Natural Regeneration in a Multi-Layered *Pinus sylvestris-Picea abies* Forest after Target Diameter Harvest and Soil Scarification

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Abstract: Forest management in Sweden can be characterized by even-aged silviculture heavily relying on three established harvest regimes: clearcutting, the seed-tree method, and the shelterwood system. Less intense, small-scale retention harvest systems such as single tree and group selection harvest are rarely used. In addition, natural regeneration dynamics without enrichment planting have barely been studied. Consequently, this study examined natural regeneration establishment in a multi-layered *Pinus sylvestris-Picea abies* forest stand in southwest Sweden after target diameter harvesting and soil scarification. The creation of forest canopy gaps had a positive effect on total seedling density five years after harvest, mainly due to a significantly higher number of *Betula pendula* individuals. Seedling density of more desirable tree species suitable for continuous cover forestry such as *Fagus sylvatica*, *Quercus petraea* and *Picea abies* also increased substantially in gaps when compared to pre-harvest conditions or the unharvested plots. In contrast, soil scarification did not increase the number of seedlings of desired tree species due to a significant decrease in *Picea abies* abundance. Soil moisture and gap size significantly improved *Betula pendula* seedling establishment while a larger number of *Quercus petraea* seedlings were observed in *Vaccinium myrtillus* patches. We conclude that canopy gaps are beneficial under the encountered stand conditions to initiate forest regeneration, and that soil scarification without the timely occurrence of a mast year of desired tree species is not effective in the type of forest studied.

1. Introduction

Managed forests in northern Europe are dominated by even-aged, single-species stands with trees forming a single canopy layer [1,2]. In order to promote more heterogeneous stand structures and to obtain more resilient, multifunctional forest ecosystems, management approaches are required that complement the prevailing systems of even-aged silviculture [3]. Some alternative management approaches such as single-tree selection in boreal Norway spruce stands and diameter limited cutting with enrichment planting in mature coniferous stands have been examined in northern and central Sweden [4–7] while the options to apply natural regeneration in multi-layered stands have rarely been studied in southern Sweden. Potential stand development trajectories including regeneration and ingrowth dynamics thus are difficult to predict. The effect of silvicultural treatments on natural regeneration has to be estimated from shelterwood trials in Sweden [8–11] and selection cuttings in

multi-layered stands in Norway and Finland [12–14]. On poor sites in northern Sweden or Finland, patch cuttings can complement alternative approaches to continuous cover forestry in mature pine stands [15–17]. In northern Germany, Tremer [18] estimated the ingrowth of new trees in mature pine stands that have been managed by target diameter harvest for the last three decades. Drössler [19] provided an overview of seedling densities, height growth and ingrowth rates reported in these studies. In addition, there are other relevant management strategies to promote more heterogeneous stand structures in central Europe and Denmark. Duncker et al. [20] summarizes them as close-to-nature forest management. They use natural forest development as an important reference for forest management and involve the transformation to more irregular forest structures mainly by target diameter harvest or group selection cutting in mature stands [21–24].

The most common managed forest types with multi-layered stand structures in southern Sweden are mature Scots pine (*Pinus sylvestris* L.) stands with advanced undergrowth of Norway spruce (*Picea abies* (L.) H. Karst.) and uneven-aged Norway spruce stands [25,26]. Mixed Scots pine-Norway spruce stands are the most frequent type of multi-layered forest in south Sweden [27], with fewer single-layered than multi-layered forest stands. Population density in southern Sweden is substantially higher compared with other regions in northern Europe, potentially affecting forest management of municipality woodlands and forested recreational areas. In fact, driven by public debate on common forestry practices, interest in the aforementioned mixed and structurally heterogeneous forest types as well as their sustainable management has increased in recent years. However, managing more heterogeneous stands is complex and alternative approaches within the concepts of continuous cover forestry or disturbance-based forest management [2,28] are thus needed to address the more diversified objectives of Swedish forest land owners [29,30]. These less intense, small-scale management approaches should be able to sustainably provide a variety of forest goods and services apart from timber, such as recreation and biodiversity values. In general, alternative methods to clearfelling and the seed-tree method are increasing in importance in the region.

By using an experiment laid out in a multi-layered Scots pine-Norway spruce forest with varying small-scale stand structure, we aimed to analyze the effects of soil scarification and partial, low intensity tree removal on natural regeneration patterns. The two main research questions were (i) How do varying site and forest conditions (e.g., stand structure, ground vegetation) influence seedling occurrence and density? and (ii) How do the implemented management measures affect regeneration characteristics?

