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Legacy effects of logging on boreal forest understorey vegetation communities in decadal time scales in northern Finland

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Nomenclature:

Species nomenclature and authority according to plantlist.org in 3.5.2018. Abbreviation of species names in Appendix A.

Abbrevations: Coarse woody debris: CWD

ABSTRACT

We followed how forest thinning, repeated twice during a period of 93 years, altered understorey plant community composition, affected the succession of forest understorey vegetation and the accumulation of logs in the long-term. The study was carried out in northern Finland by resampling 20 permanent experimental plots, established after wildfire in 1920. Understorey vegetation was inventoried in 1961, 1986 and 2013 with forest thinning treatments done in 1953 and 1987, using four and three different harvesting intensities, respectively. We found succession to override the effects of forest logging until the latest study period (2013). We observed negligible long-term effects of logging on understorey communities during the two mid-successional stages (1961, 1986), when the forest was 41 and 66 years old, respectively. The impacts of logging on understorey vegetation were strongest in the latest successional stage (2013), the forest being at the age of 93 years. In the latest successional stage (2013) logged plots had less coarse woody debris than unlogged plots. Forest management thus influenced the key feature for forest biodiversity and potential habitats for endangered species. These findings are of major interest since the studies of long-term impacts of less intensive forest management practices are scarce. Our results suggest that in addition to possible immediate impacts, harvesting treatments have legacy effects (subtle or delayed inherited effects of forestry in the past) that influence the forest understorey vegetation community composition and the amount of coarse woody debris. This finding deserves special attention when planning species conservation, multiple use of forests and sustainable forestry.

1 INTRODUCTION

Succession is described as progressive changes in species composition and community structure, caused by natural processes over time (Helms, 1998). In boreal forests, disturbances trigger forest succession (Kuuluvainen, 2002), but the increase of coniferous trees (especially spruce *Picea* spp.) along succession is an important driver for changes in understorey vegetation communities and structural diversity, as the increased shading creates unique microclimatic conditions, and affects the accumulation and quality of coarse woody debris (CWD hereafter) (Caners et al., 2013; Hedwall et al., 2013; Verstraeten et al., 2013). Gendreau-Berthiaume et al. (2015) show evidence of long-persistent effects of past disturbances on forest understorey vegetation. The amount of light reaching the forest floor is closely related to the successional stage, total canopy cover and species composition of the tree layer (Messier et al., 1998). The shift in the tree canopy structure during forest succession influences light conditions, microclimate and litter properties, thus affecting the composition of understorey vegetation (Roberts and Gilliam, 1995). The natural successional period in northern boreal forests is even 700 years (Shorohova et al. 2009), whereas a typical rotation period in the commercial forests is less than 100 years (Hedwall et al., 2013). Uotila and Kouki (2005) find that the main patterns of understorey vegetation succession can be similar between managed and unmanaged forests, but the managed and unmanaged forests still differ in the age structure of trees and in the amount of CWD.

The majority of boreal forest species have adapted to utilize spatially and temporally varying habitats and resources (Kuuluvainen, 2002), which has increased the stability of boreal forests at large scales and over long time periods (Noss, 2001). However, since the 1950s, the forest management in Finland has become more intensive to maximize timber production (Rouvinen and Kuuluvainen, 2005). Selective cuttings were replaced by clear-cuttings and currently, the forests are typically thinned two or three times during a rotation period of 60–100 years (Siiskonen, 2007; Hedwall et al., 2013). Thinnings alter canopy formation and composition (Thomaes et al., 2012), and forestry practices have homogenized stand structures, as the aim of forestry has mainly been to grow even-sized and even-aged monocultures (Rouvinen and Kuuluvainen, 2005). Nowadays, interest in a wider set of forestry practices (e.g. continuous cover forestry) is growing

(Koivula et al., 2014, Vanha-Majamaa et al. 2017) to progress towards more sustainable forestry (Peura et al. 2018).

The managed forests lack many structurally important features for maintaining biodiversity (Kuuluvainen, 2002), most importantly CWD (Jonsson and Jonsell, 1999; Paillet et al., 2010), as the natural accumulation of logs through self-thinning and disturbances is disturbed (Sturtevant et al., 1997). Consequently, many forest-dwelling organisms and nature types have become threatened (Rassi et al., 2010). According to Tonteri et al. (2016) forest logging influences especially the abundance-relationships between light-demanding and shade-tolerant species, and in Finland and in Sweden intensive forest management is a driving factor for the changes in the abundances and frequencies of understorey plant species (Reinikainen et al., 2000; Sundberg, 2014; Hedwall and Brunet, 2016). However, this development is not restricted to Finland or Northern Europe but should be a global concern, even though the European forests have been most widely utilized (Paillet et al., 2010).

When comparing the effects of different logging treatments on forest understorey species in a ten-year time scale, Vanha-Majamaa et al. (2017) have found the least intensive treatments to best maintain understorey vegetation similar to that of the unmanaged forests. Tonteri et al. (2016) show, in addition to immediate impacts, time-lag in responses of understorey species to forest management. These subtle or hidden inherited anthropogenic changes to the systems can be considered as legacy effects (James, 2015). Yet, the long-term persistence of these effects has not been much studied (Tonteri et al., 2016), and the successional patterns of understorey vegetation in the natural and managed forests are poorly documented (Uotila and Kouki, 2005). Moreover, studies focusing on less intensive forest management practices are scarce, even though such practices are widely used. Thus, there is a clear need for understanding natural long-term dynamics of boreal forest understorey vegetation as well as studying how different forest management practices alter this development.

In this study, we followed how forest thinning, repeated twice during a period of 93 years, affected the succession of forest understorey vegetation, altered understorey plant community composition, and the accumulation of logs. We also studied the responses of individual plant species that either play a key role in supporting ecosystem functions or can be used as indicator species. Twenty permanent experimental plots were established and sown by Scots pine (*Pinus sylvestris*) in year 1920, one year after a wild fire, and their understorey vegetation was inventoried three times (1961, 1986, 2013) allowing us to cover a time-span of 52 years. We hypothesized forest logging would (i) change the successional developmental pathway of understorey vegetation, (ii) alter understorey community composition, and (iii) have negative long-term effects on the amount CWD.

2 MATERIALS AND METHODS

2.1 Study area

The study was carried out in Kivalo research area, Kaihuanvaara, Northern Finland (66 ° 23'N, 26 ° 54'E). (Fig 1.) The average annual temperature in the study area varies from 0 to 1 °C, annual rainfall from 550 to 600 mm (Vanha-Majamaa and Lähde, 1991), and the length of growing season from 135 to 145 days (Finnish Meteorological Institute a). The average temperature of the coldest month (January) is −11.4 °C and the average temperature of the warmest month (July) is 15.4 °C (1981–2010) (Finnish Meteorological Institute b). Duration of the snowy period is approximately 175–190 days (from early November till late April–early May), and the average snow depth in March is 60-80cm (1981–2010) (Finnish Meteorological Institute c). In Northern Finland particularly autumns and springs have warmed, the snow cover has become thinner and precipitation during the growing season has increased in the last decades (Kivinen et al., 2017; Korpela et al., 2013). The Kaihuanvaara research forests have been used as study sites by Finnish forestry researchers (Sirén, 1955, Vanha-Majamaa and Lähde, 1991; Salminen and Jalkanen, 2007).

The experimental plot setup, used in this study (Fig. 1), was established in 1920 by the former Finnish Forest Research Institute (METLA) after a wildfire of 600 ha in 1919, in order to study the effects of different forest thinning intensities on growth of artificially regenerated Scots pine (experiment B 13 I in Heikinheimo 1961). The previous large forest fire in the same site was in 1877. In both fires most of the study area, including our study site, was burned. The study site includes 20 permanent 0.1 ha plots that are located on the western slope of the hill at an altitude range of 180–250 m a.s.l. Bedrock on Kaihuanvaara is quartzite, covered with glacial till deposits (Vanha-Majamaa and Lähde, 1991). The study site represents mesic forest vegetation, which in absence of forest management, would be dominated by Norway spruce with varying portions of Scots pine and deciduous tree species.

The study plots were first logged in 1953 and secondly in 1987, the forest being 33 and 66 years old, respectively. In both years 16 plots were logged and 4 plots remained unmanaged (Fig. 1). These unmanaged plots are used as controls. The first logging (1953) was done using four harvesting intensities: strip harvesting (all trees were cut from strips corresponding to 30% of the total area of the plot), commercial thinning (all commercially valuable co-dominant and intermediate trees were harvested), heavy thinning (all but dominant trees were removed), light thinning (intermediate trees and understorey trees were harvested, additional co-dominant trees were left) and a control treatment (no logging) (Heikinheimo, 1961). The second logging (1987) was done using three different harvesting intensities: light (700 remaining stems/ha), medium (500 remaining stems/ha), heavy (300 remaining stems/ha) and a control treatment (no logging) (Archives of Natural Resources Institute Finland, Rovaniemi, Kaihuanvaaran kasvatustiheyskokeet, unpublished documentation). The individual histories for each study plot are shown in Table 1.

Table 1. Treatments of the study plots in 1987 and 1953, organized based on the treatment in 1987.

Plot	**1987**	**1953**
B	control	control
C	control	control
S	control	control
V	control	control
A	light	strip harvesting
K	light	commercial thinning
N	light	commercial thinning
E	medium	strip harvesting
L	medium	light thinning
M	medium	light thinning
R	medium	commercial thinning
T	medium	light thinning
U	medium	heavy thinning
Y	medium	commercial thinning
D	heavy	strip harvesting
F	heavy	strip harvesting
O	heavy	heavy thinning
P	heavy	heavy thinning
X	heavy	heavy thinning
Z	heavy	light thinning

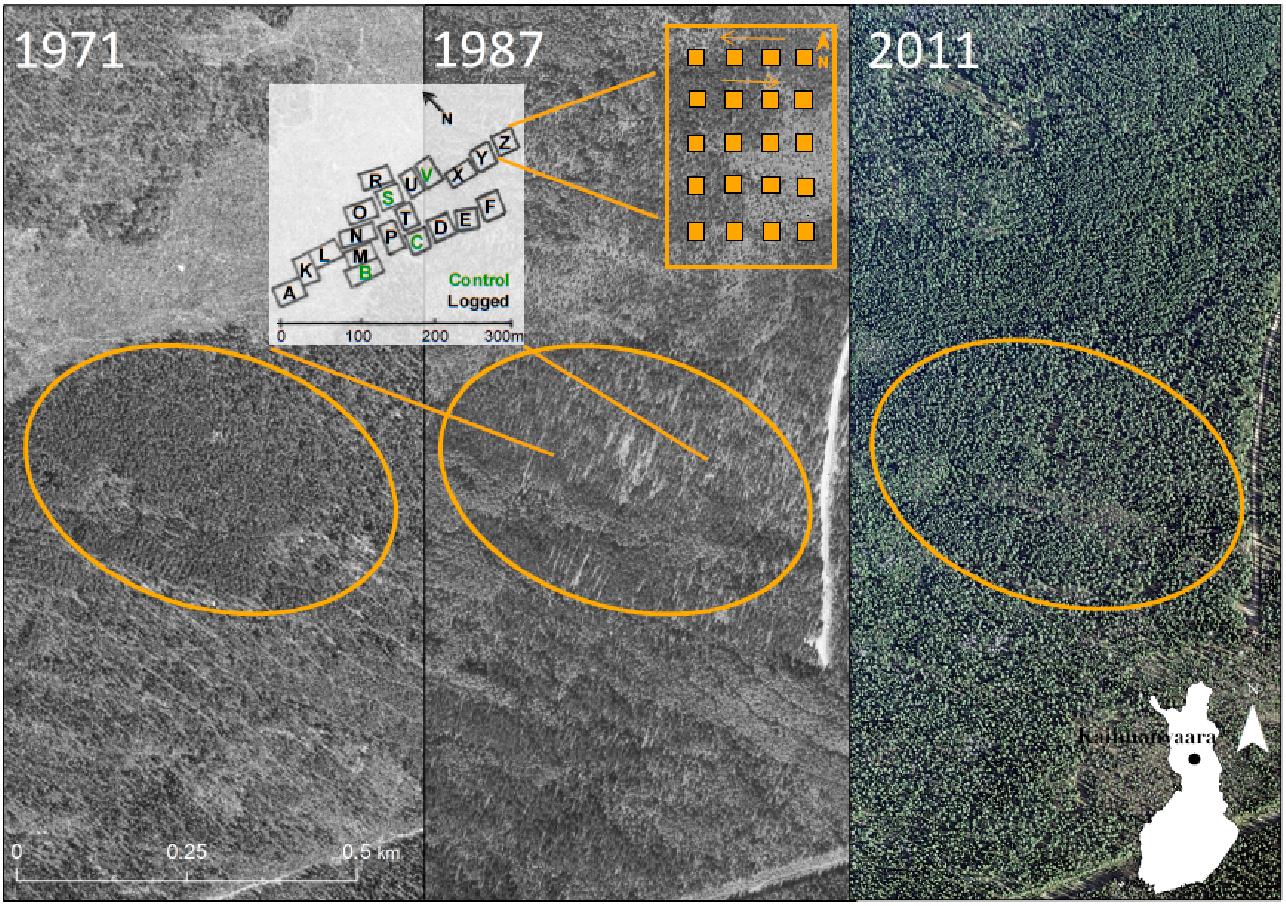

Fig. 1 Location of Kaihuanvaara and aerial photographs from the study site from the years 1971, 1987 and 2011 (18 years, same year and 24 years after the previous logging, and ten years after, one year after and two years before the vegetation inventories, respectively.) Orange circles show the location of the study plots and the locations of each study plot are shown in the insert (map according to Heikinheimo 1961). Letters indicate different study plots and green color control plots. In top center of the figure are shown the schematic positions and the order of vegetation recording of the 20 regularly placed 1 m^2 vegetation squares.

Comparisons of the effects of different harvesting treatments (1953) on the number of stems and stem volume between 1953 and 1986 are shown in Appendix B. The stem number has decreased from approximately 6000 stems/ha (1953) to 3000 stems/ha (1961) to 1000 stems/ha (1986) on logged sites due to the treatments and self-thinning. On control sites the number of stems has decreased more slowly from approximately 6000 stems/ha (1953) to 5000 stems/ha (1961) to 2500 stems/ha (1986) through self-thinning.

At the same time, the stem volume has increased from approximately 150 m^3/ha (1953) to 200 m^3/ha (1961) to 250 m^3/ha (1986) on logged sites and from 170 m^3/ha (1953) to 250 m^3/ha (1961) to over 325 m^3/ha (1986) on control sites.

2.2 Vegetation inventories

Vegetation was inventoried three times during the study period, in 1961, 1986 and 2013. The first vegetation inventory was done 8 years after the first logging (1953), the forest being 41 years old, and the second inventory 33 years after the first logging, the forest being 66 years old. The third vegetation inventory was done 60 years after the first (1953), and 27 years after the second logging (1987), the forest being 93 years old. The inventories were done in middle to late growing season: during the first weeks of July in 1961 and 2013, and in the end of July–early August in 1986. Inside each 0.1ha study plot (20 replicates) there were 20 permanent 1m^2 vegetation quadrats, placed regularly as a grid, from which the vegetation was inventoried (Fig. 1). The inventories were based on visual estimation of percentage coverage of each plant species and litter. Field and bottom layers were inventoried separately using a scale of 0.25, 0.5, 1, 2 … % (1 % intervals). The vegetation inventory methods were similar across years but conducted by different investigators each year (1961: unknown botanist, 1986: I. Vanha-Majamaa, 2013: L. Muurinen). The vegetation data were then averaged.

Taxonomic harmonization was done to minimize differences in the identification level of species. Differences in species identification and inventory methods were eliminated or minimized by grouping species, especially bryophytes and lichens, into collective species groups (genera or morpho-groups). Specialist species clearly associated only to special substrates such as stones or decaying wood were also left out from the analysis. The harmonized data included 57 taxa; 36 belonging to vascular plants, 14 to bryophytes and 7 to lichens (Appendix D). The variation in the number of species in total and in field and bottom layers separately between treatments and years is shown in Appendix C. In the analysis square root transformation was performed on the visually estimated cover percentage values to reduce the impact of highest cover values. Non-harmonized data from year 2013 were used in the analysis concerning this year only. In year 2013 altogether 70 species or taxa were found from the non-harmonized data; 37 belonging to vascular plants, 24 to bryophytes and 9 to lichens (Appendix A).

2.3 Environmental variables

For the analysis considering the whole study period, stand age was used to describe successional stage (early-mid: the forest 33 years old, mid: the forest 66 years old and late-mid: the forest 93 years old). Since based on the preliminary analysis, the impacts of the different harvesting intensities on the understorey vegetation did not differ from each other, only logged and control comparison was used. The amount of litter (as percentage cover) was also used as an explanatory environmental variable. For the analysis regarding year 2013 only, harvesting intensity of the second logging was used as an ordered factor (control, light, medium, heavy). Basal area of pine (*Pinus sylvestris*), spruce (*Picea abies*) and birch (*Betula pendula* and *B. pubescens*) was measured in 2013 in field using relascope. The proportion of birch and spruce of total basal area was calculated to describe the proportion of mixed wood. Also the numbers of snags and logs (diameter being over 10 cm) inside each study plot were counted, considered as CWD (Yan et al., 2006). The decay stage of the logs was estimated according to Maser et al., (1979), using only the first three decay stages out of five.

