**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.

Abbreviations: Coarse woody debris: CWD

21 ABSTRACT

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

39

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

66 (Koivula et al., 2014, Vanha-Majamaa et al. 2017) to progress towards more sustainable forestry (Peura et al.
67 2018).

68

69 The managed forests lack many structurally important features for maintaining biodiversity (Kuuluvainen,
70 2002), most importantly CWD (Jonsson and Jonsell, 1999; Paillet et al., 2010), as the natural accumulation
71 of logs through self-thinning and disturbances is disturbed (Sturtevant et al., 1997). Consequently, many
72 forest-dwelling organisms and nature types have become threatened (Rassi et al., 2010). According to
73 Tonteri et al. (2016) forest logging influences especially the abundance-relationships between light-
74 demanding and shade-tolerant species, and in Finland and in Sweden intensive forest management is a
75 driving factor for the changes in the abundances and frequencies of understorey plant species (Reinikainen et
76 al., 2000; Sundberg, 2014; Hedwall and Brunet, 2016). However, this development is not restricted to
77 Finland or Northern Europe but should be a global concern, even though the European forests have been
78 most widely utilized (Paillet et al., 2010).

79

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

91

92 In this study, we followed how forest thinning, repeated twice during a period of 93 years, affected the
93 succession of forest understorey vegetation, altered understorey plant community composition, and the
94 accumulation of logs. We also studied the responses of individual plant species that either play a key role in
95 supporting ecosystem functions or can be used as indicator species. Twenty permanent experimental plots
96 were established and sown by Scots pine (*Pinus sylvestris*) in year 1920, one year after a wild fire, and their
97 understorey vegetation was inventoried three times (1961, 1986, 2013) allowing us to cover a time-span of
98 52 years. We hypothesized forest logging would (i) change the successional developmental pathway of
99 understorey vegetation, (ii) alter understorey community composition, and (iii) have negative long-term
100 effects on the amount CWD.

101

102 2 MATERIALS AND METHODS

103 2.1 Study area

104 The study was carried out in Kivalo research area, Kaihuanvaara, Northern Finland (66 ° 23'N, 26 ° 54'E).
 105 (Fig 1.) The average annual temperature in the study area varies from 0 to 1 °C, annual rainfall from 550 to
 106 600 mm (Vanha-Majamaa and Lähde, 1991), and the length of growing season from 135 to 145 days
 107 (Finnish Meteorological Institute a). The average temperature of the coldest month (January) is −11.4 °C and
 108 the average temperature of the warmest month (July) is 15.4 °C (1981–2010) (Finnish Meteorological
 109 Institute b). Duration of the snowy period is approximately 175–190 days (from early November till late
 110 April–early May), and the average snow depth in March is 60–80cm (1981–2010) (Finnish Meteorological
 111 Institute c). In Northern Finland particularly autumns and springs have warmed, the snow cover has become
 112 thinner and precipitation during the growing season has increased in the last decades (Kivinen et al., 2017;
 113 Korpela et al., 2013). The Kaihuanvaara research forests have been used as study sites by Finnish forestry
 114 researchers (Sirén, 1955, Vanha-Majamaa and Lähde, 1991; Salminen and Jalkanen, 2007).

115

116 The experimental plot setup, used in this study (Fig. 1), was established in 1920 by the former Finnish Forest
 117 Research Institute (METLA) after a wildfire of 600 ha in 1919, in order to study the effects of different
 118 forest thinning intensities on growth of artificially regenerated Scots pine (experiment B 13 I in Heikinheimo
 119 1961). The previous large forest fire in the same site was in 1877. In both fires most of the study area,
 120 including our study site, was burned. The study site includes 20 permanent 0.1 ha plots that are located on
 121 the western slope of the hill at an altitude range of 180–250 m a.s.l. Bedrock on Kaihuanvaara is quartzite,
 122 covered with glacial till deposits (Vanha-Majamaa and Lähde, 1991). The study site represents mesic forest
 123 vegetation, which in absence of forest management, would be dominated by Norway spruce with varying
 124 portions of Scots pine and deciduous tree species.

125

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

137 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

139

140 Fig. 1 Location of Kaihuanvaara and aerial photographs from the study site from the years 1971, 1987 and
 141 2011 (18 years, same year and 24 years after the previous logging, and ten years after, one year after and two
 142 years before the vegetation inventories, respectively.) Orange circles show the location of the study plots and
 143 the locations of each study plot are shown in the insert (map according to Heikinheimo 1961). Letters
 144 indicate different study plots and green color control plots. In top center of the figure are shown the
 145 schematic positions and the order of vegetation recording of the 20 regularly placed 1 m² vegetation squares.

146

147 Comparisons of the effects of different harvesting treatments (1953) on the number of stems and stem
 148 volume between 1953 and 1986 are shown in Appendix B. The stem number has decreased from
 149 approximately 6000 stems/ha (1953) to 3000 stems/ha (1961) to 1000 stems/ha (1986) on logged sites due to
 150 the treatments and self-thinning. On control sites the number of stems has decreased more slowly from
 151 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 m³/ha (1953) to 200 m³/ha (1961) to 250 m³/ha (1986) on logged sites and from 170 m³/ha (1953) to 250 m³/ha (1961) to over 325 m³/ha (1986) on control sites.

155

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 1m² 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.

169

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

178 highest cover values. Non-harmonized data from year 2013 were used in the analysis concerning this year
 179 only. In year 2013 altogether 70 species or taxa were found from the non-harmonized data; 37 belonging to
 180 vascular plants, 24 to bryophytes and 9 to lichens (Appendix A).

181

182 2.3 Environmental variables

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

195

196 2.4. Statistical analysis

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

202

203 The data were ordinated with constrained distance-based redundancy analysis dbRDA (McArdle &
 204 Anderson 2001) and partial non-metric multidimensional scaling NMDS (Kruskal, 1964). These are robust
 205 ordination methods that can well cope with non-linear unimodal species response models of various shapes
 206 (Minchin, 1987). Partial NMDS is a natural extension of the dbRDA framework (McArdle & Anderson
 207 2001) where the residuals after constraints are subjected to NMDS. To focus on the successional change in
 208 vegetation, the effect of plot was partialled out before submitting the data to NMDS. This method also
 209 removes the effect of spatial distance. We used partial NMDS for the overall analysis of succession, and
 210 dbRDA for the analysis of the non-harmonized data in year 2013. Similar analysis was conducted for the
 211 other two years as well, but no differences were detected. Full model for year 2013 was built by including all
 212 environmental variables into it (e.g. harvesting intensity, basal area of pine, proportion of mixed wood,
 213 amount of litter, number of snags and the numbers of logs in each of the three decay stages) and it was
 214 reduced to final model that included only litter and harvesting intensity. Model significance was tested using
 215 randomization test with 9999 permutations.

