THE ARCTIC
UNIVERSITY
OF NORWAY

Department of Arctic and Marine Biology

Short term effects of clear cutting on the regeneration of sub-arctic birch forest following severe outbreaks by geometrid moths

Moritz Klinghardt
Master thesis in Biology BIO-3950 – November 2013

SHORT TERM EFFECTS OF CLEAR CUTTING ON THE REGENERATION OF SUB-ARCTIC BIRCH FOREST FOLLOWING SEVERE OUTBREAKS BY GEOMETRID MOTHS

Moritz Klinghardt

Department of Arctic and Marine Biology

Faculty of Biosciences, Fisheries and Economics

University of Tromsø - The Arctic University of Norway

Table of contents

Abstract

Birch forests in northern Fennoscandia experience re-occurring mass outbreaks of pest insects often resulting in severe defoliation. Here I test whether systematic clear cutting can accelerate the forest regeneration after outbreaks with uncut control plots as comparison. Basal shoot abundance was used as a main indicator for recovery but comprehensive data sampling also included the abundance of birch saplings, herbivore presence and understorey vegetation. Treatment responses of basal shoots were analyzed with generalized linear mixed models. Effects were distinguished between oligotrophic (poor) and eutrophic (rich) forest types, which were validated using vegetation data in a multi response permutation procedure. Results showed a highly significant increase of basal shoots throughout clear cut plots, with varying rich-poor differences between the two field sites. Forest regeneration through saplings showed only little improvement within the first years of the experiment.

1 Introduction

Fennoscandian mountain birch forest forms the northern and altitudinal tree line in northern Scandinavia and northwest Russia (Kola Peninsula) and is part of the unique subarctic ecotone between boreal forests and tundra areas (Wielgolaski 2001, Callaghan et al. 2002, Jepsen et al. 2008, Jepsen et al. 2012). The location of the ecotone is strongly determined by climate and the ecotone birch forest in northern Fennoscandia is hence faced with growing conditions that are on the climatic limit for continuous forest (Oksanen et al. 1995, Holtmeier and Broll 2005, Moen et al. 2008). While the birch forest in northern Fennoscandia is not utilized commercially to any greater extent, birch trees are used for fire wood and forests provide important grazing areas for reindeer. Long winters and short growing seasons mean that these forests may have a limited resilience to disturbances, eventually resulting in the loss of forest over large areas once this resilience is exceeded, e.g. by herbivory (Kallio and Lehtonen 1973, Lehtonen and Heikkinen 1995).

The main natural disturbance factor in the birch forests of Fennoscandia are mass outbreaks of moths. For more than a century recurring mass outbreaks of geometrid moths (autumnal moth (*Epirrita autumnata* Borkhausen, 1794; Figure 1) and winter moth (*Operophtera brumata* Linnaeus, 1758)) in northern Fennoscandia have been observed and described repeatedly (Tenow 1972, Nilssen et al. 2007). The latest region-wide outbreak (2002-2008) affected an area of approximately 10,000 km² or as much as 1/3 of the northern Fennoscandian birch forest belt (Jepsen et al. 2009a). Outbreaks occur in roughly decadal intervals and impact birch forests mostly by defoliation through feeding moth larvae, sometimes resulting in the death of trees (Lehtonen and Heikkinen 1995, Ruohomäki et al. 1997, Ruohomäki et al. 2000, Tenow and Bylund 2000, Jepsen et al. 2009b). Climate change may add to outbreak intensities and facilitate range expansion, as milder winters allow for moths to survive in greater numbers (Ammunét et al. 2012). Also, it is very likely that the north-eastern outbreak expansion of the less cold tolerant *O. brumata* is facilitated by climate warming, and thus adding to outbreak intensity and duration in areas that previously were only affected by *E. autumnata* (Jepsen et al. 2008). Thus, the most recent defoliation event in northeastern Fennoscandia was unusually long, due to a mass occurrence of the winter moth (2005-2009) after peak years of the autumnal moth (2001-2004) which lead to severe damages in the mountain birch forest (Klemola et al. 2008, Jepsen et al. 2009a).

In addition to insect pests, herbivory by reindeer and rodents can cause forest damage which may further affect the opportunity for, and rate of, recovery of previously defoliated areas. Herbivory by mammals is known to impede growth of basal shoots and saplings (Lehtonen and

Heikkinen 1995, Den Herder and Niemelä 2003). Permanent high grazing pressure following moth outbreaks could even lead to a change in vegetation state from forest to treeless tundra (Kallio and Lehtonen 1973, Lehtonen 1987).

Figure 1 *Epirrita autumnata.* Left: Adult male*.* Right: Larvae.

The natural regeneration of moth damaged birch forest has been addressed in studies that indicate that regrowth from basal shoots is an important factor for recovering trees (Lehtonen 1987, Lehtonen and Heikkinen 1995). The ability to form basal shoots seems to vary between trees depending on their growth form. Multi-stemmed (polycormic) trees tend to produce basal shoots faster and in greater numbers than single-stemmed (monocormic) trees (Lehtonen and Heikkinen 1995, Tenow and Bylund 2000, Karlsson et al. 2004, Tenow et al. 2004). The prevalence of the two growth forms is mostly dependent on soil characteristics such as nutrients and pH (Verwijst 1988). Lehtonen and Heikkinen (1995) suggested that rot from dead stems may have a bigger impact on sprout formation than reindeer grazing. Furthermore, they discussed the possibility that affected trees may benefit from clear-cutting, to remove the source of rot and stimulating the growth of basal shoots, that could then harness the old root system.

Despite this, specific management actions and their effect on the regeneration of birch forest, especially after severe disturbances such as moth outbreaks, have never been experimentally documented. From silviculture, clear cutting is known to be an effective method for

reforestation which may also be suitable for birch due to its ability for rapid regrowth of basal shoots after cutting or damage due to herbivory (Kauppi et al. 1988, Perala and Alm 1990, Karlsson et al. 2005, Hynynen et al. 2009, Luostarinen et al. 2009, Hytönen and Aro 2012). In addition to the vegetative regeneration through basal shoots, birch can also regenerate from seed. Sapling growth is considered slower in the earlier stages after initial establishment, but eventually catches up with the faster growing basal shoots after a few years (Hynynen et al. 2009).

In 2011, a large scale clear cutting experiment was established in northeast Finnmark, Northern Norway, a region severely defoliated by the latest and long-lasting moth outbreak (Jepsen et al. 2009a, Jepsen et al. 2009b). The long term goal is to follow up on the forest regeneration after moth outbreaks and to test whether the felling of trees can increase regeneration rates while considering the outbreak history of a forest, the vegetation and forest structure and browsing pressure of herbivores.

In this study I focus on the short term effects of the experiment within the first two years after clear cutting. I investigate whether clear cutting increases forest regeneration through basal shoots and whether its ability to do so depends in any way on the forest type (and therefore vegetation) by distinguishing between poorer and richer forests. In addition to the recovery through basal shoots I also assess the recovery through saplings. Provided that trees survive, a clear increase in basal shoots is anticipated since clear cutting is also used as a management action for short rotation biomass production (Perala and Alm 1990). Furthermore, I expect that polycormic trees which usually grow on poorer soils, would produce more basal shoots than monocormic trees, since the growth form and sprouting ability of trees is mainly determined by soil quality (Kauppi et al. 1988, Verwijst 1988). Sapling establishment is said to be primarily dependent on soil and the surrounding vegetation (Kallio and Lehtonen 1973) but may be facilitated in clear cut plots due to less shadowing by trees. However, as sapling growth and establishment may happen at slower rates than basal shoots, systematic patterns in the regeneration by saplings might not be visible yet.

2 Material and methods

2.1 Study system

The study is conducted in eastern Finnmark, northern Norway (70°N, 28°24'E - 29°20'E; Figure 2). Even though located relatively close to the sea, the sub-arctic climate in the study areas is mainly influenced by the continental landmass to the south, resulting in a yearly average temperature of -0.7°C with a mean of 12.3°C in July and -12.2°C in January. The annual precipitation averages at 455mm (Rustefjelbma weather station, www.met.no).

The predominating tree species in the study area are pubescent and mountain birch (*Betula pubescens* Ehr.; *Betula pubescens* spp. *czerepanovii* Orlova; formerly also known as ssp*. tortuosa*) (Hämet-Ahti 1963). However, there is no unified consensus on the taxonomy of *Betula* species and several theories of hybridization and introgression from other species such as *Betula nana* exist (Vaarama and Valanne 1973, Kallio et al. 1983, Väre 2001). Birch species are widely distributed throughout Scandinavia, but mountain birch forms the altitudinal and northern tree line in the forest-tundra ecotone in northern Fennoscandia (Wielgolaski 2001). The common reproduction patterns in birch are either vegetative through basal and adventitious shoots or recruitment by seedlings (Perala and Alm 1990, Odland 1994, Lehtonen and Heikkinen 1995, Hynynen et al. 2009). Birch is likely to grow as multi-stemmed (polycormic) trees on nutrient-poor and more acidic soils, whereas the single-stemmed (monocormic) form prevails in richer habitats (Kallio and Mäkinen 1978, Verwijst 1988, Karlsson et al. 2004). It is also assumed that polycormic forms facilitate the growth of basal shoots more than monocormic trees (Kallio and Lehtonen 1973, Kallio and Mäkinen 1978). Regenerating forests may therefore benefit more from growth of basal shoots on polycormic trees than from establishment of seedlings (Neuvonen et al. 2001). Other morphological traits like height and phenotype are mostly dependent on abiotic factors, such as mean temperatures and wind. Especially along the tree line with short growing seasons trees tend to be smaller (Körner 2003).