2.4. Statistical analysis

The data were standardized among years by equalizing the average total cover for each study year. In the ordination analysis a Wisconsin transformation was used: the cover of each species was first divided by its maximum, and then all sample plots were divided by their total (Faith et al., 1987). This transformation gives the classical “strict” Bray-Curtis measure (Yoshioka, 2008) and also avoids the spurious dissimilarities data, caused by different total abundances (Warton et al., 2012).

The data were ordinated with constrained distance-based redundancy analysis dbRDA (McArdle & Anderson 2001) and partial non-metric multidimensional scaling NMDS (Kruskal, 1964). These are robust ordination methods that can well cope with non-linear unimodal species response models of various shapes (Minchin, 1987). Partial NMDS is a natural extension of the dbRDA framework (McArdle & Anderson 2001) where the residuals after constraints are subjected to NMDS. To focus on the successional change in vegetation, the effect of plot was partialled out before submitting the data to NMDS. This method also removes the effect of spatial distance. We used partial NMDS for the overall analysis of succession, and dbRDA for the analysis of the non-harmonized data in year 2013. Similar analysis was conducted for the other two years as well, but no differences were detected. Full model for year 2013 was built by including all environmental variables into it (e.g. harvesting intensity, basal area of pine, proportion of mixed wood, amount of litter, number of snags and the numbers of logs in each of the three decay stages) and it was reduced to final model that included only litter and harvesting intensity. Model significance was tested using randomization test with 9999 permutations.

For the ordination figures confidence ellipses were counted as a visual tool to help the interpretation of the differences in class means. Confidence ellipses are based on standard error, which is based on standard deviation, which then is dependent on the size of the group. Confidence ellipses were calculated using Bonferroni correction.

The responses of two strongest indicator species (*Deschampsia flexuosa* as an indicator for disturbance and *Goodyera repens* for old-growth forests), and the four most dominant species (*Vaccinium myrtillus* and *V. vitis-idaea* from field layer, and *Pleurozium shreberi* and *Hylocomium splendens* from bottom layer) and litter on logging were analyzed using t-test, as there was a clear difference in variance between the groups. The impact of harvesting intensity on the number of logs, on the number of stems and stem volume, as well as the impacts of year and logging on the number of species, were analyzed using general linear models and quasi-Poisson dispersion. Model significance was tested using analysis on variance and F-test. Pairwise comparisons were done using Tukey's Honest Significant Difference. All statistical analyses were performed in the R statistical environment (R 3.3.3.). The vegan package (Oksanen et al., 2017) was used for the multivariate analysis.

3 RESULTS

3.1 Impacts of forest harvesting on understorey vegetation succession and community composition

Understorey communities strongly differed among years with only negligible effects of logging on this development in the first two study periods (years 1961, 1986), when the forest was 41 and 66 years old, respectively (Fig. 2). In the last study period (2013) the logged sites differed from control sites, 26 years after the second logging, as the forest was 93 years old (Fig. 2).

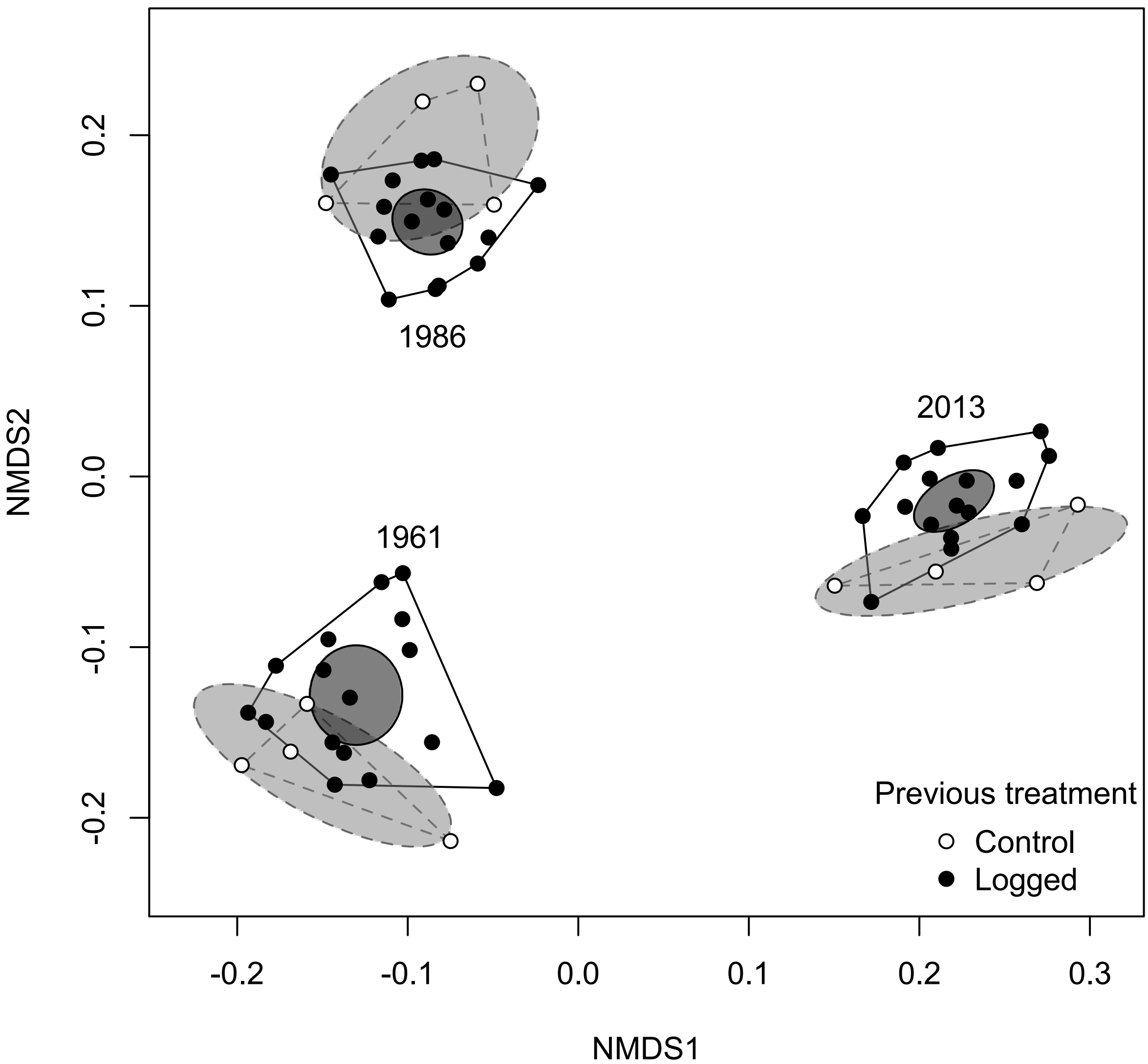

Fig. 2 Non-metric multidimensional scaling plot of understorey communities (R^2=0.991, stress=0.097) with fitted Bonferroni corrected 95% confidence interval ellipses around treatment centroids. White circles and gray dashed line indicate control plots (n=4), and black circles and solid line logged plots (n=16).

Non-harmonized data from year 2013 was used to study the impacts of the logging intensity of the second thinning in more detail. According to this reduced model, harvesting intensity significantly influenced community composition (df=3, F=1.619, p=0.005), and the amount of litter was significantly associated with community composition (df=1, F=3.447, p=0.005) (Fig. 3). The understorey vegetation communities of control plots differed from the communities of medium-logged and heavily logged plots, and the lightly logged ones differed from heavily logged ones (Fig. 3). The understorey communities were separated linearly by increasing harvesting intensity, even though the impacts of neighboring treatments did not differ from each other (Fig. 3).

Especially some herbaceous species (e.g. *Linnaea borealis, Melampyrum pratense,* and *Solidago virgaurea)*, graminoids (e.g. *Deschampsia flexuosa*) and tree seedlings (e.g. *Betula* spp.*, Populus tremula*, and *Salix* spp.) were associated with logged sites, whereas some other species (e.g.*, Goodyera repens, Lysimachia europaea, Ptilium crista-castrensis*) and liverworts, such as *Calypogeia integristipula,* were associated with control plots (Fig. 3). Especially the control plots showed high variation in the amount of litter, which was also reflected in the species assemblage of bryophytes: Brachytheciaceae –species (*Sciuro-hypnum reflexum*, *S. oedipodium* and *Brachythecium salebrosum*) and *Plagiothecium laetum* being associated to higher amounts of litter, and feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*), liverworts (e.g. *Barbilophozia* coll.), and some other mosses (e.g. *Dicranum polysetum*, *D. majus* and *Polytrichum commune*) to lower amounts of litter (Fig. 3).

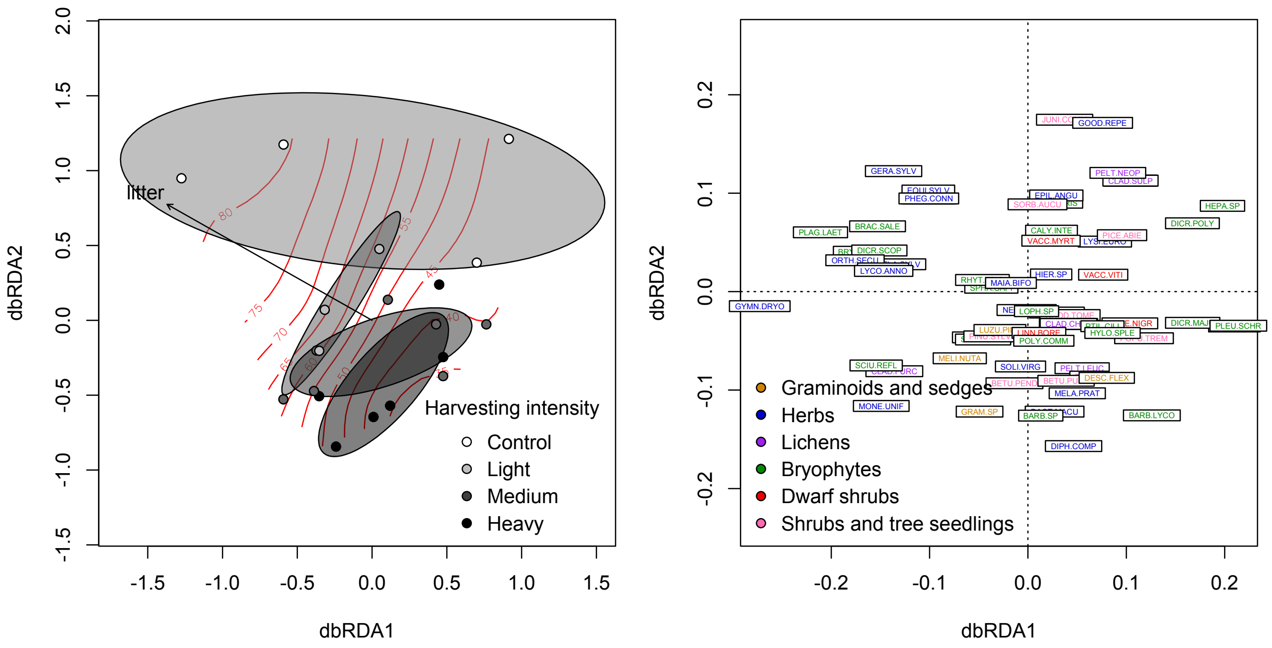

Fig. 3 Distance-based RDA ordination (dbRDA) using reduced model. Different harvesting intensities (df=3, F=1.6187, p=0.005) (control n=4, light n=3, medium n=7 and heavy n=6) are separated with fitted Bonferroni corrected 95% confidence interval ellipses around each treatment centroid. The variation in the amount of litter (df=1, F=3.4474, p=0.005) is visualized using smoothened trend surface and an arrow showing the direction of linear increase in the amount of litter. If species names have been overlapping, species are ordered with priority in abundance. Abbreviations used can be found from Appendix A.

3.2 Changes in understorey vegetation community composition during the study period

There was a clear between-year variation in species abundances (Fig. 4), but no difference in the total number of species, the number of vascular plants, or the number of bryophytes and lichens between years, harvesting treatments, or the interaction of years and harvesting treatments (Appendix C). Majority of the species maintained their populations during the whole study period and only few species were detected only once (Fig. 4). Many lichen species (*Cladonia rangiferina, C. arbuscula, Nephroma arcticum, Peltigera* sp. and *Stereocaulon* sp,) were common in 1961 but disappeared from all sites after the first vegetation inventory (Fig. 4). Similarly, some herbaceous species (e.g. *Antennaria dioica, Dactylorhiza maculata, Diphasiastrum complanatum, Epilobium angustifolium* and *Gymnocarpium dryopteris*), bryophytes (e.g.

Polytrichum juniperinum, and *Sanionia uncinata*) and lichens (*Peltigera aphthosa*) that were common in 1961 declined either in frequency, in coverage or in both from year 1961 to years 1986 and 2013 (Fig. 4). Majority of these species declined smoothly during the study period but for some species year 1986 was a threshold (Fig. 4). They either disappeared (e.g. *Antennaria dioica* and *Pyrola* sp.) or declined either in coverage (e.g. *Cladonia* sp., *Melampyrum sylvaticum* and *Ptilium crista-castrensis*) or in both coverage and frequency (e.g. *Hieracium* sp.) after this year (Fig. 4).

Some herbaceous species (e.g. *Lysimachia europaea*, *Maianthemum bifolium* and *Melampyrum pratense*), graminoids (e.g. *Deschampsia flexuosa* and *Luzula pilosa*), dwarf shrubs (*Linnaea borealis*) and bryophytes (*Pleurozium schreberi*) had a peak in 1986, while other dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-idaea)* and bryophytes (e.g. *Dicranum polysetum* and *Hylocomium splendens*) tended to increase by 2013 (Fig. 4). The species abundances returned mostly to the level of year 1961 by year 2013 except for few species (e.g. *Deschampsia flexuosa* and *Lysimachia europaea*) that decreased from the pre-peak level to year 2013. Correspondingly, some herbaceous species (e.g. *Goodyera repens, Lycopodium* s.s.*, Moneses uniflora* and *Neottia cordata*), tree seedlings and bryophytes (e.g. *Barbilophozia* coll., *Dicranum polysetum, Dicranum* sp.*, Hylocomium splendens* and *Ptilidium ciliare*) had an overall smooth increasing trend in time (despite the slight decline in 1986 for some of the species), or established after year 1986 (e.g. *Phegopteris connectilis* and *Sphagnum* sp.) (Fig. 4).

The species composition remained relatively constant during the whole study period (Fig. 4). The two most dominant species (*Pleurozium schreberi* and *Vaccinium myrtillus*) had much higher abundance than any other species (Fig. 4) They also maintained their dominance through the study period (Fig. 4). The frequency and abundances of subdominant species (e.g. *Deschampsia flexuosa, Dicranum polysetum, Gymnocarpium dryopteris, Hylocomium splendens, Linnaea borealis, Maianthemum bifolium, Polytrichum commune* and *Vaccinium vitis-idaea*), varied between the years but they still maintained their populations through the whole study period (Fig. 4). Species that can be used as indicators for valuable forest habitats (*Goodyera* *repens, Neottia cordata* and *Moneses uniflora*) (Skogsstyrelsen, 2014) increased in frequency by year 2013, and in case of *Goodyera repens* also in coverage. Detailed information about the mean coverages of individual species and species groups between different treatments in each year can be found from Appendix D.

