northward expansion has already been observed and is predicted to continue in the future (Hickler et al. 2012). Using the HadCM3 climate scenario (i.e. an increase of 4.9 °C for the period 2071-2100 relative to 1961-1990 in northern Europe), the northern boundaries of temperate and hemi-boreal forests in southern Scandinavia are projected to move 300-500 km northward to achieve equilibrium with the new climate (Hickler et al. 2012). Beech is expected to increase its tolerance of abiotic and biotic threats accompanying climate change, and thus increase its competitive advantage over spruce (Bolte et al. 2010). Consequently, Norway spruce (*Picea abies* (L.) H. Karst.; hereafter spruce) forests, are projected to be transformed to beech (*Fagus Sylvatica* L.; hereafter beech) and mixed beech forests (Bolte et al. 2014). Dominant tree species play an important role in ecosystem interactions, both aboveground and belowground (Augusto et al. 2015; Prescott & Grayston 2013; Urbanová et al. 2015; Wardle et al. 2004). Thus, a fundamental ecosystem change can be expected with a shift from spruce to beech forests.

Today, spruce is the predominant tree species on mesic soils in southeast Norway (Bjune et al. 2009) (Figure 1), and is highly valued in a commercial perspective. Spruce has a shallow root system, forms thick organic layers, and creates acidic soils (Berger & Berger 2012). The pH in soils of spruce dominated forests are normally lower than soils in beech dominated forests (Hojjati et al. 2009). Beech is late-successional, shade tolerant, and is the most abundant and dominating tree species in central Europe (Geßler et al. 2007). It forms a dense canopy and has extensive shallow and intermediate roots (Von Wuehlisch 2008). Because of its high shade tolerance, beech is able to regenerate under the canopy of other tree species, including spruce (Bolte et al. 2007). Today, the northern range of beech is discontinuous and consists of two distinct and isolated distributions in Norway: one population in Seim, western Norway, and several adjacent populations in Vestfold, southeast Norway (Bjune et al. 2013; Myking et al. 2011) (Figure 2).

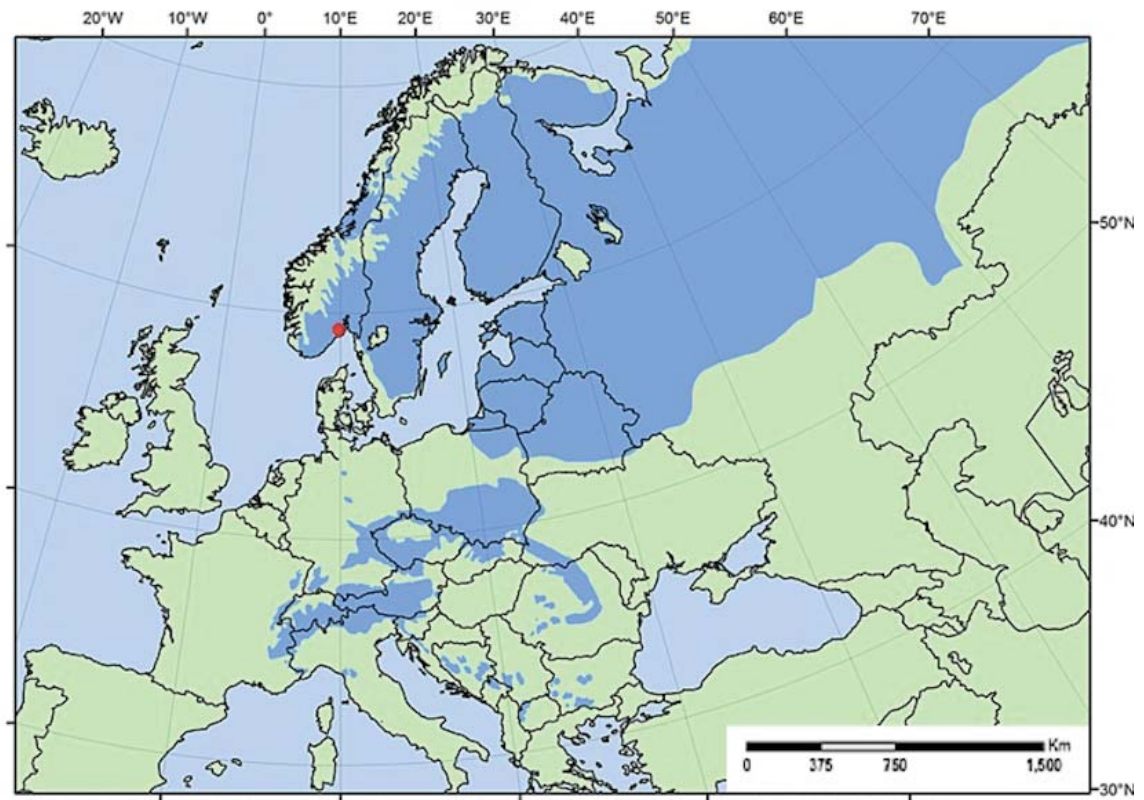


Figure 1. Distribution map of spruce in Europe (EUFORGEN 2009b). The study site is marked in red.

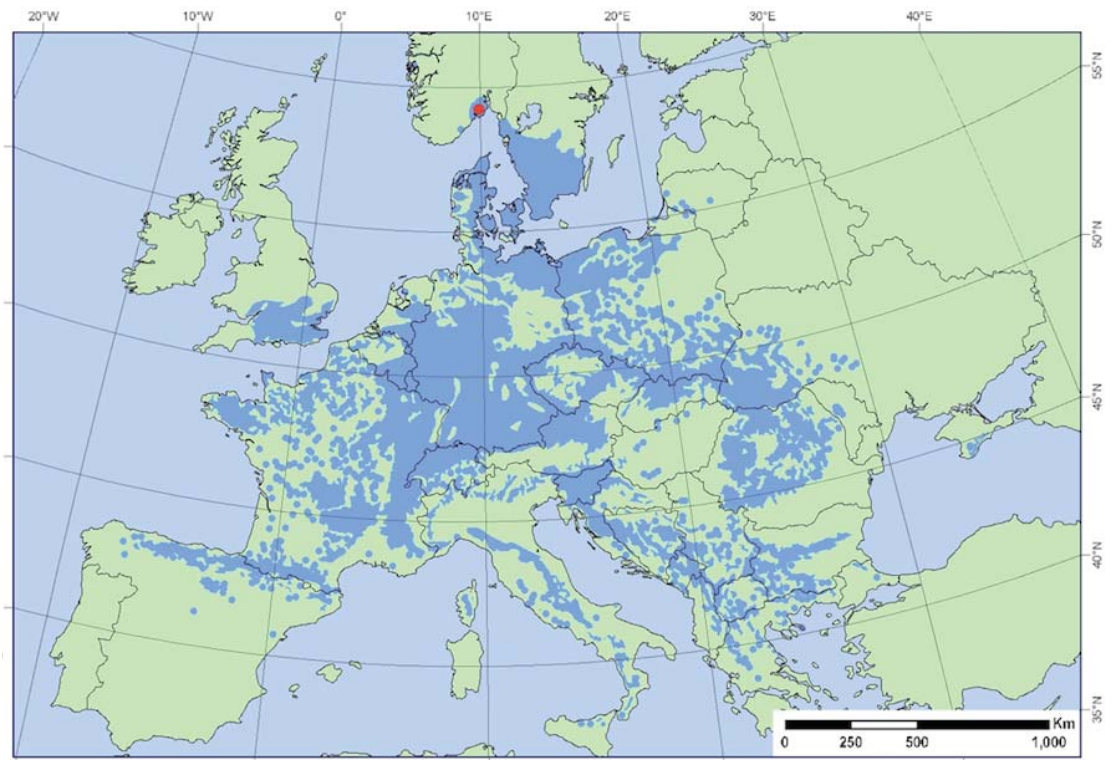


Figure 2. Distribution map of beech in Europe (EUFORGEN 2009a). The study site is marked in red.