2. Materials and Methods

2.1. Site and Initial Stand Characteristics

The study area is located 20 km east of Halmstad (56°42′02″ N, 13°7′56″ E, 115–140 m ASL) on a productive site in the northern temperate forest zone [31]. Mean annual precipitation is 1050 mm, mean annual air temperature is 7 °C and the number of days with a mean air temperature >5 °C (growing season) is 215. The soil type is a podzol developed over sandy moraine. The ground cover vegetation is mainly characterized by *Vaccinium myrtillus* and *Deschampsia flexuosa*. Site index (dominant height base age 100) is 32 m for Norway spruce and 28 m for Scots pine. Stand establishment was initiated by seeding Scots pine in 1912 to replace the *Calluna* spp. heathland while other tree species established naturally over time. Today, the stand is dominated by mature Scots pine trees in the overstory and Norway spruce trees of all size classes. Other species admixed in the under- and mid-story include sessile oak (*Quercus petraea*), silver birch (*Betula pendula*), European beech (*Fagus sylvatica*), rowan (*Sorbus aucuparia*), and aspen (*Populus tremula*).

The study stand was thinned several times before the establishment of the experiment. A detailed description of the site, the study stand, the forest structure, and the implemented experimental design can be found in [32].

2.2. Experimental Design and Data Collection

In spring 2009, the total study area of 19 ha was divided into three blocks, and four treatment areas of approximately 1 ha were randomly applied within each block. Treatments consisted of (1) control (CON) without any tree removal; (2) target diameter harvesting (TDH) where trees with a diameter at 1.3 m breast height (DBH) equal to or larger than listed in Table 1 were removed; (3) TDH complemented by soil scarification in canopy openings (TDH+); and (4) target diameter harvesting with slightly altered target diameters compared to TDH (TDH2) (Table 1). Target diameters applied in TDH and TDH+ were chosen according to economic criteria based on timber quality and average timber prices per tree species and product (e.g., sawlogs, pulpwood) published annually by the south Swedish forest owner association "Södra" for 2006. Modified target diameters in TDH2 were chosen in order to promote broadleaf tree species and to cut more Norway spruce trees. Harvesting took place in spring 2009, and soil scarification was carried out in autumn 2010 by disc-trenching (double row scarifier Bracke T21 mounted on a forwarder) resulting in approximately 0.5 m wide rows of exposed mineral soil ca. 2 m apart from each other. About one third of the area within each canopy gap was affected by this measure. The driver was instructed to scarify all canopy openings but to exclude areas with advanced natural regeneration. Detailed post-harvest stand characteristics for each treatment are provided in Table 2.

Table 1. Treatment-specific target diameter thresholds (DBH, cm) applied per tree species and timber quality class. Quality class 1 included trees with branches thinner than 6 cm while quality class 2 comprised low quality trees with thicker branches, spike-knots or forks.

Tree Species	TDH/TDH+		TDH2
	Class 1	Class 2	Class 1&2
Scots pine	40	30	40
Norway spruce	36	26	26
Silver birch	30	20	30
Sessile oak	60	30	60
European beech	50	30	50

Table 2. Mean and standard errors of post-harvest stand characteristics for the four experimental treatments.

Treatment	CON	TDH	TDH+	TDH2
N before harvest (trees·ha^{-1})	1151 ± 79	1045 ± 56	1082 ± 98	849 ± 69
N (trees·ha^{-1})	1151 ± 79	815 ± 64	905 ± 113	698 ± 81
BA (m^2·ha^{-1})	36 ± 3.6	19 ± 2.0	23 ± 2.4	20 ± 1.9
BA pine (%)	41	35	44	50
BA spruce (%)	44	52	40	28
BA oak (%)	7	18	12	14
BA birch (%)	7	1	3	5
BA others (%)	1	15	1	3
Vol (m^3·ha^{-1})	325 ± 27	160 ± 19	193 ± 17	164 ± 19
Removal (m^3·ha^{-1})	0	133 ± 24	155 ± 28	130 ± 24

Species and DBH of all living overstory trees (DBH ≥ 5 cm) were recorded on four systematically distributed circular overstory measurement plots (radius = 10 m) per treatment area before the harvest took place in 2009 and five years after the harvest in 2014. In addition, all canopy openings (termed gaps hereafter) were measured for the entire study area in 2009 and 2014. Gaps were defined as stand areas larger than 20 m^2 without overstory tree canopy cover in these pre- and post-harvest gap surveys. Gap size was calculated as the area of an ellipse using measured gap length and width while the size of non-ellipsoid gaps was estimated by several ellipse shapes or using polygons along the crowns

of edge trees [33]. If a gap was divided by different treatments, each ellipsoid canopy opening was assigned to the dominant treatment.