216

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

221

222 The responses of two strongest indicator species (*Deschampsia flexuosa* as an indicator for disturbance and
 223 *Goodyera repens* for old-growth forests), and the four most dominant species (*Vaccinium myrtillus* and *V.*
 224 *vitis-idaea* from field layer, and *Pleurozium shreberi* and *Hylocomium splendens* from bottom layer) and
 225 litter on logging were analyzed using t-test, as there was a clear difference in variance between the groups.
 226 The impact of harvesting intensity on the number of logs, on the number of stems and stem volume, as well
 227 as the impacts of year and logging on the number of species, were analyzed using general linear models and
 228 quasi-Poisson dispersion. Model significance was tested using analysis on variance and F-test. Pairwise

229 comparisons were done using Tukey's Honest Significant Difference. All statistical analyses were performed
230 in the R statistical environment (R 3.3.3.). The vegan package (Oksanen et al., 2017) was used for the
231 multivariate analysis.

232 3 RESULTS

233 3.1 Impacts of forest harvesting on understorey vegetation succession and community composition

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

238

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

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

250

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

261

262 Fig. 3 Distance-based RDA ordination (dbRDA) using reduced model. Different harvesting intensities ($df=3$,
 263 $F=1.6187$, $p=0.005$) (control $n=4$, light $n=3$, medium $n=7$ and heavy $n=6$) are separated with fitted
 264 Bonferroni corrected 95% confidence interval ellipses around each treatment centroid. The variation in the
 265 amount of litter ($df=1$, $F=3.4474$, $p=0.005$) is visualized using smoothened trend surface and an arrow
 266 showing the direction of linear increase in the amount of litter. If species names have been overlapping,
 267 species are ordered with priority in abundance. Abbreviations used can be found from Appendix A.

268

269 3.2 Changes in understorey vegetation community composition during the study period

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

278 *Polytrichum juniperinum*, and *Sanionia uncinata*) and lichens (*Peltigera aphthosa*) that were common in
 279 1961 declined either in frequency, in coverage or in both from year 1961 to years 1986 and 2013 (Fig. 4).
 280 Majority of these species declined smoothly during the study period but for some species year 1986 was a
 281 threshold (Fig. 4). They either disappeared (e.g. *Antennaria dioica* and *Pyrola* sp.) or declined either in
 282 coverage (e.g. *Cladonia* sp., *Melampyrum sylvaticum* and *Ptilium crista-castrensis*) or in both coverage and
 283 frequency (e.g. *Hieracium* sp.) after this year (Fig. 4).

284

285 Some herbaceous species (e.g. *Lysimachia europaea*, *Maianthemum bifolium* and *Melampyrum pratense*),
 286 graminoids (e.g. *Deschampsia flexuosa* and *Luzula pilosa*), dwarf shrubs (*Linnaea borealis*) and bryophytes
 287 (*Pleurozium schreberi*) had a peak in 1986, while other dwarf shrubs (*Vaccinium myrtillus* and *V. vitis-*
 288 *idaea*) and bryophytes (e.g. *Dicranum polysetum* and *Hylocomium splendens*) tended to increase by 2013
 289 (Fig. 4). The species abundances returned mostly to the level of year 1961 by year 2013 except for few
 290 species (e.g. *Deschampsia flexuosa* and *Lysimachia europaea*) that decreased from the pre-peak level to year
 291 2013. Correspondingly, some herbaceous species (e.g. *Goodyera repens*, *Lycopodium* s.s., *Moneses uniflora*
 292 and *Neottia cordata*), tree seedlings and bryophytes (e.g. *Barbilophozia* coll., *Dicranum polysetum*,
 293 *Dicranum* sp., *Hylocomium splendens* and *Ptilidium ciliare*) had an overall smooth increasing trend in time
 294 (despite the slight decline in 1986 for some of the species), or established after year 1986 (e.g. *Phegopteris*
 295 *connectilis* and *Sphagnum* sp.) (Fig. 4).

296

297 The species composition remained relatively constant during the whole study period (Fig. 4). The two most
 298 dominant species (*Pleurozium schreberi* and *Vaccinium myrtillus*) had much higher abundance than any
 299 other species (Fig. 4) They also maintained their dominance through the study period (Fig. 4). The frequency
 300 and abundances of subdominant species (e.g. *Deschampsia flexuosa*, *Dicranum polysetum*, *Gymnocarpium*
 301 *dryopteris*, *Hylocomium splendens*, *Linnaea borealis*, *Maianthemum bifolium*, *Polytrichum commune* and
 302 *Vaccinium vitis-idaea*), varied between the years but they still maintained their populations through the
 303 whole study period (Fig. 4). Species that can be used as indicators for valuable forest habitats (*Goodyera*

304 *repens*, *Neottia cordata* and *Moneses uniflora*) (Skogsstyrelsen, 2014) increased in frequency by year 2013,
 305 and in case of *Goodyera repens* also in coverage. Detailed information about the mean coverages of
 306 individual species and species groups between different treatments in each year can be found from Appendix
 307 D.

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

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

314

315 3.3 Species responses and the biodiversity impacts of the second logging

316 Forest logging significantly affected the abundance of only few species (Fig. 5). *Deschampsia flexuosa*
 317 ($df=8.431$, $t=3.427$, $p=0.008$), and *Hylocomium splendens* ($df=5.723$, $t=-2.51$, $p=0.048$) had higher coverage
 318 on logged plots, whereas *Goodyera repens* ($df=3.987$, $t=2.598$, $p=0.060$) had slightly higher coverage on
 319 control plots. Logging did not have any statistically significant effect on the coverage of the three most
 320 abundant species: *Vaccinium myrtillus*, *V. vitis-idaea* and *Pleurozium schreberi* (Fig. 5) or the amount of
 321 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).

342

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

346 4 DISCUSSION

347 4.1 Understorey vegetation succession

348 The main driver for the changes in understorey vegetation communities was time, and the impacts of the
 349 harvesting treatments on understorey communities were negligible in the first two study periods (1961,1986).
 350 The overall successional pattern of the understorey vegetation during the study period on both logged and
 351 control sites followed similar pattern from dominance of lichens, acrocarpous mosses and light demanding
 352 herbs to dominance of shrubs, pleurocarpous mosses, liverworts and shade-tolerant vascular plants, which is
 353 similar to many other reported results (e.g. Økland, 2000; Nilsson and Wardle, 2005; Uotila and Kouki,
 354 2005). The forest canopy closes relatively rapidly after forest thinning, creating only a short-term change in
 355 light conditions (Hedwall et al., 2013). Consequently, it is likely that the responses of understorey vegetation
 356 on harvesting treatments were so immediate and short-term that they were not detected in this study, due to
 357 the relatively long sampling interval of the vegetation (8 years and 27 years) after the first logging (1953).

358

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

370

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.

389

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.

438

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

450 logs. However, as the stem volume has increased and the number of stems has decreased during succession,
451 also the quality of CWD has changed, which probably has led to a continuum of uneven sized and uneven
452 aged logs.

453

454 4.3 Management implications

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

468 5 CONCLUSIONS

469 Our hypothesis

- 470 (i) logging changes the successional developmental pathway of the forest
- 471 understorey vegetation, was partly rejected, as the main driver for the
- 472 changes in understorey vegetation communities was time and the effects of
- 473 forest logging on this development were marginal.
- 474 (ii) logging alters understorey vegetation community composition, was partly
- 475 supported, as only the harvested late-mid successional communities (2013)
- 476 differed from non-harvested ones.
- 477 (iii) logging reduces the accumulation of dead logs, was supported, as the logged
- 478 stands had significantly lower amount of CWD than controls.