Decomposition is the breakdown of organic material into smaller components. The process starts with detritivores breaking down litter to smaller pieces that can be reduced chemically before being further reduced and mineralised into basic inorganic molecules (ammonium, phosphate, carbon (C) dioxide and water) by micro-organisms (bacteria and fungi). As litter decomposes, molecules are taken up by plants and micro-organisms, and released to the atmosphere via soil respiration (Swift et al. 1979). Thus, decomposition of organic matter controls the recycling of plant nutrients in terrestrial ecosystems, and determines the rate that CO₂ is released to the atmosphere (Chapin et al. 2002; Swift et al. 1979). A change in tree species composition can influence the rate that litter is decomposed directly through changes in substrate quality, and indirectly through effects on environmental conditions such as soil fertility, microclimate, and the microbial community in the forest floor (Berg et al. 2010; Cornelissen et al. 2006; Cornwell et al. 2008; Güsewell & Gessner 2009; Hobbie et al. 2006).

Soil respiration is the largest terrestrial source of CO₂ to the atmosphere (Raich et al. 2002), and in forests, about half of the soil respiration is heterotrophic, originating from decomposition of soil organic matter (SOM) (Epron et al. 2001; Nordgren et al. 2003). Thus, changes in the rate of decomposition may have a large impact on the rate of greenhouse gas (GHG) induced climate change (Bardgett et al. 2008; De Deyn et al. 2008; Raich & Schlesinger 1992). A better understanding of how a climate change induced transformation from spruce to beech forests will affect the decomposition rate in these forest ecosystems, will provide more accurate estimations of future C budgets.

Forest soils are of particular importance in this context as they represent the largest terrestrial C pools and thus play a vital role in the global C cycle (Lal 2004). Boreal forests store the second most C (272 ± 23 Pg C) after tropical forests. As much as 60% of the C is stored in the top meter of the soil, compared to only 20% in tropical forests (Pan et al. 2011). Microbial decomposition is a fundamental process for the build-up of stable humus and the accompanying storage of C and nutrients (Berg & McClaugherty 2014). Traditionally, aboveground plant litter has been assumed the principal source of soil C. However, recent studies have found that belowground roots and root-associated microorganisms contribute substantially to C sequestration (Clemmensen et al. 2013). A part of the C taken up from the atmosphere by plants during photosynthesis is directed belowground to roots, where it is transferred to mycorrhizal fungi. The fungi then incorporate some of this C into hyphae. Once hyphae die and decompose, residues of the C are converted to organic material in the soil

(Treseder & Holden 2013). This process may contribute to long-term C storage in soils (Clemmensen et al. 2013).

An extensive amount of research has shown that decomposition rates are mainly regulated by climate, litter quality and the microbial community (e.g. Aerts 1997; Cornwell et al. 2008; Coûteaux et al. 1995; Daubenmire & Prusso 1963; Gholz et al. 2000; Meentemeyer 1978; Swift et al. 1979). The relative importance of these factors, however, depends on which spatial scales are considered. For example, on a regional to global scale, climate and substrate quality often explains the largest part of the variation (Aerts 1997; Cornwell et al. 2008; Gholz et al. 2000; Parton et al. 2007). Meanwhile, at a local scale where the climate is relatively uniform, the composition of the soil community (Strickland et al. 2009a; Wall et al. 2008), and interactions among litter types (Hättenschwiler & Gasser 2005) have large effects on litter decomposition. Recent studies have shown that soils with different characteristics play an important role in the decay process (Cleveland et al. 2014; Delgado-Baquerizo et al. 2015; Keiser et al. 2013; Strickland et al. 2009b; Wallenstein et al. 2010). For instance, several studies show that litter decomposes faster under parental tree species than under different tree species (Ayres et al. 2009; Gholz et al. 2000; Keiser et al. 2013; Strickland et al. 2009b; Veen et al. 2015; Wallenstein et al. 2010). This interaction is often explained as an adaptation of the local soil community to the litter produced by the tree species above them, and is called the “home-field advantage” (HFA) (Gholz et al. 2000). However, there are several cases in which HFA has not occurred (e.g. Freschet et al. 2012).

The decomposition rate at an early stage is usually determined by the availability of nutrients needed to decompose easily decomposable substances, such as cellulose and hemicellulose (Berg & McClaugherty 2014). Nitrogen (N) is a particularly important nutrient at this early stage (Albers et al. 2004). Like other organisms, soil microbes need a balance of nutrients to build their cells and extract energy. On average, soil microbes need eight parts of C for every part of N. Only one-third of the C metabolised by microbes is incorporated into their cells, while the remainder is respired and lost as CO₂ (Brady & Weil 2013). Usually, fresh litter contains less N than the decomposer organisms need. To balance this, decomposers immobilise N from the surrounding environment. Consequently, both the amount and the concentration of N increases (Manzoni et al. 2012). At later stages, the decomposition rate is related to elements required to decompose recalcitrant components such as lignin and tannins (Güsewell and Gessner 2009; Berg et al. 2010). Polyphenols, such as tannins, are known to

affect litter quality and retard decomposition processes, through the effect on the composition and activity of decomposer organisms (Gallet & Lebreton 1995; Hättenschwiler & Vitousek 2000). In addition, polyphenols can change N availability by complexing with proteins (Hättenschwiler & Vitousek 2000; Northup et al. 1998). Spruce needles and organic layers in spruce forests are characterised by high polyphenol levels (Gallet & Lebreton 1995). While studies on polyphenol levels in beech leaves is hard to find, Kolstad et al. (2016) found higher levels of tannins in beech compared to spruce seedlings. Moreover, several studies (e.g. Aneja et al. 2006; Berger & Berger 2012; Melillo et al. 1982) have found higher concentrations of lignin in beech compared to spruce litter.

There is an extensive amount of scientific studies comparing the mineral nutrition and nutrient cycling in spruce and beech stands (see Berger & Berger 2012 and references therein). In the older literature, the established theory is that the build-up of litter and C in spruce stands is caused by slower decomposition rates in spruce forests compared to beech forests, because of the recalcitrance of spruce needles (Mardulyn et al. 1993; Nihlgård 1971). However, later studies (e.g. Albers et al. 2004; Berger & Berger 2012; Berger & Berger 2014) show that a greater accumulation of litter in spruce compared to beech stands is not due to the needles recalcitrance. Instead, the decomposition in spruce stands is retarded by adverse environmental conditions. Moreover, recent studies challenge the established assumption of faster decomposition in beech compared to spruce litter. Several studies (e.g. Albers et al. 2004; Asplund et al. submitted manuscript) have found a faster decomposition in spruce needles compared to beech leaves. Higher contents of lignin in the beech litter has been proposed as one of the explanations (Aneja et al. 2006; Melillo et al. 1982). While there exists a large amount of literature on differences in decomposition rate between beech and spruce forests, few studies have investigated the importance of the litter layer. Some studies (e.g. Sayer 2006) have looked at the effect of litter removal and additions of the same litter type. Other studies (e.g. Jonsson & Wardle 2008; Wardle et al. 2003) have investigated the effect of mixing litter types. However, to my knowledge, no other studies have looked at how replacing litter with litter from a different forest type influences decomposition rates.

