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Article

Commercial Thinning to Meet Wood Production Objectives and Develop Structural Heterogeneity: A Case Study in the Spruce-Fir Forest, Quebec, Canada

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Abstract: We evaluated the effectiveness of commercial thinning mainly from below (CT; 0, 26%, 32% and 40% merchantable basal area removals) in meeting wood production demands and developing structural heterogeneity in a balsam fir (*Abies balsamea* (L.) Mill) and spruce (*Picea* spp.) stand. After 10 years, 32%–40% removals showed a 12%–18% increase in mean diameter and 27%–38% increase in gross merchantable volume (GMV) per tree compared to the unthinned control. At the stand level, all thinning treatments generated as much cumulative GMV (harvested volume + GMV after 10 years) and gross sawlog volume per hectare as the unthinned control. As for stand structure, eight out of nine thinned experimental units showed increased structural heterogeneity after 10 years, *i.e.*, irregular, positively-skewed diameter distribution with an elongated right tail toward larger trees. The diameter distribution in the unthinned control became more symmetric, unimodal and regular over time, with fewer saplings than at the beginning of the experiment and lower density of larger trees compared to CT. Regeneration density and stocking were abundant in all treatments, largely dominated by balsam fir. Results indicate that thinning can be used to meet wood production objectives and help develop structural heterogeneity in this forest.

Keywords: commercial thinning; forest ecosystem management; partial cuts; regeneration; spruce-fir; structural heterogeneity

1. Introduction

The notion of using silviculture to help reach multiple management objectives in a sustainable manner has been evoked by generations of foresters. In the late 19th and early 20th centuries, this included Gurnaud in France, Biolley in Switzerland [1] and Simpson in Great Britain [2], advocates for a diversification of management activities in response to the silvicultural practices of their era. Ensuing generations have made similar recommendations throughout the 20th century [3]. In North America, contemporary scientists that addressed this notion using old-growth attributes or structural heterogeneity in response to societal concerns over biodiversity are numerous [4–8]. These references are examples of the use of natural variability concepts in managing ecological systems [9]. Such concepts can be useful in decision-making processes as an objective to be reached, as a benchmark, as a framework or simply to provide guidelines [9].

Natural variability concepts are used throughout the world under various ideas, such as continuous-cover forestry, disturbance-based silviculture and multi-aged forest management systems [1,10]. In northeastern North America, the forest ecosystem management concept is used to minimize the gap between preindustrial and current forest conditions [11,12], in an attempt to maintain biodiversity, as well as the ecosystem functions of managed forests. The lack of old-growth forests resulting from current or past harvest practices [11,13] generally contributes to a widening gap, particularly where minor disturbances are the main ecological driver [12,14]. Managed forests have low amounts of old-growth structural attributes, such as variation in tree sizes, including large trees, leading to large dead or dying standing trees and coarse woody debris [15].

There is some evidence suggesting that thinning could serve as a tool to increase structural heterogeneity and help accelerate the development of old-growth structural attributes. Studies where this was demonstrated include various forest types in North America and Europe [16–22]. As such, commercial thinning (CT) is a partial disturbance that reduces the density of stands that have reached the stem exclusion stage to capture mortality, redistribute growing space to fewer individuals and increase tree size [7,23]. Thus, CT offers an opportunity to meet wood production and structural heterogeneity objectives. In terms of wood production, the long-term use of CT on highly productive sites may increase merchantable stand yield in treated stands compared to unthinned stands. This potential advantage, however, depends on the timing of first entry, preharvest conditions, species, thinning intensity and the type of thinning operation (e.g., from below or from above). Hence, this advantage may not always be realized, and there is no consensus [23], particularly on less productive sites and with later entries, such as CT [24].

Long-term empirical studies investigating the usefulness of CT in meeting wood production objectives and developing structural heterogeneity in managed forests in a single study are uncommon. Modeling efforts have been carried out [22,25,26], but studies based on long-term empirical data are rare. Hence, we used an experiment aimed at investigating various intensities of thinning from below and re-examined its development over time with structural heterogeneity in mind. Although limited in terms of replication, this experiment can help guide future research efforts in this field.

The objectives of this case study were to: (1) quantify growth and yield responses; and (2) evaluate the effectiveness of CT from below in developing structural heterogeneity over a 10-year period in a conifer stand. For Objective 1, we hypothesized that: (a) mean tree size will be higher in thinned stands than in the unthinned control; (b) mean tree size will increase with increasing thinning intensity; and (c) stand yield will be similar, regardless of thinning or thinning intensity. For Objective 2, we hypothesized that CT will increase: (a) the number of large trees; (b) the heterogeneity of the shape of the diameter distribution; and (c) the regeneration density and stocking compared to the unthinned control.

2. Experimental Section

2.1. Study Site

The study site was located near the Quebec-New Brunswick border, Canada, in the Bas-Saint-Laurent region of Quebec (47°50′50″ N, 68°26′06″ W). The natural disturbance regime was characterized by recurring spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks, which can lead to small or major disturbances [27]. The site was part of the Fir-Yellow Birch (*Betula alleghaniensis* Britt.) bioclimatic subdomain of the northern temperate ecological zone. Mean annual temperature (1971–2000) was 2.2 °C; mean annual precipitation was 1134 mm; and growing season length was 153 d. Elevation was 300 m above sea level. The study site had well-drained till soil on a <10% slope. The naturally-regenerated stand was 54 years old on average (age at 1 m in height) during the year in which thinning was carried out (1997). Although this is relatively old for a first thinning entry, none of the experimental units (EUs) were overstocked prior to thinning [28,29].

Species composition included balsam fir (*Abies balsamea* (L.) Mill.) with 69% of merchantable basal area (BA of trees >9.0 cm in diameter at breast height (DBH)) and a combination of white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) with 31% of BA. Mean merchantable stand density was 1642 stems ha^{-1}, merchantable BA was 31.1 m^2 ha^{-1}, and gross merchantable volume (GMV) was 164 m^3 ha^{-1} (Table 1). Fir-dominated conifer stands of this study are more productive than typical fir-dominated stands in the region based on yield tables from Quebec [30]. At the mean tree level, the live crown ratio was 0.70, and the slenderness ratio (height/DBH) was 0.79.

Table 1. Pre- and post-harvest characteristics (mean ± SE) by commercial thinning (CT) intensity (0%, 26%, 32% and 40% merchantable basal area removals). Abbreviations: age, age at 1 m in height; BA, basal area; DBHq, mean quadratic diameter at breast height (DBH) of merchantable trees; GMV, gross merchantable volume; Ht, estimated height of all trees; live crown ratio, crown length/total height of study trees; RD, relative density; SI, mean site index of all species at age 50 at 1-m height; slenderness, ratio of estimated height/DBH. Data not measured prior to thinning are represented by a dashed line (—).

Thinning Treatment	Characteristic	Preharvest Mean	SE	Postharvest Mean	SE
CT26	Age (y)	—	—	54	8
	SI (m)	—	—	14	0.4
	DBH_q (cm)	16.1	0.5	16.9	0.5
	Ht (m)	12.3	0.4	12.1	0.5
	Density (trees ha^{-1})	1667	209	1108	110
	RD	0.56	0.06	0.41	0.04
	BA (m^2 ha^{-1})	33.6	3.5	24.9	2.2
	GMV (m^3 ha^{-1})	186	22	136	14
	Slenderness ratio	0.80	0.03	0.74	0.03
	Live crown ratio	—	—	0.55	0.08
CT32	Age (y)	—	—	58	4
	SI (m)	—	—	14	0.1
	DBH_q (cm)	16.3	0.4	17.8	0.5
	Height (m)	12.4	0.2	12.5	0.1
	Density (trees ha^{-1})	1517	228	867	145
	RD	0.53	0.07	0.36	0.05
	BA (m^2 ha^{-1})	31.4	3.3	21.3	2.6
	GMV (m^3 ha^{-1})	174	18	119	14
	Slenderness ratio	0.79	0.02	0.72	0.02
	Live crown ratio	—	—	0.72	0.04
CT40	Age (y)	—	—	48	4
	SI (m)	—	—	14	0.3
	DBH_q (cm)	14.7	0.3	16.7	0.4
	Height (m)	11.3	0.2	11.7	0.4
	Density (trees ha^{-1})	1733	242	817	85
	RD	0.49	0.04	0.30	0.02
	BA (m^2 ha^{-1})	29.5	2.2	17.8	1.5
	GMV (m^3 ha^{-1})	145	13	93	9
	Slenderness ratio	0.79	0.01	0.72	0.01
	Live crown ratio	—	—	0.75	0.05
Control	Age (y)	—	—	57	8
	SI (m)	—	—	13	1.1
	DBH_q (cm)	15.2	0.7	15.5	0.8
	Height (m)	11.7	0.5	12.0	0.6
	Density (trees ha^{-1})	1650	66	1625	76
	RD	0.49	0.04	0.50	0.05

Table 1. *Cont.*

Thinning Treatment	Characteristic	Preharvest Mean	SE	Postharvest Mean	SE
Control	BA (m^2 ha^{-1})	30.1	1.9	30.5	2.4
	GMV (m^3 ha^{-1})	153	20	162	23
	Slenderness ratio	0.80	0.01	0.80	0.01
	Live crown ratio	—	—	0.79	0.03

2.2. Experimental Design and Thinning Treatments

The completely randomized design was established in fall 1997 and was comprised of four treatments: three thinning intensities and an unthinned control. Each treatment was replicated three times, for a total of 12 EUs along a north-south orientation (Figure 1). Actual thinning intensities were 0% (unthinned control), 26% (CT26), 32% (CT32) and 40% (CT40) of merchantable BA. At the stand level, 15%–20% has to be added to each thinning treatment to account for skidding trails. Each EU was composed of a 2500 m^2 area (50 × 50 m), with a central 400 m^2 circular plot (11.28 m radius) to measure merchantable trees. An unthinned strip of 50 m was left between each EU. CT was carried out in each 2500-m^2 plot by marking merchantable trees to cut based on the following selection order: (1) diseased trees; (2) regular spatial distribution of trees; (3) crooked trees; (4) species composition (fir before spruce); and (5) smaller and less vigorous trees. Hence, the general intent was to thin mainly from below [31] by prioritizing the removal of dying and diseased trees. Trees were felled, delimbed and bucked manually using a chainsaw from late-September to mid-October 1997. Cut trees were brought to the roadside using a cable skidder. Skidding trails were 5 m in width.