Aiming at a total sampling area of 1000 m^2 to describe the initial regeneration of the stand, seedlings (height $\geq$ 20 cm and < 200 cm) and saplings (height $\geq$ 200 cm and DBH < 5 cm) were sampled in four systematically distributed circular permanent regeneration subplots (5 m^2) within each overstory measurement plot in summer 2009 (Figure 1a). The tree regeneration was resampled at the same locations but on larger subplots (10 m^2) five years later in summer 2014 (Figure 1b, Table 3). Subplot size was increased in 2014 in order to increase the total number of sampled seedlings and saplings necessary for species-specific treatment-wise comparisons. Additional information recorded for each subplot and inventory year included location specifics (skid road, scarified area, and gap ID if the plot center was located within a gap), ground vegetation type ("blueberry", "fern", "moss", and "grass"; the latter includes thin- and broad-leaved grasses according to [34]) and soil moisture class. The number of seedlings per tree species and height class (20–50, 50–100, 100–150, 150–200, and >200 cm) was recorded in summer 2009 and summer 2014. Also, browsing damage during the previous year, and annual terminal shoot length of the previous three years of the largest individual per tree species were measured on every regeneration subplot.
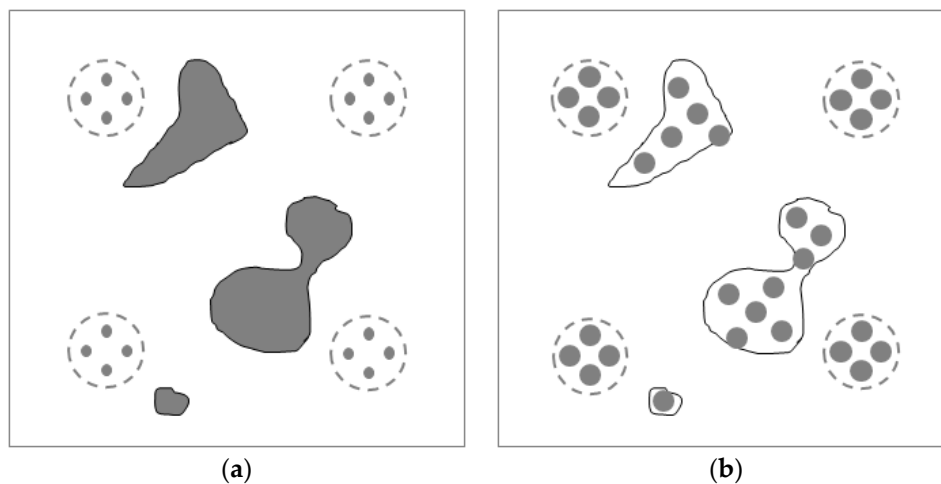

(**a**)　　　　　　　　　　　　　　　(**b**)

Figure 1. Schematic depiction of different regeneration sampling schemes used in this study (grey = sampling area): (**a**) 5 m^2 circular sample plots systematically distributed within overstory measurement plots in 2009 (dashed line) and 100% inventory of all seedlings and saplings in canopy gaps 2009 (black line); (**b**) 10 m^2 sample plots systematically distributed within overstory measurement plots in 2014 (dashed line) and 10 m^2 sample plots systematically distributed within canopy gaps in 2014 (black line).

Table 3. Sampling method and number of regeneration plots with different sizes.

	2009		2014	
	Stand	**Gaps**	**Stand**	**Gaps**
Number of sample plots	192	-	192	636
Sampling area (m^2)	960	28 620	1 920	6 360
Number of sampled seedlings	29	2 862	351	5 215

In addition to the regeneration surveys conducted in overstory measurement plots, seedlings and saplings were also recorded within every canopy gap in 2009 and 2014 (Figure 1). Sampling in 2009 was a complete enumeration, i.e., all gap seedlings and saplings were measured to capture initial variation and diversity within the forest regeneration layer in canopy openings. Due to a significant increase in gap regeneration density as well as to harmonize the surveying schemes, gap sampling in

2014 followed the procedure described above for regeneration surveys in overstory measurement plots using systematically distributed circular permanent regeneration subplots (10 m^2). Therefore, a central regeneration subplot was established at the intersection point of the previously located length and width transects within each gap. Additional permanent regeneration subplots were established every 5 m along the length and width transect lines, respectively. As a result, the number of plots per gap varied depending on gap size. Regeneration surveys conducted in 2009 were considered pre-harvest, as they reflect conditions prior to tree cutting operations.