The study area comprised two sites, each including a poorer and a richer locality. The bedrock formations of the western part of the study area are mostly characterized by sand stone with quartz and slate deposits. The eastern part of the study area comprises mostly dioritic and granitic gneiss, while there are also occurrences of gabbro, amphibolite and slate in the poorer locality of the eastern study site. Ground vegetation in the study area often consists of layers of black crowberry (*Empetrum nigrum*) in addition to grasses, mosses and *Vaccinium* species, especially in the poorer more oligotrophic habitats. In richer and wetter habitats also ferns and taller forbs can be found and often comprise more monocormic trees. However, as forest defoliation can have a strong impact ground vegetation, this assembly should be seen as a rough

approximate. For example, an increase in grasses like *Avenella flexuosa* as response to forest defoliation has been observed, as well as general shifts in understorey vegetation have been documented after moth outbreaks especially in oligotrophic forest types (Lehtonen and Yli-Rekola 1979, Jepsen et al. 2013, Karlsen et al. 2013)*.
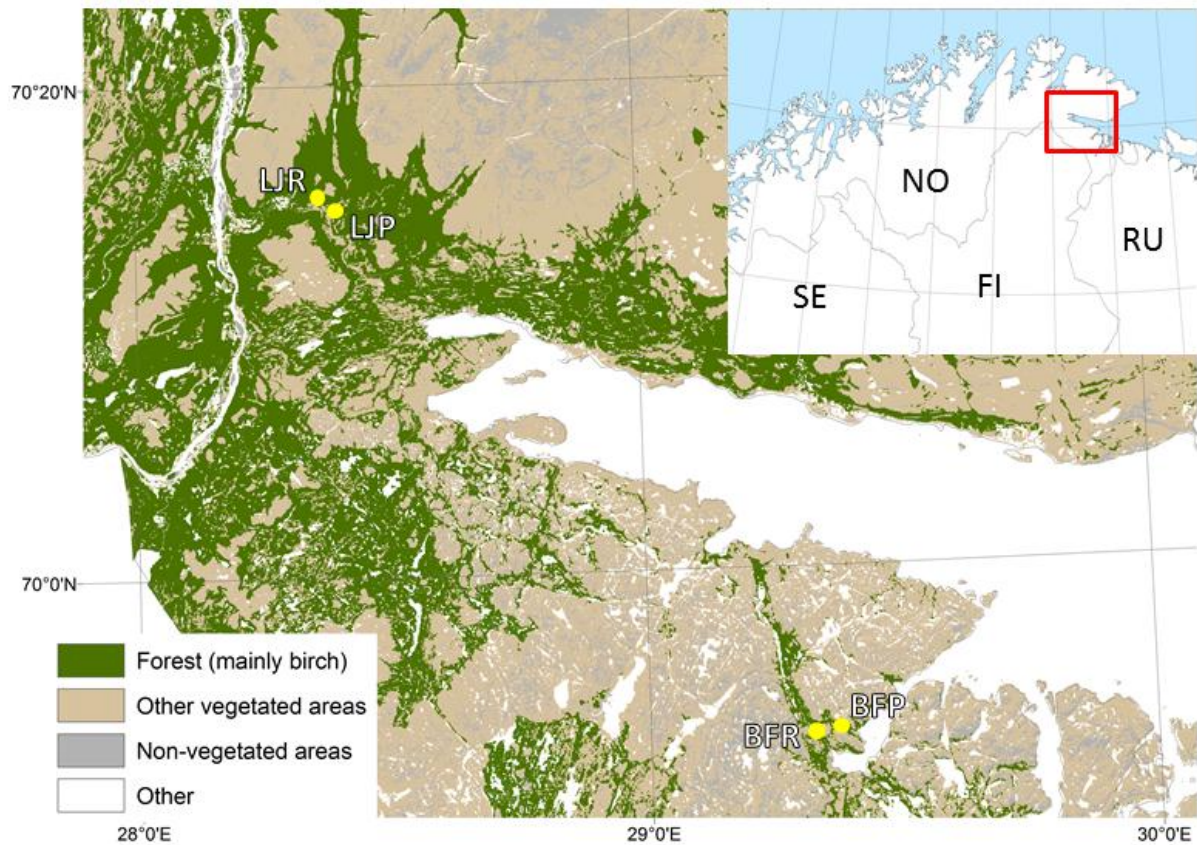

Figure 2 Map of Finnmark, Northern Norway. Yellow marks indicate field sites. **LJR** Luftjok rich, **LJP** Luftjok poor, **BFR** Bugøyfjord rich, **BFP** Bugøyfjord poor.

2.2 Study design

In 2011, 40 square plots (each 30 m x 30 m) have been laid out in the South Varanger region in northern Norway, 20 at an eastern locality near Bugøyfjord (BF) and 20 at a western locality in Luftjok valley (LJ, Figure 2). Both localities sustained severe forest defoliation by moth larvae, however the LJ site was subjected to a more intense and prolonged outbreak due to the consecutive outbreaks of two moth species (*Epirrita autumnata* and *Operophtera brumata*) whereas defoliation in the experimental plots of BF was caused only by the winter moth (Jepsen et al. 2008, Klemola et al. 2008, Jepsen et al. 2009a, Jepsen et al. 2009b). Within each site, half of the plots were located in areas with poorer soils while the remaining half was situated in richer soil (hereafter referred to as P and R respectively). This distinction was done by the land

8

owners (Finnmarkseiendommen Finnmárkkuopmodat) and the local forestry management of the county administration (Fylkesmannen i Finnmark) and refers only to differences within each site. The poor habitat in Luftjok is relatively oligotrophic with high abundances of *Empetrum nigrum*, whereas the richer plots are laid out in more eutrophic forest, comprising not only more taller forbs and denser vegetation, but also more monocormic trees. The differences in ground vegetation between poor and rich plots are not as clear in Bugøyfjord, due to higher variations between plots within a vegetation type.

The treatment (control or clear cut) was randomly assigned to plots, resulting in 5 control plots (hereafter K) and 5 clear cut plots (hereafter H) in each of the forest types (P and R).

2.3 Sampling

Prior to clear cutting 20 trees in each plot were individually marked using numbered metal tags. As the distinction between individual trees can be difficult sometimes, especially in polycormic tree stands, a 'functional' cluster of stems with no apparent root connections to nearby clusters of stems was defined as an individual tree. The number of stems was counted and the three tallest stems on a tree were classified into live and dead stems. A stem was classified as dead if it had no live foliage and no basal shoots. Stem height and diameter (at the base and at chest height) were measured on the same stems. In the following years (2012 and 2013), all stems on a tree were classified into live and dead categories, further distinguishing between standing, broken and fallen stems in the dead category. In September 2011, all stems and basal shoots of all trees in clear cut plots were cut down at their base using chainsaws and leaving stumps with estimated heights between 10 and 30 cm above ground. Since half of all marked trees were cut down, no measurements on stem heights and stem diameters were done in the years after clear cutting. In August 2012 and 2013, all marked trees were retrieved and tree stumps in clear cut plots were marked with snow poles in 2012 for better perceptibility in future years.

In all years, the basal shoots on each tree were counted. A basal shoot was defined as a shoot emerging from the base of a stem and not exceeding a length of 1.3 m. Shoots above 1.3 m were defined as stems. Basal shoots were further classified into unbrowsed and browsed shoots, depending on whether they showed bite marks from herbivores. In 2012 and 2013, base diameters and lengths of the five tallest basal shoots were measured. Birch saplings were counted in a 2 m wide transect along the diagonals of a plot (cf. Figure 3). A sapling was defined as a new recruit originating from seed (e.g. with no detectable connection to other shoots or stems) not exceeding 1.3 m in height. Saplings taller than 1.3 m were then accordingly

9

considered as individual trees. However, sapling counts showed only a minor increase over the years (average increase over two years: 0.6 saplings per plot) and were therefore not suitable for a comprehensive statistical analysis. Herbivore activity was recorded along the same diagonals as the saplings in the form of the number of droppings from moose and reindeer and the number of rodent runways that were crossing the diagonals. Because records of ungulate droppings showed too low abundances for reliable analysis at a plot level (droppings per plot (mean): Moose=0.18; Reindeer=0.3), the proportion of browsed shoots on a tree was used as an indirect measure of herbivore activity. Counts of rodent runways in 2012 and 2013 were strongly influenced by the remnants of a massive peak in lemming abundance in 2011 and were therefore excluded from further analyses.
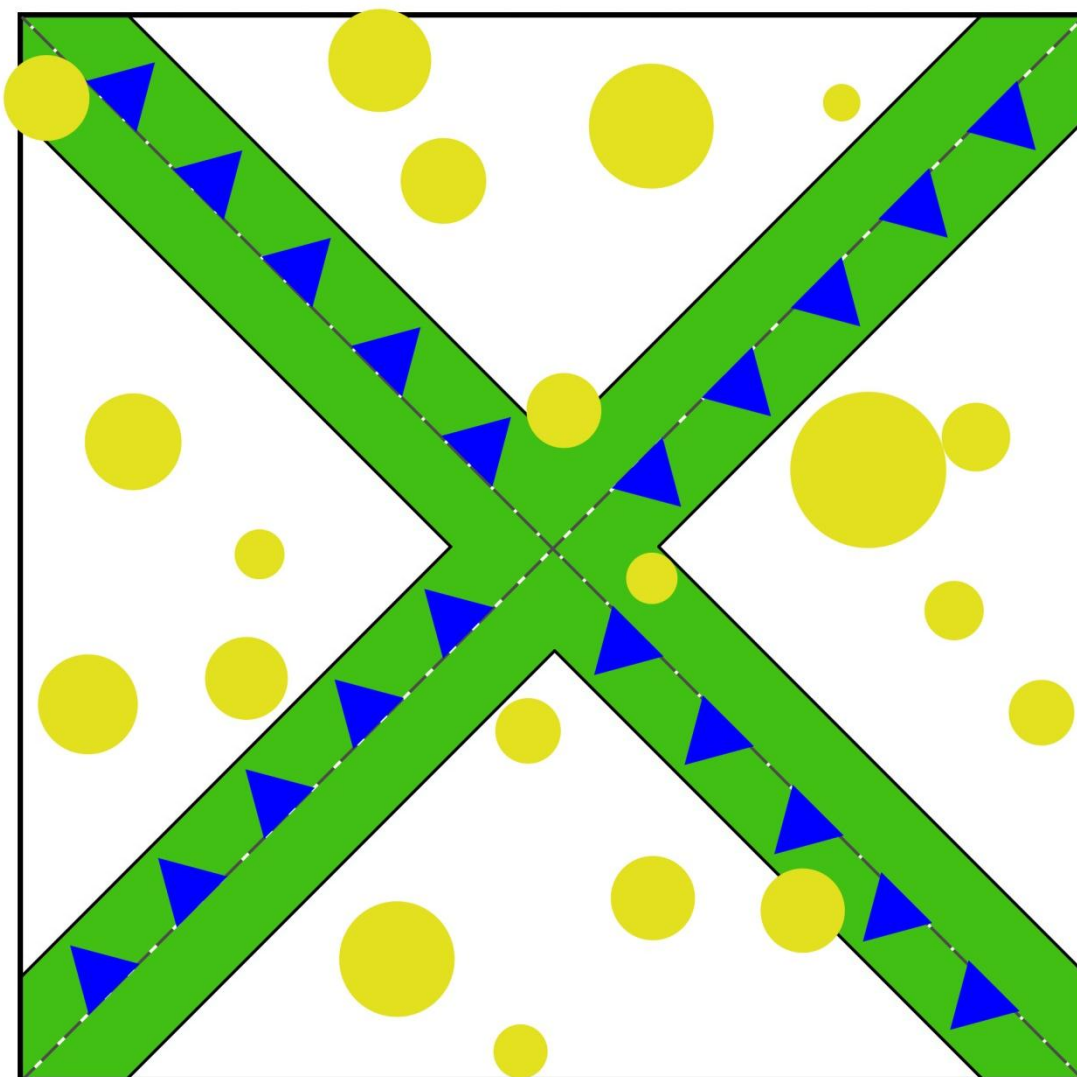

Figure 3 Schematic drawing of a plot (not to scale). Plot dimensions 30 m x 30 m. Green area along diagonals (2 m width) equals sampling area for birch saplings and ungulate droppings. Blue triangles indicate vegetation samples, each 3 m apart. Yellow circles represent marked trees (n=20 per plot).

