Structural changes and potential vertebrate responses following simulated partial harvesting of boreal mixedwood stands

Mark C. Vanderwel [a,*,1], John P. Caspersen [a], Jay R. Malcolm [a], Michael J. Papaik [b,2], Christian Messier [b]

[a] Faculty of Forestry, University of Toronto, 33 Willcocks St., Toronto, ON M5S 3B3, Canada
[b] Centre d'Études de la Forêt, Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada

ABSTRACT

Partial harvesting, where different numbers and arrangements of live trees are retained in forest stands, has been proposed for maintaining late-successional structure and associated vertebrate species within managed boreal forests. Using the stand dynamics model SORTIE-ND, we examined 80-year patterns of structural change in response to different intensities (30–70% basal area removal) and spatial patterns (22–273 m² mean patch size) of harvesting. We also applied habitat models for seven late-successional vertebrates to the structural conditions present after harvesting to assess potential species responses.

Partial harvesting increased understory and downed woody debris (DWD) cover and decreased overstory structure for the first 25 years after harvest, in comparison to unharvested stands, with this effect subsequently reversing as harvest-induced regeneration reached the canopy. Although harvesting enhanced long-term structural development in this regard, large trees, large snags, and large DWD all remained below unharvested levels throughout the simulation period. Harvesting also produced transient increases in early-decay DWD and ground exposure. Most changes in structural attributes increased in proportion to harvest intensity, but structural differences among harvest patterns were generally small. Dispersed harvesting induced somewhat less pronounced decreases in vertical structure, and produced more post-harvest slash, than aggregated harvesting.

All seven vertebrate species decreased in abundance as harvest intensity increased from 30 to 70%. In comparison to their pre-harvest abundances in old stands, vertebrates associated with DWD (redback salamander, marten, red-backed vole) showed neutral or positive responses at one or more harvest intensities, whereas those associated with large trees and snags (brown creeper, flying squirrel) consistently exhibited substantial adverse impacts.

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1. Introduction

Over the span of decades or even centuries, forest stands that escape catastrophic disturbance develop increasing live biomass, coarse woody debris, diversity in tree size and foliage height, and spatial heterogeneity (Franklin et al., 2002; Harper et al., 2003; Brassard and Chen, 2006), with the resulting structural complexity providing habitat for many late-successional vertebrate and non-vertebrate species in mature and old forest ecosystems (Penttilä et al., 2004; Fisher and Wilkinson, 2005; Schieck and Song, 2006). Natural and anthropogenic disturbances strongly influence stand structure and habitat conditions, either enhancing within-stand complexity by creating treefall gaps of various sizes (McCarthy, 2001), or reinitiating stand development by removing most or all live canopy trees. Yet, while light- and moderate-intensity mortality events are predominant characteristics of natural disturbance regimes across many forest regions (Frelich and Lorimer, 1991; Veblen et al., 1991; Lertzman et al., 1996; Bergeron et al., 2001; Seymour et al., 2002), clearcut harvesting has long been established as the favoured method for managing commercial forests across much of North America and Europe, and in the Canadian boreal forest in particular. Through time, this type of harvesting has led to simplification of stand structures through less diverse tree species composition, reduced structural legacies, and loss of spatial heterogeneity relative to naturally disturbed boreal stands (Bergeron and Harvey, 1997; Carleton, 2000; Drapeau et al., 2000; Brassard and Chen, 2006).

* Corresponding author. Tel.: +44 01223 479957; fax: +44 01223 479999.
  E-mail addresses: mark.vanderwel@utoronto.ca (M.C. Vanderwel),
john.caspersen@utoronto.ca (J.P. Caspersen), jay.malcolm@utoronto.ca
(J.R. Malcolm), papaikm@comcast.net (M.J. Papaik), messier.christian@uqam.ca
(C. Messier).
  [1] Present address: Microsoft Research, 7 JJ Thomson Ave., Cambridge, CB3 0FB, United Kingdom.
  [2] Present address: USDA-FS Southwest Research Station, 1731 Research Park Dr., Davis, CA 95618, United States.
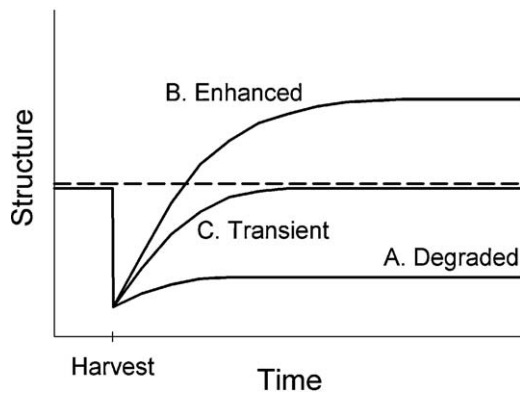
Fig. 1. Schematic representation of hypothesized stand structural dynamics following partial harvesting. The dashed line corresponds to the amount of structure in an old undisturbed stand, where features such as the distribution of tree sizes, vertical arrangement of foliage, standing and fallen dead wood, or understory cover are represented by the vertical axis. The three solid lines correspond to hypotheses where, following an initial harvest-related decrease, structural development is either degraded (A), enhanced (B), or transiently affected (C) over the long term.

Disparities between natural and anthropogenic disturbances have led to calls for employing a greater diversity of stand management practices (Harvey et al., 2002; Puettmann et al., 2009). Retaining variable numbers of residual trees at the time of harvest, either in aggregated patches, dispersed uniformly throughout a stand, or in some combination of the two patterns (as proposed by Franklin et al., 1997), may better emulate the conditions created by common disturbances, and could promote the structural complexity produced by autogenic stand development processes. Such partial harvesting concepts have garnered support as a potential means of achieving both ecological and timber-production objectives in the boreal region (Mitchell and Beese, 2002; Ruel et al., 2007; Thorpe and Thomas, 2007). Although application of partial harvesting in boreal stands is hindered by lack of direct, long-term experience, recent advances in individual-based stand growth modelling (Coates et al., 2003; DeAngelis and Mooij, 2005) now provide an opportunity to simulate different patterns and intensities partial harvesting and investigate subsequent patterns of structural change. Spatially explicit models that represent the locations of individual stems further provide a way to track the dynamics of habitat features used by vertebrate species associated with old, structurally complex forests.

