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Effects of overstory tree density, site preparation, and ground vegetation on natural Scots pine seedling emergence and survival in northern boreal pine forests

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Abstract: Natural regeneration is a commonly used forest regeneration method in northern Finland. It is not known, however, what would be the optimal overstory density and ground vegetation composition for seedling emergence and survival, and if site preparation is needed to accompany overstory density manipulation. We studied the effects of overstory density (unthinned control and thinning to 50, 150, and 250 trees·ha^{-1}) and ground vegetation removal (mechanical site preparation with disc trenching) on the number of naturally germinated pine seedlings and survival of individual seedlings over a period of 8 to 11 years. Bare mineral soil was a superior seedbed compared to intact vegetation cover, even though the mortality rate was high on mineral soil. Greater cover of lingonberry, crowberry, and slash had a negative effect on seedling number. Seedling mortality was initially high (60% died during the first 2 years) but decreased throughout the first 5 years. The survival rate of seedlings located in the mineral soil of the upper part of the disc trencher track was twice as high as that of seedlings located in the lower part of the track. High coverage of hair mosses (*Polytrichum* spp.) was associated with poorer seedling survival. An overstory density of 50–150 trees·ha^{-1} with site preparation seems to be an efficient treatment to promote regeneration under these circumstances.

Key words: natural regeneration, survival analysis, thinning, field-layer vegetation, ground-layer vegetation.

Résumé : La régénération naturelle est un mode de régénération forestière couramment utilisé dans le nord de la Finlande. Cependant, on ne connaît pas la densité optimale du couvert dominant ni la composition de la végétation au sol qui favoriseraient l’émergence et la survie des semis. De même, on ne sait pas si une préparation de terrain est nécessaire pour accompagner la manipulation de la densité du couvert dominant. Nous avons étudié les effets de la densité du couvert dominant (témoin non éclairci et éclaircies laissant 50, 150 ou 250 arbres·ha^{-1}) et de l’enlèvement de la végétation au sol (préparation mécanique de terrain avec un scarificateur à disques) sur le nombre de semis de pin naturellement régénérés et sur la survie de semis individuels pendant une période de 8 à 11 ans. Le sol minéral exposé était un meilleur lit de germination qu’un couvert intact de végétation, même si le taux de mortalité était aussi élevé sur le sol minéral. Un couvert plus important d’airelle rouge, de camarine noire et de déchets de coupe a eu un effet négatif sur le nombre de semis. La mortalité des semis était initialement élevée (60 % des semis sont morts au cours des deux premières années), mais elle a diminué au cours des cinq premières années. Le taux de survie des semis situés dans le sol minéral de la partie supérieure des sillons du scarificateur à disques était deux fois plus élevé que celui des semis situés dans la partie inférieure des sillons. Une couverture élevée de mousses du genre *Polytrichum* était associée à une plus faible survie des semis. Une densité du couvert dominant de 50 à 150 arbres·ha^{-1} jumelée à une préparation de terrain semble être une méthode efficace pour favoriser la régénération dans ces conditions. [Traduit par la Rédaction]

Mots-clés : régénération naturelle, analyse de la survie, éclaircie, strate de la végétation herbacée, strate de la végétation muscinale.

Introduction

As described in the Finnish best practices for forest management (Äijälä et al. 2019), the standard method in natural regeneration of Scots pine (*Pinus sylvestris* L.) stands in Nordic boreal forests is seed-tree cutting, where 50–100 stems·ha^{-1} are retained on the regeneration area and removed swiftly after completed regeneration. Soil is usually prepared by patch scarification or disc trenching for enhanced seed germination and survival, except for the most xeric sites.

Shelterwood cutting is similar to seed-tree cutting, except that the number of retained trees is higher, up to 250·ha^{-1} (Lehto 1970). Shelterwood cutting has been occasionally applied to Scots pine in northern areas with variable motivations like greater amenity value. Moreover, because of the dawning interest in continuous cover forestry (CCF) in the Nordic countries, regeneration

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Table 1. Pretreatment stand parameters in the three experimental sites and weather statistics (mean and min–max temperature and precipitation) during the study period.

Parameter	Savukoski	Simo	Paltamo
D_g (cm)	24.4	19.8	22.5
H_g (m)	17.9	14.8	27.2
H_{dom} (m)	19.1	16.6	21.7
N (no.·ha^{-1})	341	857	656
G (m^2·ha^{-1})	14.0	18.7	22.4
V (m^3·ha^{-1})	121	137	210
Pine (%)	99.1	99.3	90.7
Temperature (°C)			
Summertime	11.6 (10.2–13.3)	14.3 (12.7–15.6)	14.1 (12.6–15.5)
Wintertime	−11.1 (−15.3 – −7.5)	−9 (−14.5 – −5.1)	−9.1 (−14.7 – −5.1)
Precipitation (mm)			
Summertime	211 (143–275)	195 (41–263)	274 (204–353)
Wintertime	91 (56–131)	146 (73–213)	147 (98–201)

Note: D_g, quadratic mean diameter; H_g, basal area weighted mean height; H_{dom}, dominant height (mean height of the 100 thickest trees·ha^{-1}); N, number of stems·ha^{-1}; G, basal area; V, stem volume; Pine, proportion of pine of V.

regimes with higher overstory densities with substantially longer retention periods have been suggested for Scots pine forests to alleviate the adverse consequences to amenity values and biodiversity associated with clearcutting (Valkonen 2017; Äijälä et al. 2019).

The effects of overstory density and site preparation on regeneration have been addressed in many studies. The role of mature overstory trees on regeneration seems to be contradictory. Their greater density implies greater seed yield (Beland et al. 2000). Furthermore, arger number of germinates may appear under a denser overstory cover (Valtanen 1984). On the other hand, trees in the overstory can decrease seed germination (Aaltonen 1919; Lehto 1970; Moreno-Fernández et al. 2018). In addition, slower seedling growth in the proximity of mature trees has been observed in several studies (Aaltonen 1919; Lehto 1970; Valkonen et al. 2002; Hallikainen et al. 2007; Stuiver et al. 2016). Optimal overstory density after the seedling emergence stage is one of the key management issues and points of interest for research regarding shelterwood cutting and related methods. However, surprisingly little is known about actual seedling turnover rates (recruitment and mortality) in the course of time.