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

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502

503 Appendix A–D, Supplementary material

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

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- 671

672 **Appendix A**

673

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

676

677 **Graminoids and sedges**

678	CARE.SP	<i>Carex</i> sp.
679	DESC.FLEX	<i>Deschampsia flexuosa</i>
680	GRAM.SPP	Gramineae (Incl. e.g. <i>Agrostis</i> sp. <i>Calamagrostis</i> sp., <i>Deschampsia caespitosa</i> ,
681		<i>Melica nutans</i> , <i>Poa</i> sp.)
682	LUZU.PILO	<i>Luzula pilosa</i>
683	MELI.NUTA	<i>Melica nutans</i> (in 2013)

684

685 **Herbs**

686	ANTE.DIOI	<i>Antennaria dioica</i>
687	DACT.MACU	<i>Dactylorhiza maculata</i>
688	DIPH.COMP	<i>Diphasiastrum complanatum</i>
689	EPIL.ANGU	<i>Epilobium angustifolium</i>
690	EQUI.SYLV	<i>Equisetum sylvaticum</i>
691	GERA.SYLV	<i>Geranium sylvaticum</i>
692	GOOD.REPE	<i>Goodyera repens</i>
693	GYMN.DRYO	<i>Gymnocarpium dryopteris</i>
694	HIER.SP	<i>Hieracium</i> sp.
695	HUPE.SELA	<i>Huperzia selago</i>
696	LYCO.SP	<i>Lycopodium</i> sp. (Incl. <i>L. annotinum</i> and <i>L. clavatum</i>)
697	LYCO.ANNO	<i>Lycopodium annotinum</i> (in 2013)
698	LYSI.EURO	<i>Lysimachia europaea</i>
699	MAIA.BIFO	<i>Maianthemum bifolium</i>
700	MELA.PRAT	<i>Melampyrum pretense</i>
701	MELA.SYLV	<i>Melampyrum sylvaticum</i>
702	MONE.UNIF	<i>Moneses uniflora</i>
703	NEOT.CORD	<i>Neottia cordata</i>
704	ORTH.SECU	<i>Orthilia secunda</i>
705	PHEG.CONN	<i>Phegopteris connectilis</i>
706	PYRO.SP	<i>Pyrola</i> sp. (Incl. <i>P. minor</i> and <i>P. rotundifolia</i>)
707	SAUS.ALPI	<i>Saussurea alpina</i>
708	SOLI.VIRG	<i>Solidago virgaurea</i>

709

710 **Dwarf shrubs**

711	CALL.VULG	<i>Calluna vulgaris</i> (in 2013)
712	EMPE.NIGR	<i>Empetrum nigrum</i>
713	LINN.BORE	<i>Linnaea borealis</i>
714	VACC.MYRT	<i>Vaccinium myrtillus</i>
715	VACC.VITI	<i>Vaccinium vitis-idaea</i>

716

717 **Shrubs and tree seedlings**

718	BETU.SP	<i>Betula</i> sp. (Incl. <i>B. pendula</i> and <i>B. pubescens</i>)
719	BETU.PEND	<i>Betula pendula</i> (in 2013)
720	BETU.PUBE	<i>Betula pubescens</i> (in 2013)
721	JUNI.COMM	<i>Juniperus communis</i>
722	PICE.ABIE	<i>Picea abies</i>
723	PINU.SYLV	<i>Pinus sylvestris</i> (in 2013)
724	POPU.TREM	<i>Populus tremula</i>
725	RHOD.TOME	<i>Rhododendron tomentosum</i> (in 2013)
726	SALI.SP	<i>Salix</i> sp.

727	SORB.AUCU	<i>Sorbus aucuparia</i>
728		
729	Bryophytes	
730	AULA.PALU	<i>Aulacomnium palustre</i>
731	BARB.SP	<i>Barbilophozia</i> sp.
732	BARB.LYCO	<i>Barbilophozia lycopodioides</i> (in 2013)
733	BRAC.SP	<i>Brachythecium</i> sp. (Incl. e.g. <i>Brachythecium salebrosum</i> , <i>Sciurohypnum</i>
734		<i>oedipodium</i> , <i>Sciuro-hypnum reflexum</i>)
735	BRAC.SALE	<i>Brachythecium salebrosum</i> (in 2013)
736	BRYU.SP	<i>Bryum</i> sp. (in 2013)
737	CALY.INTE	<i>Calypogeia integristipula</i> (in 2013)
738	DICR.SP	<i>Dicranum</i> sp. (Incl. e.g. <i>D. fuscescens</i> , <i>D. majus</i> , <i>D. scoparium</i> ,
739		<i>D. spurium</i> , <i>D. undulatum</i>)
740	DICR.MAJU	<i>Dicranum majus</i> (in 2013)
741	DICR.POLY	<i>Dicranum polysetum</i>
742	DICR.SCOP	<i>Dicranum scoparium</i>
743	HEPA.SP	Hepaticae
744	HYLO.SPLE	<i>Hylocomium splendens</i>
745	LOPH.SP	<i>Lophozia</i> -type (in 2013)
746	PLAG.SP	<i>Plagiothecium</i> sp.
747	PLEU.SCHR	<i>Pleurozium schreberi</i>
748	POLY.COMM	<i>Polytrichum commune</i>
749	POLY.JUNI	<i>Polytrichum juniperinum</i>
750	PTIL.CRIS	<i>Ptilium crista-castrensis</i>
751	PTIL.CILI	<i>Ptilidium ciliare</i>
752	RHYT.TRIQ	<i>Rhytidiadelphus triquetrus</i>
753	RHIZ.MANG	<i>Rhizomnium magnifolium</i> (in 2013)
754	SCIU.OEDI	<i>Sciuro-hypnum oedipodium</i> (in 2013)
755	SCIU.REFL	<i>Sciuro-hypnum reflexum</i> (in 2013)
756	SANI.UNCI	<i>Sanionia uncinata</i>
757	SPHA.SP	<i>Sphagnum</i> sp. (Incl. <i>S. angustifolium</i> , <i>S. capillifolium</i> , <i>S. girgensohnii</i>)
758	SPHA.ANGU	<i>Sphagnum angustifolium</i> (in 2013)
759	SPHA.CAPI	<i>Sphagnum capillifolium</i> (in 2013)
760	SPHA.GIRG	<i>Sphagnum girgensohnii</i> (in 2013)
761		
762	Lichens	
763	CETR.ISLA	<i>Cetraria islandica</i> (in 2013)
764	CLAD.ARBUS	<i>Cladonia arbuscula</i>
765	CLAD.RANG	<i>Cladonia rangiferina</i>
766	CLAD.SP	<i>Cladonia</i> sp. (Incl. e.g. <i>C. chlorophaea</i> , <i>C. cornuta</i> , <i>C. crispata</i> ,
767		<i>C. furcata</i> , <i>C. squamosa</i> , <i>C. sulphurina</i>)
768	CLAD.CHLO	<i>Cladonia chlorophaea</i>
769	CLAD.CORN	<i>Cladonia cornuta</i>
770	CLAD.FURC	<i>Cladonia furcata</i>
771	CLAD.SULP	<i>Cladonia sulphurina</i>
772	CLAD.UNCI	<i>Cladonia uncialis</i>
773	ICMA.ERIC	<i>Icmadophila ericetorum</i> (in 2013)
774	NEPH.ARCT	<i>Nephroma arcticum</i>
775	PELT.APHT	<i>Peltigera aphthosa</i> (Incl. <i>Peltigera neopolydactyla</i> (except for 2013))
776	PELT.LEUC	<i>Peltigera leucophlebia</i> (in 2013)
777	PELT.NEOP	<i>Peltigera neopolydactyla</i> (in 2013)
778	PELT.SP	<i>Peltigera</i> sp. (Incl. e.g. <i>P. leucophlebia</i> and <i>P. canina</i>)
779	STER.SP	<i>Stereocaulon</i> sp.
780		