We hypothesized that partial harvesting could induce several different patterns of long-term structural change following an initial decrease in a given structural attribute (Fig. 1). One possibility would be that structural development remains below that in unharvested stands through time, causing a long-lasting degradation of structural conditions. For example, alleviation of density-dependent competition among canopy trees could impede production of snags and downed woody debris, or it might take a long time for densities of large diameter trees to recover to pre-harvest levels. A second possibility is that because harvesting removes trees facing imminent mortality, it increases resource availability and thereby enhances growth and structural development (Chen and Papadiouk, 2002; Harvey et al., 2002). Such changes could be particularly pronounced within the understory stratum where trees benefit most from release. In this situation, the structure of harvested stands could be better developed than in old unharvested stands. Yet another possibility is that initial post-harvest decreases (or increases) in structure are only transient effects. Light reaching the forest floor, for example, is expected to diminish through time due to crown expansion and release of understory trees (Beaudet and Messier, 2002). In time, the structure of harvested stands might recover to match levels in unharvested stands. The pattern, magnitude, and duration of structural change in each case could depend on the proportion of stand basal area removed and distribution of gap sizes created through harvest (McCarthy, 2001; Thorpe and Thomas, 2007), with more intensive harvesting expected to cause greater and longer-lasting structural changes than harvests that leave a stand more intact. Harvesting trees within aggregated groups is expected to promote more heterogeneous stand conditions, including tree species with a wider range of light requirements, and may better conserve structural and biological legacies that are sensitive to disturbance of the forest floor (Franklin et al., 1997).

In a review of wildlife responses to partial harvesting, Vanderwel et al. (2009) found that at least 38 vertebrates associated with mature or old boreal forest (out of 65 considered) were likely to decrease in abundance following relatively high-intensity (70% removal) partial harvesting. For several of those species, studies within the boreal region have produced habitat models that relate occurrence or abundance to stand-level habitat attributes (e.g., Bowman and Robitaille, 1997; Pearce and Venier, 2005). Such models provide a basis for linking the patterns of structural change that may occur following partial harvesting to consequent vertebrate responses. In this manner, one can investigate the degree to which various forms of partial harvesting might affect certain vertebrate species within stands in the boreal region.

We used the spatially explicit, individual-based stand dynamics model SORTIE-ND, parameterized for eastern Canadian boreal mixedwood stands, to investigate stand structural dynamics following various intensities and spatial patterns of partial harvesting. Our objectives were to: (1) evaluate hypotheses concerning three possible patterns of long-term structural change (degraded, enhanced, and transient) relative to unharvested stands and to each other; and (2) assess the relative susceptibility of seven late-successional vertebrate species to different types of partial harvesting. We interpret results in the context of using partial harvesting as a strategy for maintaining complex late-successional structure and vertebrate species within managed boreal stands.

2. Methods

2.1. Model description

SORTIE-ND is an individual-based, spatially explicit modelling platform for simulating forest stand dynamics through establishment, growth, seed dispersal, death, and decomposition of individual trees within a toroidal plot ($200\,m \times 200\,m$ in our simulations). SORTIE was first developed and parameterized for hardwood forests in the northeastern United States (Pacala et al., 1993, 1996), and has since been extended to tropical, temperate, and boreal forest regions in Puerto Rico, New Zealand, and Canada, respectively (Coates et al., 2003). The versatility of the model is partly attributable to its modular structure and open-source code (available online at http://www.sortie-nd.org), which enables developers to expand or modify SORTIE-ND's capabilities as needed.

Within the model, trees are represented by cylindrical crowns that compete with each other through interception of incident sunlight and crowding of neighbouring individuals. Adult trees disperse seeds locally, which probabilistically germinate and establish as seedlings under favourable light and substrate conditions. Trees experience stochastic mortality as a result of growth suppression or senescence, and can remain as snags for a period of time before falling to the ground. Upon falling, conical stems of dead trees contribute to a local pool of woody debris substrate, whose decomposition is tracked through a series of decay classes before reverting to forest floor litter and moss. Woody debris may also be added following harvesting events.

The SORTIE-ND implementation used in the present study is based upon one developed for upland boreal mixedwood stands in Quebec's Abitibi region (48°28′N, 79°21′W) (Poulin and Messier, 2008; Beaudet et al., 2011). The tree species represented by this model include trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) P. Mill.), white spruce (*Picea glauca* (Moench) Voss), white birch (*Betula papyrifera* Marsh.), and eastern white cedar (*Thuja occidentalis* L.). For this implementation, sub-models for allometric scaling, light interception, tree growth, tree mortality, and recruitment were parameterized using repeated field measurements of individual trees from the Lac Duparquet Research and Teaching Forest near Rouyn-Noranda, Quebec (Poulin and Messier, 2008). Beaudet et al. (2011) have described the light sub-model in detail, and have shown that it accurately captures understory light conditions in stands subject to a wide range of harvest intensities. At a broader scale, Papaik et al. (2010) have reported that the parameterization of SORTIE-ND used here accurately captured successional patterns on most soil types, and that long-term, landscape-level adult tree dynamics under clearcut, gap harvest, and uniform thinning regimes were in relatively good agreement with a forest landscape model.

In addition to the model formulation described above, we included additional parameters to describe snag falls, substrate decomposition, and post-harvest substrate composition based on studies of dead wood dynamics from the region. Species-specific rates of snag fall were obtained from Vanderwel et al. (2006) and Angers et al. (2009). Decay-class transition rates for woody debris were derived using an exponential decay model for wood density (Brais et al., 2006) together with decay-class-specific wood densities (Ter-Mikaelian et al., 2008) for trembling aspen. We modelled harvest-related additions and losses of woody debris in different decay classes based on pre- and post-harvest amounts of woody debris in partially harvested stands (Harvey and Brais, 2007). In our SORTIE-ND simulations, snags would stand for approximately 10–15 years before falling, woody debris would advance through 5 decay classes over about a 32 year period, and harvesting would both remove 28% of existing woody debris and add 25 m³/ha of new woody debris in decay classes 1–3. A model input file containing all parameter values is available from the first author upon request.