1.1 Aim of the study

The aim of this study was to increase the understanding of how a climate driven shift in dominant tree species will affect the decomposition rate, and consequently the rate that carbon is released to the atmosphere. More specifically, I aimed to test the relative and interactive effects of litter type, forest type, litter layer type, and their interactions as determinants of decomposition and release of N. To test this, litter bags of spruce and beech were placed in manipulated plots in neighbouring beech and spruce forests. The litter layer manipulations were: transplanted beech litter, transplanted spruce litter, and removal of litter. Un-manipulated plots served as control. After incubation, litter mass loss and nitrogen release were calculated. This study aids in the understanding of the potential impacts of climate driven tree distribution shifts on the carbon fluxes of such forest types and their feedbacks to GHG induced climate change.

The hypotheses were:

- 1) Litter will decompose faster when placed in its home-field due to a more adapted and efficient microbial community.
- 2) Both litter types will decompose faster in the beech forest than in the spruce forest, because of a more favourable environment for decomposing organisms in the beech forest.
- 3) Decomposition will be faster in transplanted beech litter compared to transplanted spruce litter and removal plots because of a more favourable environment for decomposing organisms surrounded by beech litter.
- 4) Rates of N release from the litter will show the same trends as the decomposition rates.

2 Material and methods

2.1 Study site

The study was conducted in Brånakollane Nature Reserve, in the municipality of Larvik, Vestfold, in southeast Norway, N 59° 11' E 10° 2' (Figure 3). The area was protected by law in 1980, and the area has since been disturbed only to a minor extent. The nature reserve is an area of a well-developed beech forest that has established naturally, surrounded by a spruce forest that has been planted and is still logged. There is a distinct border between the two forest types, as part of the original beech forest was clear-cut in 1956 and planted with spruce. The two forest types have established on similar types of monzonite bedrock and soil, and are thus rather alike in terms of underlying bedrock, subsoil, micro topography, and soil hydrology (see Bjune et al. 2013). Because the present southwestern border of the beech forest is overlapping the border of the boreal spruce forest in this area, it provides a natural laboratory for studying interactions between the two forest ecosystems.

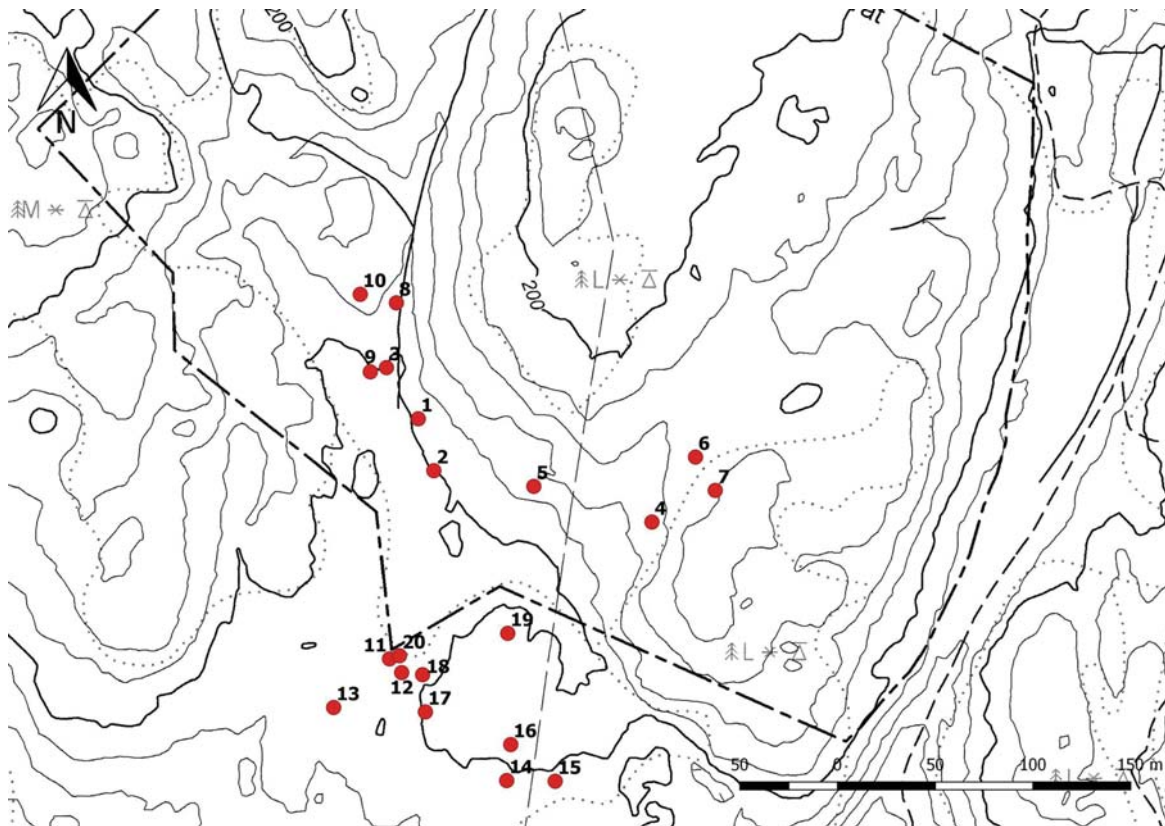


Figure 3. Map showing the location of the blocks in the study area. Blocks numbered 1 to 10 are located in the beech forest. Blocks numbered 11 to 20 are located in the spruce forest. The border of the nature reserve is presented by a dotted line.

2.2 Study design and field experiment

Twenty blocks were established in 2014, 10 in the beech forest and 10 in the spruce forest (Fig. 3). The criteria for the blocks were a homogenous surface with respect to gradient, bed rock and soil type, that there were no trees in the plots and that the cover of mosses was less than 25 %. The blocks were randomised and each block was numbered from 1 to 10 in the beech forest and 11 to 20 in the spruce forest. Each block was divided into four 50 x 150 cm plots (Figure 4; Figure 5), where the litter layer was manipulated. The manipulations (hereafter treatments) were transplanted *beech*, transplanted *spruce*, litter *removal* and *control*.

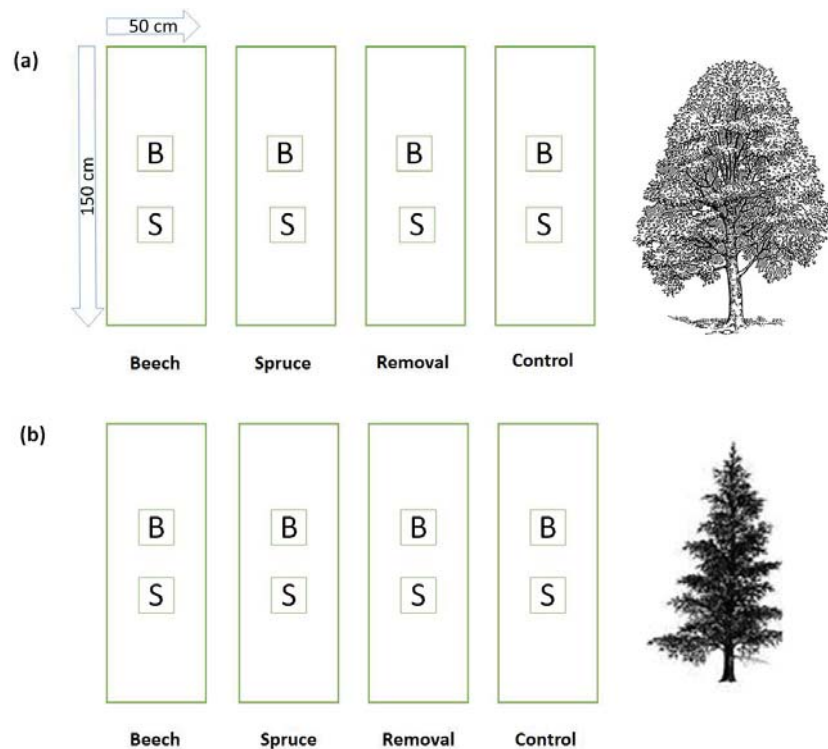


Figure 4. Illustration of the study design in the beech forest (a) and the spruce forest (b) with treatments *beech*, *spruce*, *removal* and *control*, and litter bags beech (B) and spruce (S).



