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RESEARCH ARTICLE

Effects of 80 years of forest management on landscape structure and pattern in the eastern Canadian boreal forest

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Abstract
Context Forest management alters patterns generated by natural disturbances, particularly in ecosystems with infrequent fires. Management effects can differ according to spatial scale and affect ecological processes.
Objectives To assess the effect of 80 years of forest management at both the landscape and burn/harvest scales on forest age, composition, density, spatial pattern and heterogeneity.
Methods Forest inventory maps and satellite images were used to compare two contiguous landscapes, respectively managed and unmanaged, of the eastern boreal forest of Canada, in a region with infrequent fires. Burns and harvests occurring from 1920–1950 were also compared.
Results In addition to reducing the proportion of old-growth stands in the landscape, forest management changed forest composition at both scales, favouring the late-successional species balsam fir. Landscape metrics indicated that old-growth forests and spruce-dominated ones were more fragmented, less connected, and confined to smaller patches in the managed landscape than in the unmanaged one. Forest management increased heterogeneity at the landscape scale, but decreased it at the burn/harvest scale. Logging had a homogenizing effect at the burn/harvest scale by attenuating the effect of the physical environment on forest density.
Conclusions This study provides knowledge to help reduce effects of forest management at both scales. In this forest region with low fire recurrence, the goal

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should be to manage for greater forest heterogeneity at the burn/harvest scale whereas, at the landscape scale, restoration strategies should aim to create large contiguous patches of coniferous forests to increase spatial continuity as these were reduced by past management activities.

Keywords Logging · Fires · Multi-scale · Heterogeneity · Forest composition · Old-growth forests

Introduction

Natural disturbances are key processes structuring ecological systems and driving spatial and temporal forest heterogeneity across scales (Turner 2010; Romme et al. 2011). Even very large disturbances, such as fires, which are the dominant driver in many boreal systems, create heterogeneity at multiple scales (Christensen et al. 1989; Turner 2010). The occurrence of fires over time creates a mosaic of patches of different tree compositions and stand ages (Forman 1995; DeLong and Tanner 1996; McRae et al. 2001), and given variations in fire severity, these patches are themselves heterogeneous in terms of tree composition and density (Turner et al. 1994; Chappell and Agee 1996; Haire and McGarigal 2010; Carlson et al. 2011). These patterns may persist for decades or centuries (Kashian et al. 2005; Turner 2010). Other natural disturbances such as insect outbreak, (Kulakowski et al. 2003; Gray and MacKinnon 2006; James et al. 2011), windthrow (Waldron et al. 2014) or fungal pathogens (Edman et al. 2007; Kuuluvainen 2009) may also shape forest patterns.

The increase in anthropogenic disturbances, in addition to natural ones, has had serious impacts on natural forest spatial patterns since their effects differ greatly from those generated by fire (Franklin and Forman 1987; Mladenoff et al. 1993; DeLong and Tanner 1996; McRae et al. 2001). Forest management can fundamentally alter forest spatial heterogeneity by homogenizing the structure at some scales while introducing new patterns at other scales (Mladenoff et al. 1993; Turner 2010). For example, at the landscape scale, patterns resulting from harvesting increase the fragmentation of old-growth forests (Mladenoff et al. 1993; Wang and Cumming 2010), while homogenization of composition has also been observed (Foster et al. 1998; Schulte et al. 2007).

The impact of forest harvesting on landscape patterns should be greater in ecosystems with low fire recurrence since spatio-temporal patterns of harvesting are markedly different from those resulting from natural disturbances. Low-frequency fire landscapes are naturally dominated by a matrix of old-growth forests interspersed with irregularly shaped patches of younger forests originating from fire or other intense disturbances. In comparison, managed landscapes under an even-aged regime are typically composed of a higher proportion of young stands (Östlund et al. 1997; Etheridge et al. 2005; Cyr et al. 2009), are more fragmented (Spies et al. 1994; McRae et al. 2001; Tinker et al. 2003; Wang and Cumming 2010; Dickinson et al. 2014), have a greater amount of edges (Spies et al. 1994; Gustafson and Crow 1998; Perera and Baldwin 2000) and smaller, simpler and more isolated patches of old-growth forests (Mladenoff et al. 1993; Spies et al. 1994; Tinker et al. 2003; Wang and Cumming 2010). At the stand level and up to few decades after disturbance, harvesting generally decreases stand complexity and the amount of large old trees and dead wood, and modifies stand density, in comparison with fires (Turner et al. 1994; Freedman et al. 1996; Linder and Östlund 1998; Bergeron et al. 2002; Etheridge et al. 2005; Hessburg et al. 2007; Carlson et al. 2011).

In low fire-frequency forests, management may also modify forest composition as early-successional species often establish after harvesting and their abundance increases in managed landscapes (Foster et al. 1998; Jackson et al. 2000; Etheridge et al. 2005; Friedman and Reich 2005; Ohmann et al. 2007; Schulte et al. 2007; Boucher et al. 2009). On the other hand, it has also been argued that the presence of advance regeneration in logged forests could lead to increased dominance of late-successional species (Blais 1983; McRae et al. 2001; Bouchard and Pothier 2011; Fourrier et al. 2013). Composition, density and structure at the landscape scale are further modified by forest management as harvesting occurs only in commercially viable and accessible stands.

The effects of forest management in boreal ecosystems have been primarily studied at the stand scale for variables such as forest composition, or at the landscape scale for spatial pattern (see Koivula et al. 2014). Few studies have addressed the impacts of management at multiple scales (but see Leimgruber et al. 2002; Wimberly and Ohmann 2004). It is therefore still unclear whether the impacts observed at a local scale are the same as those at the landscape scale. Considering that management leaves residual forests of varying sizes over time, the assessment of long-term effects over large landscapes enables us to understand the impacts of forest management across the landscape. For example, it is now recognized that landscape level legacies of forest management affect processes such as insect outbreaks (Raffa et al. 2008; Robert et al. 2012). Understanding the effects of such large-scale legacies after a long period of time could allow managers to plan for restoration or to reduce differences between managed and natural landscapes (Mladenoff et al. 1993; Wallin et al. 1996; Palik et al. 2000; Turner 2005; Kuuluvainen 2009).