SORTIE-ND incorporates a relatively high degree of detail in its representation of tree and stand attributes, but nonetheless simplifies several aspects of stand dynamics. For example, tree crowns maintain a fixed allometry and are unable to respond dynamically to gap creation other than through diameter and height growth. Competition from understory vegetation, which may have important effects on seedling establishment, is not explicitly considered. Also, our simulations did not introduce any spatiotemporal variation in mortality, such as might result from common secondary disturbance processes. As with any ecological simulation model, caution is warranted in interpreting SORTIE-ND's projections of a complex natural system.

2.2. Simulated harvests

We carried out simulated harvests at three levels of removal intensity (30%, 50%, and 70% of basal area) and three levels of removal aggregation (uniform, small-patch, and large-patch) to investigate structural responses to different forms of partial harvesting. These different harvests were realized by varying two aspects of the harvesting algorithm: (1) the proportion of stand basal area to remove; and (2) the patch-size distribution of groups of trees to remove or retain. Harvesting affected saplings, adult trees, and snags irrespective of size or species; seedlings were unaffected.

At the time of a simulated harvest, SORTIE-ND generated a list of all trees >1.3 m in height to be allocated for either removal or retention. The harvest algorithm would first draw a random tree from those yet to be allocated, and a random deviate from a log-normal patch-area distribution. All unallocated stems within the corresponding circular patch centered on the selected tree were removed. Another random tree and patch size were next drawn, and all unallocated trees within the new patch were retained. These two steps were repeated in turn until either the target proportion of trees to remove or to retain was met. All remaining unallocated trees were designated for either removal (if the retention criterion was already met) or retention (if the removal criterion was met).

We sought to simulate harvest scenarios where many trees were always removed individually or in small groups, but where an increasing area could be allocated to larger gaps or retention patches by varying a single characteristic of the patch-area distribution. To do so, we calculated the parameters for a log-normal distribution (μ, σ) from formulae specifying the mode and 95th percentile of a given patch-area distribution (Strom and Stansbury, 2000). We specified a common mode for all levels of harvest pattern that corresponded to the approximate area of an individual tree crown (20 m²), and selected 95th percentiles of patch area of 30, 300, and 1000 m² for uniform, small-patch, and large-patch harvest patterns, respectively. These values yielded respective mean patch sizes of 22, 94, and 273 m². Gaps in intact hardwood-dominated boreal stands reportedly range from 20 to 577 m² in size, with most of these gaps being less than 100 m² (Kneeshaw and Bergeron, 1998). Examples of post-harvest stem maps for each harvest type are depicted in Fig. 2.

2.3. Simulation runs

We first generated 15 independent, structurally complex stands by running SORTIE-ND for 120 years, starting from equal 1-cm DBH stem densities for the five species. We calibrated total initial tree density so that after 120 years, species composition approximated that found in five old boreal mixedwood stands surveyed as part of another study in the region (details on stand characteristics and field methods in Vanderwel et al., 2010). With an initial density of 2000 stems/ha, the simulated stands came to be comprised of 50% trembling aspen, 18% white spruce, 15% eastern white cedar, 12% balsam fir, and 6% white birch after 120 years. In comparison, the average relative basal areas of these respective species were 31%, 20%, 14%, 16%, and 19% in the calibration stands.

Next, we replicated each of the 120-year-old stands to implement the nine partial harvest scenarios, as well as follow the development of unharvested stands, from the same starting conditions. These scenarios were run for a further 80 years, with output generated at 5-year intervals. We averaged replicate model output ($n = 15$) for each harvest scenario and post-harvest time interval to account for a small degree of stochastic variability in structural development among runs (average coefficient of variation for all variables was 3%). At the end of the simulation runs, unharvested stands were comprised of 29% trembling aspen, 29% balsam fir, 26% cedar, 15% white spruce, and 2% white birch by basal area. The large decrease in trembling aspen, large increases in balsam fir and cedar, and small changes in white spruce and white birch, are all in good agreement with patterns of successional change apparent in long-term chronosequence data for this forest type (Bergeron, 2000). Harvested stands came to be comprised of 23–42% trembling aspen, 33–41% balsam fir, 11–22% cedar, 11–17% white spruce, and 1–2% white birch after 80 years. The increase in balsam fir and decrease in cedar as a result of harvesting are consistent with the contrasting regeneration success of these shade tolerant species following partial disturbances.
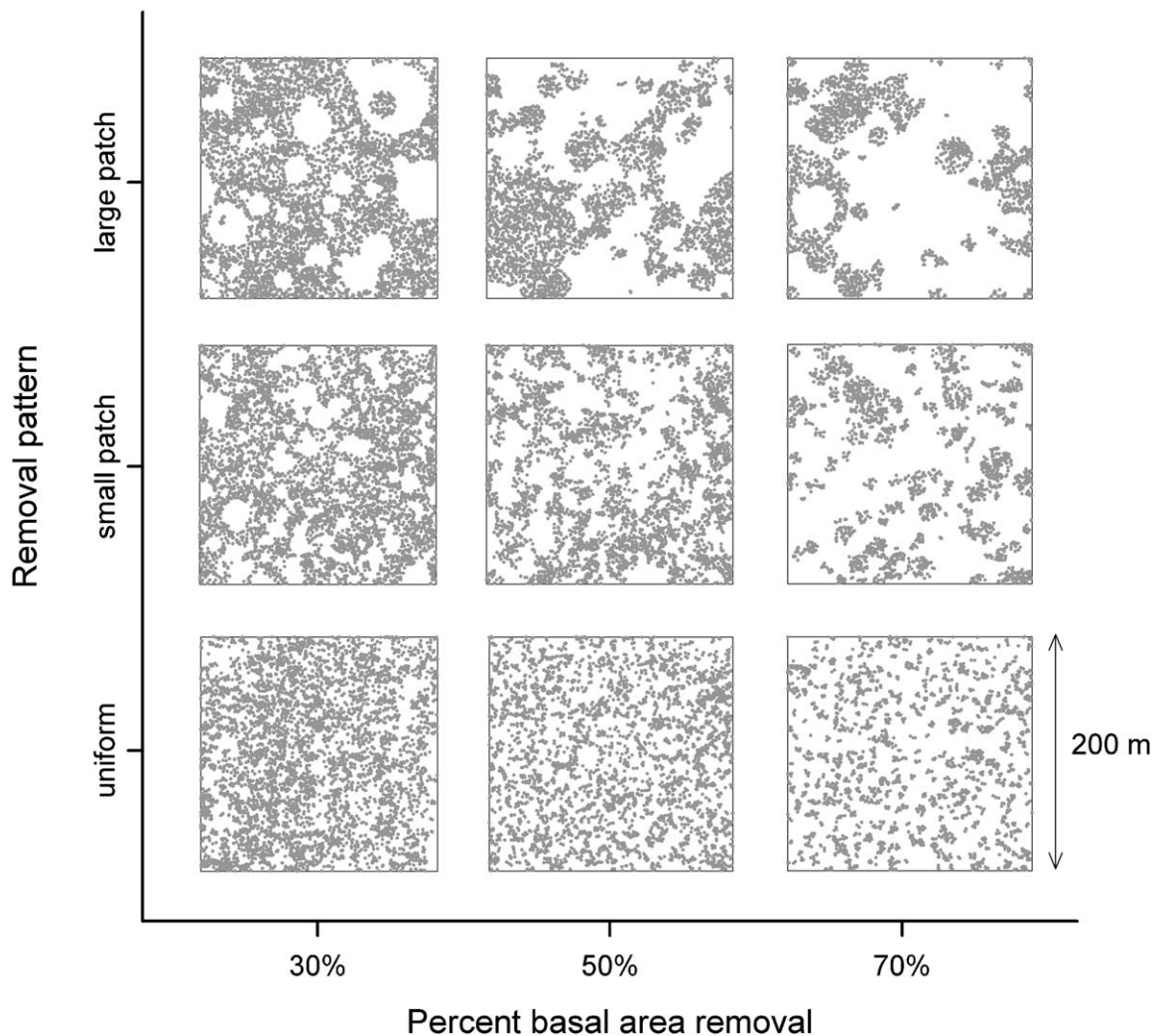
Fig. 2. Stem maps depicting examples of simulated partial harvesting at three levels of both intensity (increasing from left to right) and aggregation (increasing from bottom to top).