Figure 5. Study setup in the spruce forest with the four different treatments. *Photo: Johan Asplund*

Senesced beech leaves (autumn 2014) and spruce needles (autumn 2015) were collected directly from the trees at the study site, to avoid differences in stage of decomposition. The litter was dried at 30 °C for 48 hours and 1 gram of litter was placed in 10 x 10 cm litter bags with a mesh size of 0.5 mm, allowing the entry of micro- and meso-fauna (Bradford et al. 2002). 80 litter bags were made with beech leaves and 80 with spruce needles. Additionally, three bags of beech litter and three bags of spruce litter were weighed, dried at 70 °C for 24 hours and then weighed again. This data was used to control for differences in air humidity at the days of weighing. The excess litter was preserved in a freezer and later used for measuring initial C and N content in the litter (Table 1).

Table 1. Initial values of C and N content (%) and C:N in the beech and spruce litter.

Litter type	% C	% N	C:N
Beech	45.86	0.94	49.02
Spruce	46.46	1.27	36.67

In September 2015, the litter bags were placed on top of the litter layer in the established plots in Brånakollane and covered with litter from the plot. Cages were put on top of the litter *removal* and the *spruce* plots in the beech forest to prevent falling leaves from interfering with

the manipulated plots. Environmental variables were also measured, to control for these variables potentially interfering with my results. The environmental variables included Beam Light Index (BLI), Diffuse Light Index (DLI), and temperature. BLI and DLI were measured in all plots (*beech*, *spruce* and *removal*) during summer 2015, when the trees were fully bloomed. Temperature was only measured in two blocks (but in all tree treatments: *beech*, *spruce* and *removal*) in each forest. In addition, I had access to data for soil pH, C, N and C/N, from 2015, first presented in Hustoft (2016). This data was sampled in the 5 cm of the top soil (humus) in each plot with a 5.8 cm in diameters soil corer. In addition, I had access to the removed material from the *removal* plots. In November 2015, fallen beech leaves were removed from the cages and additional beech leaves were added to the *beech* plots in the spruce forest. In April 2016, the plots were controlled and additional litter was added to the manipulated *spruce* and *beech* treatment plots.

2.3 Lab work and chemical analyses

Weight reduction

In September 2016, after one year of incubation, the litterbags were collected and brought to the lab and dried at 40 °C. Mineral soil, plants that had grown into the litter bags and other materials that were not initially in the litter bag were removed before the litter was weighed. A small part of each litter bag was put aside after the weighing. This litter was mixed within each litter type, dried and reweighed. The data was used to calculate the weight corrected for differences in air humidity pre- and post-incubation.

C and N content

The litter samples were grinded into fine powder using a Retsch MM400 ball mill (Retsch, Haag, Germany). To measure C and N content, 5 mg (+/- 1 mg) of the grinded litter was weighed using a Mettler Toledo weight, and put in small packs of tin foil. The C and N content was determined using an Elementar Vario MICRO cube (Elementar Analysensysteme GmbH, Hanu, Germany). Initial C and N content was measured in the litter that had been frozen.

2.4 Statistical analyses

All statistical analyses were performed in R studio, version 3.3.1 (R Core Team 2016). A significance level of $P < 0.05$ was chosen. The data for one of the litterbags (B62) showed an extreme outlier in the data set and was removed from further analyses. Some of the litter bags had been opened during the time in the field, but none of these showed any clear outliers.

Mass loss was calculated as the percent difference between corrected start weight and corrected end weight. Visual inspection of residual plots for the mass loss data did not show any obvious deviations from homoscedasticity or normality. N release was calculated as the percent decrease in absolute N contents in the litter. The data for N release showed a skewness, and was ranked using aligned rank transform from the package *ARTool* (Kay & Wobbrock 2016) to obtain normal distribution. Visual inspection of residual plots of the environmental variables did not show any obvious deviations from homoscedasticity or normality after log transformation.

For both mass loss and N release, the data were analysed using a split-plot ANOVA with forest type as the main plot factor, and litter type and treatment as sub-plot factors. For comparisons between means, a Tukey's post hoc test from the package *multcomp* (Hothorn et al. 2008) was used for the mass loss data. For the N release data, a contrast test from the package *lsmeans* (Lenth 2016) was used. The Tukey post hoc test showed no significant differences between the *control* and *spruce* treatment in the spruce forest ($p = 1.00$), or between the *control* and *beech* treatment in the beech forest ($p = 1.00$). This indicates that the moving of litter itself did not have any effect on the results. Thus, the *control* treatment was removed from the N release data, but kept in the mass loss data to increase the number of observations in the model. Graphical illustrations were generated using Matplotlib version 1.5.3 with Python version 2.7. Contents of N and C were calculated using Microsoft Excel version 15.27 (Microsoft corporation 2015). For BLI, DLI and weight removal a one-way ANOVA was performed. For the soil parameters, split-plot ANOVA was used.

3 Results

3.1 Mass loss

The results showed that there was a significant difference between the mass loss of spruce and beech litter when placed in the spruce forest (Fig. 6a; Table 2). Spruce litter lost 15 % more mass than beech litter in the spruce forest. However, there were no significant differences between the two litter types when placed in the beech forest. Moreover, there were no significant differences in mass loss between the two litter types or between the two forest types. However, mass loss was significantly different between all treatments (*beech*, *spruce*, *removal*). Litter placed in the *beech* treatments lost 15 % more mass than litter placed in the *spruce* treatments, and lost 41 % more mass than litter placed in the *removal* treatments. Litter placed in the *spruce* treatments lost 31 % more mass than litter placed in the *removal* treatments.

3.2 Nitrogen release

The results showed that litter type, forest type and treatment all had significant effects on N release (Fig. 6b; Table 2). However, no interaction effects were found. The negative values (Fig. 6b) for N release indicate that N has immobilised in the litter, resulting in a higher N content than initially. The positive values (Fig. 6b) indicate that N has been released from the litter. Beech litter immobilised N, while spruce litter released N, regardless of forest type or treatment. Moreover, when placed in the spruce forest, both litter types released more N than when placed in the beech forest. Further, more N was released from litter placed in the *beech* treatments than litter placed in the *removal* treatments, and more N was released from litter placed in the *spruce* treatments than litter placed in the *removal* treatments. However, there were no significant differences between litter placed in the *beech* treatments and litter placed in the *spruce* treatments.