This study aims at assessing the effect of 80 years of forest management at both the landscape ($\approx$18,000 km^2) and burn/harvest ($\approx$300 km^2) scales in an ecosystem with infrequent fires. Specifically, our objectives are to assess the effects of management on 1) forest age, composition, density, spatial pattern and heterogeneity at the landscape scale, and 2) composition, density and heterogeneity of forest at the burn/harvest scale. We hypothesize that management will modify forest composition at both scales by increasing the abundance of late-successional species due to the dominance of shade-tolerant advance regeneration in natural stands, and will increase stand density as a consequence of decreasing stand age and the more open conditions associated with old-growth forests. We also hypothesize that management will lead to a higher fragmentation of old-growth forests since they are targeted by forest management and also because of the spatial distribution of harvests; however, fragmentation of stand composition types (e.g. fir-dominated or spruce-dominated forests) will be less pronounced since mostly late-successional species will recruit well after harvest. Finally, we hypothesize that forest management will increase landscape-scale heterogeneity (in terms of stand age, composition and density) in forests with low fire recurrence since they are naturally dominated by a matrix of old-growth forests. In contrast, management will decrease burn/harvest-scale heterogeneity since it is expected that the severity of harvests is usually less variable than fire in this region.

Methods

Study area

The study area is located in Québec's North Shore region, eastern Canada (Fig. 1). This region is characterized by a cold maritime climate. According to the closest meteorological station (Godbout: 49.32°N; 67.32°W) located at the southern border of the study area (Environment Canada 2013), mean January and July temperatures were −15.0 and 15.9 °C, respectively, during the normal period of 1971–2000, and mean annual precipitation totalled 881 mm, including 262 mm as snowfall (Environment Canada 2013). Moderately hilly topography dominates the landscape (Robitaille and Saucier 1998), with some points exceeding 800 m above sea level. Altitude gradually increases with distance from the St. Lawrence River. Undifferentiated glacial tills are the dominant surface deposit (Grondin 1996).

Québec's North Shore is part of the boreal forest, and the southernmost part of the study area is within in the balsam fir-white birch bioclimatic domain, while the remaining area is part of the black spruce–moss domain (Saucier et al. 1998). This study area is thus best considered as an ecotone between the two bioclimatic domains where black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species. White spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and white birch (*Betula papyrifera* Marsh.) are also present across the study area. Typically, shade-intolerant hardwoods (white birch and trembling aspen) establish immediately after fire, then spruce or fir gradually increase their dominance (Gauthier et al. 2010). Spruce stands can also establish immediately after fire, with balsam fir increasing in abundance and becoming dominant or co-dominant later (Bouchard et al. 2008; Gauthier et al. 2010). The fire cycle is estimated to be around 300 years and increases towards the east (Cyr et al. 2007; Bouchard et al. 2008). Although some logging occurred in the late 1800s in the southern part of the region in close proximity to the St. Lawrence River (Frenette 1996), the first substantial harvesting (clear-cuts) began around the 1920s in the southern part of the region and subsequently progressed northward according to forest inventory maps (Ministère des Ressources

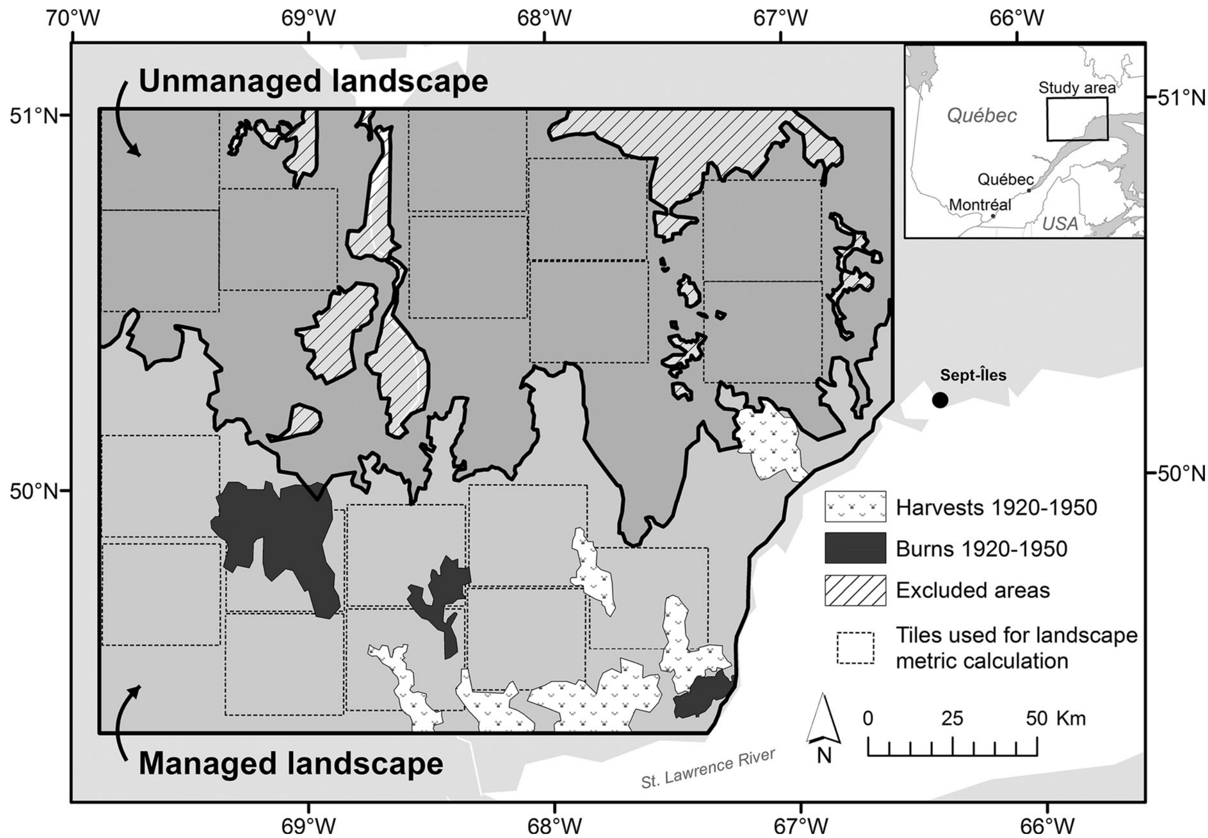

Fig. 1 Study area including the managed and the unmanaged landscapes, the 18 tiles used for landscape metric calculation, and zones of 1920–1950 burns and harvests. For clarity purpose, more recent harvests in the managed landscape are not shown

naturelles et de la Faune du Québec (MRNFQ) 2009). Up until the 1960s, the harvesting system consisted of manual felling using axes and hand saws, and transportation was by log driving in rivers. Diameter-limit clearcutting was generally applied, typically leaving behind trees with dbh < 12 cm (Minville 1944). In the 1950–1960s, chainsaws gradually replaced manual tools and skidders replaced horses; and since 1975, feller-bunchers have taken the place of felling using chainsaws. Early mechanized operations destroyed a large proportion of the advance regeneration, which was protected by earlier methods. In the early 1990s, careful logging was adopted to enhance the protection of advance regeneration during mechanized operations (Groot et al. 2005).