2.4. Analysis of output variables

Detailed information on the size and spatial distribution of stems in SORTIE-ND provides an opportunity for calculating a wide range of structural attributes beyond those traditionally used in stand dynamics models. Stand structural complexity encompasses multiple dimensions that relate to the distribution of tree sizes, vertical arrangement of foliage, standing and fallen dead wood characteristics, regeneration and understory development, and within-stand heterogeneity (McElhinny et al., 2005). We derived 24 structural output variables (Table 1) from SORTIE-ND's internal stem map and substrate grid in each 5-year timestep to describe changes in overstory, snags, understory, vertical structure, and downed woody debris (DWD). We then performed a principal components analysis (PCA) on these variables to succinctly characterize common patterns of structural variation through time and among harvest scenarios. Contributions of the original variables were assessed through their loadings on principal components that were retained for interpretation.

To assess potential vertebrate responses to the partial harvest scenarios, we coupled structural output from SORTIE-ND with empirical stand-level habitat models for seven species associated with mature or old forests (Table 2). These vertebrate species were selected to span a range of different taxonomic groups (3 classes, 4 orders, 7 families), trophic guilds, and habitat requirements. The species serve diverse ecological roles within mixedwood forests by variously consuming insects, fungi, seeds, or small mammals; by foraging, nesting or denning either at the forest floor, in the understory, or in the canopy layer; and by maintaining home ranges at a range of different spatial scales. Collectively, they encompass the habitat conditions required by a wide range of less well-studied species that are associated with mature and old boreal mixedwood forests. Three of the species (red-backed vole, northern flying squirrel and American marten) have been provincially designated as indicator species for sustainable forest management in this stand type (McLaren et al., 1998).

Published and unpublished habitat models were derived from generalized linear models of stand-level habitat features against species occurrence or abundance, based upon data from nearby regions. We evaluated the direction, magnitude, persistence, and trend of vertebrate species responses to different harvest types by comparing the ratio of estimated abundance five years after harvesting to that immediately prior to harvest, and by projecting the time required for abundance to return to pre-harvest levels. Changes in expected abundance among intensities and patterns of harvest were inspected for concordance with a predicted pattern of decrease with greater intensity of removal. We also ranked species by their relative change in abundance, and compared this to assessments of their susceptibility to different harvest intensities by Vanderwel et al. (2009).

Table 1
Loadings of 24 structural variables on three principal components describing simulated boreal mixedwood stand dynamics over 80 years in absence of harvesting and in response to nine partial harvest scenarios. Only loadings with absolute value >0.6 are shown.

Category	Variable	Principal component loadings		
		Axis 1 (48%)	Axis 2 (30%)	Axis 3 (13%)
Overstory	Stand basal area	0.94		
	Percent cover of trees ≥10 cm	0.96		
	Density of trees ≥10 cm	0.98		
	Stand quadratic mean diameter	−0.84		
	Density of trees ≥30 cm		0.66	
Understory	Density of trees <10 cm	−0.94		
	Percent cover of trees <10 cm	−0.82		
Vertical structure	Percent cover of all trees			0.86
	Mean stand height	0.64	0.67	
	Standard deviation of tree DBH		0.78	
	Foliage height diversity		0.89	
	Skewness of tree DBH	0.71		
Snags	Basal area of snags	0.74	0.61	
	Density of snags ≥10 cm	0.97		
	Mean snag diameter	−0.93		
	Density of snags ≥30 cm		0.81	
DWD	Mean DWD decay class	0.61		0.77
	SD of DWD decay class			
	Percent ground cover of DWD	−0.84		
	Volume of decay class 1–2 DWD[a]	−0.71		−0.62
	Volume of decay class 3 DWD		0.80	
	Volume of decay class 4–5 DWD		0.81	
	Volume of DWD ≥30 cm		0.89	
	Total volume of DWD		0.86	

[a] Decay classes are based on those described in Maser et al. (1979).