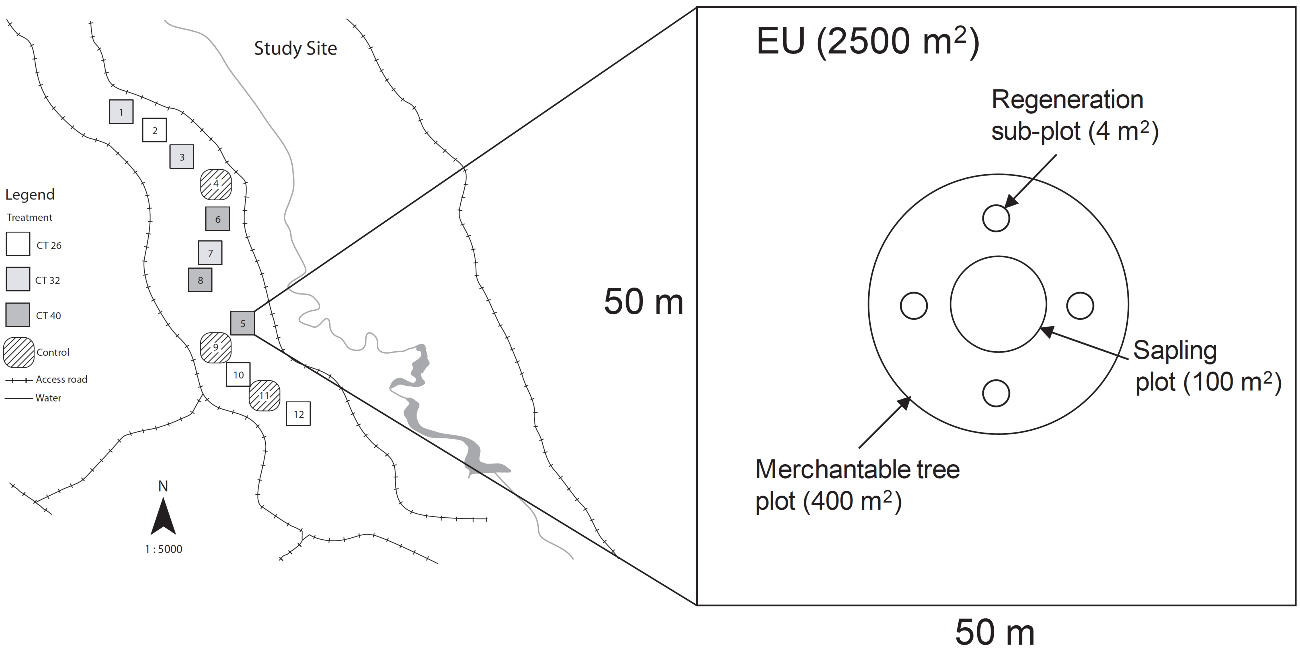

Figure 1. Layout of the study site, including details of the plot layout within experimental units.

2.3. Growth and Yield Measurements

A preharvest merchantable tree inventory was carried out from mid- to late-September in the 400-m^2 plots by tallying trees based on species and DBH class (2 cm). Postharvest measurements were carried out shortly after harvest (mid-October to mid-November 1997), as well as 5 and 10 years after thinning. All merchantable trees were numbered and tallied by species, status (live, dead, windthrow) and DBH (in mm). Detailed measurements were taken on 5 codominant trees per plot: species, age at 1 m in height, crown class, total height and live crown ratio. The height of all merchantable trees was estimated based on height-diameter relationships [32]. Height estimates and observed DBH were used to calculate GMV·tree^{-1} [33]. Thus, merchantable stand BA and GMV were calculated as the sum of all trees in each EU and expressed as per-hectare values. Gross sawlog volume (GSV) was also computed based on GMV, but with a minimum DBH of 19.1 cm. This high threshold allows a more accurate assessment of potential thinning effects on sawlog volume production, which is closer to desired thinning objectives [24]. Cumulative gross merchantable volume (CGMV) production was calculated as the sum of harvested merchantable volume and GMV after 10 years.

2.4. Structural Heterogeneity Measurements

Three attributes were used to measure structural heterogeneity: (1) the number of large trees (≥23.1 cm DBH); (2) the shape of the diameter distribution, including saplings and trees; and (3) regeneration density (number of stems ha^{-1}) and stocking (% of sub-plots containing at least one living stem). These attributes are often used to characterize stand structure in old-growth forests [15]. Unthinned EUs served as the baseline for comparisons with thinned EUs.

Large trees are often defined as ≥20 cm in the eastern boreal and temperate forest zone of Canada. This is based on evidence of wildlife use [34] and of plots with diameter distributions corresponding to old-growth coniferous stands that often show that most trees are <20 cm [35–37]. Data collection for the number of large trees and the shape of the diameter distribution was carried out through growth and yield inventory. Regeneration (all stems <9.1 cm DBH) was tallied by species and height class (1–5, 6–30, 31–60, 61–100, 101–200, 201–300 and >300 cm, but <9.1 cm DBH) in 4 sub-plots of 4 m^2 each, located 8 m away from the centre of the 400-m^2 plot in each cardinal direction. Regeneration measurements took place shortly after harvest, as well as 5 and 10 years postharvest. Saplings (>1 cm DBH) were not distinguished from smaller regeneration in the 4-m^2 plots; they were measured by species and DBH class (2 cm, 1.1–3.0 cm; 4 cm, 3.1–5.0 cm; 6 cm, 5.1–7.0 cm; 8 cm, 7.1–9.0 cm) in a separate 100-m^2 plot located at the centre of the 400-m^2 plot.

2.5. Statistical Analyses of Growth and Yield

Analyses of variance were carried out using mixed linear models (proc MIXED) in SAS (SAS 9.3, Cary, NC, USA). Dependent variables at the mean merchantable tree level were DBH and GMV. To better reflect the actual growth of residual trees, trees that died or reached merchantable size during the 10-year period were excluded. Dependent variables at the stand level were GSV, CGMV, as well as BA of ingrowth and mortality. For all statistical analyses, values were calculated at the EU level ($n = 12 \times 3$ years = 36) to avoid artificially increasing the number of degrees of freedom of the error term. Fixed effects included thinning (T), year (Y) and T × Y, with EU as a random effect. All statistical differences were reported at $p < 0.05$. Repeated measures on the same EU over time were accounted for using an autoregressive variance structure (TYPE = AR (1)) in the REPEATED statement of the MIXED procedure. This structure is appropriate when time periods are evenly spaced [38]. Because CGMV is only measured once, it was analyzed without repeated measures.

The respective preharvest value of each dependent variable was used as a covariate to account for potential differences among treatments prior to thinning [39]. Preharvest merchantable BA was used as the covariate for ingrowth. The covariate was removed from the model when non-significant. Hence, the model equation is as follows:

$$y_{ijk} = \alpha + \tau_i + \beta\, pre_{ij} + \mathrm{b}_j + \gamma_k + (\tau\gamma)_{ik} + \varepsilon_{ijk} \tag{1}$$

y_{ijk} is the dependent variable; α is the overall mean; τ_i is the thinning effect *i* (CT26, CT32, CT40, control); β is the linear effect of preharvest conditions pre_{ij} (covariate); b_j is the random effect of experimental unit *j* (1, …, 12) ($\mathrm{b}_j \sim \mathrm{N}(0, \sigma_{\mathrm{b}}^2)$); γ_k is the year effect *k* (0, 5, 10); $(\tau\gamma)_{ik}$ is the interaction between thinning *i* and year *k*; ε_{ijk} is the residual (the vector of the $\varepsilon_{ijk} \sim \mathrm{N}(\mathbf{0},\Sigma)$).

Multiple comparisons were carried out to determine differences between treatments in each measurement year [40,41]. In all multiple comparisons, the ADJUST = simulate option was used to control for potential Type I errors due to multiple testing [40,41]. Normality of residuals and homogeneity of variance were verified for all analyses using scaled residual plots. For mean DBH and GMV tree^{-1}, data transformation failed to correct for heterogeneous variances. To obtain homogeneity, we defined an effect specifying heterogeneity in the variance structure of the *R* matrix of the errors (GROUP = treatment) in the REPEATED statement [40]. As for mortality, residuals could not be normalized. Hence, descriptive statistics (mean ± SE) were used to evaluate treatment effects. Figures show adjusted means and standard error (SE) based on statistical analyses at the mean value of the covariate.

