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Natural regeneration and early development of Scots pine seedlings after gap cutting in northern Finland

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ABSTRACT
In the northern boreal region, tree growth, timber yields and economic returns are low, meaning low regeneration costs are the basis of profitable forestry. If natural regeneration is successful, it may be favoured over expensive planting or seeding. We studied the regeneration success and early growth of Scots pine in gaps in terms of seedling density and height 10 years after gap cuttings in central Finnish Lapland. Three gap sizes (diameters of 20, 40, and 80 m) were studied on patch scarified xeric and sub-xeric sites in six random blocks and a total of 18 replicates of each. The number of pine seedlings was high across the gap sizes. The proportion of empty regeneration plots (size 5 m^2) was ~ 2%. Site preparation substantially increased the number of seedlings. The growth of seedlings was faster in larger gaps, but a high proportion of exposed mineral soil decreased it. The results suggest that all studied gap sizes regenerated naturally well, and that soil scarification exposing 10–20% of the surface area or even less can be enough to achieve regeneration goals. Gaps of a diameter of 40 m or more are required to achieve an optimal balance between seedling density and growth.

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Gaps; site preparation; *Pinus sylvestris*; uneven-aged management; continuous cover forestry

Introduction

In continuous cover forestry (CCF), gap cutting, or group selection cutting, consists of the removal of all trees growing on a small area within a forest stand. The aim is to harvest timber and promote tree regeneration in the gap. It has received increasing attention in Finland, having been shown to be a relevant alternative for the management of shade-tolerant or semi-tolerant species like Norway spruce (*Picea Abies* (L.) Karst) (Valkonen et al. 2011; Valkonen and Siitonen 2016). However, it could be even more relevant for stands dominated by shade-intolerant species such as Scots pine (*Pinus sylvestris* L.), which very small-scale alternatives like single-tree selection may not fit well. Gap cutting can also be applied for the complete but stepwise regeneration of a stand, restoring its preharvest even-aged structure.

Forest gaps create environmental conditions that are suitable for the recruitment, survival, and growth of tree seedlings (Liu and Hytteborn 1991; Kuuluvainen 1994). These factors are related to the gradients of light, temperature, moisture, competition from standing trees, and seed crops from the gap edge towards the centre of the gap (Downey et al. 2018). The regeneration success of Norway spruce has been found to be generally good in small gaps, albeit quite slow (Hökkä et al. 2011; Hökkä et al. 2012; Valkonen and Siitonen 2016; Hökkä and Repola 2018). However, there is limited information regarding Scots pine regeneration success and growth in small gaps.

Quite a lot is already known about the basic factors controlling pine regeneration in gaps, e.g. about seed dispersal and competitive effects in gaps. Competition for resources such as radiation, moisture, and nutrients is known to limit the growth of seedlings at a distance of at least up to 20 m from the edge (Siipilehto 2006; Ruuska et al. 2008; Valkonen et al. 2011; Axelsson et al. 2014). In larger gaps, the competitive effects have a smaller average effect, but on the other hand, with an increasing gap size, seed dispersal may become a limiting factor. In the Finnish research and management legacy, it has been assumed that sufficient natural regeneration for Scots pine and Norway spruce is basically limited to a distance of 40–50 m from the forest edge (Lehto 1956; Ackzell 1994).

Gap size is generally one of the key features to be varied in research on regeneration success, and it is very useful for covering a large range of its variation within an experimental setup if possible. However, the approach of focusing on gradients within gaps makes it possible to interpolate, making it unnecessary to create many size variants within the experimental range (Downey et al. 2018; Hallikainen et al. 2019). Additionally, gap size should be addressed without confining oneself to the limits of current practices. In the Finnish Forest Act (Finnish Forest Act, 5 a §), gap cuttings of up to 0.3 ha are assignable to uneven-aged management, whereby the general mandatory regeneration is relinquished. However, larger gaps can be economically justifiable if regeneration success seems good, especially in northern areas,

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where topography and past practices have established and sustained stands with relatively large areas.

In this study, we examined the success of postharvest regeneration in gaps of variable size, cut in Scots pine-dominated stands in an experiment in central Finnish Lapland. Our aim was to revisit the results and conclusions from a study in the same experiment five years after its establishment (Hallikainen et al. 2019). This study focused on the situation five years later (10 years after establishment). Under our conditions, major changes are possible during such an early stage of the regeneration process, and the 10-year milestone tends to give greater consistency to conclusions. Additionally, seedling growth was added as a focus area in addition to density. We examined the effects of gap size, site preparation, and ground vegetation on the regeneration success and growth of seedlings. Our main focus was Scots pine, which is the main species in Lapland and on such infertile site types. The specific questions we addressed were:

(1) What is the average regeneration result in the number of seedlings, share of empty sample plots, and early growth in the studied gaps?
(2) Are there significant gradients in seedling density, early growth, or occurrence of empty sample plots in relation to distance from the gap edge towards the gap centre and in relation to gap size?
(3) What is the influence of site preparation and the composition of the field and ground layer vegetation on the seedling number and early growth?

Materials and methods

Experimental design and data acquisition

The study area is in central Finnish Lapland, in the northern part of the municipality of Rovaniemi (Figure 1). The study area consists of a mosaic of two site types, the sub-xeric Empetrum-Vaccinium type (EVT) and the xeric Myrtillus-Calluna-Cladonia type (MCClT) (Cajander 1926). The size of the study area is about 3 km^2. The forest comprises older pine stands with a modest degree of heterogeneity in stand structure. Stands generally contain large mature trees and younger patches that have emerged from natural regeneration during the last century related to storm damage and selective cuttings. The age of the dominant pine canopy layer is about 120–150 years. There were also scattered Norway spruce and birch and other deciduous trees in the stands. The share of species other than Scots pine was about 8% of the number of stems, or 7% of basal area. Stand density, tree size, and the exposition of the gaps varied between blocks (Appendix: Table A1). The soils are mostly podzolic moraines dominated by a silt fraction (Table 1). The average site index for pine was H100 = 16.9 m (Gustavsen 1980).

The study area was divided into six blocks (Figure 1). The average size of each block was 30 ha (range 15–40 ha). The blocks were as homogenous as possible according to their site type, stand age, and stand structure (tree size variation). Each block was covered by a rectangular grid of points at 40 m intervals. In each block, nine points on the grid were randomly selected. Gaps of variable sizes were randomly assigned to these random points, with three replicates per block. The gaps were circular, with a diameter of 20, 40, or 80 m, representing 0.03, 0.13, and 0.5 ha in area respectively. A buffer of uncut forest with a minimum width of 30 m was left between the gaps and around the blocks. A similar 30 m buffer zone was maintained between the gaps and treeless or sparsely forested areas or strongly contrasting forest types. A random point on the grid that did not fulfil these spatial criteria was discarded and replaced randomly.

Stand characteristics within the gaps were measured before cutting. Trees were measured on five circular sample plots: the first in the middle of the gap ($r = 9.77$ m, 300 m^2) and four smaller plots ($r = 5.64$ m, 100 m^2) in four directions (NE, SE, SW, and NW) 6 m from the gap edge.

The gaps were cut in March 2010. Site preparation was performed in all gaps in the early summer of 2010. The site preparation method was patch scarification with an excavator, which exposed mineral soil to a depth of 5–10 cm and placed the humus next to each newly excavated patch. The proportion of exposed soil was some 20% of the gap area.

In the summer of 2010, a set of circular regeneration plots with $r = 1.26$ m representing 5 m^2 in area were placed across each gap. Later in the text, these will be termed regeneration plots. They were positioned along south–north and east–west lines at 3.33 m intervals (Figure 2). The number of regeneration plots per gap therefore increased in relation to the gap size. In each 20 m diameter gap, there were nine regeneration plots. In 40 m diameter gap there were 21 plots and in 80 m diameter gap 45 plots. There was a total of 1350 regeneration plots. As we aimed to study only seedlings that emerged after gap cutting, all the pre-existing seedlings were removed (cut down, not torn out) on the plots in the early summer of 2010. In addition, we had four control plots per gap, located 20 m from the gap edge towards each cardinal direction to monitor the development of seedlings established before cutting.