781 Appendix B

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

787

788

789

790 Appendix C

791 Variation of the number of taxa in total, and in field and bottom layers separately in previous treatment
 792 Years are separated with dashed line to make interpretation of the figure easier. For years 1961 and 1986
 793 previous treatment was done in 1953 (control n=4, strip harvesting, n=4, commercial thinning n=4, heavy
 794 thinning n=4, light thinning n=4), and for year 2013 in 1987 (control n=4, heavy n=6, medium n=7, light
 795 n=3). Mean values are represented with black lines. Note the different scales in y-axis.
 796

Appendix D

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

Treatment	Year 1961									
	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										
<i>Luzula pilosa</i>	0.578	0.303	1.100	0.156	0.772	0.291	0.631	0.363	0.856	0.167
<i>Carex</i> 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
<i>Deschampsia flexuosa</i>	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										
<i>Huperzia selago</i>										
<i>Lycopodium</i> sp.	0.013	0.025	0.088	0.144	0.113	0.144			0.016	0.031
<i>Diphasiastrum complanatum</i>			0.013	0.025	0.038	0.075	1.263	1.555	0.438	0.875
<i>Equisetum sylvaticum</i>										
<i>Phegopteris connectilis</i>										
<i>Gymnocarpium dryopteris</i>	1.403	1.676	4.488	3.717	5.913	7.172	2.431	2.814	6.266	5.131
<i>Pyrola</i> sp.			0.066	0.131	0.019	0.030	0.006	0.013	0.063	0.070
<i>Orthilia secunda</i>	0.438	0.437	0.328	0.482	0.438	0.210	0.316	0.335	0.931	0.595
<i>Moneses uniflora</i>			0.063	0.075	0.025	0.029	0.003	0.006	0.034	0.047
<i>Lysimachia europaea</i>	0.594	0.282	1.106	0.595	0.944	0.193	0.716	0.419	0.919	0.399
<i>Epilobium angustifolium</i>	0.869	0.510	0.850	0.374	0.922	0.777	1.456	0.426	1.138	0.071
<i>Geranium sylvaticum</i>	0.003	0.006	0.063	0.125					0.041	0.081
<i>Melampyrum sylvaticum</i>	0.022	0.026	0.044	0.056	0.063	0.051	0.028	0.021	0.116	0.078
<i>M. pratense</i>	0.056	0.052	0.141	0.167	0.134	0.052	0.303	0.210	0.194	0.193
<i>Solidago virgaurea</i>	2.441	1.098	3.803	0.760	3.306	0.390	3.369	0.945	3.991	0.626
<i>Antennaria dioica</i>	0.075	0.119	0.128	0.152	0.050	0.100	0.063	0.125		
<i>Saussurea alpina</i>										
<i>Hieracium</i> sp.	0.109	0.087	0.306	0.110	0.275	0.323	0.272	0.268	0.184	0.117
<i>Maianthemum bifolium</i>	3.259	1.177	5.903	1.165	3.391	1.820	4.628	1.726	3.594	0.592
<i>Neottia cordata</i>	0.003	0.006	0.003	0.006	0.003	0.006			0.041	0.081
<i>Goodyera repens</i>	0.050	0.100	0.141	0.273					0.138	0.214
<i>Dactylorhiza maculata</i>			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										
<i>Vaccinium vitis-idaea</i>	5.150	3.141	5.878	1.338	7.300	2.218	9.213	3.206	7.044	2.389
<i>V. myrtillus</i>	35.225	18.106	25.516	12.954	32.753	18.423	26.525	14.178	27.366	8.822
<i>Empetrum nigrum</i>	0.016	0.024			0.056	0.065	0.025	0.050	0.075	0.150
<i>Linnaea borealis</i>	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										
<i>Picea abies</i>	0.003	0.006			0.003	0.006	0.028	0.048	0.063	0.125
<i>Juniperus communis</i>	0.066	0.092	0.159	0.131	0.559	0.569	0.131	0.151	0.141	0.095
<i>Betula</i> sp.	0.003	0.006	0.075	0.096	0.075	0.079	0.009	0.012	0.025	0.050
<i>Salix</i> sp.	0.019	0.024			0.025	0.035	0.038	0.048	0.063	0.125
<i>Populus tremula</i>			0.013	0.025	0.013	0.025				
<i>Sorbus aucuparia</i>	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		
<i>Ptilidium ciliare</i>										
<i>Barbilophozia</i> sp.	0.044	0.043	0.094	0.113	0.025	0.050	0.056	0.058	0.066	0.123
<i>Sphagnum</i> sp.										
<i>Dicranum</i> sp.	0.794	0.387	0.828	0.190	0.825	0.174	0.853	0.516	0.397	0.248
<i>D. polysetum</i>	1.041	0.646	2.041	0.730	2.663	2.193	1.941	1.155	2.588	1.183
<i>Aulacomium palustre</i>										
<i>Sanionia uncinata</i>	0.013	0.025			0.081	0.163	0.013	0.025		
<i>Brachyhectium</i> sp.	0.813	0.959	0.841	0.231	0.338	0.284	0.353	0.242	0.678	0.717
<i>Ptilium crista-castrensis</i>	0.100	0.091	0.756	1.209	0.113	0.131	0.244	0.407	0.238	0.221
<i>Hylacomium splendens</i>	1.150	0.372	2.713	3.569	3.225	2.743	2.028	1.874	5.484	4.758
<i>Rhytidiadelphus triquetrus</i>			0.038	0.048						
<i>Pleurozium shreberi</i>	13.375	9.114	15.369	4.309	22.625	7.282	19.688	5.069	18.525	8.886
<i>Plagiotechium</i> sp.	0.138	0.275	0.025	0.050	0.025	0.029				
<i>Polytrichum commune</i>	3.841	2.215	4.428	1.090	4.613	2.389	4.538	0.389	6.066	2.028
<i>P. juniperinum</i>	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										
<i>Cladonia</i> sp.	0.013	0.025	0.025	0.050			0.025	0.050	0.066	0.072
<i>C. arbuscula</i>	0.028	0.048	0.016	0.024	0.059	0.089	0.097	0.136	0.169	0.183
<i>C. rangiferina</i>	0.003	0.006					0.006	0.007	0.003	0.006
<i>Stereocaulon</i> sp.	0.038	0.075							0.050	0.100
<i>Nephroma arcticum</i>			0.013	0.025	0.100	0.122	0.013	0.025	0.163	0.325
<i>Peltigera</i> sp.	0.100	0.200			0.225	0.272	0.588	0.437	0.475	0.548
<i>P. aphthosa</i>	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