Table 1 Overview of sampled data.

Sampling object	Name	2011	2012	2013	Description
Marked Tree (n=20 per plot)	Stems	X	X	X	Number of stems per tree
	Live stems	X	X	X	Number of live stems (for the 3 tallest stems in 2011)
	Dead stems	X	X	X	Number of dead stems (for the 3 tallest stems in 2011)
	Tree Height	X			Height of the three tallest stems on a tree; in 0.5 m increments until 6 m height, taller stems classified as 6 m+
	Diameter Base	X			Stem diameters of the three tallest stems on a tree at their base
	Diameter Chest	X			Stem diameters of the three tallest stems on a tree at chest height
Basal Shoots	Basal shoots	X	X	X	Number of basal shoots per tree
	Browsed	X	X	X	Proportion of browsed shoots
	Length		X	X	Length [cm] of the 5 tallest shoots
	Diameter		X	X	Diameters [mm] corresponding to 'Length'
Saplings	Saplings	X	X	X	Number of birch saplings in 2m transect along diagonals
Vegetation	Vegetation	X	X	X	Vegetation abundance from sampling triangles along the plot diagonals (n=20)
Herbivores	Moose	X	X	X	Moose droppings in 2 m transect along diagonals
	Reindeer	X	X	X	Reindeer droppings in 2 m transect along diagonals
	Rodents	X	X	X	Rodent runways crossing the plot diagonals

Vegetation was registered using the point intercept method (Bråthen and Hagberg 2004), in order to get an estimate of the abundance of plants. In this method, a number of metal pins is lowered vertically into the ground vegetation and the number of hits of a given plant species on these pins is recorded. Three pins arranged in a triangle (each 40 cm apart) were used as sampling units, recording hits of all plant species (see App. 1 for list of all species/species groups registered). Vegetation sampling was repeated along the diagonal transects every three

meters counting from the center point outwards (five repetitions in each direction, n_{Plot}=20; see Table 1 for list of all measurements).

2.3 Statistical analysis

2.3.1 Initial state comparison

In order to validate the a priori distinction between poor and rich sites, non-metric multidimensional scaling (NMDS, Morisita-Horn dissimilarity index) was used on vegetation data. NMDS uses dissimilarity indices based on the species matrix, where columns represent plant species and rows representing samples (i.e. sampling triangle). Here, the occurrences were summarized to a plot level, resulting in one value per plot and plant species. The subsequent plotting of dissimilarities then visualized distances (i.e. similarities and dissimilarities) in vegetation composition between plots. Separate analyses were performed for each of the sites (BF and LJ). The three-dimensional solution yielded lower stress levels than the two-dimensional approach and was therefore the preferred solution (2D stress levels: BF=0.17, LJ=0.11; 3D: BF=0.11, LJ=0.07).

To test the significance of the differences in vegetation community structure between poor and rich sites a multi-response permutation procedure (MRPP) was performed using the `mrpp` function in the `vegan` package (Oksanen et al. 2012). By using pre-defined groups (here: poor and rich), the mean within-group distance is calculated based on a dissimilarity matrix (Morisita-Horn dissimilarity index) and weighted by the sample size of the group, resulting in observed δ. Further, an expected δ is calculated based on Monte-Carlo permutations (n=1000). The effect size (A) is then expressed as A=1-(observed δ/expected δ), giving an indication of the distance between the given groups, i.e. higher effect sizes indicate greater distances between the tested groups than within these groups. The MRPP was performed separately on each of the sites.

2.3.2 Regeneration through basal shoots

To evaluate the forest regeneration through basal shoots I created generalized linear mixed-effects models using the `lme4` library (Bates et al. 2013). The use of generalized linear mixed-models allowed to include random factors and to model repeated measurements over a time series. A two step approach was used to address zero inflation. Thus, to explain the occurrence of trees with no basal shoots, I fitted logistic models distinguishing only between the presence and absence of basal shoots. Then, for modeling the abundance of basal shoots (number of

shoots per tree), I fitted poisson models using the subset of trees with one or more basal shoots. Response variable in the logistic models was the presence/absence of basal shoots, and in the poisson models the abundance of basal shoots. Site (BF, LJ), treatment (K, H), year (2011, 2012, 2013) and vegetation type (P, R) were used as explanatory variables. Furthermore, the initial number of stems (prior to clear cutting) was used as an explanatory variable, because polycormic trees can be assumed to respond stronger to clear cutting than monocormic trees (Kallio and Lehtonen 1973, Kallio and Mäkinen 1978). Thus, polycormic trees are expected to show higher numbers of basal shoots than single stemmed trees. Random variables in all models were the individual plots and trees. Plots were created with the `ggplot2` library in R (Wickham 2009). Using the `AICcmodavg` package (Mazerolle 2012), the most parsimonious models for both model types were chosen based on their AIC-value (Akaike Information Criterion), which gives an indication of the goodness-of-fit but model simplicity as well. Parameter estimates from the selected models were then plotted with the `matplot` function.

In order to assess the effect of clear cutting qualitatively, a Wilcoxon signed-rank test was performed on the growth rate of basal shoots to test for differences between treatments. Percentual increases (and decreases respectively) were calculated for changes in shoot length from 2012 to 2013 and were used to test for differences between treatments while distinguishing between sites and vegetation types.

2.3.3 Browsing pressure through herbivores

Because records of ungulate droppings showed too low abundances for reliable analysis, browsing pressure was examined indirectly by using the abundances of unbrowsed and browsed shoots. To test for differences of browsing between treatments (K, H), Wilcoxon signed-rank tests were performed, which allows to test data that does not follow a normal distribution. Here, I compared the proportions of browsed basal shoots (as percentage of all basal shoots on a tree) between control and clear cut plots for all three years while distinguishing between sites and vegetation types (12 tests in total).

2.3.4 Tree stand dynamics

The survival of trees was assessed by comparing the proportion of dead trees in 2011 and 2013 with regard to their affiliation to site and vegetation type as well as growth form. Trees were considered dead, when neither live stems nor basal shoots were recorded. The median number of stems was used to determine the degree of polycormism and was calculated for both vegetation types at either site, based on 2011 data. As clear cutting could potentially kill trees with poor ability to regenerate from shoot and trees might respond differently to the treatment

depending on their growth form, abundances of live and dead trees in clear cut plots from 2013 were plotted based on the original number of stems to get a visual comparison of killed trees. This was also statistically analyzed by fitting a logistic model (see also 2.3.2), with the live status from 2013 as a binary response variable (live=1, dead=0), and the number of stems from 2011 as an explanatory variable.

All statistical analyses and subsequent plotting were performed using the R language (R Development Core Team 2012).

3 Results

3.1 Initial state comparison

The multidimensional scaling analysis showed a clear segregation between poor and rich (P, R) vegetation types in Luftjok (Figure 4), while there was a visible overlap between plots in Bugøyfjord (Figure 5). The relatively low stress levels for the NMDS with 3 dimensions indicated a good fit ($Stress_{BF}$=0.11, $Stress_{LJ}$=0.07). Results of the permutation tests however gave significant and similar results for both sites (Poor-Rich distinction; BF: A=0.067, p<0.001; LJ: A=0.07, p<0.001), indicating slightly bigger differences in vegetation composition between groups than within the tested groups. Nevertheless, the observed δ showed clear differences between sites ($δ_{BF}$=0.56; $δ_{LJ}$=0.35), indicating higher variances within groups in Bugøyfjord.
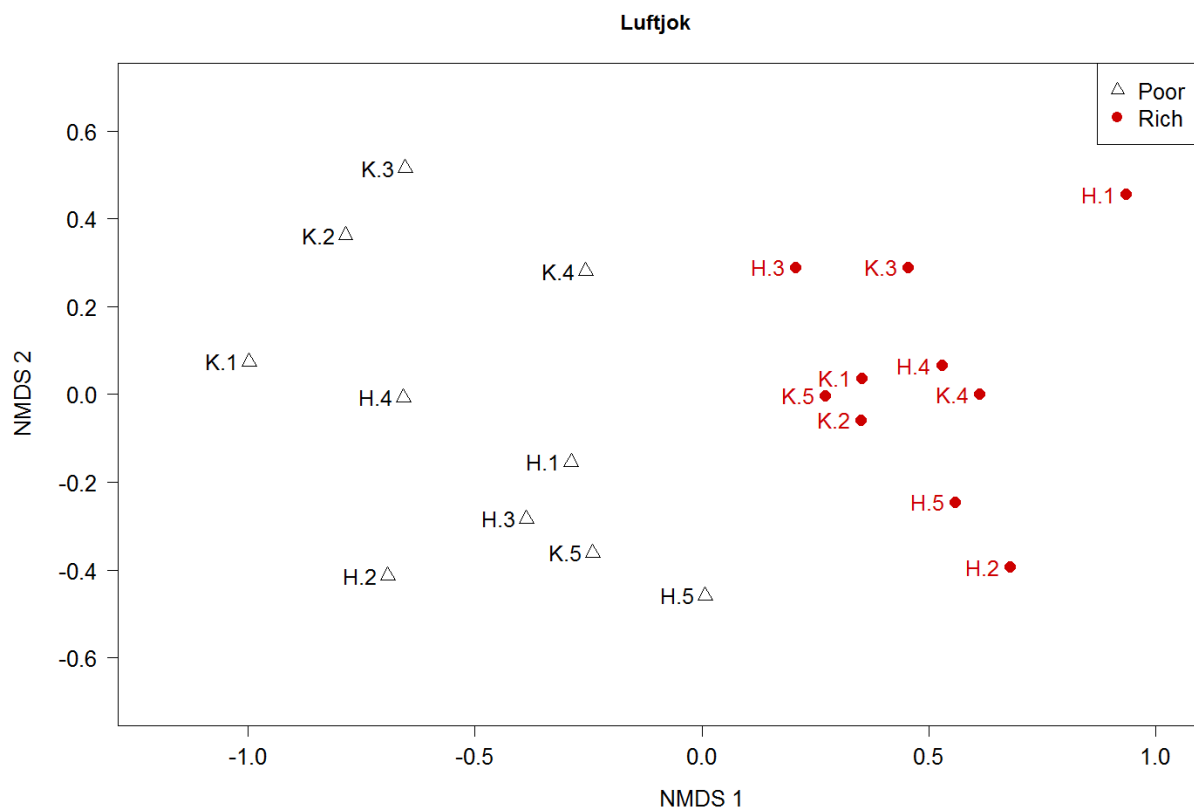

