Structural Attributes of Old-Growth and Partially Harvested Northern White-Cedar Stands in Northeastern North America

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Abstract: Forestry practitioners often need to identify old-growth stands because of their high conservation value. To identify the structural and compositional characteristics potentially unique to old-growth northern white-cedar (*Thuja occidentalis* L.) stands, we compared 16 old-growth stands and 17 partially harvested stands in Maine, USA and New Brunswick, Canada. Potential old-growth predictors included common structural metrics such as basal area (BA), quadratic mean diameter (QMD), large tree ($\geq$40 cm diameter at breast height) density, and volumes of coarse woody debris (CWD), along with six structural indices. Using generalized linear mixed-models, we identified two significant structural predictors that differentiate old-growth from partially harvested stands when used in combination: Volume of advanced-decay CWD and live tree QMD. None of the structural indices were useful in distinguishing between old-growth and partially harvested stands, nor did the two types differ with respect to tree species composition. Our results demonstrate that two metrics easily derived from standard inventory data—decayed CWD volume and QMD—effectively characterize the old-growth white-cedar stands sampled in this study. Taken together, these results can improve management decision making for white-cedar, particularly in the context of certification, while also shedding light on the effects of past partial harvesting on current forest structure.

Keywords: coarse woody debris; dead wood; forest structure; forest certification; naturalness; *Thuja occidentalis* L.

1. Introduction

Successful forest management often requires identifying areas suitable for silvicultural treatments, as well as areas to be set aside from harvest because of their high conservation value. High conservation value stands are those that provide exceptional non-commodity resources such as flood and erosion mitigation, habitat for rare organisms, or representation of locally rare ecosystems [1]. Given the importance of such stands, their identification and treatment has been institutionalized through forest certification guidelines.

One of the most challenging yet critical aspects of this process is determining which stands or communities have high conservation value. Such communities are often assumed to possess characteristics typical of old-growth, such as large live and dead trees [2–4], large volumes of coarse woody debris [2,5,6], and structural heterogeneity [4,7]. Though definitions of old-growth vary, the

Forest Stewardship Council (FSC) guidelines for the Northeastern United States specify old-growth as, "the oldest seral stage in which a plant community is capable of existing on a site, given the frequency of natural disturbances" [1]. These definitions have important management implications, as FSC guidelines specify that true old-growth requires reserve status (i.e., no harvesting).

Although certification programs contain the impetus for the conservation of old-growth and old-growth characteristics, metrics for old-growth characteristics are left to be defined by managers. Guidance has been provided for some regional forest types [3], but is incomplete or lacking for many others. Forest-type specific definitions and guidelines are clearly needed, particularly in the context of certification programs, given the large variability between types [8].

Forests dominated by northern white-cedar (*Thuja occidentalis* L.) represent a type that currently lacks metrics for old-growth characteristics. White-cedar is a very long-lived, medium-sized tree common in north-central and northeastern North America. Although it may occur as a secondary component in mixed-species stands, it is more generally found as a dominant on a range of low quality sites, such as very poorly drained soils of forested wetlands [9,10]. Two white-cedar-dominated wetland forest types are commonly recognized: cedar seepage and cedar swamp communities [11]. Both are dominated by white-cedar, with balsam fir (*Abies balsamea* (L.) Mill.), spruce (*Picea* spp.), and other species present. Seepage forests occur on gentle slopes with soils composed of a shallow organic horizon over mineral deposits with moving groundwater, while white-cedar swamps occupy basins with limited drainage and groundwater present near the soil surface [11]. White-cedar dominated communities develop under low disturbance severity over long periods of time [12,13]. The conditions necessary for the development of white-cedar stands represent a wide variety of microhabitats and potential biological niches for specialist organisms [14].

Little is known regarding the composition and structure of old-growth white-cedar forests (but see [12]), despite the species' abundance and wide distribution. Regional indices for late-successional or old-growth stands [3,15] do not include white-cedar. Any indices or criteria based on tree age alone would be especially problematic for this species, as the prevalence of internal stem decay makes age largely indeterminable by tree-ring methods, especially for large individuals [12]. Further, this species' shade tolerance variability, longevity, and slow growth make stem diameter particularly unrepresentative of age [16]. Thus, identifying the structural characteristics of old-growth white-cedar stands is warranted to assess conservation value and ultimately improve management of this forest type. The objectives of our study were to (1) characterize a range of structural and compositional attributes of both old-growth and partially harvested white-cedar stands; and (2) determine if any of these attributes can be used to differentiate between old-growth and partially harvested white-cedar stands. We addressed these objectives by analyzing detailed structural and compositional information on 16 known old-growth stands as well as 17 stands with evidence of past partial harvesting.