Treatment	Year1986									
	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										
<i>Luzula pilosa</i>	3.806	1.679	4.063	2.800	4.650	1.599	4.241	1.651	2.881	0.732
<i>Carex</i> sp.										
Gramineae	0.022	0.019	0.325	0.166	0.350	0.212	0.163	0.180	0.200	0.147
<i>Deschampsia flexuosa</i>	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										
<i>Huperzia selago</i>					0.050	0.100	0.388	0.581		
<i>Lycopodium</i> sp.	1.003	1.230	0.091	0.070	0.813	0.668	0.578	0.617	0.266	0.306
<i>Diphasiastrum complanatum</i>			0.013	0.025					0.088	0.175
<i>Equisetum sylvaticum</i>	0.013	0.025	0.013	0.025						
<i>Phegopteris connectilis</i>										
<i>Gymnocarpium dryopteris</i>	3.088	4.084	5.375	4.539	8.766	9.430	3.800	4.545	11.166	8.407
<i>Pyrola</i> sp.	0.038	0.075			0.075	0.119			0.075	0.119
<i>Orthilia secunda</i>	0.391	0.674	0.403	0.574	0.450	0.268	0.431	0.294	0.850	0.914
<i>Moneses uniflora</i>			0.050	0.071					0.003	0.006
<i>Lysimachia europaea</i>	4.125	0.859	3.134	0.855	3.291	1.781	4.678	0.751	4.166	0.991
<i>Epilobium angustifolium</i>	0.359	0.261	0.316	0.380	0.778	0.489	0.966	0.306	0.550	0.297
<i>Geranium sylvaticum</i>	0.175	0.350	0.016	0.024					0.025	0.050
<i>Melampyrum sylvaticum</i>	0.122	0.166	0.406	0.336	0.813	0.965	0.094	0.171	0.213	0.246
<i>M. pratense</i>	3.816	2.251	3.878	1.415	6.138	3.236	4.569	1.695	4.738	2.607
<i>Solidago virgaurea</i>	3.550	1.407	4.825	0.821	4.225	1.040	4.688	1.285	5.200	2.869
<i>Antennaria dioica</i>			0.013	0.025						
<i>Saussurea alpina</i>					0.038	0.075				
<i>Hieracium</i> sp.	0.016	0.031	0.150	0.178	0.150	0.173	0.075	0.119	0.113	0.131
<i>Maianthemum bifolium</i>	16.388	9.332	14.525	7.637	12.825	5.765	21.750	8.106	17.125	5.768
<i>Neottia cordata</i>	0.003	0.006	0.016	0.024						
<i>Goodyera repens</i>	0.250	0.252	0.253	0.187	0.066	0.131	0.038	0.060	0.209	0.264
<i>Dactylorhiza maculata</i>					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										
<i>Vaccinium vitis-idaea</i>	9.325	4.760	8.475	2.079	9.788	2.873	13.400	4.242	11.628	3.371
<i>V. myrtillus</i>	12.353	4.579	22.525	24.167	21.888	18.138	12.828	3.767	16.825	10.615
<i>Empetrum nigrum</i>					0.013	0.025	0.038	0.075		
<i>Linnaea borealis</i>	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										
<i>Picea abies</i>	0.984	1.846	0.225	0.384	0.425	0.718	0.638	0.950	1.544	1.831
<i>Juniperus communis</i>	0.063	0.125	0.388	0.566	0.450	0.492	0.400	0.311	0.450	0.585
<i>Betula</i> sp.	0.063	0.125	0.028	0.048	0.750	1.467	0.025	0.029	0.100	0.122
<i>Salix</i> sp.	0.003	0.006	0.025	0.050			0.063	0.125		
<i>Populus tremula</i>			0.063	0.125						
<i>Sorbus aucuparia</i>	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
Bryophytes										
Hepaticae										
<i>Ptilidium ciliare</i>	0.163	0.138	0.309	0.286	0.234	0.113	0.284	0.285	0.344	0.098
<i>Barbilophozia</i> sp.	0.422	0.455	0.409	0.447	0.188	0.165	0.375	0.377	0.669	0.967
<i>Sphagnum</i> sp.										
<i>Dicranum</i> sp.	4.053	3.040	4.681	3.528	5.394	1.123	6.391	2.853	5.431	1.462
<i>D. polysetum</i>	2.309	1.796	2.581	2.739	1.219	0.437	1.472	0.824	0.928	0.671
<i>Aulacomium palustre</i>									0.013	0.025
<i>Sanionia uncinata</i>										
<i>Brachyhectium</i> sp.	3.134	5.616	1.128	0.955	0.672	0.682	0.600	0.142	0.691	0.665
<i>Ptilium crista-castrensis</i>	0.791	0.525	1.003	1.579	1.131	1.088	2.078	1.052	2.203	1.852
<i>Hylocomium splendens</i>	2.022	0.915	3.409	2.210	5.516	4.305	1.613	0.977	7.638	5.694
<i>Rhytidiadelphus triquetrus</i>			0.088	0.175						
<i>Pleurozium shreberi</i>	50.419	34.417	59.388	19.028	69.475	12.266	76.475	9.955	64.863	9.066
<i>Plagiotechium</i> sp.			0.013	0.025	0.013	0.025			0.013	0.025
<i>Polytrichum commune</i>	3.009	1.982	8.850	3.891	7.203	3.147	5.519	1.488	7.475	4.328
<i>P. juniperinum</i>	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										
<i>Cladonia</i> sp.	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.075	0.087
<i>C. arbuscula</i>										
<i>C. rangiferina</i>										
<i>Stereocaulon</i> sp.										
<i>Nephroma arcticum</i>										
<i>Peltigera</i> sp.										
<i>P. aphthosa</i>									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