In addition to competition caused by shelterwood trees, emerging seedlings are subjected to competition by understory vegetation. Lehto (1956) estimated that the effect of ground vegetation on pine seedling emergence and survival is larger than the effect of the main canopy trees. However, the ground vegetation can have a contradictory role in regeneration. Some ground vegetation species can have positive and some negative effects on seedling regeneration. For example, Brown and Mikola (1974) showed that lichens have negative allelopathic effects on mycorrhizas and tree seedlings (pine, spruce, and birch), but later Steijlen et al. (1995) and Kytöviita and Stark (2009) found that the effects of lichens may be neutral or even beneficial for pine seedlings. Furthermore, in a study by Hyppönen et al. (2013), the presence of crowberry (*Empetrum nigrum* subsp. *hermaphroditum*), feather moss (*Pleurozium shreberi*), or *Dicranum* moss species increased the mortality of pine seedlings, but pine seedling emergence and survival increased, and seedling growth decreased with the cover of heather (*Calluna vulgaris* L.). In contrast, heather was found to be harmful to pine regeneration in a study by Nilsson and Zackrisson (1992). According to Hertz (1934), on the other hand, shrubs do not disturb pine regeneration.

The purpose of mechanical site preparation on submesic to xeric Scots pine sites in the northern areas is to establish patches of bared mineral or organic soil free from competing vegetation and with improved ecophysiological characteristics as seedbeds. Better regeneration results following site preparation have been found in several studies (e.g., Karlsson and Örlander 2000; Hyppönen et al. 2005, 2013; Karlsson et al. 2002; Rosenvald et al. 2020).

The purpose of this study was to focus on the processes of tree seedling recruitment and survival to find out how seedling turnover develops in time, and how it is affected by the density of an overstory of mature trees and by the ground- and field-layer vegetation, and by raw humus. The study is based on a large-scale field experiment covering northern Finland, where we (*i*) manipulated the overstory density, (*ii*) removed the ground- and field-layer vegetation and raw humus to uncover the mineral soil with mechanical site preparation, (*iii*) monitored the recruitment and mortality of individual seedlings and ground vegetation for 8–11 years, and (*iv*) applied Cox proportional hazard model to the seedling monitoring data to reveal favorable and risky microhabitats for seedling survival.

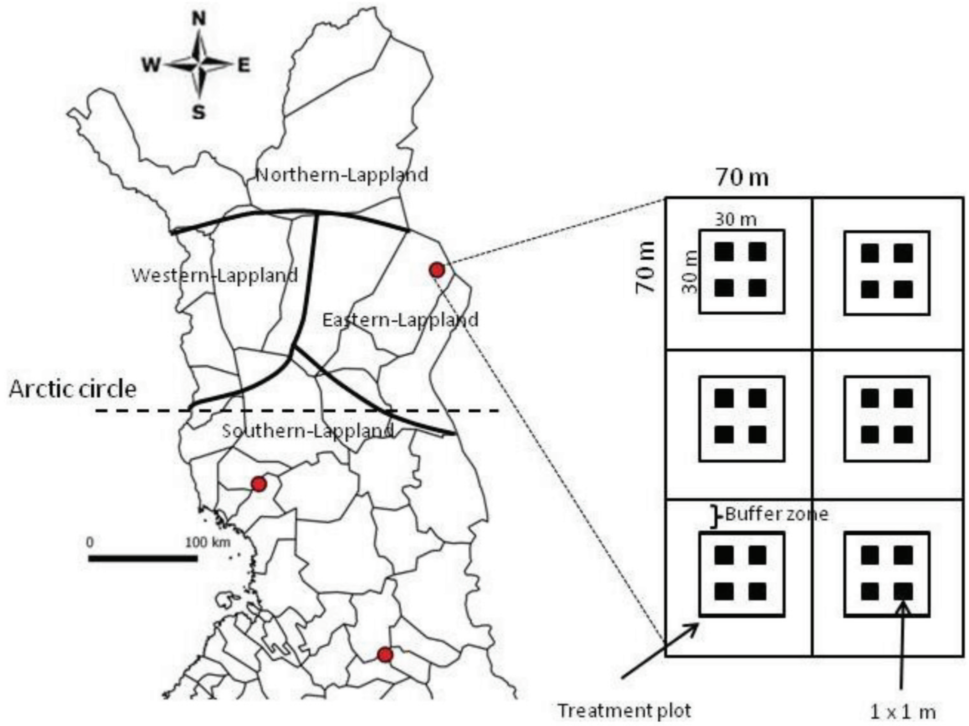
Materials and methods

Location, experimental setup, and data sampling

The climate in the study area is influenced by the North Atlantic Ocean and the Gulf Stream. The area is defined by cold winters (in winter the mean temperature remains below 0 °C) and relatively warm summers (in summer the mean daily temperature is consistently above 10 °C), with July being the warmest month of the year. During the observation periods, the mean summer temperature varied in the experimental sites (Fig. 1) between 11.6 and 14.1 °C and the winter temperature between −9 and 11.1 °C (Table 1). The amount of summertime precipitation varied between 195 and 274 mm and wintertime precipitation (mostly snow) between 91 and 147 mm. Snow cover generally lasts from early November to early May in the south and from late October to late May in the north (the long-term average (1981–2010)). The temperature sum (sum of daily values by which the average temperature exceeds a threshold of 5 °C during the growing season) varies from 1000 °C days in south to <800 °C days in north (Finnish Meteorological Institute 2020).

The experiment was established at three locations in northern Finland in 2004–2007 (Fig. 1). The locations were positioned in climatically different areas at least 200 km apart. Within the locations, the experimental site was selected among homogenous forest stands that were large enough for the experiment and close to the age of final cutting based on the forest stand data of Metsähallitus (State Forest Enterprise that administers and manages state owned forests in Finland). More specifically, chosen stands had to fulfil these criteria: area >3 ha with homogeneous site and

Fig. 1. Location of the three experimental sites (red dots) with one stand in each. Each study stand had six 70 m × 70 m treatment plots and for each of these one of the six treatments was randomly allocated. In each treatment plot seedlings were individually monitored in four 1 m × 1 m square seedling monitoring subplots. [Colour online.]



National Land Survey of Finland 2016. Transverse Mercator. GCS Euref Fin. www.avoindata.fi/data/fi/dataset/maastotietokanta

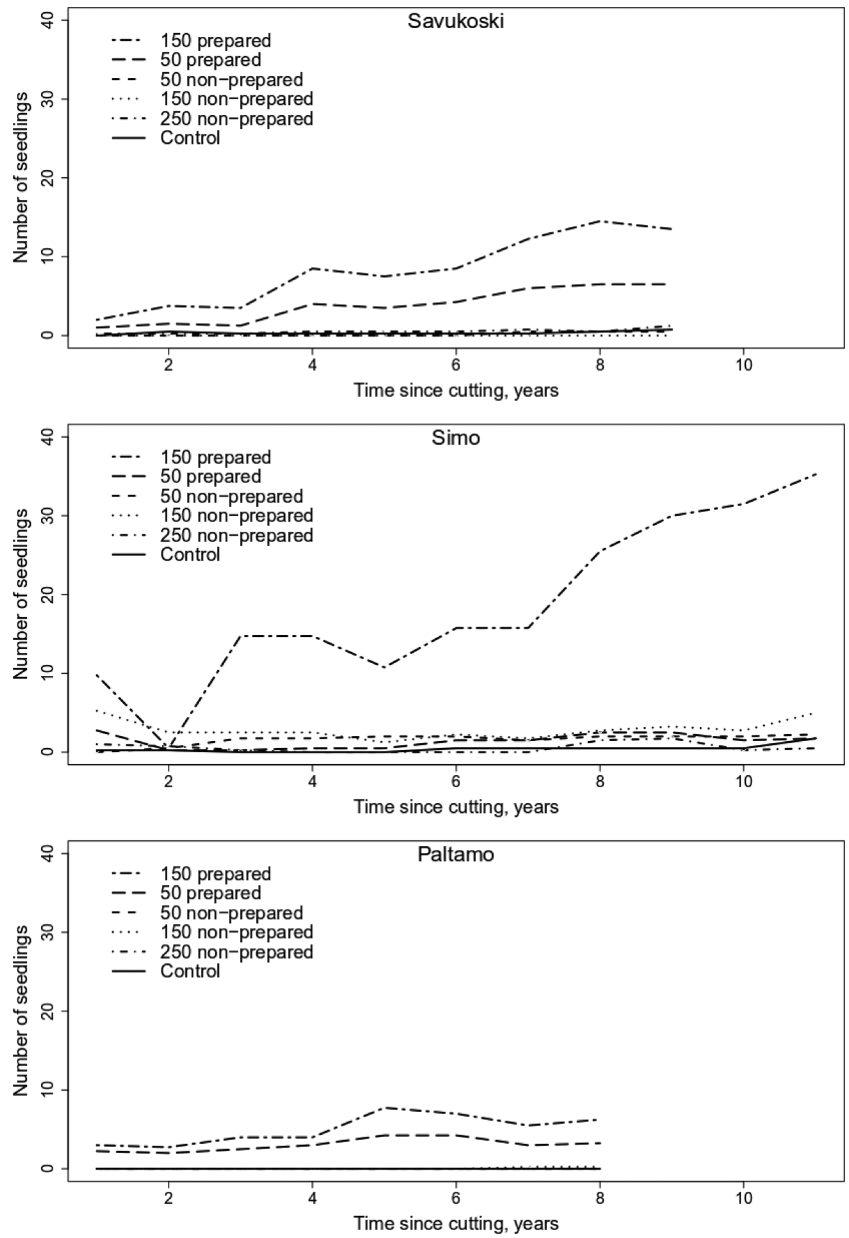
stand characteristics, site type subxeric forest (*Empetrum–Myrtillus* or *Empetrum–Vaccinium* Type (Hotanen et al. 2018)), age above or close to the stage of final cutting (80–150 years), main tree species Scots pine (*Pinus sylvestris* L.), and density >250 stems·ha^{-1}. Stand parameters prior to the treatments are shown in Table 1.

In each experimental site, six treatment plots were established. The size of the treatment plot was 70 m × 70 m. Each treatment gross-plot contained a 30 m × 30 m net-plot at its center that was surrounded by a 20 m buffer zone towards all directions (Fig. 1). The gross plots, including the 20 m buffer zones, were treated similarly as the net-plots; the term treatment plot (including both gross- and net-plots) is used hereinafter. Treatment plots were either thinned to densities of 50, 150, or 250 stems of overstory trees per hectare or left unthinned (control). Stem densities in the control plots were 330 stems·ha^{-1} in the northernmost site (in Savukoski, Lat. 67°50′13.68″N, Long. 29°16′3.55″E), 640 stems·ha^{-1} at the central location (Simo, 66°1′8.52″N, 25°22′5.52″E), and 720 stems·ha^{-1} in the southernmost site (Paltamo, 64°33′48.95″N, 27°58′13.03″E). In addition to the four basic density plots, two plots with mechanical site preparation combined with the two lowest density variants were added. Site preparation (disc trenching) was thus conducted on the two treatment plots with the lowest stem number 50 or 150·ha^{-1} during the following summer after thinning. Site preparation was not considered technically feasible either on the densest treatment (250 stems·ha^{-1}) or on the control plots. A substantial proportion of the tree stems and root collars would probably been damaged if the large machinery had been operated in the limited space between the trees. Above six treatments were placed randomly on the experimental plots.

On each of the six treatment plots, four 1 m ×1 m subplots were systematically placed to monitor individually seedling emergence and survival (Fig. 1). These seedling monitoring subplots were carefully marked with plastic sticks in the corners and in the middle of the squares. All existing tree seedlings were removed on these subplots prior to the initial measurements.

On treatment plots where site preparation was applied, the seedling monitoring subplots were slightly moved to represent the trench with bared mineral soil with 30%–50% of the plot area, the rest remaining in the untouched ground. The square 1 m × 1 m seedling monitoring subplots were inventoried annually. Each emerged seedling of all species was individually monitored throughout the period. The first inventory was made in 2005 in Simo, 2007 in Savukoski, and 2008 in Paltamo, and the last inventory in 2015, i.e., the maximum age of a seedling that was emerged during the monitoring period could be 11 years in Simo, 9 years in Savukoski, and 8 years in Paltamo (Fig. 2). The shortest monitoring period in the study stands was 8 years, and we compared the number of the naturally regenerated seedlings 8 years after the cuttings in all study stands. The surrounding environment (microsite) and surrounding ground-layer vegetation of each emerged seedling within 3 cm from the seedling was determined when a seedling was first recorded. The microsite surrounding each seedling was categorized as mineral soil furrow (the bottom part of disc trencher track), mineral soil ridge (the elevated part of disc trencher track), humus with and without vegetation, and the border zone of mineral soil and humus. The ground-layer vegetation in the close proximity (3 cm diameter) of each seedling was classified as peat mosses (*Sphagnum* spp.), hair mosses (*Polytrichum* spp.), other mosses than the previous, lichens (mainly reindeer lichens *Cladonia* spp.), and no ground-layer vegetation. Ground-layer species and species groups were recorded also on the 1 m^2 subplots. The cover of field-layer species or groups of species that was measured on the 1 m^2 subplots were lingonberry (*Vaccinium vitis-idaea* L.), bilberry (*Vaccinium myrtillus*

Fig. 2. The number of seedlings on a subplot (1 m^2) in the three experimental sites (Savukoski, Simo, and Paltamo) during 1–11 years after cuttings. Numbers in the legend refer to the stem densities·ha^{-1} used in the treatments. Prepared versus non-prepared denote that the treatment plot was either disc trenched or left intact.



L.), northern bilberry (*V. uliginosum* L.), heather (*Calluna vulgaris* L.), crowberry (*Empetrum nigrum* L. and *E. nigrum* subsp. *hermaphroditum*), northern Labrador tea (*Ledum palustre* L.), other vascular plants, and no field-layer vegetation. In addition to the proportions of the species or groups of species listed above also the proportion of exposed mineral soil was determined on the 1 m^2 subplots to be used as the independent variables in the seedling density model (see below). The distance from a seedling to its nearest neighboring seedling was also recorded.

Statistical analysis

The study design consisted of seventy-two 1 m^2 regeneration sample plots (later referred to as subplots). The lowest level in the data hierarchy consisted of individual seedlings on the subplots. Part of the subplots remained empty (no seedlings emerged) during the monitoring period, and the total number of plots with recruited seedlings that could be used in the survival analysis was 33, in 14 treatment plots in the three stands.

The four-level hierarchy consisting of experimental site, treatment plot, subplot, and seedling was used in the *survival model*. The response variable in the survival model was seedling's lifetime (measured in years). The tested independent categorical variables in the survival model in addition to seedling's age were (*i*) treatment, (*ii*) seedling microsite (site where a seedling had recruited, measured from 3 cm radius from seedling's base), and (*iii*) dominating ground-layer vegetation. The categories of treatment were (*i*) 50, (*ii*) 150, and (*iii*) 250 overstory trees·ha^{-1} without site preparation, (*iv*) 50 and (*v*) 150 trees·ha^{-1} with site preparation, and (*vi*) control without thinning or site preparation. In addition to the microsite and vegetation variables, the distance to the nearest neighboring seedling was tested as a continuous covariate in the statistical model.

The seedling *density model* had three level hierarchy: a subplot within a treatment plot within an experimental site. The same treatment factor with six levels as in survival model was applied also in the seedling density model. In addition, the cover of field- and ground-layer species, as well as the exposed cover of mineral soil (proportion of cover of exposed mineral soil by mechanical site preparation or otherwise) and cover of slash (i.e., cutting residues) were measured on the 1 m^2 subplots and tested in the seedling density model. The response variable in the seedling density model was the seedling count i.e., the number of seedlings in the 1 m^2 subplot measured after 8 years since the beginning of the experiment. The 8-year period was used to have equally long period for each of the three locations. The cover of vegetation and mineral soil were measured from the subplots in the end of the observation period. Thus, they might have been changed from the beginning of the period. Though in the north, i.e., in the whole study area, the change in vegetation during the 10-year period is very small and concerns mainly the site prepared plots where the bare humus of mineral soils is gradually occupied by mainly *Polytrichum* species.

In the models for seedling density, zero-inflated negative binomial distribution was used in the modelling of the over-dispersed distribution of the number of pine seedlings on the 1 m^2 square plots. Zero-inflation was taken into account by estimating a zero-inflated coefficient in the model. The model was estimated using R package glmmADMB, using function glmmadmb (Fournier et al. 2012). The function estimates the zero inflated coefficient with its standard error. NB2 parametrization was used in the estimation of over-dispersion. The NB2 parametrization estimates variance (var) using the following formula:

$$\text{var} = \mu(1 + \mu/k) \qquad (1)$$

where μ denotes an expected mean value and k denotes a clumping parameter (size parameter). When k approaches ∞, the distribution approaches the Poisson distribution. On the other hand, when $k = 1$, distribution is called geometric distribution. Because the pine seedlings usually emerge naturally in groups, the aggregation with rather high over-dispersion (small k values) can be expected. The function glmmadmb estimates the over-dispersion and the zero-inflated parameter.

The predictions with their 95% confidence intervals by the explanatory variables were computed using R-package effects (Fox 2003; Fox and Weisberg 2019). There was a slight bias in the mean and median values when comparing observed and predicted distributions of the number of seedlings. However, the predicted minimum and maximum values fitted well with the observed values.

Cox mixed effects survival model was used for modelling of the right-censored survival data of the pine seedlings. The development of Cox frailty or mixed effects models have been intensive during the last two decades (Therneau and Grambsch 2000; Therneau 2020). However, the hierarchical structure in the data must be considered for the appropriate standard errors and tests. The clustered structure in the data also raises a question whether the proportional hazard should be computed based on the base hazards within the clusters, or on the average baseline hazard (marginal model). If there are two hierarchy levels in the data, R-function coxph (in R-package survival, Therneau and Grambsch 2000) with cluster- or frailty-options could be appropriate. We used R mixed effects Cox package coxme (Therneau 2020), because the survival data for the seedlings consisted of four hierarchical levels. Similar survival curves to coxph models are not yet available with the coxme package. However, the coxme model enables the computation of predicted proportional risk estimates for the seedlings. The distributions of risk computed for each of the seedlings can be illustrated using e.g., box plots, in addition to the predicted point estimates for the categories of categorical variables using R package lsmeans (Lenth 2016). Because the least-squares means (lsmeans) estimates for the categories were available, seedling's age was treated as a categorical variable. Thus, the coefficients for the ages and the lsmeans estimates could be interpreted, and the change in the risk of death could be computed.

A general form of the Cox mixed effects model can be described as

$$\lambda(t) = \lambda_0(t)e^{\mathbf{X}\beta + \mathbf{Zb}} \qquad (2)$$

$$\boldsymbol{b} \sim \mathrm{G}(0, \boldsymbol{\Sigma}(\theta)) \qquad (3)$$

where λ_0 is an unspecified baseline hazard function. $\mathbf{X}$ and $\mathbf{Z}$ are the design matrices for the fixed and random effects, respectively. $\boldsymbol{\beta}$ denotes the vector of fixed effects coefficients and $\boldsymbol{b}$ is the vector of random effects coefficients. The distribution of random effects is modelled as Gaussian (G), with mean zero and a variance matrix $\boldsymbol{\Sigma}$, which in turn depends on a vector of parameters, $\boldsymbol{\theta}$.

The computation of the fixed values of model parameters (β, b), and defined usual Cox partial likelihood (PL) is described in Therneau and Grambsch (2000) and Therneau (2020).

In Cox marginal models, the proportional hazard for an individual is computed based on the unspecified average hazard function, whereas in the mixed or frailty models the proportional risk is computed based on the conditional base hazards, depending on the cluster structure (hierarchy) in the data. The proportional hazard values (predictions) can be interpreted as interval scale values, not as the probabilities. Thus, the proportional hazard value 0.2 can be interpreted as two times higher risk to die compared to value 0.1. Proportional hazard or risk could be derived by taking the exponent of the coefficients in the model.

The modelled dying risk by a seedling's age followed well the observed proportion of dead seedlings in the age classes. On the other side, the proportional risk levels in the categories of the position and ground-layer vegetation followed only moderately the observed proportions. This could be expected because the ages in the categories of the position and ground layer varied. The model predictions were computed at the mean values (levels) of the other predictions.

Results

Eight years after treatment, the number of seedlings on the plots without site preparation did not increase during the observation period (Fig. 2) but did increase in Savukoski and Paltamo throughout the observation period on the site prepared plots, especially when combined with an overstory density of 150 trees·ha^{-1}. The highest seedling recruitment was found in Simo and the treatment of 150 trees·ha^{-1} with site preparation (Fig. 2).

The computation based on the raw data revealed that about 80% of the seedling observations were on microsites free of vegetation, that is on mineral soil, humus, or the mix of humus and mineral soil formed in the site preparation. According to the seedling density model, the predicted number of seedlings on the plots without site preparation varied between 1000 and 4400 seedlings·ha^{-1}, whereas on the site-prepared plots, the average number varied between about 32 000 and 92 000 seedlings·ha^{-1} (Fig. 3). Significant explanatory variables in the seedling density model were treatment (including site preparation), and the cover of lingonberry, crowberry, and slash. Greater cover of lingonberry, crowberry, and slash had a negative effect on the number of seedlings (Table 2; Fig. 3).

The age of the seedling, seedling's microsite, and ground-layer vegetation clearly affected the seedling survival probability (Table 3; Figs. 4*a*–4*c*). The lifetime of the monitored seedlings varied a lot. About 60% of the dead seedlings died during the first 2 years. The risk of death decreased strongly during the first 5 years (Fig. 4*a*). After that, the risk to die remained low.

If a seedling had emerged on the mineral soil or on bare humus, the estimated average risk to die was about 2.7 times higher

Fig. 3. The predictions for the number of seedlings per hectare, with 95% confidence intervals for the explanatory variables of the seedling density model. In panel *a*, 50 NS, 150 NS, and 250 NS are trees·ha^{-1} in non-treated plots (no site preparation), 50 S and 150 S are trees·ha^{-1} in the plots with site preparation (disc trenching). In panels *b–d*, the predictions are for number of seedlings·ha^{-1} in relation to the cover (%) of lingonberry, crowberry, and slash.

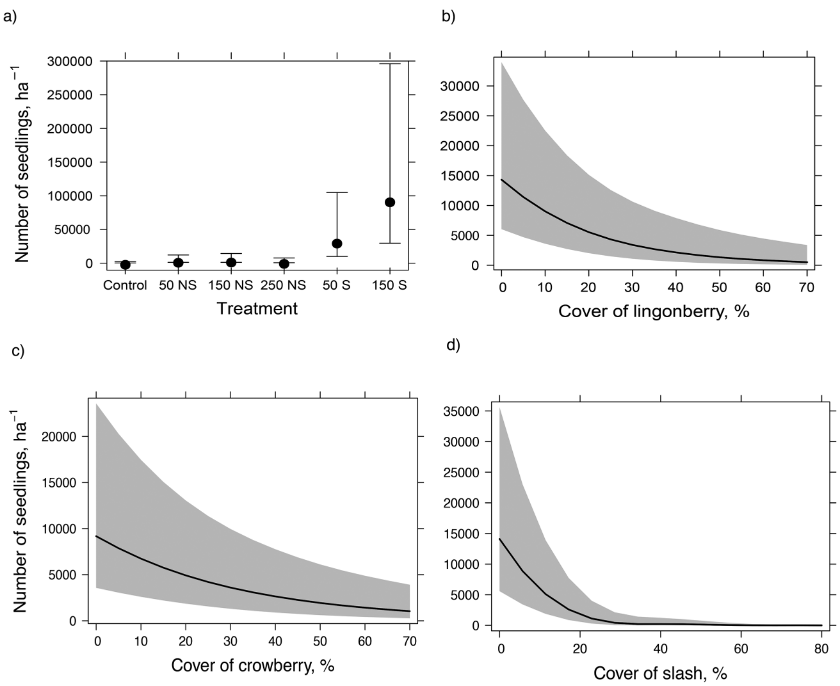


Table 2. Parameter estimates and tests for the seedling density model.

Variable	Estimate	Std. error	z or χ^2 value	p
Fixed parameters				
Intercept	−0.653	0.768	−0.85	0.392
Treatment (reference category = Control)			5.174 (df = 5)	<0.001
50 trees·ha^{-1}, no soil treatment	1.360	0.756	1.80	0.072
150 trees·ha^{-1}, no soil treatment	1.445	0.730	1.98	0.048
250 trees·ha^{-1}, no soil treatment	0.850	0.759	1.12	0.263
50 trees·ha^{-1}, soil treatment	3.445	0.690	4.99	<0.001
150 trees·ha^{-1}, soil treatment	4.505	0.669	6.74	<0.001
Lingonberry cover (%)	−0.048	0.023	−2.06	0.040
Crowberry cover (%)	−0.031	0.014	−2.27	0.023
Slash cover (%)	−0.104	0.038	−2.76	0.006
Random parameters				
Experimental site	0.562			
Treatment plot nested within experimental site	3.772×10^{-9}			
Dispersion parameter	1.660	0.648		
Zero-inflation coefficient	1×10^{-6}	4.465×10^{-6}		

Note: The independent variable is the number of seedlings on a square plot (1 m^2). Std. error denotes the standard error of the estimate, z values are for the tests of parameter estimates, and χ^2 values are for the deviance tests (for the significance of the categorical variables).

compared to vegetation-covered microsites (category "Humus, vege" in Fig. 4*b*). The vegetation cover was associated with very large variation depending on the type of vegetation (Fig. 4*c*). Bare humus was a much riskier environment for seedlings than the mixture of mineral soil and humus or a mineral soil ridge. Mineral soil ridge was about two times better substrate for the survival compared to mineral soil furrow (Fig. 4*b*).

Moss species other than hair mosses (e.g., *Polytrichum juniperinum* and *P. piliferum*) and *Sphagnum* spp. offered a rather safe environment for the seedlings; the average dying risk being less than half of that for lichen-covered microsites that were the riskiest of the vegetation types. On the other hand, other mosses were about twice as safe environment compared to *Polytrichum* species (Fig. 4*c*).

There was a large variation in the probability of mortality when the seedlings regenerated on the lichen bed. On the average the dying risk on the lichen bed was about 14 times higher compared to the safest seed bed, a ground layer covered with *Sphagnum* species, and more than double compared to the seedlings growing on the mineral soil (category "No g-layer" in Fig. 4*c*).

Discussion

Our study focused on how tree seedling turnover from seed germination to seedling mortality develops in time, and how it

Table 3. Parameter estimates and tests for the mixed-effects proportional risk (hazard) Cox model.

Variable	Coefficient	Exp. of coefficient	Standard error of coefficient	z and (or) χ^2 value of deviance table	p
Fixed parameters					
Age (reference category = 1 year)				78.275 (df = 7)	<0.001
2 years	−0.499	0.607	0.161	−3.10	0.002
3 years	−1.202	0.300	0.226	−5.32	<0.001
4 years	−1.400	0.247	0.279	−5.02	<0.001
5 years	−2.170	0.115	0.427	−5.08	<0.001
6 years	−3.528	0.030	1.010	−3.49	<0.001
7 years	−3.147	0.043	1.013	−3.11	0.002
8 years	−23.035	0.991×10^{-10}	2.749×10^{4}	0.00	<0.001
Seedling microsite (reference category = Mineral soil, furrow)				10.189 (df = 4)	0.038
Mineral soil, ridge	−0.630	0.533	3.224	−1.95	0.051
Mineral soil / humus (mixed)	−0.690	0.501	0.383	−1.81	0.071
Humus, covered with vegetation	−0.939	0.391	0.375	−2.51	0.012
Bare humus (no vegetation)	0.015	1.015	0.559	0.003	0.980
Ground-layer vegetation (reference category = No ground layer vegetation)				15.021	0.005
Polytrichum spp. (%)	0.477	1.611	0.184	2.59	0.010
Sphagnum spp. (%)	−1.981	0.138	1.042	−1.90	0.057
Other moss (%)	−0.229	0.795	0.250	−0.92	0.360
Lichen (mostly *Cladina* spp.) (%)	0.730	2.075	0.493	1.48	0.140
Random parameters	Std. dev.	Variance			
Experimental site	0.020	3.989×10^{-4}			
Treatment plot nested within experimental site	0.733	0.538			
Subplot nested within treatment plot nested within experimental site	1.019	1.039			

Note: The deviance tests for the fixed effects were based on the ANOVA-function in R package car (Fox and Weisberg 2019). The number of censored observations (seedling died during the observation period) was 235, total number of observations was 1243.

was affected by microsite properties and overstory density. The study combined detailed monitoring of the regeneration process with attempts to involve new analysis methods that could better fit the multidimensional, hierarchical experimental setup to produce tangible results for research and practice.

The number of seedlings developed in time through the antagonistic processes of seedling emergence and mortality which were controlled by a variety of factors. On average, the number of seedlings tended to increase throughout the study period, which shows that new seedlings emerged even over 10 years after the thinning (and site preparation). For an annual seedling cohort, mortality was momentously largest during its first year of life, from where it constantly decreased to a minuscule fraction (about 1/24) for the eighth year.

The role of years of abundant seed crops in northern Finland has often been emphasized in silvicultural research and practice (Henttonen et al. 1986; Hilli et al. 2008). The present results with steadily increasing seedling number through the study period rather support the viewpoint that gradual and constant seedling emergence is possible on favorable seedbeds as some viable seed is produced in most years (Heikinheimo 1932, 1937) and seedling number tends to increase constantly in time (e.g., Hyppönen et al. 2005).

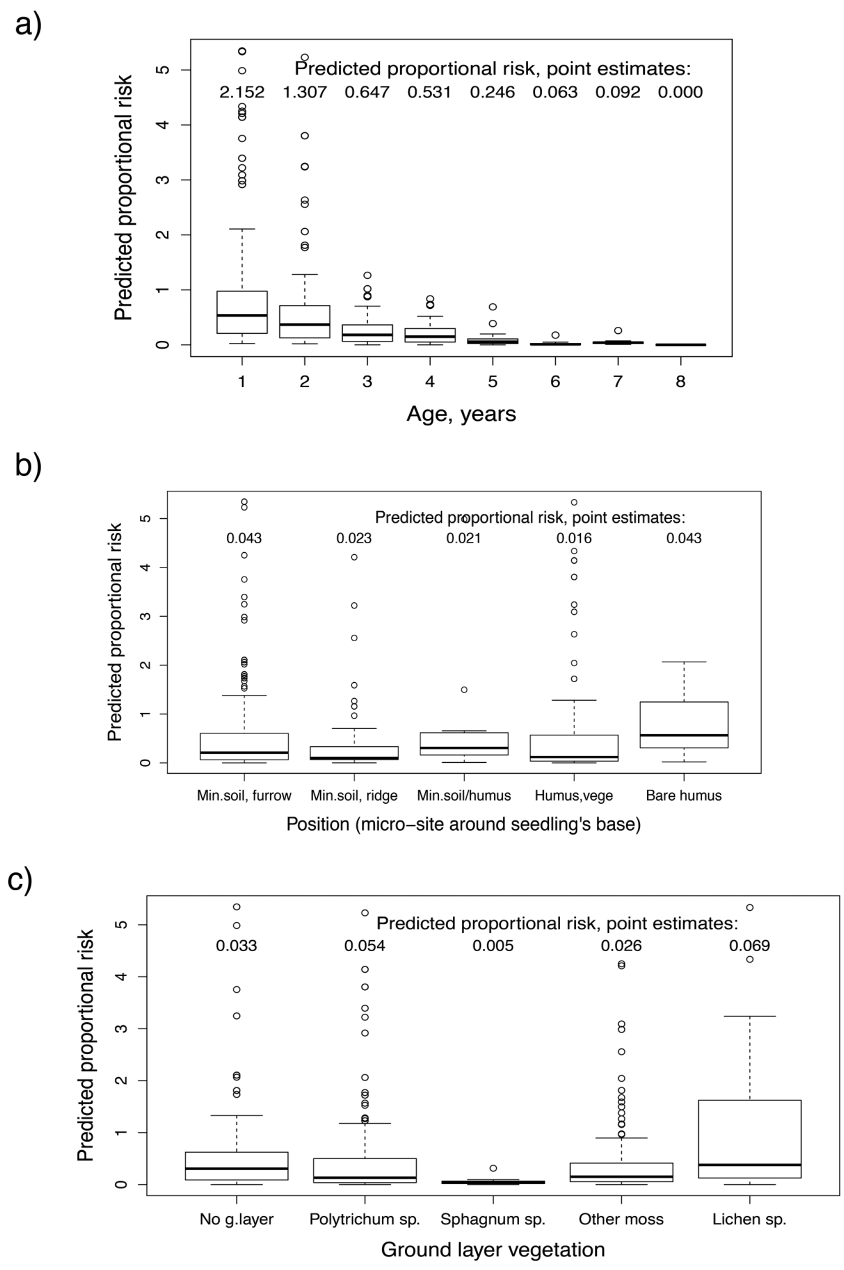
The overwhelmingly most important division in seedling emergence and survival was observed between places where the site was prepared or not prepared (i.e., whether ground- and field-layer vegetation was present or not). On non-site prepared plots, the number of seedlings remained low throughout the observation period, and mortality and recruitment canceled each other out. Both emergence and mortality were larger with site preparation, but emergence was clearly greater, and the number of seedlings increased throughout the period. Consequently, mechanical site preparation hugely increased the number of seedlings present on the plots from 1000–4400·ha^{-1} without site preparation to 32 000 – 92 000·ha^{-1} on prepared plots. This is in agreement with many earlier studies (Karlsson and Örlander 2000; Hyppönen et al. 2005, 2013; Nilsson et al. 2002; Hallikainen et al. 2019; Sikström et al. 2020). On the other hand, bare mineral soil is also associated with large temperature and moisture variations and frequent droughts (Pohtila 1977; Wennström et al. 2007; Hyppönen and Hallikainen 2011; Helenius 2012) creating a challenging environment inducing high mortality in small seedlings. That is probably the main factor behind the high mortality rate observed during the first 2 years.

The results indicated that ground vegetation cover (or its absence) affected seedling survival, but the strength and the direction of the effect varied largely between species. Any of the surveyed main ground-layer plant species was not significantly associated with seedling emergence, but of the field-layer species, lingonberry and crowberry clearly decreased seedling emergence. Wardle et al. (2008) also found that lingonberry had a negative impact on the number of pine seedlings. Crowberry has also been found to decrease seedling emergence (Nilsson and Zackrisson 1992; Zackrisson et al. 1995; Hyppönen et al. 2013). Slash tended to decrease the number of seedlings, which was in line with the findings of Hyppönen et al. (2013).

Seedling mortality was very low on *Sphagnum* mosses, while other mosses, particularly hair mosses (*Polytrichum* spp.) were associated with much greater mortality. Moss carpet is usually not a favorable substrate for seedling survival (Steijlen et al. 1995; Hyppönen et al. 2013). Mosses can compete with seedlings for light, space, and nutrients (Hörnberg et al. 1997; Zackrisson et al. 1998; Stuiver et al. 2014). Mosses in general create microhabitats that appear very dry for seedlings because evaporation is high, and precipitation will not easily reach down to the topsoil with thick moss layers (Hertz 1934; Yli-Vakkuri 1961). This is obviously not the case with *Sphagnum*, which are also an indicator of microsites with higher moisture levels.

Thinning, or shelterwood cutting, was effective in promoting pine regeneration under the given conditions. The overstory density of 150 trees·ha^{-1} with the highest seedling density had about four times as many seedlings as the non-thinned control. But on the other hand, as the overstory density of 150 trees·ha^{-1} produced

Fig. 4. Predicted proportional risks of mortality according to the fixed variables, (*a*) age, (*b*) microsite, and (*c*) ground-layer vegetation, of the mixed effects Cox proportional risk (hazard) survival model. The box and the whiskers illustrate the distributions of the predictions. Numbers above the boxes denote predicted point estimates of the risk when other predictors have been fixed to their mean values (levels). Values along *y* axis are proportional risk levels that enable comparisons between the categories. "Min. soil" denotes mineral soil, "vege" vegetation cover, "Humus, vege" humus covered with vegetation, "No g.layer" no ground-layer vegetation, and "Other moss" mosses other than *Sphagnum* or *Polytrichum* species.



slightly more seedlings compared to 50 trees·ha^{-1}, and when combined with site preparation this difference was even larger, our results did not show the negative impact of overstory density to regeneration observed in many earlier studies (e.g., Aaltonen 1919; Hagner 1962; Ackzell and Lindgren 1992). Rather our results were in line with, e.g., Valkonen et al. (2002), who observed no clear negative effects of retained trees on seedling production.

The applied experimental methodology was successful in the acquisition of detailed information on the drivers of the basic dynamic processes in natural regeneration, i.e., seedling recruitment and mortality, and some of the principal factors involved at a fine scale. Such a research approach that can yield basic information is still remarkably scarce in the area of natural forest regeneration despite a tradition of silvicultural research spanning numerous decades. This study hopefully makes a major contribution in helping to focus further research efforts in relevant contexts.

To our knowledge the present study is the first to apply statistical survival analysis to follow individual naturally regenerated pine seedlings in situ for this long period (up to 11 years). In this analysis we successfully applied Cox mixed effects survival models in the R-environment to the multilevel data. However, there are some interesting alternatives (e.g., coxph function in R) but they do not allow more than two hierarchy levels and need further development in that respect. The alternative that we applied instead (coxme) to the four-level hierarchy in our data, does not on the other hand allow the computation of predicted proportional risk point estimates and their confidence intervals, but only the estimates for single cases (seedlings). Hence, also this statistical package needs further development.

The large number of seedlings observed indicated that successful regeneration in terms of seedling density had been generally achieved on the mechanically site prepared plots, but less so without site preparation. However, the actual regeneration results need to be focused on in a further study. The size of the sample plots was designed to optimally fit the gathering of data at the individual seedling level and in their immediate vicinity, but it was far less suited for the evaluation the seedling density and distribution. The sampling intensity was too low for that purpose. The large number of empty plots was also one of the adverse features in this respect. Furthermore, silviculturally relevant regeneration results must be assessed by the number of crop seedlings, whereby the spatial and size distribution of vigorous good quality seedlings is taken into account on each plot and mirrored against target densities set by silvicultural considerations. Plot sizes of 5 or 10 m^2 have worked best for the purpose, as the common target densities of 2000–4000$\cdot$$ha^{-1}$ would represent one to four crop seedlings per plot. One of the key features to focus on would be the optimal overstory density. The thinning treatment with 150 stems$\cdot$$ha^{-1}$ seemed best in terms of seedling density in this case, but the other thinned treatments (50 and 250$\cdot$$ha^{-1}$) were not much poorer either. In optimal regimes one must also consider the competition influence of the greater overstory density on seedling growth and survival, which tends grow cumulatively greater in time (Valkonen et al. 2002).

Mechanical site preparation was not conducted in the treatment with the highest overstory density (250$\cdot$$ha^{-1}$) due to technical reasons, and the possible interaction of the two factors could not be examined. A greater degree of shading could moderate the temperature and moisture extremes of site preparation but reduce light and moisture availability through overstory competition. To disentangle these potentially contradictory effects one should test a site preparation method that is not causing damage to root and trunks in dense stands to find out if thinning is unnecessary for natural regeneration in case site preparation is carried out.

Conclusions

Seedling mortality decreased constantly from a maximum in the first year to a fraction with 8 or more years after emergence. In studies and practical forest management with natural regeneration, the assessment of the success of regeneration makes sense only after seedling mortality has stabilized sufficiently after the emergence of the main seedling cohort. Under these circumstances (infertile northern pine stands) the earliest point would hence be around 5 years. Results clearly show that mechanical site preparation is a key component for successful natural regeneration under these circumstances. The bare mineral soil exposed by disc trenching is a superior seedbed compared to intact vegetation cover, and its somewhat greater mortality rate is unimportant in this respect. Microsites covered with mosses are associated with poorer seedling survival and regeneration potential, except for *Sphagnum* species that are indicators of microsites with high moisture. An overstory density of 50–150 trees$\cdot$$ha^{-1}$ with site preparation seems to work best for pine regeneration under these circumstances, but further studies are required to verify and improve the estimate for practical relevance.

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Author contributions

All authors contributed substantially to the manuscript.

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