Understorey vegetation and microsite properties were recorded to the level of either individual species or species groups on the regeneration plots during the summer of 2010 (Table 1). The upper (shrub) layers were extremely weakly developed due to the sub-xeric to xeric site conditions. Only the field and ground layers were therefore included in the vegetation survey. The cover proportion of ground and field layer vegetation, stumps, exposed humus layer (organic layer), stones, exposed mineral soil and double humus were estimated using a scale of 0%, 1%, 2.5%, 5%, 10%, 15%, … , 100%. Double humus was recorded to indicate a microsite established in the soil scarification by overturning a patch of field and ground layer vegetation and the humus layer beneath it on top of the adjacent untouched vegetation, with the overturned humus on top.

The number of tree seedlings and the average seedling height were measured for pine, spruce, birch, and a group containing all other deciduous tree species. Age of pine and spruce seedlings was determined by counting the number of annual shoots in the main stem, i.e. the internodes

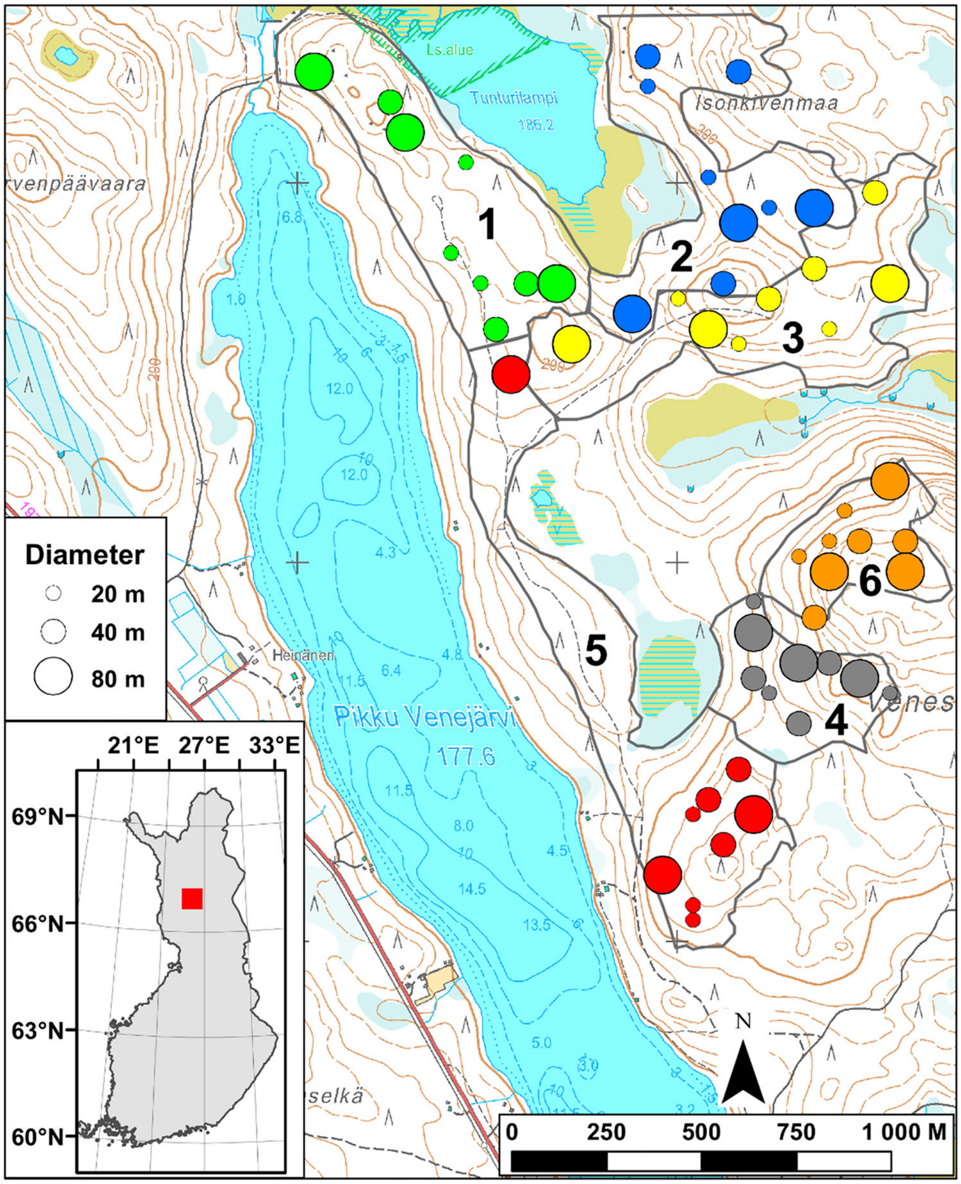

Figure 1. Location of the study area and experimental layout. Gaps of 20, 40, and 80 m diameters were randomly placed in six blocks (marked in different colours). Each gap size was replicated three times in each block.

between annual whorl of branches or branch scar knots in case branches were shed. The age of the seedlings was at most 10 years as all visible seedlings were cut down in the sample plots when the sample plots were established. The vegetation and microsite survey of 2010 was not repeated in 2020 because the change from 2010 seemed minimal, and the main goal was to study the effect of the vegetation at the initial timepoint.

After cutting, the five nearest dominant trees to the gap edge were selected and measured as sample trees in sectors representing the main directions to characterise the shading intensity of the edge stands. Two dominant trees from the southern and northern side of each gap were also selected to monitor seed production. The number of cones per tree was assessed (in August) in 2010 and 2020, using a 7-point ordinal index scale (1 = 0 cones per tree, 2 = 1–20, 3 = 21–50, 4 = 51–100, 5 = 101–200, 6 = 201–500, 7 = 501–). The cumulative cone index was calculated as the sum of the annual observed categorical values for 2010–2014, i.e. for the first five years, which were relevant for seedling emergence. A value of 0 would indicate no cones at all during the period, while a maximum of 70 would indicate >500 cones per tree (index value = 7) in each of the 10 observation years. The gaps were inventoried in 2015 (seedling numbers) and 2020 (also seedling height and age, highest healthy, suffering, and dead seedling).

Statistical modelling: negative binomial models for the seedling number

Models were constructed for the number of all observed living seedlings on the 5 m^2 circular regeneration plots. The models therefore described recruitment potential, not the number of crop seedlings.

A generalised linear mixed model with a negative binomial distribution assumption and log-link function was applied,

Table 1. Basic statistics for the regeneration and stand parameters.

