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Can Retention Harvest Maintain Natural Structural Complexity? A Comparison of Post-Harvest and Post-Fire Residual Patches in Boreal Forest

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Abstract: Variable retention harvest promotes biodiversity conservation in managed boreal forests by ensuring forest continuity and structural complexity. However, do post-harvest and post-fire patches maintain the same structural complexity? This study compares post-harvest and post-fire residual patches and proposes retention modalities that can maintain the same structural complexity as in natural forests, here considering both continuous forest stands and post-fire residual patches. In boreal black spruce forests, 41 post-fire residual patches, and 45 post-harvest retention patches of varying size and ages (exposure time to disturbed matrix) and 37 continuous forest stands were classified into six diameter structure types. Types 1 (inverted-J) and 2 (trunked-unimodal) characterized stands dominated by small trees. The abundance of small trees decreased and the abundance of large trees increased from Type 1 to Type 6. Type 6 had the most irregular structure with a wide range of diameters. This study indicates that: (1) old post-harvest residual retentions maintained the range of structural complexity found in natural stands; (2) Types 1 and 2 were generally associated with young post-fire patches and post-harvest retention clumps; (3) the structure of residual patches containing only small trees was usually younger (in terms of the age of the original forest from which residual patches were formed) than those with larger trees. To avoid the risk of simplifying the structure, retention patches should be intentionally oriented towards Types 3–6, dominated by intermediate and large trees.

Keywords: diameter structure; structural attributes; ecosystem based management; disturbance; black spruce-feathermoss forest; continuous forest

1. Introduction

In boreal forests, landscape mosaics are now as likely to have been shaped by harvest as by fire [1]. At the landscape scale, fire severity is spatially heterogeneous, with partially or entirely intact tree patches in the burned matrix, here called post-fire residual patches. These residual patches are believed to preserve pre-fire continuous forest structure, including old growth structure. By preserving the structural attributes of old-growth forests, post-fire residual patches could represent a refuge habitat for many forest species [2–4], and could also constitute a source of propagules for recolonization of the burned matrix [5,6]. However, in managed landscapes, harvesting, including large-scale clearcuts practiced in the last half century, progressively homogenizes the forest mosaic and simultaneously reduces the proportion of old-growth forests [7,8]. Consequently, the simplification of internal structure of forest stands could cause a loss of habitat for species that require structures associated with irregular old-growth forests [9,10]. It is increasingly recognized that increasing the structural complexity in managed forests by mimicking natural disturbance patterns can promote biodiversity [11]. Therefore, it is necessary to develop forest practices that maintain the structural complexity of natural forest stands [12], such as that observed within unburned continuous forests or post-fire residual patches [13,14].

The internal structure of forest stands, i.e., the vertical and horizontal arrangement of trees, is a key attribute in maintaining forest productivity and biodiversity of old-growth forests [15,16]. Forest stand dynamics are usually evaluated by observing the changes in structure and composition over time [17]. Forest stand dynamics are marked by several stages ranging from establishment, structural maturity, canopy closure and finally by reopening of the stand during the breakup phase [17]. Consequently, the structural changes induced by the closure and reopening of the canopy can affect several species, particularly plants and mosses occupying the forest floor [18,19] or birds and insects associated with internal stand structure [20,21]. In the boreal forest, an unimodal regular diameter structure is often associated with a juvenile stand, while mature stands often have an irregular diameter structure with stem density in all sizes and a reopening of the canopy [22]. Many factors may influence both forest stand dynamics and structure after fire or after harvest, including the type of original disturbance [15], the magnitude of past human impact [23,24], the initial local conditions before disturbance [25–28], time since last fire and soil characteristics [29].

In managed boreal forests, variable retention harvesting is the most frequently suggested technique to retain the structural attributes of original continuous forest stands within a cutblock. Variable retention harvesting leaves living and dead trees and woody debris of the original forest stand in unharvested forest patches, called "post-harvest retention patches" [30,31]. However, it is currently unknown whether the selection of post-harvest residual patches in cutblocks, which is generally based on operational criteria such as the market value of the residual patch, proximity to water bodies, field accessibility and tree age, permits post-harvest residual patches to preserve a variety of structural types similar to those characterizing post-fire residual patches or continuous forest stands [32,33]. In addition, it is also unknown whether the structural characteristics of retention patches are maintained throughout time after harvest, because of their susceptibility to windthrow [34,35]. A comparison of forest structure of post-harvest and post-fire residual patches is required for developing forestry strategies that can maintain biological diversity after harvest.

This study aims to compare the structural complexity of current post-harvest and post-fire residual patches and unburned continuous forest stands (as controls) in black spruce dominated stands located in northwestern Quebec, Canada. More specifically, we wish (1) to develop a classification of post-fire and post-harvest residual patch structural types and continuous forest stands based on their diameter distribution; (2) to describe the internal structural complexity and forest canopy closure of the generated structural types; (3) to identify factors that may explain the differences between structural types; (4) to determine if stands of post-harvest residual patches maintain the variety of structural types observed in post-fire residual patches and continuous forest stands. Finally, in order to evaluate the link between patch structural complexity and their temporal dynamics in black spruce boreal forests, we have characterized the structural types in terms of their deadwood dynamics on a deadwood diagram developed by Moussaoui et al. [28].

2. Materials and Methods

2.1. Study Area

The study area is located between 74°–80° W and 49°–51° N (Figure 1), in the eastern Canadian boreal black spruce-feathermoss forest characterized by dense stands (canopy cover 40%–80%) and dominated by black spruce (*Picea mariana* Mill., BSP) with jack pine (*Pinus banksiana* Lamb), balsam fir (*Abies balsamea* [L.] Mill), birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides*

Michx.). The topography of this area forms an undulating plain. The mineral soil type is composed primarily of glaciolacustrine clay in the west, and clay till in the east [36]. The mean annual temperature varies between −2.5 and 0.0 °C, and the mean annual precipitation varies between 700 and 900 mm and the climate is subpolar, continental sub-humid [37,38].

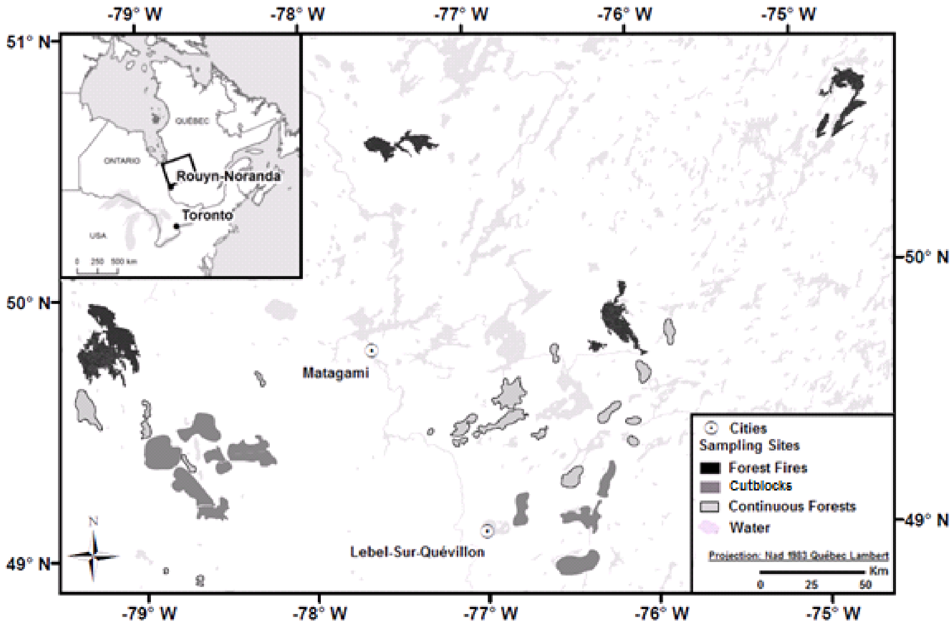

Figure 1. Location of 125 study sites in the black spruce boreal forest. Forty-one post-fire residual patches located in forest fires (black); 47 post-harvest residual patches located in cutblocks (dark gray) and 37 continuous forest stands are represented in pale gray surrounded in black.