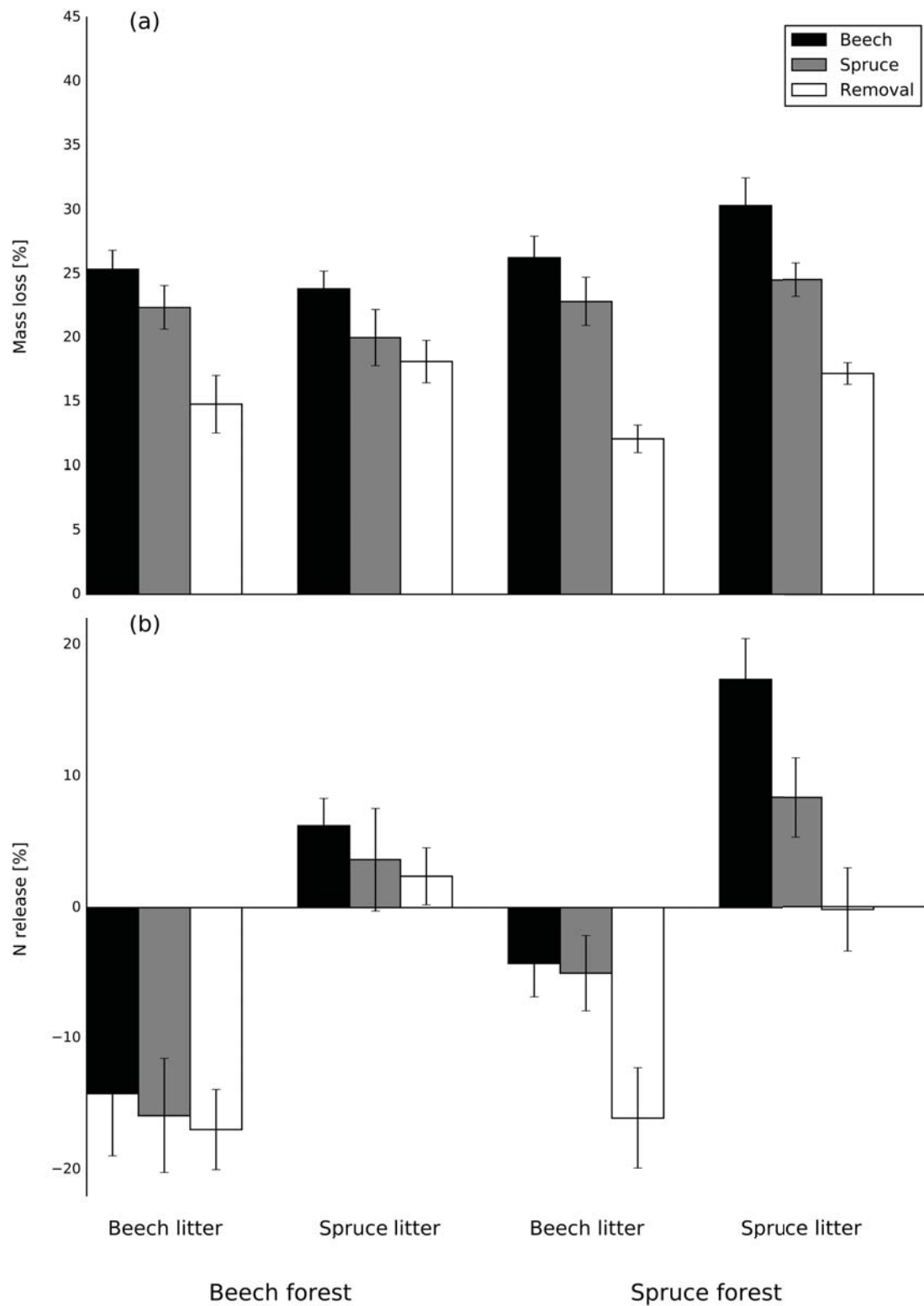


Figure 6. Mean (\pm SE) for mass loss (a) and nitrogen release (b) from the interactions between forest type, litter type and litter layer treatments. The bottom line (beech forest, spruce forest) shows forest type, the line above (beech litter, spruce litter, beech litter, spruce litter) shows litter type, and the different colours (black, grey, white) show type of treatment.

Table 2. ANOVA output, F and (P)-values, for mass loss and N release for litter type, forest type, treatment and the interaction effects.

	Litter type (L)	Forest type (F)	Treatment (T)	L x F	L x T	F x T	L x F x T
Mass loss	2.88 (0.092)	0.92 (0.3498)	30.32 (< 0.001)	7.78 (0.0061)	1.29 (0.2792)	2.22 (0.0894)	0.60 (0.6176)
N release	127.62 (< 0.001)	6.06 (0.024)	10.76 (< 0.001)	0.61 (0.439)	0.77 (0.468)	2.78 (0.067)	0.65 (0.523)

Degrees of freedom: Mass loss: L and L x F = 1, 125, F = 1, 125, F x T and L x F x T = 3, 125, N release: L and L x F = 1, 90, F = 1, 18, T, L x T, F x T and L x F x T = 2, 90. Bold values indicate significant effects at P = 0.0

3.3 Environmental variables

The environmental variables were all significantly different between the beech and the spruce forest (Table 3). All variables were higher in the spruce forest than the beech forest, except for soil pH. Because of few replicates the temperature data could not be analysed statistically. However, visual inspection of the data reveals that there were no large differences in temperature between the two forest types (Fig. 7; Appendix Fig. 1 and 2).

Table 3. ANOVA output, F and (P)-values, for Beam Light Index (BLI) and Diffuse Light Index (DLI) (during summer only), soil pH, soil carbon (C), soil nitrogen (N), soil carbon nitrogen ratio (C:N), and weight of the litter removed from the *removal* treatments. The values are shown for forest type (F), treatment (T) and the interaction of forest type and treatment. The two rightmost columns show mean values \pm SE for the beech forest and spruce forest.

	F	T	F x T	Beech forest	Spruce forest
BLI	57.14 (<0.001)			0.10 \pm 0.005	0.20 \pm 0.013
DLI	88.78 (<0.001)			0.12 \pm 0.002	0.23 \pm 0.012
Soil pH	7.45 (0.014)	1.09 (0.346)	0.33 (0.718)	4.02 \pm 0.043	4.03 \pm 0.037
Soil C	10.51 (0.005)	1.07 (0.354)	0.35 (0.705)	23.36 \pm 2.252	35.90 \pm 1.729
Soil N	7.14 (0.016)	3.33 (0.047)	0.36 (0.698)	1.09 \pm 0.089	1.48 \pm 0.063
Soil C:N	6.28 (0.022)	0.54 (0.589)	0.11 (0.893)	20.72 \pm 0.883	24.29 \pm 0.677
Removal	10.66 (0.005)			1018.29 \pm 74.32	1733.58 \pm 216.32

Degrees of freedom: BLI and DLI: F = 1, 18, Soil pH, C and C:N: F = 1, 18, T = 2, 35, F x T = 2, 35.

Bold values indicate significant effects at P = 0.05

BLI, DLI, soil C, soil N, soil C:N and weight removal all show significantly higher levels in the spruce forest compared to the beech forest (Table 3). For soil N, there was also a significantly higher content of N in the *spruce* treatment than the *removal* treatment (treatment mean \pm SE: B = 1.296 \pm 0.117, S = 1.416 \pm 0.097, R = 1.155 \pm 0.092). Soil pH was significantly higher in the beech forest than in the spruce forest.