Variable	Mean	Sd.	Median	Min.	Max.
Number of Scots pine seedlings, ha^{-1}	21757	19054	16000	0	176,000
Number of Scots pine seedlings on scarified mineral soil, ha^{-1}	739	2195	0	0	24,000
Number of Norway spruce seedlings, ha^{-1}	151	715	0	0	12,000
Number of birch seedlings, ha^{-1}	7138	18139	0	0	2,02,000
Number of other deciduous seedlings, ha^{-1}	156	760	0	0	16,000
Height of Scots pine seedlings, cm	9.10	8.89	6	1	63
Height of Norway spruce seedlings, cm	4.56	3.12	4	1	15
Height of birch seedlings, cm	9.30	8.77	7	1	62
Height of other deciduous seedlings, cm	10.65	9.00	9	1	50
Proportion of exposed mineral soil, %	22.53	17.08	20	0	85
Proportion of bare stones, %	8.83	8,49	5	0	55
Proportion of stumps, %	1.49	3.97	0	0	25
Proportion of cutting residues, %	17.86	14.20	15	0	100
Proportion of exposed humus, %	21.86	13.68	19	0	74
Proportion of double humus overturned in site preparation, %	20.01	18.62	15	0	80
Coverage of *Vaccinium myrtillus*, %	7.03	7.04	5	0	65
Coverage of *Vaccinium vitis-idaea*, %	7.65	6.89	5	0	55
Coverage of *Vaccinium uliginosum*, %	0.15	0.76	0	0	8
Coverage of *Empetrum nigrum / E. hermaphroditum*, %	4.90	6.40	3	0	50
Coverage of *Calluna vulgaris*, %	2.43	4.63	1	0	50
Coverage of *Ledum palustre*, %	0.01	0.18	0	0	5
Coverage of hays and sedges, %	0.16	0.89	0	0	20
Coverage of other vascular plants, %	0.10	0.39	0	0	5
Coverage of *Polytrichum* species %	0.22	0.55	0	0	5
Coverage of *Sphagnum* species %	0.03	1.09	0	0	40
Coverage of other moss species, %	40.45	18.97	40	0	90
Coverage of *Cladina* species, %	4.28	6.55	2	0	65
Coverage of other ground lichen species, %	0.36	0.83	0	0	10
Variables measured at larger sample plot level, categorical					
Soil type, % (*n*)	Moraine 97.6 (1265)	Sorted 2.4 (31)			
Coarseness, % (*n*)	Gravel < 1 (1)	Sand 3.3 (43)	Silt 95.0 (1231)	Loam 1.6 (21)	
Variables measured at gap level					
Direction from gap midpoint % (number of the openings, total = 54), categorical variable	North 25.9 (14)	East 7.4 (4)	South 16.7 (9)	West 37.0 (20)	Flat 13.0(7)
Cumulative cone index (sum of years 2011–2014), continuous variable, maximum values for north and south for the cumulative sum is 20					
North	9.57	2.74	9.25	5.00	16.50
South	7.85	1.81	7.50	4.50	12.00

All the sample plots are pooled without any consideration of hierarchy in the data. The counts in the data are expressed as numbers ha^{-1}. All the variables were tested in the models. Variables were measured at regeneration plot level. Seedling number and height variables are in the middle of the study period (2014), the others at the beginning prior to gap harvesting.

consisting of three hierarchical levels, blocks, gap nested within the block, and regeneration plots nested within the gap. The models were estimated using the R package glmmTMB, using NB2 parametrisation, which estimated the clumping parameter, called theta (Brooks et al. 2017). General or generalised linear mixed models tend to underestimate the mean. A ratio estimator (ratio of observed and predicted mean, Snowdon 1991) was therefore computed.

The most relevant independent fixed variables in the models were gap diameter (20, 40, and 80 m) or distance from the forest edge. These variables could not be included in the same models together because they describe the same phenomena. Separate models were therefore computed based on these variables. The tested potential explanatory variables describing the ecological characteristics on the regeneration plots and those in the gaps (e.g. tree cover on the forest edge of the gap, average inclination of the gap ground surface, and so on) are presented in Table 1. Because of the many potential independent fixed variables, the model building could not be done by starting with the full model as suggested by e.g. Zuur et al. (2009). Instead, a preselection of the variables with at least a slight contribution to the response was carried out. The selected candidate variables and their possible two-way interactions were then simultaneously tested using several include-drop stages. A possible multicollinearity in the main effects models between the selected variables was tested using R package performance (Lüdecke et al. 2021). Typically, the Variance Inflation Factor, VIF, with a value of 10 (Hair et al. 1998) or as low as 5 or 3 (Hair et al. 2021), has been suggested as the upper limit that should not be exceeded to avoid multicollinearity. In our case, the VIF for all the main effects was below 2.

The plots in the centre of the gaps were excluded from the models where the variable inclination was included in the models. A separate count model was therefore constructed for the centre plots. The fixed variables in that model were gap size, and the covariates used in the other presented count models. In addition, the only random effect of the model was block, because only block and gap levels were present in this model.

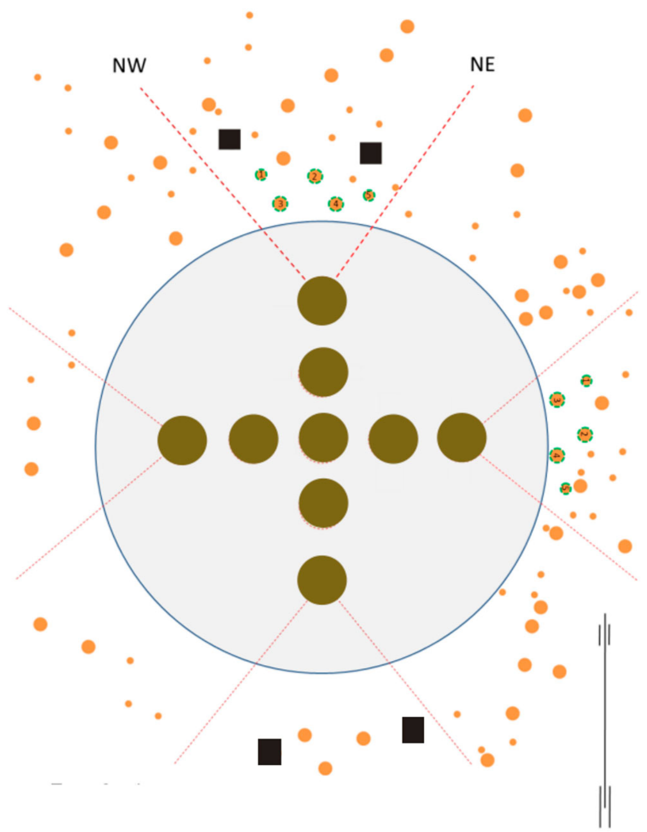

Figure 2. An example of the sampling design within a gap ($d = 20$ m). Circular regeneration plots (nine plots) are shown within the gap. Small orange dots outside the gap represent trees of the forest edge and the numbers in the tree symbols on the northern and eastern sides of the cap indicate the sample trees, which are the 5 nearest trees in that direction. The black rectangles represent trees that were used for the evaluation of cone production (*Scots pine*). In addition, there were four control plots per gap in the uncut forest matrix, located 20 m from the gap edge, towards each cardinal direction.

Statistical modelling: linear models for seedling height development

Ten-year height development (the height of the highest seedling on a regeneration plot that had emerged during the experiment) was modelled using a log-normal linear mixed model. The most important explanatory variables were gap diameter and distance from the forest edge. The direction was also tested in the models (without the centre plot). The other variables, model hierarchy, and model construction were similar to those described in the model for seedling number. The linear models were computed using R package nlme (Pinheiro et al. 2020). R^2 values were computed using R package MuMIn (Bartoń 2020). Model predictions were computed and drawn using R packages ggeffects (Lüdecke 2018) and ggplot2 (Wickham 2016)

Results

The average total number of pine seedlings was large: there were 14.55 pine seedlings on each regeneration plot within the gaps, representing 29,100 seedlings ha^{-1}. The proportion of exposed mineral soil (EMS) explained most of the variation in the number of pine seedlings (Table 2, Figure 3(a)). An increasing proportion of cowberry (*Vaccinium vitis-idaea*) significantly decreased the number of pine seedlings (Figure 3(b)). Furthermore, the direction from the nearest gap edge influenced the number of pine seedlings; the western direction had fewer pine seedlings than the northern direction (Table 2). However, this effect appeared only in the 20 m gap, as there was no significant difference between the directions in the 40 and 80 m gaps (Figure 3(c)). The total model fit for the pine seedling number model was 35.20% in the marginal model and 57.70% in the conditional model (Table 2).

Table 2. The generalised linear mixed model with a negative binomial distribution assumption for the number of seedlings with direction (Model 1).

Variable, parameter	Estimate	Std. error	*t*- /chi-value	*p*
(Intercept)	2.360E + 00	1.568E-01	15.049	<0.001
Direction (ref. North)			13.495 (3)	0.004
East	2.162E-01	1.362E-01	1.587	0.113
South	−9.772E-03	1.368E-01	−0.071	0.943
West	−2.867E-01	1.386E-01	−2.069	0.039
Gap diameter (ref. 20 m)			8.077 (2)	0.018
40 m	−1.218E-01	1.606E-01	−0.758	0.448
80 m	−4.000E-01	1.541E-01	−2.596	0.009
Cover of cowberry, %	−1.590E-02	3.088E-03	−5.148	<0.001
Cover of exposed mineral soil, %	2.367E-02	1.189E-03	19.916	<0.001
Direction:Diameter			33.060 (6)	<0.001
East:40 m	−7.684E-02	1.613E-01	−0.476	0.634
South:40 m	−1.851E-01	1.629E-01	−1.137	0.256
West:40m	3.512E-01	1.637E-01	2.146	0.032
East:80 m	−2.126E-01	1.490E-01	−1.427	0.154
South:80 m	1.052E-01	1.496E-01	0.703	0.482
West:80 m	4.286E-01	1.514E-01	2.831	0.005
Variance: Block	4.161E-02			
Variance: Plot nested within block	1.111E-01			
Theta (NB2)	3.79			

The results of type 3 ANOVA tests are computed for the categorical variables; the degrees of freedom of the tests are in parentheses. $R^2 = 35.20\%$ (marginal model) / 57.70% (conditional model).

Smaller gaps had greater seedling densities than larger gaps. If the model with the gap diameter (see Table A2 in the appendix) was constructed without direction from the gap centre, using only the gap diameter, the predicted number of Scots pine seedlings for different gap diameters were: 20 m had 33,639 seedlings ha^{-1}, 40 m had 29,750 seedlings ha^{-1}, and 80 m had 23,411 seedlings ha^{-1} (the chi-squared value = 9.652, df = 2, $p = 0.008$).

The number of empty regeneration plots (no pine seedlings found on a plot) in the gaps was very small – about 30 of the total of 1,350 regeneration plots (Figure 4). In contrast, there were many empty plots in the control plots, i.e. regeneration plots within the uncut edge stand. On the control plots, there were an average of 0.73 pine seedlings (1,460 seedlings ha^{-1}).

The height of pine seedlings increased significantly with a greater gap size and increasing proportion of exposed humus cover (Table 3, Figure 5(a)). The height of pine seedlings was lower when the proportion of exposed mineral soil increased (Figure 5(b)). The interaction between the age of the seedlings and the number of all the seedlings on a regeneration plot suggested that seedlings' growth increased with an increasing number of seedlings on the sample plot, which can be seen as a steeper slope from 1 to 15 or 30 stems per plot (Table 3, Figure 5(c)). Furthermore, the increasing

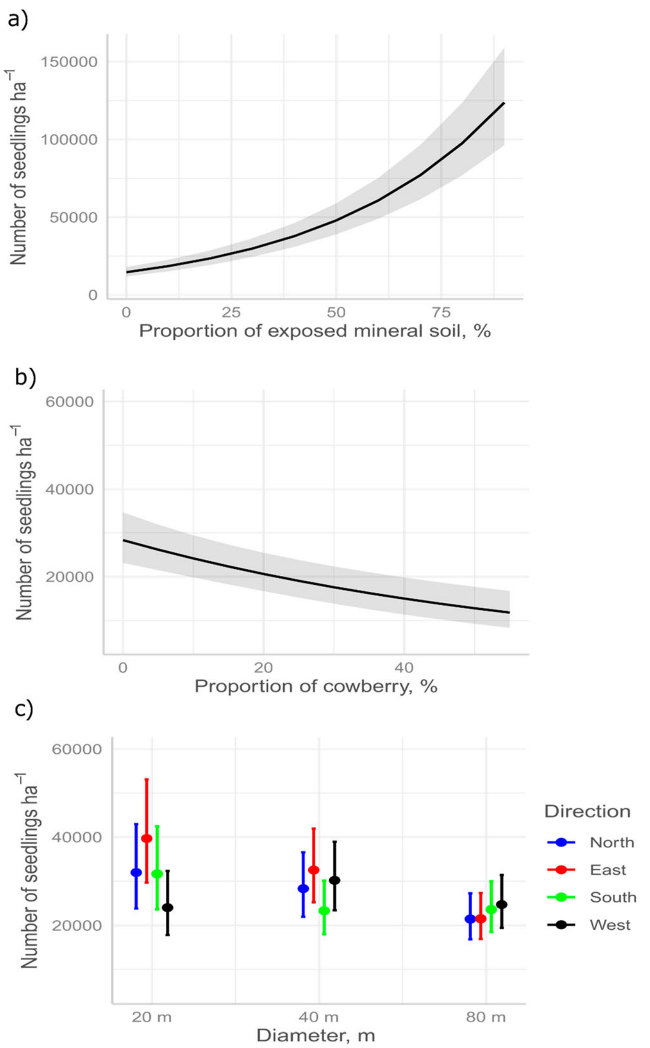

Figure 3. Predictions (with 95% confidence intervals) for the generalised linear model (Model 1) using a negative binomial distribution assumption explaining the number of Scots pine seedlings in the gaps of different size. The predictions are presented for: (a) the proportion of exposed mineral soil; (b) the proportion of cowberry; and (c) the interaction effects of gap diameter and the direction from the gap centre.

lichen cover decreased seedlings' height increment in the function of seedlings' age, which can be seen as a more gentle slope from 1% to 30% or 60% lichen proportion (Table 3, Figure 5(d)). Furthermore, the pine seedlings were

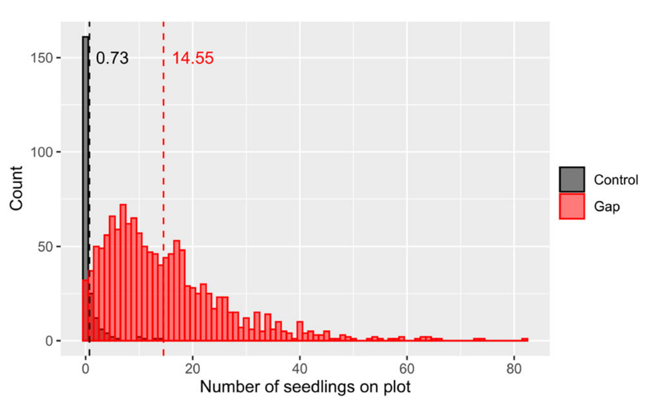

Figure 4. Distribution of the observed number of pine seedlings on regeneration plots in gaps (red) and on control plots in the uncut forest matrix (grey).

Table 3. The log-normal linear mixed model for the seedlings height with direction (Model 2).

Variable, parameter	Estimate	Std. error	Df	*t*- /chi -value	*p*
(Intercept)	−3.038E + 00	6.996E-01	1141	−4.342	0.000
Direction (ref. North)			3	10.130	0.017
East	−1.314E-01	1.219E-01	1141	−1.077	0.282
South	−7.155E-02	1.207E-01	1141	−0.593	0.553
West	2.207E-01	1.198E-01	1141	1.842	0.066
Gap diameter (ref. 20 m)			2	15.537	0.000
40 m	2.683E-01	1.114E-01	46	2.408	0.020
80 m	4.034E-01	1.039E-01	46	3.884	0.000
Age of pine seedlings, years	−2.245E-01	1.427E-01	1141	−1.573	0.116
Sqrt(Age of pine seedlings), years	2.785E + 00	6.188E-01	1141	4.500	0.000
log(Number of pine seedlings)	5.278E-01	9.435E-02	1141	5.594	0.000
Cover of *Cladonia* spp, %	−5.153E-02	1.206E-02	1141	−4.272	0.000
Cover of humus layer, %	5.675E-03	1.216E-03	1141	4.668	0.000
Cover of exposed mineral soil, %	−6.752E-03	1.177E-03	1141	−5.737	0.000
Age of pine seedlings: log (number of pine seedlings)	−3.494E-02	1.423E-02	1141	−2.455	0.014
Age of pine seedlings: Cover of *Cladonia* spp.	5.232E-03	1.617E-03	1141	3.236	0.001
Direction:Diameter			6	10.867	0.093
East: 40 m	3.799E-02	1.438E-01	1141	0.264	0.792
South: 40 m	7.896E-02	1.430E-01	1141	0.552	0.581
West:40 m	−2.156E-01	1.417E-01	1141	−1.522	0.128
East:80 m	6.187E-02	1.322E-01	1141	0.468	0.640
South:80 m	7.741E-03	1.309E-01	1141	0.059	0.953
West:80 m	−3.010E-01	1.302E-01	1141	−2.313	0.021
Variance: Block	7.625E-03				
Variance: Plot nested within block	1.697E-02				
Residual	2.374E-01				

R^2 = 53.02% (marginal model) / 57.44% (conditional model).

taller in 40 and 80 m gaps than in 20 m gaps (Table 3), and the combined effect of diameter and direction was seen in the 20 m diameter class in the western direction (Figure 5 (e)). The total model fit for the negative binomial models for the seedling number was 53.02% in the marginal model and 57.44% in the conditional model (Table 3).

If the model with the gap diameter was constructed without direction from the gap centre (see Table A3 in appendix) using only the main effect of gap diameter, the predicted height of Scots pine seedlings for different gap sizes were: 20 m 33.93 cm, 40 m 41.13 cm, and 80 m 45.22 cm (the chi-squared value = 19.760, df = 2, $p < 0.001$).

The height of pine seedlings as a function of seedling age increased quite steadily in the gaps, whereas in the control plots (regeneration plots within the uncut buffer zone), the height was very low, less than 20 cm at the age of 10 years (Figure 6).

Discussion

Our results showed excellent regeneration results in terms of a large number of seedlings and small share of empty regeneration plots. However, the seedlings' early height development was relatively slow. The results reflect and confirm the

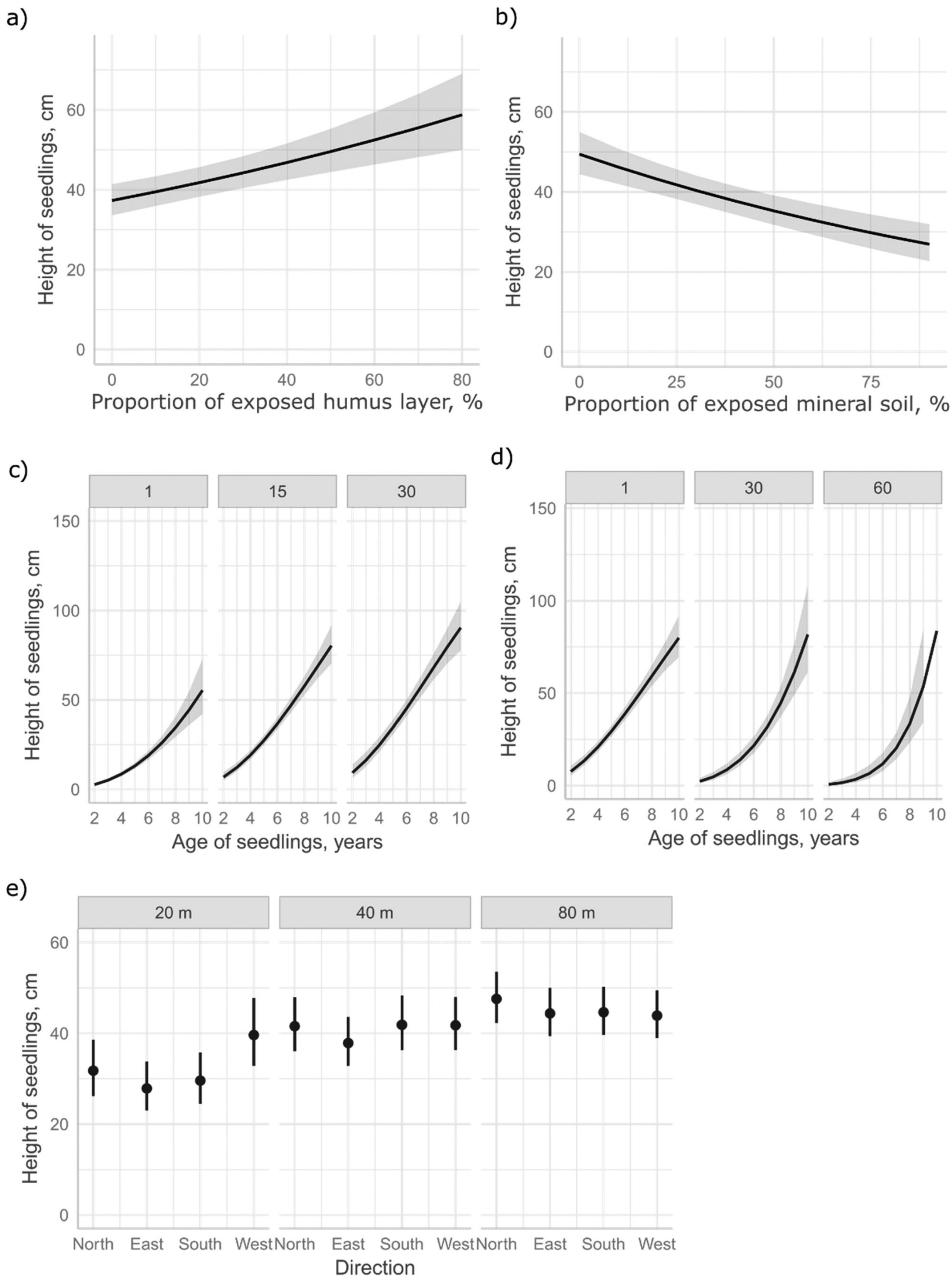

Figure 5. Predictions (with 95% confidence intervals) for the general linear mixed model for seedling height (Model 2). The predictions are presented for: (a) the proportion of the exposed humus cover; (b) the proportion of exposed mineral soil; (c) the interaction of the age of the seedlings and number of seedlings in numbers 1, 15, and 30 seedlings per plot; and (d) the interaction of the gap diameter and the cover of Cladonia lichens in cover proportions 1%, 30%, and 60%; and (e) the combined effect of diameter and direction in 20, 40 and 80 m diameter gaps.

Figure 6. The height of pine seedlings on regeneration plots in gaps (red) and in closed forest, i.e. control plots in the buffer zone (black). The scatterplot was based on raw data of observed ages and the corresponding heights of the seedlings.

preliminary findings of Hallikainen et al. (2019), providing new information about the early growth of pine seedlings in northern boreal forests.

The average number of established pine seedlings was very high in all studied gap sizes. There were fewer pine seedlings in the larger gaps, but even in the largest 80 m diameter gaps, it was over 23,000 ha^{-1}. This, with the finding that only a very small fraction, about 2% of the 5 m^2 regeneration plots, were empty, suggests that all the studied gap sizes showed abundant pine regeneration. In contrast, the proportion of empty plots was high, and growth was extremely slow in the control plots outside the gaps, i.e. in the uncut forest matrix. These control plot characteristics were very similar to the results of Rautio, Hallikainen et al. (2023) in closed forests or in forests with high a basal area.

When the early height development of pine seedlings is added to this picture, the larger gaps seem preferable from the silvicultural perspective, as seedlings were taller in the larger gaps. Although there were slightly fewer seedlings in the larger gaps and the number of seedlings decreased towards the gap centre, there were still more than enough seedlings for silvicultural needs. The minimum limit for the number of crop seedlings in the Finnish Forest Act (11 §) for Lapland is just 1,200 seedlings ha^{-1}. As only 2% of the regeneration plots were empty, the number of potential crop seedlings is certainly much higher than the minimum limit in most gaps. In the Finnish forest management guidelines, a specific target density has not been set for natural regeneration, but for the production of high-quality timber, the aim is to have 4,000–5,000 seedlings ha^{-1} in direct seeding (Äijälä et al. 2019). The densities here were therefore manifold compared with that figure.

In addition to gap diameter (Kuuluvainen 1994; Kuuluvainen and Ylläsjärvi 2011), direction showed an effect on the number and height of pine seedlings. This effect was most pronounced in the smallest gap, where the western side showed the fewest seedlings but highest growth. As direction probably does not affect root competition as much as the amount of light, this suggests that in addition to root competition (see e.g. Häggström et al. 2023), light competition has an effect on regeneration success.

The proportion of exposed mineral soil was the most powerful variable for predicting the number of established pine seedlings. However, many pine seedlings (about 20,000 ha^{-1}) were established even without site preparation. A recent study by Miettinen et al. (2022) in Finnish and Swedish Lapland concluded that site preparation was needed to secure regeneration, but even the lightest preparation methods would provide sufficient regeneration results. Our conclusions are similar, but even more pronounced. Our results also support the hypothesis that on xeric and sub-xeric sites in Lapland, the available time window for the pine seedling establishment is relatively long, at least 10 years (Hyppönen and Kemppe 2001; Hallikainen et al. 2007; Kyrö et al. 2022), as the number of pine seedlings nearly doubled compared with those in the inventory conducted five years earlier by Hallikainen et al. (2019).

Of the studied ground and field layer species, the proportion of cowberry was a strong predictor of the number of pine seedlings. This reverse relationship agrees with recent findings of Kyrö et al. (2022), although in their study, the number of pine seedlings was about ten times lower. In our results, the number of pine seedlings exceeded 10,000, even with the highest cowberry proportions. Cowberry proportion is related to higher soil productivity. In this light, it seems obvious that higher fertility means challenges in seedling recruitment even on such infertile sites – but on the other hand, faster growth. The proportion of the exposed humus cover was in turn related to the faster growth of pine seedlings. The proportion of humus cover may also be related to the site fertility, as in places with thick humus layer, indicating fertility, it is more likely that more humus remains on the spot after patch scarification with an excavator. On the other hand, also thin layer of humus can improve the surface for seedling establishment compared to the bare mineral soil, as the water holding capacity is better and it is also less prone to frost heaving of seedlings (Kyrö et al. 2022).

Additionally, a positive correlation between the number of seedlings on a regeneration plot and seedling height was detected. This could be connected with the phenomenon that in a larger group of seedlings, the dominant height tends to be higher. There was also a negative relationship between the cover of *Cladonia* lichens and seedling height. This reverse relationship may be connected with a low availability of nutrients, as *Cladonia* lichens indicate low soil fertility.

The height development of pine seedlings was slow, and it was not substantially faster in greater gap sizes. The average height of the tallest seedlings in different gap sizes ranged from 34 to 45 cm 10 years after gap cutting. This is very well in line with previous findings in Lapland (Hyppönen et al. 2005; Hallikainen et al. 2007; Hyppönen and Hallikainen 2011). Slow early growth increases the risk of many types of forest damage such as browsing damages caused by moose (*Alces alces*) and reindeer (*Rangifer tarandus tarandus*, Miettinen et al. 2022) or some fungal diseases such as scleroderris canker (*Gremmeniella abietina*, Kaitera et al. 2015) or snow blight (*Phacidium infestans*, Lilja et al. 1997), which can slow down the regeneration process even more.

Planting would provide better early growth in many cases, but on poor sites and in a cool climate, it cannot necessarily provide a profitable alternative to natural regeneration. This is due to high costs and low and distant future revenues, which makes many investments unprofitable, even at low-interest rates (Ahtikoski et al. 2012). In future, the possible use of carbon offsets may change the optimal solutions (e.g. Ahtikoski et al. 2022). For example, carbon offsets could also promote the use of planting on slightly poorer sites and in slightly poorer environments. In any case, securing fast and sufficient natural regeneration with minimal costs seems an attractive alternative to planting. For this, small gaps without site preparation and larger gaps combined with light site preparation – and perhaps spatially limited to gap core areas and a western direction – could provide a useful solution (see also Rautio, Lindeskog et al. 2023). Additionally, practitioners have suggested that direct seeding conducted mechanically in combination with site preparation would be an economically justifiable inexpensive way to accelerate regeneration and utilise the benefits of tree breeding, but specific research results remain absent.

Pine seedlings grew somewhat faster in larger gaps than in smaller ones. This was expected, as it is well known that the edge forest limits the growth of seedlings in a gap up to 20 m from the edge (Siipilehto 2006; Ruuska et al. 2008; Valkonen et al. 2011; Axelsson et al. 2014). Larger gaps may accelerate stand development, but small gaps can be preferable when other ecosystem services in addition to timber production are considered. For example, for some bird species, small gaps are needed to maintain habitat quality. An example of such a species is capercaillie, which needs its lekking sites to be highly forested and can tolerate only small gaps within them (Valkeajärvi and Ijäs 1986; Rolstad and Wegge 1987; Valkeajärvi and Ijäs 1991). Blueberry (*Vaccinium myrtillus*), which is closely connected with both recreational use of forests and biodiversity via connections with many associated species, may also benefit from smaller gaps because the reduction of blueberry is found to depend on cutting intensity (Bergstedt and Milberg 2001). In addition, small gaps have been shown not to have impacts on bird assemblage diversity (Versluijs et al. 2017) or on the diversity of vascular plants or bryophytes (del Alba et al. 2021).

To conclude, our study shows that gap cutting using diameters of 20, 40, and 80 m showed successful results in the regeneration of xeric and sub-xeric pine forests in central Lapland, especially when light site preparation was applied. In terms of the number of pine seedlings, the results were almost overwhelming in the smaller gaps. In larger gaps, there were fewer seedlings, although there were still enough seedlings from the silvicultural perspective, and their average growth was faster than in smaller gaps. To achieve both sufficient recruitment and fast early growth, gaps of 40 metres or larger in diameter are needed. Improved regeneration results advocate the use of low-intensity site preparation with its low costs, low environmental effects, and less adverse effects on other land use forms compared with more intensive methods. Optimal combinations could probably be found by using various site preparation strategies, depending on the gap size. Future studies could focus on larger gaps and more fertile site types, as well as including some hybrid methods where site preparation intensities are modified at the gap edges, gap core areas, or in some selected directions.

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References

Ackzell L. 1994. Natural regeneration on planted clear-cuts in boreal Sweden. Scand J For Res. 9:245–250.

Ahtikoski A, Rämö J, Juutinen A, Shanin V, Mäkipää R. 2022. Continuous cover forestry and cost of carbon abatement on mineral soils and peatlands. Front Environ Sci. 10:837878. doi:10.3389/fenvs.2022.837878.

Ahtikoski A, Salminen H, Hökkä H, Kojola S, Penttilä T. 2012. Optimising stand management on peatlands: the case of northern Finland. Can J For Res. 42:2.

Äijälä O, Koistinen A, Sved J, Vanhatalo K, Väisänen P. 2019. Metsänhoidon suositukset. Tapion julkaisuja. Finnish.

Axelsson EP, Lundmark T, Högberg P, Nordin A. 2014. Belowground competition directs spatial patterns of seedling growth in boreal pine forests in Fennoscandia. Forests. 5(9):2106–2121. doi:10.3390/f5092106.

Bartoń K. 2020. MuMIn: multi-model inference. R Package Version 1.43.17. https://CRAN.R-project.org/package = MuMIn.

Bergstedt J, Milberg P. 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. For Ecol Manag. 154:105–115.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. Glmmtmb balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9(2):378–400.

Cajander A. 1926. The theory of forest types. Acta For Fenn. 29(3):108.

del Alba CE, Hjältén J, Sjögren J. 2021. Restoration strategies in boreal forests: differing field and ground layer response to ecological restoration by burning and gap cutting. For Ecol Manag. 494:119357.

Downey M, Valkonen S, Heikkinen J. 2018. Natural tree regeneration and vegetation dynamics across harvest gaps in Norway spruce dominated forests in southern Finland. Can J For Res. 48:524–534.

Gustavsen HG. 1980. Talousmetsien kasvupaikkaluokittelu valtapituuden avulla. abstract: site index curves for conifer stands in Finland. Folia For. 454:1–31.

Häggström B, Gundale M, Nordin A. 2023. Environmental controls on seedling establishment in a boreal forest: implications for Scots pine regeneration in continuous cover forestry. Eur J For Res. doi:10.21203/rs.3.rs-3014303/v1.

Hair Jr JF, Anderson RE, Tatham RL, Black WC. 1998. Multivariate data analysis. 5th ed. Upper Saddle River: Prentice Hall, p. 730.

Hair Jr JF, Hult GTM, Ringle CM, Sarstedt M, Danks NP, Ray S. 2021. Partial least squares structural equation modeling (PLS-SEM) using R. A workbook. Springer, p. 179. doi:10.1007/978-3-030-80519-7.

Hallikainen V, Hökkä H, Hyppönen M, Rautio P, Valkonen S. 2019. Natural regeneration after gap cutting in Scots pine stands in northern Finland. Scand J For Res. 34(2):115–125. doi:10.1080/02827581.2018.1557248.

Hallikainen V, Hyppönen M, Hyvönen J, Niemelä J. 2007. Establishment and height development of harvested and naturally regenerated Scots pine near the timberline in North-East Finnish Lapland. Silva Fenn. 41(1):71–88.

Hartig F. 2021. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Rpackage version 0.4.4. https://CRAN.R-project.org/package = DHARMa.

Hökkä H, Repola J. 2018. Pienaukkohakkuun uudistumistulos Pohjois-Suomen korpikuusikossa - 10-vuotisinventoinnin tulokset [Regeneration result in gap harvesting in a drained spruce mire in Northern Finland - survey results 10 years after harvesting]. Metsät Aikak. 2018–7808. doi:10.14214/ma.7808. (In Finnish).

Hökkä H, Repola J, Moilanen M, Saarinen M. 2011. Seedling survival and establishment in small canopy openings in drained spruce mires in northern Finland. Silva Fenn. 45(4):633–645.

Hökkä H, Repola J, Moilanen M, Saarinen M. 2012. Seedling establishment on small cutting areas with or without site preparation in a drained spruce mire - a case study in northern Finland. Silva Fenn. 46(5):695–705.

Hyppönen M, Alenius V, Valkonen S. 2005. Models for the establishment and height development of naturally regenerated *Pinus sylvestris* in Finnish Lapland. Scand J For Res. 20:347–357.

Hyppönen M, Hallikainen V. 2011. Factors affecting the success of autumn direct seeding of *Pinus sylvestris* L. in Finnish Lapland. Scand J For Res. 26:515–529.

Hyppönen M, Kemppe T. 2001. Maanmuokkauksen ja kylvön vaikutus mäntysiemenpuualan taimettumiseen Etelä-Lapissa. Metsätieteen Aikakauskirja. 1/2002:19–27. (In Finnish).

Kaitera J, Mäkitalo K, Hantula J. 2015. Incidence of *Gremmeniella abietina* in planted seedlings of *Picea abies* and *Pinus sylvestris* in northern Finland. For. Path. 45:14–20. doi:10.1111/efp.12118.

Kuuluvainen T. 1994. Gap disturbance, ground micro topography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annal Zool Fenn. 31:35–51.

Kuuluvainen T, Ylläsjärvi I. 2011. On the natural regeneration ofdry heath forests in Finnish Lapland: a review of V. T. Aaltonen (1919). Scand J For Res. 26(S10):34–44. doi:10.1080/02827581.2011.517951.

Kyrö MJ, Hallikainen V, Valkonen S, Hyppönen M, Puttonen P, Bergsten U, Winsa H, Rautio P. 2022. Effects of overstory tree density, site preparation and ground vegetation on natural Scots pine seedling emergence and survival in northern boreal pine forests. Can J For Res. 52:1–10.

Lehto J. 1956. Tutkimuksia männyn luontaisesta uudistumisesta Etelä-Suomen kangasmailla. Summary: Studies on the natural reproduction of Scots pine on the upland soils of Southern Finland. Acta For Fenn. 66(2):106.

Lilja A, Lilja S, Kurkela T, Rikala R. 1997. Nursery practices and management of fungal diseases in forest nurseries in Finland. A review. Silva Fenn. 31(1):79–100.

Liu Q, Hytteborn H. 1991. Gap structure, disturbance and regeneration in a primeval Picea abies forest. J Veg Sci. 2(3):391–402.

Lüdecke D. 2018. Ggeffects: tidy data frames of marginal effects from regression models. J Open Source Software. 3(26):772. doi:10.21105/joss.00772.

Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D. 2021. Performance: an R package for assessment, comparison and testing of statistical models. J Open Source Software. 6(60):3139. doi:10.21105/joss.03139.

Miettinen J, Hallikainen V, Hyppönen M, Bergsten U, Winsa H, Välikangas P, Hiltunen A, Aatsinki P, Rautio P. 2022. Effects of site preparation and reindeer grazing on the early-stage success of Scots pine regeneration from seeds in northern Finland and Sweden. Scand J For Res. 37:338–351.

Pinheiro J, Bates D, DebRoy S, Sarkar D, Core Team R. 2020. nlme: Linear and Nonlinear MixedEffects Models. R package version. 3:1–150. https://CRAN.R-project.org/package = nlme.

Rautio P, Hallikainen V, Valkonen S, Karjalainen J, Puttonen P, Bergsten U, Winsa H, Hyppönen M. 2023. Manipulating overstory density and mineral soil exposure for optimal natural regeneration of Scots pine. For Ecol Manag. 539:120996.

Rautio P, Lindeskog H, Bergsten U, Karlberg M. 2023. Lean forestry – a paradigm shift from economies of scale to precise and sustainable use of ecosystem services in forests. For Ecol Manag. 530:120766. doi:10.1016/j.foreco.2022.120766.

Rolstad J, Wegge P. 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. Oecologia. 72:389–394.

Ruuska J, Siipilehto J, Valkonen S. 2008. Effect of edge stands on the development of young *Pinus sylvestris* stands in southern Finland. Scand J For Res. 23:214–226.

Siipilehto J. 2006. Height distributions of Scots pine sapling stands affected by retained tree and edge stand competition. Silva Fenn. 40(3):473–486.

Snowdon P. 1991. A ratio estimator for bias correction in logarithmic regressions. Canadian Journal of Forest Research. 21(5). https://doi.org/10.1139/x91-101.

Valkeajärvi P, Ijäs L. 1986. On the display requirements of capercaillie in central Finland. Suomen Riista. 33:5–18. (In Finnish with English summary).

Valkeajärvi P, Ijäs L. 1991. The impact of clearcutting on a capercaillie lek centre. Suomen Riista. 37:44–55. (In Finnish with English summary).

Valkonen S, Koskinen K, Mäkinen J, Vanha-Majamaa I. 2011. Natural regeneration in patch clear-cutting in I stands in Southern Finland. Scand J For Res. 26:530–542.

Valkonen S, Siitonen J. 2016. Tree regeneration in patch cutting in Norway spruce stands in northern Finland. Scand J For Res. 31:271–278.

Versluijs M, Eggers S, Hjältén J, Löfroth T, Roberge JM. 2017. Ecological restoration in boreal forest modifies the structure of bird assemblages. For Ecol Manag. 401:75–88.

Wickham H. 2016. Ggplot2: elegant graphics for data analysis. New York: Springer-Verlag. 213 p. eISBN: 978-0-387-98141-3, doi:10.1007/978-0-387-98141-3.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and their extensions in ecology with R. New York: Springer. 574 p. ISBN 978-0-378-87457-0, doi:10.1007/978-0-387-87458-6.

Appendix

Experimental design and data acquisition

Stand density, tree size, and the exposition of the gaps varied between blocks (Table A1).

Statistical modelling: negative binomial models for the seedling number

In the negative binomial defined R function glmmTMB, the variance was defined in two ways: NB1 variance = $\mu(1+\alpha)$ and NB2 variance = $\mu(1+\mu/\theta)$ (Brooks et al. 2017). NB1 parametrisation suggested the linear mean-variance relationship, while NB2 parametrisation suggested the quadratic relationship between the expected value and variance. The two parametrisations were tried, and the best parametrisation selected, using AIC and R2 and comparing the predicted and observed counts. Both parametrisations produced reasonable results, and the same interpretations of the results. NB2 parametrisation proved slightly better as a whole, and it was used in the computation of the final models. The Poisson distribution was also tested, but it was not used because of considerable over-dispersion.

R package glmmTMB also allowed the zero-inflation modelling. The possible existence of a zero-inflation problem was tested in the count models, but the zero-inflation in terms of excess zeroes was not an obvious problem in these data, although the lack of zeroes was a problem when the number of zeroes was tested using R package DHRMa (Hartig 2021). The null hypothesis of the suitable number of observed zeroes compared with the simulated ones tested using the function "testZeroInflation" suggested the lack of observed zeroes in the data ($p < 0.050$). The zero-inflation modelling possibilities in glmmTMB did not help the problem either. Using a "ziformula" option in the glmmTMB model produced slightly better predicted value distributions than the presented models, but with warnings of convergence or Hessian matrix problems. The (pseudo) R^2 values for the negative binomial models were computed using wide-functioning R package performance (Lüdecke et al. 2021). VIF, variance inflation factor was used in order to check possible multicollinearity of the predictors. All the VIF-values of the main effects remained low, below 5 (Hair et al. 2021).

Results

Models were constructed also with the gap diameter without direction from the gap centre, using only the gap diameter for the number (Table A2) and for the height (Table A3) of Scots pine seedlings.

Table A1. Mean values of the basic parameters by blocks.

Variable / block	1	2	3	4	5	6	*p*
Total number of tree stems ha^{-1} (min. $d_{1.3} = 7$ cm)	611.11	546.03	515.87	606.35	712.70	871.43	**0.001**
Total basal area of trees (m^2ha^{-1})	17.12	17.19	13.02	19.81	18.77	21.45	**0.001**
Diameter of trees (all species) weighted by basal area	27.01	25.80	24.26	28.45	25.95	25.94	0.939
Height of trees (all species) weighted by basal area	17.24	17.65	15.66	18.33	17.39	16.91	0.956
Crown height of trees, m (all tree species)	5.91	7.03	5.49	7.11	6.21	6.19	0.876
Number of Norway spruce stems ha^{-1} (min. $d_{1.3} = 7$ cm)	12.70	3.18	1.59	30.16	6.35	7.94	0.796
Basal area of Norway spruce stems m^2 ha^{-1} (min. $d_{1.3} = 7$ cm)	0.22	0.04	0.01	0.48	0.05	0.13	0.953
Number of deciduous stems ha^{-1} (min. $d_{1.3} = 7$ cm)	15.87	58.73	38.10	61.91	49.21	33.33	0.478
Basal area of deciduous stems m^2 ha^{-1} (min. $d_{1.3} = 7$ cm)	0.90	1.41	0.80	1.54	1.08	1.08	0.806
Dominant Diameter of Scots pines (min. $d_{1.3} = 7$ cm)	32.81	31.82	28.44	34.74	32.92	34.54	0.060
Dominant Height of Scots pines (min. $d_{1.3} = 7$ cm)	19.13	19.75	17.40	20.23	19.80	19.50	0.282
Average slope (%)	6.45	6.87	7.70	9.99	5.65	10.00	0.256
Direction of the slope (% of the openings, $n = 54$):	North	East	South	West	Flat		Chi-test *p*
Block 1	22	23	00	22	33		0.021
Block 2	33	00	11	56	00		
Block 3	00	11	56	11	22		
Block4	11	00	22	56	11		
Block5	33	00	11	45	11		
Block6	56	11	00	33	00		

The values have been calculated from the data describing the original forest, which had been measured before the cutting of the small cap openings (based on the five circular plots, see Chapter 2.1). The data have been aggregated (mean) to the small canopy opening level (54 openings in six blocks). *P*-values denote the significances of the ANOVA describing the differences in the means between the blocks. Dominant diameter denotes the diameter of the 100 biggest ($d_{1.3}$) trees ha^{-1}. All tree species denotes Scots pine, Norway spruce, and deciduous trees together. The main directions of the slope are also presented by the blocks with a chi-squared test using the simulated *p*-values.

Table A2. Model for the number of pine seedlings according to gap diameter.

Variable, parameter	Estimate	Std. error	*t*- /chi-value	*p*
(Intercept)	2.416E + 00	1.200E-01	20.126	0.000
Diameter (ref. 20)			9.652	0.008
Diameter 40	−1.228E-01	1.222E-01	−1.006	0.315
Diameter 80	−3.625E-01	1.203E-01	−3.013	0.003
The cover of cowberry, %	−1.399E-02	3.024E-03	−4.625	0.000
The cover of exposed mineral soil, %	2.205E-02	1.120E-03	19.686	0.000
Variance, Block	1.082E-01			
Variance, Small gap nested within block	0.02869			
NB2 overdispersion parameter (Theta)	4.31			

$R^2 = 33.70\%$ (marginal model) / 56.50% (conditional model).

Table A3. Model for the length of pine seedlings according to gap diameter.

Variable, parameter	Estimate	Std. error	Df	*t*- /chi-value	*p*
(Intercept)	−3.058E + 00	6.909E-01	1201	−4.427	0.000
Diameter (ref. Diameter 20)				19.760	0.000
Diameter 40	1.923E-01	6.687E-02	46	2.876	0.006
Diameter 80	2.871E-01	6.462E-02	46	4.444	0.000
Age_living_pines	−2.375E-01	1.422E-01	1201	−1.670	0.095
sqrt(Age of living pines)	2.863E + 00	6.167E-01	1201	4.642	0.000
log(Number of pine seedlings)	5.194E-01	9.353E-02	1201	5.553	0.000
Cover of Cladonia spp, %	−5.238E-02	1.199E-02	1201	−4.368	0.000
Cover of humus layer, %	5.624E-03	1.200E-03	1201	4.688	0.000
The cover of exposed mineral soil, %	−6.470E-03	1.156E-03	1201	−5.596	0.000
Age of pine seedlings:log(number of pine seedlings)	−3.540E-02	1.409E-02	1201	−2.513	0.012
Age of pine seedlings:Cover of Cladonia spp.	5.213E-03	1.611E-03	1201	3.236	0.001
Variance: Block	7.306E-03				
Variance: Plot nested within block	1.932E-02				
Residual	2.405E-01				

$R^2 = 51.55\%$ (marginal model) / 56.38% (conditional model).