Treatment	Year2013							
	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								
<i>Luzula pilosa</i>	0.284	0.199	0.540	0.180	0.463	0.228	0.933	0.198
<i>Carex</i> sp.								
Gramineae	0.003	0.006	0.104	0.120	0.116	0.114	0.163	0.102
<i>Deschampsia flexuosa</i>	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								
<i>Huperzia selago</i>								
<i>Lycopodium</i> sp.	0.994	1.323	0.556	0.406	0.543	0.486	0.088	0.111
<i>Diphasiastrum complanatum</i>			0.013	0.021	0.011	0.020		
<i>Equisetum sylvaticum</i>								
<i>Phegopteris connectilis</i>	0.050	0.10						
<i>Gymnocarpium dryopteris</i>	1.016	1.829	0.908	1.072	1.137	1.131	2.196	0.805
<i>Pyrola</i> sp.								
<i>Orthilia secunda</i>	0.309	0.516	0.150	0.216	0.223	0.259	0.646	0.418
<i>Moneses uniflora</i>	0.003	0.006	0.013	0.016	0.011	0.011	0.013	0.022
<i>Lysimachia europaea</i>	0.375	0.264	0.308	0.213	0.341	0.428	0.167	0.131
<i>Epilobium angustifolium</i>	0.038	0.048	0.027	0.043	0.011	0.018	0.017	0.029
<i>Geranium sylvaticum</i>			0.021	0.051				
<i>Melampyrum sylvaticum</i>	0.006	0.007	0.017	0.035	0.004	0.009	0.008	0.014
<i>M. pratense</i>	0.144	0.022	0.410	0.146	0.445	0.095	0.375	0.111
<i>Solidago virgaurea</i>	0.741	0.180	1.796	0.912	1.789	0.762	1.767	0.488
<i>Antennaria dioica</i>								
<i>Saussurea alpina</i>								
<i>Hieracium</i> sp.	0.003	0.006	0.004	0.010	0.002	0.005	0.025	0.043
<i>Maianthemum bifolium</i>	1.863	0.849	2.044	0.860	2.800	1.356	2.638	1.241
<i>Neottia cordata</i>	0.025	0.027	0.040	0.051	0.021	0.021	0.021	0.026
<i>Goodyera repens</i>	2.097	0.834	0.544	0.344	1.318	0.400	0.813	1.215
<i>Dactylorhiza maculata</i>			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								
<i>Vaccinium vitis-idaea</i>	10.313	5.998	10.827	2.293	13.00	2.784	11.700	2.901
<i>V. myrtillus</i>	43.425	9.266	43.758	5.623	42.057	3.768	43.583	6.663
<i>Empetrum nigrum</i>	0.056	0.113	0.050	0.100	0.382	0.665		
<i>Linnaea borealis</i>	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								
<i>Picea abies</i>	0.725	0.725	0.742	0.661	0.275	0.328	0.321	0.295
<i>Juniperus communis</i>	0.556	0.130	0.225	0.312	0.234	0.259	0.817	0.718
<i>Betula</i> sp.	0.019	0.030	0.396	0.425	0.213	0.255	0.367	0.153
<i>Salix</i> sp.			0.006	0.010				
<i>Populus tremula</i>	0.006	0.013			0.009	0.019		
<i>Sorbus aucuparia</i>	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
Bryophytes								
Hepaticae	0.222	0.341	0.573	0.338	0.393	0.264	0.225	0.142
<i>Ptilidium ciliare</i>	0.134	0.175	0.275	0.338	0.280	0.203	0.029	0.026
<i>Barbilophozia</i> sp.	0.178	0.211	2.144	1.497	1.123	0.693	0.333	0.272
<i>Sphagnum</i> sp.			0.175	0.405			0.033	0.058
<i>Dicranum</i> sp.	4.963	2.848	7.256	1.413	7.345	2.939	5.046	1.266
<i>D. polysetum</i>	4.728	2.918	7.079	1.507	7.189	2.798	5.000	1.277
<i>Aulacomium palustre</i>								
<i>Sanionia uncinata</i>	0.006	0.013						
<i>Brachyhectium</i> sp.	0.834	1.504	0.279	0.298	0.521	0.443	0.579	0.484
<i>Ptilium crista-castrensis</i>	0.022	0.012	0.004	0.006	0.034	0.052	0.013	0.022
<i>Hylocomium splendens</i>	5.013	2.911	8.681	3.425	9.536	3.496	10.204	5.832
<i>Rhytidiadelphus triquetrus</i>			0.017	0.041			0.500	0.866
<i>Pleurozium shreberi</i>	19.688	12.375	32.573	6.588	26.438	12.078	10.479	1.631
<i>Plagiotrichum</i> sp.	0.088	0.102	0.021	0.040	0.032	0.047		
<i>Polytrichum commune</i>	2.278	1.976	4.067	2.207	4.027	1.052	5.825	1.401
<i>P. juniperinum</i>	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								
<i>Cladonia</i> sp.	0.013	0.010	0.019	0.025	0.007	0.019		
<i>C. arbuscula</i>								
<i>C. rangiferina</i>								
<i>Stereocaulon</i> sp.								
<i>Nephroma arcticum</i>								
<i>Peltigera</i> sp.								
<i>P. aphthosa</i>	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

0.2

0.1

0.0

-0.1

-0.2

1986

1961

2013

Previous treatment

○ Control

● Logged

-0.2

-0.1

0.0

0.1

0.2

0.3

NMDS1

Vaccinium myrtillus ***Pleurozium schreberi*** ***Vaccinium vitis-idaea*** ***Hylocomium splendens*** ***Deschampsia flexuosa*** ***Goodyera repens***