Figure 4 NMDS plots for Luftjok. Black triangles represent poor plots, red circles rich plots. **K** Control plots; **H** Clear cut plots.
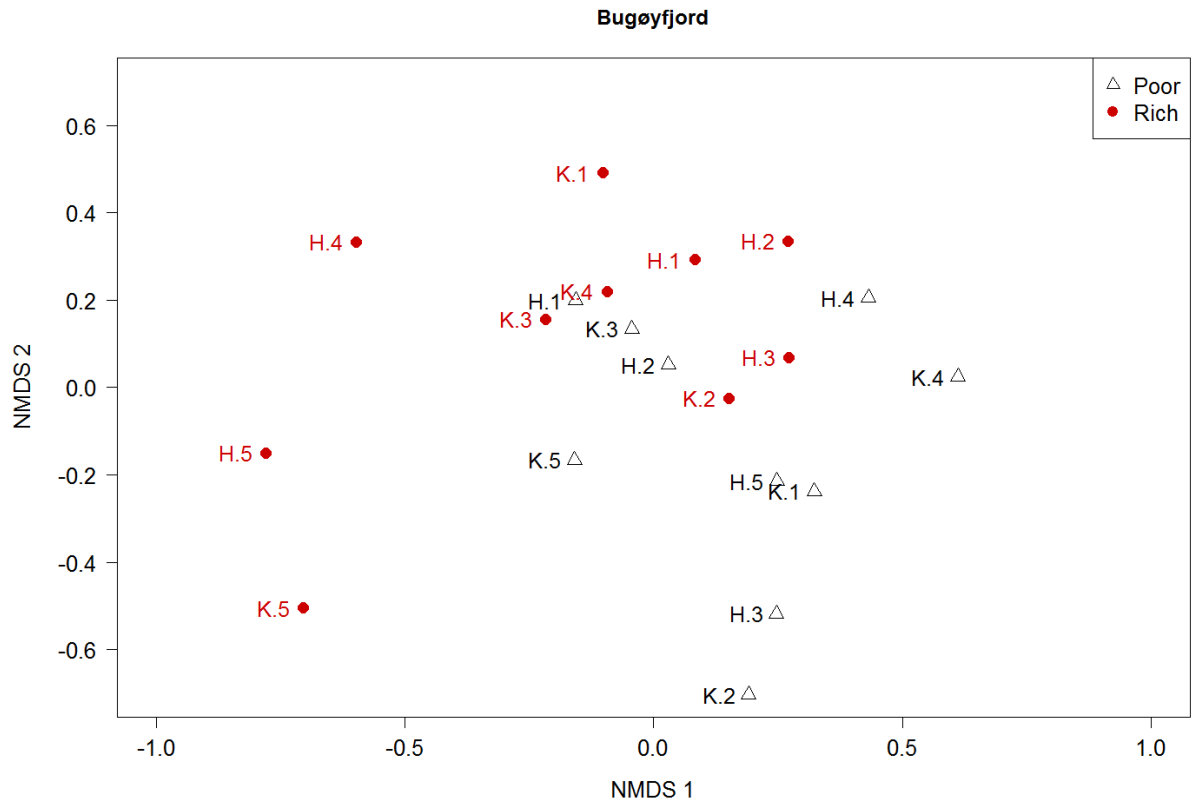
15

Figure 5 NMDS plots for Bugøyfjord. Black triangles represent poor plots, red circles rich plots. **K** Control plots; **H** Clear cut plots.

3.2 Regeneration through basal shoots

The number of basal shoots per tree ranged from 0 to 60 in 2011 (Median=2; first and third quartile $Q_{1(2011)}=0$, $Q_{3(2011)}=7$), increasing to 0 to 264 in 2013 (Median=6; $Q_{1(2013)}=0$, $Q_{3(2013)}=16$) (cf. Figure 6). Thus, within two years after clear cutting, the number of basal shoots increased by 6951 to a total of 11174. The vast majority of this increase happened in clear cut plots (n=6542; 94.12% of the increase). Further, two thirds (67.08%) of all new basal shoots between 2011 and 2013 grew in the first year after the treatment. However, together with the number of basal shoots, variance also increased considerably.
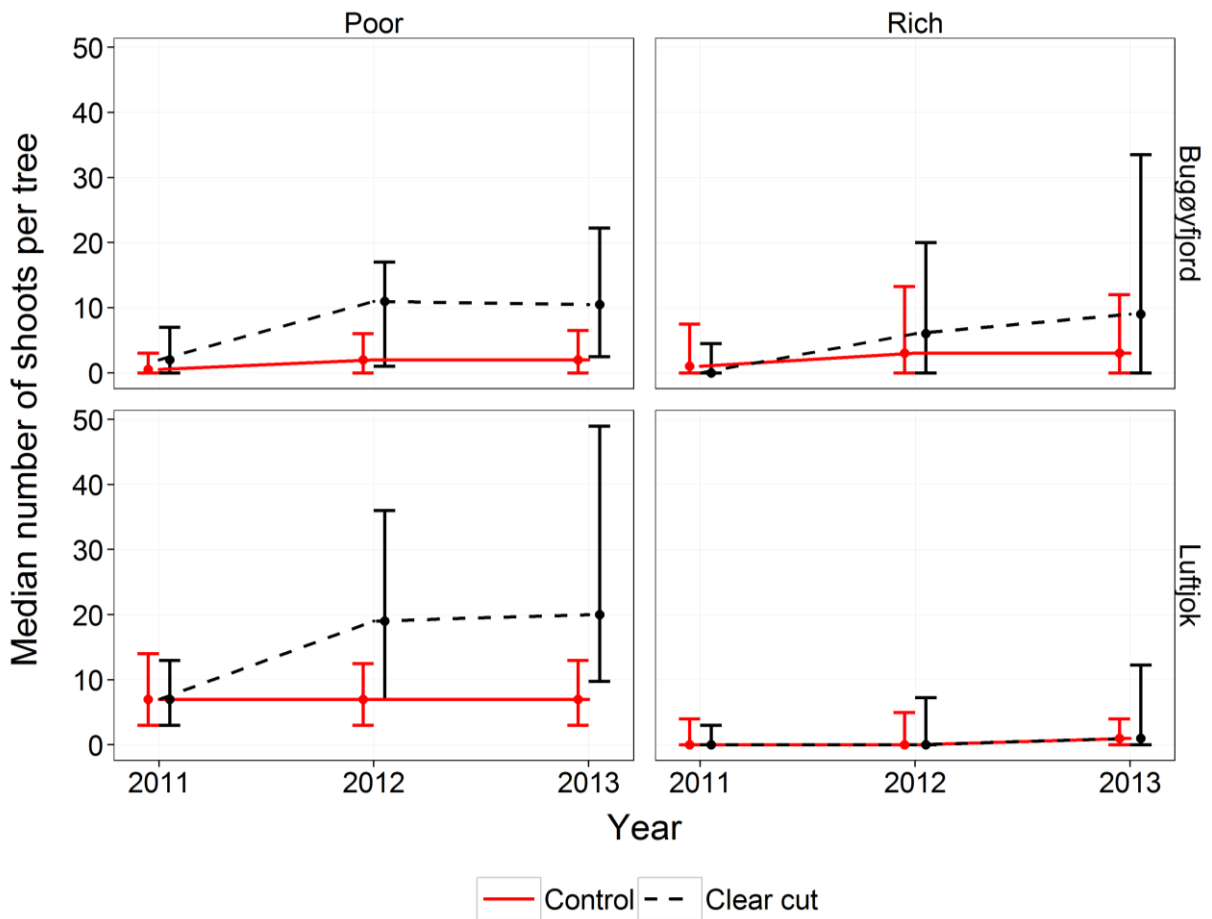
Figure 6 Basal shoots per tree (Medians with 1st and 3rd quartiles), from 2011 to 2013 on a plot level.

Candidate models for the presence and absence of basal shoots are presented in Table 2 together with AIC values and the log-likelihood for each model. The model with best support was chosen based on the lowest AIC value, which indicates the level of support for the model being the most parsimonious. All models included single trees (n=798) and plots (n=40) as random factors.

Table 2 Table of all fitted logistic models with AIC values and LogLikelihood (LL). Fixed factors: Treatment (Clear cut/Control), Year (2011/2012/2013), Quality (Poor/Rich), Site (BF/LJ), Stems (Number of stems in 2011). Asterisks mark interaction terms (included factors are also treated individually), '+' indicates additive effects. Random factors in all models: plots (n=40) and trees (n=798). Response variable: the presence of basal shoots on a tree (i.e. trees having any basal shoots).

Model structure (fixed effects)	AIC	LL
Treatment*Year+ Quality*Site+ Stems	1847.80	-911.84
Treatment*Year+ Quality*Site+ Stems*Year	1850.79	-911.31
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Quality	1851.75	-909.76
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Quality+ Stems*Site	1852.26	-909.00
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems	1852.86	-911.33
Quality*Site+ Treatment+ Year+ Stems	1852.94	-916.43
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Site	1854.01	-910.89
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Treatment	1854.78	-911.28
Treatment*Year+ Quality+ Site+ Stems	1870.50	-924.19
Treatment+ Year+ Quality+ Site+ Stems	1875.03	-928.48
Year*Quality+ Site*Treatment+ Year*Treatment+ Stems	1875.68	-923.75
Year*Quality+ Treatment+ Site+ Stems	1878.06	-927.98
Year*Quality+ Site*Treatment+ Stems	1880.07	-927.97