2.6. Statistical Analyses of Structural Heterogeneity

The diameter distribution of each EU was plotted immediately postharvest and after 10 years to assess the number of large trees and the shape of the diameter distribution, including saplings. Decennial changes in the density of saplings and larger trees, as well as in the shape of the diameter distribution, were assessed visually and with computed descriptive statistics in each EU [42,43]. The Weibull function [44], where *c* is the shape parameter, the coefficient of Kurtosis (*k*) [45] and the symmetry index (I_s) [46] were calculated to describe the shape of the diameter distribution based on threshold values. Distributions were grouped into four classes [43]: (a) normal (regular); (b) unimodal, negatively skewed (regular); (c) unimodal, positively skewed (irregular); and (d) bimodal (irregular) (Figure 2).

To simplify the analysis and presentation of regeneration data, height classes with a similar postharvest density were grouped into two classes (≤30 cm and >30 cm). The 30-cm threshold is a good indicator of regeneration survival after harvest [47]. Regeneration was analyzed using the same procedure as growth and yield, but without covariates due to a lack of preharvest data. Logarithmic transformation was used on regeneration density (≤30 cm and >30 cm), and arcsine transformation was used on regeneration stocking ≤30 cm to meet the homogeneity of variance and normality assumptions. Regeneration stocking >30 cm in height could not be normalized. Hence, we used descriptive statistics (mean ± SE) to evaluate treatment effects.

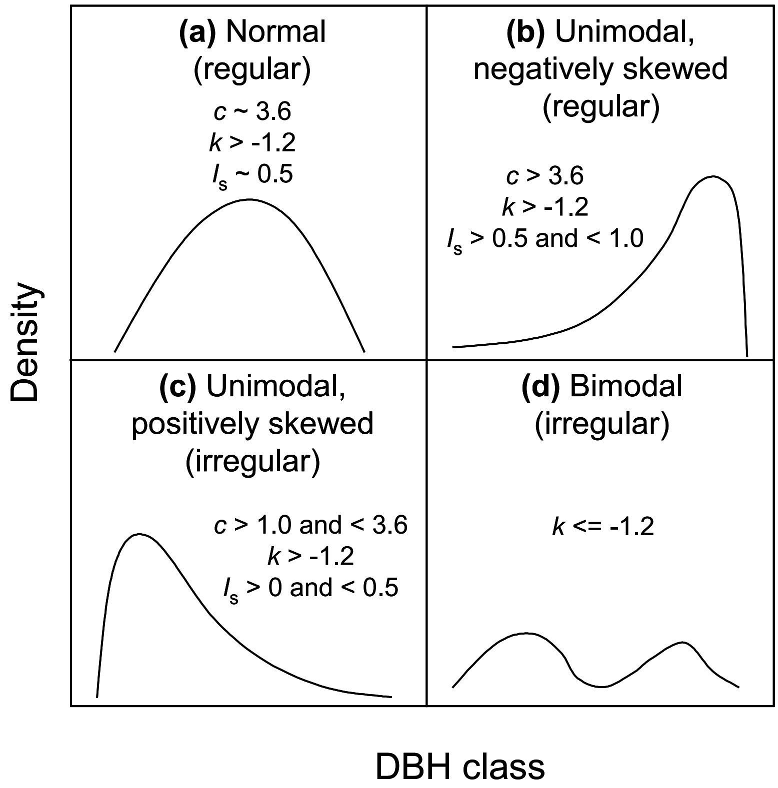

Figure 2. Theoretical diameter distributions and respective statistical thresholds as defined by the Weibull function (*c*), kurtosis (*k*) and the symmetry index (I_s): (**a**) normal, regular; (**b**) unimodal, negatively skewed, regular; (**c**) unimodal, positively skewed, irregular; (**d**) bimodal, irregular.

3. Results

3.1. Growth and Yield

3.1.1. Mean Tree Level

For the first five years after harvest, mean DBH of residual trees was similar among treatments. After 10 years, however, both CT32 and CT40 had higher mean DBH than the control (T × Y, $p < 0.001$, Table 2, Figure 3A). These differences translate into mean decennial gains of 2.2 cm in CT32 (12%) and 3.1 cm (18%) in CT40 over the unthinned control. CT40 was also higher than CT26 after 10 years.

After five years, mean GMV tree^{-1} in CT40 was higher than CT26 and the unthinned control (T × Y, $p = 0.002$, Table 2, Figure 3B). After 10 years, both CT32 and CT40 had higher GMV tree^{-1} than CT26 and the control (Figure 3B). These differences translate into decennial gains of 47 dm^3 tree^{-1} in CT32 (28%) and 62 dm^3 tree^{-1} in CT40 (37%) over the unthinned control.

Table 2. Analyses of variance of the response variables after four commercial thinning intensities (0, 26, 32, 40% merchantable basal area removals). Abbreviations are as follows: DBH and GMV, mean diameter at breast height and gross merchantable volume of residual merchantable trees; CGMV, cumulative GMV ha^{-1}; ddf, denominator degrees of freedom; GSV, gross sawlog volume; ndf, numerator degrees of freedom. Significance ($p < 0.05$) indicated in bold.

Objective	Response Variable	Source of Variation	ndf	ddf	F-Value	*p*-Value
Mean Tree Level	DBH (cm)	Thinning (T)	3	5.9	19.7	0.002
		Year (Y)	2	8.4	1345.0	<0.001
		T × Y	6	4.9	43.1	<0.001
		Covariate (C)	1	5.6	62.7	<0.001
	GMV (dm^3 $tree^{-1}$)	T	3	15.7	19.5	<0.001
		Y	2	11.6	724.6	<0.001
		T × Y	6	8.4	10.6	0.002
		C	1	1.6	120.6	0.018
Stand Yield	GSV (m^3 ha^{-1})	T	3	6.8	1.98	0.209
		Y	2	15.2	131.46	<0.001
		T × Y	6	15.2	0.17	0.982
		C	1	6.7	31.65	<0.001
	CGMV (m^3 ha^{-1})	T	3	7.0	0.35	0.791
		C	1	7.0	79.42	<0.001
	Ingrowth (m^2 ha^{-1})	T	3	10.2	2.03	0.172
		Y	2	17.5	19.81	<0.001
		T × Y	6	17.5	0.95	0.489
		C	1	10.3	7.23	0.022
Old-Growth Attributes (Regeneration)	Density ≤ 30 cm (stems ha^{-1})	T	3	8.0	1.43	0.303
		Y	2	15.3	49.65	<0.001
		T × Y	6	15.3	1.14	0.386
	Density > 30 cm (stems ha^{-1})	T	3	8.0	1.80	0.226
		Y	2	10.5	11.83	0.002
		T × Y	6	10.5	2.89	0.064
	Stocking ≤ 30 cm (%)	T	3	7.7	1.11	0.403
		Y	2	11.4	1.55	0.254
		T × Y	6	11.4	0.86	0.548

3.1.2. Stand Level

GSV increased over time, but the increase was similar among treatments (Y, $p < 0.001$, Table 2, Figure 3C). CGMV did not vary among treatments (T, $p = 0.791$, Table 2, Figure 3D). Ingrowth increased for the first five years after harvest and leveled off afterward (Y, $p < 0.001$, Table 2, Figure 3E). Ingrowth accounted for <1 m^2 ha^{-1} in each 5-year period, was mostly composed of balsam fir and did not vary among treatments (T, $p = 0.172$, Table 2). Mortality was low (Figure 3F) and mainly comprised of balsam fir (64%) over spruce (23%) and birch (13%). Nearly 85% of mortality was comprised of stems smaller than the mean DBH of all living trees at time of death. Mortality was similar among treatments for the first five years, but appeared to be higher in the unthinned control by year 10 (Figure 3F).