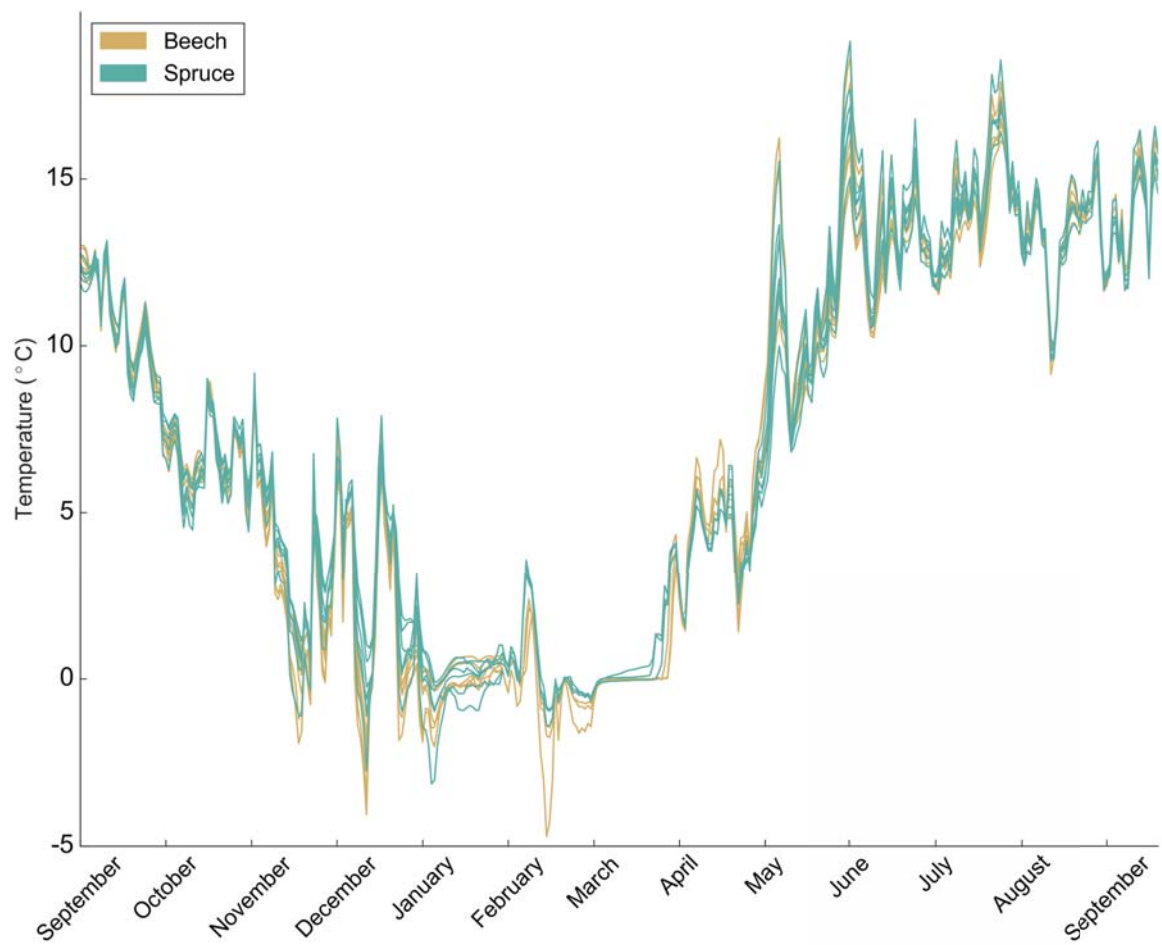


Figure 6. Daily mean temperature of the beech and spruce forest during the litter bag exposure time in the field (September 2015 - September 2016).

4 Discussion

4.1 Mass loss

Spruce needles lost significantly more mass than beech leaves in the spruce forest. This finding shows support for the HFA and my first hypothesis, in accordance with several other studies (Ayres et al. 2009; Gholz et al. 2000; Keiser et al. 2013; Strickland et al. 2009b; Veen et al. 2015; Wallenstein et al. 2010). However, the difference in mass loss could also be explained by differences in initial litter quality. Since there was no difference in the decomposition rate between the two forest types, one explanation could be that the changes seen in the spruce forest are due to a combination of both HFA and higher recalcitrance in beech leaves compared to spruce needles. In the beech forest, the HFA would lead to faster decomposition of beech leaves, while higher levels of N in the spruce needles, and potentially higher concentrations of recalcitrant compounds in the beech leaves, would lead to a faster decomposition of spruce needles. Thus, we may not see a difference between the litter types in the beech forest because the effect of the HFA is outweighed by the effect of the initial litter quality. In addition to lignin concentration, differences in concentration of polyphenols between the two litter types could be a part of the explanation. Since my study only covered the first year of decomposition, N content has likely played a larger role than the concentrations of lignin and tannins. Partly in line with my results, Albers et al. (2004) found that spruce needles decomposed faster than beech litter. However, in contrast to my results, Albers et al. (2004) found that the decomposition of spruce needles was faster compared to beech leaves regardless of the incubation site, and that the difference was higher in the beech forest than in the spruce forest.

Further, my study shows that mass loss was significantly different between all treatments (*beech*, *spruce* and *removal*). Litter placed in the *beech* treatment decomposed faster than litter placed in the *spruce* and *removal* treatments, and litter placed in the *spruce* treatment decomposed faster than litter placed in the *removal* treatment. This shows support for my second hypothesis. In general, beech litter creates a better environment for decomposing organisms than spruce litter (Berger & Berger 2012), partly because of higher pH. In my study, the pH was significantly higher in the beech forest compared to the spruce forest, but there were no differences in pH between the treatments (Table 3). Thus, pH did not seem to have played a major role in controlling the decomposition rate. Moreover, soil characteristics

not measured in this study must explain the difference between the *beech* and the *spruce* treatments. The slower decomposition in the *removal* treatment compared to the *beech* and the *spruce* treatments is also in line with other studies. Sayer (2006) showed that removal of litter depleted the forest of nutrients, increased fluctuations in temperature and disturbed the soil water balance. These changes led to changes in the fungal species composition and diversity, and caused a decline in soil fauna populations. However, this study was conducted for a longer period than my study. In my study, N content was significantly lower in the *removal* treatment compared to the *spruce* treatment (Table 3), indicating less nutrient availability in the *removal* treatment.

The results did not show a significant difference in mass loss between the two forest types, which was surprising. Because of a more favourable environment with higher soil pH, decomposition rates are usually faster in beech stands than in spruce stands (Berger & Berger 2012). My results are particularly surprising since Asplund et al. (submitted manuscript) found a 49 % higher litter mass loss in the beech forest compared to the spruce forest, in the same study area as where my study was conducted. However, Asplund et al. (submitted manuscript) did not include litter layer manipulations. My results showing that treatment had a significant effect on mass loss, but not forest type, indicate that the litter layer is more important for determining decomposition rates than the forest type.