There was a significant overall increase in trees with basal shoots in both years after clear cutting (Estimate E_{2012}=0.95, p=0.002; E_{2013}=1.13, p<0.001). Also, there was a higher proportion of trees with basal shoots in Luftjok than in Bugøyfjord throughout all three years (E_{LJ}=5.36, p<0.001). Furthermore, the significant interaction term between treatment and year (both 2012 and 2013) indicates the increase in the number of trees with basal shoots after treatment was greater in clear cut plots than in the control plots ($E_{Cut2012}$=0.91, p=0.04); $E_{Cut2013}$=1.32, p=0.004). The initial number of stems present in 2011 had a positive effect on the probability of having basal shoots ($E_{Stems2011}$=0.4, p<0.001). A significant negative effect was present for the interaction between vegetation type and site, indicating a higher number of shootless trees in the rich plots of Luftjok (E_{LJRich}=-7.22, p<0.001; cf. Figure 7, see App. 2 for all estimates).
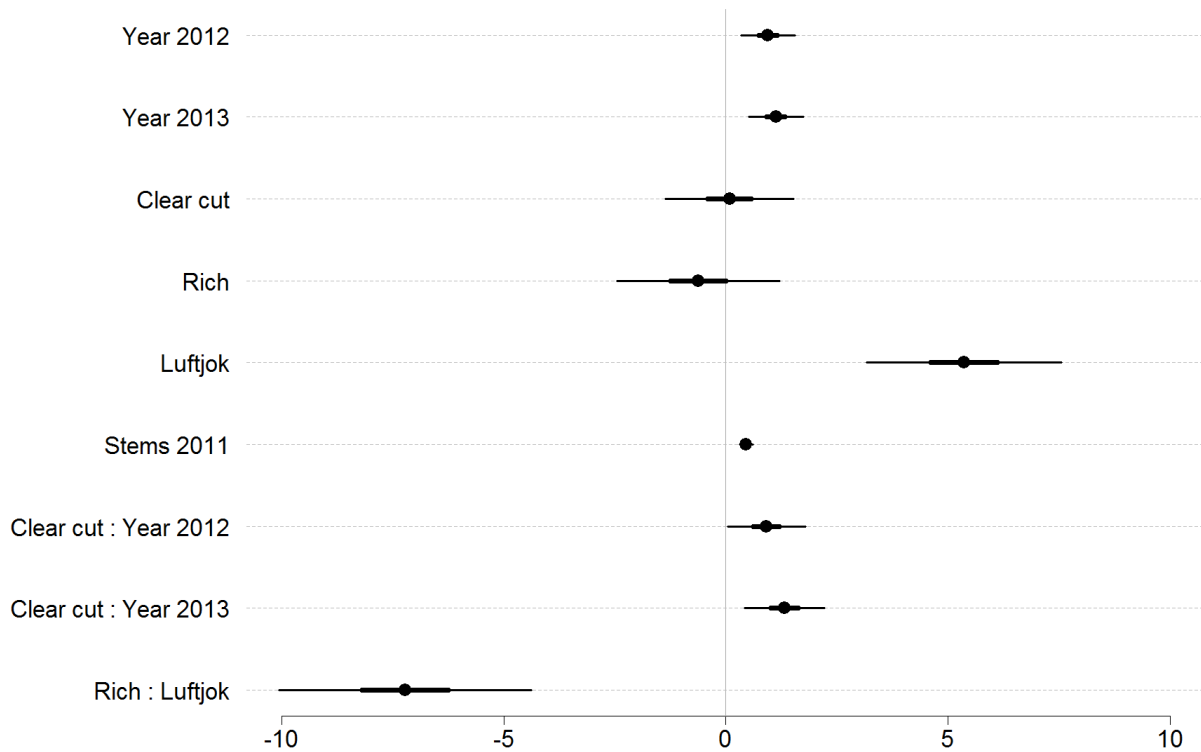
Figure 7 Estimates for the generalized linear mixed models focusing on the presence and absence of basal shoots. Results give estimates of the effect size on a logit scale in comparison to the reference level (depending on factor: Year 2011, Control, Poor, Bugøyfjord). Thick lines indicate the 50% confidence interval (1 SD), thin lines the 95% CI (2 SD). Colons mark interaction terms.

Analogously to the logistic models, candidate models for the abundance of basal shoots are presented in Table 3. For the poisson model a subset was used, that only contained trees with at least one basal shoot per tree. Single trees (n=590) and plots (n=40) were again used as random factors in all given models.

The most parsimonious model of basal shoot counts indicated higher numbers of basal shoots per tree in the Luftjok plots (E_{LJ}=0.59, p<0.001). However, for the rich plots in Luftjok a negative estimate was calculated (E_{LJRich}=-1.04, p<0.001). Highly significant increases in the number of basal shoots per tree were also found in all clear cut plots after trees had been cut down ($E_{Cut2012}$=0.93, p<0.001; $E_{Cut2013}$=1.2, p<0.001). Furthermore, plots in the rich vegetation type also showed a significantly higher increase in basal shoots in the years after clear cutting ($E_{Rich2012}$=0.18, p<0.001; $E_{Rich2013}$=0.39, p<0.001). Concurrent with expectations, trees in clear cut plots showed slightly higher, yet significant increases in basal shoots the more stems they initially had in 2011 ($E_{CutStem2011}$=0.078, p<0.001; cf. Figure 8, see App. 2 for all estimates).

Table 3 Table of all fitted poisson models with AIC values and LogLikelihood (LL). Fixed factors: Treatment (Clear cut/Control), Year (2011/2012/2013), Quality (Poor/Rich), Site (BF/LJ), Stems (Number of stems in 2011). Asterisks mark interaction terms (included factors are also treated individually), '+' indicates additive effects. Random factors in all models: plots (n=40) and trees (n=560). Response variable: abundance of basal shoots on a tree.

| Model structure (fixed effects)	AIC	LL
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Treatment	5006.68	-2487.16
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems	5021.92	-2495.81
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Site	5022.93	-2495.29
Year*Quality+ Site*Treatment+ Treatment*Year+ Site*Quality+ Stems*Quality	5023.96	-2495.81
Year*Quality+ Site*Treatment+ Treatment*Year Site*Quality+ Stems*Quality+ Stems*Site	5024.91	-2495.26
Year*Quality+ Site*Treatment+ Year*Treatment+ Stems	5045.58	-2508.65
Treatment*Year+ Quality*Site+ Stems*Year	5117.42	-2544.58
Treatment*Year+ Quality*Site+ Stems	5132.47	-2554.13
Treatment*Year+ Quality+ Site+ Stems	5155.92	-2566.88
Year*Quality+ Treatment+ Site+ Stems	6001.75	-2989.79
Year*Quality+ Site*Treatment+ Stems	6003.02	-2989.41
Quality*Site+ Treatment+ Year+ Stems	6036.70	-3008.28
Treatment+ Year+ Quality+ Site+ Stems	6060.73	-3021.31
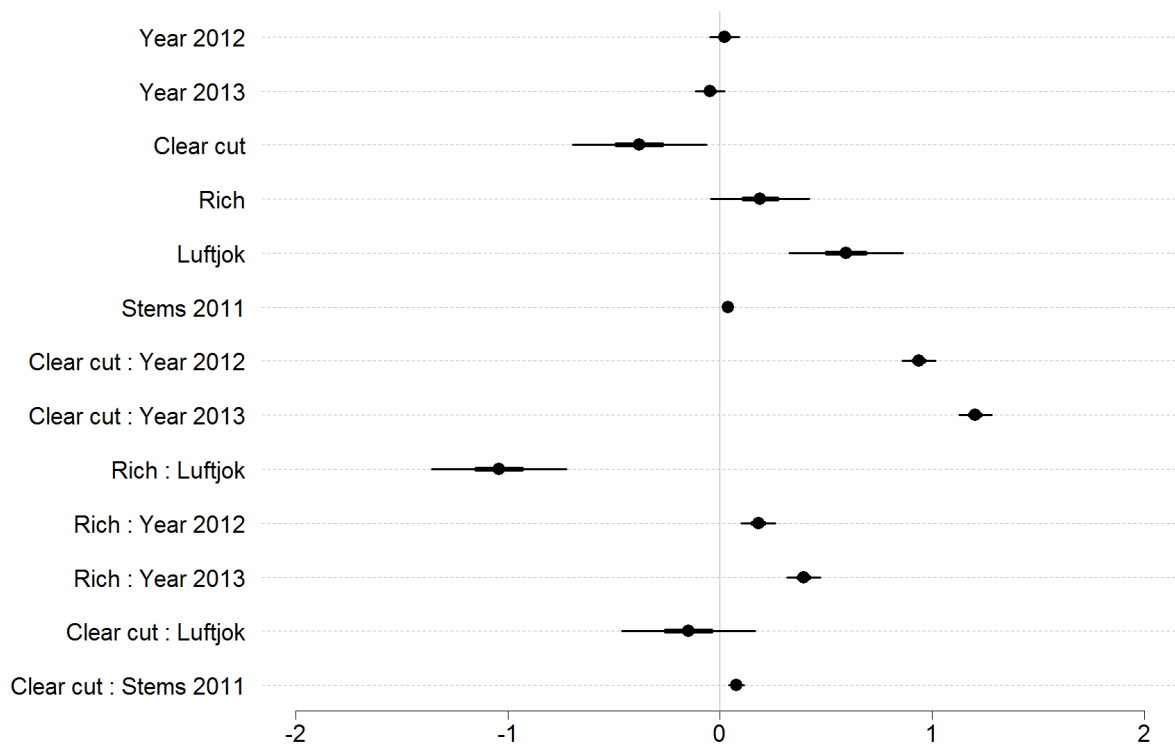
Figure 8 Estimates for the generalized linear mixed models focusing on the abundance of basal shoots. Results give estimates of the effect size on a logit scale in comparison to the reference level (depending on factor: Year 2011, Control, Poor, Bugøyfjord). Thick lines indicate the 50% confidence interval (1 SD), thin lines the 95% CI (2 SD). Response variable: abundance of basal shoots per tree.