2. Methods

2.1. Study Site Selection

For the purpose of this study, we define old-growth sites as those in late developmental stages with no known or visible history of harvesting (such as cut stumps), that is, 'primary forests' as defined by Frelich and Reich [17]. Potential old-growth sites were identified through consultation with regional scientists, state/provincial agencies, conservation organizations, and published accounts [15]. Four sites, out of 15 suggested for field reconnaissance, ultimately met our old-growth criteria and were selected for this study. All four sites are currently protected areas in Maine and New Brunswick, including Deboullie Ecological Reserve (Maine), Big Reed Forest Reserve (Maine), Baker Branch Reserve on the St. John River (Maine), and MacFarlane Brook Protected Natural Area (New Brunswick).

Partially harvested sites were those from which some proportion of the trees had been removed in the past 15 to 40 years, as evidenced by cut stumps in varying stages of decay. Although we were unable to obtain logging records, we note that stump numbers varied among sites, with a mean of

151 per ha (standard deviation = 89), and a range of 30–320 per ha (see below). Our intent was to select partially harvested sites near or adjacent to the old-growth sites, thus forming a paired sampling design. Although we were able to do this for three of the four old-growth sites, we were not able to do so for the Big Reed old-growth site. An additional partially harvested site was sampled at the Penobscot Experimental Forest, Maine, to provide a wider range of stand conditions in analyses.

In this region, large homogenous stands of white-cedar are uncommon; instead, small stands intergrade with other forest types, forming a patchwork of white-cedar 'micro-stands' (*sensu* Boulfroy et al. [18]), which in most cases limited our sampling to one plot per stand (see below). At each site, we sampled all stands dominated by northern white-cedar; that is, stands in which this species had the highest relative basal area of all species present. Our sampled stands spanned the gradient from apparent white-cedar swamps to apparent white-cedar seepage forests. The differences between swamp and seepage forests are subtle and often characterized by understory plant species composition and slight topographic changes [11]. Because preliminary ordinations of stands based on tree species composition did not suggest groupings that could be attributable to these two forest types, we did not attempt to separate them for further analyses.

2.2. Site Description

Mean annual temperature across sites ranged from 3.1 to 6.4 °C, and annual precipitation ranged from 1075 to 1155 mm [19]. Elevations ranged from 41 m a.s.l. at the Penobscot Experimental Forest to 383 m a.s.l. at the Big Reed Forest Reserve. All sites (old-growth and partially harvested) had loamy soils derived from glacial till with varying levels of organic material ranging from deep, predominately organic soils to soils with a shallow organic horizon over mineral deposits. Drainage of all sites ranged from very poorly drained to somewhat poorly drained with an average depth to water table ranging from 0 to 30 cm [20].

2.3. Field Sampling and Calculations

Our sampling included 17 partially harvested and 16 old-growth stands across the five sites. At each stand, we established randomly located fixed-radius circular plots (0.1 ha) to record tree species, diameter at breast height (DBH, 1.37 m), and location (distance and azimuth from plot center) for all living and dead trees ≥10 cm DBH. As above, the small size of most stands limited our sampling to just one plot per stand in most cases. However, three of the old-growth stands were large enough to permit up to four plots per stand, maintaining a minimum distance of 80 m between plots. In these cases plot values were averaged to produce stand-level values for analysis. Downed coarse woody debris (CWD) volume was estimated by the line-intercept method [21], using three 40 m transects (120 m total) radiating equi-angularly outward from plot center at fixed azimuths. For each coarse woody debris piece ≥10 cm diameter at the point of intersection with the sampling transect, we recorded diameter at intersection, species, and decay class (following the standard five-class system [22]). These values were converted to volumes using standard formulae [23]. Volumes of decay class 4 and 5 pieces were reduced to account for their collapse resulting from advanced decay [24]. From these data we calculated stand structural and compositional measures commonly used in forest management, including live and dead tree basal area (BA; $m^2 \cdot ha^{-1}$), number of trees per hectare (TPH), quadratic mean diameter (QMD; cm) of live and dead trees, BA and TPH of live and dead large trees (≥40 cm DBH), and volumes of CWD by decay class ($m^3 \cdot ha^{-1}$) (Table 1). Additional details on the sites and sampling protocol can be found in Wesely [25].

