

# Wildfire and forest harvest disturbances in the boreal forest leave different long-lasting spatial signatures

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## Abstract

**Aims** Natural disturbances leave long-term legacies that vary among landscapes and ecosystem types, and which become integral parts of successional processes at a given location. As humans change land use, not only are immediate post-disturbance patterns altered, but the processes of recovery themselves are likely altered by the disturbance. We assessed whether short-term effects on soil and vegetation that distinguish wildfire from forest harvest persist over 60 years after disturbance in boreal black spruce forests, or post-disturbance processes of recovery promote convergence of the two disturbance types.

**Methods** Using semi-variograms and Principal Coordinates of Neighbour Matrices, we formulated precise, a priori spatial hypotheses to discriminate spatial signatures

following wildfire and forest harvest both over the short- (16–18 years) and long-term (62–98 years).

**Results** Both over the short- and the long-term, wildfire generated a wide spectrum of responses in soil and vegetation properties at different spatial scales, while logging produced simpler patterns corresponding to the regular linear pattern of harvest trails and to pre-disturbance ericaceous shrub patches that persist between trails.

**Conclusions** Disturbance by harvest simplified spatial patterns associated with soil and vegetation properties compared to patterns associated with natural disturbance by fire. The observed differences in these patterns between disturbance types persist for over 60 years. Ecological management strategies inspired by natural disturbances should aim to increase the complexity of patterns associated with harvest interventions.

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## Introduction

Major natural disturbances, such as fire and insect outbreaks, are inherent and ubiquitous phenomena, which affect all levels of biological organization (Esser 2001) and leave long-lasting signatures in natural ecosystems (Turner et al. 2001). The particular characteristics of these ecological legacies vary among landscapes and ecosystem types, but they are integral to successional processes in a given location (Walker

and Willig 1999). By changing land use, humans modify, suppress or reinforce natural disturbance regimes, while also introducing novel disturbances (Esser 2001), thereby altering post-disturbance patterns and the processes of recovery, and potentially leaving unique long-term spatial legacies (Foster et al. 2003).

In black spruce-feathermoss forests of boreal Quebec, large catastrophic fires drive stand composition and structure (Saucier et al. 2009). These forests typically have two dominant species groups (Bloom and Mallik 2004); black spruce (*Picea mariana* (Mill.) BSP) forms the canopy, while ericaceous shrubs dominate the understory. The past 60 years, however, have witnessed a shift from fire to timber harvesting as the predominant disturbance agent in northern conifer and boreal mixed-wood forests, with further shifts from clearcutting to careful logging (See methods; MRNQ 1994). By restricting circulation of skidding machinery to evenly spaced trails, while leaving understory vegetation and soils intact between trails, careful logging was envisaged as a means of reducing damage to residual trees and soil. However, this practice may be accompanied by rapid proliferation of the existing ericaceous understory, which takes advantage of full-light conditions and interferes with advance conifer regeneration.

Ericaceous shrubs may compete directly with conifers for nutrients (Peterson 1965; Thiffault et al. 2004; Castells 2008), but also compete indirectly by modifying humus quality (Joanisse et al. 2009), or by imposing potential allelopathic effects (e.g., Zhu and Mallik 1994). Indeed, certain life history characteristics (e.g., thick, long-lived leaves with high concentrations of phenolic compounds and other secondary metabolites) have predisposed some ericaceous species to act as 'ecosystem engineers' (*sensu* Jones et al. 1994) promoting positive feedbacks leading to an alternate persistent vegetation state (Bloom and Mallik 2004). Yet, as Mallik (2003) has stressed, the 'afterlife effects' exerted by their decaying litter are also considerable; the soil becomes acidified, resulting in the loss of base cations (Bloom and Mallik 2004), while compounds that are leached from these tissues can form protein and other N complexes, rendering the habitat even more deficient in sources of available N (Bennett and Prescott 2004; Joanisse et al. 2007; Kraus et al. 2003).

Ecosystem management (Grumbine 1994; Kohm and Franklin 1997), which has developed over the last 20 years in North America, promotes interventions that better mimic spatiotemporal patterns of natural

disturbances, thus approaching natural structural attributes and processes. Wildfire is characterized by variable intensities, which results in a heterogeneous pattern of burn severities at different scales (Brown et al. 1999). This heterogeneity manifests itself through variable residual patch sizes (Eberhart and Woodward 1987), tree mortality (DeLong and Kessler 2000) and volume of coarse woody debris (Clark et al. 1998). Forest harvesting, however, only very crudely approximates wildfire effects (McRae et al. 2001) and can impose unintentional effects on subsequent stand development (Bloom and Mallik 2004). Harvest practices that create evenly-spaced trails may directly or indirectly influence subsequent patterns of black spruce establishment and growth and, hence, stand structure. On harvest trails, soil compaction associated with mechanical harvester traffic can directly result in tree growth reduction and mortality (Brais and Camiré 1992; Thorpe et al. 2008). Once established under full-light conditions, post-harvest ericaceous shrub growth may indirectly promote persistence of two types of patterns: (a) repetitive patterns that are related to trails, and (b) on protection strips, patterns related to shrub patches that are pre-established in canopy gaps. Thus, it is critical to better understand how anthropogenic disturbance regimes may create spatial patterns of soil properties and vegetation regeneration that diverge significantly from those patterns associated with natural disturbance.