On average, 42%–45% of the 320 m$^3 \cdot$ha^{-1} initial standing volume was removed by the first cutting in spring 2009. The pre-harvest total gap area was 3%, and the post-harvest total gap area amounted to 15% of the total stand area in 2009. About 6% of the total gap area of the stand was located in treatment CON, while gap area and sizes were evenly distributed in the three management treatments. Windthrow of individual trees was rare throughout the five-year study period and thus influenced gap characteristics only marginally. Gap size distribution and a more detailed description of the stand are given in [20]. The regeneration within the two experimental treatments TDH and TDH2 is jointly presented in this study, as preliminary analysis revealed very small differences in regeneration density and composition between the two target diameter harvest treatments. TDH+ with the additional soil scarification treatment, however, is presented separately.

Other information recorded for every stand and gap regeneration subplot comprised soil moisture class [35], vegetation type [34] and canopy closure class (0–33%, 34%–66%, 67%–100%) estimated using a spherical densiometer [36].

2.3. Data Analysis

Regeneration establishment was first quantified using seedlings 20–200 cm in height to evaluate overall density per treatment and in gaps. In addition, tree species composition and height growth were compared between treatments and in gaps. The regeneration sampled 2009 in overstory measurement plots was analyzed as a single stratum without the consideration of treatments applied in that year. Student's two-tailed *t*-test was applied to detect statistical differences in species-specific annual seedling height growth between gaps and treatment TDH/TDH+. The test was also used to compare seedling densities between non-scarified and scarified gaps in 2014, and to compare the 2014 gap regeneration subplots with the following subplot subsamples of the same inventory: (1) gaps >100 m^2; (2) scarified gaps >100 m^2; and (3) individual canopy closure classes.

To further gain insight into the factors influencing seedling establishment and relative species proportion, regeneration models were developed and evaluated using all regeneration subplot data. Due to the hierarchical structure (spatial correlation: regeneration subplots within overstory measurement plots within treatment areas within blocks) and the zero-inflation (i.e., a large number of subplots with no seedlings or saplings) of the combined regeneration data set, generalized linear mixed effects modelling was applied using the R package "glmmADMB" [37,38]. In a first step, a model analyzing total subplot seedling density was developed using standardized seedling density (# of seedlings per 10 m^2) because of the varying regeneration subplot size used in surveys during 2009 and 2014 [39]. In a second step, we developed species-specific relative proportion models using the subsample of stocked regeneration subplots only [40]. A species-specific relative proportion was calculated for each analyzed species as the subplot-specific percentage of the total number of seedlings and saplings. Zero-inflated negative binomial and binomial error structures were used in modeling steps 1 and 2, respectively [41]. Various nested random effect structures on the intercept (e.g., plots within treatment areas within blocks) were tested [42]. However, best model performance evaluated using Akaike's information criterion (AIC) was achieved with the inclusion of random block terms only. Potential predictor variables were first tested for collinearity. Subsequent preliminary analyses examining the predictive power of explanatory variables within each modeling step showed that gap size was a better predictor to quantify overstory tree density than canopy closure class. Total basal area could not be included because overstory tree data were not collected for gaps. Consequently,

considered predictor variables included gap size (m^2; 0–1155 with 0 for regeneration subplots under closed canopy), time since harvest (years; 0 or 5), and various binomial indicator variables (0 or 1) namely soil scarification, skid road, soil moisture classes "moist" and "wet", as well as the vegetation types "blueberry", "fern", "grass", and "moss". Starting with a null model containing an intercept only, predictor variables were added stepwise and retained in the model if the inclusion showed a significant effect ($p < 0.05$) and resulted in improved model performance which was evaluated using AIC [42].