Table 1. Means (with standard deviation: SD) and ranges of stand structural variables for old-growth and partially harvested white-cedar stands (*n* = number of stands).

Stand Variable	Old-Growth (*n* = 16)		Partial Harvest (*n* = 17)	
	Mean (SD)	Range	Mean (SD)	Range
Living trees (DBH $\geq$ 10 cm)				
Basal area (m²·ha⁻¹)	51.8 (17.9)	26.6–94.2	54.5 (11.1)	37.3–76.3
Trees density (No. ha⁻¹)	765 (220)	300–1130	1051 (98)	560–1680
Quadratic Mean Diameter (cm)	29.4 (3.4)	24.2–34.4	26.3 (4.8)	19.8–34.9
Large trees ($\geq$40 cm DBH) (No. ha⁻¹)	135 (67)	70–280	97 (68)	0–210
Standing dead trees (DBH $\geq$ 10 cm)				
Basal area (m²·ha⁻¹)	12.7 (10.0)	3.2–31.9	7.5 (2.5)	2.5–12.0
Trees per ha (No. ha⁻¹)	164 (63)	70–280	182 (79)	90–350
Quadratic Mean Diameter (cm)	26.7 (4.4)	18.7–36.2	23.3 (3.1)	18.9–27.6
Large trees ($\geq$40 cm DBH) (No. ha⁻¹)	34 (42)	0–110	10 (7)	0–20
Coarse woody debris ($\geq$10 cm diam.)				
Total volume (m³·ha⁻¹)	168.1 (49.3)	74.1–240.5	125.1 (80.2)	36.4–314.1
Advanced decay volume (m³·ha⁻¹)	60.6 (40.5)	2.5–147.7	20.8 (21.1)	0–70.2
Cut stumps				
Density (No. ha⁻¹)	0	0	151 (89)	30–320

These same data also allowed us to calculate six structural indices, including both spatially explicit and non-spatially explicit indices, that we hoped would capture potentially subtle structural differences between old-growth and partially harvested stands. Three of these indices (numbers 1–3 below) are considered neighborhood indices, which make use of both sizes and spatial locations of plot trees and thus require mapped inventory plots, as described above. These indices are typically calculated for each 'focal' tree in the plot, using the species, size, proximity, azimuth, etc. of neighbor trees relative to the reference tree. These reference-tree indices can then be averaged to produce a plot-level index. Neighborhood indices used here include (1) diameter differentiation index, a measure of the spatial distribution of tree sizes with values ranging from 0 to 1, with increasing values representing greater difference between the diameter of a reference tree and its single nearest neighbor [26,27]; (2) mingling index, a measure of the species diversity in reference to a focal tree and its four closest neighbors [26–28]; and (3) mean directional index, a measure of the arrangement of four neighboring trees around a focal tree, with a value of 0 for a square lattice and higher values representing greater clustering [27]. Additional indices used here include (1) Gini index, a measure of the range of variability represented in diameters with the theoretical value of 0 representing a stand of all similar sized trees and a value of 1 representing maximum heterogeneity [29]; (2) Shannon-Weaver index based on tree diameters, a relative measure of diversity or variability represented across groups [26,27]; and (3) Clark-Evans index of aggregation, a measure of the regularity of the distribution of trees across a horizontal axis, with a value of 1 pertaining to a random configuration, lower values representing aggregation, and higher values increased regularity [26,27]. The mean number of trees per plot was 91 (range 30 to 168 trees per plot).

2.4. Statistical Analysis

We first tested if the two site types (old-growth vs. partially harvested) differed with respect to tree species composition, using multivariate techniques applied to species' relative basal areas. Specifically, we used multi-response permutation procedures (MRPP), a nonparametric procedure that tests the hypothesis of no difference between groups based on a matrix of Sørensen distances. MRPP produces a chance-corrected within-group agreement value *A*, which is a measure of heterogeneity within groups compared to random expectation. Tests were performed using PC-ORD Version 6.08 (MjM Software, Gleneden Beach, OR, USA) [30].

To determine if our structural metrics could distinguish old-growth from partially harvested white-cedar stands, we first needed to screen the large number of potential metrics to determine an appropriate subset for inclusion in a generalized linear model. To this end, we used a non-parametric approach, namely the variable selection using random forest (VSURF) package [31] in R (R Foundation for Statistical Computing, Vienna, Austria) [32]. The resulting top ranked predictors were then used to construct a generalized linear mixed-effects model using the lme4 [33] package in R. Here, old-growth status was used as the binary response variable while testing stand structural metrics as predictors. Location, site productivity (parent material, lithology, and soil drainage [20]), and a measure of climate (climate site index [34]), were also included as predictors (as random effects) in these models. Models were refined by iteratively excluding non-significant predictor variables in a stepwise procedure until only significant predictors remained. The model best supported by the data was identified based on the Akaike information criterion (AIC) score and area under the curve (AUC). A significance level of 0.05 was used for all main effects. Given that QMD was ultimately shown to be among the top predictors, we tested if the diameter distributions differed between old-growth and partially harvested forests (stands pooled), using a Kolmogorov-Smirnov test [35].

3. Results

Tree Species Composition and Forest Structure

Northern white-cedar dominated all stands, with an average relative basal area of $77 \pm 18\%$ (stands pooled), with a range of 32% to 98%. We had considered dropping, as an outlier, the stand with the 32% relative basal area from analyses, but ultimately retained it because white-cedar was still the dominant species, and the stand did not appear to be an outlier regarding structural metrics. Commonly associated species (in order of decreasing abundance by basal area) included red spruce (*P. rubens* Sarg.), black spruce (*P. mariana* (Mill.) B.S.P.), balsam fir, red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and black ash (*Fraxinus nigra* Marsh.). Tree species composition did not differ significantly between old-growth and partially harvested stands ($A = 0.023$, $p = 0.073$).

Our initial screening of potential predictors using random forest analysis produced the following top predictors for distinguishing old-growth from partially harvested stands: volume of advanced-decay CWD, quadratic mean diameter of live trees, live trees per hectare, total CWD volume, and quadratic mean diameter of standing dead trees (snags). The mixed-effects model that was best supported by the data (i.e., lowest AICc score) included just two predictors that, when used in combination, allowed us to distinguish old-growth status: advanced-decay CWD ($p = 0.013$) and QMD ($p = 0.039$ (Table 2). Parameter estimates for this model are provided in Table 3. Advanced-decay CWD volume averaged 60.6 ± 40.5 and 20.8 ± 21.1 m$^3 \cdot$ha^{-1} and QMD averaged 29.4 ± 3.4 and 26.3 ± 4.8 cm for old-growth and partially harvested stands respectively (Table 1). The majority of the remaining standard structural variables were quite similar between old-growth and partially harvested stands (Table 1). Decay class distributions of CWD in old-growth and partially harvested stands are presented in Figure 1.

Table 2. Ranking of models (increasing AICc) using variables identified in the preliminary random forest analysis used to predict old-growth status; CWD_{ADV} = advanced-decay coarse woody debris volume; QMD = quadratic mean diameter, live trees; CWD_{TOT} = total coarse woody debris volume; TPH = live trees per hectare; SN_QMD = standing dead (snag) quadratic mean diameter. * denotes significance ($p \leq 0.05$); k = number of model parameters; AICc = corrected Akaike information criterion; ΔAIC = change in Akaike information criterion; AICc wt. = corrected Akaike information criterion weights; AUC = Area under the curve, an assessment of model fit; R^2 refers to a pseudo R^2 calculated for a binomial distribution.

| Model Predictors	k	AICc	ΔAICc	AICc wt.	AUC	R^2
CWD_{ADV} * + QMD *	4	37.8	0.0	0.62	0.84	0.69
CWD_{ADV} * + QMD * + CWD_{TOT}	5	39.3	1.6	0.28	0.75	0.77
CWD_{ADV} * + QMD + CWD_{TOT} + TPH	6	42.0	4.2	0.08	0.71	0.79
CWD_{ADV} * + QMD + CWD_{TOT} + TPH + SN_QMD	7	45.2	7.5	0.01	0.70	0.79

Table 3. Parameter estimates for fixed effects in final binary model, in the form old-growth status = a + b(CWD_{ADV}) + c(QMD); CWD_{ADV} = advanced-decay coarse woody debris volume.

| Variable	Parameter	Parameter Value (Standard Error)	*p*-Value
Intercept	a	−10.44 (4.60)	0.023
Advanced-decay CWD volume	b	0.060 (0.02)	0.013
Quadratic mean diameter (QMD)	c	0.294 (0.14)	0.039
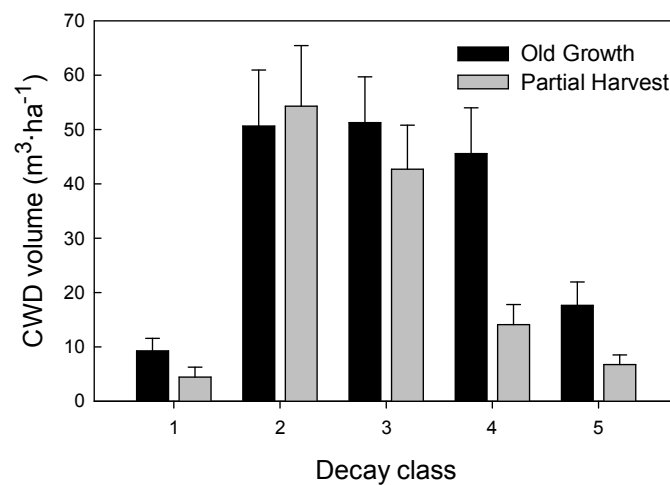
Figure 1. Decay class distributions of coarse woody debris between old-growth and partially harvested stands. Error bars represent one standard error of the mean. CWD: coarse woody debris.

The combined influence of advanced-decay CWD volume and QMD, as predictors of old-growth status, can be readily seen in Figure 2, which demonstrates that as the values of both metrics simultaneously increase, so does the probability that a given stand can be classified as old-growth. Despite the significance of QMD in our final model for distinguishing old-growth from partially harvested stands, diameter distributions did not differ significantly between these two types (Kolmogorov-Smirnov tested at $\alpha = 0.05$; Figure 3).
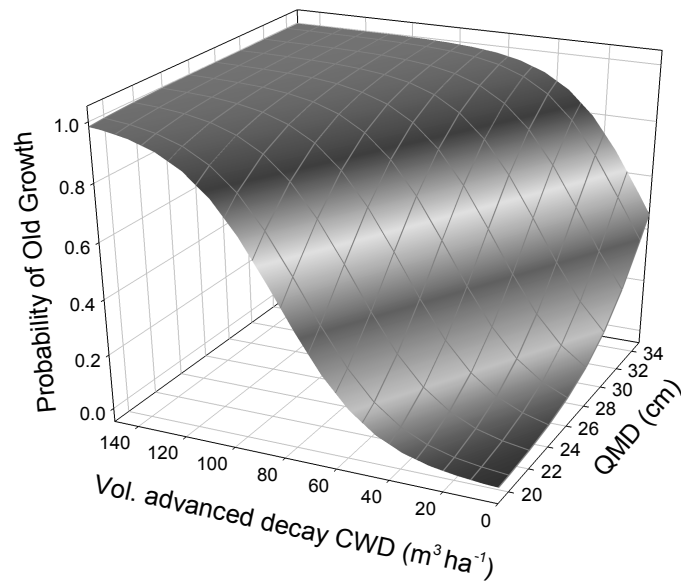
Figure 2. Probability of old-growth white-cedar as a function of volume of advanced-decay coarse woody debris (CWD) and quadratic mean tree diameter (QMD). As values of either one or both increase, so does the probability that a given stand can be classified as old-growth.
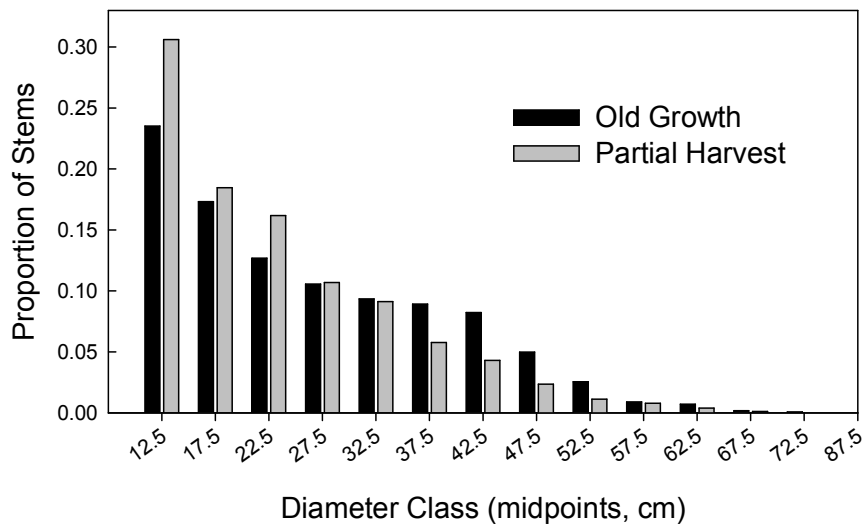
Figure 3. Diameter distributions of old-growth and partially harvested white-cedar stands (pooled data).

None of the six structural indices were significant in predicting old-growth status; indeed, the means, standard deviations, and ranges for all metrics were quite similar between old-growth and partially harvested stands (Table 4). Similarly, the location and site productivity variables were not useful in separating the old-growth and partially harvested stands.

Table 4. Mean (standard deviation) and range of structural indices for old-growth and partially harvested stands. (*n* = number of stands).

Indices	Old-Growth (*n* = 16)		Partial Harvest (*n* = 17)	
	Mean (SD)	Range	Mean (SD)	Range
Diameter differentiation	0.35 (0.04)	0.28–0.44	0.33 (0.03)	0.27–0.39
Mingling	0.50 (0.19)	0.18–0.77	0.43 (0.15)	0.17–0.64
Clark-Evans	0.30 (0.02)	0.27–0.34	0.29 (0.03)	0.24–0.33
Shannon-Weaver (diameters)	1.08 (0.44)	0.38–1.64	0.86 (0.30)	0.40–1.35
Mean directional	1.86 (0.12)	1.56–2.04	1.94 (0.09)	1.78–2.15
Gini (diameters)	0.26 (0.03)	0.22–0.29	0.24 (0.04)	0.18–0.29
Simpson (diameters)	0.54 (0.20)	0.19–0.77	0.45 (0.16)	0.19–0.70

4. Discussion

Although forest managers worldwide have a clear need to identify old-growth characteristics, few quantitative criteria exist to aid in this process. Our results suggest that old-growth (never harvested) northern white-cedar stands in the study region can be distinguished from partially harvested stands by using two easy-to-obtain metrics. Specifically, old-growth stands in our study had a greater volume of advanced-decay CWD and larger QMDs (Table 1, Figure 1). When used together, and in in conjunction with surveys of cut stumps, these metrics constitute practical old-growth criteria that can be obtained from standard forest inventories, a feature that greatly benefits forest managers [36].

4.1. Tree Species Composition

It is recognized that late-successional, shade-tolerant species often characterize old-growth forests [37], and some definitions of old growth rely heavily on tree species composition [38]. Although previous studies report differences in tree species composition between old-growth and harvested stands of various forest types [36,39], our study found no significant differences in overstory species composition with regard to management history. Our stand selection criterion was based on dominance of white-cedar by basal area, thereby focusing on one end of this white-cedar forest type continuum. This may have confounded our ability to detect differences in tree species composition potentially evident in less pure white-cedar stands.

In addition, our study differs from many previous studies in that we did not use for comparison true second-growth stands (those that developed following stand-replacing harvest); instead, we used stands that had experienced only partial harvesting. This intensity of harvesting may have been insufficient to cause the shift in tree species composition evident in true second-growth stands [35]. White-cedar is a slow-growing, shade-tolerant species that often dominates stands that develop with repeated, small-scale disturbances, which further favor shade-tolerant species [12,40]. The stands we sampled for comparison with old-growth had received moderate partial harvests, which like small-scale natural disturbances would favor more shade-tolerant species, as opposed to silvicultural treatments such as clearcutting that would favor shade-intolerant species. Thus our partially harvested stands would be more likely to maintain their pre-harvest species composition. Similar stability in composition has been observed in regional forests where small-scale disturbances (natural or harvest-related) maintain shade-tolerant tree species [41,42].

4.2. Forest Structure

Many previous studies have examined differences in forest structure between old-growth forests and those that have been actively managed. Results from studies worldwide conclude that old-growth forests generally have greater structural diversity [4–6], more large trees [4,5,43], more diverse diameter distributions [2,5,6], greater snag size and abundance [4,5,36], greater woody debris volume [6,43–45], and greater total above-ground biomass [4,46], when compared to actively managed forests. Our work

is similar to these previous studies in many ways, yet it has a subtle but important difference: the stands we assessed, for comparison to old-growth, had only been partially harvested, and harvesting occurred some distance in the past. As such, our study is quite similar to a growing number of recent studies worldwide aimed at identifying criteria associated with forest 'naturalness' [47,48]. Use of this concept recognizes that stands having experienced light harvesting in the past, or stands recovering from long-ago harvests, often have high conservation value [6,49,50]. The degree to which they contain pre-management structures, species composition, and processes can be taken as a direct measure of naturalness [51]. Many of these studies assess compositional and structural attributes similar to those addressed in the current study, and they have identified important structural attributes associated with naturalness that are quite similar to those mentioned above: larger tree diameters, greater volumes of woody debris (including snags), greater structural diversity [6,44,45,49,52]. Nevertheless, Brumelis et al. [51] argue that criteria for forest naturalness must be forest-type and location specific. Even with such specific criteria, old-growth and semi-natural forests can be difficult to distinguish [6,50,52]. Indeed, our study suggests that partially harvested stands did not differ appreciably from old growth regarding a number of structural attributes, as well as tree species composition.

However, our results did identify two metrics—volume of advanced-decay coarse woody debris (CWD, decay classes 4 and 5) and the quadratic mean diameter (QMD)—that when used in combination, provided the best means of separating old growth from partially harvested stand structures, with old-growth having higher values of both metrics. Thus our findings largely corroborate those of these previous studies regarding CWD and tree diameters when assessing forest naturalness.

Similar to our findings, Angers et al. [53] report greater volumes of advanced decay CWD in old-growth when compared to stands that had experienced two types of partial harvest (single-tree selection and diameter-limit cutting) in hardwood-dominated forests of Quebec, and Motta [6] found higher volumes of CWD in old growth, when compared to stands withdrawn for management for many decades and stands harvested by single-tree selection. CWD is a prominent feature of old forests [4,36] and is often used as an identifying characteristic for old-growth stands [6,54]. CWD is critical to maintaining biological diversity in forested ecosystems because a large number of organisms depend on dead wood at some stage in their life cycle [54,55]. Furthermore, large volumes of CWD can be used as a surrogate for species richness of deadwood-dependent organisms, which comprise a major portion of forest biodiversity [55,56]. Large volumes of advanced-decay CWD is among the structural attributes that take the longest time to develop in previously managed forests [57], yet it represents a particularly important substrate for rare organisms [55]. Because of consistent inputs in various size classes to the CWD pool as the result of small-scale natural disturbances [12], along with slow decomposition rates [58], white-cedar stands have the potential to accrue high volumes of CWD across a range of decay classes. Given that harvesting activities remove trees that would otherwise have entered the CWD pool [55], it follows that unharvested white-cedar stands would possess greater volumes of CWD, particularly in advanced stages of decay (Figure 1).

Large trees are also a prominent feature of old forests and are often used to identify late-successional or old-growth stands worldwide [6,36,59]. In particular, the density of trees over 40 cm diameter is taken as a suitable indicator of late-successional forest of high conservation value for northern hardwood forests [3], as well as old-growth forests in Alberta [60], although a diameter threshold of 50 cm has been suggested based on a review of temperate forests worldwide [4]. This metric (40 cm diameter) however did not improve our ability to distinguish old-growth from partially harvested white-cedar stands, nor did the diameter distributions differ between the two types. This finding might be explained by practitioners' choice to leave the largest white-cedars unharvested, given the well-known likelihood of internal decay for this species. Indeed, the probability of internal decay increases with diameter for this species, with trees over 40 cm diameter having a ca. 70% probability of being decayed (Fraver, unpublished data). Instead, we found live tree QMD, when used in combination with volume of advanced-decay coarse woody debris, to be more useful in

distinguishing old-growth from partially harvested stands (Figure 2), with old-growth stands having a larger QMD.

Large trees are increasingly uncommon forest structures, yet they serve an important role in forest processes and offer substrate for rare organisms [14,61]. Although the actual size of trees can be important in providing habitat structures for associated organisms [62,63], in some cases the developmental changes of the tree, such as deepening bark fissures, decorticated wood, and changes in acidity, are particularly important to rare epiphytes [14]. Further, the actual size of a "large" tree is relative to a particular ecosystem and species; in the northeastern U.S. and New Brunswick, trees are generally smaller than those found in other areas where old-growth definitions have been developed.