Fire is the main natural disturbance that shapes the forest landscape in the study area [39]. The fire cycle was historically relatively short, in the order of 100–200 years [40] and currently it is lengthening and is estimated at over 400 years. Accordingly, the effects of forest harvest have become the main source of disturbance to the landscape [8,41]. Since the late 1980s, the harvesting method commonly used has been harvest with protection of regeneration and soils (CPRS in French), which consists of harvesting all merchantable stems (DBH > 9 cm) in cutblocks with a maximum size of 250 hectares. Retention patches were placed linearly between these cutblocks (separators) with a width of 60–100 m and in the form of large patches (3–10 ha) within the cutblocks for moose [42]. In the last decade, small forest clumps and large intact forest patches are two new retention types that have been used in order to maintain structural attributes similar to those created by fires [43,44].

2.2. Location of the Study Stands

Three stand origins were studied: Post-fire residual patches, post-harvest retention patches and undisturbed continuous forests. Six fires, including three young fires (0–19 years old) and three old fires (20–40 years), were selected using the fire maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF). Then, five to eight residual patches were selected per fire for a total of 41 post-fire residual patches (Figure 1). The selection of cutblocks was undertaken using eco-forestry maps and recent harvest GIS layers of three forestry companies and harvest licenses (TEMBEC UAF 085-51, and EACOM UAF 086-64 and PF Résolu PRAN 087-62). Thirteen cutblocks were studied: Seven young cutblocks (0–19 years) with retention in clumps and large islands, and six old cutblocks (20–40 years) with linear separators and large islands. Three to five retention patches were selected per cutblock for a total of 47 post-harvest retention patches (Figure 1). The residual patches were: (1) randomly selected from accessible patches (<1 km from a road) using ArcGis 10.2

mapping software (ESRI, Redlands, CA, USA, 2013) based on the fire and eco-forestry maps, and recent harvest GIS layers and harvest licenses; then (2) validated in the field according to the criteria of representativeness of size and position, accessibility, presence of late successional species (*Picea mariana* Mill., BSP) and absence of salvage logging in the case of fires. A total of 37 continuous forest stands (controls, C), aged between 74 and 1320 years were selected from the same landscape [45].

Six residual patch types of varying size [28] were considered in some analyses based on their origin (fire or cut), their age (exposure time (EXT) to disturbed matrix) and the retention type: (1) young clump retention patches YCc (3–7 years old); (2) young island retention patches YCi (1–2 years old); (3) old island retention patches OCi (21–24 years old); (4) old separator retention patches OCs (21–24 years old); (5) old fire residual patches OF (27–37 years old); and (6) young fire residual patches YF (15–17 years old) [28] (p. 20).

2.3. Data Collection

Stand structure and local factors characterizing the study sites were measured in post-fire residual patches during the summers of 2012 and 2013 and in post-harvest retention patches during the summer of 2014. At the core of each retention or residual patch, one representative circular plot with a radius of 11.28 m (400 m^2) was established. Because edge influence is believed to extend approximately 5 m into the forest from the disturbed matrix in boreal forest as Harper et al. [46], in the young clump retentions with an area less than 400 m^2, a circular 200 m^2 plot was used to avoid edge effects.

In each circular plot, diameter at breast height (DBH) of all commercial stems of all trees (DBH $\geq$ 9 cm) and saplings (DBH < 9 cm) was measured, their species was noted, and their average height was measured with a clinometer. The DBH and the decomposition class of all snags were also measured. The volume of living trees and snags (per hectare) was calculated following Fortin et al. [47]. The line intersect method was used to sample fallen deadwood (logs) $\geq$5 cm in diameter by decay class, and their volume per hectare was calculated as in Van Wagner [48]. Proportion and volume of recent deadwood and old deadwood in post-fire residual patches, and post-harvest retention patches and in the continuous forest stands were evaluated as in Moussaoui et al. [28]. Following Moussaoui et al. [28], recent deadwood volume of post-fire patches, post-harvest retention patches and continuous forest stands was estimated as the sum of recent snag volumes (Classes 3 and 4), and the recent log volumes (Classes 1 and 2). Decomposition stage was based on Thomas et al.'s [49] decay classification system for snags and logs, and their old deadwood volume was the sum of snag volumes in Classes 5, 6 and 7 and log volumes in the last three classes of decaying woody debris on the ground based on Thomas et al. [28].

The average shape index (MSI) was calculated from the perimeter and the area of each residual patch according to McGarigal and Marks [50]. The perimeter and the area of each residual patch were measured by (1) tracing the exterior of the patches on foot with a handheld GPS; then (2) generating polygons from the lines generated by the GPS and (3) calculating the perimeter and area of the polygons using ArcGis® mapping software. The thickness of the organic layer (TOL) of each site representing the tree anchoring substrate, was determined in a soil pit dug in the center of each sample plot. The time since last fire (TSF), i.e., the age of the original forest from which the patch was formed, was estimated using one of two methods. Time since last fire was estimated in most stands by coring and counting growth rings in 10 individuals of the tallest cohort [51]. However, in some natural stands where the TOL was around 1 m and TSF approached the average maximum age of black spruce (i.e., 200 years) [52], radiocarbon dating (^{14}C) by accelerator mass spectrometry (AMS) was used to date the most recent local fire event based on the methodology of Chaieb et al. [45]. AMS was conducted on charcoal samples by the radiochronology laboratory C.E.N. (Centre d'Étude Nordique, Laval, QC, Canada) and the earth System Science Department (Irvine, California, CA, USA).

In the data analyses, we started by classifying the post-fire and post-harvest residual patches and continuous forest stands based on diameter structure. Secondly, we described the internal structural complexity and forest canopy closure of the six structural types found in residual patches and continuous forest stands. Thirdly, environmental factors influencing stand structural types were identified and the structural types found in post-harvest and post-fire and continuous forest were compared. Then, we tested if Types 1 and 2 without large timber were associated with particular residual patch types. Finally, the link between patch structural complexity and the temporal dynamics of their deadwood was evaluated.

2.4. Structural Classification of Stands

A structural classification of 125 residual patches and continuous forest stands (C, OF, YF, OCi, OCs, YCc, YCi) was developed based on DBH class data, following a method developed by Moss [53]. More specifically: (1) determine from the DBH data of each site diametric classes of 2 cm, and to determine the class with the highest DBH; (2) build a matrix that contains the density (number of trees/ha) and the basal area of living trees per DBH class for each site; (3) transform the absolute data into the inverse cumulative data for each DBH class. Trees were cumulated to reduce the number of zeros and make distributions insensitive to the width of classes starting from the largest class (30 cm) to the smallest (10 cm). Then, in order to control for variations in density and basal area, the cumulative data was transformed to a percentage (relative scale). In this way, the structural types were only based on the shape of diameter class distributions.

Subsequently, using the two inverse cumulative matrices of density and basal area of residual post fire and harvest patches and continuous forest stands, structural types were determined using a clustering algorithm k-means [54]. K-means clustering is a heuristic technique used to partition observations into a limited number of groups in order to minimize intra-group distance [54–56]. The optimal number of clusters was evaluated following exploratory tests using the clValid function in R. The clValid function integrates three validation criteria, the connectivity, width and Silhouette Dunn index, which measure the compactness, connection and separation of different numbers of clusters. The classification was validated by visually comparing the diameter distributions of the different structural types.