2.5. Model evaluation

Partial harvesting has not been widely applied in boreal mixedwood stands to date – particularly over the long timeframes used in our simulations – and so it is difficult to identify appropriate empirical data for evaluating our harvest simulations. However, harvesting operations in the 1940s, 1950s and early 1960s used horse-skidding techniques that left many unmerchantable stems (including understory and non-spruce trees) in mixedwood stands intact (Carleton, 2000). Although such practices cannot easily be described in terms of retention level, they resemble the partial harvesting scenarios that we simulate here in many respects, particularly in drawing relative comparisons to old, unharvested stands. We therefore compare the difference in field-surveyed attributes between old, unmanaged stands and younger (47–64 year old) stands previously harvested using horse skidding (Vanderwel et al., 2010), to the long-term difference in

these attributes between our unharvested and harvested model scenarios. Given the necessarily approximate nature of this evaluation approach, we place more emphasis on patterns and directions of change than specific quantitative values produced by the model.

Several structural attributes, such as tree basal area, large snag density, and DWD volume, showed reasonable agreement between modelled and field-surveyed stands (Fig. 3). Other structural features, including large tree density and snag basal area, did not correspond particularly well to the field data. The model correctly reproduced an observed long-term decrease in large tree density, large snag density, and DWD volume between unharvested stands and stands previously harvested using horse skidding. It also correctly predicted that there would be little long-term difference in tree basal area between the two groups of stands. Observed differences in snag basal area and mean DWD decay class were not consistent with model projections, however, which suggests that

Table 2
Regression models relating habitat use by selected late-successional vertebrate species to stand-level structural habitat characteristics in northern forests, and the expected relative sensitivity of these species to partial harvesting from Vanderwel et al. (2009).

Species	Habitat model	Source	Expected sensitivity
Eastern redback salamander (*Plethodon cinereus*)	ln(Relative abundance) = 1.743 − 0.013(basal area)/(quadratic mean diameter)$^{1/2}$ − 2.325(class 1–2 DWD cover) + 11.160(class 3–5 DWD cover)	McKenny et al. (2006)	Low
Brown creeper (*Certhia americana*)	Logit(Pr(nest presence)) = −1.9490 + 0.0142(density of trees ≥30 cm) + 0.0053(snag density)	Poulin et al. (2008)	High
Ovenbird (*Seiurus aurocapilla*)	Relative abundance = 1.000 + 0.019(percent canopy cover) − 0.178(seedling density per m^2)	King and Degraaf (2000)	High
Least flycatcher (*Empidonax minimus*)	Logit(Pr(detection)) = 0.0863 − 0.1094(CV of canopy cover)	Thompson (unpublished data)	Moderate
Southern red-backed vole (*Myodes gapperi*)	Relative abundance = −2.850 − 0.017(class 5 DWD volume) + 0.009(DWD volume) + 1.060(cover at 50–250 cm height) + 2.428(cover at 5–10 m height)	Pearce and Venier (2005)	Low
Northern flying squirrel (*Glaucomys sabrinus*)	Density = 0.130 + 0.028(density of spruce ≥25 cm) + 0.007(density of hardwoods ≥25 cm) − 0.004(class 1–3 DWD volume)	Holloway and Malcolm (2006)	Moderate
American marten (*Martes americana*)	Logit(Pr(detection)) = −4.958 + 0.026(percent spruce/fir trees) + 0.081(stand height) + 0.121(DWD cover) + 0.014(canopy cover)	Bowman and Robitaille (1997)	Moderate
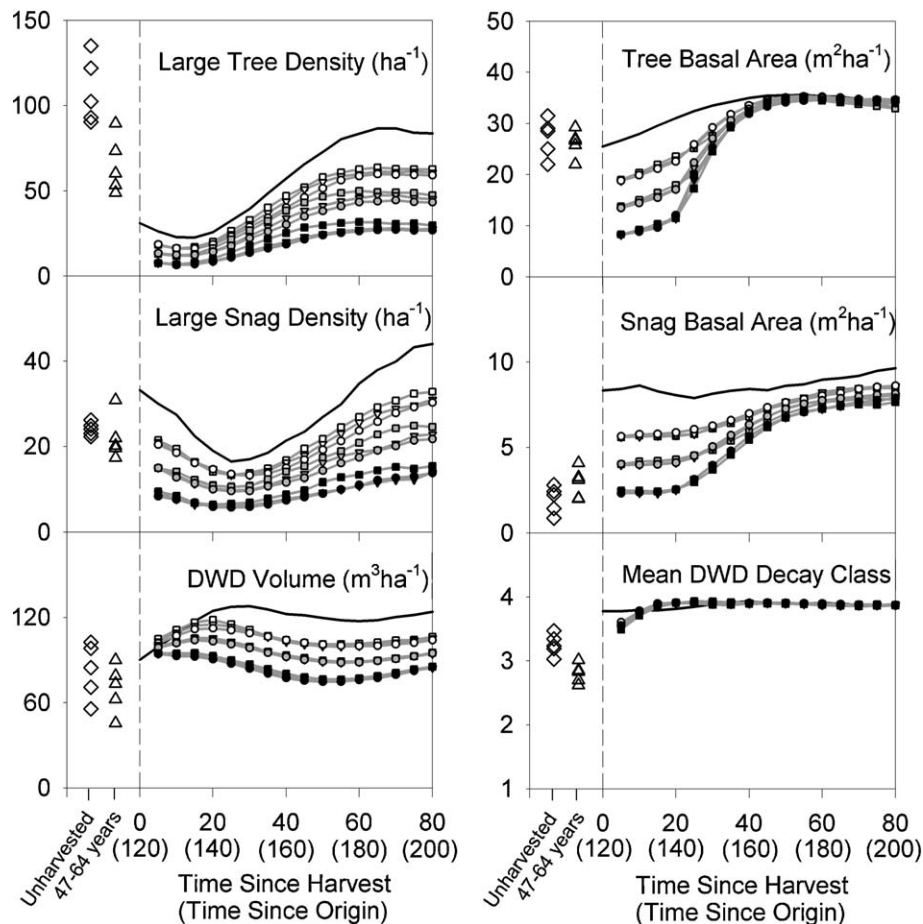
Fig. 3. Values of selected structural attributes in simulated 120–200 years old unharvested boreal mixedwood stands (solid black lines), in simulated partially harvested stands (grey lines with symbols), in five field-surveyed, old, unharvested stands (◇), and in five field-survey stands harvested using horse skidding 47–64 years earlier (△). For the simulated partial harvest scenarios, symbol shading represents different intensities of harvesting (white, 30% removal; grey, 50% removal; black, 70% removal), and shape represents different spatial patterns of harvesting (triangles, uniform; squares, small-patch; circles, large-patch).

the model may have some difficulty in accurately representing the mortality and decomposition of small diameter trees.