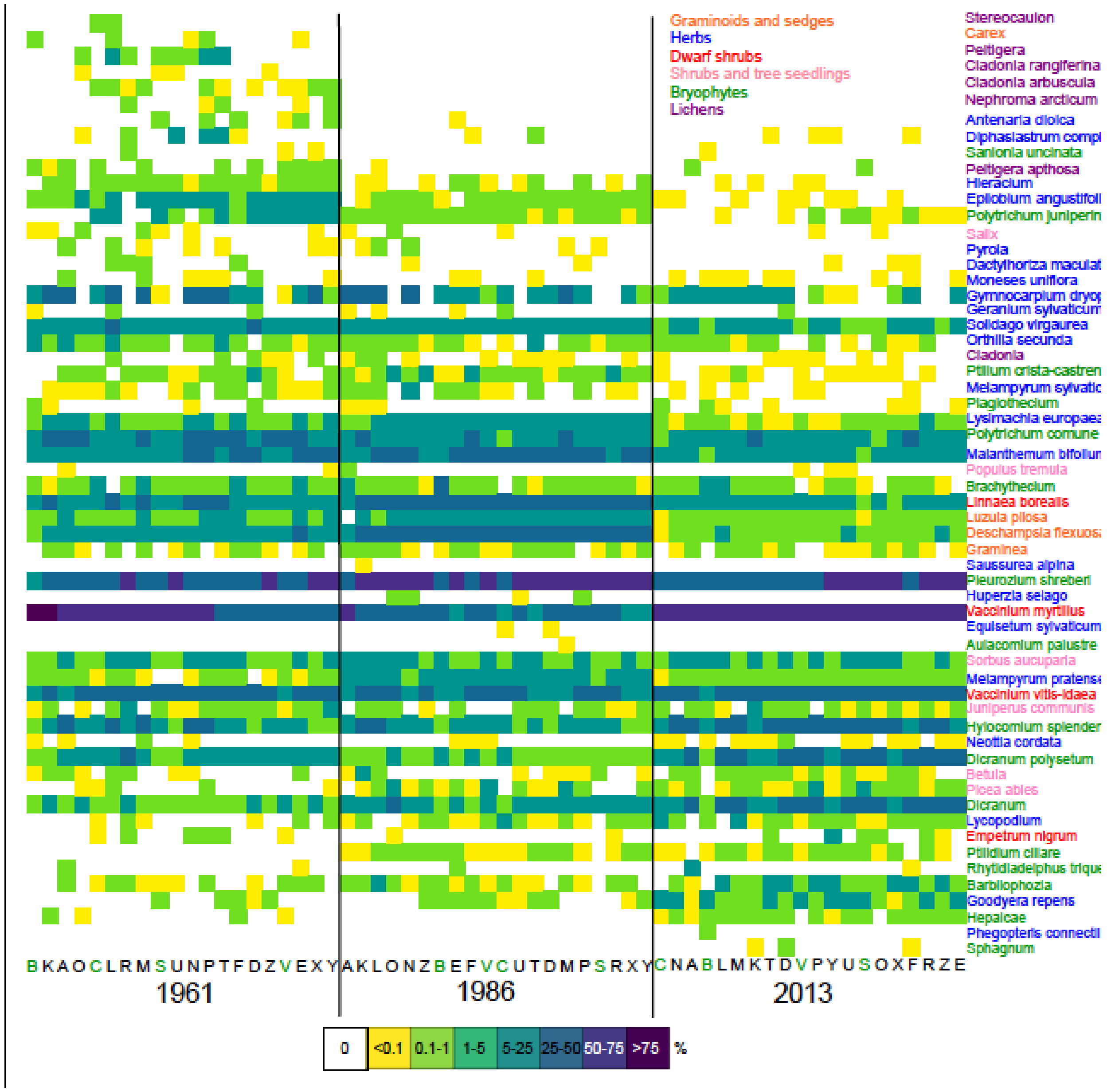

Fig. 4 Changes in understorey species assemblages during the study period. Plots are arranged within years to emphasize the gradual change in species composition and they are separated with black lines. Control plots (B, C, V, S) are indicated using green color. Species belonging to different species groups are written

using different colors. The species coverage has been harmonized using square root transformation and equalizing the average total cover for each study year, and is visualized using Braun-Blanquet scale.

3.3 Species responses and the biodiversity impacts of the second logging

Forest logging significantly affected the abundance of only few species (Fig. 5). *Deschampsia flexuosa* (df=8.431, t=3.427, p=0.008), and *Hylocomium splendens* (df=5.723, t=–2.51, p=0.048) had higher coverage on logged plots, whereas *Goodyera repens* (df=3.987, t= 2.598, p=0.060) had slightly higher coverage on control plots. Logging did not have any statistically significant effect on the coverage of the three most abundant species: *Vaccinium myrtillus, V. vitis-idaea* and *Pleurozium schreberi* (Fig. 5) or the amount of litter (Fig. 6).

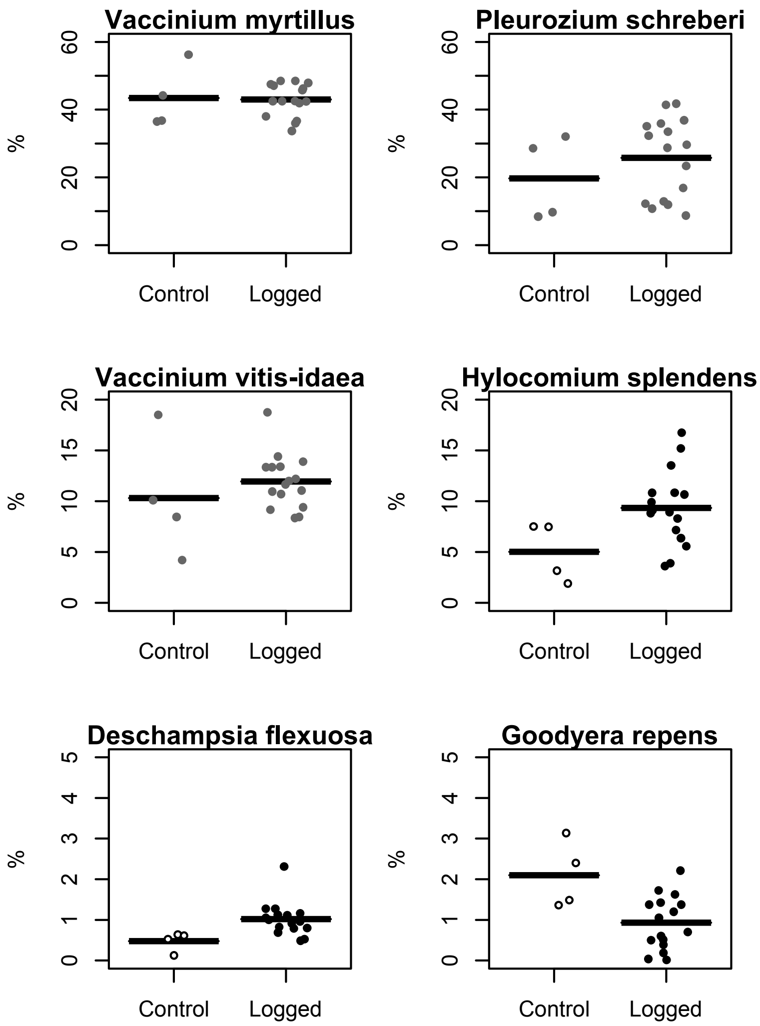

Fig. 5 Variation in the coverage of four most dominant species, and species used as indicators for disturbance and late successional conditions (*Deschampsia flexuosa* and *Goodyera repens,* respectively) between logged (n=16) and control (n=4) plots in year 2013. Means are represented with black lines and a statistically significant difference is indicated by difference in dot color (white and black), whereas similar dot color (gray) indicates no statically significant difference. Note the different scales in y-axis.

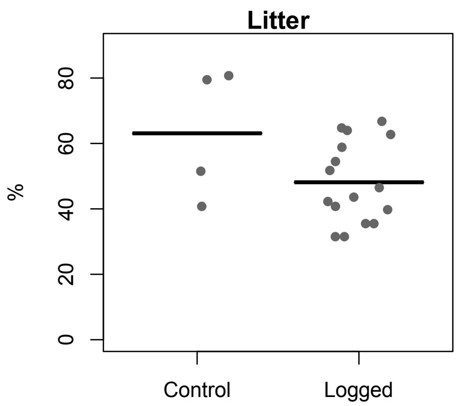

Fig. 6 The amount of litter (% cover) between logged (n=16) and control (n=4) plots in 2013. Means are represented with black lines and similar dot color (gray) indicates no statically significant difference.

The harvesting intensity of the second logging significantly affected the total number of logs (df= 3, F=51.279, $p<0.001$) as well as the number of the logs in all three decay stages (stage 1: df=3, F=6.761, $p<0.001$; stage 2: df=3, F=28.182, $p<0.001$; stage 3: df=3, F=37.904, $p<0.001$) (Fig. 7). The number of logs slightly decreased with increasing logging intensity, but the difference between pairwise comparisons was statistically significant only between the different harvesting intensities and control treatment (Fig. 7). The accumulation of logs has been rather fast during the first half of the study period (1953–1986) (Appendix B, reduction of approx. 3000 stems/ha during 1953–1961 and approx. 1000 stems/ha during 1961–1986 on control sites). At this time, the tree volume has increased rapidly in control plots, which must have resulted from increase in trunk size (Appendix B). During the latter half (1986–2013) the accumulation of logs has slowed down, as there is four, five times less newly fallen logs (Stage 1) than older logs (Stages 2 and 3) on control sites (Fig. 7) On the logged experimental plots there were only a couple of logs, regardless to the decay stage (Fig. 7).

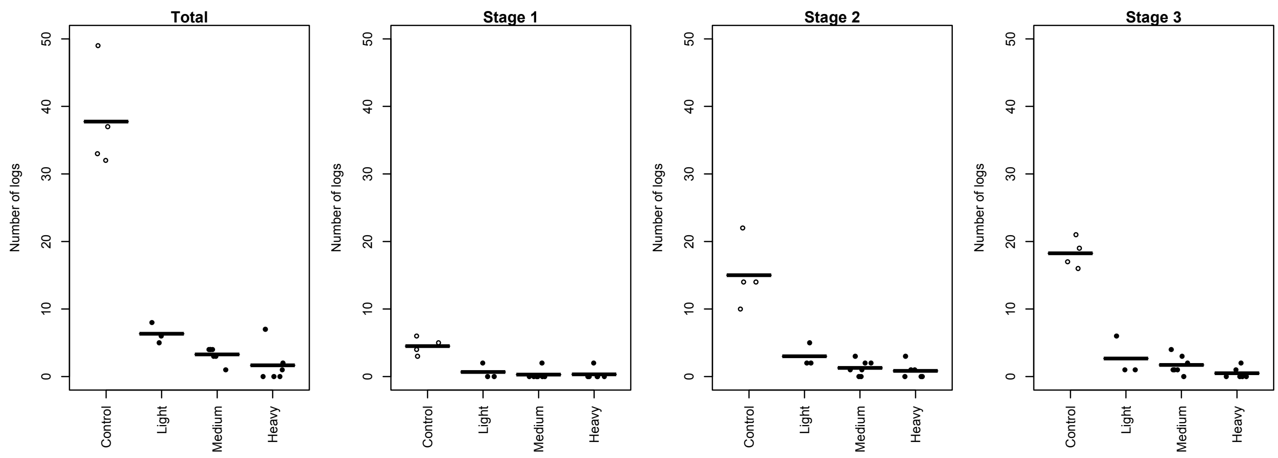

Fig. 7 Variation in the number of logs in total and in each decay stage (1-3) in 2013. Means are represented as black lines. Difference in dot color (white and black) indicates statistically significant difference in the number of logs between the harvesting treatments (control n=4, light n=3, medium n=7, heavy n=6).

4 DISCUSSION

4.1 Understorey vegetation succession

The main driver for the changes in understorey vegetation communities was time, and the impacts of the harvesting treatments on understorey communities were negligible in the first two study periods (1961,1986). The overall successional pattern of the understorey vegetation during the study period on both logged and control sites followed similar pattern from dominance of lichens, acrocarpous mosses and light demanding herbs to dominance of shrubs, pleurocarpous mosses, liverworts and shade-tolerant vascular plants, which is similar to many other reported results (e.g. Økland, 2000; Nilsson and Wardle, 2005; Uotila and Kouki, 2005). The forest canopy closes relatively rapidly after forest thinning, creating only a short-term change in light conditions (Hedwall et al., 2013). Consequently, it is likely that the responses of understorey vegetation on harvesting treatments were so immediate and short-term that they were not detected in this study, due to the relatively long sampling interval of the vegetation (8 years and 27 years) after the first logging (1953).

Successional stage and logging was not observed to affect the number of species contrary to e.g. Uotila and Kouki (2005), and the changes in species presence along the study period and between thinning treatments were minor. Our result may be partly due to the fact that majority of species in the studied forest sites common forest floor generalists that have wide physical tolerance ranges and large and well connected regional species pool, affiliating them to maintain their populations in time, and increasing their resistance and resilience to disturbances (Kuuluvainen, 2002; Bergeron et al. 2010). These generalist forest species can tolerate both early and late successional conditions and forest management practices even though they are not necessarily favored by them (e.g. Nilsson and Wardle, 2005; Økland, 2000; Tonteri et al., 2016; Uotila and Kouki, 2005). The abundances of species varied between years, but did not remarkably differ between the harvesting intensities. Consequently, the differences in community assemblages were caused mainly by the changes in abundances of species, but not by the species presence, as has been found by Nieppola (1992).

Even though the overall gradient in changes in understorey communities was mainly similar as reported in literature (e.g. Økland, 2000; Nilsson and Wardle, 2005; Uotila and Kouki, 2005), a shift in understorey vegetation community composition in year 1986 from dominance of dwarf shrubs to dominance of herbs and graminoids was detected. Also *Pleurozium schreberi* increased in the expense of other bryophytes, especially *Hylocomium splendens* and *Dicranum polysetum,*The trend was similar on both control and logged plots. *Deschampsia flexuosa* can be classified as light, *Linnaea borealis, Solidago virgaurea, Vaccinium vitis-idaea, Dicranum polysetum* and *Pleurozium schreberi* as semi-light, *Goodyera repens* and *Vaccinium myrtillus* as semi-shade and *Hylocomium splendens* as shade species (see Tonteri et al. 2016). As many of the species with higher cover in 1986 were light-favored based on Ellenberg light indicator values (Ellenberg et al., 1991), some disturbance or stress event may have reduced canopy closure (e.g. a storm event, insect outbreak, massive snow load or extreme winter), leading to increase in the amount of light on forest floor. However, at that time the logging residue (branches, tree tops, stumps) was left in the site in loggings, which has likely increased nitrogen levels of the site (Palviainen et al. 2004). Also, it is possible that changes in reindeer grazing pressure may have favored grazing tolerant graminoids (*Deschampsia flexuosa)* and bryophytes (*Pleurozium schreberi*) over palatable dwarf-shrubs (*Vaccinium myrtillus*) and lichens. (Väre et al. 1995; Bråthen and Oksanen, 2001; statistics of Reindeer Herder's Association, data from LUKE). However, the different timing of the inventory, annual variation in vegetation cover and the impact of the researcher on estimating species coverage may also affect the result.

4.2 Impacts of logging

Forest logging changes tree canopy closure, and causes a sudden disturbance on soil (Peltzer et al., 1999; Uotila and Kouki, 2005) and on ground vegetation, which alters the environmental conditions for understorey species (Tonteri et al., 2016). The severity of soil disturbance is known to affect the community assemblages between managed and non-managed stands (Peltzer et al., 1999; Uotila and Kouki, 2005). In our results, the species assemblages did not differ between logged and control sites in 1961 and 1986. Yet, there may be several reasons to this. The severity of disturbance created by the thinning treatments was not accurately known, as neither the exact timing nor the method of timber harvesting was known. Logging as lumberjack-work or with forest machinery, and logging season evidently affects the amount of disturbance to understorey vegetation. It is likely that at least the later logging has been done by forest machinery, which probably partly explains the stronger responses of understorey vegetation to logging. Plot size was relatively small (0.1ha), causing edge effect between the plots with different harvesting intensities, which may have disturbed detection of the responses of understorey communities on logging. Sampling interval was relatively long, and it is possible that majority of the impacts have been immediate and the communities have mainly recovered after logging at the time of the vegetation inventory. Moreover, the majority of species used in the harmonized data were common forest floor generalists, as specialist species growing on stones and decaying wood were not included in the analyses. However, many of the sensitive specialist species (Kuuluvainen, 2002) as well as endangered species (Rassi et al., 2010) are dependent on special substrates like decaying wood. Thus the actual impacts of the harvesting treatments probably differ from the detected impacts on understorey vegetation.

On the other hand, the community assemblages between logged and control sites differed from each other during the last study period (2013), as the forest was 93 years old. Increase in logging intensity of the second logging in 1987 resulted to larger differences in the understory vegetation communities in 2013. In addition to immediate impacts, some species have been noticed to react to forestry practices with time delay (Nieppola 1992; Bergstedt and Milberg 2001; Tonteri et al. 2016). Based on the data, we cannot firmly infer, whether the communities of control sites and logged sites are diverging in 2013, or are they recovering from the previous logging achieving increasing convergence, or are the results a combination of both.

Only a few understorey vegetation species (*Deschampsia flexuosa*, *Goodyera repens* and *Hylocomium splendens*) showed significant long-term responses on the second logging (1987). *Deschampsia flexuosa,* used as an indicator for disturbances, had higher abundance on logged sites in 2013, 26 years after the second logging. The higher abundance of *Hylocomium splendens*, was likely due to the lower amount of litter at the time of the inventory, not necessarily due to being favored by disturbance, and changes in abiotic conditions created by timber harvesting. Even though some individual species (e.g. *Pleurozium schreberi*) may benefit from increased light (Gundale et al. 2012), most forest bryophytes are able to survive in shade and are favored by humid microclimate, which are abiotic conditions characteristic of older forests (Frisvoll and Prestø 1997). In general these bryophytes are often negatively affected by forestry practices (Jalonen and Vanha-Majamaa 2001; Paillet et al., 2010).. Also changes in nutrient levels due to the decaying logging residue may have favored some bryophytes on logged sites (Palviainen et al. 2004). The coverage of three most dominant understorey species (*Pleurozium schreberi, Vaccinium myrtillus* and *V. vitis-idaea*) was not affected by the logging in the long-term and they maintained their dominance in all plots throughout the study period. The only species having lower abundance on logged sites was *Goodyera repens,* which is known to be associated to increasing amounts of spruce and old-growth forests (Økland, 2000). Boreal forest understorey vegetation and its associations with symbiotic cyanobacteria and high diversity of fungi plays a key role in maintaining and regulating ecosystem processes (DeLuca et al., 2002; Read et al., 2005; Kolari et al., 2006; Kauserud et al., 2008). Therefore, the long-term impacts and legacy effects of forest thinning on ecosystem functioning deserves to be further studied.