3. Results

3.1. Regeneration Establishment

Only 10% of the regeneration subplots contained seedlings in 2009. On average, the number of seedlings was 300 individuals per hectare in the entire stand, but increased in all treatments in 2014. After cutting, the number increased considerably to 1400 (TDH+) and 1800 (TDH) individuals ha^{-1} (Table 4). While Norway spruce dominated the seedlings initially, its relative proportion decreased substantially in the harvest treatments five years after cutting. The decrease was mainly caused by the large number of new birch and rowan seedlings. Dividing the regeneration into two height classes, the proportion of spruce in year 2014 was 12% of small seedlings (20–100 cm height) and 30% of larger seedlings (101–200 cm).

Table 4. Number of seedlings ha^{-1} and standard error by tree species (height 20–200 cm) before and after treatment.

Tree Species	2009		2014			
	Stand	Gaps	Stand			Gaps
			TDH	TDH+	CON	
Spruce	135 ± 42	422 ± 65	229 ± 144	104 ± 106	354 ± 427	929 ± 93
Oak	10 ± 69	36 ± 8	167 ± 160	83 ± 80	21 ± 41	263 ± 23
Beech	63 ± 53	37 ± 16		21 ± 41	125 ± 173	41 ± 10
Birch	10 ± 10	167 ± 31	771 ± 619	500 ± 400		5031 ± 271
Rowan	42 ± 21	220 ± 70	458 ± 243	375 ± 192	83 ± 80	925 ± 59
Pine		5 ± 2				149 ± 25
Willow		14 ± 11	42 ± 82	83 ± 80		357 ± 45
Aspen				21 ± 41		94 ± 18
Others	52 ± 34	98 ± 43	146 ±148	188 ± 183		472 ± 48
Total N·ha^{-1}	300 ± 80	1000 ± 158	1800 ± 440	1400 ± 270	600 ± 250	8300 ± 320
N of plots	192	174 gaps	48	48	48	636

In canopy gaps, on average 1000 seedlings ha^{-1} were found in 2009. The proportion of spruce was 50%. In total, the proportion of birch and rowan was higher in gaps than in the entire stand already and similar to the proportion of spruce (Table 4). Five years after harvest, an eightfold increase of total seedling density was observed, mainly due new birch seedlings (Table 4). The more shade-tolerant tree species spruce, oak and beech, increased in total from 208 to 306 individuals ha^{-1} in the stand on the overstory measurement plots. The seedling density after soil scarification in treatment TDH+ was lower with 224 individuals ha^{-1}. In gaps, the absolute density of these three tree species together increased from 450 to 1200 individuals ha^{-1} while their relative proportion decreased (Table 4).

3.2. Seedling Height Growth

While seedling number was large enough for comparisons between the stand and gaps in 2014, only Norway spruce provided enough seedlings to describe the height growth in the stand in 2009 and in the CON treatment in 2014 (Table 5). Annual terminal shoot length of spruce was 3 cm on average in 2009, and 5 cm in the CON treatment in 2014. In contrast, spruce height growth in gaps and the treatments TDH or TDH+ substantially increased to 10 cm per year in 2014. More pronounced

differences between gaps in 2014 and the entire stand were found for broadleaf tree species and Scots pine (Table 5). Leader shoot growth in beech and pine was on average 5 cm greater in gaps compared to the treatments TDH/TDH+. A small difference was also found for oak, accompanied with the highest browsing damage (Table 5). Over all tree species, no effect of scarification in TDH+ on seedling height growth could be found.

Table 5. Top shoot length with standard error (cm per year) of the tallest individual per tree species and per gap or subplot of different inventories (if available; see Table 3) and initial browsing damage of the top shoot per tree species.

| Tree Species | 2009 | | 2014 | | | Browsing Damage |
| | Stand | Gaps | Stand | | Gaps | 2009 |
			TDH/TDH+	CON		
Spruce	3 ± 0.5	8 ± 0.6	10 ± 1.9	5 ± 0.7	10 ± 1.0	2%
Oak		8 ± 0.8	6 ± 0.8		8 ± 0.6	51%
Beech		11 ± 0.9	11 ± 2.7		16 ± 3.0	37%
Birch		18 ± 1.2	14 ± 1.3		17 ± 0.8	42%
Pine		8 ± 0.8	5.5 ± 0.7		11 ± 0.7	33%

3.3. Influence of Soil Scarification, Soil Moisture, Vegetation Type and Gap Size

Table 4 pointed out a somewhat lower total regeneration density in treatment TDH+ with soil scarification (1400 seedlings) compared with treatment TDH (1800 seedlings). In canopy gaps, however, there was still a reduction in the number of seedlings after scarification but this difference diminished with 8600 seedlings ha^{-1} in non-scarified gaps and 8200 seedlings ha^{-1} in scarified gaps. A statistically significant difference was found only for spruce ($p = 0.03$), when comparing the 900 spruce seedlings ha^{-1} in non-scarified gaps with 500 seedlings ha^{-1} in gaps with soil scarification. Pine and willow increased their small number by 25%–35% after scarification, but the differences were not statistically significant.