Finally, the structural classification of stands was plotted in a triangle of structures in R, which is a structural representation method that has been used for over a century in Europe [57] and more than a decade in Quebec [58]. A triangle of structures is a ternary graph with three inputs for the proportion of three size classes of timber determined by the user, small timber (ST), medium timber (MT) and large timber (LT), which can be estimated using density, basal area or volume of trees [58]. In this study, the three timber size classes, ST (9 cm > DBH > 13 cm), MT (13 cm > DBH > 17 cm) and LT (DBH >17 cm), were based on natural breaks in the diameter distribution of black spruce (data not shown). So, based on these three size classes, we illustrated the relative contribution of small, medium and large stems within each structural type.

2.5. Description of Structural Types

2.5.1. Internal Structure Complexity

Our classification method was based on only the shape of the diameter class distribution. Therefore, to determine whether the structural stand types also differed in living tree density, basal area and volume, we used single factor analysis of variance (ANOVA), followed by a Tukey multiple mean comparison, by the means of a mixed linear model [59], using the package nlme in R [60]. The geographic location (cutblock, or fire or continuous forest) was considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically in R. The analyzed stand characteristics are presented in Table 1.

Table 1. Mean and standard error of stand characteristics and environmental factors of the structural types. Letters illustrate the significantly different values among structural types following ANOVA and Tukey's HSD post hoc tests ($p < 0.05$). ST (9 cm > DBH > 13 cm), MT (13 cm > DBH > 17 cm) and LT (DBH > 17 cm).

Variable	T1 (n = 14)	T2 (n = 14)	T3 (n = 22)	T4 (n = 29)	T5 (n = 30)	T6 (n = 16)
Living Wood						
Mean height of living trees (m)	9.8 ± 0.3 [a]	12.5 ± 0.5 [b]	13.7 ± 0.4 [bc]	14.8 ± 0.3 [c]	16.1 ± 0.4 [e]	16.3 ± 0.6 [e]
Mean tree diameter at breast height (cm)	11.1 ± 0.2 [a]	12.9 ± 0.4 [ab]	13.7 ± 0.3 [bc]	14.7 ± 0.3 [ce]	15.4 ± 0.3 [e]	17.7 ± 0.8 [d]
Mean total tree density (trees/ha)	1153.6 ± 105.2 [b]	1712.5 ± 182.1 [ab]	2114.8 ± 174.6 [a]	1881.9 ± 108.5 [a]	1449.1 ± 109.6 [b]	1139.1 ± 85.8 [b]
Mean tree basal area (m^2/h)	11 ± 1.1 [a]	20.5 ± 2.3 [a]	30.6 ± 2.5 [b]	33.1 ± 1.9 [b]	31.2 ± 2.4 [b]	34 ± 2.4 [b]
Mean total tree volume (m^3/h)	40.82 ± 7 [a]	98.1 ± 14.7 [ac]	146.2 ± 13.1 [bc]	173.8 ± 12.8 [bc]	173.3 ± 17.2 [b]	188.4 ± 22.5 [b]
Mean sapling density (saplings/ha)	4941.7 ± 771.4 [a]	4177.8 ± 867.8 [a]	2081.3 ± 486.7 [b]	1356.3 ± 419.4 [b]	1718.2 ± 346.5 [b]	1353.8 ± 352.9 [b]
Mean sapling basal area (m^2/h)	7.2 ± 1.2 [a]	5.4 ± 0.6 [ac]	3.9 ± 0.9 [bc]	2.1 ± 0.5 [b]	3.1 ± 0.7 [bc]	1.7 ± 0.5 [b]
Mean small timber basal area (m^2/h)	9.5 ± 0.9 [ab]	11.5 ± 1.2 [a]	10.6 ± 1 [a]	7.2 ± 0.4 [b]	4.4 ± 0.4 [c]	2.2 ± 0.4 [c]
Mean medium timber basal area (m^2/h)	1.5 ± 0.3 [a]	7.6 ± 1 [c]	12.8 ± 1.2 [b]	13.6 ± 1.1 [b]	9.1 ± 1 [c]	4.8 ± 0.7 [ac]
Mean large timber basal area (m^2/h)	0.2 ± 0.1 [a]	1.6 ± 0.3 [a]	7.3 ± 0.8 [b]	12.4 ± 0.9 [c]	17.2 ± 1.3 [d]	26.8 ± 2.1 [e]
Deadwood						
Mean diameter of snags (cm)	11.1 ± 0.4 [a]	12.1 ± 0.4 [ab]	12.8 ± 0.4 [ab]	13.6 ± 0.5 [bc]	15.6 ± 0.5 [c]	18.5 ± 1.1 [d]
Mean total volume of snags (m^3/h)	2.2 ± 0.6 [a]	5.5 ±1.1 [a]	11.6 ± 1.7 [ab]	19.3 ± 2.7 [b]	31.3 ± 3.5 [bc]	36.3 ± 5.5 [c]
Mean total volume of logs (m^3/h)	7.9 ± 1.6 [a]	19.22 ± 4.2 [a]	53.1 ± 12.5 [ab]	75.5 ± 11.8 [b]	85.6 ± 9.1 [bc]	123.7 ±19.5 [c]
Recent deadwood volume (m^3/h)	4.6 ± 0.7 [a]	10.5 ± 1.8 [a]	26.6 ± 6.1 [ab]	41.5 ± 5.3 [bc]	47.7 ± 5.9 [bc]	62.1 ± 13.6 [c]
Old deadwood volume (m^3/h)	5.4 ± 1.6 [a]	14.2 ± 2.8 [a]	38.1 ± 10.8 [ab]	53.3 ± 10.1 [b]	69.1 ± 7.1 [bc]	98.1 ± 12.5 [c]
Environmental Factors						
Thickness of the organic layer (cm)	43.4 ± 6.4 [a]	38.6 ± 4.8 [a]	44.7 ± 9.1 [a]	35.8 ± 4 [a]	41.6 ± 4.5 [a]	49.2 ± 9.1 [a]
Mean shape index	1.2 ± 0.07 [a]	1.1 ± 0.02 [a]	1.2 ± 0.05 [a]	1.1 ± 0.03 [a]	1.3 ± 0.05 [a]	1.2 ± 0.03 [a]
Area of residual patch (ha)	4.5 ± 2.4 [a]	10.6 ± 4.9 [a]	8.4 ± 2.3 [a]	11.7 ± 2.4 [a]	7.4 ± 1.3 [a]	9.3 ± 4.2 [a]
Time since the last fire (year)	97 ± 7.3 [a]	115.2 ± 13.6 [ab]	120 ± 12.1 [ab]	126.7 ± 12.7 [ab]	149.2 ± 11.2 [b]	143.6 ± 11.7 [b]

2.5.2. Forest Canopy Closure

Because our classification method was performed on the relative abundance of trees to emphasize differences in shape of the diameter class distribution, it does not indicate whether a particular structural type was mainly dominated by a closed canopy. Canopy closure results from a particular combination of living tree size and density. In order to illustrate the relationship between forest canopy closure and structural types, the canopy closure threshold was assessed for each site by using modular-based structural stand density management (SDMMD) developed by Newton [61], for stands of pure black spruce. This is to show graphically, in each forest stand, the relationships between the average volume of living trees (dm^3) and their total density (stems/ha) on a base 10 logarithmic scale. This graphic is then divided into two parts, formed by a theoretical line suggested by Newton [61], which corresponds to the minimum threshold for natural black-spruce forest canopy closure. Forest stands to the right are considered as closed stands, while stands to the left are considered as open stands [61] (p. 181).

2.6. Factors Influencing Stand Structure

In order to examine the local environmental factors that may explain the differences among structural types, we considered four factors: Time since last fire, which corresponds to the age of the original forest from which the patch was formed; tree anchoring substrate, estimated by the thickness of the organic layer; and site area and shape. First, we hypothesize that the structure of stands without large stems and with an inverted-J diameter structure would be juvenile stands, and the structure stands with stems in all sizes would be older stands [58–60]. Moreover, as site productivity (soil richness) can influence the rate of maturation of forest stands [62,63], we anticipate that structural types including large trees appear sooner on rich soils than on poor soils. Finally, we anticipate that due to their high susceptibility to windthrow, small stands will have collapsed structures without larger stems. The four factors were examined using ANOVA followed by a Tukey multiple mean comparison, by means of one factor linear mixed models [59], using the package nlme in R [60]. The assumptions of homogeneity of variance and normality of residues were verified graphically in R. The location of a stand in a particular cutblock, or fire or continuous forest was considered a random effect.