CWD is in system level one of the most important features for forest biodiversity and endangered species (Rassi et al., 2010). Even slight extraction of timber is known to affect the amount and the quality of dead wood (Tikkanen et al., 2014) as the natural accumulation of CWD through self-thinning and disturbances is disrupted (Sturtevant et al., 1997). This was supported by our results as the thinning treatments reduced the accumulation of dead logs, regardless to the thinning intensity. Sturtevant et al. (1997) show that coniferous tree logs accumulate especially when the forest is between 50 and 90 years old, but this development is largely dependent on disturbances and site properties. In our data rather constant accumulation during the first half of the study period (1953–1986) can be assumed. During the latter half (1986–2013) the accumulation possibly has slowed down. As no timber harvesting was done after the second logging, majority of the logs on the logged sites can be assumed to have accumulated after year 1987, whereas control sites also preserve earlier accumulated logs. This can be seen in the high number of most highly decayed logs. However, as the stem volume has increased and the number of stems has decreased during succession, also the quality of CWD has changed, which probably has led to a continuum of uneven sized and uneven aged logs.

4.3 Management implications

Our results strongly suggest that multiple forest thinnings in the past have legacy effects that influence the forest understorey community composition and the amount of CWD, a key indicator for forest biodiversity. Because harvesting intensity affected the responses of the understorey communities (the most intensive harvestings leading to the strongest legacy effects) it may to be possible to support more natural-state understorey community composition using lighter thinning intensities. However, according to our results, thinnings clearly reduced the accumulation of CWD in later-successional stage, regardless to the thinning intensity. Apparently, forest thinning during earlier successional stages disturbs the successional patterns and development of biodiversity values (CWD), emphasizing the importance of leaving the natural later successional forests outside of forestry use to support existing forest biota, as well as allowing the forests to develop unmanaged over long time periods to maintain forest biodiversity in the future. The key message of accumulating legacy effects on understorey communities and biodiversity indicators should be considered when developing and evaluating sustainable forest management practices, multiple use of the forests and planning nature conservation.

5 CONCLUSIONS

Our hypothesis

(i) logging changes the successional developmental pathway of the forest understorey vegetation, was partly rejected, as the main driver for the changes in understorey vegetation communities was time and the effects of forest logging on this development were marginal.

(ii) logging alters understorey vegetation community composition, was partly supported, as only the harvested late-mid successional communities (2013) differed from non-harvested ones.

(iii) logging reduces the accumulation of dead logs, was supported, as the logged stands had significantly lower amount of CWD than controls.

The results indicate that succession of the forest understorey vegetation may override the effects of multiple forest loggings until late-mid successional stages. Successional stage and logging did not affect the total number of species and the changes in community assemblages in time were mainly driven by the abundances of common forest-floor species, possibly supporting rather similar ecosystem functioning on both logged and control sites. However, in the latest successional stage (2013), when the forest was 93 years old, logging intensity together with the possible accumulation of legacy effects led to differences between understorey communities and the amount of CWD. These findings are of major interest since the studies on long-term impacts of less intensive forest management practices are scarce.

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Appendix A–D, Supplementary material

Supplementary data associated with this article can be found in the online version.

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Appendix A

Species abbrevations used and description of taxa classification. Marking “in 2013” means that species was included in non-harmonised data in year 2013 though it was not used in the harmonized data.

Graminoids and sedges

CARE.SP	*Carex* sp.
DESC.FLEX	*Deschampsia flexuosa*
GRAM.SPP	Gramineae (Incl. e.g. *Agrostis* sp. *Calamagrostis* sp., *Deschampsia caespitosa*, *Melica nutans*, *Poa* sp.)
LUZU.PILO	*Luzula pilosa*
MELI.NUTA	*Melica nutans* (in 2013)

Herbs

ANTE.DIOI	*Antennaria dioica*
DACT.MACU	*Dactylorhiza maculata*
DIPH.COMP	*Diphasiastrum complanatum*
EPIL.ANGU	*Epilobium angustifolium*
EQUI.SYLV	*Equisetum sylvaticum*
GERA.SYLV	*Geranium sylvaticum*
GOOD.REPE	*Goodyera repens*
GYMN.DRYO	*Gymnocarpium dryopteris*
HIER.SP	*Hieracium* sp.
HUPE.SELA	*Huperzia selago*
LYCO.SP	*Lycopodium* sp. (Incl. *L. annotinum* and *L. clavatum*)
LYCO.ANNO	*Lycopodium annotinum* (in 2013)
LYSI.EURO	*Lysimachia europaea*
MAIA.BIFO	*Maianthemum bifolium*
MELA.PRAT	*Melampyrum pretense*
MELA.SYLV	*Melampyrum sylvaticum*
MONE.UNIF	*Moneses uniflora*
NEOT.CORD	*Neottia cordata*
ORTH.SECU	*Orthilia secunda*
PHEG.CONN	*Phegopteris connectilis*
PYRO.SP	*Pyrola* sp. (Incl. *P. minor* and *P. rotundifolia*)
SAUS.ALPI	*Saussurea alpina*
SOLI.VIRG	*Solidago virgaurea*

Dwarf shrubs

CALL.VULG	*Calluna vulgaris* (in 2013)
EMPE.NIGR	*Empetrum nigrum*
LINN.BORE	*Linnaea borealis*
VACC.MYRT	*Vaccinium myrtillus*
VACC.VITI	*Vaccinium vitis-idaea*

Shrubs and tree seedlings

BETU.SP	*Betula* sp. (Incl. *B. pendula* and *B. pubescens*)
BETU.PEND	*Betula pendula* (in 2013)
BETU.PUBE	*Betula pubescens* (in 2013)
JUNI.COMM	*Juniperus communis*
PICE.ABIE	*Picea abies*
PINU.SYLV	*Pinus sylvestris* (in 2013)
POPU.TREM	*Populus tremula*
RHOD.TOME	*Rhododendron tomentosum* (in 2013)
SALI.SP	*Salix* sp.

SORB.AUCU	*Sorbus aucuparia*

Bryophytes

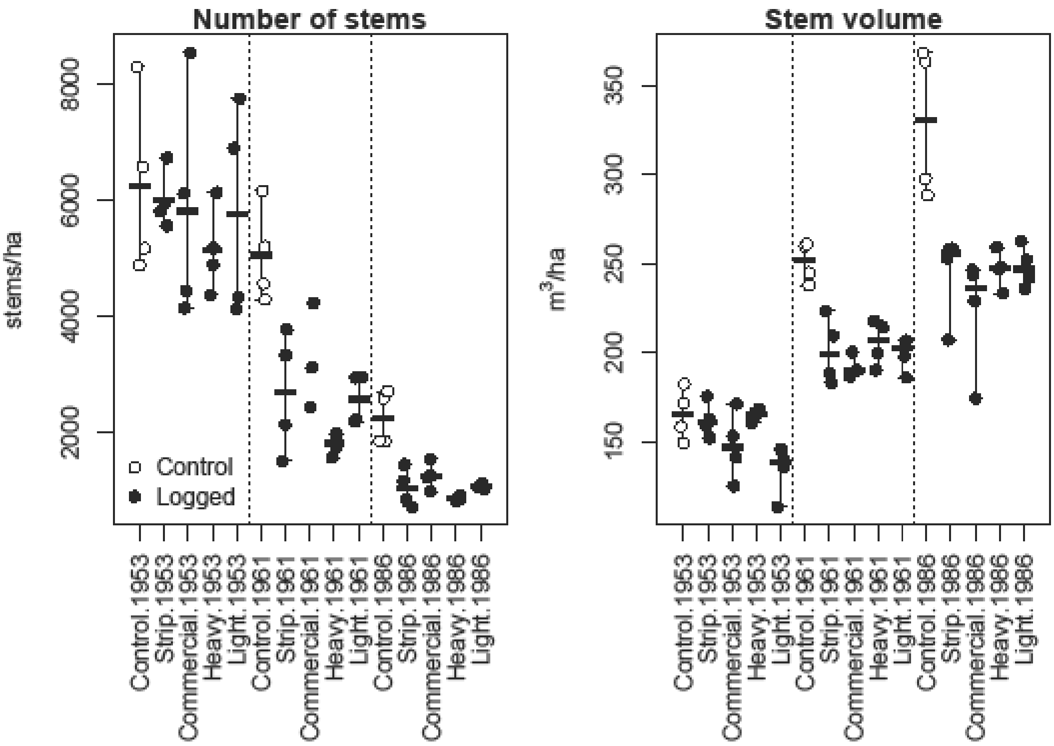
AULA.PALU	*Aulacomnium palustre*
BARB.SP	*Barbilophozia* sp.
BARB.LYCO	*Barbilophozia lycopodioides* (in 2013)
BRAC.SP	*Brachythecium* sp. (Incl. e.g. *Brachythecium salebrosum*, *Sciurohypnum oedipodium*, *Sciuro-hypnum reflexum*)
BRAC.SALE	*Brachythecium salebrosum* (in 2013)
BRYU.SP	*Bryum* sp. (in 2013)
CALY.INTE	*Calypogeia integristipula* (in 2013)
DICR.SP	*Dicranum* sp. (Incl. e.g. *D. fuscescens*, *D. majus, D. scoparium, D. spurium, D. undulatum*)
DICR.MAJU	*Dicranum majus* (in 2013)
DICR.POLY	*Dicranum polysetum*
DICR.SCOP	*Dicranum scoparium*
HEPA.SP	Hepaticae
HYLO.SPLE	*Hylocomium splendens*
LOPH.SP	*Lophozia*-type (in 2013)
PLAG.SP	*Plagiothecium* sp.
PLEU.SCHR	*Pleurozium schreberi*
POLY.COMM	*Polytrichum commune*
POLY.JUNI	*Polytrichum juniperinum*
PTIL.CRIS	*Ptilium crista-castrensis*
PTIL.CILI	*Ptilidium ciliare*
RHYT.TRIQ	*Rhytidiadelphus triquetrus*
RHIZ.MANG	*Rhizomnium magnifolium* (in 2013)
SCIU.OEDI	*Sciuro-hypnum oedipodium* (in 2013)
SCIU.REFL	*Sciuro-hypnum reflexum* (in 2013)
SANI.UNCI	*Sanionia uncinata*
SPHA.SP	*Sphagnum* sp. (Incl. *S. angustifolium, S.capillifolium, S. girgensohnii*)
SPHA.ANGU	*Sphagnum angustifolium* (in 2013)
SPHA.CAPI	*Sphagnum.capillifolium* (in 2013)
SPHA.GIRG	*Sphagnum girgensohnii* (in 2013)

Lichens

CETR.ISLA	*Cetraria islandica* (in 2013)
CLAD.ARBU	*Cladonia arbuscula*
CLAD.RANG	*Cladonia rangiferina*
CLAD.SP	*Cladonia* sp. (Incl. e.g. *C. chlorophaea, C. cornuta, C. crispata, C. furcata, C. squamosa, C. sulphurina*)
CLAD.CHLO	*Cladonia chlorophaea*
CLAD. CORN	*Cladonia cornuta*
CLAD. FURC	*Cladonia furcata*
CLAD.SULP	*Cladonia sulphurina*
CLAD.UNCI	*Cladonia uncialis*
ICMA.ERIC	*Icmadophila ericetorum* (in 2013)
NEPH.ARCT	*Nephroma arcticum*
PELT.APHT	*Peltigera aphthosa* (Incl. *Peltigera neopolydactyla* (except for 2013))
PELT.LEUC	*Peltigera leucophlebia* (in 2013)
PELT.NEOP	*Peltigera neopolydactyla* (in 2013)
PELT.SP	*Peltigera* sp. (Incl. e.g. *P. leucophlebia* and *P. canina*)
STER.SP	*Stereocaulon* sp.

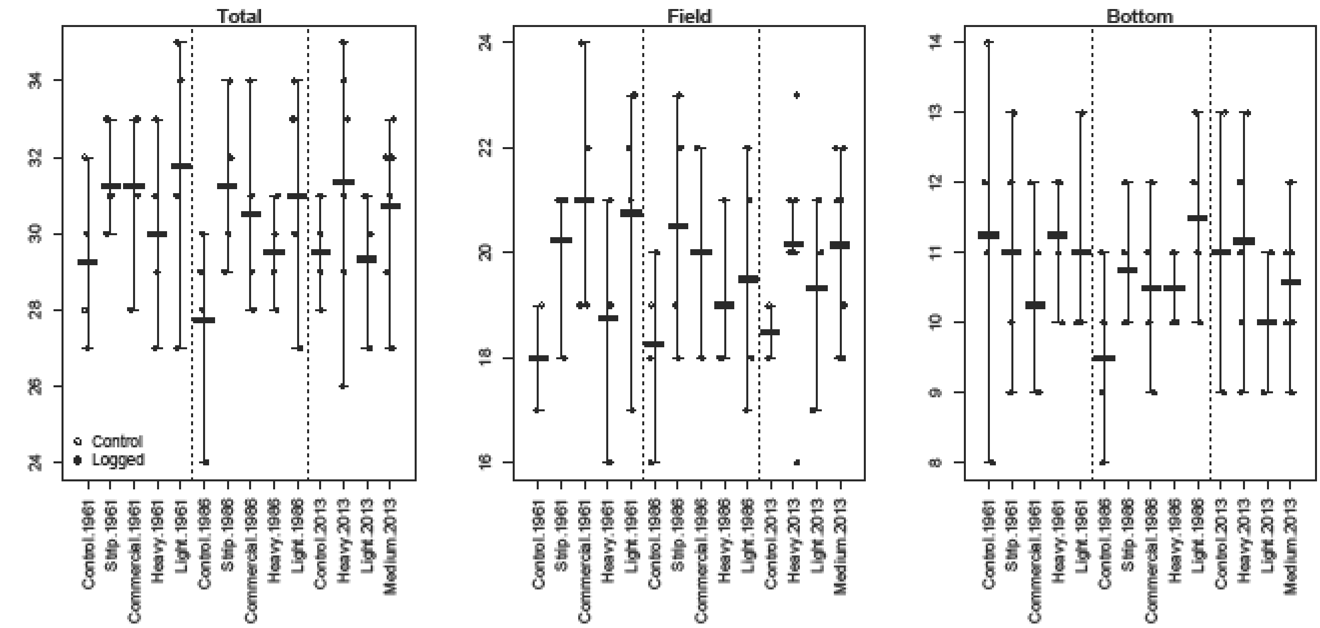
Appendix B

Variation in the number of stems and stem volume in different harvesting treatments in years 1953 (before the first logging), 1961 and 1986 (after the first logging). Names indicate different harvesting intensities in each year (control n=4, strip harvesting n=4, commercial thinning n=4, heavy thinning n=4, light thinning n=4). Mean values are represented with black lines. Years are separated with dashed line to make interpretation of the figure easier. Note the different scales in y-axis.



Appendix C

Variation of the number of taxa in total, and in field and bottom layers separately in previous treatment Years are separated with dashed line to make interpretation of the figure easier. For years 1961 and 1986 previous treatment was done in 1953 (control n=4, strip harvesting, n=4, commercial thinning n=4, heavy thinning n=4, light thinning n=4), and for year 2013 in 1987 (control n=4, heavy n=6, medium n=7, light n=3). Mean values are represented with black lines. Note the different scales in y-axis.



Appendix D

Table of the mean values and standard deviations of species or species group in the previous harvesting treatments in each year.