In gaps larger than 100 m^2, seedling density increased to 9200 ± 430 (SE) individuals ha^{-1} in 2014, but no significant difference compared with the total regeneration in gaps was found. The density in scarified gaps larger than 100 m^2 was 8400 ± 880 individuals ha^{-1}. Also in these gaps, a significant decrease was revealed for spruce with 490 individuals ha^{-1} (less than half the value in non-scarified larger gaps).

A lower total density of 6100 ± 730 seedlings was found on mesic micro-sites in large, scarified gaps (compared with the average in all gaps). On such sites, the number of birch seedlings (3200 ± 520) was lower than on moister sites (7300 ± 830). The same trend was found for all gaps surveyed in 2014, where fewer birch seedlings occurred on mesic sites than on moist sites. Norway spruce, on the contrary, was more abundant on mesic subplots.

Comparing the regeneration density in gaps in 2014 between the two dominant ground vegetation types "blueberry" and "grass" with total gap regeneration density, a higher seedling density of 9100 ($\pm$470) individuals ha^{-1} was found on the vegetation type "grass". Total seedling density on regeneration subplots dominated by blueberry was slightly lower than the average with 7400 ($\pm$ 460) individuals ha^{-1}. As suggested in the respective proportion model, a higher number of oak seedlings was found in the blueberry type with 380 ± 40 individuals ha^{-1}, compared to 249 oak seedlings ha^{-1} across all vegetation types.

In Table 6, three different classes of light conditions in gaps were compared. In 2014, total seedling density was significantly higher in subplots with 0–33% canopy coverage (11000 ind. ha^{-1}), and significantly lower in subplots with 67%–100% coverage (6500 ind. ha^{-1}). At the species level, the number of birch, pine and oak seedlings was significantly lower in subplots in the highest canopy coverage class, while the number of spruce seedlings was higher in these subplots (Table 6).

Table 6. Effect of canopy closure on seedling density in forest gaps. *p*-values refer to the comparison with all 636 regeneration plots in gaps 2014 (Table 3).

| Tree Species | Canopy Coverage | | | | | | | | | | | |
| | 0–33% | | | | 34%–66% | | | | 67%–100% | | | |
	Plot No.	N·ha^{-1}	SE	*p*	Plot No.	N·ha^{-1}	SE	*p*	Plot No.	N·ha^{-1}	SE	*p*
Spruce	121	**620**	110	0.04	298	970	140	0.83	217	1100	180	0.52
Oak	121	370	60	0.10	298	280	40	0.68	217	**180**	30	0.03
Birch	121	**7600**	770	<0.01	298	5100	400	0.94	217	**3600**	360	<0.01
Pine	121	170	50	0.79	298	220	50	0.16	217	**40**	20	<0.01
Total	121	**11,000**	890	<0.01	298	8500	470	0.67	217	**6500**	440	<0.01

Generalized linear mixed effects modelling revealed that time since harvest, gap size, and the vegetation type "grass" were among the most influential predictors for total seedling density. All three predictors exhibited a positive relationship (Table 7). In addition, skid road and soil moisture class "moist" also significantly increased regeneration density. No statistically significant effect was found for soil scarification on regeneration density. A significantly negative effect on the relative proportion of spruce was observed for gap size, soil scarification, skid road and vegetation type "grass". Increasing gap size also significantly decreased the relative proportions of beech and rowan. In contrast, gap size as well as soil moisture were positively correlated with the relative proportion of birch. Proportion models for pine, aspen and willow could not be derived due to their low total seedling number.