Managed and unmanaged landscapes

The North Shore boreal forest provides a rare opportunity to compare managed landscapes with natural ones since large areas were still only partly managed at the beginning of the 21st century. The 235 × 185 km study area (49.3°–51.1°N; 66.6°–69.9°W; Fig. 1) was chosen to cover both the landscape in which past harvesting was concentrated (Managed landscape) and a landscape essentially free from logging (Unmanaged landscape). In the latter landscape, we excluded the few zones of logged forest that were found within its perimeter (Fig. 1). Net total areas of the managed and unmanaged (without excluded zones) landscapes were 17,796 and 19,350 km^2, respectively.

The comparison of managed and unmanaged landscapes requires that the two landscapes be comparable in terms of environmental variables and natural disturbance regime or requires that inter-landscape environmental heterogeneity be taken into account (see Hargrove and Pickering 1992; Mladenoff et al. 1993; Wyatt and Silman 2010). The two landscapes were contiguous and very similar in terms of surface deposit types and mean slope (Table 1). According to

Table 1 Comparative description of the managed and unmanaged landscapes, in terms of environmental factors, natural disturbance and bioclimatic domain

	Managed	Unmanaged
Surface deposit type (% area)		
Thick tills	19.9	19.6
Medium thickness tills	28.1	24.9
Thin tills	21.0	20.0
Very thin tills	13.6	16.8
Rocks	3.8	7.2
Elevation (m, mean ± std dev)	374.5 (±129)	509.3 (±139)
Slope inclination (%, mean ± std dev)	11.0 (±9.4)	12.7 (±10.0)
Fires (% area)		
<1880	76.5	75.4
1880–1920	7.0	14.9
1920–1960	9.3	9.3
1960–2000	7.2	0.4

the historical reconstruction of past fires (Bouchard et al. 2008), ~75 % of both landscapes originated from fire prior to 1880 (Table 1). The unmanaged landscape has a higher average elevation. A good way to verify whether the two landscapes are comparable is to evaluate the similitude between their old-growth stands. In both landscapes, old-growth stands are of natural origin (since the oldest harvested stands are only 80 years-old). An absence of difference between old-growth forests in the two landscapes would indicate that the two landscapes were similar before management. The inclusion of stand age in our statistical analyses (see Analyses section), in addition to deposit thickness, slope and elevation, allowed us to verify this postulate.

Database

Forest data

Stand age and forest composition were obtained from forest inventory maps (Ministère des Ressources naturelles et de la Faune du Québec (MRNFQ) 2009). These maps were created by interpretation, with field validation, of 1:15,000 aerial photographs taken in 1999. Data were compiled in forest stand polygons that are ≥4 ha in size. For analysis purposes, inventory composition classes were grouped into nine classes (Table 2). We estimated the proportion of balsam fir (%) in each stand from inventory composition classes using the median value of balsam fir proportion in each class (Table 2). Recently logged polygons were excluded from the analyses. We assigned the age class of the stand based on the age of the dominant cohort using the following classes: 10 (0–20 years), 30 (21–40 years), 50 (41–60 years), 70 (71–80 years), 90 (81–100 years) and 120 (>100 years). Since these stand age values are approximated from photo-interpretation (based on tree height, stand density and forest structure), they are in effect proxies for the successional status of each stand rather than real stand age. Disturbance type and year of origin were also obtained from forest inventory maps and were used to exclude logged zones in the unmanaged landscape.

Forest density (as percent crown closure) was obtained from land cover maps produced from Landsat-7 Enhanced Thematic Mapper Plus (ETM+) images by the Earth Observation for Sustainable Development of Forests (EOSD) group (http://www.nrcan.gc.ca/forests/remote-sensing/13433). These land cover maps represent circa year 2000 conditions and depict 23 land cover classes of the forested ecozones of Canada at a resolution of 25 m (Wulder et al. 2008). We chose this database rather than inventory maps because of its finer spatial resolution and thus more accurate estimation of forest density at the polygon scale. We assigned a median density value to each density class of the land cover map: original density classes >60, 26–60 and 10–25 % become respectively 80, 43 and 18 %. The values were then summarized for each inventory map polygon by calculating the standwise average (mean of the density values of the pixels occurring in each polygon).

Table 2 Description of stand composition classes (grouped from inventory data composition classes) and the estimated percentage of balsam fir used in statistical analyses

Class	Composition (in basal area)	Estimated % fir
Spruce	Conifers ≥75 %; Spruce ≥75 % of conifers	0
Spruce-Fir	Conifers ≥75 %; Spruce 50–75 % of conifers; Fir 2nd most numerous sp.	32
Fir-Spruce	Conifers ≥75 %; Fir 50–75 % of conifers; Spruce 2nd most numerous sp.	54
Fir	Conifers ≥75 %; Fir ≥75 % of conifers	76
Spruce-Hardwoods	Conifer 50–75 %; Spruce the most dominant conifer	0
Fir-Hardwoods	Conifer 50–75 %; Fir the most dominant conifer	47
Hardwoods	Hardwoods ≥50 %	0: *only hardwoods, or with spruce component*
		12: *with conifer component*
		28: *with fir component*
Jack pine	Conifer ≥75 %; Jack pine ≥25 % of conifers	0
Other	*Larix* and unidentified conifers	0
		20: *mixed with 50–75 % unidentifed conifers*

Physical variables

Local elevation (m) and slope (%) were derived from the Canadian Digital Elevation Data product (CDED) of Natural Resources Canada at a scale of 1:50,000 using ArcGIS™Spatial Analyst 10.0 (www.esri.com). Elevation and slope values were averaged within each forest polygon to adjust data to a common resolution. Surface deposit data were also extracted from forest inventory maps. Deposit thickness found in this database is estimated by a photo-interpreter based on landform and position on the slope. Since the study area is mainly composed of undifferentiated till of varying thickness (89 % of the area is covered with tills), we simplified the surface deposit information by recording only their thickness as one of four classes: (1) thick (>1 m with no or rare bedrock outcrops); (2) medium (0.5–1 m with rare bedrock outcrops); (3) thin (0.25–0.5 m with rare bedrock outcrops); and (4) very thin (0–0.5 m with frequent bedrock outcrops, up to 50 % of the area).