Year 1961

Treatment	**Control** (n=4)		**Strip harvesting** (n=4)		**Commercial thinning** (n=4)		**Heavy thinning** (n=4)		**Light thinning** (n=4)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges										
Luzula pilosa	0.578	0.303	1.100	0.156	0.772	0.291	0.631	0.363	0.856	0.167
Carex sp.	0.025	0.050	0.013	0.025	0.013	0.025	0.044	0.088	0.106	0.213
Gramineae			0.116	0.057	0.091	0.114	0.038	0.043	0.144	0.128
Deschampsia flexuosa	1.894	1.100	2.600	2.447	2.172	0.856	1.903	0.527	1.422	0.766
In total	2.497	1.155	3.828	2.526	3.047	1.161	2.616	0.494	2.528	0.628
Herbs										
Huperzia selago										
Lycopodium sp.	0.013	0.025	0.088	0.144	0.113	0.144			0.016	0.031
Diphasiastrum complanatum			0.013	0.025	0.038	0.075	1.263	1.555	0.438	0.875
Equisetum sylvaticum										
Phegopteris connectilis										
Gymnocarpium dryopteris	1.403	1.676	4.488	3.717	5.913	7.172	2.431	2.814	6.266	5.131
Pyrola sp.			0.066	0.131	0.019	0.030	0.006	0.013	0.063	0.070
Orthilia secunda	0.438	0.437	0.328	0.482	0.438	0.210	0.316	0.335	0.931	0.595
Moneses uniflora			0.063	0.075	0.025	0.029	0.003	0.006	0.034	0.047
Lysimachia europaea	0.594	0.282	1.106	0.595	0.944	0.193	0.716	0.419	0.919	0.399
Epilobium angustifolium	0.869	0.510	0.850	0.374	0.922	0.777	1.456	0.426	1.138	0.071
Geranium sylvaticum	0.003	0.006	0.063	0.125					0.041	0.081
Melampyrum sylvaticum	0.022	0.026	0.044	0.056	0.063	0.051	0.028	0.021	0.116	0.078
M. pratense	0.056	0.052	0.141	0.167	0.134	0.052	0.303	0.210	0.194	0.193
Solidago virgaurea	2.441	1.098	3.803	0.760	3.306	0.390	3.369	0.945	3.991	0.626
Antennaria dioica	0.075	0.119	0.128	0.152	0.050	0.100	0.063	0.125		
Saussurea alpina										
Hieracium sp.	0.109	0.087	0.306	0.110	0.275	0.323	0.272	0.268	0.184	0.117
Maianthemum bifolium	3.259	1.177	5.903	1.165	3.391	1.820	4.628	1.726	3.594	0.592
Neottia cordata	0.003	0.006	0.003	0.006	0.003	0.006			0.041	0.081
Goodyera repens	0.050	0.100	0.141	0.273					0.138	0.214
Dactylorhiza maculata			0.025	0.050	0.025	0.050			0.050	0.058
In total	9.334	1.463	17.556	3.325	15.656	7.918	14.853	7.214	18.150	6.046
Dwarf shrubs										
Vaccinium vitis-idaea	5.150	3.141	5.878	1.338	7.300	2.218	9.213	3.206	7.044	2.389
V. myrtillus	35.225	18.106	25.516	12.954	32.753	18.423	26.525	14.178	27.366	8.822
Empetrum nigrum	0.016	0.024			0.056	0.065	0.025	0.050	0.075	0.150
Linnaea borealis	2.178	1.308	2.325	0.504	4.872	3.022	4.656	2.066	6.216	1.848
In total	42.569	16.220	33.719	11.789	44.981	18.924	40.419	13.039	40.700	7.587
Shrubs and tree seedlings										
Picea abies	0.003	0.006			0.003	0.006	0.028	0.048	0.063	0.125
Juniperus communis	0.066	0.092	0.159	0.131	0.559	0.569	0.131	0.151	0.141	0.095
Betula sp.	0.003	0.006	0.075	0.096	0.075	0.079	0.009	0.012	0.025	0.050
Salix sp.	0.019	0.024			0.025	0.035	0.038	0.048	0.063	0.125
Populus tremula			0.013	0.025	0.013	0.025				
Sorbus aucuparia	0.578	0.133	1.097	0.279	1.106	0.372	0.981	0.483	1.322	0.406
In total	0.091	0.669	0.226	1.344	0.318	1.781	0.910	1.188	0.652	1.613
Bryophytes										
Hepaticae	0.003	0.006	0.025	0.050	0.025	0.050	0.013	0.025		
Ptilidium ciliare										
Barbilophozia sp.	0.044	0.043	0.094	0.113	0.025	0.050	0.056	0.058	0.066	0.123
Sphagnum sp.										
Dicranum sp.	0.794	0.387	0.828	0.190	0.825	0.174	0.853	0.516	0.397	0.248
D. polysetum	1.041	0.646	2.041	0.730	2.663	2.193	1.941	1.155	2.588	1.183
Aulacomium palustre										
Sanionia uncinata	0.013	0.025			0.081	0.163	0.013	0.025		
Brachyhecium sp.	0.813	0.959	0.841	0.231	0.338	0.284	0.353	0.242	0.678	0.717
Ptilium crista-castrensis	0.100	0.091	0.756	1.209	0.113	0.131	0.244	0.407	0.238	0.221
Hylocomium splendens	1.150	0.372	2.713	3.569	3.225	2.743	2.028	1.874	5.484	4.758
Rhytidiadelphus triquetrus			0.038	0.048						
Pleurozium shreberi	13.375	9.114	15.369	4.309	22.625	7.282	19.688	5.069	18.525	8.886
Plagiotechium sp.	0.138	0.275	0.025	0.050	0.025	0.029				
Polytrichum commune	3.841	2.215	4.428	1.090	4.613	2.389	4.538	0.389	6.066	2.028
P. juniperinum	1.188	0.940	1.666	1.521	0.688	1.375	1.066	1.480	1.163	0.861
In total	22.497	11.758	28.822	1.985	35.244	5.915	30.791	5.362	35.203	7.857
Lichens										
Cladonia sp.	0.013	0.025	0.025	0.050			0.025	0.050	0.066	0.072
C. arbuscula	0.028	0.048	0.016	0.024	0.059	0.089	0.097	0.136	0.169	0.183
C. rangiferina	0.003	0.006					0.006	0.007	0.003	0.006
Stereocaulon sp.	0.038	0.075							0.050	0.100
Nephroma arcticum			0.013	0.025	0.100	0.122	0.013	0.025	0.163	0.325
Peltigera sp.	0.100	0.200			0.225	0.272	0.588	0.437	0.475	0.548
P. aphthosa	0.316	0.324	0.178	0.154	0.078	0.118	0.063	0.125	0.363	0.419
In total	0.497	0.306	0.231	0.172	0.463	0.270	0.791	0.276	1.288	1.082
Litter	79.313	11.903	71.663	3.046	64.700	8.156	67.125	3.367	50.013	30.922

Appendix D

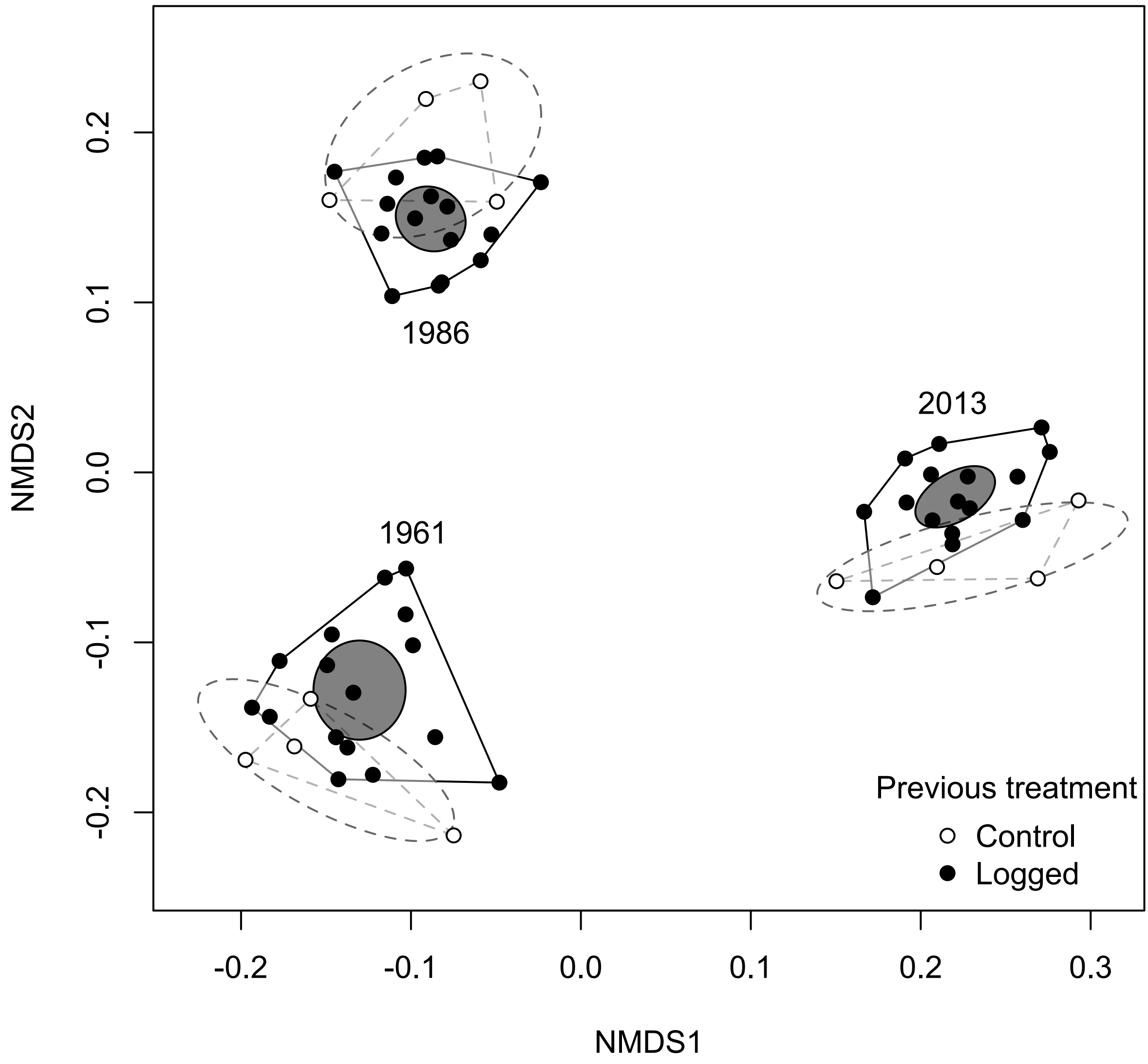
Year1986

Treatment	**Control** (n=4)		**Strip harvesting** (n=4)		**Commercial thinning** (n=4)		**Heavy thinning** (n=4)		**Light thinning** (n=4)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges										
Luzula pilosa	3.806	1.679	4.063	2.800	4.650	1.599	4.241	1.651	2.881	0.732
Carex sp.										
Gramineae	0.022	0.019	0.325	0.166	0.350	0.212	0.163	0.180	0.200	0.147
Deschampsia flexuosa	18.447	6.559	14.903	4.180	23.063	1.059	15.850	4.336	25.588	11.835
In total	22.275	7.755	19.291	6.954	28.063	2.511	20.253	5.015	28.669	11.905
Herbs										
Huperzia selago					0.050	0.100	0.388	0.581		
Lycopodium sp.	1.003	1.230	0.091	0.070	0.813	0.668	0.578	0.617	0.266	0.306
Diphasiastrum complanatum			0.013	0.025					0.088	0.175
Equisetum sylvaticum	0.013	0.025	0.013	0.025						
Phegopteris connectilis										
Gymnocarpium dryopteris	3.088	4.084	5.375	4.539	8.766	9.430	3.800	4.545	11.166	8.407
Pyrola sp.	0.038	0.075			0.075	0.119			0.075	0.119
Orthilia secunda	0.391	0.674	0.403	0.574	0.450	0.268	0.431	0.294	0.850	0.914
Moneses uniflora			0.050	0.071					0.003	0.006
Lysimachia europaea	4.125	0.859	3.134	0.855	3.291	1.781	4.678	0.751	4.166	0.991
Epilobium angustifolium	0.359	0.261	0.316	0.380	0.778	0.489	0.966	0.306	0.550	0.297
Geranium sylvaticum	0.175	0.350	0.016	0.024					0.025	0.050
Melampyrum sylvaticum	0.122	0.166	0.406	0.336	0.813	0.965	0.094	0.171	0.213	0.246
M. pratense	3.816	2.251	3.878	1.415	6.138	3.236	4.569	1.695	4.738	2.607
Solidago virgaurea	3.550	1.407	4.825	0.821	4.225	1.040	4.688	1.285	5.200	2.869
Antennaria dioica			0.013	0.025						
Saussurea alpina					0.038	0.075				
Hieracium sp.	0.016	0.031	0.150	0.178	0.150	0.173	0.075	0.119	0.113	0.131
Maianthemum bifolium	16.388	9.332	14.525	7.637	12.825	5.765	21.750	8.106	17.125	5.768
Neottia cordata	0.003	0.006	0.016	0.024						
Goodyera repens	0.250	0.252	0.253	0.187	0.066	0.131	0.038	0.060	0.209	0.264
Dactylorhiza maculata					0.013	0.025	0.013	0.025		
In total	33.334	3.096	33.475	4.525	38.488	8.319	42.066	13.978	44.784	14.639
Dwarf shrubs										
Vaccinium vitis-idaea	9.325	4.760	8.475	2.079	9.788	2.873	13.400	4.242	11.628	3.371
V. myrtillus	12.353	4.579	22.525	24.167	21.888	18.138	12.828	3.767	16.825	10.615
Empetrum nigrum					0.013	0.025	0.038	0.075		
Linnaea borealis	14.656	1.979	11.500	3.513	17.275	3.370	22.188	5.647	20.275	4.947
In total	36.334	1.729	42.500	21.186	48.963	21.455	48.453	8.727	48.728	15.84
Shrubs and tree seedlings										
Picea abies	0.984	1.846	0.225	0.384	0.425	0.718	0.638	0.950	1.544	1.831
Juniperus communis	0.063	0.125	0.388	0.566	0.450	0.492	0.400	0.311	0.450	0.585
Betula sp.	0.063	0.125	0.028	0.048	0.750	1.467	0.025	0.029	0.100	0.122
Salix sp.	0.003	0.006	0.025	0.050			0.063	0.125		
Populus tremula			0.063	0.125						
Sorbus aucuparia	2.469	0.961	2.122	2.333	2.250	1.059	3.050	0.356	2.113	0.884
In total	0.582	3.581	2.731	2.850	3.200	3.875	2.876	4.175	1.397	4.206
Bryphytes										
Hepaticae										
Ptilidium ciliare	0.163	0.138	0.309	0.286	0.234	0.113	0.284	0.285	0.344	0.098
Barbilophozia sp.	0.422	0.455	0.409	0.447	0.188	0.165	0.375	0.377	0.669	0.967
Sphagnum sp.										
Dicranum sp.	4.053	3.040	4.681	3.528	5.394	1.123	6.391	2.853	5.431	1.462
D. polysetum	2.309	1.796	2.581	2.739	1.219	0.437	1.472	0.824	0.928	0.671
Aulacomium palustre									0.013	0.025
Sanionia uncinata										
Brachyhecium sp.	3.134	5.616	1.128	0.955	0.672	0.682	0.600	0.142	0.691	0.665
Ptilium crista-castrensis	0.791	0.525	1.003	1.579	1.131	1.088	2.078	1.052	2.203	1.852
Hylocomium splendens	2.022	0.915	3.409	2.210	5.516	4.305	1.613	0.977	7.638	5.694
Rhytidiadelphus triquetrus			0.088	0.175						
Pleurozium shreberi	50.419	34.417	59.388	19.028	69.475	12.266	76.475	9.955	64.863	9.066
Plagiotechium sp.			0.013	0.025	0.013	0.025			0.013	0.025
Polytrichum commune	3.009	1.982	8.850	3.891	7.203	3.147	5.519	1.488	7.475	4.328
P. juniperinum	0.397	0.164	1.097	0.643	0.906	0.533	0.563	0.339	0.288	0.257
In total	66.719	34.277	82.956	16.202	91.950	6.744	95.369	10.995	90.553	9.553
Lichens										
Cladonia sp.	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.075	0.087
C. arbuscula										
C. rangiferina										
Stereocaulon sp.										
Nephroma arcticum										
Peltigera sp.										
P. aphthosa									0.013	0.025
In total	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.088	0.111
Litter	36.538	16.72	17.663	8.808	20.688	6.511	15.688	3.751	20.438	1.338