Table 7. Parameter estimates and significance levels of predictor variables including various soil moisture classes (SMC) and vegetation types (VT) of generalized linear mixed effects models for regeneration subplot-level total seedling density and relative species-specific proportion.

| Predictor | Seedling Density | | Relative Proportion | | | | | | | | | |
			Beech		Birch		Oak		Rowan		Spruce	
Intercept	−0.7066	***	−4.2552	***	−2.7897	***	−3.8160	***	−0.9641	*	−1.1238	***
Time since harvest	0.4165	***							−0.2767	**		
Gap size	0.0007	***	−0.0218	*	0.0011	*			−0.0035	**	−0.0038	**
Soil scarification											−0.8925	**
Skid road	0.3894	***									−2.0437	*
SMC 'moist'	0.3521	***			0.9051	**						
SMC 'wet'					2.9427	***						
VT 'blueberry'					−0.6955	*	0.9130	*				
VT 'grass'	0.4002	***									−1.3305	***
VT 'moss'												
VT 'fern'			7.2066	**	1.6109	*			2.0296	*		

[1] Significance: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

4. Discussion

This study is one of the first to analyze regeneration establishment without enrichment planting in managed multi-layered stands under transition towards an uneven-aged forest structure on fertile forest sites in southern Sweden. Target diameter harvesting, and the creation of gaps in particular, significantly increased seedling density over the five-year study period. This was mostly due to an increase in the number of birch seedlings. However, seedling density of other, more desirable species such as spruce, oak, and beech also significantly increased in studied canopy gaps. Soil scarification, in contrast, did not prove to be an effective management practice to improve regeneration establishment under the studied forest conditions. Gap size, soil moisture, and ground vegetation type were most influential in predicting species-specific relative proportions of the forest regeneration layer. The creation of gaps also increased annual height growth rates of the regeneration, in line with other regeneration studies in the boreal and temperate region of Europe [43–45].

4.1. Regeneration Establishment

Many ecological studies have emphasized the importance of canopy gaps for initiating regeneration processes and maintaining stand structural complexity in natural forests, including their role for pioneer tree species [2,43–47]. Our case-study highlighted the importance of canopy gaps for forest regeneration establishment in a managed forest, which has not been reported in previous studies in southern Sweden. The total regeneration density was on average approximately four times greater in gaps than elsewhere in the stand. Despite covering only 15% and 11% of the total stand area in 2009 after cutting and 2014, respectively, half of the seedlings were found in canopy gaps. Consequently, gap size was found to be crucial in initiating forest regeneration. Earlier work in boreal Scots pine forests in northern Sweden found that competition for nutrients is crucial [16,48], while studies in temperate Norway spruce stands highlighted the importance of light for successful regeneration [49]. In boreal Norway spruce single-tree selection forests of central Sweden, no relationship between seedling occurrence and canopy gaps was found [50]. Hence, the role of above- and below-ground competition remains unclear under southern Swedish conditions and for the study stand in particular.

Strong relationships between harvest removal levels and seedling occurrence as well as seedling height growth were reported for managed pine- and spruce-dominated stands in previous experimental trials across Sweden, in line with the findings for undisturbed soil in the present study. For example, Nilsson et al. [8] recorded approximately 2000 seedlings ha^{-1} five years after shelterwood cutting (95 and 155 shelter trees ha^{-1}) in a spruce-dominated stand on a similar site. However, the number of seedlings increased 2- to 3-fold after soil preparation. Irrespective of the soil disturbance, Norway spruce seedlings dominated the newly established regeneration layer [8]. Also, within an experimental shelterwood trial containing 22 mature pine stands across Sweden, an average 10,000 seedlings ha^{-1} were counted five to eight years after harvest, and almost 20,000 seedlings ha^{-1} with an additional soil preparation treatment [9]. Here, the difference in seedling density was mainly caused by a substantially higher number of birch seedlings, as observed in our study. In addition, positive significant effects of shelter and scarification on pine seedling density in comparison to clearcutting were revealed for the whole trial in Sweden, but not for the southern or northern region with a large natural variation between stands [9]. Even in a single stand, seedling density can range from 14,000 to 321,000 ha^{-1} depending on stand density [51]. Regeneration occurrence and survival are highly stochastic processes compared with individual tree growth dynamics following seedling establishment and are influenced by various factors apart from management-generated variation in canopy closure and soil disturbance [52]. However, in the majority of the above-mentioned studies, the number of seedlings was significantly lower in non-harvested areas, a finding that was verified in our study (Table 4). Only for spruce and beech did the absolute number remain constant.

4.2. Seedling Height Growth

A substantial increase in annual height growth was observed for spruce seedlings after harvest. The silvicultural intervention in general caused the difference as height growth was the same in gaps and post-harvest in the stand (Table 5). High browsing pressure by ungulates may have confounded the results for other tree species, especially oak.