2.7. Structural Types in Post-Harvest Residual Patches versus Natural Stands

Comparison of structural types encountered in post-harvest retention patch stands to those observed in naturel stands (post-fire residual patches and continuous forests) was realized by comparing the frequency of structural types present per type of residual patch or continuous forest stand (C, OF, YF, OCi, OCs, YCc, YCi) in a 2 × 2 contingency table. The relationship between the two categorical variables, residual patch type and structural type, was analyzed in R, with the Fisher-exact test (for small theoretical values <5). We tested the null hypothesis that each structure type could be in any residual patch type or continuous forest stand, i.e., the structure was independent of the disturbance (fire, cut). If the p-value was less than the critical value of 0.05, the null hypothesis was rejected, i.e., residual patch types and structural types were associated.

In order to determine whether inverted-J structure and truncated unimodal structures without large trees (structure of Types 1 and 2) were more abundant within certain residual patches, we generated two contrasts, first between Type 1 and other structural types (Type 2 to Type 6) and second between Types 1 and 2 and others (Type 3 to Type 6). We tested in this way if Types 1 and 2 could be associated to particular residual patch types. The null hypothesis for each contrast was that each structure was equally likely to be found in each residual patch type. The association was tested statistically with the Fisher-exact test (p-value = 0.05) in R. Then, to determine whether there were differences between fire and harvest origin patches of Types 1 and 2, we determined the age of the original forest from which the patch was formed (TSF) and thickness of the organic layer (TOL) for each origin and compared them with ANOVA.

Deadwood is an important functional and structural component of forest stands and it is related to the initial forest structure and dynamics [17,28]. So, in order to evaluate the link between the patch structural complexity and their temporal dynamics in black spruce boreal forests, we have characterized structural types in terms of their deadwood dynamics on a deadwood diagram suggested by Moussaoui et al. [28].

3. Results

3.1. Structural Classification of Residual Patch Stands

K-means classified the 125 residual patches and continuous forest stands into six stand structural types (14 as Type 1; 14 as Type 2; 22 as Type 3; 29 as Type 4; 30 as Type 5 and 16 as Type 6). Average absolute basal area and stem density by DBH class of the six structural types generated by k-means clustering are presented in Figure 2. Type 1 had an inverted-J structure, dominated by saplings (DBH < 9 cm; Table 1) and trees of small DBH classes varying between 9.1 and 14 cm. Types 2–4 had a truncated unimodal structure with regular diameter structures, dominated by trees of small and intermediate DBH classes (10–18 cm). In the case of Type 2, the stands had practically no large trees. Type 5 had an intermediate bimodal irregular structure, dominated by trees of intermediate and relatively large DBH classes. Finally, Type 6 had an irregular structure, with a wide range of diameters, with higher abundance of the largest DBH class (Figure 2a,b).

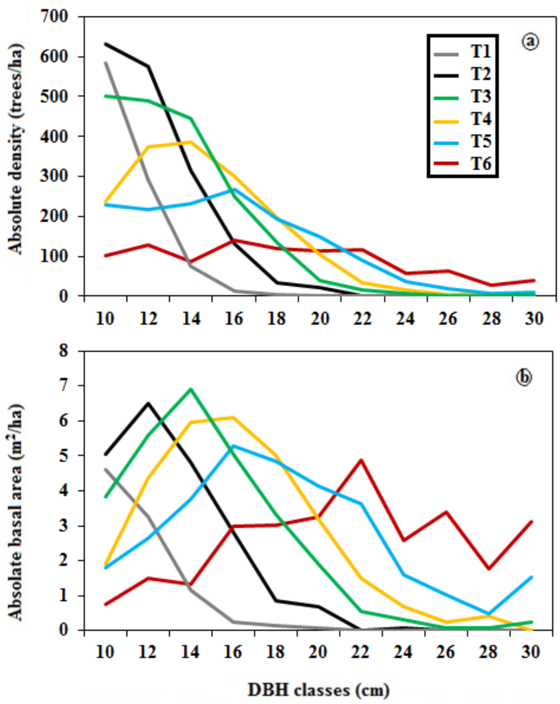

Figure 2. Representation of the six structural types (T1–T6) present in residual patches and continuous forest stands (k-means structural types) with the distribution of the absolute average tree (**a**) density and (**b**) basal area plotted by DBH class. T: Structural type.

The variation in the proportion of tree size classes among the six structural types is illustrated in Figure 3. Structural Types 1 and 2 (1, 2 in Figure 3) were dominated by small timber with 85.1% and 55.4%, respectively, while the structural Type 6 (6), which seemed to have a more irregular structure, had an average of 79.9% of large timber. The proportion of medium timber was highest in the three structural Types 3–5. There is a structural evolution from Type 1 to Type 6 with a decrease in the proportion of ST and an increase in the proportion of LT (Figure 3).

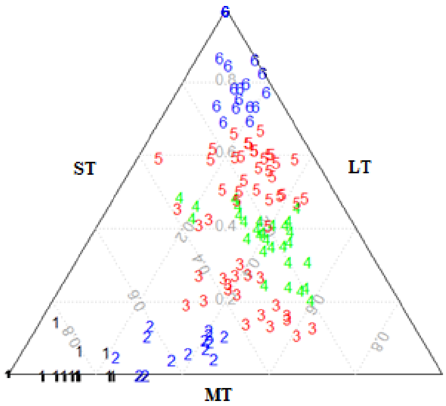

Figure 3. Ternary diagram (ternary plot) representing structural variability within and among structural types (from 1 to 6) by timber size (small timber ST (9 cm > DBH > 13 cm): Left oblique axis; medium timber MT (13 cm > DBH > 17 cm): Horizontal axis, and large timber LT (DBH >17 cm): Right oblique axis).

3.2. Complexity of Structural Stand Types

Structural characteristics differed among the six structural types (T1–T6; Table 1). For almost all characteristics, the inverted-J structure (Type 1) was characterized by minimum values, while maximum values were typical of the stands of irregular structure (Type 6), except in the case of small and medium timber (ST, MT), where, the maximum values were recorded in the trunked-unimodal structure Types 2 and 4, respectively (Table 1). The characteristics of the residual patches and continuous forest stands with an inverted-J structure (T1) differed significantly ($p < 0.05$) from Types 4–6 (Table 1). In addition, the analyses showed that generally Types 2 and 3 (trunked-unimodal structure) differed significantly ($p < 0.05$) from Type 6, which had an irregular structure characterizing stands dominated by a wide range of diameters (Table 1). The intermediate structure type (T5) and irregular structure type (T6) were not significantly different in terms of the average DBH of living and dead trees.

In terms of forest canopy closure, stands with an inverted-J structure or a truncated unimodal structure without relatively large trees (Types 1 and 2) had generally an open forest canopy (Figure 4). The structural Types 3–6, however, tended to have relatively closed structures.

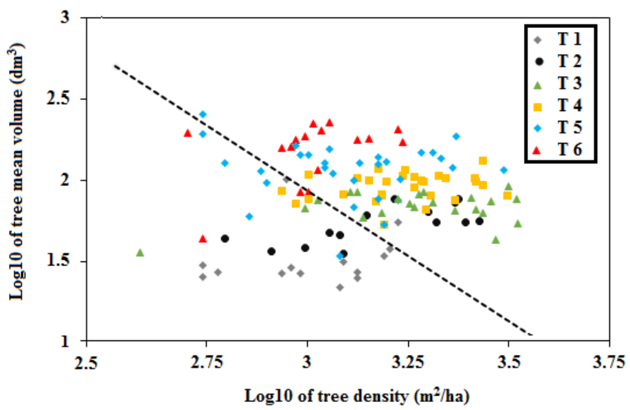

Figure 4. Average volume of trees (Log10 dm^3) based on their total density (Log10 m^2/ha) in the six structural types (from T1 to T6). The dotted line represents the minimum threshold for natural black-spruce forest canopy closure suggested by Newton [61]. Forest stands to the right are considered as closed stands, while stands to the left are considered as open stands.