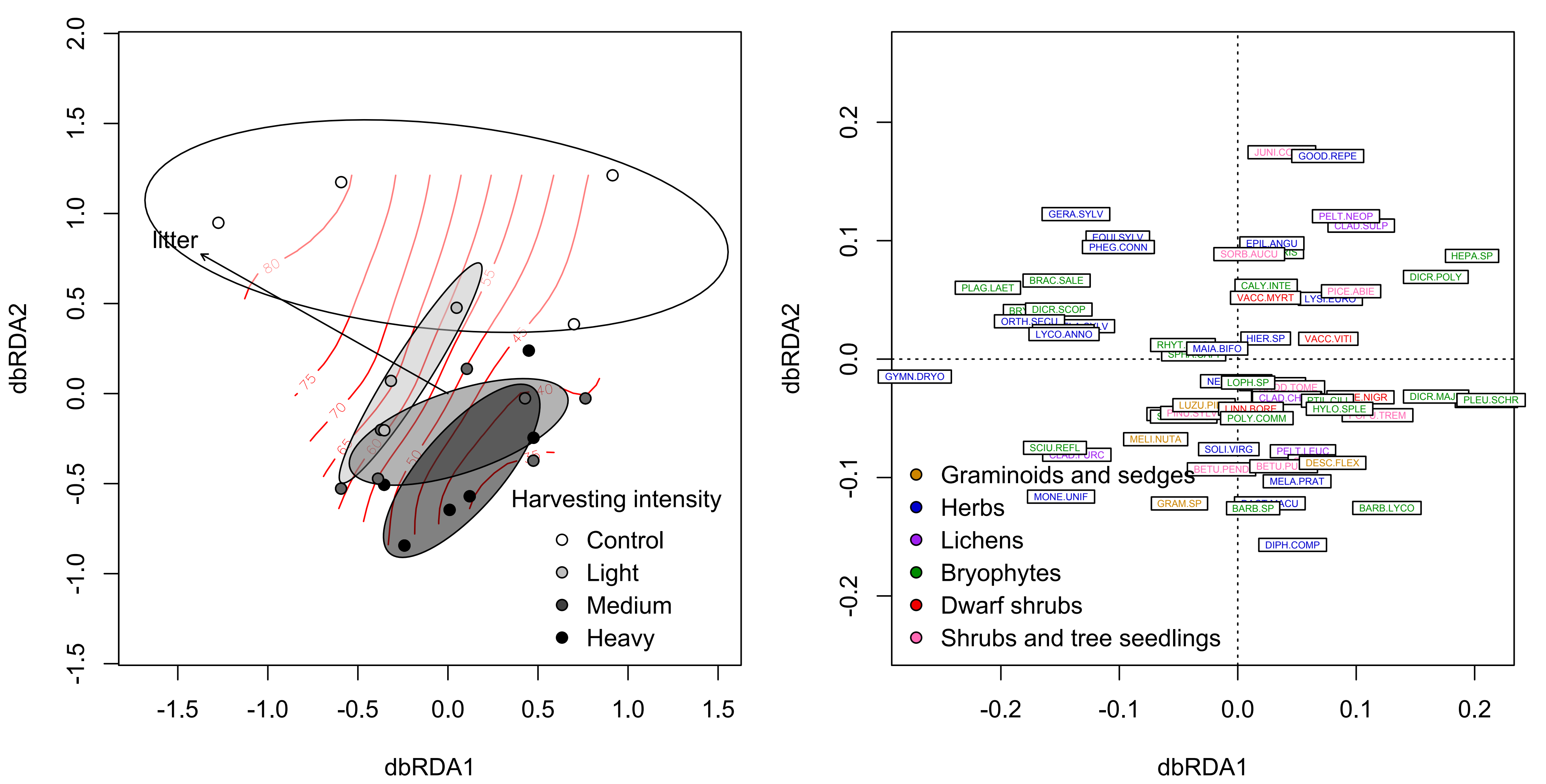
Appendix D

Year2013

Treatment	**Control** (n=4)		**Heavy thinning** (n=6)		**Medium thinning** (n=7)		**Light thinning (n=3)**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges								
Luzula pilosa	0.284	0.199	0.540	0.180	0.463	0.228	0.933	0.198
Carex sp.								
Gramineae	0.003	0.006	0.104	0.120	0.116	0.114	0.163	0.102
Deschampsia flexuosa	0.472	0.244	1.229	0.544	0.977	0.267	0.658	0.158
In total	0.759	0.387	1.873	0.581	1.555	0.500	1.754	0.304
Herbs								
Huperzia selago								
Lycopodium sp.	0.994	1.323	0.556	0.406	0.543	0.486	0.088	0.111
Diphasiastrum complanatum			0.013	0.021	0.011	0.020		
Equisetum sylvaticum								
Phegopteris connectilis	0.050	0.10						
Gymnocarpium dryopteris	1.016	1.829	0.908	1.072	1.137	1.131	2.196	0.805
Pyrola sp.								
Orthilia secunda	0.309	0.516	0.150	0.216	0.223	0.259	0.646	0.418
Moneses uniflora	0.003	0.006	0.013	0.016	0.011	0.011	0.013	0.022
Lysimachia europaea	0.375	0.264	0.308	0.213	0.341	0.428	0.167	0.131
Epilobium angustifolium	0.038	0.048	0.027	0.043	0.011	0.018	0.017	0.029
Geranium sylvaticum			0.021	0.051				
Melampyrum sylvaticum	0.006	0.007	0.017	0.035	0.004	0.009	0.008	0.014
M. pratense	0.144	0.022	0.410	0.146	0.445	0.095	0.375	0.111
Solidago virgaurea	0.741	0.180	1.796	0.912	1.789	0.762	1.767	0.488
Antennaria dioica								
Saussurea alpina								
Hieracium sp.	0.003	0.006	0.004	0.010	0.002	0.005	0.025	0.043
Maianthemum bifolium	1.863	0.849	2.044	0.860	2.800	1.356	2.638	1.241
Neottia cordata	0.025	0.027	0.040	0.051	0.021	0.021	0.021	0.026
Goodyera repens	2.097	0.834	0.544	0.344	1.318	0.400	0.813	1.215
Dactylorhiza maculata			0.013	0.021	0.004	0.009		
In total	7.663	1.401	6.862	2.351	8.658	2.560	8.771	2.427
Dwarf shrubs								
Vaccinium vitis-idaea	10.313	5.998	10.827	2.293	13.00	2.784	11.700	2.901
V. myrtillus	43.425	9.266	43.758	5.623	42.057	3.768	43.583	6.663
Empetrum nigrum	0.056	0.113	0.050	0.100	0.382	0.665		
Linnaea borealis	1.728	0.604	2.673	0.980	3.182	0.791	2.546	0.813
In total	55.522	9.814	57.308	5.848	58.621	2.225	57.829	6.589
Shrubs and tree seedlings								
Picea abies	0.725	0.725	0.742	0.661	0.275	0.328	0.321	0.295
Juniperus communis	0.556	0.130	0.225	0.312	0.234	0.259	0.817	0.718
Betula sp.	0.019	0.030	0.396	0.425	0.213	0.255	0.367	0.153
Salix sp.			0.006	0.010				
Populus tremula	0.006	0.013			0.009	0.019		
Sorbus aucuparia	1.747	0.691	1.425	0.340	1.102	0.450	2.692	0.128
In total	2.480	3.053	1.504	2.794	1.317	1.832	0.752	4.196
Bryphytes								
Hepaticae	0.222	0.341	0.573	0.338	0.393	0.264	0.225	0.142
Ptilidium ciliare	0.134	0.175	0.275	0.338	0.280	0.203	0.029	0.026
Barbilophozia sp.	0.178	0.211	2.144	1.497	1.123	0.693	0.333	0.272
Sphagnum sp.			0.175	0.405			0.033	0.058
Dicranum sp.	4.963	2.848	7.256	1.413	7.345	2.939	5.046	1.266
D. polysetum	4.728	2.918	7.079	1.507	7.189	2.798	5.000	1.277
Aulacomium palustre								
Sanionia uncinata	0.006	0.013						
Brachyhecium sp.	0.834	1.504	0.279	0.298	0.521	0.443	0.579	0.484
Ptilium crista-castrensis	0.022	0.012	0.004	0.006	0.034	0.052	0.013	0.022
Hylocomium splendens	5.013	2.911	8.681	3.425	9.536	3.496	10.204	5.832
Rhytidiadelphus triquetrus			0.017	0.041			0.500	0.866
Pleurozium shreberi	19.688	12.375	32.573	6.588	26.438	12.078	10.479	1.631
Plagiotechium sp.	0.088	0.102	0.021	0.040	0.032	0.047		
Polytrichum commune	2.278	1.976	4.067	2.207	4.027	1.052	5.825	1.401
P. juniperinum	0.053	0.106	0.092	0.099	0.038	0.063		
In total	38.206	19.157	63.235	8.306	56.955	13.902	38.267	1.536
Lichens								
Cladonia sp.	0.013	0.010	0.019	0.025	0.007	0.019		
C. arbuscula								
C. rangiferina								
Stereocaulon sp.								
Nephroma arcticum								
Peltigera sp.								
P. aphthosa	0.063	0.125					0.050	0.087
In total	0.075	0.125	0.019	0.025	0.007	0.019	0.050	0.087
Litter	63.125	20.121	40.083	7.656	47.921	11.498	64.750	2.00



NMDS2
NMDS1
0.2
0.1
0.0
-0.1
-0.2
-0.2
-0.1
0.0
0.1
0.2
0.3
1986
2013
1961
Previous treatment
Control
Logged



litter
Harvesting intensity
Control
Light
Medium
Heavy
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dbRDA2
-1.5
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-0.5
0.0
0.5
1.0
1.5
2.0
80
75
70
65
60
55
50
45
40
35
GOOD.REPE
GERA.SYLV
PELT.NEOP
CLAD.SULP
PHEG.CONN
EPIL.ANGU
SORB.AUCU
HEPA.SP
BRAC.SALE
PLAG.LAET
CALY.INTE
DICR.POLY
VACC.MYRT
PICE.ABIE
DICR.SCOP
ORTH.SECU
LYCO.ANNO
HIER.SP
VACC.VITI
MAIA.BIFO
GYMN.DRYO
LOPH.SP
DICR.MAJ
PLEU.SCHR
HYLO.SPLE
POLY.COMM
MELI.NUTA
SCIU.REFL
SOLI.VIRG
DESC.FLEX
MELA.PRAT
MONE.UNIF
GRAM.SP
BARB.SP
BARB.LYCO
DIPH.COMP
Graminoids and sedges
Herbs
Lichens
Bryophytes
Dwarf shrubs
Shrubs and tree seedlings
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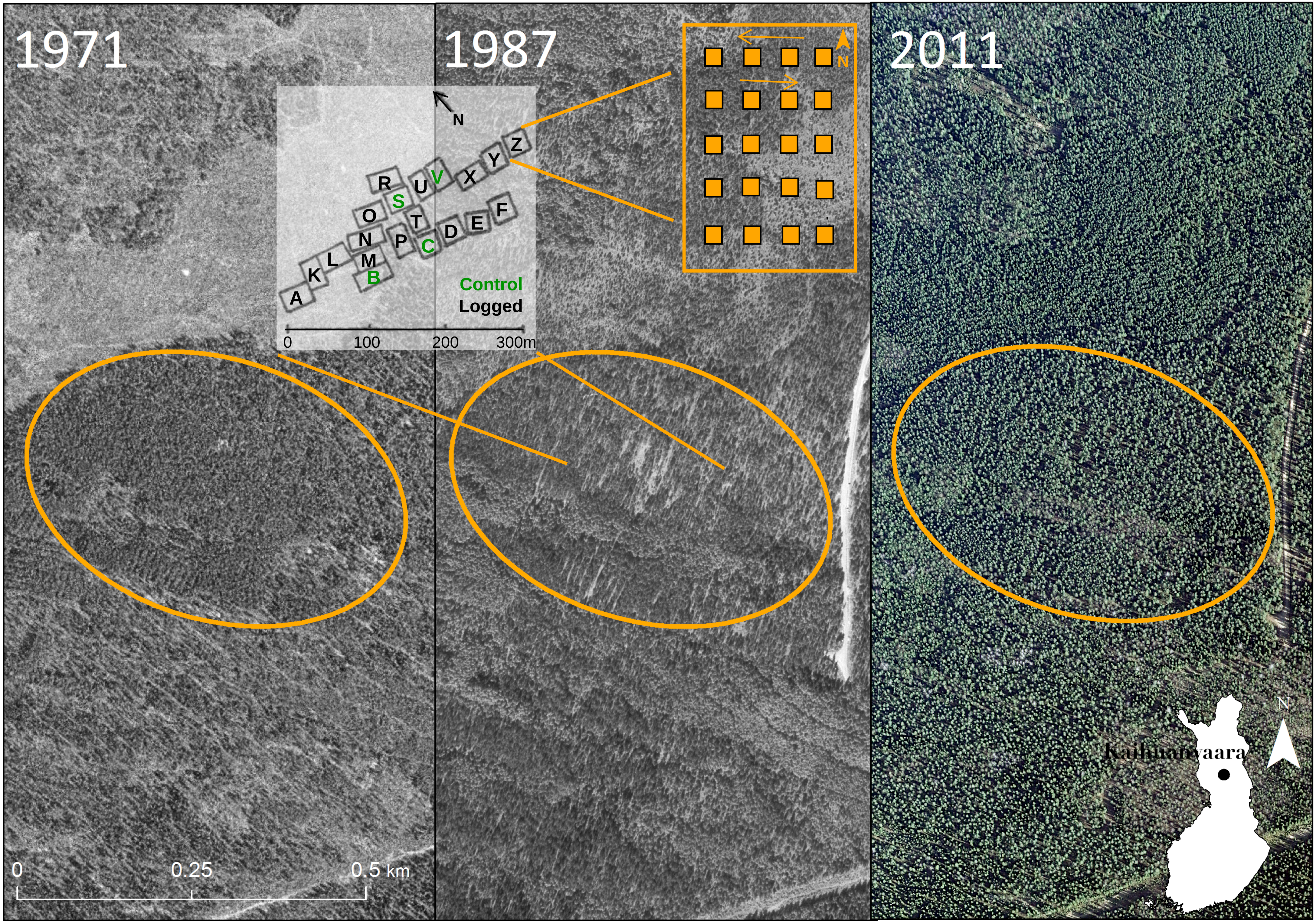
-0.1
0.1
0.2


1971
1987
2011
N
R
U
V
X
Y
Z
S
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T
F
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D
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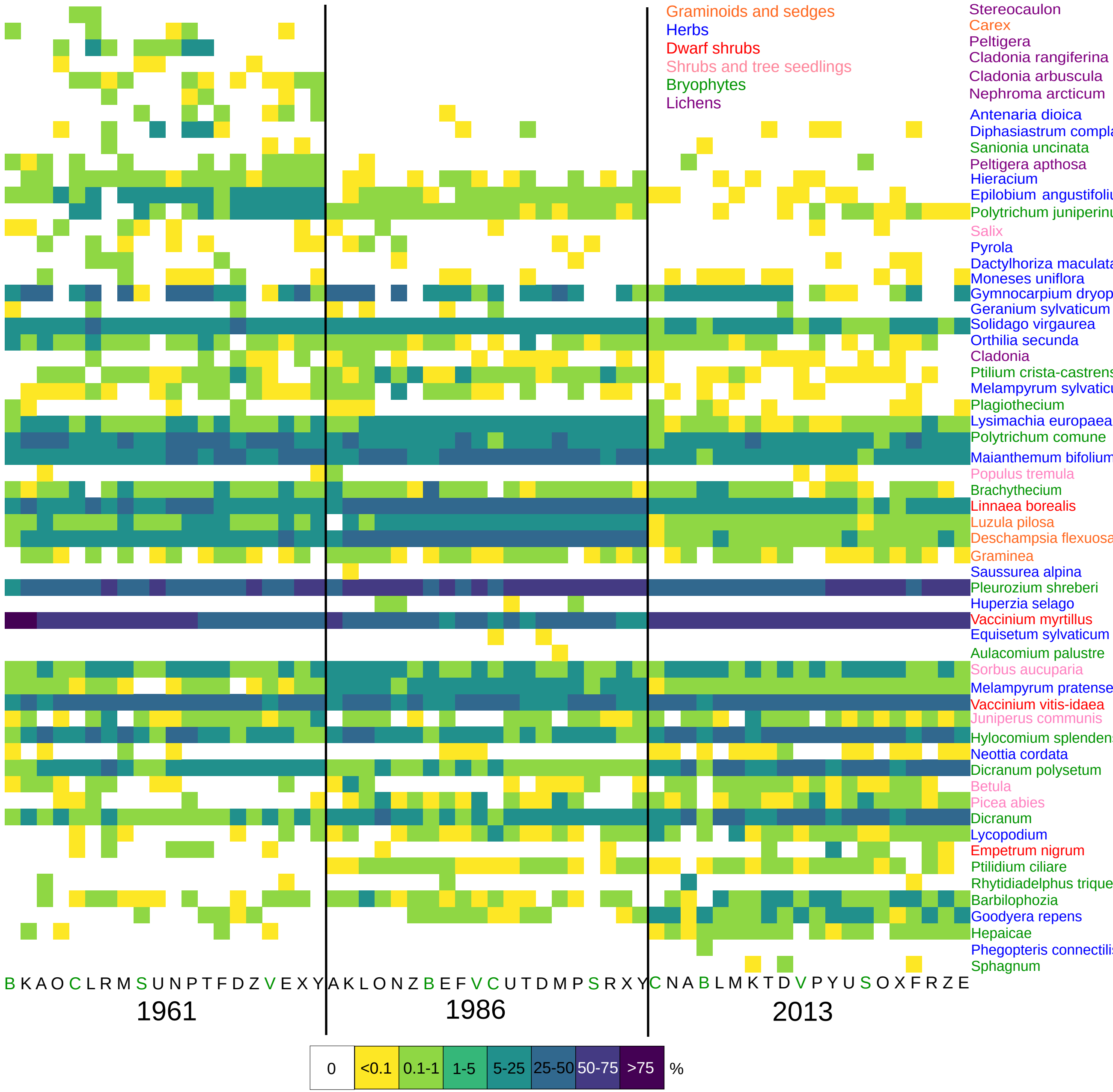
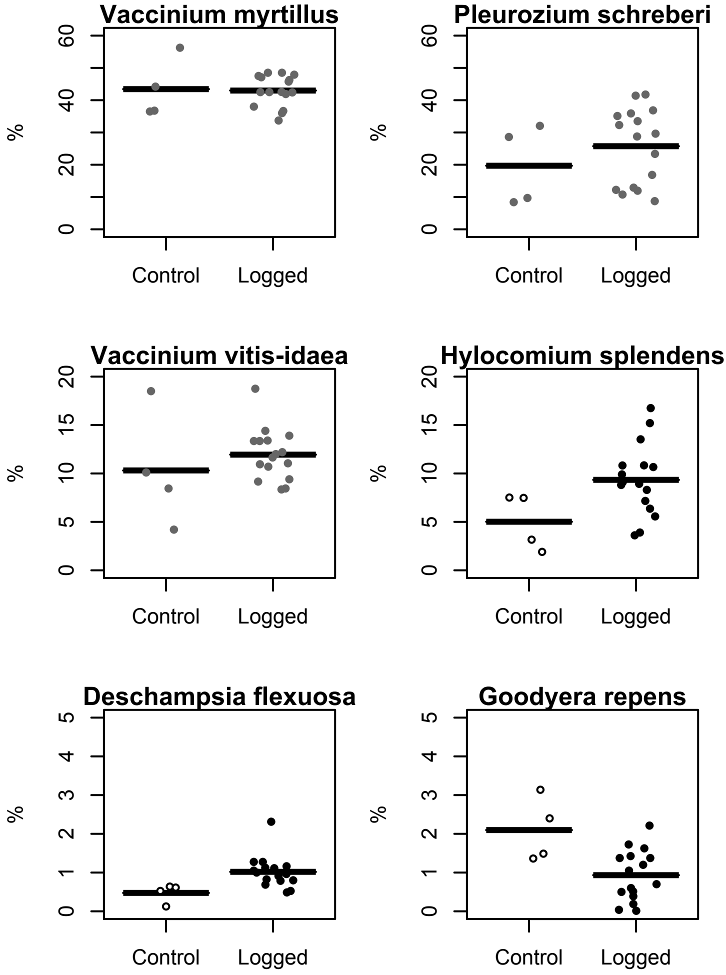
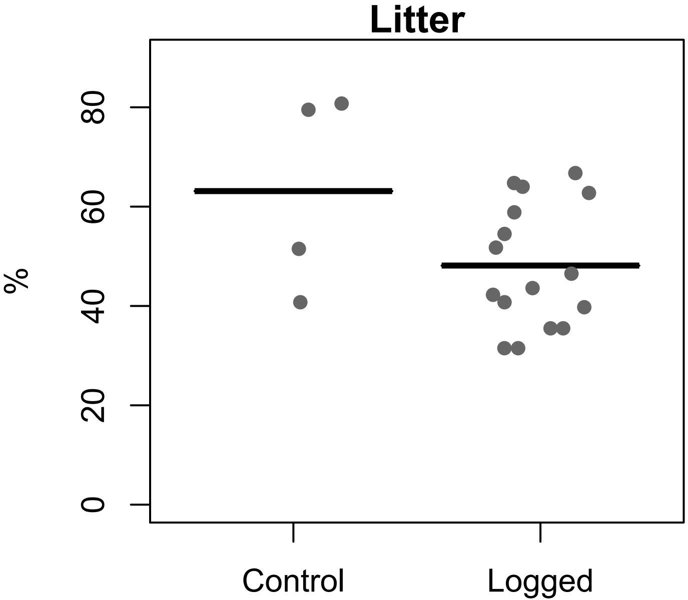
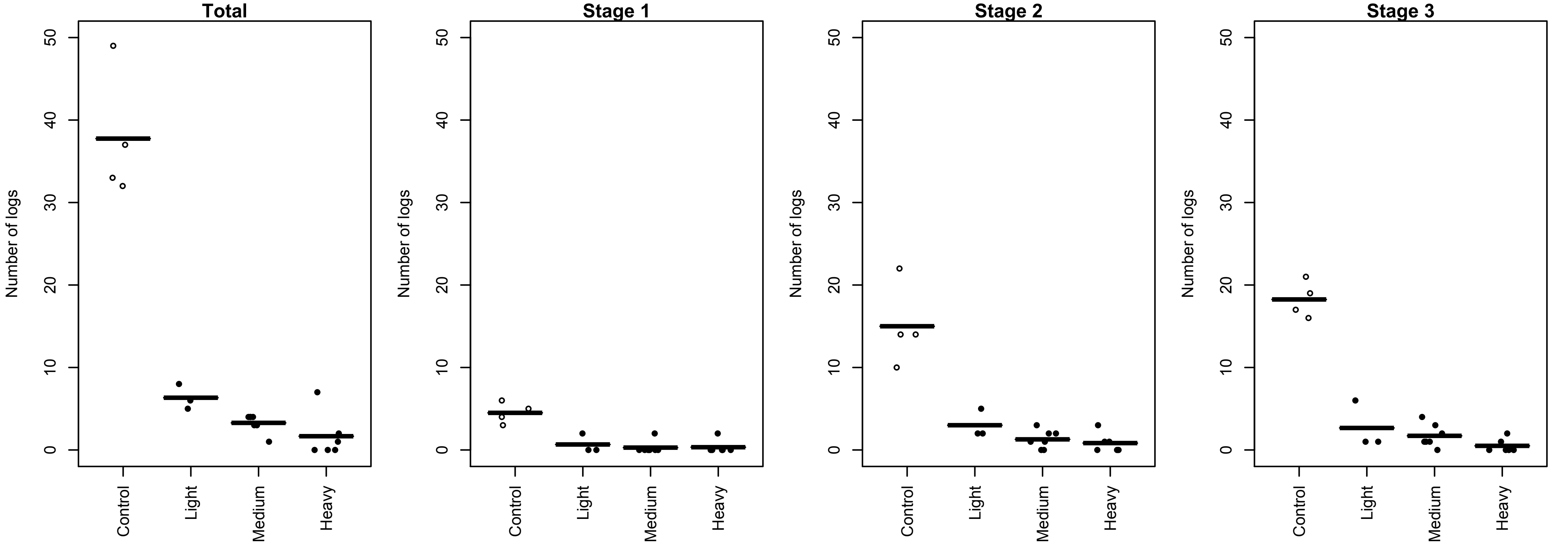
P
C
A
K
L
M
B
Control
Logged
0
100
200
300m
N
Kaihuanvaara
N
0
0.25
0.5 km