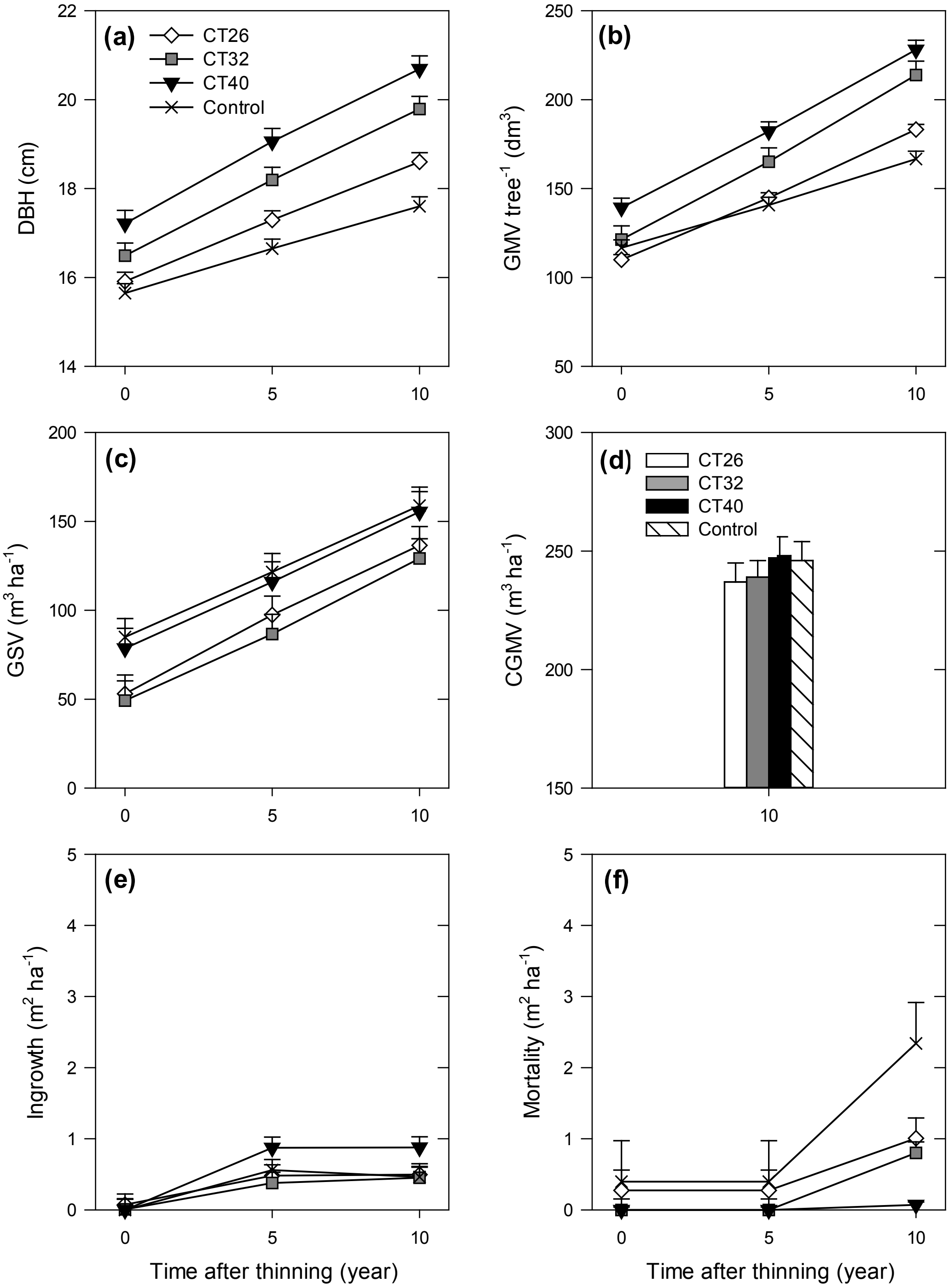

Figure 3. Mean tree- and stand-level development after four commercial thinning intensities from below (0%, 26%, 32%, 40% merchantable basal area removals). Dependent variables were: (**a**) mean diameter at breast height (DBH) of residual merchantable trees; (**b**) mean gross merchantable volume (GMV) of residual merchantable trees; (**c**) gross sawlog volume (GSV) per·ha^{-1}; (**d**) cumulative gross merchantable volume (CGMV) per·ha^{-1}; (**e**) ingrowth; and (**f**) mortality. Means (± SE) represent adjusted values from statistical analyses at the mean value of the covariate and are based on three replicates per treatment.

3.2. Structural Heterogeneity

3.2.1. Number of Large Trees and Shape of the Diameter Distribution

Thinning from below was generally respected, but harvesting also occurred in intermediate diameter classes (>16 cm) in all thinning treatments (Figure 4). In eight out of nine thinned EUs, diameter distributions were irregular immediately after thinning and became increasingly positively skewed over time (I_s closer to zero, except EU 2, Table 3, Figure 5 and Supplementary Figures S1 and S2). Thinning resulted in 240 large trees ha^{-1} compared to only 158 trees ha^{-1} in unthinned EUs at the end of the decennial period, for a gain of 51%. Given that total stand density after 10 years was 2230 trees ha^{-1} in thinned EUs and 2792 trees ha^{-1} in unthinned EUs, a greater proportion of density could be found as large trees in thinned EUs (11%) compared to the unthinned control (6%). The diameter distribution remained positively skewed and elongated its right tail with the development of two modes in EUs 1 and 3 ($k \leq -1.2$). Thus, thinned EUs tended to become more irregular over time (Table 3).

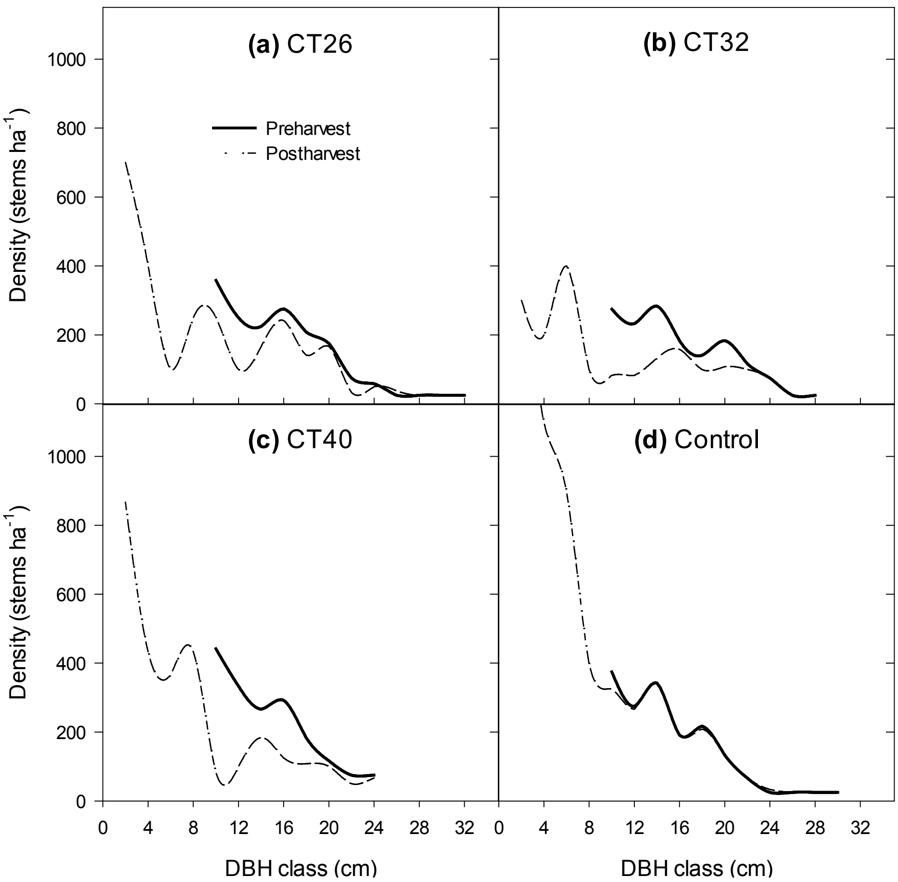

Figure 4. Preharvest and postharvest diameter distribution (2-cm classes) of four intensities of commercial thinning from below (26%, 32%, 40% and 0% merchantable basal area removals) (**a**–**d**). Lines are based on three replicates per treatment.

Table 3. Statistical parameters and structure of the diameter distribution of all trees (DBH >1.0 cm) for each experimental unit (EU) immediately postharvest (post) and after 10 years according to: the Weibull function (*c*), the coefficient of kurtosis (*k*), the symmetry index (I_s) and the interpretation of the structure. Abbreviations: bim, bimodal distribution; trt, thinning treatment.

Trt	**EU**	***c***		***k***		**I_s**		**Structure**	
		Post	**10 y**	**Post**	**10 y**	**Post**	**10 y**	**Post**	**10 y**
CT26	2	3.8	5.4	0.4	0.1	0.65	0.68	Regular	Regular
	10	1.1	1.0	−0.6	1.0	0.05	0.04	Irregular	Irregular
	12	1.7	1.1	0.5	−0.4	0.14	0.04	Irregular	Irregular
CT32	1	1.8	1.9	−1.0	−1.2	0.22	0.20	Irregular	Irregular, bim
	3	1.2	1.5	−1.3	−1.4	0.04	0.04	Irregular, bim	Irregular, bim
	7	1.7	1.1	−0.9	−0.8	0.24	0.04	Irregular	Irregular
CT40	5	1.2	1.1	1.5	0.1	0.05	0.04	Irregular	Irregular
	6	1.7	1.6	−0.2	−0.8	0.37	0.04	Irregular	Irregular
	8	1.4	1.5	−0.3	−0.9	0.05	0.04	Irregular	Irregular
Control	4	1.1	1.0	−1.1	−1.1	0.05	0.04	Irregular	Irregular
	9	1.5	1.6	0.3	−1.1	0.06	0.14	Irregular	Irregular
	11	1.3	2.3	−0.7	−0.6	0.06	0.43	Irregular	Irregular

The initial diameter distribution of unthinned EUs was also irregular (Table 3). In EUs 9 and 11, however, the diameter distribution became more symmetric, unimodal and closer to a regular structure as I_s moved toward 0.5 over the 10-year period (Table 3, Figure 5 and Supplementary Figure 1 and 2). This consolidation was centered on one mode in intermediate diameter classes (16 cm) with 1700 fewer saplings ha^{-1} on average after 10 years than immediately postharvest (Figure 5).

3.2.2. Regeneration Density and Stocking

Mean postharvest regeneration density for all height classes combined was over 75000 stems ha^{-1}, with the vast majority (63400 stems ha^{-1}) ≤30 cm in height and composed of balsam fir (96%). Balsam fir was well stocked with an average distribution of 88% for the study site, compared to 17% for white spruce and 7% for black spruce.

Over the first 5-year period, the mean density of regeneration ≤30 cm in height decreased from 63400 stems ha^{-1} postharvest to 17800 stems ha^{-1} at year 5 and increased substantially to 176400 stems ha^{-1} after 10 years (Y, $p < 0.001$, Table 2, Figure 6A). Fluctuations were statistically similar among thinning treatments. The density of regeneration >30 cm in height decreased slightly over the 10-year period (Y, $p = 0.002$, Table 2, Figure 6B), but did not vary among treatments.