Analyses

We performed the analyses at two scales: (1) that of the landscape (managed and unmanaged, $\approx$18,000 km^2 each), and (2) that of the harvest or burn (100–700 km^2) during the 1920–1950 period (Fig. 1). The first scale allowed us to assess the general effect of 80 years of forest management, including both logged and intact forests in the same area. The second scale allowed us to understand the differences observed between harvests and burns from the same period.

Management effects at the landscape scale

To avoid spatial autocorrelation in statistical analyses, a grid of sample points using a 5 km mesh was generated using ArcGIS 10.0 (www.esri.com). The mesh interval was chosen after calculating a semi-variogram to evaluate the distance at which autocorrelation was non-significant (range of the semi-variogram). For each sample point, data on forest, physical attributes and disturbances were extracted from the different spatial layers. After removing points falling under water and non-forested cover types and those without composition classes, we had 909 sample points.

Differences in stand composition between managed and unmanaged landscapes were tested with two analyses, one using the composition classes as a categorical variable and the other using the estimated percentage of balsam fir as a continuous variable since abundance of this species is thought to increase after logging due to recruitment from advance regeneration. The analysis of composition classes allowed us to evaluate differences in classes other than those including fir, whereas the analysis of the percentage of fir in a stand allowed us to test the interactions with explanatory variables.

Specifically, Freeman-Tukey deviate statistics (Legendre and Legendre 1998) were used to compare the frequency of composition classes between managed and unmanaged landscapes. A Bonferroni correction was applied.

To evaluate the difference in the proportion of fir between managed and unmanaged landscapes, an analysis of variance was performed using stand percentage of fir as the dependent variable, and management type (managed/unmanaged), stand age class, surface deposit thickness class, % slope, elevation and their double interactions as independent variables. Similarly, an analysis of variance was performed using stand density (mean of forest polygons) as the dependent variable, and management type, stand age class, composition class, surface deposit thickness class, slope inclination, elevation and their double interactions as independent variables. Non-significant variables and non-significant interactions were removed from both models to obtain the most parsimonious models. Residuals were plotted to confirm assumptions of normality and homoscedasticity (Sokal and Rohlf 1995).

Spatial patterns were characterized in terms of fragmentation and connectivity (the degree to which a landscape facilitates the movement of organisms between resource patches; McGarigal and Cushman 2002; Fahrig 2003). Fragmentation and decrease in connectivity are important elements for landscape ecological process (Taylor et al. 1993), and even though they are difficult to dissociate from habitat loss (Andrén 1994; McGarigal and Cushman 2002; Fahrig 2003; Wang et al. 2014), their analyses complement the result on composition change and can be used to guide restoration strategies. We used the Landscape Division Index as a measure of fragmentation because of its consistency over a wide range of subdivision patterns (Jaeger 2000; McGarigal 2014). The Patch Cohesion Index, a widely recognized measure of connectivity (Schumaker 1996; Tischendorf and Fahrig 2000; Calabrese and Fagan 2004), Mean Patch Area, and Coefficient of Variation of Patch Area are used as complementary measures of spatial pattern. These metrics are described in Appendix 1.

To compare spatial patterns between landscapes, nine 30 $\times$ 35 km (1050 km^2) tiles were delimited in both landscapes (Fig. 1). This allowed us to standardize the extent and the shape of the sample area units since many landscape metrics are affected by the extent and amount of edges in a study area (McGarigal 2014). Landscape metrics were calculated for each age class in each tile using FRAGSTATS v4.2 (McGarigal et al. 2013). Metrics were also calculated for spruce-dominated (Spruce, Spruce-Fir and Spruce-Hardwoods classes) and for fir-dominated stands (Fir, Fir-Spruce and Fir-Hardwoods classes) in the same analysis. For this purpose, the polygon-based age and composition data were rasterized with a pixel size of 25 m. This resolution was smaller than half the size of the narrowest dimension of the smallest patch, as suggested by McGarigal (2014). The 8-neighbour criterion was used to define patches.

Each of the metrics was compared between landscapes using nonparametric Wilcoxon tests (two-sided exact tests). Comparisons were performed between managed and unmanaged landscapes for the same composition and age class. We also compared old stands in the unmanaged landscape with young stands in the managed landscape. This comparison could be useful, in a restoration perspective, to assess the differences in patterns created by logging from those resulting from the natural disturbance regime.

Management effects at the scale of harvests and burns in 1920–1950

More specifically, we analyzed forest areas that originated from harvests conducted between 1920 and 1950 (the 1920 harvests are the oldest clearcuts in the North Shore region) and forest areas that originated from fires during the same period (Fig. 1). Three major fires occurred in this period in our study area (one in 1925 and two in 1941). Both the selected burns and the harvests were located in the managed landscape. Since harvests were spatially agglomerated, samples points from any given harvesting agglomeration (or burn) had a greater probability of being similar than if they were sampled randomly from the entire landscape. Therefore, they cannot be considered independent samples. In order to deal with this autocorrelation, we created well-defined zones (hereafter named "disturbance polygons") surrounding each burn and each harvest agglomeration (Fig. 1), which were then included in our statistical model. The disturbance polygons measured between 137 and 680 km^2. In each of these disturbance polygons, we generated sample points that were 1.5 km apart (20–137 points per polygon, depending on the size). A semi-variogram was used to determine that spatial autocorrelation could no longer be observed beyond this distance within each polygon. A total of 513 points were used.

Differences in stand composition between harvests and burns were also tested using both composition class as a categorical variable and the estimated percentage of fir as a continuous variable. Freeman-Tukey deviate statistics (Legendre and Legendre 1998) were used to compare the frequency of composition classes between harvests and burns. A Bonferroni correction was applied.

To test the difference in the proportion of balsam fir between harvests and burns, a mixed model analysis was performed with the percentage of fir as a dependant variable and disturbance type (harvest/burn), surface deposit thickness class, % slope, elevation, and all interaction levels as independent fixed effects. The random effect was disturbance polygons nested within disturbance type. Non-significant ($P > 0.05$) interactions or variables (when not included in a significant interaction) were removed to obtain the most parsimonious model possible. To test differences in stand density, a similar mixed model was used with density as the dependent variable, and with composition class added to the other independent fixed effects. Assumptions of normality and homoscedasticity (Sokal and Rohlf 1995) were met based on plots of analysis residuals.

Heterogeneity

At the landscape scale, heterogeneity of stand composition, age and density were assessed using Shannon's diversity index (Shannon and Weaver 1949). This index was calculated on composition, age and density rasters within the 18 tiles (Fig. 1) using FRAGSTATS.