3. Results

3.1. Structural dynamics following partial harvests

The first three principal component axes together accounted for 91% of the variance among harvest scenarios over an 80-year period. All variables but one loaded highly onto at least one axis, indicating that these principal components were effective in summarizing patterns of variation present in the original variables (Table 1).

Axis 1 (48% variance explained) was interpretable as an 'overstory, snags, and DWD cover' gradient. It was positively associated with the density and basal area of both live trees and snags, and negatively associated with sapling (<10 cm DBH) density and DWD cover. Partially harvested stands had lower scores on this axis than unharvested stands ≤25 years after harvest (Fig. 4), reflecting direct removal of the overstory and snags as well as promotion of understory development and creation of harvest slash. After 35 years, as post-harvest regeneration reached the canopy and harvest-origin DWD was lost, harvested stands had lower values on this axis than stands left unharvested.

Axis 2 (30% variance explained) was interpretable as a 'large size and vertical complexity' gradient. It was positively associated with the density of trees and snags >30 cm DBH, and the volume of DWD

in most decay classes (particularly that >30 cm diameter). Stands with high values on this axis also tended to have greater diversity in tree size, both in terms of the standard deviation of DBH and foliage height diversity, and a taller canopy. Harvested stands had lower values on this axis than unharvested stands throughout the simulation period, and showed only modest recovery over 80 years.

Axis 3 (13% variance explained) was interpretable as an 'early-decay woody debris and ground exposure' gradient. It reflected a sharp but transient increase in decay classes 1 and 2 woody debris five years after harvesting. It was also associated with low combined sapling and canopy cover prior to the growth of post-harvest regeneration into the sapling stratum.

3.2. Variation among harvest scenarios

Effects of harvesting on the first two axes varied most strongly among different intensities of removal. For both the 'overstory, snags, and DWD cover' and 'large size and vertical complexity' axes, differences from unharvested stands were nearly in proportion to relative basal area removal (Figs. 4 and 5). In contrast, harvesting tended to have comparable impacts on the 'early-decay woody debris and ground exposure' axis at each intensity level.

Harvest pattern had smaller effects on stand structure than removal intensity. Dispersed harvesting patterns had somewhat less pronounced impacts on the second axis than aggregated harvesting for up to 50 years (Figs. 4 and 5). Inspection of individual variables loading on to this axis showed that this effect was
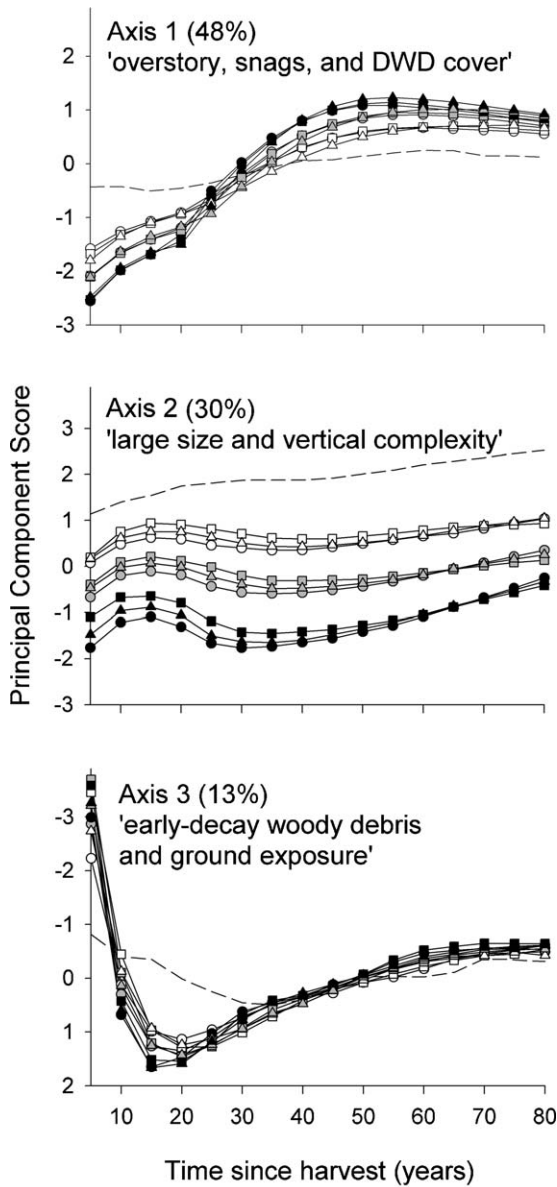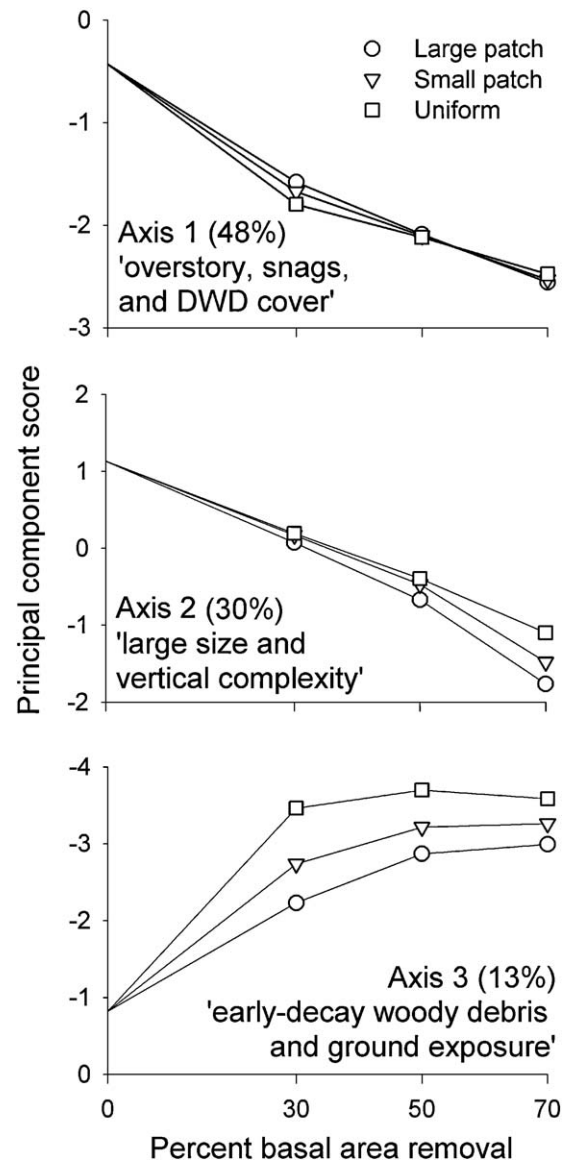
Fig. 4. Changes in the principal component scores of boreal mixedwood stands in nine partial harvest scenarios (solid lines), relative to corresponding points in time in unharvested stands (dashed lines), as simulated within the stand dynamics model SORTIE-ND. Symbol shading represents different intensities of harvesting (white, 30% removal; grey, 50% removal; black, 70% removal), and shape represents different spatial patterns of harvesting (triangles, uniform; squares, small-patch; circles, large-patch).