Graminoids and sedges
Herbs
Dwarf shrubs
Shrubs and tree seedlings
Bryophytes
Lichens
Stereocaulon
Carex
Peltigera
Cladonia rangiferina
Cladonia arbuscula
Nephroma arcticum
Antenaria dioica
Diphasiastrum compla
Sanionia uncinata
Peltigera apthosa
Hieracium
Epilobium angustifoliu
Polytrichum juniperinu
Salix
Pyrola
Dactylhoriza maculata
Moneses uniflora
Gymnocarpium dryop
Geranium sylvaticum
Solidago virgaurea
Orthilia secunda
Cladonia
Ptilium crista-castrens
Melampyrum sylvaticu
Plagiothecium
Lysimachia europaea
Polytrichum comune
Maianthemum bifolium
Populus tremula
Brachythecium
Linnaea borealis
Luzula pilosa
Deschampsia flexuosa
Graminea
Saussurea alpina
Pleurozium shreberi
Huperzia selago
Vaccinium myrtillus
Equisetum sylvaticum
Aulacomium palustre
Sorbus aucuparia
Melampyrum pratense
Vaccinium vitis-idaea
Juniperus communis
Hylocomium splenden
Neottia cordata
Dicranum polysetum
Betula
Picea abies
Dicranum
Lycopodium
Empetrum nigrum
Ptilidium ciliare
Rhytidiadelphus trique
Barbilophozia
Goodyera repens
Hepaicae
Phegopteris connectilis
Sphagnum
B K A O C L R M S U N P T F D Z V E X Y
1961
A K L O N Z B E F V C U T D M P S R X Y
1986
C N A B L M K T D V P Y U S O X F R Z E
2013
0
<0.1
0.1-1
1-5
5-25
25-50
50-75
>75
%


Vaccinium myrtillus
Pleurozium schreberi
Vaccinium vitis-idaea
Hylocomium splendens
Deschampsia flexuosa
Goodyera repens
%
Control
Logged
0
20
40
60
0
5
10
15
20
0
1
2
3
4
5



Litter
%
0
20
40
60
80
Control
Logged


Total
Stage 1
Stage 2
Stage 3
Number of logs
0
10
20
30
40
50
Control
Light
Medium
Heavy

Year 1961

Treatment	**Control** (n=4)		**Strip harvesting** (n=4)		**Commercial thinning** (n=4)		**Heavy thinning** (n=4)		**Light thinning** (n=4)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges										
Luzula pilosa	0.578	0.303	1.100	0.156	0.772	0.291	0.631	0.363	0.856	0.167
Carex sp.	0.025	0.050	0.013	0.025	0.013	0.025	0.044	0.088	0.106	0.213
Gramineae			0.116	0.057	0.091	0.114	0.038	0.043	0.144	0.128
Deschampsia flexuosa	1.894	1.100	2.600	2.447	2.172	0.856	1.903	0.527	1.422	0.766
In total	2.497	1.155	3.828	2.526	3.047	1.161	2.616	0.494	2.528	0.628
Herbs										
Huperzia selago										
Lycopodium sp.	0.013	0.025	0.088	0.144	0.113	0.144			0.016	0.031
Diphasiastrum complanatum			0.013	0.025	0.038	0.075	1.263	1.555	0.438	0.875
Equisetum sylvaticum										
Phegopteris connectilis										
Gymnocarpium dryopteris	1.403	1.676	4.488	3.717	5.913	7.172	2.431	2.814	6.266	5.131
Pyrola sp.			0.066	0.131	0.019	0.030	0.006	0.013	0.063	0.070
Orthilia secunda	0.438	0.437	0.328	0.482	0.438	0.210	0.316	0.335	0.931	0.595
Moneses uniflora			0.063	0.075	0.025	0.029	0.003	0.006	0.034	0.047
Lysimachia europaea	0.594	0.282	1.106	0.595	0.944	0.193	0.716	0.419	0.919	0.399
Epilobium angustifolium	0.869	0.510	0.850	0.374	0.922	0.777	1.456	0.426	1.138	0.071
Geranium sylvaticum	0.003	0.006	0.063	0.125					0.041	0.081
Melampyrum sylvaticum	0.022	0.026	0.044	0.056	0.063	0.051	0.028	0.021	0.116	0.078
M. pratense	0.056	0.052	0.141	0.167	0.134	0.052	0.303	0.210	0.194	0.193
Solidago virgaurea	2.441	1.098	3.803	0.760	3.306	0.390	3.369	0.945	3.991	0.626
Antennaria dioica	0.075	0.119	0.128	0.152	0.050	0.100	0.063	0.125		
Saussurea alpina										
Hieracium sp.	0.109	0.087	0.306	0.110	0.275	0.323	0.272	0.268	0.184	0.117
Maianthemum bifolium	3.259	1.177	5.903	1.165	3.391	1.820	4.628	1.726	3.594	0.592
Neottia cordata	0.003	0.006	0.003	0.006	0.003	0.006			0.041	0.081
Goodyera repens	0.050	0.100	0.141	0.273					0.138	0.214
Dactylorhiza maculata			0.025	0.050	0.025	0.050			0.050	0.058
In total	9.334	1.463	17.556	3.325	15.656	7.918	14.853	7.214	18.150	6.046
Dwarf shrubs										
Vaccinium vitis-idaea	5.150	3.141	5.878	1.338	7.300	2.218	9.213	3.206	7.044	2.389
V. myrtillus	35.225	18.106	25.516	12.954	32.753	18.423	26.525	14.178	27.366	8.822
Empetrum nigrum	0.016	0.024			0.056	0.065	0.025	0.050	0.075	0.150
Linnaea borealis	2.178	1.308	2.325	0.504	4.872	3.022	4.656	2.066	6.216	1.848
In total	42.569	16.220	33.719	11.789	44.981	18.924	40.419	13.039	40.700	7.587
Shrubs and tree seedlings										
Picea abies	0.003	0.006			0.003	0.006	0.028	0.048	0.063	0.125
Juniperus communis	0.066	0.092	0.159	0.131	0.559	0.569	0.131	0.151	0.141	0.095
Betula sp.	0.003	0.006	0.075	0.096	0.075	0.079	0.009	0.012	0.025	0.050
Salix sp.	0.019	0.024			0.025	0.035	0.038	0.048	0.063	0.125
Populus tremula			0.013	0.025	0.013	0.025				
Sorbus aucuparia	0.578	0.133	1.097	0.279	1.106	0.372	0.981	0.483	1.322	0.406
In total	0.091	0.669	0.226	1.344	0.318	1.781	0.910	1.188	0.652	1.613
Bryphytes										
Hepaticae	0.003	0.006	0.025	0.050	0.025	0.050	0.013	0.025		
Ptilidium ciliare										
Barbilophozia sp.	0.044	0.043	0.094	0.113	0.025	0.050	0.056	0.058	0.066	0.123
Sphagnum sp.										
Dicranum sp.	0.794	0.387	0.828	0.190	0.825	0.174	0.853	0.516	0.397	0.248
D. polysetum	1.041	0.646	2.041	0.730	2.663	2.193	1.941	1.155	2.588	1.183
Aulacomium palustre										
Sanionia uncinata	0.013	0.025			0.081	0.163	0.013	0.025		
Brachyhecium sp.	0.813	0.959	0.841	0.231	0.338	0.284	0.353	0.242	0.678	0.717
Ptilium crista-castrensis	0.100	0.091	0.756	1.209	0.113	0.131	0.244	0.407	0.238	0.221
Hylocomium splendens	1.150	0.372	2.713	3.569	3.225	2.743	2.028	1.874	5.484	4.758
Rhytidiadelphus triquetrus			0.038	0.048						
Pleurozium shreberi	13.375	9.114	15.369	4.309	22.625	7.282	19.688	5.069	18.525	8.886
Plagiotechium sp.	0.138	0.275	0.025	0.050	0.025	0.029				
Polytrichum commune	3.841	2.215	4.428	1.090	4.613	2.389	4.538	0.389	6.066	2.028
P. juniperinum	1.188	0.940	1.666	1.521	0.688	1.375	1.066	1.480	1.163	0.861
In total	22.497	11.758	28.822	1.985	35.244	5.915	30.791	5.362	35.203	7.857
Lichens										
Cladonia sp.	0.013	0.025	0.025	0.050			0.025	0.050	0.066	0.072
C. arbuscula	0.028	0.048	0.016	0.024	0.059	0.089	0.097	0.136	0.169	0.183
C. rangiferina	0.003	0.006					0.006	0.007	0.003	0.006
Stereocaulon sp.	0.038	0.075							0.050	0.100
Nephroma arcticum			0.013	0.025	0.100	0.122	0.013	0.025	0.163	0.325
Peltigera sp.	0.100	0.200			0.225	0.272	0.588	0.437	0.475	0.548
P. aphthosa	0.316	0.324	0.178	0.154	0.078	0.118	0.063	0.125	0.363	0.419
In total	0.497	0.306	0.231	0.172	0.463	0.270	0.791	0.276	1.288	1.082
Litter	79.313	11.903	71.663	3.046	64.700	8.156	67.125	3.367	50.013	30.922

Year1986

Treatment	Control (n=4)		Strip harvesting (n=4)		Commercial thinning (n=4)		Heavy thinning (n=4)		Light thinning (n=4)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges										
Luzula pilosa	3.806	1.679	4.063	2.800	4.650	1.599	4.241	1.651	2.881	0.732
Carex sp.										
Gramineae	0.022	0.019	0.325	0.166	0.350	0.212	0.163	0.180	0.200	0.147
Deschampsia flexuosa	18.447	6.559	14.903	4.180	23.063	1.059	15.850	4.336	25.588	11.835
In total	22.275	7.755	19.291	6.954	28.063	2.511	20.253	5.015	28.669	11.905
Herbs										
Huperzia selago					0.050	0.100	0.388	0.581		
Lycopodium sp.	1.003	1.230	0.091	0.070	0.813	0.668	0.578	0.617	0.266	0.306
Diphasiastrum complanatum			0.013	0.025					0.088	0.175
Equisetum sylvaticum	0.013	0.025	0.013	0.025						
Phegopteris connectilis										
Gymnocarpium dryopteris	3.088	4.084	5.375	4.539	8.766	9.430	3.800	4.545	11.166	8.407
Pyrola sp.	0.038	0.075			0.075	0.119			0.075	0.119
Orthilia secunda	0.391	0.674	0.403	0.574	0.450	0.268	0.431	0.294	0.850	0.914
Moneses uniflora			0.050	0.071					0.003	0.006
Lysimachia europaea	4.125	0.859	3.134	0.855	3.291	1.781	4.678	0.751	4.166	0.991
Epilobium angustifolium	0.359	0.261	0.316	0.380	0.778	0.489	0.966	0.306	0.550	0.297
Geranium sylvaticum	0.175	0.350	0.016	0.024					0.025	0.050
Melampyrum sylvaticum	0.122	0.166	0.406	0.336	0.813	0.965	0.094	0.171	0.213	0.246
M. pratense	3.816	2.251	3.878	1.415	6.138	3.236	4.569	1.695	4.738	2.607
Solidago virgaurea	3.550	1.407	4.825	0.821	4.225	1.040	4.688	1.285	5.200	2.869
Antennaria dioica			0.013	0.025						
Saussurea alpina					0.038	0.075				
Hieracium sp.	0.016	0.031	0.150	0.178	0.150	0.173	0.075	0.119	0.113	0.131
Maianthemum bifolium	16.388	9.332	14.525	7.637	12.825	5.765	21.750	8.106	17.125	5.768
Neottia cordata	0.003	0.006	0.016	0.024						
Goodyera repens	0.250	0.252	0.253	0.187	0.066	0.131	0.038	0.060	0.209	0.264
Dactylorhiza maculata					0.013	0.025	0.013	0.025		
In total	33.334	3.096	33.475	4.525	38.488	8.319	42.066	13.978	44.784	14.639
Dwarf shrubs										
Vaccinium vitis-idaea	9.325	4.760	8.475	2.079	9.788	2.873	13.400	4.242	11.628	3.371
V. myrtillus	12.353	4.579	22.525	24.167	21.888	18.138	12.828	3.767	16.825	10.615
Empetrum nigrum					0.013	0.025	0.038	0.075		
Linnaea borealis	14.656	1.979	11.500	3.513	17.275	3.370	22.188	5.647	20.275	4.947
In total	36.334	1.729	42.500	21.186	48.963	21.455	48.453	8.727	48.728	15.84
Shrubs and tree seedlings										
Picea abies	0.984	1.846	0.225	0.384	0.425	0.718	0.638	0.950	1.544	1.831
Juniperus communis	0.063	0.125	0.388	0.566	0.450	0.492	0.400	0.311	0.450	0.585
Betula sp.	0.063	0.125	0.028	0.048	0.750	1.467	0.025	0.029	0.100	0.122
Salix sp.	0.003	0.006	0.025	0.050			0.063	0.125		
Populus tremula			0.063	0.125						
Sorbus aucuparia	2.469	0.961	2.122	2.333	2.250	1.059	3.050	0.356	2.113	0.884
In total	0.582	3.581	2.731	2.850	3.200	3.875	2.876	4.175	1.397	4.206
Bryphytes										
Hepaticae										
Ptilidium ciliare	0.163	0.138	0.309	0.286	0.234	0.113	0.284	0.285	0.344	0.098
Barbilophozia sp.	0.422	0.455	0.409	0.447	0.188	0.165	0.375	0.377	0.669	0.967
Sphagnum sp.										
Dicranum sp.	4.053	3.040	4.681	3.528	5.394	1.123	6.391	2.853	5.431	1.462
D. polysetum	2.309	1.796	2.581	2.739	1.219	0.437	1.472	0.824	0.928	0.671
Aulacomium palustre									0.013	0.025
Sanionia uncinata										
Brachyhecium sp.	3.134	5.616	1.128	0.955	0.672	0.682	0.600	0.142	0.691	0.665
Ptilium crista-castrensis	0.791	0.525	1.003	1.579	1.131	1.088	2.078	1.052	2.203	1.852
Hylocomium splendens	2.022	0.915	3.409	2.210	5.516	4.305	1.613	0.977	7.638	5.694
Rhytidiadelphus triquetrus			0.088	0.175						
Pleurozium shreberi	50.419	34.417	59.388	19.028	69.475	12.266	76.475	9.955	64.863	9.066
Plagiotechium sp.			0.013	0.025	0.013	0.025			0.013	0.025
Polytrichum commune	3.009	1.982	8.850	3.891	7.203	3.147	5.519	1.488	7.475	4.328
P. juniperinum	0.397	0.164	1.097	0.643	0.906	0.533	0.563	0.339	0.288	0.257
In total	66.719	34.277	82.956	16.202	91.950	6.744	95.369	10.995	90.553	9.553
Lichens										
Cladonia sp.	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.075	0.087
C. arbuscula										
C. rangiferina										
Stereocaulon sp.										
Nephroma arcticum										
Peltigera sp.										
P. aphthosa									0.013	0.025
In total	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.088	0.111
Litter	36.538	16.72	17.663	8.808	20.688	6.511	15.688	3.751	20.438	1.338