3.3. Influence of TSF on Structure

Organic layer thickness, stand size and shape did not vary among the structural types (Table 1). The results indicated that the time since the last fire (TSF), i.e., minimum age of original forest from which the patch was formed, varied among the structural types. Structural Type 1, characterized by trees of small DBH classes, showed an average TSF lower than structural Types 5 (intermediate) and 6 (irregular structure), which had higher TSF mean values (Table 1).

3.4. Structural Types: Post-Harvest versus Post-Fire Residual Patches

The analysis of the relationship between structural types (T1, T2, T3, T4, T5, T6) present in natural stands (post-fire residual patches and continuous forest) and post-harvest retention patches showed that generally the structural variety observed in natural stands was maintained in post-harvest stands (Fisher's exact test, p-value = 0.257; Figure 5). We observed that over 60% of the old post-harvest retentions (EXT $\geq$ 20 years) had an intermediate or irregular diametric structure (Types 5 and 6). In fires, residual patches seemed to be characterized by variable structures similar to those characterizing the continuous forest stands (Figure 5). Stands with an inverted-J structure or a truncated unimodal structure without relatively large trees (Types 1 and 2) were primarily young residual patches (EXT: 0–19 years), particularly, post-harvest retention in the shape of clumps (YCc) and post-fire residual patches (YF; Figure 5; Fisher exact test, p = 0.01).

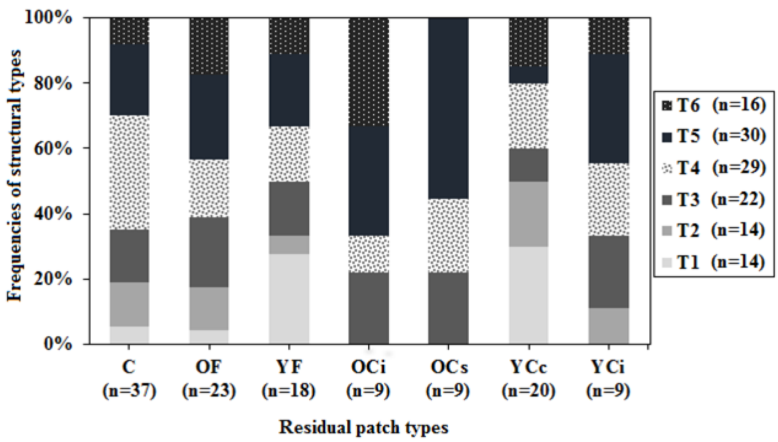

Figure 5. Stacked bars representing the frequencies of structural types (T1–T6) in each residual patch type and continuous forest stand. Young cut clump (YCc); young cut island (YCi), and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT $\geq$20 years and continuous forest (C): Control.

The results indicated that organic layer thickness did not differ significantly ($F_{1,14}$ = 0.55, p = 0.47) between young post-fire residual patches (YF) and young retention in the shape of clumps YCc dominated by structure of Types 1 and 2. The time since the last fire (TSF), i.e., minimum age of the original forest from which the patch was formed, differed significantly between YF (138.8 years) and YCc (82.1 years; $F_{1,14}$ = 18.42, p = 0.0007).

The relationship between the density of trees and their volume indicated that based on the threshold suggested by Newton [61], that all stands of Type 1 were open and characterized as young post-disturbance patches (YF, YCc; Figures 4 and 5) with the exception of a single continuous forest stand. Four of the six open stands of Type 2 were young post-harvest retentions. In Types 3–6, the majority of stands were closed and were composed of continuous forest stands and old post-disturbance residual patches (OF, OCs, OCi and C; Figures 4 and 5).

When we plotted structural types on the deadwood diagram suggested by Moussaoui et al. [28], we observed in terms of deadwood dynamics, that some structural types, especially, Types 1 and 2 characterizing some of young fire (YF) and half of young harvest (clump; YCc) patches are characterized by low living volumes and also by low volumes of deadwood (Figure 6). The occurrence of open canopy in others structural types (Types 3–6) appeared to be associated with a high relative volume of deadwood (Figure 6).

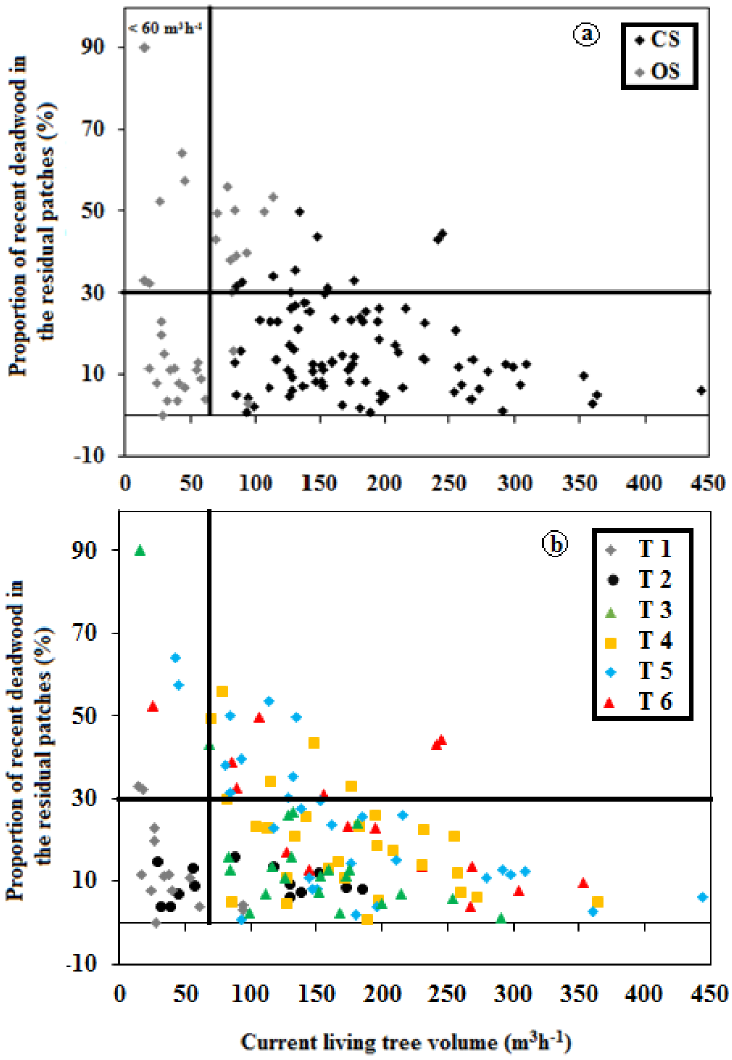

Figure 6. Relationship between the proportion of recent deadwood volume (%) and the current living wood volume (m^3/ha) in the residual patches and continuous forest stands in terms of (**a**) canopy closure and (**b**) structural diameter types. The proportion of the recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. The initial stand volume (ISV) at the time of the formation of each residual patch is estimated as the sum of current living volume and recent deadwood volume.

4. Discussion

The results of this study show that the structural complexity in post-harvest retention patches is generally similar to that characterizing natural stands of post-fire residual patches and continuous forests as previously suggested by Gandhi et al. [20] and Heikkala et al. [64]. Furthermore, our results also indicate that post-fire residual patches generally fall within the natural variability present in continuous forest stands. Our structural classification approach, based on the analysis of the size distribution of the merchantable trees, suggested that there are six distinct structural types characterizing residual patches (post-fire or post-harvest) and continuous forest stands in black spruce boreal forests. Type 1 (inverted-J diameter structure) and trunked-unimodal structure (type 2) characterize stands dominated by trees in small DBH classes, while, Type 6 had a more irregular structure with a wide range of diameters. In stands ranging from Type 1 to Type 6, the merchantable volume and basal area, and degree of the canopy closure could be influenced over time by of the development of large trees [65,66].