Litter

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										
<i>Luzula pilosa</i>	0.578	0.303	1.100	0.156	0.772	0.291	0.631	0.363	0.856	0.167
<i>Carex</i> 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
<i>Deschampsia flexuosa</i>	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										
<i>Huperzia selago</i>										
<i>Lycopodium</i> sp.	0.013	0.025	0.088	0.144	0.113	0.144			0.016	0.031
<i>Diphasiastrum complanatum</i>			0.013	0.025	0.038	0.075	1.263	1.555	0.438	0.875
<i>Equisetum sylvaticum</i>										
<i>Phegopteris connectilis</i>										
<i>Gymnocarpium dryopteris</i>	1.403	1.676	4.488	3.717	5.913	7.172	2.431	2.814	6.266	5.131
<i>Pyrola</i> sp.			0.066	0.131	0.019	0.030	0.006	0.013	0.063	0.070
<i>Orthilia secunda</i>	0.438	0.437	0.328	0.482	0.438	0.210	0.316	0.335	0.931	0.595
<i>Moneses uniflora</i>			0.063	0.075	0.025	0.029	0.003	0.006	0.034	0.047
<i>Lysimachia europaea</i>	0.594	0.282	1.106	0.595	0.944	0.193	0.716	0.419	0.919	0.399
<i>Epilobium angustifolium</i>	0.869	0.510	0.850	0.374	0.922	0.777	1.456	0.426	1.138	0.071
<i>Geranium sylvaticum</i>	0.003	0.006	0.063	0.125					0.041	0.081
<i>Melampyrum sylvaticum</i>	0.022	0.026	0.044	0.056	0.063	0.051	0.028	0.021	0.116	0.078
<i>M. pratense</i>	0.056	0.052	0.141	0.167	0.134	0.052	0.303	0.210	0.194	0.193
<i>Solidago virgaurea</i>	2.441	1.098	3.803	0.760	3.306	0.390	3.369	0.945	3.991	0.626
<i>Antennaria dioica</i>	0.075	0.119	0.128	0.152	0.050	0.100	0.063	0.125		
<i>Saussurea alpina</i>										
<i>Hieracium</i> sp.	0.109	0.087	0.306	0.110	0.275	0.323	0.272	0.268	0.184	0.117
<i>Maianthemum bifolium</i>	3.259	1.177	5.903	1.165	3.391	1.820	4.628	1.726	3.594	0.592
<i>Neottia cordata</i>	0.003	0.006	0.003	0.006	0.003	0.006			0.041	0.081
<i>Goodyera repens</i>	0.050	0.100	0.141	0.273					0.138	0.214
<i>Dactylorhiza maculata</i>			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										
<i>Vaccinium vitis-idaea</i>	5.150	3.141	5.878	1.338	7.300	2.218	9.213	3.206	7.044	2.389
<i>V. myrtillus</i>	35.225	18.106	25.516	12.954	32.753	18.423	26.525	14.178	27.366	8.822
<i>Empetrum nigrum</i>	0.016	0.024			0.056	0.065	0.025	0.050	0.075	0.150
<i>Linnaea borealis</i>	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										
<i>Picea abies</i>	0.003	0.006			0.003	0.006	0.028	0.048	0.063	0.125
<i>Juniperus communis</i>	0.066	0.092	0.159	0.131	0.559	0.569	0.131	0.151	0.141	0.095
<i>Betula</i> sp.	0.003	0.006	0.075	0.096	0.075	0.079	0.009	0.012	0.025	0.050
<i>Salix</i> sp.	0.019	0.024			0.025	0.035	0.038	0.048	0.063	0.125
<i>Populus tremula</i>			0.013	0.025	0.013	0.025				
<i>Sorbus aucuparia</i>	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		
<i>Ptilidium ciliare</i>										
<i>Barbilophozia</i> sp.	0.044	0.043	0.094	0.113	0.025	0.050	0.056	0.058	0.066	0.123
<i>Sphagnum</i> sp.										
<i>Dicranum</i> sp.	0.794	0.387	0.828	0.190	0.825	0.174	0.853	0.516	0.397	0.248
<i>D. polysetum</i>	1.041	0.646	2.041	0.730	2.663	2.193	1.941	1.155	2.588	1.183
<i>Aulacomium palustre</i>										
<i>Sanionia uncinata</i>	0.013	0.025			0.081	0.163	0.013	0.025		
<i>Brachyhegium</i> sp.	0.813	0.959	0.841	0.231	0.338	0.284	0.353	0.242	0.678	0.717
<i>Ptilium crista-castrensis</i>	0.100	0.091	0.756	1.209	0.113	0.131	0.244	0.407	0.238	0.221
<i>Hylocomium splendens</i>	1.150	0.372	2.713	3.569	3.225	2.743	2.028	1.874	5.484	4.758
<i>Rhytidiadelphus triquetrus</i>			0.038	0.048						
<i>Pleurozium shreberi</i>	13.375	9.114	15.369	4.309	22.625	7.282	19.688	5.069	18.525	8.886
<i>Plagiotechium</i> sp.	0.138	0.275	0.025	0.050	0.025	0.029				
<i>Polytrichum commune</i>	3.841	2.215	4.428	1.090	4.613	2.389	4.538	0.389	6.066	2.028
<i>P. juniperinum</i>	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										
<i>Cladonia</i> sp.	0.013	0.025	0.025	0.050			0.025	0.050	0.066	0.072
<i>C. arbuscula</i>	0.028	0.048	0.016	0.024	0.059	0.089	0.097	0.136	0.169	0.183
<i>C. rangiferina</i>	0.003	0.006					0.006	0.007	0.003	0.006
<i>Stereocaulon</i> sp.	0.038	0.075							0.050	0.100
<i>Nephroma arcticum</i>			0.013	0.025	0.100	0.122	0.013	0.025	0.163	0.325
<i>Peltigera</i> sp.	0.100	0.200			0.225	0.272	0.588	0.437	0.475	0.548
<i>P. aphthosa</i>	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										
<i>Luzula pilosa</i>	3.806	1.679	4.063	2.800	4.650	1.599	4.241	1.651	2.881	0.732
<i>Carex</i> sp.										
Gramineae	0.022	0.019	0.325	0.166	0.350	0.212	0.163	0.180	0.200	0.147
<i>Deschampsia flexuosa</i>	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										
<i>Huperzia selago</i>					0.050	0.100	0.388	0.581		
<i>Lycopodium</i> sp.	1.003	1.230	0.091	0.070	0.813	0.668	0.578	0.617	0.266	0.306
<i>Diphasiastrum complanatum</i>			0.013	0.025					0.088	0.175
<i>Equisetum sylvaticum</i>	0.013	0.025	0.013	0.025						
<i>Phegopteris connectilis</i>										
<i>Gymnocarpium dryopteris</i>	3.088	4.084	5.375	4.539	8.766	9.430	3.800	4.545	11.166	8.407
<i>Pyrola</i> sp.	0.038	0.075			0.075	0.119			0.075	0.119
<i>Orthilia secunda</i>	0.391	0.674	0.403	0.574	0.450	0.268	0.431	0.294	0.850	0.914
<i>Moneses uniflora</i>			0.050	0.071					0.003	0.006
<i>Lysimachia europaea</i>	4.125	0.859	3.134	0.855	3.291	1.781	4.678	0.751	4.166	0.991
<i>Epilobium angustifolium</i>	0.359	0.261	0.316	0.380	0.778	0.489	0.966	0.306	0.550	0.297
<i>Geranium sylvaticum</i>	0.175	0.350	0.016	0.024					0.025	0.050
<i>Melampyrum sylvaticum</i>	0.122	0.166	0.406	0.336	0.813	0.965	0.094	0.171	0.213	0.246
<i>M. pratense</i>	3.816	2.251	3.878	1.415	6.138	3.236	4.569	1.695	4.738	2.607
<i>Solidago virgaurea</i>	3.550	1.407	4.825	0.821	4.225	1.040	4.688	1.285	5.200	2.869
<i>Antennaria dioica</i>			0.013	0.025						
<i>Saussurea alpina</i>					0.038	0.075				
<i>Hieracium</i> sp.	0.016	0.031	0.150	0.178	0.150	0.173	0.075	0.119	0.113	0.131
<i>Maianthemum bifolium</i>	16.388	9.332	14.525	7.637	12.825	5.765	21.750	8.106	17.125	5.768
<i>Neottia cordata</i>	0.003	0.006	0.016	0.024						
<i>Goodyera repens</i>	0.250	0.252	0.253	0.187	0.066	0.131	0.038	0.060	0.209	0.264
<i>Dactylorhiza maculata</i>					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										
<i>Vaccinium vitis-idaea</i>	9.325	4.760	8.475	2.079	9.788	2.873	13.400	4.242	11.628	3.371
<i>V. myrtillus</i>	12.353	4.579	22.525	24.167	21.888	18.138	12.828	3.767	16.825	10.615