Compared to the stand average, beech, birch and pine exhibited accelerated height growth in gaps. However, the absolute height growth of all seedlings was less than previously reported for advanced regeneration under shelterwood and in stands under transformation towards more heterogeneous stand structure [10,13,14,51]. On the other hand, the magnitude was larger than observed for newly established seedlings under shelterwood [8,9] and in boreal Norway spruce single-tree selection stands [4,5,53]. Only a southern site in central Sweden [4] showed comparable annual height growth rates that ranged from 1–19 cm on average. In addition, further increases in height growth rates can be expected in subsequent years given results reported from older experiments [12,13].

4.3. Influence of Soil Scarification, Soil Moisture, Vegetation Type and Gap Size

Soil scarification did not increase seedling density but instead had a significant negative effect on the number of spruce seedlings (Tables 4 and 7). While rather unexpected, [9] reported similar findings for spruce regeneration in shelterwood cuttings. No frost heaving damage was observed after scarification and thus can be excluded as a potential cause for the decline [54]. We therefore consider unintended mechanical damage from soil scarification as the main reason for the reduction of spruce seedling density. As the less browsed, initially more abundant, and shade-tolerant Norway spruce can be considered as one of the important tree species to constitute the future forest, the additional soil scarification treatment was not effective in improving conditions for future ingrowth. Beside mechanical damage to existing regeneration, the delayed timing and insufficient seed crops following soil preparation may explain the poor results of this measure [55]. Given more promising findings in earlier experimental shelterwood trials using various methods of soil preparation [8,56,57], additional scarification measures should be planned only when a lack of regeneration becomes evident and a mast year of desired species is expected.

As shown in previous studies, gap size increased seedling density in birch and pine [58,59]. Despite the small number of pine seedlings found in our study, seed years provide opportunities for successful Scots pine regeneration, especially on drier sites, in larger gaps or by reducing overstory canopy levels rapidly [56].

In contrast and likely in addition to the lack of seed trees, high frost sensitivity of the late successional beech is likely to explain the negative relationship with gap size as temperature extremes occur, especially in larger canopy openings [60]. In a beech shelterwood experiment in southern Sweden, a higher density of beech seedlings was found on scarified soil than on undisturbed soil [61]. Karlsson and Nilsson [57] concluded that scarification and shelterwood cutting are efficient tools to promote natural regeneration under conditions similar to this study. The authors highlighted the importance of sufficient seed supply and concluded that wind-dispersed tree species including birch and willow were favored by scarification, while animal-dispersed tree species such as beech and oak were more favored by shelterwood than by clearcutting [57].

Concerning other factors, a significantly higher density of birch seedlings was found with increasing soil moisture, while spruce tended to be less frequent under such conditions (Table 7). Although Norway spruce is well adapted to moist sites, the competition with birch or other vegetation can be a reason for the observed lower density in spruce. Furthermore, a significantly higher proportion of oak was observed in blueberry patches. This could be related to the seed dispersal activities of the Eurasian jay (*Garrulus glandarius*), known to preferably hide acorns under dwarf shrub vegetation [62].

5. Conclusions

The observed increase in post-harvest seedling density to around 1500 ha^{-1} after target diameter harvest provides sufficient ingrowth potential for sustainable management if future target diameter harvests will have similar positive effects on regeneration. Subsequent inventories in coming years will show if the current, rather undesired high proportion of birch will decrease substantially as a result of the observed and ongoing rapid gap closure [20,58,63]. Consequently, future management activities should promote recruitment of late-successional species as phytosociological and silvicultural experiences point to the long-term disappearance of light-demanding tree species under close-to-nature management practices [60,64].

We conclude that heterogeneously structured stands like the one studied here appear to provide feasible silvicultural options to develop uneven-aged stand structures [24]. Under such a management goal, a more explicit spatial consideration of advanced regeneration and the creation of canopy gaps become crucial silvicultural tools to enhance stand regeneration processes [65,66]. Schütz [24] highlighted that transformation to more irregular stand structures needs time and frequent interventions. To develop the study stand into an uneven-aged single-tree selection forest with a sustainable supply of smaller trees [32,67] therefore, will take many decades. Aiming at the

transformation to a spruce-dominated single-tree selection forest, more attention should be paid to tree species with vital growth under varying levels of canopy closure. Given our findings and current management conditions in the study region, Norway spruce, European beech and sessile oak appear to be the most suitable species in this regard [26,68]. To balance removal and ingrowth of trees over time, both gaps to initiate or release regeneration and closed canopy sections without regeneration are necessary, as this will assure the continuous supply of regeneration and mature, harvestable trees.

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