	Year2013							
Treatment	**Control** (n=4)		**Heavy thinning** (n=6)		**Medium thinning** (n=7)		**Light thinning (n=3)**	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Graminoids and sedges								
Luzula pilosa	0.284	0.199	0.540	0.180	0.463	0.228	0.933	0.198
Carex sp.								
Gramineae	0.003	0.006	0.104	0.120	0.116	0.114	0.163	0.102
Deschampsia flexuosa	0.472	0.244	1.229	0.544	0.977	0.267	0.658	0.158
In total	0.759	0.387	1.873	0.581	1.555	0.500	1.754	0.304
Herbs								
Huperzia selago								
Lycopodium sp.	0.994	1.323	0.556	0.406	0.543	0.486	0.088	0.111
Diphasiastrum complanatum			0.013	0.021	0.011	0.020		
Equisetum sylvaticum								
Phegopteris connectilis	0.050	0.10						
Gymnocarpium dryopteris	1.016	1.829	0.908	1.072	1.137	1.131	2.196	0.805
Pyrola sp.								
Orthilia secunda	0.309	0.516	0.150	0.216	0.223	0.259	0.646	0.418
Moneses uniflora	0.003	0.006	0.013	0.016	0.011	0.011	0.013	0.022
Lysimachia europaea	0.375	0.264	0.308	0.213	0.341	0.428	0.167	0.131
Epilobium angustifolium	0.038	0.048	0.027	0.043	0.011	0.018	0.017	0.029
Geranium sylvaticum			0.021	0.051				
Melampyrum sylvaticum	0.006	0.007	0.017	0.035	0.004	0.009	0.008	0.014
M. pratense	0.144	0.022	0.410	0.146	0.445	0.095	0.375	0.111
Solidago virgaurea	0.741	0.180	1.796	0.912	1.789	0.762	1.767	0.488
Antennaria dioica								
Saussurea alpina								
Hieracium sp.	0.003	0.006	0.004	0.010	0.002	0.005	0.025	0.043
Maianthemum bifolium	1.863	0.849	2.044	0.860	2.800	1.356	2.638	1.241
Neottia cordata	0.025	0.027	0.040	0.051	0.021	0.021	0.021	0.026
Goodyera repens	2.097	0.834	0.544	0.344	1.318	0.400	0.813	1.215
Dactylorhiza maculata			0.013	0.021	0.004	0.009		
In total	7.663	1.401	6.862	2.351	8.658	2.560	8.771	2.427
Dwarf shrubs								
Vaccinium vitis-idaea	10.313	5.998	10.827	2.293	13.00	2.784	11.700	2.901
V. myrtillus	43.425	9.266	43.758	5.623	42.057	3.768	43.583	6.663
Empetrum nigrum	0.056	0.113	0.050	0.100	0.382	0.665		
Linnaea borealis	1.728	0.604	2.673	0.980	3.182	0.791	2.546	0.813
In total	55.522	9.814	57.308	5.848	58.621	2.225	57.829	6.589
Shrubs and tree seedlings								
Picea abies	0.725	0.725	0.742	0.661	0.275	0.328	0.321	0.295
Juniperus communis	0.556	0.130	0.225	0.312	0.234	0.259	0.817	0.718
Betula sp.	0.019	0.030	0.396	0.425	0.213	0.255	0.367	0.153
Salix sp.			0.006	0.010				
Populus tremula	0.006	0.013			0.009	0.019		
Sorbus aucuparia	1.747	0.691	1.425	0.340	1.102	0.450	2.692	0.128
In total	2.480	3.053	1.504	2.794	1.317	1.832	0.752	4.196
Bryphytes								
Hepaticae	0.222	0.341	0.573	0.338	0.393	0.264	0.225	0.142
Ptilidium ciliare	0.134	0.175	0.275	0.338	0.280	0.203	0.029	0.026
Barbilophozia sp.	0.178	0.211	2.144	1.497	1.123	0.693	0.333	0.272
Sphagnum sp.			0.175	0.405			0.033	0.058
Dicranum sp.	4.963	2.848	7.256	1.413	7.345	2.939	5.046	1.266
D. polysetum	4.728	2.918	7.079	1.507	7.189	2.798	5.000	1.277
Aulacomium palustre								
Sanionia uncinata	0.006	0.013						
Brachyhecium sp.	0.834	1.504	0.279	0.298	0.521	0.443	0.579	0.484
Ptilium crista-castrensis	0.022	0.012	0.004	0.006	0.034	0.052	0.013	0.022
Hylocomium splendens	5.013	2.911	8.681	3.425	9.536	3.496	10.204	5.832
Rhytidiadelphus triquetrus			0.017	0.041			0.500	0.866
Pleurozium shreberi	19.688	12.375	32.573	6.588	26.438	12.078	10.479	1.631
Plagiotechium sp.	0.088	0.102	0.021	0.040	0.032	0.047		
Polytrichum commune	2.278	1.976	4.067	2.207	4.027	1.052	5.825	1.401
P. juniperinum	0.053	0.106	0.092	0.099	0.038	0.063		
In total	38.206	19.157	63.235	8.306	56.955	13.902	38.267	1.536
Lichens								
Cladonia sp.	0.013	0.010	0.019	0.025	0.007	0.019		
C. arbuscula								
C. rangiferina								
Stereocaulon sp.								
Nephroma arcticum								
Peltigera sp.								
P. aphthosa	0.063	0.125					0.050	0.087
In total	0.075	0.125	0.019	0.025	0.007	0.019	0.050	0.087
Litter	63.125	20.121	40.083	7.656	47.921	11.498	64.750	2.00

Appendix A

Species abbreviations used and description of taxa classification. "in 2013" means that species was included in non-harmonised data in year 2013 though it was not used in the harmonized data.

Graminoids and sedges

CARE.SP	*Carex sp.*
DESC.FLEX	*Deschampsia flexuosa*
GRAM.SPP	Gramineae (Incl. e.g. *Agrostis* sp. *Calamagrostis* sp., *Deschampsia caespitosa*, *Melica nutans, Poa* sp.)
LUZU.PILO	*Luzula pilosa*
MELI.NUTA	*Melica nutans* (in 2013)

Herbs

ANTE.DIOI	*Antennaria dioica*
DACT.MACU	*Dactylorhiza maculata*
DIPH.COMP	*Diphasiastrum complanatum*
EPIL.ANGU	*Epilobium angustifolium*
EQUI.SYLV	*Equisetum sylvaticum*
GERA.SYLV	*Geranium sylvaticum*
GOOD.REPE	*Goodyera repens*
GYMN.DRYO	*Gymnocarpium dryopteris*
HIER.SP	*Hieracium* sp.
HUPE.SELA	*Huperzia selago*
LYCO.SP	*Lycopodium* sp. (Incl. *Lycopodium annotinum* and *Lycopodium clavatum*)
LYCO.ANNO	*Lycopodium annotinum* (in 2013)
LYSI.EURO	*Lysimachia europaea*
MAIA.BIFO	*Maianthemum bifolium*
MELA.PRAT	*Melampyrum pretense*
MELA.SYLV	*Melampyrum sylvaticum*
MONE.UNIF	*Moneses uniflora*
NEOT.CORD	*Neottia cordata*
ORTH.SECU	*Orthilia secunda*
PHEG.CONN	*Phegopteris connectilis*
PYRO.SP	*Pyrola* sp. (Incl. *Pyrola minor* and *Pyrola rotundifolia*)
SAUS.ALPI	*Saussurea alpina*
SOLI.VIRG	*Solidago virgaurea*

Dwarf shrubs

CALL.VULG	*Calluna vulgaris* (in 2013)
EMPE.NIGR	*Empetrum nigrum*
LINN.BORE	*Linnaea borealis*
VACC.MYRT	*Vaccinium myrtillus*
VACC.VITI	*Vaccinium vitis-idaea*

Shrubs and tree seedlings

BETU.SP	*Betula* sp. (Incl. *B. pendula* and *B. pubescens*)
BETU.PEND	*Betula pendula* (in 2013)
BETU.PUBE	*Betula pubescens* (in 2013)
JUNI.COMM	*Juniperus communis*
PICE.ABIE	*Picea abies*
PINU.SYLV	*Pinus sylvestris* (in 2013)
POPU.TREM	*Populus tremula*
RHOD.TOME	*Rhododendron tomentosum* (in 2013)
SALI.SP	*Salix* sp.
SORB.AUCU	*Sorbus aucuparia*

Bryophytes

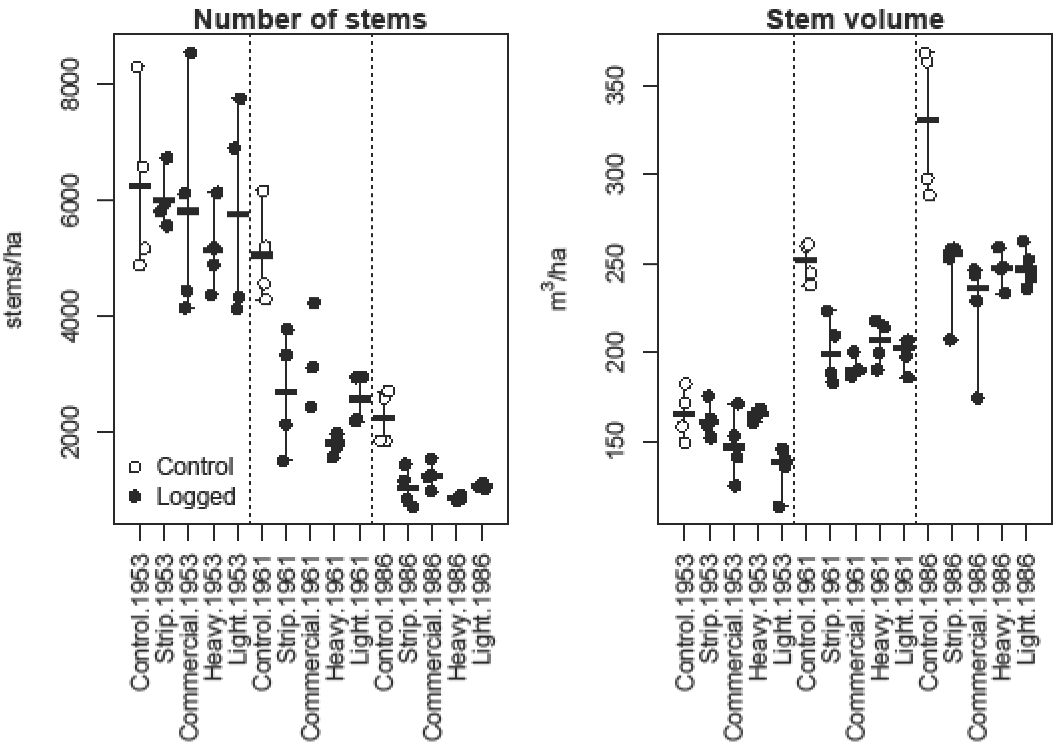
AULA.PALU	*Aulacomnium palustre*
BARB.SP	*Barbilophozia* sp.
BARB.LYCO	*Barbilophozia lycopodioides* (in 2013)
BRAC.SP	*Brachythecium* sp. (Incl. e.g. *Brachythecium salebrosum, Sciuro-hypnum oedipodium, Sciuro-hypnum reflexum*)
BRAC.SALE	*Brachythecium salebrosum* (in 2013)
BRYU.SP	*Bryum* sp. (in 2013)
CALY.INTE	*Calypogeia integristipula* (in 2013)
DICR.SP	*Dicranum* sp. (Incl. e.g. *Dicranum fuscescens, D. majus, D. scoparium, D. spurium, D. undulatum)*
DICR.MAJU	*Dicranum majus* (in 2013)
DICR.POLY	*Dicranum polysetum*
DICR.SCOP	*Dicranum scoparium*
HEPA.SP	Hepaticae
HYLO.SPLE	*Hylocomium splendens*
LOPH.SP	*Lophozia*-type (in 2013)
PLAG.SP	*Plagiothecium* sp.
PLEU.SCHR	*Pleurozium schreberi*
POLY.COMM	*Polytrichum commune*
POLY.JUNI	*Polytrichum juniperinum*
PTIL.CRIS	*Ptilium crista-castrensis*
PTIL.CILI	*Ptilidium ciliare*
RHYT.TRIQ	*Rhytidiadelphus triquetrus*
RHIZ.MANG	*Rhizomnium magnifolium* (in 2013)
SCIU.OEDI	*Sciuro-hypnum oedipodium* (in 2013)
SCIU.REFL	*Sciuro-hypnum reflexum* (in 2013)
SANI.UNCI	*Sanionia uncinata*
SPHA.SP	*Sphagnum* sp. (Incl. *Sphagnum angustifolium*, *S.capillifolium, S. girgensohnii*)
SPHA.ANGU	*Sphagnum angustifolium* (in 2013)
SPHA.CAPI	*Sphagnum.capillifolium* (in 2013)
SPHA.GIRG	*Sphagnum girgensohnii* (in 2013)

Lichens

CETR.ISLA	*Cetraria islandica* (in 2013)
CLAD.ARBU	*Cladonia arbuscula*
CLAD.RANG	*Cladonia rangiferina*
CLAD.SP	*Cladonia* sp. (Incl. e.g. *Cladonia chlorophaea, C. cornuta, C. crispata, C. furcata, C. squamosa, C. sulphurina*)
CLAD.CHLO	*Cladonia chlorophaea*
CLAD. CORN	*Cladonia cornuta*
CLAD. FURC	*Cladonia furcata*
CLAD.SULP	*Cladonia sulphurina*
CLAD.UNCI	*Cladonia uncialis*
ICMA.ERIC	*Icmadophila ericetorum* (in 2013)
NEPH.ARCT	*Nephroma arcticum*
PELT.APHT	*Peltigera aphthosa* (Incl. *Peltigera neopolydactyla* (except for 2013))
PELT.LEUC	*Peltigera leucophlebia* (in 2013)
PELT.NEOP	*Peltigera neopolydactyla* (in 2013)
PELT.SP	*Peltigera* sp. (Incl. e.g. *Peltigera leucophlebia* and *P. canina*)
STER.SP	*Stereocaulon* sp.

Appendix B

Variation in the number of stems and stem volume in different harvesting treatments in years 1953 (before the first logging), 1961 and 1986 (after the first logging). Names indicate different harvesting intensities in each year (control n=4, strip harvesting n=4, commercial thinning n=4, heavy thinning n=4, light thinning n=4). Mean values are represented with black lines. Years are separated with dashed line to make interpretation of the figure easier. Note the different scales in y-axis.



Appendix C

Variation of the number of taxa in total, and in field and bottom layers separately in previous treatment Years are separated with dashed line to make interpretation of the figure easier. For years 1961 and 1986 previous treatment was done in 1953 (control n=4, strip harvesting, n=4, commercial thinning n=4, heavy thinning n=4, light thinning n=4), and for year 2013 in 1987 (control n=4, heavy n=6, medium n=7, light n=3). Mean values are represented with black lines. Note the different scales in y-axis.