At the burn/harvest scale, heterogeneity of stand composition and density classes were assessed using Shannon's diversity index for values extracted from the 513 sample points with 1.5 km post spacing (we did not use rasters because much unburned or unlogged areas occurred in the disturbance polygons). For stand density, since values for each point represent the mean of density class of the forest polygon (see above), values were reclassified as original classes of the Landsat image. Differences in diversity between managed and unmanaged landscapes and between harvests and burns of the same period were tested using nonparametric Wilcoxon tests (two-sided exact tests).

All statistical analyses were performed using SAS (SAS Institute Inc. 2010).

Results

Management effects at the scale of the landscapes

In the unmanaged landscape, 72 % of the forests stands were 120 years or older, whereas only 28 % of such stands were present in the managed landscape (Fig. 2). Stands in the 70-year age class and lower were almost absent in the unmanaged landscape, whereas 31, 16 and 10 % of 10-, 30- and 50-year age class stands, respectively, were observed in the managed landscape.

The composition of the managed landscape differed significantly from that of the unmanaged one (Fig. 3). The managed landscape had significantly more stands

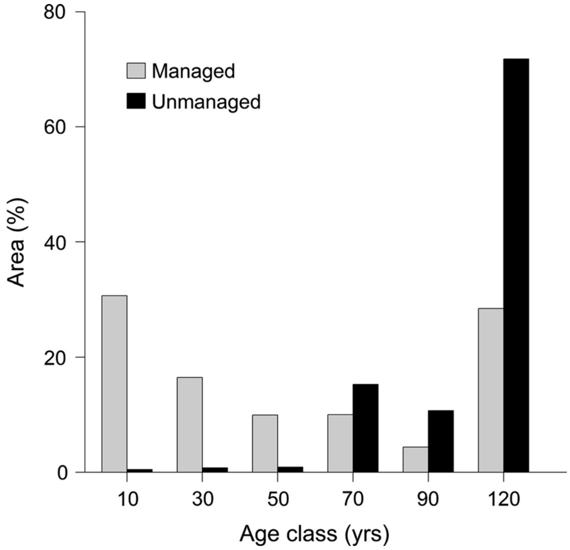

Fig. 2 Area (%) of stand age classes in managed and unmanaged landscapes

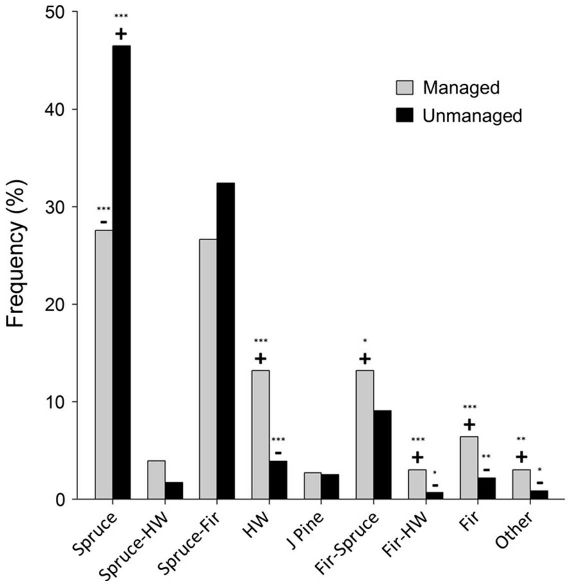

Fig. 3 Percentage of stand composition classes observed among sample points of managed and unmanaged landscapes. *Symbols* "+" and "−" indicate significant excess and deficiency of a composition class, respectively, according to Freeman-Tukey deviate statistics with a Bonferroni correction. *HW* Hardwoods; *J Pine* Jack pine. $***P < 0.0001$; $**P < 0.001$; $*P < 0.01$

dominated by fir (Fir, Fir-Spruce and Fir-Hardwoods classes), and less Spruce class stands than the unmanaged landscape, according to Freeman-Tukey deviate statistics ($P \leq 0.01$; Fig. 3). The analysis of variance also indicated that stands in the managed landscape were composed of a significantly higher percentage of fir than those in the unmanaged landscape (Table 3a). However, it is worth noting that the percentage of fir was similar in the 90- and 120-year age classes (those stands that are older than the oldest harvests) between the two landscapes, but that the percentage of fir was higher in the managed landscape for younger age classes (Table 3a; Fig. 4a). This indicates that stands within the managed landscape were not initially different in composition from those in the unmanaged landscape, and that differences in composition are due to management.

Stand density (as percentage of crown closure) was significantly higher in the managed landscape than in the unmanaged one (Table 3b). Again, stand density was similar between old stands (90–120 years) in the two landscapes, but was higher in 70-year-old stands of the managed one (Table 3b; Fig. 4b). Density

Table 3 Analysis of variance testing (A) the percentage of balsam fir, and (B) stand density (% crown closure) between managed and unmanaged landscapes (Management type), surface deposit thickness class, stand age class, % slope, stand composition class and elevation

Source	Df	*F*	$Pr > F$
A			
Management type	1	4.68	0.0308
Age	5	0.56	0.7289
Deposit thickness	3	5.12	0.0016
Slope	1	2.24	0.1348
Elevation	1	8.15	0.0044
Management type × age	3	5.04	0.0018
Deposit × age	15	2.29	0.0035
Slope × deposit thickness	3	17	<0.0001
Slope × age	5	2.71	0.0196
B			
Management type	1	5.02	0.0253
Composition	8	8.59	<0.0001
Age	5	18.55	<0.0001
Deposit thickness	3	5.43	0.0011
Slope	1	27.47	<0.0001
Elevation	1	109.45	<0.0001
Management type × age	3	5.55	0.0009
Slope × management type	1	3.84	0.0503
Slope × deposit thickness	3	5.38	0.0011
Slope × composition	8	2.26	0.0214

increased with % slope, but the relationship tended to be more pronounced in the unmanaged landscape.

Spatial patterns differed greatly between the two landscapes. Older forests (120-year age class), which were less abundant in the managed landscape, were more fragmented, less connected, and patches were smaller than for old forests in the unmanaged landscape (Table 4). In contrast, spatial patterns of forests in the 90- and 70-year age classes were similar between the two landscapes (Table 4). Spatial patterns of old stands in the unmanaged landscape *versus* young post-logging stands in the managed landscape differed greatly: young post-logging stands, i.e. those in the 10-, 30- and 50-year age classes, were more fragmented, less connected, and had smaller and less variable patches in the managed landscape than old forests in the unmanaged one (Table 4).