Treatment or period effects were not found in the stocking of regeneration ≤30 cm in height, which remained >60% in all treatments after 10 years ($p \geq 0.254$, Table 2, Figure 6C). Stocking of regeneration >30 cm in height decreased from 100% to 67% in CT32, while remaining stable in other treatments over the 10-year period. Stocking appeared to be higher in CT26 and CT40 (both 100%) compared to CT32 after 10 years (Figure 6D). Combining all treatments, height classes and species, stocking after 10 years remained quite similar to postharvest stocking at 93%. Balsam fir was still dominant with 90% stocking, followed by black spruce with 10% and white spruce with 3%.

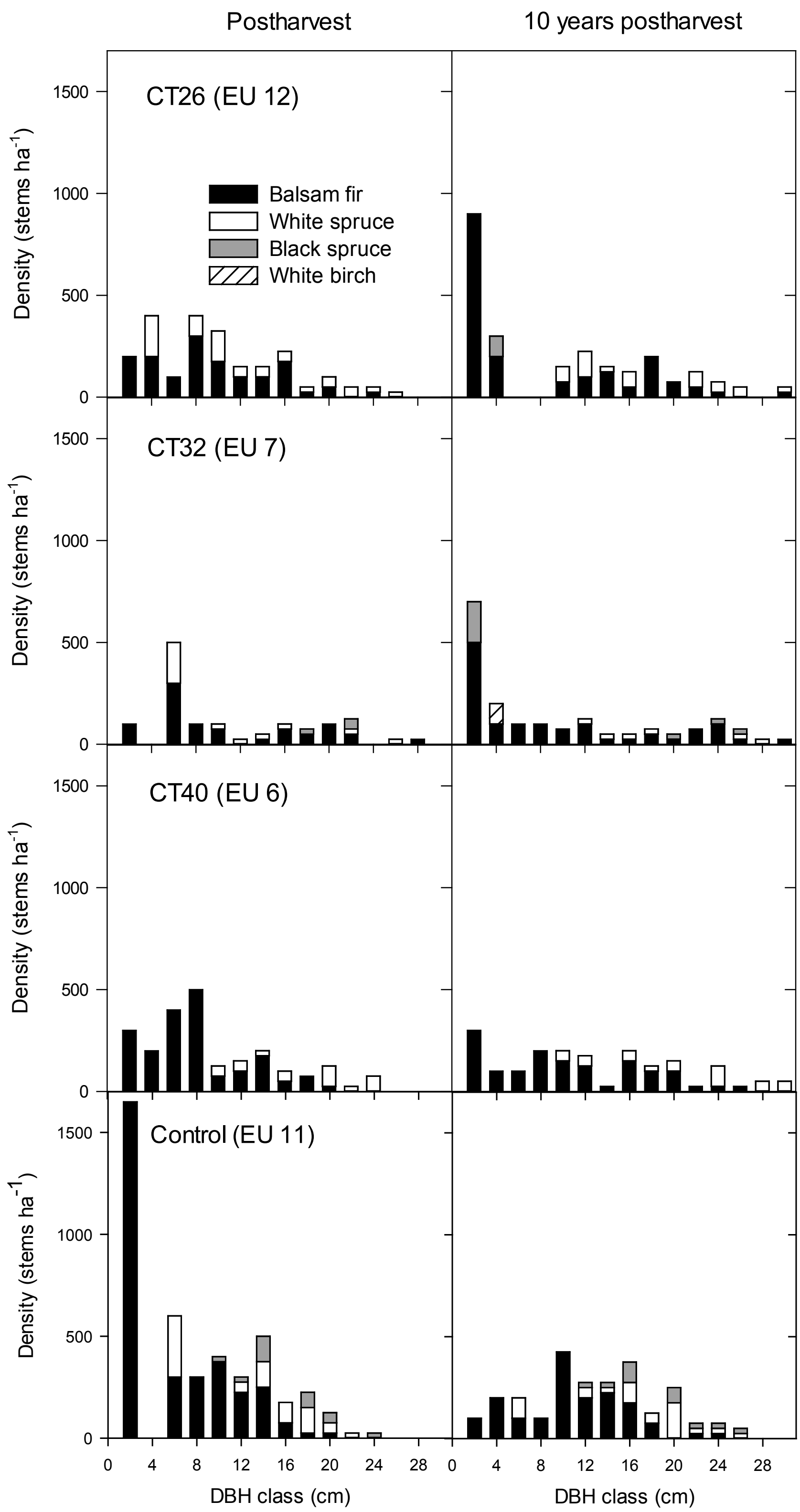

Figure 5. Diameter distribution (2-cm classes) of selected experimental units (EUs) in each commercial thinning treatment: 26% (EU 12), 32% (EU 7) and 40% (EU 6) merchantable basal area removals and an unthinned control (EU 11). Distributions are presented immediately postharvest and 10 years after thinning. Distributions for the remaining EUs can be found online as Supplementary Figures.

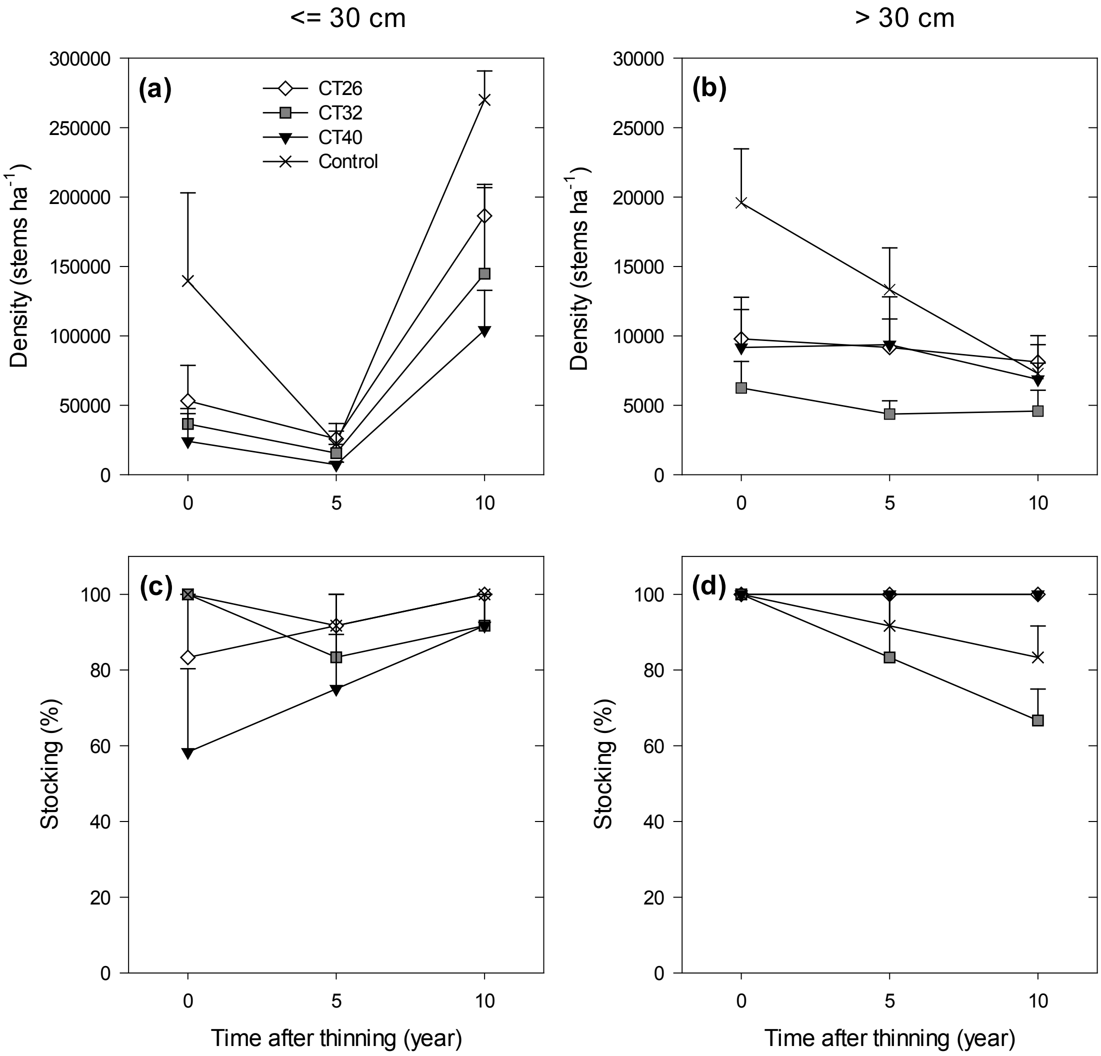

Figure 6. Decennial development of (**a**,**b**) regeneration density and (**c**,**d**) stocking by height class (≤30 cm; >30 cm) after four commercial thinning intensities from below (0%, 26%, 32% and 40% merchantable basal area removals).

4. Discussion

4.1. Growth and Yield

4.1.1. Mean Tree Level

Compared to the unthinned control, CT32 and CT40 resulted in increases of 2.2–3.1 cm in mean DBH and 47–62 dm^3 in GMV·$tree^{-1}$ after 10 years. These gains are substantial, especially in terms of volume, and reflect the high productivity of this site. Results are in line with Hypotheses 1a and 1b, except for CT26. A lack of differences among treatments in year 0 suggests that increased tree size resulted mainly from increased growth of residual trees rather than immediate removal of smaller trees [48]. Results also indicate a delay in response of at least five years, which may be explained by the late thinning entry.

The benefits of thinning on radial growth response have long been recognized in Europe and North America [24,49]. Evidence of increased tree size in species, like Norway spruce (*Picea abies* (L.)