<i>Empetrum nigrum</i>					0.013	0.025	0.038	0.075		
<i>Linnaea borealis</i>	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										
<i>Picea abies</i>	0.984	1.846	0.225	0.384	0.425	0.718	0.638	0.950	1.544	1.831
<i>Juniperus communis</i>	0.063	0.125	0.388	0.566	0.450	0.492	0.400	0.311	0.450	0.585
<i>Betula</i> sp.	0.063	0.125	0.028	0.048	0.750	1.467	0.025	0.029	0.100	0.122
<i>Salix</i> sp.	0.003	0.006	0.025	0.050			0.063	0.125		
<i>Populus tremula</i>			0.063	0.125						
<i>Sorbus aucuparia</i>	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
Bryophytes										
Hepaticae										
<i>Ptilidium ciliare</i>	0.163	0.138	0.309	0.286	0.234	0.113	0.284	0.285	0.344	0.098
<i>Barbilophozia</i> sp.	0.422	0.455	0.409	0.447	0.188	0.165	0.375	0.377	0.669	0.967
<i>Sphagnum</i> sp.										
<i>Dicranum</i> sp.	4.053	3.040	4.681	3.528	5.394	1.123	6.391	2.853	5.431	1.462
<i>D. polysetum</i>	2.309	1.796	2.581	2.739	1.219	0.437	1.472	0.824	0.928	0.671
<i>Aulacomium palustre</i>									0.013	0.025
<i>Sanionia uncinata</i>										
<i>Brachyhegium</i> sp.	3.134	5.616	1.128	0.955	0.672	0.682	0.600	0.142	0.691	0.665
<i>Ptilium crista-castrensis</i>	0.791	0.525	1.003	1.579	1.131	1.088	2.078	1.052	2.203	1.852
<i>Hylocomium splendens</i>	2.022	0.915	3.409	2.210	5.516	4.305	1.613	0.977	7.638	5.694
<i>Rhytidiadelphus triquetrus</i>			0.088	0.175						
<i>Pleurozium shreberi</i>	50.419	34.417	59.388	19.028	69.475	12.266	76.475	9.955	64.863	9.066
<i>Plagiotrichum</i> sp.			0.013	0.025	0.013	0.025			0.013	0.025
<i>Polytrichum commune</i>	3.009	1.982	8.850	3.891	7.203	3.147	5.519	1.488	7.475	4.328
<i>P. juniperinum</i>	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										
<i>Cladonia</i> sp.	0.025	0.050	0.016	0.024	0.175	0.287	0.022	0.030	0.075	0.087
<i>C. arbuscula</i>										
<i>C. rangiferina</i>										
<i>Stereocaulon</i> sp.										
<i>Nephroma arcticum</i>										
<i>Peltigera</i> sp.										
<i>P. aphthosa</i>									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								
<i>Luzula pilosa</i>	0.284	0.199	0.540	0.180	0.463	0.228	0.933	0.198
<i>Carex</i> sp.								
Gramineae	0.003	0.006	0.104	0.120	0.116	0.114	0.163	0.102
<i>Deschampsia flexuosa</i>	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								
<i>Huperzia selago</i>								
<i>Lycopodium</i> sp.	0.994	1.323	0.556	0.406	0.543	0.486	0.088	0.111
<i>Diphasiastrum complanatum</i>			0.013	0.021	0.011	0.020		
<i>Equisetum sylvaticum</i>								
<i>Phegopteris connectilis</i>	0.050	0.10						
<i>Gymnocarpium dryopteris</i>	1.016	1.829	0.908	1.072	1.137	1.131	2.196	0.805
<i>Pyrola</i> sp.								
<i>Orthilia secunda</i>	0.309	0.516	0.150	0.216	0.223	0.259	0.646	0.418
<i>Moneses uniflora</i>	0.003	0.006	0.013	0.016	0.011	0.011	0.013	0.022
<i>Lysimachia europaea</i>	0.375	0.264	0.308	0.213	0.341	0.428	0.167	0.131
<i>Epilobium angustifolium</i>	0.038	0.048	0.027	0.043	0.011	0.018	0.017	0.029
<i>Geranium sylvaticum</i>			0.021	0.051				
<i>Melampyrum sylvaticum</i>	0.006	0.007	0.017	0.035	0.004	0.009	0.008	0.014
<i>M. pratense</i>	0.144	0.022	0.410	0.146	0.445	0.095	0.375	0.111
<i>Solidago virgaurea</i>	0.741	0.180	1.796	0.912	1.789	0.762	1.767	0.488
<i>Antennaria dioica</i>								
<i>Saussurea alpina</i>								
<i>Hieracium</i> sp.	0.003	0.006	0.004	0.010	0.002	0.005	0.025	0.043
<i>Maianthemum bifolium</i>	1.863	0.849	2.044	0.860	2.800	1.356	2.638	1.241
<i>Neottia cordata</i>	0.025	0.027	0.040	0.051	0.021	0.021	0.021	0.026
<i>Goodyera repens</i>	2.097	0.834	0.544	0.344	1.318	0.400	0.813	1.215
<i>Dactylorhiza maculata</i>			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								
<i>Vaccinium vitis-idaea</i>	10.313	5.998	10.827	2.293	13.00	2.784	11.700	2.901
<i>V. myrtillus</i>	43.425	9.266	43.758	5.623	42.057	3.768	43.583	6.663
<i>Empetrum nigrum</i>	0.056	0.113	0.050	0.100	0.382	0.665		
<i>Linnaea borealis</i>	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								
<i>Picea abies</i>	0.725	0.725	0.742	0.661	0.275	0.328	0.321	0.295
<i>Juniperus communis</i>	0.556	0.130	0.225	0.312	0.234	0.259	0.817	0.718
<i>Betula</i> sp.	0.019	0.030	0.396	0.425	0.213	0.255	0.367	0.153
<i>Salix</i> sp.			0.006	0.010				
<i>Populus tremula</i>	0.006	0.013			0.009	0.019		
<i>Sorbus aucuparia</i>	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
Bryophytes								
Hepaticae	0.222	0.341	0.573	0.338	0.393	0.264	0.225	0.142
<i>Ptilidium ciliare</i>	0.134	0.175	0.275	0.338	0.280	0.203	0.029	0.026
<i>Barbilophozia</i> sp.	0.178	0.211	2.144	1.497	1.123	0.693	0.333	0.272
<i>Sphagnum</i> sp.			0.175	0.405			0.033	0.058
<i>Dicranum</i> sp.	4.963	2.848	7.256	1.413	7.345	2.939	5.046	1.266
<i>D. polysetum</i>	4.728	2.918	7.079	1.507	7.189	2.798	5.000	1.277
<i>Aulacomium palustre</i>								
<i>Sanionia uncinata</i>	0.006	0.013						
<i>Brachyhegium</i> sp.	0.834	1.504	0.279	0.298	0.521	0.443	0.579	0.484
<i>Ptilium crista-castrensis</i>	0.022	0.012	0.004	0.006	0.034	0.052	0.013	0.022
<i>Hylocomium splendens</i>	5.013	2.911	8.681	3.425	9.536	3.496	10.204	5.832
<i>Rhytidiadelphus triquetrus</i>			0.017	0.041			0.500	0.866
<i>Pleurozium shreberi</i>	19.688	12.375	32.573	6.588	26.438	12.078	10.479	1.631
<i>Plagiotechium</i> sp.	0.088	0.102	0.021	0.040	0.032	0.047		
<i>Polytrichum commune</i>	2.278	1.976	4.067	2.207	4.027	1.052	5.825	1.401
<i>P. juniperinum</i>	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								
<i>Cladonia</i> sp.	0.013	0.010	0.019	0.025	0.007	0.019		
<i>C. arbuscula</i>								
<i>C. rangiferina</i>								
<i>Stereocaulon</i> sp.								
<i>Nephroma arcticum</i>								
<i>Peltigera</i> sp.								
<i>P. aphthosa</i>	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	<i>Carex</i> sp.
DESC.FLEX	<i>Deschampsia flexuosa</i>
GRAM.SPP	Gramineae (Incl. e.g. <i>Agrostis</i> sp. <i>Calamagrostis</i> sp., <i>Deschampsia caespitosa</i> , <i>Melica nutans</i> , <i>Poa</i> sp.)
LUZU.PILO	<i>Luzula pilosa</i>
MELI.NUTA	<i>Melica nutans</i> (in 2013)

Herbs

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

Dwarf shrubs

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

Shrubs and tree seedlings

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

Bryophytes

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

Lichens

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