4.2 Nitrogen release

The results of N release did not support my fourth hypothesis. No support for N release following the same trends as the mass loss rate was found. While spruce litter lost significantly more mass than beech litter in the spruce forest, there was no interaction effect between litter type and forest type for N release. However, individually, litter type and forest type affected the release of N significantly. For the litter type, spruce litter lost N (except in the *removal* treatment in the spruce forest), while beech litter gained N (Fig. 6b). According to Melillo et al. (1982), increases in N during early stages of decomposition have been reported repeatedly since first described by Tenney and Waksman (1929). When N concentrations are insufficient in organic material, decomposing organisms must gain N from the surroundings. This can occur via one or more of the following mechanisms: immobilisation, fixation, absorption of atmospheric ammonia, insect frass, green litter, fungal

translocation through fall and/or dust (Melillo et al. 1982). My measurements show that there was a higher initial content of N in the spruce needles than in the beech leaves (Table 1), which is consistent with previous studies on beech and spruce. For instance, Albers et al. (2004) and Asplund et al. (submitted manuscript) both found that N accumulated more rapidly in beech leaves than in spruce needles during decomposition. My results also showed that there was a significantly higher release of N in the spruce forest than the beech forest. This can be explained by a higher N content in the spruce forest than the beech forest (Table 3).

Further, my results showed a higher release in the *beech* and *spruce* treatments compared to the *removal* treatment. This can be explained by the soil N measurements, showing higher content of N in the *spruce* treatment compared to the *removal* treatment (Table 3). There was no significant difference in N release between the *beech* and *spruce* treatments, which contrasts with the result for mass loss. This may be explained by similar soil N content between the *beech* and *spruce* treatments (Table 3). Initial litter N content and N availability in the soil seems to explain a part of the N release rates found in this study. However, factors not measured in this study could also be part of the explanation. One possible explanation for N immobilisation in the beech litter could be caused by polyphenols altering N availability by complexing with proteins (Hättenschwiler & Vitousek 2000). Differences in content of polyphenols between spruce and beech litter, and their role in decomposition processes, should therefore be investigated in future decomposition studies.

4.3 Implications of a transformation from spruce to beech

My results show that both beech and spruce litter decompose faster with beech in the litter layer compared to spruce in the litter layer. However, the forest type did not influence the litter decomposition rate. This indicates that the surrounding litter type is more determining for the decomposition rate than the forest type. Moreover, my results indicate that the decomposition rate will likely increase with a transformation from spruce to beech, particularly in the mixed forests that will occur in the transition phase. Consequently, it is likely that the rate at which CO₂ is released to the atmosphere will increase, contributing to increased GHG induced climate warming. However, how a change in dominant tree species will influence the total C budget in forests depends on a range of factors, such as C storage in deeper soil layers, nutrient availability for plant productivity, and the albedo effect (see e.g.

Randerson et al. 2006). Hence, it is still unclear to what extent a transformation from spruce to beech forests may lead to a net increase in GHG induced climate change.

4.4 Limitations of my study

Understanding decay processes is complicated by the fact that microbial community structure and function are likely to both affect and be affected by the quality and chemistry of the organic matter (Cleveland et al. 2014). The composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees (Urbanová et al. 2015), and could potentially explain a large part of my results. Unfortunately, abundance and diversity of decomposer organisms was not included in this study. However, a study by Asplund et al. (submitted manuscript), from the same study area, found that both fungal and bacterial communities were dependent on both litter and forest type. In addition, Asplund et al. (submitted manuscript) found a correlation between the fungal community and litter mass loss.

The largest part of the literature on decomposition only studies the first year of decomposition (Berg & McClaugherty 2014). Whether initial rates of decay provide a useful indication of decomposition has been questioned in several studies. Prescott (2005) questioned if it matters how quickly different species reaches their maximum limit if mass loss curves of different species all converge at a similar maximum limit. Several long-term studies have found convergence, and even crossing over of mass loss curves (Berg & Ekbohm 1991; Prescott et al. 2000; Yang & Janssen 2002). Prescott et al. (2000) found that despite a faster initial decomposition of broadleaf litter, there were little differences in the litter mass remaining after four years of exposure. Instead of measuring early rates of decay, Prescott (2005) suggested to measure annual litter input and determining the maximum decomposition limit and nutrient content at that stage. This method may provide more insight into nutrient cycling and C storage in ecosystems than measuring early rates of decay.

4.5 Factors that may have influenced my results

An extensive body of research show that climatic differences play a major role in regulating decomposition rates across large regional spatial scales. However, on smaller spatial scales, as in this study, climatic differences between the sites are likely to be small, and will

consequently play only a minor role as determinants of decomposition rates. Moreover, this is corroborated by the temperature measurements in the study area which showed only minor differences between the two forest types (Fig. 7) and between blocks (Fig 1 and 2, appendix). In addition, Berg et al. (2000) found that decomposition of spruce needle litter is little affected by variations in climate.

Soil pH was significantly higher in the beech forest compared to the spruce forest. This is not surprising, since spruce stands are known for creating acid soils (e.g. Berger & Berger 2012; Berger et al. 2002; Hojjati et al. 2009; Nihlgård 1971). Although there is a common understanding that higher pH leads to more favourable soil conditions, some studies have shown that variations in pH does not have a large effect on decomposition of spruce needles (Smolander et al. 1996) or beech leaves (Albers et al. 2004). Moreover, pH did not seem to affect my studies noteworthy, since there was no difference in mass loss between the forest types despite a higher pH in the beech forest compared to the spruce forest. In addition, there were differences in mass loss between the different treatments though there was no difference in pH.

Soil moisture can influence the decomposition rate (Von Haden & Dornbush 2014), but was not measured directly in this study. However, BLI/DLI could be an indirect measure of soil moisture, because light intensity may influence the soil moisture. Albers et al. (2004) found that litter decomposition was limited by the availability of water, though the precipitation in the study area was high. BLI/DLI may also have affected my results through a change in micro climate.

The mesh size of the litterbags is too small to allow penetration by macro fauna. However, in the same study area, Asplund et al. (submitted manuscript) found no effect on litter mass loss or microbial species composition when excluding soil meso fauna and macro fauna. Thus, the mesh size of the litter bags in this study has likely not affected my results.

5 Conclusions

Since soil respiration is the largest terrestrial source of CO₂ to the atmosphere, small changes in rates of decomposition could have a large effect on the global carbon budget. My results showed that spruce litter decomposed faster than beech litter when placed in the spruce forest. This could be explained by either the home-field advantage, differences in initial litter quality, or a combination of both. Surprisingly, the results did not show a significant difference in mass loss between the two forest types. This finding is in contrast with most of the existing literature. However, both spruce and beech litter decomposed faster in stands with beech litter in the litter layer, regardless of the original forest type. This indicates that the litter type in the litter layer is more determining for the decomposition rate than the forest type. This study is, to my knowledge, the first that looks at how the rate of decomposition is influenced by replacing litter from parental trees with litter from a different tree species. My findings indicate that a transformation from spruce to beech forests will lead to a faster decomposition rate, particularly in the mixed forests that will occur in the transition phase. The implication of a transformation from spruce to beech dominated forests may thus be a faster release of CO₂ to the atmosphere, contributing to increased global warming. However, the total forest C budget is determined by several factors, such as the availability of nutrients for plant growth, C sequestration in deeper soil layers, and the albedo effect. Hence, whether a transformation from spruce to beech forests will lead to a net increase in GHG induced climate change is still unknown.