Stands dominated by spruce (Spruce, Spruce-Fir and Spruce-Hardwoods classes), which were less

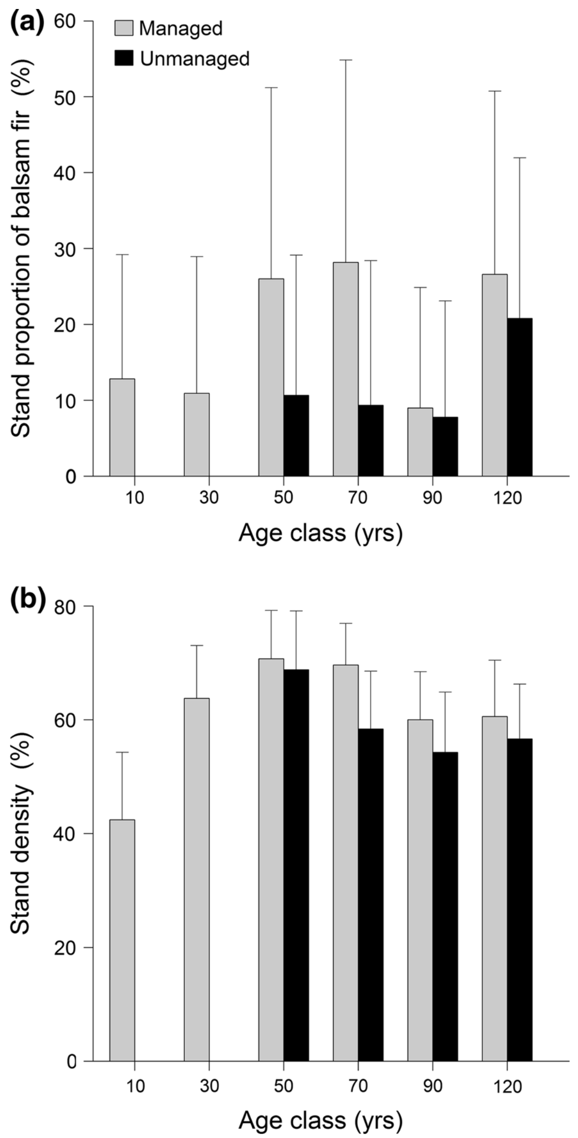

Fig. 4 Stand proportion of balsam fir (%) (**a**) and stand density (% crown closure) (**b**) by stand age class in managed and unmanaged landscapes, illustrating the significant Management type × Age interactions (see Table 3). *Error bars* are the standard deviations

abundant in the managed landscapes, were also more fragmented, had a lower connectivity, and smaller patches than in the unmanaged one (Table 4). However, there were no differences in the patterns of fir-dominated classes (Fir, Fir-Spruce and Fir-Hardwoods classes) between the two landscapes (Table 4), despite the increased presence of those stands in the managed landscape.

Management effects at the scale of harvests and burns in 1920–1950

Forest harvesting resulted in significant differences in forest composition as compared to fire. Harvested sites contained significantly more stands with an abundant fir component (Spruce-fir, Fir-spruce and Fir classes) and fewer with abundant spruce, hardwoods and jack pine (Spruce, Spruce-hardwoods, Hardwoods and Jack pine classes) compared with burns ($P \leq 0.01$, Freeman-Tukey deviate statistics; Fig. 5).

The percentage of fir tended to be higher in harvests than in burns ($P = 0.0637$; Table 5a). Furthermore, disturbance type also affected the relationship between fir abundance and elevation (Table 5a): fir abundance increased with elevation in harvests while it decreased in burns.

There was no significant difference in stand density between harvests and burns, but the Disturbance type × Deposit thickness interaction effect was significant (Table 5b). In fact, differences in stand density were observed between surface deposit thickness classes in burns (thin and medium thickness sites had higher stand density than thick and very thin deposits), but no differences were observed between thickness classes in harvests, suggesting a homogenizing effect of harvesting.

Heterogeneity

At the landscape scale, forest heterogeneity, measured in terms of stand age and density diversity, was greater in the managed landscape as compared with the unmanaged one (Table 6), resulting in a landscape composed of a variety of stand ages and density classes. Note that variability of surface deposit thickness types was very similar between the two landscapes (Table 1); therefore, it could not explain this heterogeneity in stand density. At the burn/harvest scale, burns were more heterogeneous in terms of stand density than harvests. Heterogeneity of stand composition was similar between managed and unmanaged landscapes and between burns and harvests (Table 6).

Discussion

By comparing large managed and unmanaged landscapes, this study shows that 80 years of forest

Table 4 Means (standard deviations) of four landscape metrics for stand age and composition classes

Landscape metrics	Index means (std)		*P*
	Unmanaged	Managed	
Landscape division index (*Fragmentation*)			
120 years unmanaged versus 120 years managed	0.7736 (0.2372)	0.9880 (0.0251)	**0.0048**
90 years unmanaged versus 90 years managed	0.9933 (0.0137)	0.9990 (0.0022)	n.s.
70 years unmanaged versus 70 years managed	0.9541 (0.1108)	0.9987 (0.0016)	n.s.
120 years unmanaged versus 50 years managed	0.7736 (0.2372)	0.9966 (0.0076)	**0.0012**
120 years unmanaged versus 30 years managed	0.7736 (0.2372)	0.9737 (0.0651)	**0.0168**
120 years unmanaged versus 10 years managed	0.7736 (0.2372)	0.9639 (0.0682)	0.0852
Spruce-dominated stands	0.6463 (0.1652)	0.9909 (0.0068)	**<0.0001**
Fir-dominated stands	0.9998 (0.0002)	0.9997 (0.0003)	n.s.
Patch cohesion index (*Connectivity*)			
120 years unmanaged versus 120 years managed	99.7475 (0.2653)	98.7039 (0.8620)	0.0720
90 years unmanaged versus 90 years managed	97.3918 (2.7806)	96.0528 (2.7004)	n.s.
70 years unmanaged versus 70 years managed	98.5903 (1.6407)	97.6078 (1.7271)	n.s.
120 years unmanaged versus 50 years managed	99.7475 (0.2653)	97.4366 (2.0017)	**0.0048**
120 years unmanaged versus 30 years managed	99.7475 (0.2653)	97.5145 (2.4315)	**0.0468**
120 years unmanaged versus 10 years managed	99.7475 (0.2653)	98.3911 (2.4052)	0.1128
Spruce-dominated stands	99.9378 (0.0424)	99.0270 (0.4391)	**<0.0001**
Fir-dominated stands	96.9671 (0.6349)	96.5581 (1.1771)	n.s.
Mean patch area (ha)			
120 years unmanaged versus 120 years managed	441.3450 (399.3258)	40.7286 (19.6313)	**<0.0001**
90 years unmanaged versus 90 years managed	83.6111 (72.9955)	34.1391 (38.7456)	n.s.
70 years unmanaged versus 70 years managed	133.0802 (156.4801)	31.5053 (18.2836)	0.3750
120 years unmanaged versus 50 years managed	441.3450 (399.3258)	50.4022 (39.7251)	**0.0018**
120 years unmanaged versus 30 years managed	441.3450 (399.3258)	60.3955 (65.2213)	**0.0072**
120 years unmanaged versus 10 years managed	441.3450 (399.3258)	116.7077 (94.0655)	0.2400
Spruce-dominated stands	380.1112 (212.0779)	34.4626 (12.1767)	**<0.0001**
Fir-dominated stands	28.7209 (7.7012)	23.0223 (11.8955)	n.s.
Patch area coefficent of variation (%)			
120 years unmanaged versus 120 years managed	782.4269 (242.5288)	701.9019 (540.5681)	n.s.
90 years unmanaged versus 90 years managed	316.6858 (254.1551)	250.6839 (193.5979)	n.s.
70 years unmanaged versus 70 years managed	567.7618 (306.8103)	458.8060 (267.7186)	n.s.
120 years unmanaged versus 50 years managed	782.4269 (242.5288)	326.7964 (221.0946)	**0.0114**
120 years unmanaged versus 30 years managed	782.4269 (242.5288)	502.5778 (420.7314)	0.3750
120 years unmanaged versus 10 years managed	782.4269 (242.5288)	499.1347 (364.4355)	0.1464
Spruce-dominated stands	1201.4950 (396.8942)	833.1467 (418.0136)	0.6250
Fir-dominated stands	204.4020 (68.0841)	220.1313 (54.9223)	n.s.