H. Karst.) and European beech (*Fagus sylvatica* L.), were reported across several countries, including Germany, Switzerland, Denmark and Sweden [23]. In North America, examples include deciduous angiosperms of the central and northern regions [50,51] and conifers of the northern region [52–54]. There is no universal response, however, and results vary with site quality, timing of first thinning, type of thinning, species and the definition of the response variable [7]. The advantages of increased diameter and volume per tree include reaching a given technical rotation age earlier and reducing harvesting and processing costs during final overstory removal.

4.1.2. Stand Level

Thinning generated as much GSV or CGMV as the unthinned control with fewer trees. Results are in accordance with our initial hypothesis (1c), as well as the current yield hypothesis used in Quebec, Canada, which states that the CGMV produced in a commercially thinned stand at the end of the rotation is equivalent to that of an unthinned stand [55]. These results can be explained by the increased growth of residual trees in thinned EUs, low and similar ingrowth among treatments, and low mortality in the unthinned control. A 10% mortality threshold in BA has been recommended to determine the success of partial cuts [56]. Mortality ranged from 1%–3% after thinning and 6% in the control. Low mortality can be attributed to the conservation of mature forest surrounding the study site and large buffer zones (50 m) between each EU that could have helped reduce windthrow. Furthermore, EUs were not placed adjacent to skidding trails, and this may have helped prevent potential mortality. Our findings do not support the suggestion that CT increases sawlog volume or merchantable stand yield. Results can vary depending on several factors, including site quality and tree species. In Sweden, CT can lead to lower CGMV compared to unthinned stands across a wide range of sites and thinning treatments for Scots pine (*Pinus sylvestris* L.) [57].

4.2. Structural Heterogeneity

4.2.1. Number of Large Trees and Shape of the Diameter Distribution

In eight out of nine thinned EUs, we found a diversification of stand structure reflected by decreases in I_s, with an increasingly positively-skewed diameter distribution and an elongated right tail toward larger trees. This is in line with Hypothesis 2b and can be attributed to the type of thinning operation, which was mainly from below. Thinning maintained an important component of large trees and favored sapling survival, both of which helped develop heterogeneity in the shape of the diameter distribution. Despite the greater abundance of sapling density in unthinned EUs (2900 saplings ha^{-1}) compared to thinned EUs (1300 saplings ha^{-1}), a consolidation of the structure occurred toward a unimodal regular structure, and the diameter distribution became more symmetrical in two of the three unthinned EUs after 10 years. This can be mainly attributed to low sapling survival and fewer large trees than in thinned EUs.

Thus, the type of CT can be used to target specific diameter distributions. Examples include variable density thinning [21,58] and conversion thinning [22], whereby operations are deliberately aimed at increasing structural heterogeneity. Thinning from below can generate an increase in positive skewness, because the removal of smaller diameter trees truncated the left-hand tail of the distribution curve [23]. Thinning from above, however, can lead to a bimodal distribution, with peaks for ingrowth and larger trees, respectively [23]. Further investigations into the long-term effects of such thinning approaches on wood production objectives would be useful to determine the range of thinning operations that can meet both objectives. The potential influence of plot size also warrants further evaluation because 400 m^2 plots may not be optimal in describing diameter distributions.

For large trees, the 51% gain reported in our study corroborates our initial hypothesis (2a) and findings from the literature [59,60], albeit not at the same level of magnitude. Over a long-term period (≥25 years), increases of at least 400 larger trees ha^{-1} were reported after 42%–45% BA removals in Norway spruce and Scots pine stands of Finland [59,60]. Also noteworthy in our study is the potential benefit of species mixtures in meeting structural heterogeneity objectives. As shown by Figure 5 and Supplementary Figures, the spruce component represented 21% of all large trees in thinned EUs after 10 years. Spruce differs from fir in terms of shade tolerance (white spruce is moderately shade tolerant), growth rate and longevity. Favoring spruce over fir during the thinning operation offers additional opportunities to further develop structural attributes, especially if final harvesting is delayed, because spruce has greater longevity than fir. Species mixtures can provide increased flexibility against insects, diseases and climate change. Tree species richness in managed forests has also shown positive relationships with the production of tree biomass, soil carbon storage and game [61].

One of the novel findings from our study is that thinning mainly from below can be used to develop structural heterogeneity in managed forests rather than simplifying them. Increasing structural heterogeneity can provide several benefits to forest biodiversity conservation by sustaining species, increasing habitat diversity, improving connectivity and sustaining ecosystem processes [62]. Results are corroborated by another thinning study in lodgepole pine (*Pinus contorta* Doug. ex. Loud.) stands of British Columbia, Canada [63]. Modeling work in coniferous stands of the Pacific Northwest, USA, is also in accordance with our finding that CT can expedite the development of large live trees without reducing CGMV [25]. While different aspects of old-growth stand structures can be created in a short time frame through silviculture, developing the full suite of attributes, such as coarse woody debris, will require more time [7].

There is a potential caveat in developing old-growth structural attributes in fir-dominated stands: balsam fir is a short-lived, decay-prone species and susceptible to spruce budworm outbreaks. It should be noted, however, that gap-driven old-growth balsam fir stands with a complex structure can occupy up to 75% of the landscape area in many perhumid ecosystems of eastern North America, where widespread stand-initiating events are rare events [35,64]. Furthermore, management actions can prevent or limit budworm damage in areas targeted for developing old-growth structure (e.g., spraying). Even if the balsam fir component in these stands may not always last beyond 85 years, the stand would still provide increased structural heterogeneity for 30 years (55 to 85) or until final overstory removal. Moreover, the spruce component (>25% merchantable BA) is much longer-lived than fir and could play an important role in stand development. For these reasons, attempts at developing structural heterogeneity in these stands should not be overlooked.

4.2.2. Regeneration Density and Stocking

Balsam fir dominated the understory over time and thinning provided similar tree regeneration density and stocking compared to the unthinned control. This does not corroborate our initial hypothesis (2c). The density of regeneration ≤30 cm increased substantially during the second 5-year period. This increase was mostly comprised of seedlings <6 cm that likely became established after a heavy seed year from mature balsam fir trees in the stand [36]. Ten years after crown thinning in spruce-fir stands of Maine, USA, small (11–60 cm) coniferous and hardwood regeneration were much more abundant in thinned stands compared to unthinned stands [65]. However, lower regeneration densities should be expected when thinning from below due to smaller canopy openings and lower windthrow mortality [65]. Comparisons with our study are also limited because we included seedlings <11 cm in height in our analyses.

As for taller regeneration (>30 cm in height), we did not find differences among treatments 10 years after CT. We hypothesize that tree removal increased available light in the understory, and tree mortality had a similar effect in the unthinned control. Lack of differences between thinned and unthinned stands were also reported for medium (61–140 cm) and large (≥141 cm) coniferous regeneration density in fir-dominated sites 10 years postharvest [65]. In terms of stocking, all thinning treatments remained relatively well stocked after 10 years (≥60%). Hence, thinning compared favorably to the unthinned control in most cases, and the regenerating cohort should be sufficient to ensure stand renewal if well protected during final overstory removal [66].

Findings from the literature are inconsistent, because tree regeneration is a highly stochastic process [67], and the response after thinning can show large variability due to stand and site conditions, microsite heterogeneity, seedling clustering and thinning intensity [68]. Hence, more research is needed to better understand regeneration mechanisms after thinning.

5. Conclusions

Results from our case study suggest that thinning mainly from below was generally successful. At the mean tree level, 32%–40% basal area removals resulted in gains of 12%–18% (2.2–3.1 cm) in diameter and 28%–37% (47–62 dm^3) in gross merchantable volume $tree^{-1}$ compared to the unthinned control. At the stand level, all thinning intensities generated as much gross sawlog volume and cumulative gross merchantable volume as the unthinned control with fewer trees despite being carried out in a relatively old stand for a first thinning entry. Compared to the unthinned control, thinning also helped develop structural heterogeneity as measured by the shape of the diameter distribution and the number of large trees. Thinning compared favorably with the unthinned control in terms of regeneration density and stocking, with a dense and well-distributed cohort of balsam fir in all treatments after 10 years. Developing silvicultural approaches, such as this one, is in line with using natural variability concepts in managing ecological systems.

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Author Contributions

All authors contributed equally to this work.