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Appendix

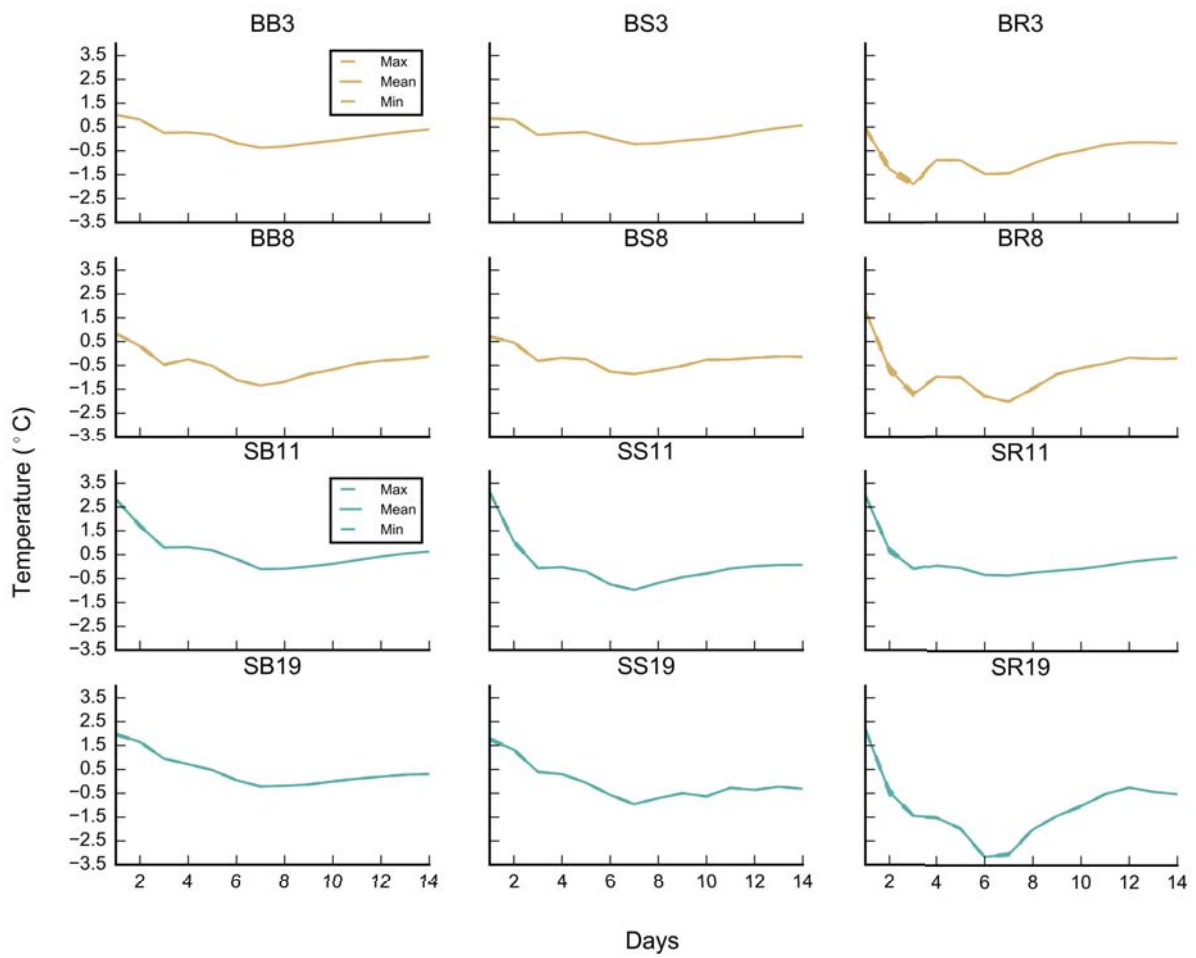


Figure 1. Measured temperature in the litter layer during the 14 first days of January (2016). BB3 (top left) means beech forest, beech treatment and block number 3. Brown colour represents the beech forest, and green colour represents the spruce forest.

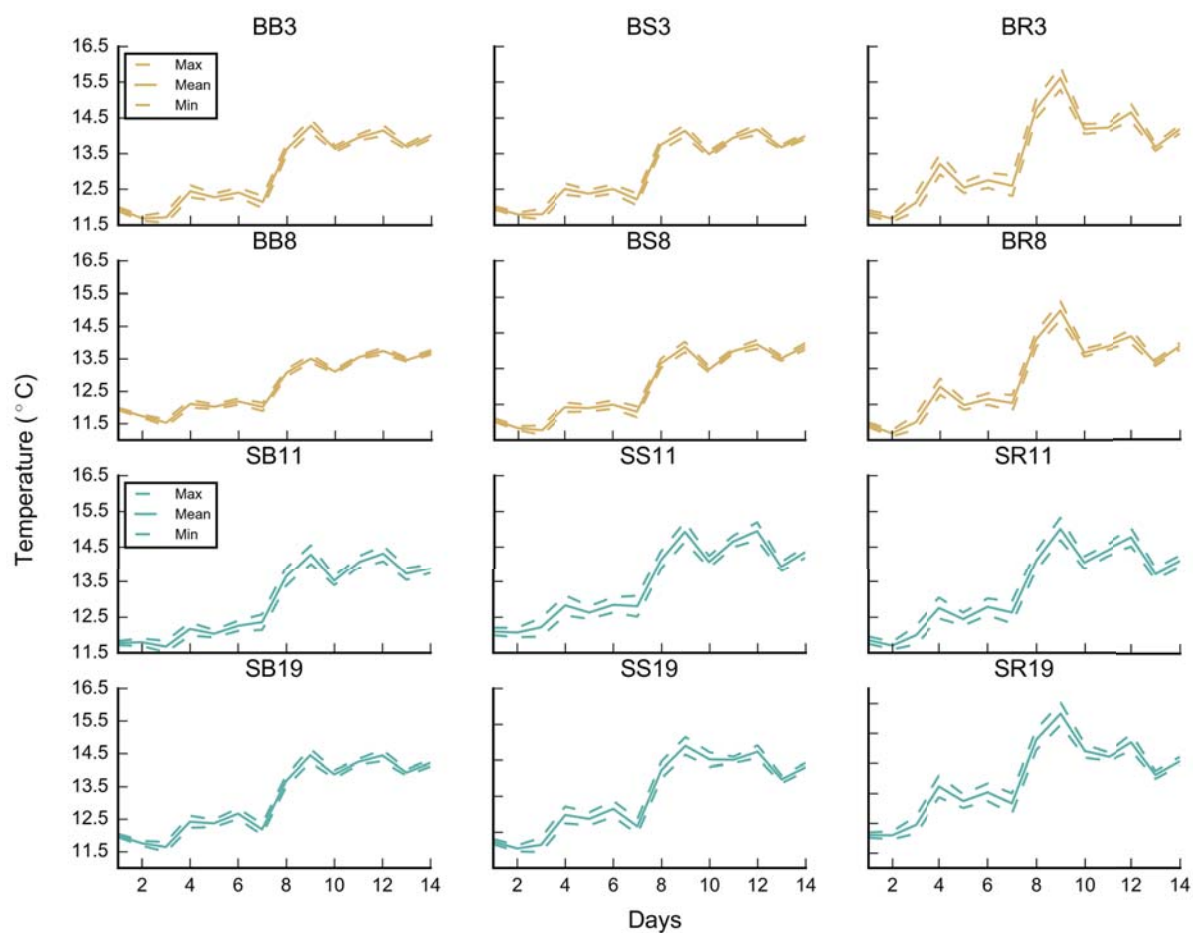


Figure 2. Measured temperature in the litter layer during the 14 first days of July (2016). BB3 (top left) means beech forest, beech treatment and block number 3. Brown colour represents the beech forest, and green colour represents the spruce forest.



Norges miljø- og biovitenskapelig universitet
Noregs miljø- og biovitenskapelige universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway