Forest Ecology and Management 617 (2026) 123929

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Natural regeneration of Scots pine seedlings in northern Finland after small gap, selection and shelterwood cuttings and site preparation

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ARTICLE INFO

Keywords:
Continuous cover forestry
LiDAR
Aerial imaging
Track preparation
Patch scarification
Area-based approach

ABSTRACT

The interest in continuous cover forestry (CCF) has increased in Northern Europe over the last decade. Its sustainability depends on successful natural regeneration, which can be limited by the demanding growing conditions in northern Fennoscandia. We studied the early success of, and factors influencing, natural regeneration of Scots pine seedlings on xeric and mesic sites in northern Finland after small gap, selection and shelterwood cuttings and site preparation (none, track and patch scarification). The six study stands treated in 2020–2021 were inventoried in 2024, 3–4 years after cuttings. We evaluated the factors affecting the number of Scots pine seedlings established after cuttings using generalised linear mixed modelling, considering both field-measured and remote-sensing-based predictors. We found that the modelled number of pine seedlings increased in the small gap stands along with increasing distance from the forest edge and coverage of bare humus and lichen. In the selection and shelterwood cutting stands it decreased along with increasing stoniness and moss (excluding *Sphagnum* spp.) coverage. In both cases, site preparation (especially track preparation) improved the regeneration result. Based on the best fitting model, the mean number of pine seedlings in the small gap stands was 1500 ha^{-1} and in the selection and shelterwood cutting stands 1000 ha^{-1}. To conclude, the establishment of seedlings was low, but it may increase in the coming years.

1. Introduction

Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.) are the economically most important species in Finland. Forests dominated by them have been managed in Finland in past decades using even-aged rotation forestry (RF) (Brunner et al., 2025; Korhonen et al., 2024). In RF, different stand development classes (e.g. open area, young sapling stand, young thinning stand, mature stand) can be clearly distinguished (Äijälä et al., 2019; Brunner et al., 2025; Lula et al., 2025). In RF, forest regeneration is achieved by planting, sowing or using natural regeneration with seed-tree or shelterwood methods (Äijälä et al., 2019). As an alternative to RF, in uneven-aged forestry (i.e. continuous cover forestry [CCF]), a mixed stand structure is maintained where several age classes occur together. Such forests can be treated with selection or small gap cuttings. To enhance preconditions for sufficient natural regeneration, the CCF stand should consist of larger number of younger (smaller) trees than older (larger) ones, which are gradually harvested and replaced by younger ones (Äijälä et al., 2019; Lula et al., 2025). In CCF, sufficient natural regeneration is crucial, because forest regeneration relies solely on natural regeneration and seedling ingrowth (Lula et al., 2025). However, the success of natural regeneration can be highly variable, depending on several environmental factors, such as the moisture content of the soil, available light, site fertility, rainfall and size of seed crops (Lula et al., 2025). It can be especially challenging under more northerly (i.e. colder) climates, where good seed crops occur approximately once in every 10 years and germination is often delayed (Lula et al., 2025).

The interest in CCF has increased in Finland since updating the Forest

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https://doi.org/10.1016/j.foreco.2026.123929
Received 28 February 2026; Received in revised form 18 May 2026; Accepted 19 May 2026

Act in 2014, which permitted its wider use. CCF is expected to improve the multiple use of forests and nature values compared to RF. This is due to continuous forest coverage which is beneficial for biodiversity, provision of non-timber products and forest landscape values compared to clear-cut areas of RF (Peura et al., 2018; Juutinen et al., 2020; Miina et al., 2020; Tuulentie et al., 2025). CCF is considered as a particularly interesting option for the pine-dominated upland (mineral) forests of the northern region where natural wood production is low and forest regeneration costs are high (Norokorpi and Lähde, 2013; Rautio et al., 2023). Although the principles of forest regeneration and the factors contributing to it are well understood in RF due to its long use, the corresponding knowledge for CCF in boreal forests is limited (Brunner et al., 2025).

The Finnish Forest Act allows small gap cuttings to be performed over forest areas with a maximum size of 0.3 ha without requiring active forest regeneration. However, outside of these small gaps, the remaining basal area of the forest stand after cuttings must fulfil the required minimum level by the Forest Act. Otherwise, the harvesting is classed as a forest regeneration cutting of RF. In selection cutting, sufficient number of larger overstory trees and basal area (above the required minimum level) should be maintained in a forest, to provide preconditions for natural regeneration. In shelterwood cutting, mainly larger (seed) trees are left in forest for seeding the new tree generation and they are removed after establishment of sufficient number of seedlings (Kellomäki, 2022a). The recommended basal area left in a stand after selection and shelterwood cuttings are quite equal in practical forestry in Finland (Äijälä et al., 2019).

Rotation forestry is often combined with mechanical site preparation, which is used to enhance the establishment and survival of seedlings. It reduces competition between seedlings and other vegetation, and increases the soil temperature, moisture and nutrient uptake in the planting spot (Örlander et al., 1996; Sikström et al., 2020; Thiffault et al., 2025). The site preparation methods recommended for coarse or medium-coarse soil texture in natural regeneration are disc trenching and patch scarification which both expose the mineral soil by removing the humus layer. In patch scarification, a patch of mineral soil is exposed using an excavator. In disc trenching strips of mineral soil are exposed with rotating discs. Whereas in new (novel) track preparation method forwarder tracks break up the ground, exposing some of the mineral soil, but mostly the humus layer (Miettinen et al., 2022). Site preparation is rarely used in CCF due to its costs, even though it may improve the results of regeneration, particularly in mineral soils with abundant moss coverage in northern Finland (Lula et al., 2025; Miettinen et al., 2022; Rautio et al., 2023).

In addition to climate, dense overstory and the quality of the ground surface affect seedling emergence. Although a dense overstory produces more seeds, it simultaneously reduces the rainfall and sunlight to the seedlings below the overstory canopy and causes greater below-ground competition (Béland et al., 2000; Lehto, 1969; Nygren, 2003). In southern Finland, a recent study on Norway spruce showed that the low stand basal area (8–10 m^2 ha^{-1}) promoted the natural regeneration (Peltola et al., 2026, unpublished). Because Scots pine is a light-demanding species, its seedling survival rates can vary greatly between small gap, selection and shelterwood cuttings and depending on the stand basal area left after cuttings (Miettinen et al., 2024; Nystrand and Granström, 2000).

Ground- and field-layer vegetation characteristics can both hinder and advance seed germination and seedling ingrowth. An extensive coverage of moss and thick humus layer decrease seedling establishment and survival as they form dry seedbeds and growing conditions (Hallikainen et al., 2019; Miettinen et al., 2022; Peltola et al., 2025; Rautio et al., 2023). During snowless periods, reindeer in regions with active reindeer husbandry mainly graze on lichens and can trample on seedlings. But abundant lichens may indicate less reindeer grazing, which in turn might result in less mechanical damage to tree seedlings. Miettinen et al. (2022) reported a positive correlation between lichen coverage and seedling density. Conversely, bilberry (*Vaccinium myrtillus* L.) and stones as ground surface hinder the establishment of seedlings, by causing competition (Downey et al., 2018; Jäderlund et al., 1997).

In addition to the vegetation, the gap size affects seedling density, with smaller gap diameters tending to enhance seed germination and seedling establishment (Axelsson et al., 2014; Hallikainen et al., 2019; Miettinen et al., 2024). Downey et al. (2018) found seedling emergence to be at its greatest 5 m from the forest edge in small gaps. Too large gap diameter may decrease seed dispersal, whereas forest edge causes both above- and below-ground competition to seedlings nearby it (Axelsson et al., 2014; Hallikainen et al., 2019).

Most of previous studies on the success of, and factors influencing, natural regeneration in CCF have been based on field inventories in Finland. A few previous studies exist on successful use of airborne laser scanning (ALS) or other remote sensing methods in predicting the number of naturally regenerated seedlings (Bollandsås et al., 2008; Maltamo et al., 2023; Stoddart et al., 2023) or tending needs of sapling stands or their characteristics in RF (Imangholiloo et al., 2019; Korhonen et al., 2013; Närhi et al., 2008; Tokola et al., 2019). Remote sensing, including ALS, is now a mainstream tool in predicting forest attributes in RF (Korhonen et al., 2013; Maltamo et al., 2023). In CCF, dense overstory may prevent the laser pulses reaching the understory, causing inaccuracy for prediction. However, new LiDAR data by the National Land Survey of Finland, with an improved pulse density (5 m^{-2}) allows now more pulses to reach the forest floor, improving the detection accuracy of the understory trees (National Land Survey of Finland, 2025). Despite this, determining the understory trees by remote sensing is still a difficult task in CCF (Korpela et al., 2012; Maltamo et al., 2026). Thus, there is still need for research on the use of ALS data in CCF forests with several canopy layers to predict accurately the success of natural regeneration.

The aim of this study was to investigate the early success of natural regeneration and to determine the factors influencing it in Scots pine stands in northern Finland after small gap, selection and shelterwood cuttings with no site preparation, patch scarification and track preparation. The factors affecting the number of Scots pine seedlings established after the cuttings were evaluated using generalised linear mixed modelling, with both field-measured and remotely-sensed predictors. We considered the following combinations of cutting and site preparation treatments: 1) small gap cutting with no site preparation; 2) small gap cutting with patch scarification; 3) small gap cutting with track preparation; 4) selection cutting with no site preparation; 5) shelterwood cutting with no site preparation; 6) shelterwood cutting with patch scarification; and 7) shelterwood cutting with track preparation. We aimed to answer the following questions: 1) how does the cutting type affect the number of established new pine seedlings?; 2) does the site preparation improve the number of established pine seedlings compared to no site preparation?; and 3) can the number of established pine of seedlings be predicted using only remotely sensed data?

2. Materials and methods

2.1. Study area and experimental design

The study area was 6500 ha of northern boreal forest in the municipality of Suomussalmi in the Kainuu region of Finland (Fig. 1). This is part of a CCF test site that is managed in co-operation with Metsähallitus and the Natural Resources Institute Finland. Kainuu, located in central Finland, typically has higher prevalence of less fertile sites than southern Finland. The average mean annual temperature over the last 30 years (according to the Kuusamo meteorological station) is 0.7ºC and the mean annual precipitation 617 mm (Finnish et al., 2025). The site fertility type ranged from sub-xeric to mesic (*Vaccinium*- and *Myrtillus*-type based on the Cajander (1949) classification).

Study data were obtained from six Scots pine-dominated experimental stands (Fig. 1). One of the stands had selection cutting without

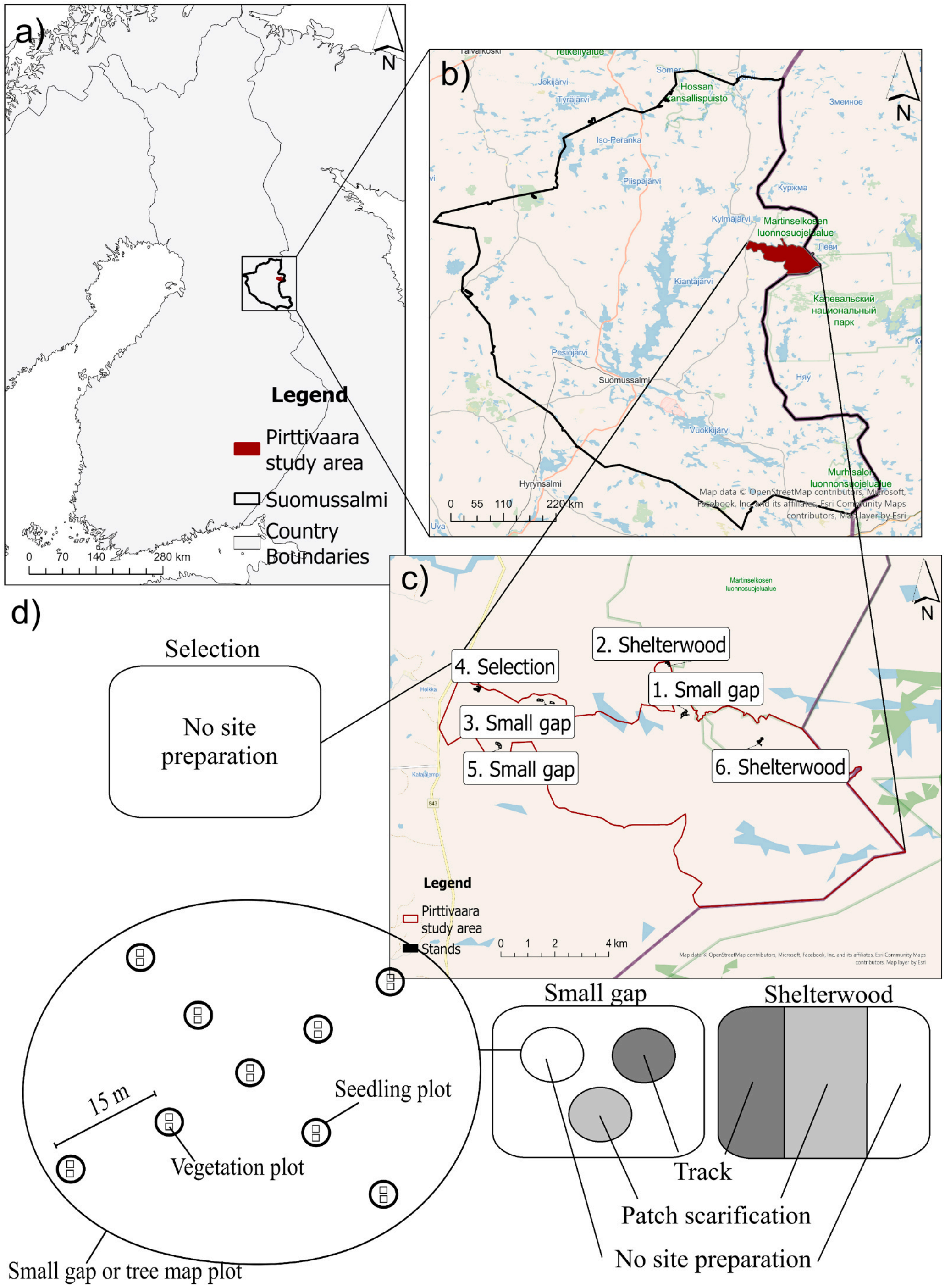

Fig. 1. (a–c) Locations of the study stands. (c and d) Location of different site treatments and plot layout. Each site preparation treatment included one treemap plot (1000–1500 m^2 / 100–200 trees). Stands with no site preparation (selection cutting stand and forest edges in small gap cutting stands) had two treemap plots. A batch of nine seedling plots (20 m^2) was located inside the treemap plot or in the small gap (max. 0.3 ha). Each seedling plot included two vegetation plots (0.25 m^2).

site preparation. Two stands had a shelterwood cutting with three site preparation treatments. Three stands had small gap cuttings using three site preparation treatments (Fig. 1). The site preparation treatments used in the shelterwood and small gap cutting stands were unprepared, patch scarification and track preparation. The forest edges of the small gaps were also treated with selection cutting with no site preparation, similarly to the individual selection cutting stands (Table 1; Fig. 1).

In the study stands, the seedling plots, vegetation plots for the ground- and field-vegetation inventory, and the tree-level plots (i.e. treemap plots) were measured. In each stand, a set of nine seedling plots was located inside a treemap plot and inside a small gap (Fig. 1). A seedling plot was replaced if more than 50% of its area was covered with slash, rocks or other unsuitable substrates. The selection cutting stand had two treemap plots, the shelterwood stands had six, the small gap stands also had six located at the forest edges. In total, we considered 14 treemap plots and 207 seedling plots, of which 81 represented small gap cutting stands, 54 the shelterwood cutting stands and 72 the selection cutting stands.

The stands were cut in 2020–2021 and the data were collected in the summer of 2024. The treemap plots were measured using electronic calipers with GPS detection of tree locations (Kostensalo et al., 2023). The treemap plots included 100–200 individually measured trees from

Table 1
Field-measured stand attributes under different types of cuttings and site preparation treatments.

	n	N		V, m^3 ha^{-1}	N, ha^{-1}	BA, m^2 ha^{-1}	D, cm	H, m
Small gap–edge		3*	p-value$_1$	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
NT	3			55.6 ± 12.4	180 ± 23	6.6 ± 1.5	20.7 ± 1.3	16.0 ± 0.7
PS	3			60.2 ± 12.3	193 ± 40	7.1 ± 1.5	20.7 ± 1.1	16.1 ± 0.5
TP	3			52.1 ± 16.4	189 ± 11	6.4 ± 1.6	19.8 ± 2.4	15.4 ± 1.1
Selection		1	p-value$_2$	> 0.05	< 0.05	> 0.05	> 0.05	< 0.05
NT	2			60.5 ± 11.3	261 ± 126	7.6 ± 1.6	19.1 ± 1.3	15.0 ± 0.8
Shelterwood		2	p-value$_2$	> 0.05	< 0.05	> 0.05	> 0.05	< 0.05
NT	2			67.7 ± 4.8	214 ± 67	7.7 ± 0.1	20.2 ± 3.5	14.4 ± 1.6
PS	2			56.0 ± 14.7	215 ± 37	6.6 ± 1.5	17.8 ± 0.5	13.6 ± 1.3
TP	2			59.9 ± 13.6	204 ± 19	7.2 ± 1.3	20.0 ± 1.9	15.1 ± 0.3

Note: NT = no site preparation, PS = patch scarification, TP = track preparation, n = number of treemap plots, N = number of stands/trees, V = volume, BA = basal area, D = diameter, H = height, p-value$_1$ = test statistic between small gap and selection + shelterwood cutting stands combined, p-value$_2$ = test statistic between selection and shelterwood cutting stands. *The forest edges of the small gaps were managed using selection cutting with no site preparation, consistent with the management applied in the individual selection cutting stands.

an irregular area of 1000–1500 m^2. The height, diameter at 1.3 m and tree species of each tree were determined. Accurate locations of the trees were also logged. The stand attributes were calculated from the tree measurements, including the species-specific average height (in metres), diameter (in centimetres), volume (cubic metres per hectare), volume of dead trees (cubic metres per hectare) (Laasasenaho, 1982), number of tree stems (per hectare) and basal area (square metres per hectare) (Table 1). The geometry of the treemap plots was created using a 10 m buffer around the tree locations and then dissolving the buffered points into a single vector layer. For the seedling plots in the small gaps, the stand attributes from the treemap plot at the forest edge were used in the modelling.

From the seedling plots (r = 2.52 m, area = 20 m^2), all the pine seedlings that emerged after the cuttings (diameter <4.5 cm) were individually inventoried regardless of their location relative to other seedlings. The seedling plot locations were systematically predefined at two crossing lines, 15 m apart (Fig. 1). The height, age and condition (1 = good, 2 = slightly damaged, 3 = dead) of each pine seedling were measured. Seedlings (age <1 year) that emerged in the inventory year were not measured. The other tree species were divided into spruce, birch and other. For these groups, the total number in each plot and their average heights were measured, but only if the seedling height was > 10 cm and the diameter < 4.5 cm. The stoniness of ground surface in each plot was measured as a three-level factor variable (0 = 0–30 cm, 1 = 30–60 cm, 2 = >60 cm) by measuring the depth of soil until first stone(s) in the middle of the seedling plots.

The different ground surface coverages in the ground and field layers were estimated (as percentages) in two (0.5 × 0.5 m, 0.25 m^2) vegetation plots located in the seedling plots. The species considered in the ground layer were mosses (excluding *Sphagnum* spp.) and lichens, along with the litter, deadwood (downed and standing), exposed soil and humus layer, rocks and stumps. The field-layer coverage measurements included the vascular plants bilberry (*Vaccinium myrtillus*), cowberry (*V. vitis-idaea* L.), heather (*Calluna vulgaris* [L.] Hull.), northern Labrador tea (*Ledum palustre* L.), bog bilberry (*Vaccinium uliginosum* L.) and crowberry (*Empetrum nigrum* L.) along with herbs (including grasses). The averages from these two plots were generalised to the seedling plot (Supplementary material Table A.1).

2.2. Remote sensing

The stand-level attributes were also predicted using airborne LiDAR data (density 5 pulses m^{-2}) and an area-based approach (ABA) (Nasset et al., 2014). This was done mainly because, in the small gaps, all the surrounding trees acted as seeding trees, whereas the stand attributes from the treemap plots represented only one edge of the gap. The LiDAR features such as point height, density and intensity percentiles and averages, were calculated using the R software package lidR (Roussel et al., 2020). For raster manipulation, the R software package terra (Hijmans et al., 2026) was used. The handling of the vector layers needed for the ABA was conducted using the R software package sf (Pebesma and Bivand, 2023). The ABA attributes were extrapolated to the stands surrounding each seedling plot batch (i.e. each site preparation treatment). Thus, the small gap cutting stands were divided into two parts; the stand surrounding the seedling plots in a small gap and the stand surrounding the seedling plots at the forest edge treated with selection cutting. The ABA stand attribute estimates were extrapolated to 23 stands (nine small gap forest edges, eight selection cutting stands and six shelterwood stands). In this way, the most accurate stand attributes could be linked with the seedling plots based on whether they were in the gaps or in the surrounding selection cutting stands.

The attributes extrapolated to the stands using remote sensing and the ABA were the average height (in metres), diameter (in centimetres), volume (cubic metres per hectare), number of tree stems (per hectare) and basal area (square metres per hectare). On average, 88% of the stands were dominated by pine (9% Norway spruce, 3% deciduous trees [mainly *Betula* spp.]), and so we did not consider species-specific estimates of the stand attributes, species-specific estimation being also more inaccurate (see, e.g., Vauhkonen et al., 2014). First, the LiDAR was height-normalised and features were calculated to the treemap plots along with aerial image features. The aerial image features calculated were the minimum, maximum, mean, median and variance of the red/green/blue (RGB), colour infrared (CIR), (each band) and Normalised Difference Vegetation Index (NDVI) rasters. The aerial image features were extrapolated using zonal statistics from a 0.5 m resolution orthoimage to the geometry of the treemap, so that the minimum, maximum, mean, median and variance from approximately 15 700 raster image cells to the geometry of treemap. Both the LiDAR data and aerial images were provided by the National Land Survey of Finland, except for the LiDAR for the easternmost shelterwood stand, which was collected by drone (National Land Survey of Finland, 2025).

Generalised linear models were constructed using this treemap plot dataset to predict stand attributes from previously described LiDAR and aerial image features. The explanatory variables for these models were selected using exhaustive variable search in R. The three best variables were chosen from a feature set that contained both the LiDAR and aerial image features, but only the statistically significant ones were included in the ABA models.

The stands for extrapolation were divided into 16 × 16 m grids. The same LiDAR and aerial image features as treemaps had in the previous phase were calculated to each grid cell. Then, using previously created ABA models, the stand attributes were predicted for each grid cell. Using zonal statistics, the average values of these cells were calculated for each stand (Supplementary material Tables A.2 and A.3). The stand attribute estimates were also extrapolated to stands from the Finnish Forest Centre's open source similarly produced 16 × 16 -m grid to the stands

(Finnish Forest Centre, 2023).

In addition to these stand attribute estimates, a canopy height model (CHM) was created by rasterising the height-normalised LiDAR (Fig. 2). In the small gap cutting stands, the distance between the seedling plots and the edge of the forest was calculated using the CHM and geospatial tools. In the final modelling phase, the stand attribute estimates (including distance from the forest edge) were linked to the seedling plots by the batch number. The aerial images and LiDAR features were also calculated to the geometries of the stands.

2.3. Statistical data analysis and modelling

The seedling plot statistics from the field inventory data and their distribution among the different site preparations and treatments were calculated using R's built in functions and the dplyr package (Wickham et al., 2026). The number of established new pine seedlings was evaluated using four different explanatory models, to study which explanatory variable types and combinations provide the most accurate prediction of number of naturally regenerated seedlings and to study if field-measured variables can be replaced with remote sensing ones. Because the selection and shelterwood cutting stands did not differ statistically in their stand attributes 3–4 years after cuttings (Table 1), they were grouped together for the modelling. The differences in the stand attributes were tested using the student's *t*-test for independent samples. Test results with p values greater than 0.05 for three out of five attributes (volume, basal area and mean diameter) indicated no statistical difference.

Separate models were constructed for the small gap cutting stands and the combined selection and shelterwood cutting stands. This was done because the natural regeneration conditions differed in the open small gap cutting stands from those under tree canopies in the selection and shelterwood cutting stands. All the models included the same random effect, seedling plot. For the small gap cutting models, the fixed effect included distance from the forest edge. In both the small gap cutting and the selection and shelterwood cutting models, the fixed effects included site preparation as a categorical variable. The alternative models tested included other explanatory variables, including:

a) site preparation (+ distance) + **LiDAR/aerial image features** | plot
b) site preparation (+ distance) + **ABA stand attribute estimates** | plot
c) site preparation (+ distance) + **field-measured stand attributes** + **other seedling variables** | plot
d) site preparation (+ distance) + **field-measured substrate coverages** | plot

The seedlings, coverage, LiDAR and aerial image features were calculated at the plot level (20 m^2). The field-measured stand attributes were calculated at the treemap level (~0.1–0.15 ha) and the stand attribute estimates and LiDAR features were predicted/calculated at the stand level (~1 ha). The LiDAR features were then calculated for both the seedling plots and the stands. Because the stand-level LiDAR features were not statistically significant, all their reported features are at the seedling plot level. Stand attributes were assigned to the seedling plots by a batch number that was the same for the set of nine seedling plots, the treemap and the surrounding stand. After creating the models, the replaceability of the field-measured stand attributes was evaluated by replacing them with open-source ABA estimates in **Model c** (Finnish Forest Centre, 2023). The use of open-source ABA attributes instead of ones created for this study is reasonable considering the operational use of these kinds of models. Statistical difference in plot-wise predictions between **Model c** with field-observed and **Model c** with field-observed stand attributes replaced with ABA attributes was evaluated with non-parametric Mann–Whitney–*U* test. Models created using remotely sensed variables can be applied to other areas that have the same variables available. Models that use field-measured stand attributes can be applied in the same way to other areas by replacing them with stand attribute estimates.

A generalised linear mixed model with a negative binomial distribution assumption was used to estimate the Scots pine seedling density. The models estimated the number of established Scots pine seedlings per 20 m^2 plot after the selection or shelterwood cuttings and small gap

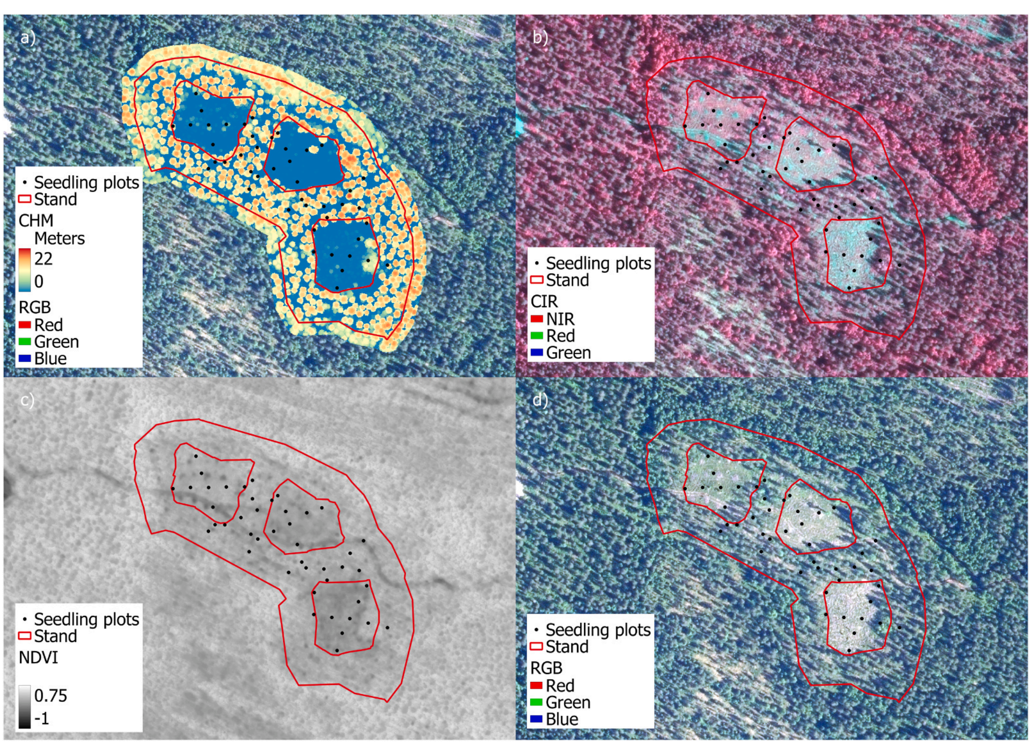

Fig. 2. Illustration of a small gap cutting stand and location of seedling plots: (a) CHM; (b) CIR image; (c) NDVI; and (d) RGB image layers.

cuttings, regardless of their height or location in relation to other seedlings. The models were computed using the R glmmTMB package (Brooks et al., 2017). In glmmTMB, the negative binomial model variance function of NB1 was defined as follows:

$$variance = \mu(1+\alpha) \quad (1)$$

where μ is the expected value and α is the ratio between the expected value and the dispersion parameter, as follows:

$$\alpha = \frac{\mu}{\theta} \quad (2)$$

Initially, four variables for each model (a–d) were chosen using an exhaustive variable search. The variable was included in the model if: 1) it improved the coefficient of determination (R^2) and the root mean square error (RMSE) of the model; 2) studying the effect of the variable on the response variable regardless of its statistical significance; 3) if it did not correlate with other variables in the model, causing singularity issues; and 4) if it was ecologically reasonable.

The models used one different hierarchical level—seedling plot. The variance of random effects was tested using glmmTMB and, as a result, seedling plot was chosen as a random effect (Brooks et al., 2017). The variance between the batches or stands was very close to zero and therefore excluded. Possible multicollinearity and singularity between selected variables were tested using the R software package performance (Lüdecke et al., 2021). For multicollinearity, the variance inflation values had to be < 5, and for the singularity, the variance–covariance matrix had to be greater than 1×10^{-5}. The spatial correlation checked using the nlme package (Pinheiro et al., 2025) between the plots was small, and consideration of this did not improve the model. The possible zero inflation was tested using the DHRMa package (Hartig et al., 2024), but it was not a problem in this dataset.

The R^2 values for all the models were calculated using the R software package multi-model inference (Bartoń, 2025). Predictions with 68% (i.e. one standard deviation [SD]) confidence intervals (CIs) and plotting were computed using the R software packages ggeffect and ggplot (Lüdecke et al., 2021; Wickham, 2016). For plotting purposes, the predicted number of seedlings in a plot was scaled up to the per-hectare level. The accuracy of the created models was evaluated using the RMSE, as follows:

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{(y_i - \hat{y}_i)^2}{n}} \quad (3)$$

where n is the number of plots, y_i is the observed value for plot i, and $\hat{y}_i$ is the predicted value for plot i. The models chosen for prediction and more detailed analysis were evaluated using the smallest RMSE values and the Akaike information criterion (AIC).

3. Results

3.1. Number of seedlings observed

In the small gap cutting stands, there was an average of 1971 seedlings ha^{-1} after the cuttings (Table 2). Seedling emergence was highest (3407 ha^{-1}) in the small gap cutting stands with track preparation and lowest (537 ha^{-1}) in the small gap cutting stands with no site preparation. In the selection cutting stands with no site preparation, the average number of new seedlings was 1417 ha^{-1}. On average, there were 1204 seedlings ha^{-1} in the shelterwood cutting stands (Table 2). Seedling emergence was highest with the track preparation (1417 ha^{-1}) and lowest (389 ha^{-1}) with no site preparation. In all the cutting and site preparation combinations majority of established new seedlings were in good condition and their average height was about 9 cm (Table 2).

3.2. Modelled number of seedlings

For the small gap cutting stands, the best model was **Model d** (coverages), which provided the smallest RMSE value (Table 3). The modelled average number of seedlings was 1500 ha^{-1} (3 plot^{-1}) as the mean of all site preparation treatments (Table 4). The corresponding observed average number of seedlings in the small gap cutting stands was 1971 ha^{-1} (4 plot^{-1}). The highest R^2 value was also found for **Model d.** Unexpectedly, the model with the lowest AIC value was **Model a** (LiDAR and aerial image features), although it was barely different from **Model d** (Table 3). In the selection and shelterwood cutting stands, **Model d** also provided the smallest RMSE and AIC values (Tables 3 and 5). Regardless of site preparation treatment, the modelled seedling density for the selection and shelterwood cutting stands was 1000 seedlings ha^{-1} with **Model d**, and the observed density was 1417 ha^{-1}.

In the small gap cutting stands, models were also produced by replacing the field-observed stand attributes in **Model c** with their

Table 3
Performance of the **Models a-d** by RMSE, AIC and predicted and observed number of seedlings.

Seedlings plot^{-1}	RMSE	PRED.	OBS.	AIC
Small gap				
Model a*	5.5	2.9	3.7	**351.7**
Model b	5.9	2.7	3.7	362.1
Model c	5.6	2.7	3.7	360.6
Model d	**4.5**	**3.1**	3.7	355.0
Selection + shelterwood				
Model a	3.7	1.9	2.3	485.5
Model b	3.6	1.9	2.3	485.8
Model c	3.6	1.9	2.3	490.0
Model d*	**3.5**	**2.0**	2.3	**481.7**

Note: Bold type highlights the smallest RMSE values. PRED. = predicted, OBS. = observed. *The best model according to the AIC.

Table 2
Number, height and age of Scots pine seedlings established after cuttings under different cutting and site preparation treatments, calculated as stand-level means.

	n	N	Empty plots, %	Condition good, %	Seedlings ha^{-1}	Height, cm	Age, years
Small gap	81	3	36	90	1971 ± 758	9.4 ± 0.7	1.1 ± 0.1
NT	27	3	67	100	537 ± 306	11.2 ± 1.1	1 ± 0
PS	27	3	19	91	1556 ± 475	9.8 ± 1.6	1.1 ± 0.1
TP	27	3	22	86	3407 ± 1696	8.3 ± 0.5	1.2 ± 0.1
Selection	72	1 + 3*	54	88	1417 ± 278	8.9 ± 2.0	1.2 ± 0.1
NT	72	1 + 3*	54	88	1417 ± 278	8.9 ± 2.0	1.2 ± 0.1
Shelterwood	54	2	39	91	1204 ± 314	7.7 ± 1.1	1.1 ± 0
NT	18	2	78	75	389 ± 236	9.1 ± 4.9	1.1 ± 0.1
PS	18	2	17	93	1139 ± 511	7.5 ± 2.2	1 ± 0
TP	18	2	22	93	1417 ± 196	8.2 ± 0.8	1.1 ± 0.1

Note: n = number of seedling plots, N = number of stands, NT = no site preparation, PS = patch scarification, TP = track preparation. Neither the minimum distance between the seedlings nor their minimum height was considered. *In addition to the actual selection cutting stand, the edges of the small gaps were treated using selection cutting.

Table 4
Models and parameter estimates for the number of Scots pine seedlings established after small gap cuttings.

Variable	Estimate	Standard error	Chi/z-value	p-value
Model a: R^2 (marginal model) = 0.510, R^2 (conditional model) = 0.724, AIC = 351.7				
Fixed effects				
Intercept	–148.7	44.88	–3.313	< 0.01
l_p95	145.6	44.81	3.248	< 0.01
ndvi_min	4.008	1.828	2.193	0.03
rgb1_min	0.02167	0.009	2.345	0.02
cir2_var	0.003034	0.001	3.269	< 0.01
Distance from forest edge, m	0.03045	0.0241	1.260	0.208
Site preparation (reference unprepared)	—	—	—	< 0.01
– Patch scarification	1.410	0.432	3.267	< 0.01
– Track preparation	1.529	0.420	3.641	< 0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.470			
Theta	2.6			
Model b: R^2 (marginal model) = 0.378, R^2 (conditional model) = 0.621, AIC = 362.1				
Fixed effects				
Intercept	2.47116	1.614	1.531	0.126
ABA-estimated mean diameter, cm	–0.19385	0.098	–1.987	0.047
Distance from forest edge, m	0.04369	0.022	1.975	0.048
Site preparation (reference unprepared)	—	—	—	< 0.01
– Patch scarification	1.22150	0.417	2.929	< 0.01
– Track preparation	2.07737	0.425	4.893	< 0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.543			
Theta	1.4			
Model c: R^2 (marginal model) = 0.387, R^2 (conditional model) = 0.626, AIC = 360.6				
Fixed effects				
Intercept	2.11660	1.236	1.713	0.087
Height of deciduous trees, m	–0.31511	0.134	–2.359	0.018
Distance from forest edge, m	0.045367	0.022	2.075	0.038
Site preparation (reference unprepared)	—	—	—	< 0.01
– Patch scarification	1.17793	0.417	2.824	< 0.01
– Track preparation	2.02846	0.412	4.920	< 0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.527			
Theta	1.4			
Model d: R^2 (marginal model) = 0.387, R^2 (conditional model) = 0.549, AIC = 355.0				
Fixed effects				
Intercept	–0.642920	0.415	–1.550	0.121
Coverage of lichen, %	0.753284	0.201	3.747	< 0.01
Coverage of exposed humus, %	0.017049	0.007	2.355	0.019
Distance from forest edge, m	0.041383	0.022	1.921	0.055
Site preparation (reference unprepared)	—	—	—	< 0.01
– Patch scarification	1.045976	0.414	2.529	0.011
– Track preparation	1.391824	0.420	3.315	< 0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.323			
Theta	1.4			

Note: l_p95 = 95% percentile of last echo density, ndvi_min = minimum NDVI value, rgb1_min = minimum value of red band and cir2_var = variance of red band.

Table 5
Models and parameter estimates for the number of Scots pine seedlings established after selection and shelterwood cuttings.

Variable	Estimate	Standard error	Chi/z-value	p-value
Model a: R^2 (marginal model) = 0.098, R^2 (conditional model) = 0.286, AIC = 485.5				
Fixed effects				
Intercept	–2.2151	0.916	–2.419	0.016
f_p30	3.1699	1.040	3.047	< 0.01
Site preparation (reference unprepared)	—	—	—	0.119
– Patch scarification	0.5315	0.339	1.567	0.117
– Track preparation	0.5654	0.337	1.679	0.093
Random effects, dispersal parameter				
Seedling plot, variance	0.500			
Theta	0.5			
Model b: R^2 (marginal model) = 0.089, R^2 (conditional model) = 0.268, AIC = 485.8				
Fixed effects				
Intercept	–1.54257	0.685	–2.253	0.024
ABA-estimated mean height, m	0.11524	0.035	3.317	< 0.01
Site preparation (reference unprepared)	—	—	—	< 0.01
– Patch scarification	0.56048	0.336	1.666	0.096
– Track preparation	1.03476	0.358	2.892	< 0.01
Random effects, dispersal parameter				
Seedling plot, variance	0.465			
Theta	0.5			
Model c: R^2 (marginal model) = 0.067, R^2 (conditional model) = 0.067, AIC = 490.0				
Fixed effects				
Intercept	1.179360	0.298	3.959	< 0.01
Height of deciduous seedlings, cm	–0.008164	0.004	–2.233	0.026
Site preparation (reference unprepared)	—	—	—	0.474
– Patch scarification	0.271888	0.330	0.823	0.411
– Track preparation	0.380398	0.324	1.175	0.240
Random effects, dispersal parameter				
Seedling plot, variance	0.000			
Theta	0.4			
Model d: R^2 (marginal model) = 0.155, R^2 (conditional model) = 0.292, AIC = 481.7				
Fixed effects				
Intercept	2.082452	0.449	4.641	< 0.01
Coverage of mosses, %	–0.013778	0.005	–2.728	0.006
Coverage of bilberry, %	–0.021967	0.010	–2.245	0.025
Stoniness (Reference category 0–30 cm)	—	—	—	0.038
– 30–60 cm	–0.481822	0.307	–1.569	0.117
– > 60 cm	–0.957193	0.429	–2.231	0.026
Site preparation (reference unprepared)	—	—	—	0.905
– Patch scarification	0.078128	0.365	0.214	0.830
– Track preparation	0.146359	0.334	0.438	0.661
Random effects, dispersal parameter				
Seedling plot, variance	0.3508			
Theta	0.6			

Note: f_p30 = 30% of the first echo density.

corresponding open-source ABA stand attribute estimates. This was done only to model for small gap stands since **Model c** for selection and shelterwood cutting stands did not include field-observed stand attributes. The modelled number of seedlings was 2 plot^{-1}, with the RMSE value being slightly higher at 6.4 seedlings plot^{-1}. The non-parametric Mann–Whitney–*U* test revealed that there was a statistically significant difference between the plot-wise predictions when the field-measured stand attributes were replaced with the ABA estimates.

For the small gap cutting stands, the modelled number of seedlings with **Model d** was 460 ha^{-1} if no site preparation was used, 1310 ha^{-1} with patch scarification and 1850 ha^{-1} with track preparation (Fig. 3a and Table 4). Distance from the forest edge increased the modelled number of seedlings for the small gap cutting stands. At 10 m inside the forest edge, the number of Scots pine seedlings was 521 ha^{-1}, whereas

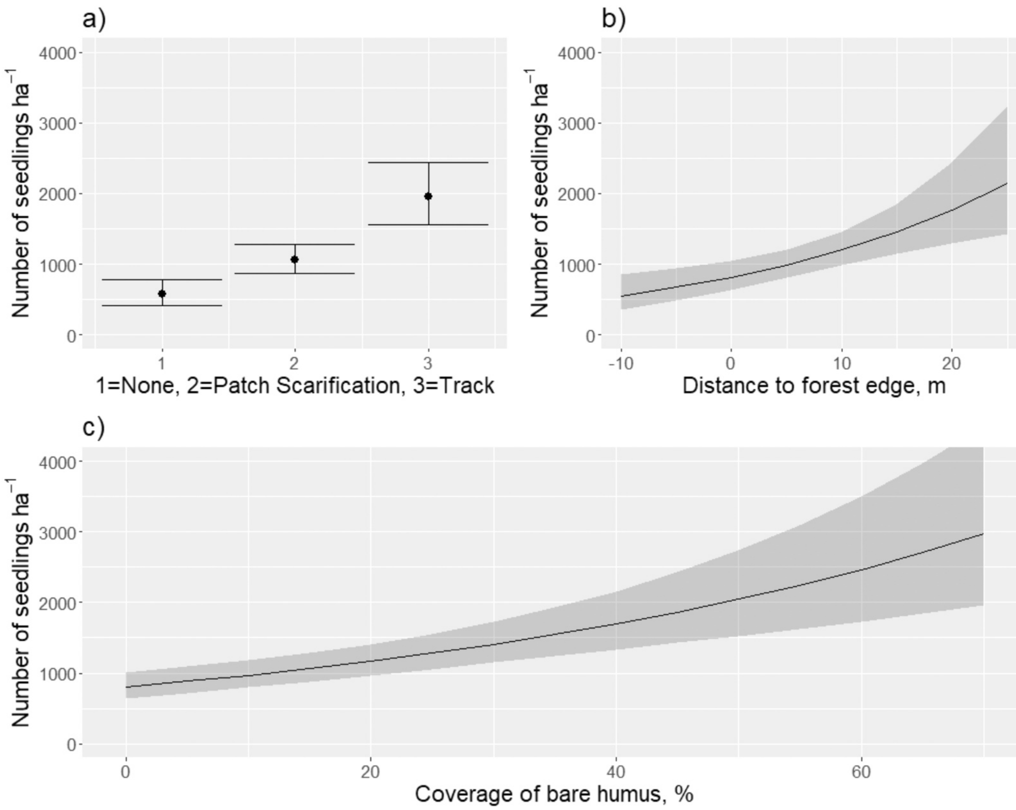

Fig. 3. Modelled number of Scots pine seedlings established after small gap cuttings, with point estimates and 1 SD confidence intervals for **Model d** (lowest RMSE value): a) site preparation (1 = unprepared, 2 = patch scarification, 3 = track preparation); b) distance from forest edge; c) bare humus cover.

10 m outside the forest edge, there were 1192 seedlings ha^{-1} (Fig. 3b). The modelled number of seedlings also increased with an increase in the coverage of bare humus. With 5% bare humus coverage, the number of seedlings was 882 ha^{-1}, whereas with 55%, it was 2069 ha^{-1} (Fig. 3c). This also increased with increasing lichen coverage, no matter how small the coverage (Table 4).

Smaller NDVI (–1–1) values accounted for the lower number of seedlings based on the second-best model, **Model a** (Fig. A.1a). When the minimum NDVI value in a seedling plot was 0, the modelled number of seedlings was 860 ha^{-1}. Similarly, smaller values of the red band in the RGB image (rgb1_min) and a smaller variance in the red band in the CIR image (cir2_var) accounted for smaller numbers of seedlings. When the red band (0–255) minimum was 30, the number of seedlings was 400 ha^{-1}, and where there was a 500-unit variance in the red band, it was 1645 ha^{-1} (Figs. A.1b and A.1c). The LiDAR feature l_p95 (95% percentile of the last echo density) accounted for a larger number of seedlings. With an l_p95 value of 1.0, the number of seedlings was 735 ha^{-1}, but with a value of 1.007, it was 2000 ha^{-1} (Fig. A.1d).

The modelled number of Scots pine seedlings with **Model d** for the selection and shelterwood cutting stands was 787 ha^{-1} with no site preparation, 851 ha^{-1} with patch scarification and 911 ha^{-1} with track preparation (Table 5 and Fig. 4a). The modelled number of seedlings with a stoniness level of 1 (0–30 cm) was 1115 ha^{-1} and with a stoniness level of 3 (>60 cm) was 428 seedlings ha^{-1} (Fig. 4b). An increasing coverage of mosses on bilberry accounted for the lower number of seedlings. With 20% moss coverage of the ground surface, the modelled number of seedlings was 1582 ha^{-1} and with a corresponding coverage of bilberry, it was 759 ha^{-1} (Figs. 4c and 4d).

4. Discussion

4.1. *Observed number of Scots pine seedlings in different cutting methods*

In our study, the observed average number of living Scots pine seedlings (age >1 year) was in a range of 389–3407 ha^{-1} 3–4 years after small gap, selection and shelterwood cuttings and different site preparation treatments. However, in our study, no minimum height or distance from other seedlings was required in the seedling counting. According to the Finnish Forest Act, there is not given any minimum requirement for the number of naturally regenerated seedlings in CCF, but in RF the regeneration result should be sufficient in 20 years in this region.

The lowest seedling numbers were found in the shelterwood cutting stands with no site preparation and the highest in the small gap cutting stands with track preparation. Likewise, the highest seedling numbers (1417 ha^{-1}) in the shelterwood cutting stands were found with track preparation. Previous studies have also reported lower seedling densities with no site preparation (Kyrö et al., 2022; Rautio et al., 2023). In stands with no site preparation, seed germination and the establishment of seedlings are affected by drought and competition. Also in our study, the number of seedlings was lowest with no site preparation. Number of seedlings was also lower in the selection and shelterwood cutting stands compared to the small gap cutting stands since larger trees shade the light-demanding Scots pine seedlings and cause above- and below-ground competition (Béland et al., 2000; Kellomäki, 2022b; Lehto, 1969; Nygren, 2003). Recently Peltola et al. (2025) reported an average of 2140 Scots pine seedlings ha^{-1} (h > 10 cm, no minimum requirement for distance from other seedlings), 12–34 years after selection cuttings in northern Finland without site preparation. Rautio et al. (2023) reported in Northern Finland 10 000 Scots pine seedlings (h ≥ 10 cm, no minimum requirement for distance from other seedlings) ha^{-1} 11 years after cuttings, with site preparation, and 2000–4000

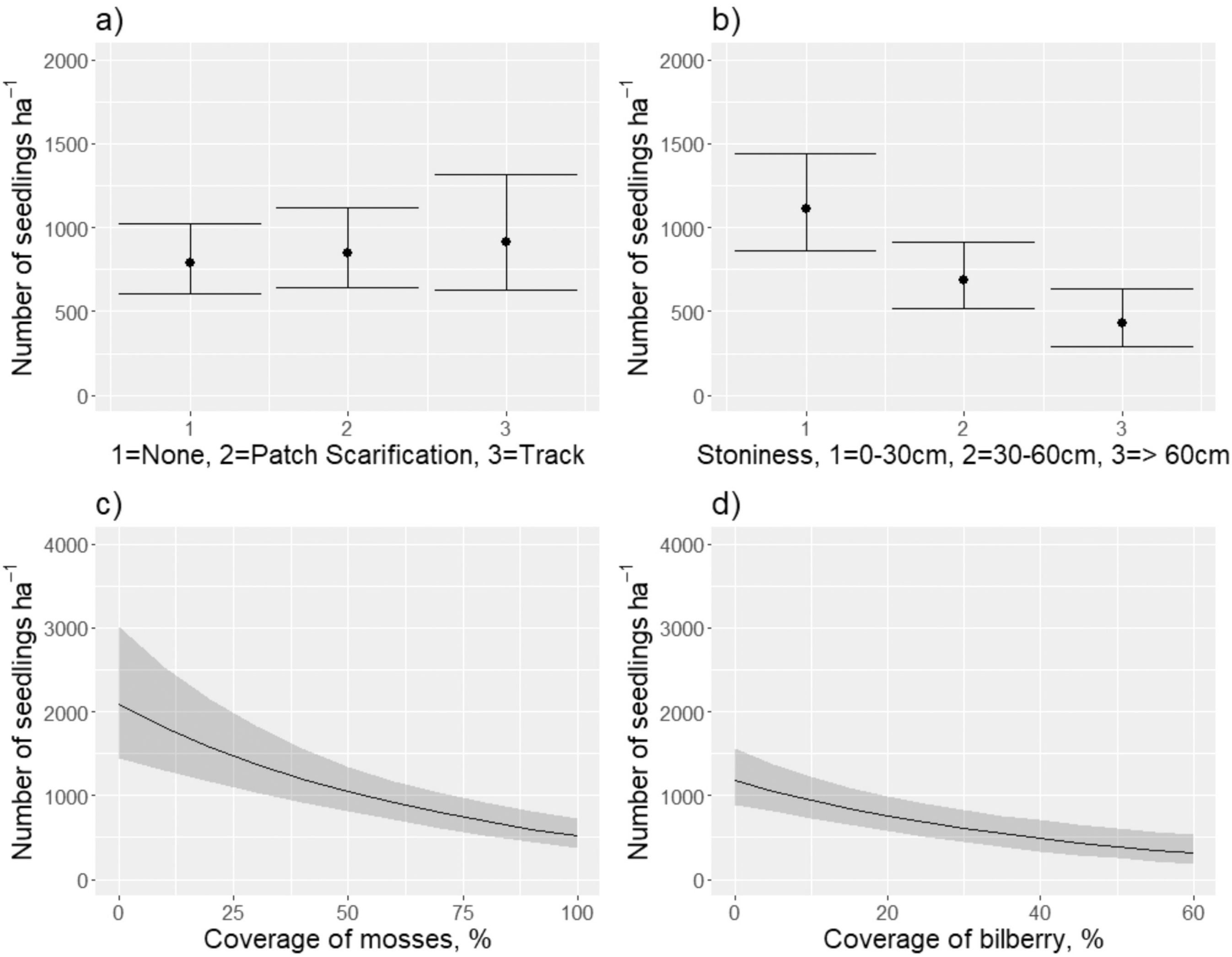

Fig. 4. Modelled number of Scots pine seedlings established after selection and shelterwood cuttings, with point estimates and 1 SD confidence intervals for **Model d** (lowest AIC and RMSE values)**:** a) site preparation (1 = unprepared, 2 = patch scarification, 3 = track preparation); b) stoniness, defined here as the soil depth to the first stone (1 = 0–30 cm, 2 = 30–60 cm, 3 = >60 cm); c) moss cover; d) bilberry cover.

seedlings ha^{-1} with no site preparation.

4.2. Effects of distance from forest edge on number of Scots pine seedlings in small gaps

In our study, the modelled number of seedlings increased slightly in small gaps with increasing distance from forest edge. At the edge of the gap, seedling establishment is hindered by both below-ground competition and shading from mature trees (Axelsson et al., 2014; Hallikainen et al., 2019). In our study, at the edge of the small gap, the number of pine seedlings was 796 ha^{-1}, and at 25 m from the edge, it was 1420 ha^{-1}. By contrast, Hallikainen et al. (2019) observed a decrease in pine seedling numbers with increasing distance from the forest edge, their numbers ranging from about 20 000 ha^{-1} at the edge of the gap to 14 000 ha^{-1} 40 m from the edge of the gap, 5 years after cutting. However, the contradictory results observed between these studies may be explained by differences in gap sizes, their shapes and orientations. In the study by Hallikainen et al. (2019), the maximum gap diameter was 80 m, whereas in our study it was about 50 m. Also, the forest edge around small gaps providing seed material was in a study of Hallikainen et al. (2019) denser. Its basal area was in a range of 13–21.5 m^2 ha^{-1} with 516–871 trees ha^{-1} while in our study it was only 6.4–7.1 m^2 ha^{-1} with 180–193 trees ha^{-1}. They also had patch scarification in all the gaps while in our study one third of the gaps were without site preparation. Whereas Axelsson et al. (2014) found that the number of Scots pine seedlings established was low at up to 10 m from the forest edge, which our findings support.

4.3. Modelled number of seedlings in different cutting methods

For the small gap cutting stands, **Model a**, which included remotely sensed features, surprisingly produced the lowest AIC (Akaike information criterion) value. The openness of the small gap cutting stands enhanced the performance of **Model a** compared to its performance in the selection and shelterwood cutting stands. Laser pulses reach the forest floor in open areas, unlike in densely forested areas, where most laser pulses are absorbed or reflected in the upper canopy layers. Similarly, aerial images of the selection and shelterwood cutting stands could only partially capture the forest floor due to canopy coverage (see Fig. 2 for clarification). Therefore, in small gap cutting stands, **Model a** best described the seedling-level properties because there was no interfering canopy cover. Aerial image features especially were strong explanatory variables in the small gap cutting stands. Smaller minimum NDVI values (ndvi_min) predicted lower numbers of seedlings, with NDVI values closer to –1 revealing bare soils or less green vegetation (Weier and Herring, 2000). At the same time, a greater variance in red wavelengths (cir2_var) accounted for a larger number of seedlings. Chlorophyll absorbs mostly red wavelengths and abundant vegetation reflects less red wavelengths (Virtanen et al., 2022). The large variance in red wavelengths may indicate a mosaic of bare soils and vegetation (i.e. plots with site preparation and seedlings). Smaller red wavelength values (rgb1_min) indicated lower numbers of seedlings. Smaller reflectance at red wavelengths can indicate larger competing vegetation and thus a lower number of seedlings. Also, the density feature, l_p95, which describes the density of the last echoes (95% percentile of the last echo density), was a statistically significant variable in **Model a** in the small gap cutting stands. Higher l_p95 values mean more echoes reached the ground, potentially indicating sparser vegetation and thus less competition for the seedlings and a higher number of seedlings.

The increasing coverage of bare humus in **Model d** seemed to increase the average number of seedlings in the small gap cutting stands. Bare humus offers a good seedbed and growing surface for pine seeds and seedlings by decreasing the competition between other species in the ground- and field-layer. Miettinen et al. (2022) reported that the establishment of sowed pine seedlings was better in bare humus compared to moss coverage. In our study, increasing lichen coverage was associated with an increasing number of seedlings, although overall its coverage was small and the variation large.

The best model, based on the AIC and RMSE (root mean square error) values, for the selection and shelterwood cutting stands was **Model d**, which used substrate coverages as predictors. In the selection and shelterwood cutting stands, the abundant mosses and bilberry coverages indicated lower numbers of seedlings. This finding seems logical because mosses and bilberry hinder the germination of seeds and the growth of seedlings (Jäderlund et al., 1997; Downey et al., 2018). Hallikainen et al. (2019) found that, with no moss coverage, 27 000 seedlings ha^{-1} were established, and with moss coverage of 80%, there were 10 000 seedlings ha^{-1} 5 years after cuttings. In our study, with no moss coverage, the modelled number of seedlings was 2500 ha^{-1} and with moss coverage of 80%, it was 700 ha^{-1}. Both study sites were located on mineral soils, but Hallikainen et al.'s (2019) study area was located over 200 km northwest of ours. Mosses have been found to be unfavourable as seed beds or growing surface because they tend to be too dry and compete with seeds and seedlings (Kyrö et al., 2022). In our stands, which were treated with cuttings quite recently, variation in the overstory density was low. This may explain why ground surface coverages were more significant as predictors. Greater stoniness indicated lower seedling numbers, especially when comparing the stoniest ground surface to the least stony ones, which may be due to stony soils being unfavourable for seed germination and seedling growth.

4.4. *Potential of remote sensing for predicting stand attributes and seedling numbers*

The ABA (area-based approach) stand (overstory) attribute estimates seemed fairly accurate. When the field-measured stand attributes were replaced with stand attribute estimates from remote sensing, and vice versa, the RMSE values of our models were similar to those of other predictive models. This indicates that the predicted ABA stand attribute estimates were successful. It also suggests that, for future predictions, field-measured stand attributes could be replaced with ABA stand attribute estimates to give relatively reliable results, and that stand attribute estimates provide accurate information on the stands surrounding seedling plots. The relative RMSE values were on the same scale within the models a-d. Therefore, predictions on seedling numbers could possibly be drawn solely from remote-sensing-based models, reducing the need for field inventories. However, it should be noted that remote-sensing-based models, and especially those employing LiDAR features, describe more the conditions favourable for seedling germination rather than the individual seedlings, which were, on average, about 9 cm tall. It should also be noted that constructed models are not entirely comparable. Remote-sensing-based models can be considered as applied models because remote sensing data is widely available, allowing these models to be used wherever such data exists. By contrast, field-inventory-based models may be more investigative because they focus on analysing the effects of different variables.

Also, for small gap cutting stands and selection and shelterwood cutting stands, **Models b** and **c** did not perform as well because the variation in the stand attributes was very low. Contrastingly, the remote sensing variables used in **Model a** in the small gap cutting stands were more varied and the model was able to predict the seedling numbers well. Similarly, **Model a** better accounted for the homogeneous overstory level than the forest floor in the selection and shelterwood cutting stands, and therefore did not predict the seedling number as well in the small gaps.

4.5. *Conclusions*

The number of naturally established Scots pine seedlings (age >1 year) was on average low 3–4 years after small gap, selection and shelterwood cuttings, considering that no minimum height or distance from other seedlings was required in the seedling counting. However, the success of natural regeneration may improve in the coming years, based on previous studies with typically longer time spans since their cuttings. This could be confirmed in field inventories in the future. We found that small gap cuttings combined with site preparation, and especially track preparation, seem to enhance the natural regeneration of Scots pine. Also, the prediction of seedling numbers using remote sensing, was successful. Based on this, some estimates of forest regeneration could be predicted in the future solely through remote sensing, and field-measured stand attributes could be replaced by ABA stand attribute estimates in the models.

CRediT authorship contribution statement

Antti Kilpeläinen: Writing – review & editing. **Heli Peltola:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition. **Petra Peltola:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pasi Rautio:** Writing – review & editing, Supervision, Methodology. **Ville Hallikainen:** Writing – review & editing, Methodology. **Laura Pikkarainen:** Writing – review & editing, Writing – original draft. **Lauri Korhonen:** Writing – review & editing, Data curation, Conceptualization. **Fan Yang:** Data curation. **Viivi Pääkkönen:** Data curation. **Aaron Petty:** Writing – review & editing, Data curation. **Matti Maltamo:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Tuukka Poutiainen:** Investigation, Data curation.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the writing of this study, the authors occasionally used Microsoft Copilot and openAI ChatGPT to improve the grammar, spelling and readability, and review and edit the content as needed. The authors take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Metsähallitus Forestry Ltd. is acknowledged for establishing the study area used, in co-operation with the UNITE Flagship and the

Natural Resources Institute of Finland. The data analyses and writing of this article were supported by the UNITE flagship [grant numbers 357906, 359172] through funding obtained from the Research Council of Finland. The text has been improved using the proofreading services offered by Cambridge Proofreading LLC.

Appendix

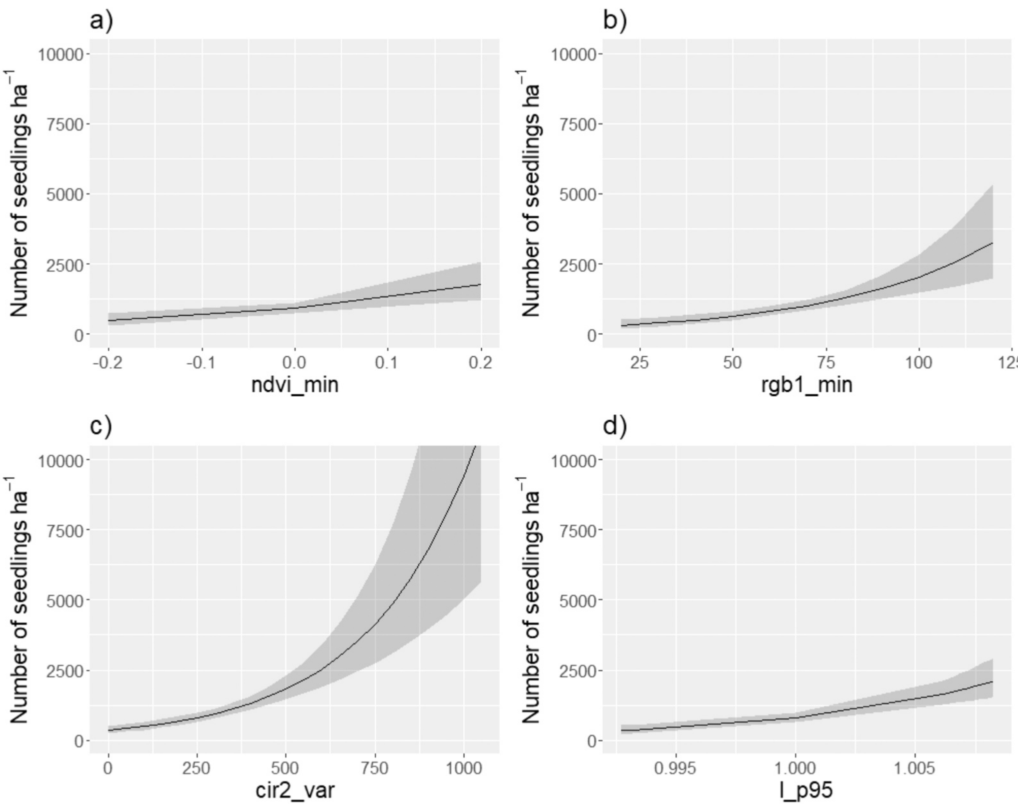

Fig. A.1. Modelled number of Scots pine seedlings established after small gap cuttings, with point estimates and 1 SD confidence intervals for **Model a** (lowest AIC): a) ndvi_min (minimum NDVI value); b) rgb1_min (minimum red band value); c) cir2_var (red band variance); d) l_p95 (95% percentile of the last echo density)

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123929.

Data availability

Data will be made available on request.

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