P-values are from Wilcoxon two-sided exact rank tests comparing managed to unmanaged landscapes. A Bonferroni correction was applied. Significant ($P \leq 0.05$) differences are in bold. See Appendix 1 for metric descriptions

management has profoundly modified the boreal landscape in many ways. Since the comparison of landscapes could raise concerns because of the lack of real replication of the landscapes (i.e. this study is based on many sample points but on only one managed and one unmanaged landscape), it is worth discussing our methodological approach. Many landscape-scale studies are faced with the problem of not having

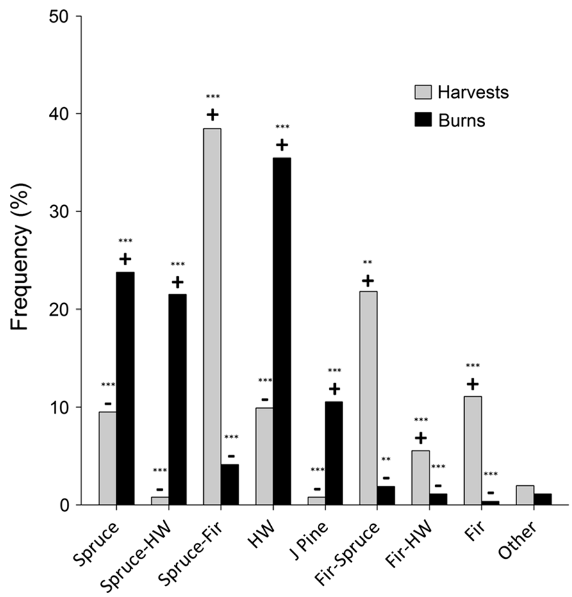

Fig. 5 Percentage of stand composition classes observed among sample points of harvests and burns for the 1920–1950 period. *Symbols* "+" and "−" indicate significant excess and deficiency of a composition class, respectively, according to Freeman-Tukey deviate statistics with a Bonferroni correction. *HW* Hardwoods; *J Pine* Jack pine. ***$P < 0.0001$; **$P < 0.001$

replicated landscapes due to the lack of similar units at the scale of the study. Such studies are considered relevant and useful by many ecologists when the comparability of the landscapes is carefully assessed and results are interpreted with caution (Hargrove and Pickering 1992; Mladenoff et al. 1993; Oksanen 2001). We took many precautions to make this comparison valid, by choosing contiguous landscapes with comparable environmental factors and natural disturbance regimes (see Methods section & Table 1). Also, the inclusion of environmental variables in our statistical analyses enabled us to make comparisons by considering the influence of these variables. In this way, our results on the percentage of fir and on stand density indicate that these two variables differed between landscapes but were similar in pre-management old-growth stands (90–120 years, thus from natural origin) between managed and unmanaged landscapes. This demonstrates that, at least for these two variables, the landscapes are comparable.

One of the most important consequences of forest management is the complete inversion of the age class distribution in the managed landscape. The fire cycle approximates 300 years (Cyr et al. 2007; Bouchard et al. 2008) in the area and it is thus naturally dominated by old stands (72 %), but this proportion decreases to as low as 28 % in the managed landscape.

Another major impact of forest management is the resulting change in forest composition, characterized, as hypothesized, mainly by the increasing proportion of balsam fir at both scales. While the establishment of early-successional species has been observed after logging (Foster et al. 1998; Jackson et al. 2000;

Table 5 Mixed model testing (A) the percentage of fir and (B) stand density (% crown closure) between the 1920–1950 harvests and burns (Disturbance type), surface deposit thickness class, % slope inclination, stand composition class and elevation

Source	Num. Df	Den. Df	F	$Pr > F$
A				
Disturbance type	1	17.2	3.93	0.0637
Deposit thickness	3	498	7.49	<0.0001
Slope	1	501	12.17	0.0005
Elevation	1	374	11.12	0.0009
Type × elevation	1	336	4.72	0.0306
Deposit × elevation	3	497	3.46	0.0164
B				
Disturbance type	1	7.36	2.07	0.1916
Composition	8	481	3.84	0.0002
Deposit thickness	3	479	5.63	0.0009
Slope	1	483	13.23	0.0003
Elevation	1	437	0.2	0.6528
Type × deposit	3	479	3.55	0.0145
Elevation × composition	8	481	2.94	0.0032
Deposit × slope	3	479	3.79	0.0104

Table 6 Mean (standard deviation) of the Shannon diversity index for stand age, composition and density classes at the landscape and burn/harvest scales

Landscape scale	*N*	Shannon diversity index		*P*
		Managed	Unmanaged	
Stand age	18	1.468 (0.236)	0.959 (0.279)	**0.0012**
Stand composition	18	1.579 (0.234)	1.410 (0.138)	0.0939
Stand density	18	0.823 (0.069)	0.757 (0.038)	**0.0400**
Burn/harvest scale		Harvests	Burns	
Stand composition	9	1.420 (0.323)	1.471 (0.290)	0.9050
Stand density	9	0.149 (0.161)	0.594 (0.073)	**0.0238**