Supplementary

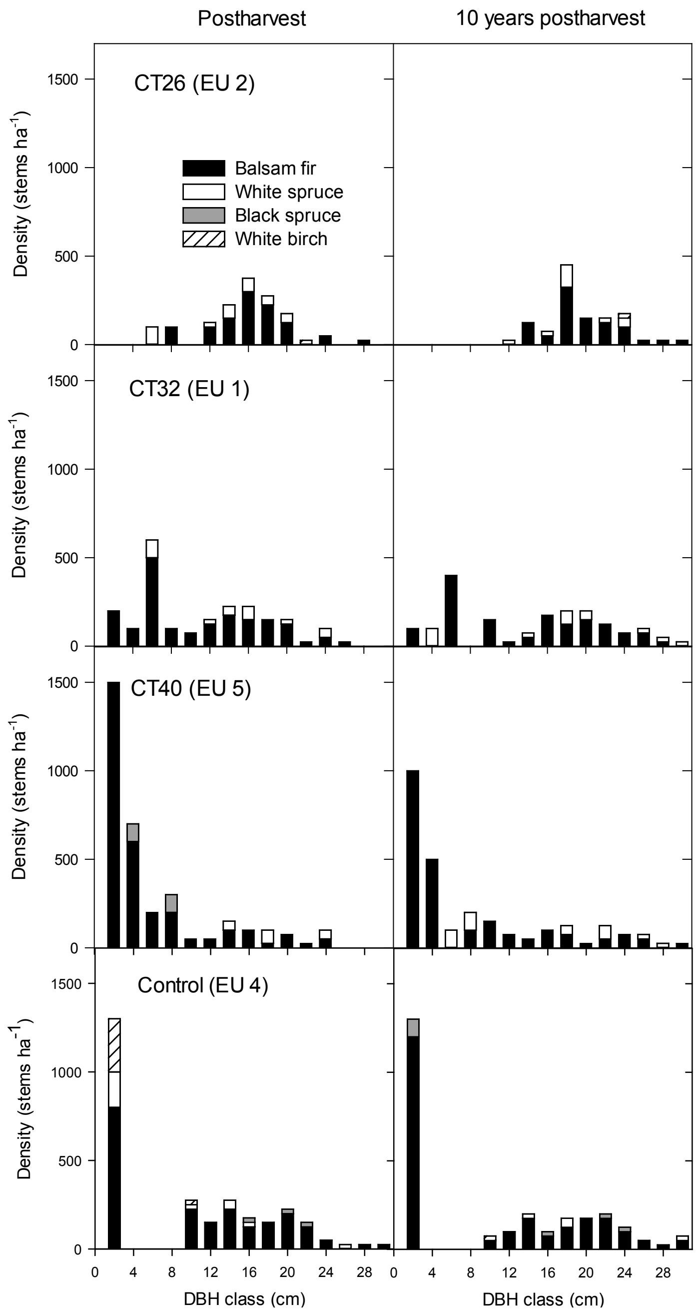

Figure S1. Diameter distribution (2-cm classes) of experimental units (EUs) in each commercial thinning treatment: 26% (EU 2), 32% (EU 1) and 40% (EU 5) merchantable basal area removals and an unthinned control (EU 4). Distributions are presented immediately postharvest and 10 years after thinning.

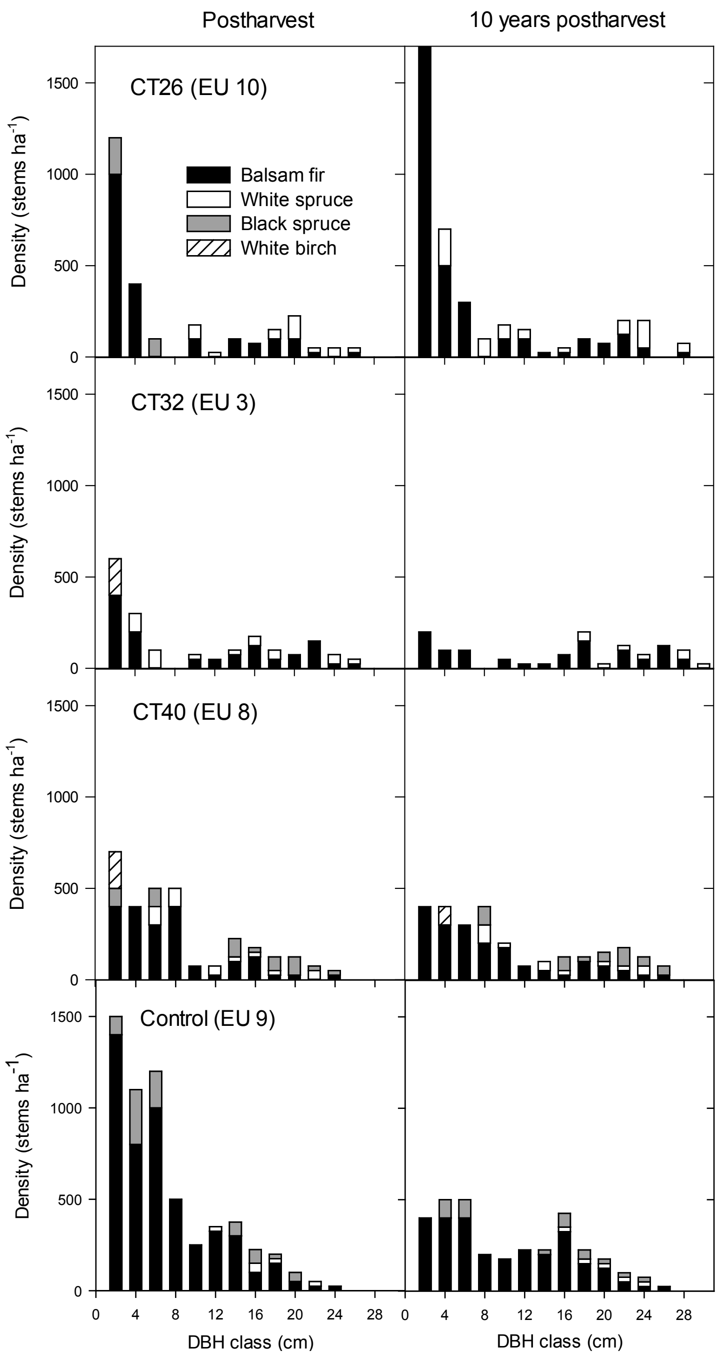

Figure S2. Diameter distribution (2-cm classes) of experimental units (EUs) in each commercial thinning treatment: 26% (EU 10), 32% (EU 3) and 40% (EU 8) merchantable basal area removals and an unthinned control (EU 9). Distributions are presented immediately postharvest and 10 years after thinning.

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Schütz, J.P.; Pukkala, T.; Donoso, P.J.; von Gadow, K. Historical emergence and current application of CCF. In *Continuous Cover Forestry*, 2nd ed.; Pukkala, T., von Gadow, K., Eds.; Springer: Dordrecht, The Netherlands, 2012; pp. 1–28.
2. Simpson, J. 1903. *The New Forestry*, 2nd ed.; Pawson & Brailsford Ltd: Sheffield, UK, 1903; p. 220.
3. Kerr, G. The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. *Forestry* **1999**, *72*, 191–205.
4. Franklin, J.F. Toward a new forestry. *Am. For.* **1989**, *95*, 37–44.
5. Seymour, R.S.; Hunter, M.L. *New forestry in eastern spruce-fir forests: Principles and applications to Maine*. Maine Agricultural and Forest Experiment Station Miscellaneous: Orono, ME, USA, 1992; p. 36.
6. Lorimer, C.G.; Freelich, L.E. Natural disturbance regimes for old-growth northern hardwoods: Implications for restoration efforts. *J. For.* **1994**, *92*, 33–38.
7. Oliver, C.; Larson, B. *Forest Stand Dynamics*, 2nd ed.; Wiley: New York, NY, USA, 1996; p. 520.
8. O'Hara, K.L. Silviculture for structural diversity: A new look at multiaged systems. *J. For.* **1998**, *96*, 4–10.
9. Landres, P.B.; Morgan, P.; Swanson, F.J. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* **1999**, *9*, 1179–1188.
10. O'Hara, K.L.; Ramage, B.S. Silviculture in an uncertain world: Utilizing multi-aged management systems to integrate disturbance. *Forestry* **2013**, *86*, 401–410.
11. Gauthier, S.; Vaillancourt, M.A.; Kneeshaw, D.; Drapeau, P.; de Granpré, L.; Claveau, Y.; Paré, D. Aménagement écosystémique: Origines et fondements. In *Aménagement Ecosystémique en Forêt Boréale*; Presses del'Université du Québec: Québec, Canada, 2008; pp. 11–40.
12. Boucher, Y.; Arseneault, D.; Sirois, L.; Blais, L. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Landsc. Ecol.* **2009**, *24*, 171–184.
13. Puettmann, K.J.; Coates, K.D.; Messier, C. *A Critique of Silviculture: Managing Complexity*; Island Press: Washington, DC, USA, 2008; p. 208.
14. Arielle Angers, V.; Messier, C.; Beaudet, M.; Leduc, A. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manag.* **2005**, *217*, 275–293.
15. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537.
16. Schütz, J.P. Opportunities and strategies of transforming regular forests to irregular forests. *For. Ecol. Manag.* **2001**, *151*, 87–94.
17. Singer, M.T.; Lorimer, C.G. Crown release as a potential old-growth restoration approach in northern hardwoods. *Can. J. For. Res.* **1997**, *27*, 1222–1232.
18. Lindh, B.C.; Muir, P.S. Understory vegetation in young Douglas-fir forest: Does thinning help restore old–growth composition? *For. Ecol. Manag.* **2004**, *192*, 285–296.

19. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Long-term responses of ecosystem components to stand thinning in young lodgepole pine forest. III Growth of crop trees and coniferous stand structure. *For. Ecol. Manag.* **2006**, *228*, 69–81.
20. Choi, J.; Lorimer, C.G.; Vanderwerker, J.M. A simulation of the development and restoration of old–growth structural features in northern hardwoods. *For. Ecol. Manag.* **2007**, *249*, 204–220.
21. O'Hara, K.L.; Leonard, L.P.; Keyes, C.R. Variable–Density thinning and a marking paradox: Comparing prescription protocols to attain stand variability in coast redwood. *West. J. Appl. For.* **2012**, *27*, 143–149.
22. Drössler, L.; Nilsson, U.; Lundqvist, L. Simulated transformation of even-aged Norway spruce stands to multi–layered forests: An experiment to explore the potential of tree size differentiation. *Forestry* **2014**, *87*, 239–248.
23. Assmann, E. *The Principles of Forest Yield Study*; Pergamon Press Ltd: New York, NY, USA, 1970; p. 506.
24. Ministère des Ressources Naturelles (MRN). *Avis Scientifique: Éclaircie Commerciale Pour le Groupe de Production Prioritaire SEPM*; Gouv du Québec, Ministère des Ressources Naturelles (MRN): Quebec City, QC, Canada, 2003; p. 80.
25. Busing, R.T.; Garman, S.L. Promoting old–growth characteristics and long-term wood production in Douglas–fir forests. *For. Ecol. Manag.* **2002**, *160*, 161–175.
26. Lafond, V.; Cordonnier, T.; de Coligny, F.; Courbaud, B. Reconstructing harvesting diameter distribution from aggregate data. *Ann. For. Sci.* **2012**, *69*, 235–243.
27. Boulanger, Y.; Arseneault, D. Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Can. J. For. Res.* **2004**, *34*, 1035–1043.
28. Frank, R.M.; Bjorkbom, J.C. A silvicultural guide to spruce-fir in the northeast. In *Gen. Tech. Rep. NE-6*; USDA Forestry Service.: Asheville, NC, USA,1973; p. 29.
29. Bégin, E.; Bégin, J.; Bélanger, L.; Rivest, L.P.; Tremblay, S. Balsam fir self-thinning relationship and its constancy among different ecological regions. *Can. J. For. Res.* **2001**, *31*, 950–959.
30. Pothier, D.; Savard, F. *Actualisation des Tables de Production Pour les Principales Espèces Forestières du Québec*; Gouv Québec, Min. Ress. Nat., Dir. Inv. For., Ministère des Ressources naturelles: Québec, Canada, 1998; p. 183.
31. Zeide, B.L. Thinning and growth: a full turnaround. *J. For.* **2001**, *99*, 20–25.
32. Fortin, M.; Bernier, S.; Saucier, J.P.; Labbé, F. Une relation hauteur–diamètre tenant compte de l'influence de la station et du climat pour 20 espèces commerciales du Québec. *In Mathieu Fortin*; Direction de la recherche forestière: Québec, Canada, 2009; p. 22.
33. Fortin, M.; DeBlois, J.; Bernier, S.; Blais, G. Mise au point d'un tarif de cubage général pour les forêts québécoises: Une approche pour mieux évaluer l'incertitude associée aux prévisions. *For. Chron.* **2007**, *83*, 754–765.
34. Nappi, A.; Drapeau, P. Pre–fire forest conditions and fire severity as determinants of the quality of burned forests for deadwood-dependent species: The case of the black-backed woodpecker. *Can. J. For. Res.* **2011**, *41*, 994–1003.
35. McCarthy, J.W.; Weetman, G. Stand structure and development of an insect–mediated boreal forest landscape. *For. Ecol. Manag.* **2007a**; *241*, 101–114.

36. McCarthy, J.W.; Weetman, G. Self–thinning dynamics in a balsam fir (*Abies balsamea* (L.) Mill.) insect-mediated boreal forest chronosequence. *For. Ecol. Manag.* **2007b**; *241*, 295–309.
37. Ruel, J.C.; Fortin, D.; Pothier, D. Partial cutting in old-growth boreal stands: An integrated experiment. *For. Chron.* **2013**, *89*, 360–369.
38. Brown, H.; Prescott, R. *Applied Mixed Models in Medicine*, 2nd ed.; John Wiley & Sons, Inc: Chichester, UK, 2006; p. 455.
39. Mead, R. *The Design of Experiments-Statistical Principles for Practical Application*; Cambridge University Press: New York, NY, USA, 1988; p. 620.
40. Littell, R.C.; Milliken, G.A.; Stroup, W.W.; Wolfinger, R.D.; Schabenberger, O. *SAS for Mixed Models*, 2nd ed.; SAS Institute: Cary, NC, USA, 2006; p. 814.
41. Westfall, P.H.; Tobias, R.D.; Wolfinger, R.D. *Multiple Comparisons and Multiple Tests Using SAS*, 2nd ed.; SAS Institute: Cary, NC, USA, 2011; p. 625.
42. Côté, G.; Bouchard, M.; Pothier, D.; Gauthier, S. Linking stand attributes to cartographic information for ecosystem management purposes in the boreal forest of eastern Québec. *For. Chron.* **2010**, *86*, 511–519.
43. Barrette, M.; Bélanger, L. Reconstitution historique du paysage préindustriel de la région écologique des hautes collines du Bas-Saint-Maurice. *Can. J. For. Res.* **2007**, *37*, 1147–1160.
44. Bailey, R.L.; Dell, T.R. Quantifying diameter distributions with the Weibull function. *For. Sci.* **1973**, *19*, 97–104.
45. Wyszomirski, T. Detecting and displaying size bimodality: Kuz trtosis, skewness and bimodalizable distributions. *J. Theor. Biol.* **1992**, *158*, 109–128.
46. Lorimer, C.G.; Krug, A.G. Diameter distributions in even–aged stands of shade-tolerant and midtolerant tree species. *Am. Midl. Nat.* **1983**, *109*, 331–345.
47. Ruel, J.C.; Doucet, R.; Boily, J. Mortality of balsam fir and black spruce advance growth 3 years after clear-cutting. *Can. J. For. Res.* **1995**, *25*, 1528–1537.
48. Ministry of Forests. *Guidelines for Developing Stand Density Management Regimes*; British Columbia Ministry Forestry, Forestry Practices British: Victoria, Canada, 1999; p. 94.
49. Büsgen, M.; Münch, E. *The Structure and Life of Forest Trees*; Chapman & Hall Ltd: London, UK, 1929; p. 436.
50. Schlesinger, R.C. Increased growth of released white oak poles continues through two decades. *J. For.* **1978**, *76*, 726–727.
51. Ward, J.S. Crop tree release increases growth of mature red oak sawtimber. *North J. Appl. For.* **2002**, *19*, 149–154.
52. Pelletier, G.; Pitt, D.G. Silvicultural responses of two spruce plantations to midrotation commercial thinning in New Brunswick. *Can. J. For. Res.* **2008**, *38*, 851–867.
53. Krause, C.; Laplante, S.; Plourde, P.Y. Transversal tracheid dimension in thinned black spruce and Jack pine stands in the boreal forest. *Scand. J. For. Res.* **2011**, *26*, 477–487.
54. Gagné, L.; Lavoie, L.; Binot, J.M. Croissance et propriétés mécaniques du bois après éclaircie commerciale dans une plantation d’épinette blanche (*Picea glauca*) âgée de 32 ans. *Can. J. For. Res.* **2012**, *42*, 291–302.
55. Poulin, J. Bureau du forestier en chef. Manuel de détermination des possibilités forestières 2013–2018. In *Fascicule 35*; Gouv. Québec: Roberval, Canada, 2013; pp. 95–98.

56. Coates, K.D. Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the Interior Cedar–Hemlock forests of Northwestern British Columbia. *Can. J. For. Res.* **1997**, *27*, 1695–1701.
57. Nilsson, U.; Agestam, E.; Ekö, P.M.; Elfving, B.; Fahlvik, N.; Johansson, U.; Karlsson, K.; Lundmark, T.; Wallentin, C. Thinning of Scots pine and Norway spruce monocultures in Sweden -Effects of different thinning programmes on stand level gross-and net stem volume production. *Stud. For. Suec.* **2010**, *219*, 46.
58. Carey, A.B. Bioheterogeneity and restoration of biodiversity in temperate coniferous forest: Inducing spatial heterogeneity with variable-density thinning. *Forestry* **2003**, *76*, 127–136.
59. Mäkinen, H.; Isomäki, A. Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. *For. Ecol. Manag.* **2004a**, *201*, 295–309.
60. Mäkinen, H.; Isomäki, A. Thinning intensity and long-term changes in increment and stem form of Scots pine trees. *For. Ecol. Manag.* **2004b**, *203*, 21–34.
61. Lindenmayer, D.B.; Franklin, J.F.; Fisher, J. General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biol. Conserv.* **2006**, *131*, 433–445.
62. Gamfeldt, L.; Snäll, T.; Bagchi, R.; Jonsson, M.; Gustafsson, L.; Kjellander, P.; Ruiz-Jaen, M.C.; Fröberg, M.; Stendahl, J.; Philipson, C.D.; *et al*. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* **2013**, *4*, 1340.
63. Sullivan, T.P.; Sullivan, D.S.; Lindgren, P.M.F.; Ransome, D.B. Stand structure and the abundance and diversity of plants and small mammals in natural and intensively managed forests. *For. Ecol. Manag.* **2009**, *258S*, S127–S141.
64. Barrette, M.; Bélanger, L.; de Grandpré, L. Preindustrial reconstruction of a perhumid midboreal landscape, Anticosti Island, Quebec. *Can. J. For. Res.* **2010**, *40*, 928–942.
65. Olson, M.G.; Meyer, S.R.; Wagner, R.G.; Seymour, R.S. Commercial thinning stimulates natural regeneration in spruce-fir stands. *Can. J. For. Res.* **2014**, *44*, 173–181.
66. Pothier, D. Évolution de la régénération après la coupe de peuplements récoltés selon différents procédés d'exploitation. *For. Chron.* **1996**, *72*, 519–527.
67. Bataineh, M.M.; Kenefic, L.S.; Weiskittel, A.R.; Wagner, R.G.; Bissette, J.C. Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian Forest of Maine, USA. *For. Ecol. Manag.* **2013**, *306*, 96–106.
68. Ares, A.; Neill, A.R.; Puettmann, K.J. Understory abundance, species diversity and functional attribute response to thinning in coniferous stands. *For. Ecol. Manag.* **2010**, *260*, 1104–1113.