attributable to smaller changes in mean stand height and foliage height diversity under dispersed versus aggregated harvesting. Conversely, aggregated harvesting had a less pronounced short-term effect on the 'early-decay woody debris and ground exposure' axis than dispersed harvesting (Fig. 5).

3.3. Vertebrate responses to harvesting

Although modelled habitat value for all seven vertebrates decreased as harvesting intensified from 30 to 70%, only five species showed the expected pattern of decline relative to unharvested stands (Table 3). Habitat value for both marten and redback salamanders increased following most types of partial harvesting. Abundances of red-backed voles were projected to modestly decrease (≤30%) in the short term, but would recover within 15 years. The model for ovenbirds likewise showed modest decreases

Fig. 5. Comparison of principal component scores for unharvested boreal mixedwood stands and those harvested 5 years previously under different intensities and patterns of harvesting, as simulated within the stand dynamics model SORTIE-ND.

under light- and moderate-intensity harvesting, but this species required 25–30 years to recover afterwards. The two large tree and snag associates, brown creeper and northern flying squirrel, were expected to show substantial decreases (33–74%) and require the longest timeframes for their habitat to recover from intensive harvesting. Least flycatchers could decrease by more than half even under light harvesting, and this species was predicted to be virtually absent from stands subject to aggregated patterns of removal. Aside from least flycatchers, no species models predicted pronounced differences in 5-year responses to different spatial patterns of harvesting.

4. Discussion

4.1. Impacts on structure

Different facets of stand structure exhibited the three patterns of change that we hypothesized could follow partial harvesting. The greatest impact on stand structure was an initial (0–25

Table 3
Proportion of pre-harvest vertebrate species abundance five years after various intensities of partial harvesting in simulated boreal mixedwood stands, and the time required to recover to pre-harvest abundances. For all species except least flycatcher, reported short-term changes are averaged across harvest patterns and recovery times are given as a range across harvest patterns. Species are sorted from least-adverse to most-adverse impacts.

Species	Modelled pre-harvest value	Response variable type	Short-term change (proportion of pre-harvest abundance)			Recovery time (years)		
			30%	50%	70%	30%	50%	70%
Eastern redback salamander	12.8	Relative abun.	1.51	1.46	1.43	0	0	0
American marten	0.42	Pr(Detection)	1.33	1.18	0.94	0	0	5–15
Southern red-backed vole	9.64	Relative abun.	0.90	0.80	0.70	10–15	15	15
Ovenbird	1.98	Relative abun.	0.85	0.74	0.63	25	25–30	25–30
Brown creeper	0.45	Pr(Nest presence)	0.67	0.53	0.41	30	35	35
Northern flying squirrel	0.60	Density (ha^{-1})	0.68	0.48	0.26	15–20	25–40	80+
Least flycatcher (uniform)	0.23	Pr(Detection)	0.45	0.09	0.03	30	30	30
Least flycatcher (small-patch)	0.23	Pr(Detection)	0.20	0.02	0.00	30	30	30
Least flycatcher (large-patch)	0.23	Pr(Detection)	0.04	0.00	0.00	30	30	30

years) decrease in overstory-related characteristics and increase in understory development and DWD cover (Fig. 4). In the longer term (≥35 years), however, this relationship was reversed such that harvesting promoted overstory structure and led to decreased understory development and DWD. Because these dynamics occurred faster than senescence and mortality in unharvested stands, partial harvesting effectively accelerated the canopy turnover process and led to enhanced long-term structural development. Partial overstory removal acts to increase light availability and thus promote regeneration and growth within the understory (Prevost and Pothier, 2003). At the same time, harvesting activities often produce a pulse of downed woody debris associated with slash and post-harvest treefalls (Fraver et al., 2002; Morneault et al., 2004). Through time, understory stems reach the canopy, light levels decrease and suppress further understory development (Beaudet and Messier, 2002), and harvest-related downed wood becomes incorporated into the forest floor. In our simulations, these changes were most pronounced following high-intensity partial harvests that maximized light availability in the understory.

Partial harvesting had an adverse long-term impact on large trees, snags, and DWD in simulated stands, as has been reported for other forest types (McGee et al., 1999; Holloway and Malcolm, 2006). Increased growth and decreased mortality of smaller residual trees were inadequate to offset lower densities of large live trees and snags following harvest. As a result, we observed a long-lasting reduction in the number of large features, both live and dead, in partially harvested stands relative to unharvested stands. Vertical complexity was also degraded over the long term by harvesting, particularly when trees were removed in aggregated patches. Vertical diversification occurs as stands develop uneven-aged structure through continuous growth and recruitment of new individuals. The pulse of regeneration created by partial harvesting, along with the accompanying loss of large-diameter trees, is expected to lower the diversity of tree sizes present until recruitment and senescence mortality return to their continuous pre-harvest levels. A linear relationship between the 'large size and vertical complexity' axis scores and removal intensity (Fig. 5) reflected the direct importance of basal area after harvest for these features; thus, greater removals of large trees and snags are expected to increase the time required for these features to return to levels in unharvested stands.