Differences between managed and unmanaged landscapes and between harvests and burns were tested using Wilcoxon two-sided exact rank tests. Significant ($P \leq 0.05$) differences are in bold

Etheridge et al. 2005; Friedman and Reich 2005; Ohmann et al. 2007; Schulte et al. 2007; Boucher et al. 2009), in our study, it is principally the late-successional species balsam fir that dominates the logged forest (Bouchard and Pothier 2011; Fourrier et al. 2013). The dominance of balsam fir in logged areas results from abundant advance fir regeneration in the understory at the time of logging. This species is adapted to survive for long periods of time in a shaded understory and can take advantage of sudden increases in light to maintain or increase its dominance over other species such as black spruce and hardwoods (Parent and Messier 1995; Claveau et al. 2002). While wildfires kill advance regeneration and partially or totally burn the organic layer, logging keeps both advance regeneration and the organic layer nearly intact. The oldest harvests (1920–1950) were not mechanized. It is thus probable that advance regeneration was more protected at that time (Fourrier et al. 2013). However, it has been suggested by some that recent logging methods designed to protect advance regeneration have a similar protection impact (Cimon-Morin et al. 2010). These post-harvest conditions are suboptimal for both black spruce and hardwood species, such as trembling aspen, and this is reflected in their lower abundance in harvested areas compared with burns of the same age.

Despite the decrease in hardwood species at the harvest scale, this was not the case at the landscape scale since the managed landscape had a higher proportion of hardwood stands. This could be explained by the lower number of young post-burn forests in the natural landscape and the fact that aspen disappears during succession and is absent in old-growth forests that dominate the natural landscape.

Composition change as well as the reduction in old forests in the landscape caused by forest management could have several ecological impacts. Such habitat changes could modify the composition and abundance of associated organisms, and could have repercussions on future disturbances. For instance, the increase in balsam fir at the landscape scale could lead to more severe spruce budworm outbreaks (Blais 1983), this species being the most vulnerable host of this pest (Blais 1957; Nealis and Régnière 2004; Hennigar et al. 2008). Furthermore, the reduction in hardwoods in the landscape could increase forest susceptibility to spruce budworm as these species are recognized to reduce mortality and defoliation by the spruce budworm (Su et al. 1996; Cappuccino et al. 1998; Quayle et al. 2003).Balsam fir is also known to be highly vulnerable to windthrow (Ruel and Benoit 1999; Ruel 2000). Finally, considering that black spruce is the preferred species of the forest industry in this region, both for lumber and pulp (Barrette et al. 2013), shifts from higher spruce to higher fir volumes will not only have ecological impacts; they will also have economic ones.

Spatial patterns in terms of stand age were strongly different between landscapes. As we hypothesized, the remaining mature and old-growth forests in the managed landscape were much more fragmented, presented less connectivity and were confined to smaller patches (surrounded by younger forests) than old-growth forests in the unmanaged landscape. Several earlier studies also found fragmentation and lack of connectivity between residual patches in the landscape to be a result of forest management (Ripple et al. 1991; Spies et al. 1994; Kouki et al. 2001; Löfman and Kouki 2001) and recognized them to affect several old-growth-associated species (e.g. Franklin and Forman 1987; Halpern and Spies 1995; Schmiegelow et al. 1997; Lomolino and Perault 2000; Kivinen et al. 2012; Olsson et al. 2012). Furthermore, the spatial pattern of spruce-dominated forest was more fragmented and less connected in the managed landscape than in the unmanaged one, but no differences in spatial pattern were found between landscapes for fir-dominated forest. This is probably because, due to abundant advance regeneration, fir is favoured by logging and consequently it is widely distributed throughout the managed landscape.

Our results could help indicate where to perform stand-level restoration practices in the landscape in order to reduce differences in patterns between managed and natural landscapes. Restoration efforts should aim to promote structural complexity and increase the recruitment of spruce at the stand scale, and concentrate operations at the landscape scale. This would reduce fragmentation and create a forest matrix that would eventually be comparable to the old-growth matrix observed in the unmanaged landscape.

As expected, the effects of forest management on natural heterogeneity depend on the scale of observation. We found higher forest heterogeneity in terms of stand age, density and spatial pattern in the managed landscape. In ecosystems with very low fire recurrence, natural landscapes are very homogeneous since they are largely dominated by old-growth forests. Harvesting thus increases landscape heterogeneity by creating new patches of younger and denser forests. In contrast at the burn/harvest scale, harvesting is more homogenizing since logging intensity is constant in the boreal forest (usually total cut with or without protection of regeneration). Fire is recognized to have heterogeneous effects on forests at this scale, due to variable severity within a given fire (Hessburg et al. 2007; Carlson et al. 2011; Romme et al. 2011). Furthermore, we found that stand density was principally related to environmental factors (surface deposit thickness) in burned forests, but these relationships were not observed in harvested forests. This suggests that harvesting attenuates the relationships between forest density and the physical environment. In terms of stand composition, contrary to our expectations, management did not alter heterogeneity at either of the scales evaluated.

Our results on heterogeneity provide insights in terms of goals for restoration purposes. Forest management has often been found to homogenize landscapes (Bobiec 1998; Foster et al. 1998; Schulte et al. 2007), and the recovery of landscape heterogeneity has often been suggested as a restoration strategy. Our results highlight the fact that restoration objectives should be based on the natural disturbance regime of the ecosystem, as well as on the variables being considered. In a low fire recurrence ecosystem, restoration strategies should aim to decrease the heterogeneity created by harvesting at the landscape scale (age and density), but to increase heterogeneity at the harvest scale (density).

Conclusion

Eighty years of forest management in a region where the natural fire cycle is long have strongly modified the landscape by reducing the proportion of old-growth forests and modifying forest composition and spatial patterns. Lessons derived from studies on long-term management effects can be used in landscape restoration: silvicultural treatments should be developed that can rapidly convert logged stands dominated by balsam fir to stands structurally and compositionally similar to old-growth forests (i.e. by preserving live and dead wood of all sizes to increase the structural complexity of stands, for example) to attenuate management effects at the landscape scale (Harvey et al. 2002; Seymour et al. 2002). However, silvicultural strategies should also be developed that favour recruitment by black spruce and, to a lesser extent, by hardwoods, such as prescribed burns, soil scarification and conservation of natural forests. To create more natural landscapes, managers should reconfigure spatial patterns of harvested forests by reducing fragmentation of old-growth and black spruce forests and by increasing their connectivity.

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