The median length of basal shoots increased by 17.5 cm from 30 cm in 2012 (Q_1=19 cm; Q_3= 60 cm) to 47.5 cm in 2013 (Q_1=31 cm; Q_3=77 cm). Results from the Wilcoxon signed-rank test showed a significantly faster growth rate in clear cut plots than in control plots (W=41956, p<0.001). This difference was found throughout all plots in Luftjok and in the rich plots of Bugøyfjord, whereas the poor plots in Bugøyfjord did not reveal any significant differences in growth rate (Figure 9).
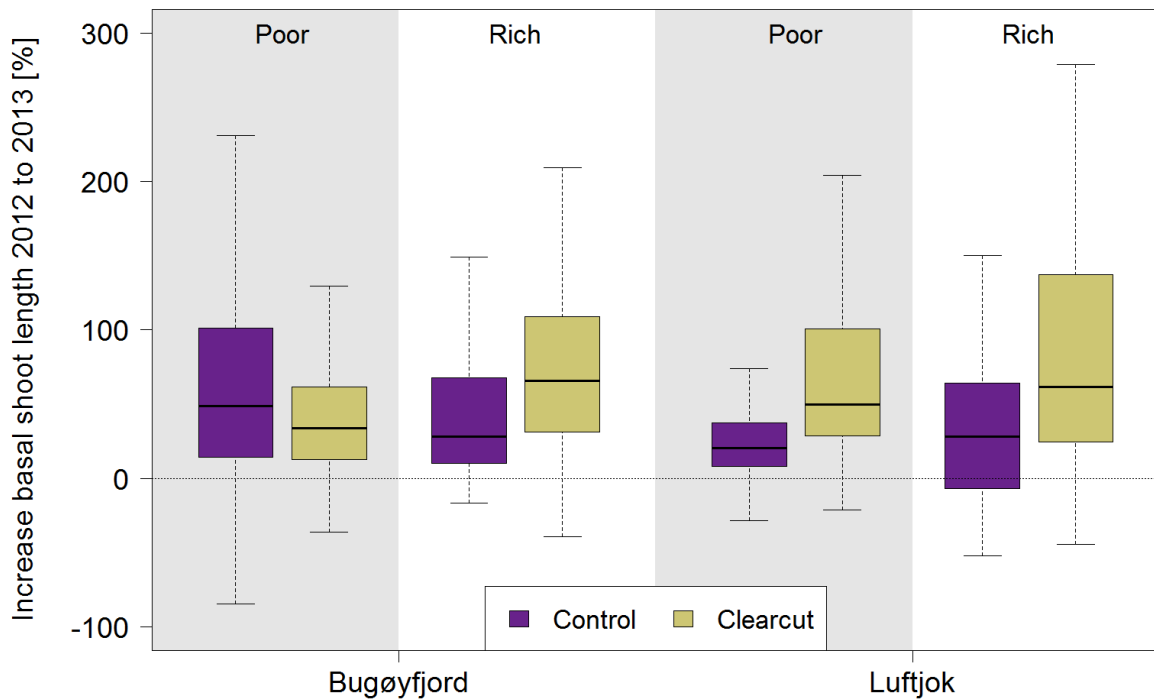
Figure 9 Basal shoot growth per tree. Changes in percent from 2012 to 2013.

3.3 Browsing pressure through herbivores

Over the years there was a visible increase in browsing in the majority of all plots. The analyses of browsing pressure further revealed systematic differences between control and clear cut plots. In Luftjok, control plots experienced significantly higher browsing pressure throughout all three years in both vegetation types (Wilcoxon signed-rank; W_{LJRich}=679, p=0.005; W_{LJPoor}=2161, p<0.001; Figure 10). In contrast, plots in Bugøyfjord did not show any significant differences in browsing between control and clear cut plots before cutting the trees in 2011. One year later, significantly more browsing was visible in clear cut plots of the poor vegetation type ($W_{BFPoor2012}$=3317.5, p<0.001), until in 2013 eventually all plots in Bugøyfjord showed the same differences in browsing between control and clear cut plots, with significantly higher browsing proportions in clear cut plots ($W_{BFPoor2013}$=1308.5, p<0.001; $W_{BFRich2013}$=807.5, p<0.001). Thus, plots in Bugøyfjord then showed the opposite pattern to plots in Luftjok, where the majority of browsing happened in control plots.
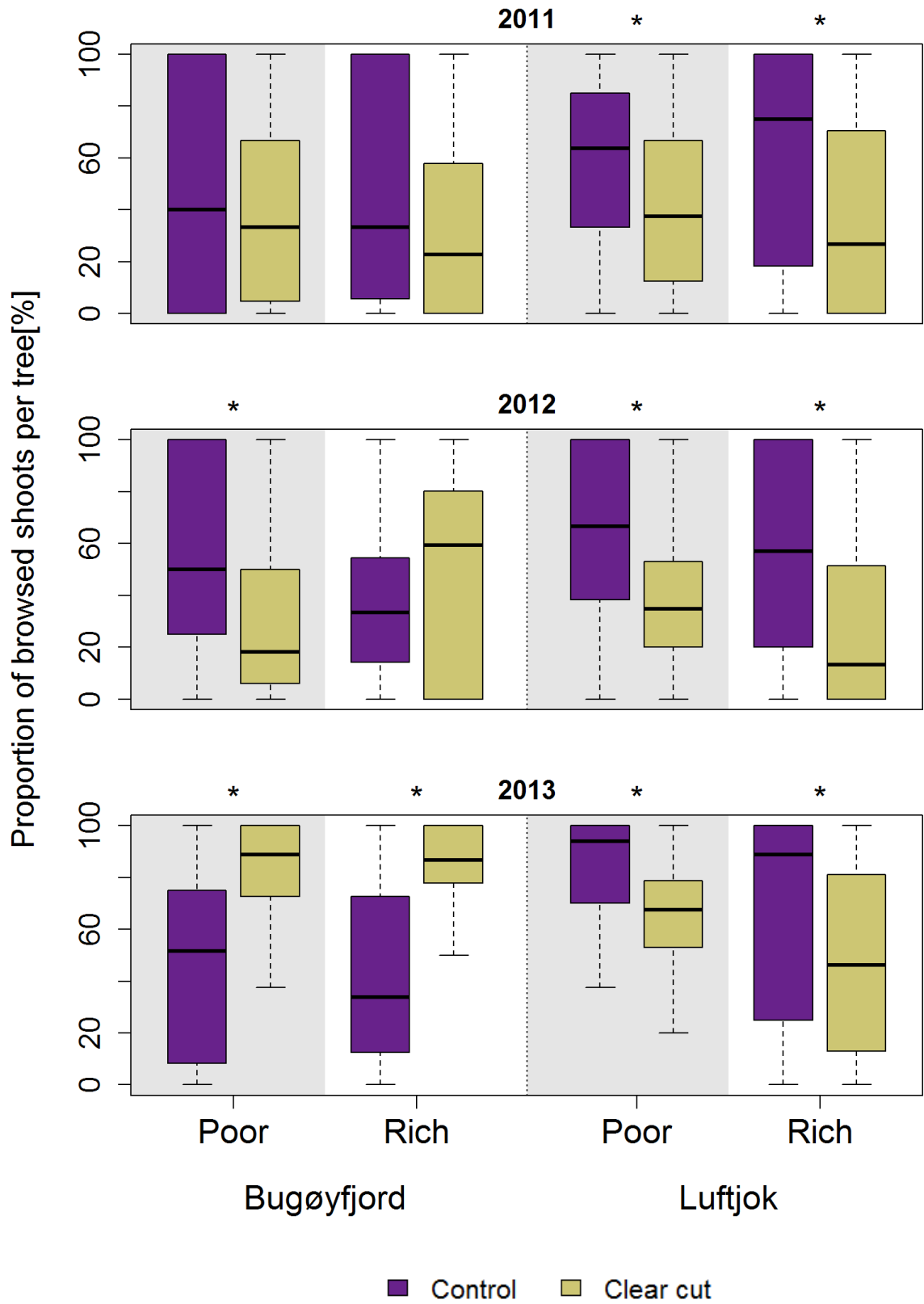
Figure 10 Ratios of browsed shoots during the experiment. Asterisks mark significant differences at a 0.05 significance level.

3.4 Tree stand dynamics

The median number of stems revealed that the highest stem abundances were found in poor vegetation types (Median$_{LJPoor}$=5, Median$_{BFPoor}$=5), whereas most monocormic trees were recorded in the rich plots in Luftjok (Median$_{LJRich}$=3; Median$_{BFRich}$=4). Prior to clear cutting 44 trees were assumed dead, the vast majority of them in Bugøyfjord (n=39).

Table 4 Abundances of dead trees in 2011 and 2013.

Site	Bugøyfjord		Luftjok		
Vegetation type	Poor	Rich	Poor	Rich	Sum
2011	23	16	1	4	44
2013	31	41	5	47	124
Increase	+8	+25	+4	+43	+80

After two years, 13 of these trees had recovered and were no longer classified as dead. However, due to clear cutting and the loss of stems, counts of dead trees increased to a total of 124, whereas 106 of them were found in clear cut plots, with the highest increase in the rich plots in Luftjok (Table 4). Live trees in clear cut plots from 2013 had significantly more stems in 2011 than dead trees (Estimate from logistic model: E$_{Stems2011}$=0.19, p<0.001), indicating a lower degree of polycormism among dead trees, which is further supported by the histograms of live and dead trees (Figure 11).
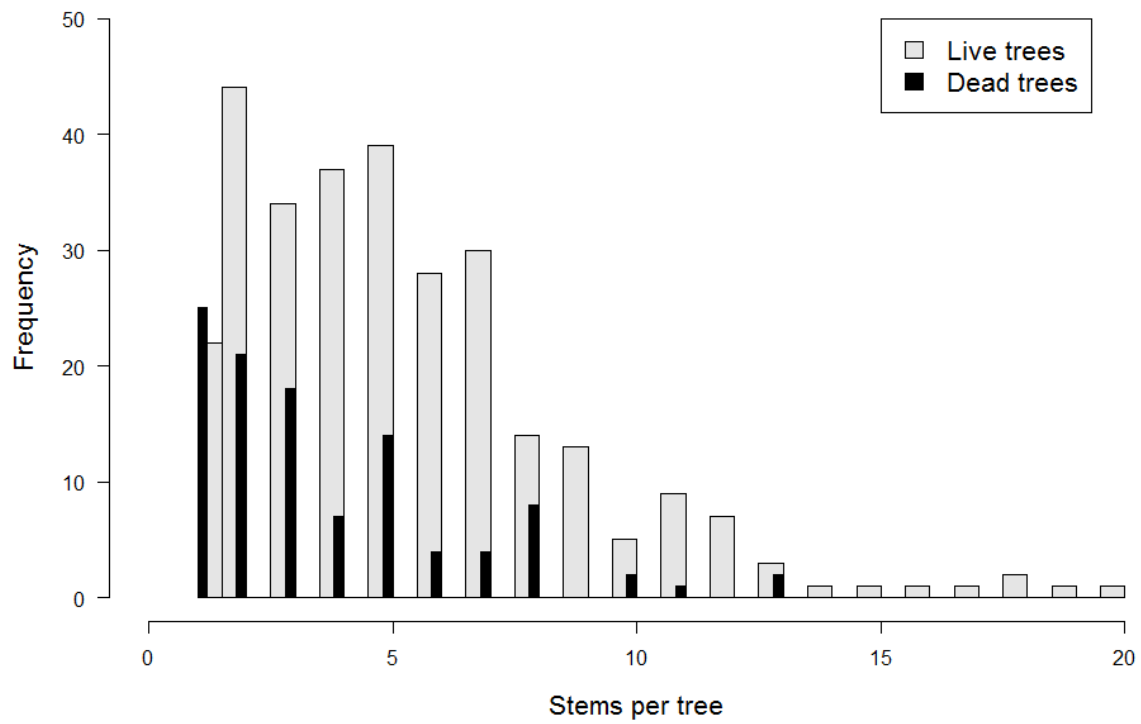
Figure 11 Histograms of stem numbers in 2013 clear cut plots based on stem abundance from 2011.