Various structural indices have recently provided insight into vertical and horizontal stand structure that may not be captured in basic inventory data [26,28,29,52]. As old-growth forest can possess aspects of structural complexity that are unrepresented in younger forests [64], these indices can offer greater insight into that complexity. To our surprise, these indices did not enhance our ability to differentiate old-growth from partially harvested stands (Table 4). Similarly, Kuehne et al. [65] report only marginal differences in structure, using these same structural indices, between various silvicultural treatments and unharvested control stands. Our finding could result from a large degree of structural and spatial heterogeneity in many white-cedar stands, even at earlier stages of recovery from harvest [66]. Field observation suggested that all study stands, regardless of harvesting history, exhibited clumping of white-cedar trees, which could confound any distinction of types based on the Clark-Evans or mean directional indices. The finding that harvesting history had no bearing on tree species composition could explain the inability of the mingling index to differentiate stands based on previous harvesting. In addition, the plot size used in this study (0.1 ha) may have been too small to adequately characterize structural complexity [64,67]; more work is needed on identifying appropriate plot sizes for application of structural indices. Finally, we note that several newly applied structural complexity indices based on laser scanning (e.g., [68,69]), may have allowed us to differentiate old-growth from partially harvested stands; however, we did not have access to these data types, and our intent was to identify differences that could be derived from currently available field inventory data. Current active research on interpretation of laser-scanning point clouds, as well as the increased availability of such data worldwide, may ultimately prove useful in differentiating forest structures that may have been missed by the field methods employed in our study [69,70].

Because of the long history of logging in the northeastern U.S., old-growth forests are particularly rare. Although our sites represent the full set of known old-growth white-cedar in the region, we recognize the limitations of a relatively small sample size (16 old-growth stands from four locations, with often just one plot per stand). Small sample sizes can decrease the power of statistical tests and limit inference to the population of focus [71]. For these reasons, our results cannot be generalized to other white-cedar populations across the species' geographic range. Nevertheless, our results are supported by previous work that has drawn attention to CWD abundance and tree size in old-growth forest of the region [3,5,59]. Successful old-growth definitions build on well-recognized structural attributes, such as those found here, yet need to be "calibrated" for specific forest types and regions [8,36]. This can be particularly useful when metrics are based on common forest inventory data, resulting in old-growth definitions that are easily understandable by land managers and can more readily be implemented in management.

4.3. Management Implications

A particular challenge for land managers is the distinction between old-growth and previously managed late successional forests. The structural features typical of old-growth vary in the time they take to accumulate following disturbance or the cessation of management [46]. Because these structures are dynamic, white-cedar stands that do not currently possess old-growth features (i.e., large average tree sizes and high volumes of advanced-decay CWD) can be managed in a way that promotes their development. In fact, a growing focus in forest management is the creation and maintenance of

unique structural features associated with old-growth through ecological forestry [72,73]. Our results may aid those interested in developing ecologically based silvicultural prescriptions for white-cedar stands by suggesting structural features (i.e., large diameter trees and CWD) on which to focus. Irregular shelterwood and other types of partial cutting suggested for white-cedar stands [18] may be compatible with the development of old-growth structural features [72] if individual trees or micro-stands are retained over multiple rotations. In addition, white-cedar trees respond well to release from competition [40], suggesting that thinning can be used to focus growth on residual trees, both to accelerate growth to larger sizes and diversify diameter distributions over time [7].

Recent studies have suggested methods to increase coarse woody debris abundance in post-harvest stands by felling some low value or cull trees [74]. Other operational considerations include avoiding areas of coarse woody debris accumulation during harvest layout, and in-woods retention of tree tops and branches to increase the pool of coarse woody debris in harvested stands. Such practices may also facilitate regeneration, and thus long-term sustainability of white-cedar stands, because of the importance of CWD as a substrate for white-cedar germination [75] and the potential for intact tree tops and branches to provide low shade and limit herbivore access to seedlings [76].

Finally, our findings have relevance in the context of Forest Stewardship Council (FSC) certification. FSC guidelines for the Northeastern United States [1] specify that true old-growth requires reserve status (i.e., no harvesting), while semi-natural forests (those that that have retained old-growth characteristics despite past partial harvests) could be harvested, providing that such characteristics are maintained during management operations. Currently this distinction between true old-growth and partially harvested is not well defined or quantified. Our results should aid in this distinction for the white-cedar forest type in this region.

5. Conclusions

We tested a large number of metrics that could potentially be used to distinguish old-growth (never harvested) northern white-cedar stands from partially harvested stands. Our findings suggest that two easy-to-obtain metrics, namely the volume of advanced-decay CWD and quadratic mean diameter, when used together, could effectively distinguish these types; both metrics were higher in old-growth stands. To our surprise, none of the more complex structural indices improved the model's ability to distinguish between these types. Further, the forest types did not differ with respect to tree species composition. Taken together, these results can improve management decision making for white-cedar, while also shedding light on the effects of past partial harvesting on current forest structure. These findings may be used to develop ecologically based silvicultural prescriptions for white-cedar stands by suggesting structural features (i.e., CWD and large diameter trees) on which to focus.

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