Harvesting produced a transient (5-year) increase in early-decay downed woody debris and ground exposure that was largely unrelated to removal intensity. After this brief period, harvest-related downed wood advanced to later decay classes and sapling regeneration increased total cover to pre-harvest levels. The rapid turnaround of these structural elements precluded any persistent long-term effect.

4.2. Impacts on selected vertebrate species

The conceptual soundness of structural changes following harvesting was supported by negative relationships between harvest intensity and habitat use for all seven late-successional vertebrate species considered (Vanderwel et al., 2009 and references therein). Both species that were expected to show low sensitivity to harvesting (Table 2) were modelled to be less adversely affected than the two species expected to be highly sensitive (Table 3) (the three moderately sensitive species showed variable responses). Our model results also showed that species using common habitat features exhibited consistent responses to harvesting.

Most species associated with downed woody debris (redback salamander, marten, red-backed vole) showed neutral or positive responses at one or more harvest intensities, suggesting that either the modelled post-harvest abundance of DWD was excessively high, or that these habitat models did not extrapolate well to the high DWD levels expected to occur after harvest. Although there may be an upper limit to the value of DWD for some species (Thompson, 2006), these findings support the habitat benefits of retaining abundant DWD within partially harvested stands.

Ovenbirds also were not as sensitive to harvesting as expected. In addition to reducing canopy cover, harvesting may negatively affect ovenbirds if it promotes growth of low shrubs in the understory (Jobes et al., 2004). Shrub cover was not represented by SORTIE-ND, and the exclusion of this habitat feature may have lead to underestimates of harvesting effects on ovenbird abundance.

Modelled decreases in large trees and snags were reflected by the responses of brown creepers and northern flying squirrels to harvesting. Both of these species rely on large trees, either alive or dead, for foraging or nesting. The direct removal of these structures through harvesting, coupled with the long timeframes required for their replenishment, suggests that partially harvested stands will not provide good habitat for snag- and cavity-dependent species unless specific, effective measures are taken to conserve large trees and snags.

Least flycatchers were found to be highly sensitive to harvesting, particularly aggregated harvests that strongly increased canopy heterogeneity. Decreases in least flycatcher abundance could be partially mitigated by applying low-intensity harvesting in a uniform rather than aggregated pattern. Least flycatchers were the only species for which we detected a strong response to harvest pattern, as theirs was the only habitat model that included an explicit term for the spatial variability of habitat structure, and non-spatial differences in habitat structure were minor. In reality, species show diverse responses to habitat alteration, some aspects of which cannot be readily predicted by simple stand-level models. It is likely that, for many vertebrates, spatial patterns have a greater role in shaping habitat use than was predicted by the models in Table 2.

In interpreting these vertebrate responses, it must be noted that habitat models often extrapolate poorly outside the data set used for their development (Vernier et al., 2008). Such problems are likely exacerbated by using structural output from a stand dynamics model, by considering partially harvested stands with novel habitat structure, and in some cases by applying the models to a different forest region or stand type. Habitat conditions in the surrounding landscape are also relevant to some of the species considered (e.g., marten; Fuller and Harrison, 2005), and will affect the local use of harvested stands to varying degrees. While the absolute changes in vertebrate habitat value modelled here are likely unreliable, the relative changes among species lend insight into susceptibility to habitat alteration. Commonalities in the responses of vertebrates using similar habitat features, such as DWD or large trees, also provide information on the importance of shared structural attributes.

4.3. Implications for forest ecosystem management

Many consider the maintenance of ecosystem structure and function to be a major objective of contemporary forest management practices (Kohm and Franklin, 1997). To realize this objective, it has been proposed that partial harvesting systems that retain variable numbers of residual trees (Franklin et al., 1997) and promote the development of complex structure (Puettmann et al., 2009) can emulate conditions created through stand development and natural disturbance processes in some stand types (Harvey et al., 2002). In doing so they may succeed in maintaining suitable habitat for species associated with late-successional forests.

Our results support the proposition that light- or moderate-intensity harvesting could be effective in this regard, particularly if additional measures are taken to conserve large diameter trees and snags (Burton et al., 1999). Although we did not observe strong thresholds in the modelled responses of vertebrates or structure to harvesting, 6 of the 7 species considered maintained close to 70% of their pre-harvest abundance (or more) at 30% basal area removal, and close to 50% of their pre-harvest abundance (or more) at 50% basal area removal (Table 3). The time required for recovery to pre-harvest abundance was also substantially shorter for a large-tree associate (northern flying squirrel) following 30% and 50% basal area removals than 70% removal. It should be noted, however, that these effects are for a single harvest event and do not consider the cumulative impacts of a periodic harvesting regime. Some species and structural features did not recover to pre-harvest levels for 30 or more years. The persistence of such mature-forest legacies may be uncertain if stands undergo repeated harvest entries over time.

Even though we used a spatial model of stand dynamics, few species or structural features were strongly affected by harvest pattern in our simulations. Among the differences that we found, dispersed harvesting maintained a taller mean canopy height, fostered a greater diversity of vertical structure, produced more post-harvest slash, and caused less severe decreases in least flycatcher habitat use. Aggregated patterns of harvesting promoted greater regeneration of shade-intolerant trembling aspen and decreased regeneration by eastern white cedar and white spruce. Despite the relatively weak spatial effects in our simulations, it is likely desirable to create gaps of various sizes to account for variability in species' habitat requirements (Rosenvald and Lõhmus, 2008). Conventional uneven-aged silvicultural systems, such as individual-tree or group selection, tend to create a much narrower range of gap sizes than those occasionally produced by natural disturbances (Hanson and Lorimer, 2007). Regimented harvesting systems that fail to maintain structural heterogeneity and species diversity will ultimately restrict the successional and developmental pathways of managed stands to a subset of those experienced by natural stands.

The scenarios modelled here cannot be considered specific management prescriptions, but they do provide predictions of structural and vertebrate species responses to partial harvesting that may be expected to occur in boreal mixedwood stands. Coupled with experience from other forest regions and stand types, these simulations provide a sound basis for generating more detailed hypotheses for maintaining the habitat functions of late-successional forests through partial harvesting. In turn, these hypotheses can be translated into real-world experiments to be evaluated, refined, and either accepted or rejected within an adaptive management framework (Burton et al., 2006).

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