4 Discussion

The first two years of the experiment showed clear trends in forest regeneration and confirmed most expectations. Clear cutting had positive effects on the formation of basal shoots and thus clearly facilitated forest regeneration in comparison to control plots. The response in basal shoots to clear cutting showed differences between poor and rich vegetation types, though not in a consistent manner between sites. The expectations of this aspect – a greater increase of basal shoots in poorer plots - were confirmed in Luftjok, whereas plots in Bugøyfjord showed a contrasting response. The role of saplings in forest regeneration could not be assessed, since saplings show slower growth rates and may therefore contribute to the recovery in a greater extent not until future years. Further, the impact of herbivore browsing was documented, but the exact implications for forest regeneration are difficult to assess at this point, as e.g. reindeer presence may be strongly influenced by herding regimes.

4.1 Initial state comparison

The vegetation community composition confirms the a priori division of sample plots into poorer and richer sites. In Luftjok there was a very clear distinction between the poor and the rich site supported both by the NMDS-plots and the MRPP. In Bugøyfjord the distinction was evident, but less clear. Even though the results of the MRPP are highly significant (p<0.001), their effect size (A-value) is relatively small, which also indicates only small differences in the composition of the vegetation communities. Nevertheless sample sizes were relatively big, which can result in more robust results on the one hand, but may also increase variation on the other. Since the `mrpp` function estimated if the difference between rich and poor plots is bigger than the variance within one of these groups, it is also likely that variance between plots of one group increased the within-group difference, resulting in lower overall-difference. Especially in Bugøyfjord, the distinction between poor and rich plots was not as clear due to a broader range in vegetation composition throughout plots, resulting in an overlap between rich and poor localities in the NMDS-plots, which is further substantiated by the comparably high δ value for Bugøyfjord plots.

Further it should be mentioned that composition and abundances not only vary between plots, but are also subject to annual variations due to changing climatic factors (e.g. temperature, precipitation). NMDS plotting however (especially in LJ) suggests that the distinction into poorer and richer habitats is indeed applicable. Apart from annual and plot-wise variations, a general shift in the vegetation composition can be expected across all plots, as moth outbreaks

on their own are known to cause change in plant communities (Karlsen et al. 2013), let alone in combination with clear cutting. Thus, this transformation is likely to become more drastic in clear cut plots due to changing light levels on the ground.

4.2 Regeneration through basal shoots

Clear cutting clearly increased the formation of and regeneration through basal shoots in all experimental plots, with varying intensities depending on site and forest type. Thus, poor plots in Luftjok showed distinctly more basal shoots after clear cutting than the rich plots at the same locality. In contrast, plots in Bugøyfjord showed more similar responses in both forest types. Results from modeling the presence and absence of basal shoots on a tree, indicated a higher probability for basal shoots in trees that also had more stems before clear cutting. This is further supported by the fact that there are distinctly fewer trees with basal shoots in the rich vegetation plots in Luftjok, where trees show a lower degree of polycormism. These findings further confirm the findings of Kallio and Mäkinen (1978), which suggested polycormic trees to be more inclined to vigorous basal shoot formation. As model results also show significantly more trees with basal shoots in Luftjok than in Bugøyfjord, it can be assumed that this increase is mostly caused by and confined to the plots in the poor vegetation type, which is accordance with results from the abundance models (see below). Further, in the years after clear cutting significantly more trees with basal shoots were found. This is very likely caused by the clear cutting itself, as removing any parts that were (at least potentially) capable of performing photosynthesis, forces trees to regain this feature.

The results from the abundance models show that clear cutting does in fact significantly accelerate forest regeneration through basal shoots and is in line with expectations. Even though the response to the treatment varied between sites and vegetation types, the amount of basal shoots was consistently higher throughout clear cut plots. The distinction between rich and poor plots should be treated separately within the respected site, as clear cut plots in Luftjok showed the strongest increase in poor plots, whereas the stronger response in Bugøyfjord was visible in rich plots. Control plots showed neither significant nor visible changes regardless of affiliation with site or vegetation type and throughout all three years of the experiment. The strong response in basal shoots to the felling of trees is in line with expectations, as felling trees and subsequent formation of basal shoots is a well-known management action for forest rejuvenation (Kauppi et al. 1988, Hytönen and Issakainen 2001) and could further be explained by the theory of Lehtonen and Heikkinen (1995) that clear cutting preserves the root system from rot radiating from stems and at the same time facilitates

growth of basal shoots, which then are nurtured by an entire adult-tree-sized root system. The aspect of self-thinning between basal shoots has not been unitarily answered especially with regard to the given combination of a post-outbreak phase and clear-cutting of trees (Verwijst 1988). Considering the maximum number of 264 basal shoots on a single tree, long term observations are likely to give insight to the dynamics of stem development. Analogous to the logistic model results, higher abundances of basal shoots were found in originally polycormic trees. Thus, fewer basal shoots were counted in the rich plots of Luftjok that have fewer polycormic trees than the poor plots of the same site. But as there are significantly more basal shoots in all plots in Luftjok, this increase must be caused by poor plots, which is accordance with the results from the logistic model and is best explained by the different responses from mono- and polycormic trees.

Despite promising results, ecological consequences should be considered for clear cutting at large scales. It can be assumed that systematic clear cutting on large scales entails drastic changes to an ecosystem. With respect to the increase in dead trees after the treatment, selective cutting could be an alternative to clear cutting. This could avoid the felling of live (especially monocormic) trees for which clear cutting would rather impede regeneration than facilitating it. Also, dead trees can constitute an ecological niche for e.g. saproxylic insects, which would be destroyed at once when felling all trees in an affected area (Jonsson and Siitonen 2012).

In addition to the steep increase in basal shoot abundance in clear cut plots, shoot growth proved to be consistently higher in clear cut plots as well, with the exception of trees in poor plots in Bugøyfjord. The higher growth rate in cut trees seems likely, when considering that basal shoots have recourse to a fully grown root system while no stems withdraw nutrients or water, thus allowing for vigorous growth. The exception of the poor plots in Bugøyfjord can be most likely attributed to herbivores, as results for grazing pressure, show also an increase in browsing in said plots from 2012 to 2013 (cf. 3.3).

4.3 Regeneration through saplings

For birch saplings, only a slight increase was recorded over the years. As saplings need to establish their own root system they tend to grow slower than basal shoots, presumably making their contribution to forest regeneration properly detectable not until future years. Initial establishment of seedlings may be additionally aggravated by the changing vegetation (Karlsen et al. 2013), which theoretically could impede sapling establishment by shadowing or the

presence of allelopathic shrubs, such as *Empetrum nigrum*. This would also be in accordance with the theory that seedling establishment is facilitated in areas with low vegetation cover (Kallio and Lehtonen 1973) and will eventually surpass basal shoot growth, thus increasingly contributing to forest regeneration. However, due to the slower establishment and growth, saplings are more susceptible to severe damage by herbivore browsing, which may impede the regeneration through saplings even more than regeneration through basal shoots (Den Herder and Niemelä 2003).

4.4 Browsing pressure through herbivores

Even though it is very likely that herbivores impact forest regeneration, records for ungulate droppings did not allow for a comprehensive statistical analysis at a plot level. Because moose and especially reindeer roam over long distances (Tveraa et al. 2007), it seems probable that many of the plots that experienced grazing did not show any signs in form of droppings, as plots could have been grazed and crossed relatively fast without leaving any proof but grazing marks. Thus, analysis of browsing in trees revealed changes in grazing pressure over the years. While trees in Luftjok showed more signs of herbivore browsing in control plots during all years, browsing seemed to shift from control plots to clear cut plots in Bugøyfjord. Although there may be differences in herbivore densities between sites, they would not explain the differing patterns between treatments. Other explanations, such as diverging preferences in moose and reindeer for a given treatment (i.e. forest or open spaced plots), would be unsubstantiated, even though theoretically conceivable. However, there was a bias in browsing towards control plots before clear cutting. As mentioned above, treatments were assigned at random, suggesting the influence of other factors on herbivore grazing preferences.

In contrast to ungulate droppings, rodent presence was clearly visible in 2011, either directly or indirectly through runways and droppings. Runway counts from the following years were remainders from the peak year. Therefore, it is difficult to assess the amount of rodent influence on browsing in particular and forest regeneration in general. However, lemmings usually show cyclic fluctuations in population density, becoming potentially visible as long term patterns in browsing. And although ungulates are likely to be more efficient grazers (i.e. they can cause more browsing in a short period of time), rodents may cause similar damage by longer dwelling times and recurrent browsing throughout a year. The influence of herbivores on forest regeneration seems also substantiated by fencing experiments currently conducted in the Polmak area in the border area of northeastern Norway and Finland (Biuw et al. 2013). Even

though fencing can protect recovering trees from herbivory by moose or reindeer, excluding rodents from trees on larger scales would not be feasible.

4.5 Tree stand dynamics

The comparison of growth forms showed, that the oligotrophic forest areas in the rich plots of Luftjok yielded more monocormic trees than the poorer habitats. Also, it is apparent that clear cutting can kill trees, and more so in monocormic tree stands. Even though the development of trees revealed that trees are capable of recovery even after two years of no live signs, there was a considerable increase of dead trees especially in clear cut plots. The highest increase being recorded in the rich plots in Luftjok. As these plots also comprised the most monocormic trees, it stands to reason that this increase in dead trees was facilitated by the poorer ability of basal shoot formation of monocormic trees (Kallio and Lehtonen 1973, Kallio and Mäkinen 1978). This is further substantiated by the comparison of live and dead trees in clear cut plots in 2013, which revealed a higher proportion of living polycormic trees. With regard to these results, clear cutting as a management action for regenerating forest, seems to be better suitable for polycormic trees.

Acknowledgements

References

Ammunét, T., T. Kaukoranta, K. Saikkonen, T. Repo, and T. Klemola. 2012. Invading and resident defoliators in a changing climate: cold tolerance and predictions concerning extreme winter cold as a range-limiting factor. Ecological Entomology 37:212-220.

Bates, D., M. Maechler, and B. Bolker. 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.

Biuw, M., J. U. Jepsen, J. Cohen, S. H. Ahonen, M. Tejesvi, S. Aikio, P. R. Wäli, O. P. Vindstad, A. Markkola, P. Niemelä, and R. A. Ims. 2013. Long-term impacts of contrasting management of large ungulates int he arctic tundra-forest ecotone: Ecosystem structure and climate feedback (Article in review).

Bråthen, K. A. and O. Hagberg. 2004. More efficient estimation of plant biomass. Journal of Vegetation Science 15:653-660.

Callaghan, T. V., B. R. Werkman, and R. M. M. Crawford. 2002. The Tundra-Taiga interface and its dynamics: Concepts and Applications. Ambio:6-14.