Our results indicate that the residual patches containing only small timber were generally younger (in terms of the age of the forest stand) than those with timber in all size classes. This supports studies that suggest that stand structural complexity in boreal forests increases with the time since fire [67–69]. This is not surprising because the time since last fire, i.e., the age of a forest stand, describes the natural structural maturation of trees. Initially, the young forest develops significant merchantable volume until the age of collapse, followed by a stage of transition to uneven structures [69,70], then the merchantable volume will be again reduced with forest age [71]. However, although the structure of residual patches and continuous forest stands is influenced by time since last fire, this influence is highly variable (Table 1), probably due to the interaction with site productivity, as a higher growth rate in productive stands is likely to induce earlier senescence and thus an earlier passage to an uneven-sized structure [69]. Otherwise, some residual patches may have simply preserved the original structures of unproductive sites, which typically have an uneven-sized structure.

In fact, in addition to time since fire, site productivity has often been cited as an important factor influencing the structure of the coniferous boreal forest [72,73]. As site productivity (soil richness) can influence the rate of maturation of forest stands [62,63], structural types including large trees appear sooner on rich soils than on poor soils. In this study, no significant effect of tree anchoring substrate on the structure of residual patches and continuous forest stands was found. This inconsistency in our results with previous studies [62,74,75] could possibly be explained by the small range of variation in the mean thickness of the organic layer among our identified structural types (Table 1).

The hypothesis on the relationship between residual patch area and mean shape index on structural complexity in residual patches and continuous forest stands was also not supported. This may be due to an interaction with the exposure time of patches and their post-disturbance temporal dynamics. However, our results also show that regardless of the origin of the residual patch (fire or cut), in terms of exposure time (EXT) to the disturbance matrix, Types 1 and 2 are generally associated with young post-disturbance residual patches (YCc, YF). Humidity, as indicated by a thick organic matter layer, could be a factor influencing the creation of some young post-fire residual patches as they had thick organic layers despite a relatively young forest age [76]. Fire escape stands of Types 1 and 2 could maintain this structure for a long period of time as tree growth is relatively slow in these environments [73]. In these fires, our raw data show that the post-fire structure of the patches is usually aged of more than 120 years. In the case of cutblocks, these retentions have usually less than 95 years and may have resulted from a selection bias of the operator, who selected retention patches with a low market value.

Furthermore, when we plot structural types on the deadwood diagram suggested by Moussaoui et al. [28], our results show that despite the fact that half of young clump retention patches YCc (10 of 20) and some of young post-fire YF residual patches are characterized by low living volumes, the low volume of deadwood in these retentions (Figure 6) suggests that their structures did not result from a collapse of more advanced structural types, but simply reflect a legacy of the original forests. In this case, the open, inverted-J structure of young fire and young harvest (clump) patches may have simply preserved their original open structures, which are more resistant to post-disturbance mortality [77]. However, the occurrence of open canopy in some other structural types (Types 3–6) appears to be associated with a high relative volume of deadwood (Figure 6). Thus, this suggests that this canopy openness could come from a collapse of the original forest structure. In this case, even if these residual patches have low living volumes, the high proportion of recent deadwood would not indicate stand collapse but rather a structural retrogression to intermediate stages or a truncated bell shape as they maintain some larger timber (Figure 6).

5. Conclusions and Silvicultural Implications

It is increasingly recognized that conservation of biodiversity requires the preservation of the structural attributes of natural forest stands in the context of forest management [11]. Consequently, foresters need to develop forestry practices that maintain key structural complexity similar to that found in natural forests [12]. This study indicates that current post-harvest residual retentions in black spruce forests maintain much of the natural range of structural complexity found in post-fire residual patches and also within continuous forest stands. In addition, although there is a high volume of deadwood especially in stands in structural Types 3–6, our result show that this mortality does not result in a significant loss of structural complexity. This suggests that despite the fact that some of stands in Types 3–6 are partially collapsed, as shown in the deadwood diagram, these structural types persist or retrogress to intermediate stages such as a truncated bell shape as they maintain some larger timber. In our study area, we suggest that operators chose retention patches with a low merchantable value. This bias appears only in the young retentions in the shape of clump YCc, but not in other types of old retention (separator OCs or island OCi) in which the operator had no choice in the type of forest retained. So, our results suggest that selection bias of the operator may simplify the structural diversity of retention patches favoring sectors devoid of large stems and with little merchantable volume.

As structural Types 1 or 2, which are devoid of large stems, are created naturally by fire as well as by harvest, we might be tempted to conclude that the retention of Types 1 and 2 are acceptable targets. However, only Types 3–6 generated by past practices retain intermediate and large trees over time. In harvest areas, retention of some large trees and of large closed patches in the shape of an island or separator (Types 3–6) can contribute both to the preservation of natural structural complexity and to the maintenance of natural dynamics of deadwood (similar to residual patch or continuous forest deadwood dynamics) [28] while the surrounding harvested forest regenerates. In addition, as structural attributes of natural forests are important for different forest dwelling species, these retention patches could represent a refuge habitat for many species. To support all of these results, it will be important to compare also edge effects on stand structure of post-fire residual patches versus of post-harvest residual retentions, that can vary depending on the type of edge (post-fire or post-harvest), edge age (exposure time to disturbed matrix) and forest structure and composition [78].

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References

1. Bergeron, Y.; Engelmark, O.; Harvey, B.; Morin, H.; Sirois, L. Key issues in disturbance dynamics in boreal forests: Introduction. *J. Veg. Sci.* **1998**, *9*, 464–468. [CrossRef]
2. Hylander, K.; Johnson, S. In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. *J. Veg. Sci.* **2010**, *21*, 1099–1109. [CrossRef]