Den Herder, M. and P. Niemelä. 2003. Effect of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow. Rangifer 23:3-12.

Holtmeier, F.-K. and G. Broll. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14:395-410.

Hynynen, J, P. Niemisto, A. Vihera-Aarnio, A. Brunner, S. Hein, and P. Velling. 2009. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. Forestry 83:103-119.

Hytönen, J. and L. Aro. 2012. Biomass and nutrition of naturally regenerated and coppiced birch on cutaway peatland during 37 years. Silva Fennica 46:377-394.

Hytönen, J. and J. Issakainen. 2001. Effect of repeated harvesting on biomass production and sprouting of *Betula pubescens*. Biomass and Bioenergy 20:237-245.

Hämet-Ahti, L. 1963. Zonation of the Mountain Birch Forest in Northernmost Fennoscandia. Societas zoologica-botanica Fennica Vanamo.

Jepsen, J., M. Biuw, R. Ims, L. Kapari, T. Schott, O. Vindstad, and S. Hagen. 2013. Ecosystem Impacts of a Range Expanding Forest Defoliator at the Forest-Tundra Ecotone. Ecosystems 16:561-575.

Jepsen, J. U., M. Biuw, R. A. Ims, L. Kapari, T. Schott, O. P. L. Vindstad, and S. B. Hagen. 2012. Ecosystem impacts of a range expanding forest defoliator at the Forest-Tundra Ecotone. Ecosystems.

Jepsen, J. U., S. B. Hagen, K. A. Hogda, R. A. Ims, S. R. Karlsen, H. Tømmervik, and N. G. Yoccoz. 2009a. Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. Remote Sensing of Environment 113:1939-1947.

Jepsen, J. U., S. B. Hagen, R. A. Ims, and N. G. Yoccoz. 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. Journal of Animal Ecology 77:257-264.

Jepsen, J. U., S. B. Hagen, S. R. Karlsen, and R. A. Ims. 2009b. Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. Proceedings of the Royal Society B-Biological Sciences 276:4119-4128.

Jonsson, B. G. and J. Siitonen. 2012. Dead wood and sustainable forest management. Biodiversity in Dead Wood. Cambridge University Press.

Kallio, P. and J. Lehtonen. 1973. Birch forest damage caused by *Oporinia autumnata* (Bkh.) in 1965-66 in Utsjoki, N Finland. Rep. Kevo Subarctic Res. Stat. 10:55-69.

Kallio, P. and Y. Mäkinen. 1978. Vascular flora of Inari Lapland: Betulaceae. University of Turku, Turku.

Kallio, P., S. Niemi, and M. Sulkinoja. 1983. The fennoscandian birch and its evolution in the marginal forest zone. Nordicana 47:101-110.

Karlsen, S. R., J. U. Jepsen, A. Odland, R. A. Ims, and A. Elvebakk. 2013. Outbreaks by canopy feeding geometrid moth cuase state-dependent shifts in understorey plant communities.

Karlsson, P. S., O. Tenow, H. Bylund, J. Hoogesteger, and M. Weih. 2004. Determinants of mountain birch growth in situ: effects of temperature and herbivory. Ecography 27:659-667.

Karlsson, P. S., M. Weih, and C. Borg. 2005. Mountain birch growth in relation to climate and herbivores. Pages 71-83 *in* F. E. Wielgolaski, editor. Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests. Springer, Berlin.

Kauppi, A., P. Rinne, and A. Ferm. 1988. Sprouting ability and significance for coppicing of dormant buds on *Betula pubescens* Ehrh. stumps. Scandinavian Journal of Forest Research 3:343-354.

Klemola, T., T. Andersson, and K. Ruohomäki. 2008. Fecundity of the autumnal moth depends on pooled geometrid abundance without a time lag: implications for cyclic population dynamics. Journal of Animal Ecology 77:597-604.

Körner, C. 2003. Alpine plant life: Functional plant ecology of high mountain ecosystems. Springer-Verlag, Berlin.

Lehtonen, J. 1987. Recovery and development of birch forests damaged by *Epirrita autumnata* in Utsjoki area, North Finland. Rep. Kevo Subarctic Res. Stat. 20:35-39.

Lehtonen, J. and R. K. Heikkinen. 1995. On the recovery of mountain birch after *Epirrita* damage in Finnish Lapland, with a particular emphasis on reindeer grazing. Ecoscience 2:349-356.

Lehtonen, J. and M. Yli-Rekola. 1979. Field and ground layer vegetation in birch forests after *Oporinia* damage. Rep. Kevo Subarctic Res. Stat. 15:27-32.

Luostarinen, K., N. Huotari, and E. Tillman-Sutela. 2009. Effect of regeneration method on growth, wood density and fibre properties of downy birch (*Betula pubescens* Ehrh.). Silva Fennica 43:329-338.

Mazerolle, M. J. 2012. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 1.26.

Moen, J., D. M. Cairns, and C. W. Lafon. 2008. Factors structuring the treeline ecotone in Fennoscandia. Plant Ecol Divers 1:77-87.

Neuvonen, S., K. Ruohomäki, H. Bylund, and P. Kaitaniemi. 2001. Insect herbivores and herbivory effects on Mountain birch dynamics. Pages 207-222 *in* F. E. Wielgolaski, editor. Nordich mountain birch ecosystems. The Parthenon Publishing group, London.

Nilssen, A. C., O. Tenow, and H. Bylund. 2007. Waves and synchrony in *Epirrita autumnata /Operophtera brumata* outbreaks. II. Sunspot activity cannot explain cyclic outbreaks. Journal of Animal Ecology 76:269-275.

Odland, A. 1994. Bjørkeartenes spredning, etablering og samspill med naturmiljøet. Norsk institutt for naturforskning.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2012. Community Ecology Package.

Oksanen, L., J. Moen, and T. Helle. 1995. Timberline patterns in northernmost Fennoscandia. Acta Bot. Fennica 153:93-105.

Perala, D. A. and A. A. Alm. 1990. Regeneration silviculture of birch - a review. Forest Ecology and Management 32:39-77.

R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ruohomäki, K., M. Tanhuanpaa, M. P. Ayres, P. Kaitaniemi, T. Tammaru, and E. Haukioja. 2000. Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. Population Ecology 42:211-223.

Ruohomäki, K., T. Virtanen, P. Kaitaniemi, and T. Tammaru. 1997. Old mountain birches at high altitudes are prone to outbreaks of *Epirrita autumnata* (Lepidoptera: Geometridae). Environmental Entomology 26:1096-1104.

Tenow, O. 1972. The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountainchain and northern Finland 1862-1968. Uppsala University, Uppsala.

Tenow, O. and H. Bylund. 2000. Recovery of a *Betula pubescens* forest in northern Sweden after severe defoliation by *Epirrita autumnata*. Journal of Vegetation Science 11:855-862.

Tenow, O., H. Bylund, P. S. Karlsson, and J. Hoogesteger. 2004. Rejuvenation of a mountain birch forest by an *Epirrita autumnata* (Lepidoptera : Geometridae) outbreak. Acta Oecologica-International Journal of Ecology 25:43-52.

Tveraa, T., P. Fauchald, N. Gilles Yoccoz, R. Anker Ims, R. Aanes, and K. Arild Høgda. 2007. What regulate and limit reindeer populations in Norway? Oikos 116:706-715.

Vaarama, A. and T. Valanne. 1973. On the taxonomy, biology and origin of *Betula tortuosa* Ledeb. Rep. Kevo Subarctic Res. Stat. 10:70-94.

Verwijst, T. 1988. Environmental correlates of multiple-stem formation in *Betula pubescens* ssp. *tortuosa*. Vegetatio 76:29-36.

Väre, H. 2001. Mountain birch taxonomy and floristics of mountain birch woodlands. Pages 35-46 *in* F. E. Wielgolaski, editor. Nordic mountain birch ecosystems. The Parthenon Publishing Group, London.

Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer Publishing Company, Incorporated.

Wielgolaski, F. E. 2001. Vegetation sections in Northern Fennoscandian mountain birch forests. Pages 23-34 *in* F. E. Wielgolaski, editor. Nordic mountain birch ecosystems. The Parthenon Publishing Group, London.

Appendix

App. 1 Overview of sampled plant species.

Species	Growth form	Species	Growth form
Alnus spp.	Tall woody	*Avenella flexuosa*	Grass
Betula nana		*Luzula sylvatica*	
Betula pubescens		*Juncus* sp.	
Juniperus sp.		Unspecified grasses	
Ledum palustris		*Cornus suecica*	Small forbs
Salix spp.		*Linnea borealis*	
Sorbus aucuparia		*Rubus chamaemorus*	
Arctostaphylos alpinus	Small woody	*Rubus saxatilis*	
Empetrum nigrum		*Trientalis europaea*	
Vaccinium myrtillus		*Equisetum* sp.	Cryptogams
Vaccinium uliginosum		*Lycopodium* sp.	
Vaccinium vitis-idaea		Unspecified small ferns	
Chaemonerion spp.	Tall forbs	Unspecified tall ferns	
Solidago virgauea		Unspecified mosses	Moss
Unspecified tall forbs		Unspecified lichens	Lichen

App. 2 Estimates, standard errors and probabilities of basal shoot models according to Figures 7 and 8. Top: logistic model. Bottom: poisson model.

Factor	Estimate	Standard Error	Pr(>|z|)
Clear cut	0.08	0.73	0.91
Year 2012	0.95	0.3	0.0022
Year2013	1.13	0.31	<0.001
Rich	-0.62	0.93	0.5
Luftjok	5.36	1.12	<0.001
Stems 2011	0.45	0.078	<0.001
Clear cut : Year 2012	0.91	0.45	0.04
Clear cut : Year 2013	1.32	0.46	0.0043
Rich : Luftjok	-7.22	1.45	<0.001

Factor	Estimate	Standard Error	Pr(>|z|)
Year 2012	-0.14	0.048	0.0042
Year 2013	-0.2	0.047	<0.001
Rich	0.17	0.13	0.17
Luftjok	0.61	0.15	<0.001
Clear cut	0.088	0.12	0.48
Stems 2011	0.051	0.0098	<0.001
Year 2012 : Rich	0.21	0.041	<0.001
Year 2013 : Rich	0.42	0.04	<0.001
Luftjok : Clear cut	-0.19	0.17	0.27
Year 2012 : Clear cut	0.94	0.04	<0.001
Year 2013 : Clear cut	1.2	0.039	<0.001
Rich : Luftjok	-1.06	0.17	<0.001
Year2012 : Stems 2011	0.02	0.0043	<0.001
Year2013 : Stems 2011	0.02	0.0042	<0.001