3. Perhans, K.; Appelgren, L.; Jonsson, F.; Nordin, U.; Söderström, B.; Gustafsson, L. Retention patches as potential refugia for bryophytes and lichens in managed forest landscapes. *Biol. Conserv.* **2009**, *142*, 1125–1133. [CrossRef]
4. Schmiegelow, F.K.; Stepnisky, D.P.; Stambaugh, C.A.; Koivula, M. Reconciling salvage logging of boreal forests with a natural-disturbance management model. *Conserv. Biol.* **2006**, *20*, 971–983. [CrossRef] [PubMed]
5. DeLong, S.C.; Kessler, W.B. Ecological characteristics of mature forest remnants left by wildfire. *For. Ecol. Manag.* **2000**, *131*, 93–106. [CrossRef]
6. Madoui, A.; Leduc, A.; Gauthier, S.; Bergeron, Y. Spatial pattern analyses of post-fire residual stands in the black spruce boreal forest of western Quebec. *Int. J. Wildland Fire* **2011**, *19*, 1110–1126. [CrossRef]
7. Bergeron, Y.; Drapeau, P.; Gauthier, S.; Lecomte, N. Using knowledge of natural disturbances to support sustainable forest management in the northern clay belt. *For. Chron.* **2007**, *83*, 326–337. [CrossRef]
8. Cyr, D.; Gauthier, S.; Bergeron, Y.; Carcaillet, C. Forest management is driving the eastern north American boreal forest outside its natural range of variability. *Front. Ecol. Environ.* **2009**, *7*, 519–524. [CrossRef]
9. Franklin, J.F.; Berg, D.R.; Thornburgh, D.A.; Tappeiner, J.C. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems. In *Creating a Forestry for the 21st Century: The Science of Ecosystem Management*; Island Press: Washington, DC, USA, 1997; pp. 111–139.
10. Drapeau, P.; Nappi, A.; Giroux, J.-F.; Leduc, A.; Savard, J.-P. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. *Ecol. Manag. Dead Wood West. For.* **2002**, 193–205.
11. Franklin, J.F.; Spies, T.A.; Van Pelt, R.; Carey, A.B.; Thornburgh, D.A.; Berg, D.R.; Lindenmayer, D.B.; Harmon, M.E.; Keeton, W.S.; Shaw, D.C. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using douglas-fir forests as an example. *For. Ecol. Manag.* **2002**, *155*, 399–423. [CrossRef]
12. Bauhus, J.; Puettmann, K.; Messier, C. Silviculture for old-growth attributes. *For. Ecol. Manag.* **2009**, *258*, 525–537. [CrossRef]
13. Gauthier, S.; Leduc, A.; Harvey, B.; Bergeron, Y.; Drapeau, P. Les perturbations naturelles et la diversité écosystémique. *Nat. Can.* **2001**, *125*, 10–17.
14. Beese, W.; Dunsworth, B.; Zielke, K.; Bancroft, B. Maintaining attributes of old-growth forests in coastal BC through variable retention. *For. Chron.* **2003**, *79*, 570–578. [CrossRef]
15. Hunter, M.L.J. *Wildlife, Forests, and Forestry: Priciples of Managing Forests for Biological Diversity*; Prentice-Hall: Englewood Cliffs, NJ, USA, 1990; p. 370.
16. Kuuluvainen, T. Natural variability of forests as a reference for restoring and managing biological diversity in boreal fennoscandia. *Silva Fenn.* **2002**, *36*, 97–125. [CrossRef]
17. Larson, B.C.; Oliver, C.D. *Forest Stand Dynamics*, 2nd ed.; John Wiley and Sons Inc.: New York, NY, USA, 1996; p. 520.
18. Fenton, N.J.; Frego, K.A. Bryophyte (moss and liverwort) conservation under remnant canopy in managed forests. *Biol Conserv.* **2005**, *122*, 417–430. [CrossRef]
19. Lachance, É.; Pothier, D.; Bouchard, M. Forest structure and understory plant communities inside and outside tree retention groups in boreal forests. *Ecoscience* **2013**, *20*, 252–263. [CrossRef]
20. Gandhi, K.J.; Spence, J.R.; Langor, D.W.; Morgantini, L.E.; Cryer, K.J. Harvest retention patches are insufficient as stand analogues of fire residuals for litter-dwelling beetles in northern coniferous forests. *Can. J. For. Res.* **2004**, *34*, 1319–1331. [CrossRef]
21. Bouchard, M.; Hébert, C. Beetle community response to residual forest patch size in managed boreal forest landscapes: Feeding habits matter. *For. Ecol. Manag.* **2016**, *368*, 63–70. [CrossRef]
22. Smith, D.M.; Larson, B.C.; Kelty, M.J.; Ashton, P.M.S. *The Practice of Silviculture: Applied Forest Ecology*; John Wiley and Sons, Inc.: New York, NY, USA, 1997.
23. Angelstam, P.; Kuuluvainen, T. Boreal forest disturbance regimes, successional dynamics and landscape structures: A european perspective. *Ecol. Bull.* **2004**, *51*, 117–136.
24. Gauthier, S.; Bernier, P.; Kuuluvainen, T.; Shvidenko, A.; Schepaschenko, D. Boreal forest health and global change. *Science* **2015**, *349*, 819–822. [CrossRef] [PubMed]
25. Smith, F. Mortality in the Yukon: Post-Harvest Effects on Structural Retention. Master's Thesis, University of Toronto, Toronto, ON, USA, 2010.
26. Ouarmim, S.; Asselin, H.; Bergeron, Y.; Ali, A.A.; Hély, C. Stand structure in fire refuges of the eastern Canadian boreal mixedwood forest. *For. Ecol. Manag.* **2014**, *324*, 1–7. [CrossRef]

27. Bolton, D.K.; Coops, N.C.; Wulder, M.A. Characterizing residual structure and forest recovery following high-severity fire in the western boreal of canada using landsat time-series and airborne lidar data. *Remote Sens. Environ.* **2015**, *163*, 48–163. [CrossRef]
28. Moussaoui, L.; Fenton, N.J.; Leduc, A.; Bergeron, Y. Deadwood abundance in post-harvest and post-fire residual patches: An evaluation of patch temporal dynamics in black spruce boreal forest. *For. Ecol. Manag.* **2016**, *368*, 17–27. [CrossRef]
29. Lindenmayer, D.; Mackey, B.; Mullen, I.; McCarthy, M.; Gill, A.; Cunningham, R.; Donnelly, C. Factors affecting stand structure in forests–are there climatic and topographic determinants? *For. Ecol. Manag.* **1999**, *123*, 55–63. [CrossRef]
30. Gustafsson, L.; Baker, S.C.; Bauhus, J.; Beese, W.J.; Brodie, A.; Kouki, J.; Lindenmayer, D.B.; Lõhmus, A.; Pastur, G.M.; Messier, C. Retention forestry to maintain multifunctional forests: A world perspective. *BioScience* **2012**, *62*, 633–645.
31. Lindenmayer, D.; Franklin, J.; Lõhmus, A.; Baker, S.; Bauhus, J.; Beese, W.; Brodie, A.; Kiehl, B.; Kouki, J.; Pastur, G.M. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* **2012**, *5*, 421–431. [CrossRef]
32. Harper, K.A.; Drapeau, P.; Lesieur, D.; Bergeron, Y. Forest structure and composition at fire edges of different ages: Evidence of persistent structural features on the landscape. *For. Ecol. Manag.* **2014**, *314*, 131–140. [CrossRef]
33. Work, T.T.; Shorthouse, D.P.; Spence, J.R.; Volney, W.J.A.; Langor, D. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the ecosystem management emulating natural disturbance (emend) landbase in northwestern Alberta. *Can. J. For. Res.* **2004**, *34*, 417–430. [CrossRef]
34. Lavoie, S.; Ruel, J.-C.; Bergeron, Y.; Harvey, B.D. Windthrow after group and dispersed tree retention in eastern Canada. *For. Ecol. Manag.* **2012**, *269*, 158–167. [CrossRef]
35. Urgenson, L.S.; Halpern, C.B.; Anderson, P.D. Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the pacific northwest, USA. *For. Ecol. Manag.* **2013**, *308*, 116–127. [CrossRef]
36. Robitaille, A.; Saucier, J. *Paysages Régionaux du Québec Méridional. Direction de la Gestion des Stocks Forestiers et Direction des Relations Publiques, Ministère des Ressources Naturelles du Québec*; Les Publications du Quebec: Québec, QC, Canada, 1998.
37. Bergeron, J.-F.; Grondin, P.; Blouin, J. *Rapport de Classification Ecologique du Sous-Domaine Bioclimatique de la Pessière à Mousses de L'ouest*; Ministere des Ressources Naturelles, Forêt Québec: Ville de Québec, QC, Canada, 1999.
38. Blouin, J.; Berger, J. Guide de reconnaissance des types écologiques de la région écologique 6a—436 plaine du lac matagami et 6b—plaine de la baie de rupert. In *Ministère des Ressources Naturelles du Québec, Forêt-Québec, Direction des Inventaires Forestiers, Division de la Classification Ecologique et Productivité des Stations*; Forêt-Québec: Québec, QC, Canada, 2005; p. 188.
39. Payette, S. Fire as a controlling process in the north american boreal forest. In *A Systems Analysis of the Boreal Forest*; Shugart, H.H., Leemans, R., Bonan, G.B., Eds.; Cambridge University Press: Cambridge, UK, 1992; pp. 144–169.
40. Bergeron, Y.; Gauthier, S.; Kafka, V.; Lefort, P.; Lesieur, D. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. *Can. J. For. Res.* **2001**, *31*, 384–391. [CrossRef]
41. Bergeron, Y.; Gauthier, S.; Flannigan, M.; Kafka, V. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* **2004**, *85*, 1916–1932. [CrossRef]
42. Gouvernement du Québec. *Règlement sur les Normes D'intervention dans les Forêts du Domaine de L'état-loi sur les Forêts*; LRQ c. F-4.1, a: Québec, QC, Canada, 1988; p. 171.
43. Bergeron, Y.; Harvey, B.; Leduc, A.; Gauthier, S. Forest management guidelines based on natural disturbance dynamics: Stand-and forest-level considerations. *For. Chron.* **1999**, *75*, 49–54. [CrossRef]
44. Harvey, B.D.; Leduc, A.; Gauthier, S.; Bergeron, Y. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. *For. Ecol. Manag.* **2002**, *155*, 369–385. [CrossRef]
45. Chaieb, C.; Fenton, N.J.; Lafleur, B.; Bergeron, Y. Can we use forest inventory mapping as a coarse filter in ecosystem based management in the black spruce boreal forest? *Forests* **2015**, *6*, 1195–1207. [CrossRef]
46. Harper, K.A.; Lesieur, D.; Bergeron, Y.; Drapeau, P. Forest structure and composition at young fire and cut edges in black spruce boreal forest. *Can. J. For. Res.* **2004**, *34*, 289–302. [CrossRef]

47. 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. [CrossRef]
48. Van Wagner, C. The line intersect method in forest fuel sampling. *For. Sci.* **1968**, *14*, 20–26.
49. Thomas, J.W.; Anderson, R.G.; Maser, C.; Bull, E.L. *Wildlife Habitats in Managed Forests of the Blue Mountains of Oregon and Washington*; United States Department of Agriculture, Forest Service, Agricultural Handbook; US Forest Service: Washington, DC, USA, 1979; p. 553.
50. McGarigal, K.; Marks, B.J. Spatial pattern analysis program for quantifying landscape structure. *Dolores (CO) PO Box* **1994**, *606*, 67.
51. Wagner, C.V. Age-class distribution and the forest fire cycle. *Can. J. For. Res.* **1978**, *8*, 220–227. [CrossRef]
52. Burns, R.M.; Honkala, B.H. Silvics of north america. Volume 1. Conifers. In *Agriculture Handbook*; Forest Service, USDA: Washington, DC, USA, 1990; p. 654.
53. Moss, I. Stand Structure Classification, Succession, and Mapping Using Lidar. Ph.D. Thesis, The University of British Columbia, Vancouver, BC, Canada, 2012.
54. Nock, R.; Nielsen, F. On weighting clustering. *IEEE Trans. Pattern Anal. Mach. Intell.* **2006**, *28*, 1223–1235. [CrossRef] [PubMed]
55. Borcard, D.; Gillet, F.; Legendre, P. *Numerical Ecology with R*; Springer: Breinigsville, PA, USA, 2011; p. 306.
56. Brock, G.; Pihur, V.; Datta, S.; Datta, S. Clvalid, an r package for cluster validation. *J. Stat. Softw.* **2008**, *1*, 22–25.
57. De Liocourt, F.D. De l'amenagement des sapinieres. *Bull. Soc. Franche-Comté Belfort* **1898**, *4*, 396–409.
58. Lessard, G.; Côté, S. Détermination des paramètres des forêts aptes au régime du jardinage (phase i). *Centre Collégial de Transfert de Technologie en Foresterie (CERFO), Rapport du CERFO* **2005**, *4*, 289.
59. Pinheiro, J.; Bates, D. *Mixed-Effects Models in S and S-Plus*; Chambers, J., Eddy, W., Hardle, W., Sheather, S., Tierney, L., Eds.; Springer: New York, NY, USA, 2000.
60. R Development-CORE-TEAM. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2011. Available online: http://www.R-project.org/ (accessed on 12 December 2011).
61. Newton, P.F. A decision-support system for forest density management within upland black spruce stand-types. *Environ. Model. Softw.* **2012**, *35*, 171–187. [CrossRef]
62. Simard, M.; Bernier, P.Y.; Bergeron, Y.; Pare, D.; Guérine, L. Paludification dynamics in the boreal forest of the james bay lowlands: Effect of time since fire and topography. *Can J. For. Res.* **2009**, *39*, 546–552. [CrossRef]
63. Nlungu-Kweta, P.; Leduc, A.; Bergeron, Y. Climate and disturbance regime effects on aspen (*Populus tremuloides* Michx) stand structure and composition along an east-west transect in Canada's boreal forest. *Int. J. For. Res.* **2016**. [CrossRef]
64. Heikkala, O.; Seibold, S.; Koivula, M.; Martikainen, P.; Müller, J.; Thorn, S.; Kouki, J. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. *For. Ecol. Manag.* **2016**, *359*, 51–58. [CrossRef]
65. Clark, D.F.; Antos, J.A.; Bradfield, G.E. Succession in sub-boreal forests of west-central british columbia. *J. Veg. Sci.* **2003**, *14*, 721–732. [CrossRef]
66. Lee, P.C.; Crites, S.; Nietfeld, M.; Nguyen, H.V.; Stelfox, J.B. Characteristics and origins of deadwood material in aspen-dominated boreal forests. *Ecol. Appl.* **1997**, *7*, 691–701. [CrossRef]
67. Brassard, B.W.; Chen, H.Y. Stand structural dynamics of north american boreal forests. *Crit. Rev. Plant Sci.* **2006**, *25*, 115–137. [CrossRef]
68. Kneeshaw, D.D.; Burton, P. Canopy and age structures of some old sub-boreal picea stands in British Columbia. *J. Veg. Sci.* **1997**, *8*, 615–625. [CrossRef]
69. Boucher, D.; Gauthier, S.; De Grandpré, L. Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of québec. *Ecoscience* **2006**, *13*, 172–180. [CrossRef]
70. Chen, H.Y.; Popadiouk, R.V. Dynamics of north american boreal mixedwoods. *Environ. Rev.* **2002**, *10*, 137–166. [CrossRef]
71. Smyth, C.; Schieck, J.; Boutin, S.; Wasel, S. Influence of stand size on pattern of live trees in mixedwood landscapes following wildfire. *For. Chron.* **2005**, *81*, 125–132. [CrossRef]

72. Brassard, B.W.; Chen, H.Y.; Wang, J.R.; Duinker, P.N. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. *Can. J. For. Res.* **2008**, *38*, 52–62. [CrossRef]
73. Simard, M.; Lecomte, N.; Bergeron, Y.; Bernier, P.Y.; Paré, D. Forest productivity decline caused by successional paludification of boreal soils. *Ecol. Appl.* **2007**, *17*, 1619–1637. [CrossRef] [PubMed]
74. Ruel, J.-C. Understanding windthrow: Silvicultural implications. *For. Chron.* **1995**, *71*, 434–445. [CrossRef]
75. Laamrani, A.; Valeria, O.; Bergeron, Y.; Fenton, N.; Cheng, L.Z.; Anyomi, K. Effects of topography and thickness of organic layer on productivity of black spruce boreal forests of the canadian clay belt region. *For. Ecol. Manag.* **2014**, *330*, 144–157. [CrossRef]
76. Cyr, D.; Gauthier, S.; Bergeron, Y. Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. *Landsc. Ecol.* **2007**, *22*, 1325–1339. [CrossRef]
77. Rich, R.L.; Frelich, L.E.; Reich, P.B. Wind-throw mortality in the southern boreal forest: Effects of species, diameter and stand age. *J. Ecol.* **2007**, *95*, 1261–1273. [CrossRef]
78. Harper, K.A.; Macdonald, S.E.; Mayerhofer, M.S.; Biswas, S.R.; Esseen, P.A.; Hylander, K.; Stewart, K.J.; Mallik, A.U.; Drapeau, P.; Jonsson, B.G. Edge influence on vegetation at natural and anthropogenic edges of boreal forests in Canada and Fennoscandia. *J. Ecol.* **2015**, *103*, 550–562. [CrossRef]