We assessed whether or not short-term effects that distinguish natural from anthropogenic disturbances persist 60 years after disturbance of black spruce forests, and if post-disturbance processes of recovery promote convergence. We expected that spatial patterns of soil and vegetation properties would reflect complexity that is related to different burn intensities (Brown et al. 1999) following wildfire, versus the regular structure imposed by trails and shrub patches following forest harvest. To maximize our inference about this conjecture, we used an a priori multiple-hypotheses approach (Chamberlin 1965; Burnham and Anderson 2002) applied to spatial pattern analyses. In this approach, processes are inferred from spatial patterns. We tied our precise a priori hypotheses to multiple processes (e.g., McIntire and Fajardo 2009) to link disturbance signatures with short- (16–18 years) and long-term (62–98 years) post-disturbance successional processes (ericaceous shrub presence) and to compare between- and within-disturbances imposed

by wildfire and forest harvest. We evaluated these spatial hypotheses using semi-variograms (Isaaks and Srivastava 1989) and Principal Coordinates of Neighbour Matrices (PCNM, Borcard and Legendre 2002).

To understand wildfire effects, we recognize the positive spatial autocorrelation that exists in terrestrial ecosystems as a primary response to large scale disturbance (e.g., Robertson et al. 1988). Thus, we hypothesized that this non-repeating spatial pattern would be best fitted by exponential or spherical variogram models (see Methods for description of this and other models). We selected the latter because its sill (i.e., equal to the variance of a variable) has a finite range (i.e., distance at which the variance levels off) that is appropriate to defining patch dimensions. Model range was not constrained to allow for uncertainty regarding processes associated with positive spatial autocorrelation. We hypothesized that harvest trails would create repeating patterns, thereby following the “wave” model. Furthermore, since trails are created parallel to one another at fixed distances, we can strengthen inference by fitting the data to a constrained wave model that runs perpendicular to the trails, with a range equal to half the inter-trail distance (~6 to 10 m). Any wave pattern occurring parallel to the trails or at a different scale would not represent the signature of forest harvesting. In harvested landscapes and, in contrast to the wave model, the alternative spherical model would best fit the irregular patches of soil and vegetation with well-defined boundaries that can be generated by non-anthropogenic processes.

In the PCNM analysis, we deduced that a fine-scale model (<6 m) represents spruce spatial distribution, as determined by ericaceous shrub patches (shrub patch size: ~<6 m); the medium-scale model (>6 and <14 m) represents spruce distribution, as determined by the presence of trails (trails: ~3 m wide; strips between trails: ~14 m wide); and the broad-scale model (>14 m) represents spruce distribution at scales greater than trail locations and shrub patches. Hence, we hypothesized that the broad-scale model would describe natural patterns (i.e., independent of trails) in spruce. We predicted that both medium- and fine-scale models would describe the two abovementioned anthropogenic types of patterns in spruce distribution: (a) the regular structure (i.e., trails),

and (b) the effects of shrub patches remaining intact in protected strips between the trails.

## Material and methods

### Study area

The study was conducted in the Chibougamau-Lac St. Jean region of Quebec, Canada (49°19' to 50°06'N, 73°59' to 75°29'W). Our sites were in the spruce-feathermoss domain, which is part of the B.1b Chibougamau-Natashquan boreal forest region (Rowe 1972). The sites were black spruce stands with an ericaceous understory dominated by sheep laurel (*Kalmia angustifolia* L.), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), lowbush blueberry (*Vaccinium angustifolium* Aiton) and velvetleaf blueberry (*V. myrtilloides* Michaux) (referred to collectively as *Vaccinium*). A variable cover of feathermosses, sphagnum mosses and reindeer lichens completed the ground cover composition. The sandy loam soils are Humo-Ferric Podzols (Soil Classification Working Group 1998) or Orthic Podzols in the FAO system, with a 2- to 25-cm thick mor humus.

Four plots were established in two burned stands (originating in 1906 and 1986, respectively) and two harvested stands (harvested in 1942 and 1988). The old burn and old harvest had regenerated naturally since disturbance. The recent burn originated from a lightning-caused fire (Smith et al. 1998). The recent harvest was subject to careful logging. Careful logging has gradually replaced clearcutting (i.e., logging of an area by removing all trees at one time) in Quebec since 1980, as a strategy for reducing soil erosion, while maintaining genetic diversity, density and growth of advance natural regeneration. Clearcutting typically damages advanced natural tree regeneration, while surface soils are disturbed and compacted, and frequently the organic and mineral horizons are mixed. In contrast, careful logging protects natural regeneration and soils by restricting the circulation of machinery to trails that occupy a maximum of ~25 % of the harvested area (MRNQ 1994). The old harvest site was subject to horse-logging, which also created a regular structure of parallel trails (Walker and Stevens 1947), allowing us to verify if this pattern was still evident more than 60 years after disturbance. The four treatments were not mixed; each site represented one disturbance type and a corresponding time-since-disturbance.

Replication was not possible, due to biological and operational constraints. Consequently, we used the aforementioned precise a priori models to overcome this lack of replication (McIntire and Fajardo 2009). Moreover, multi-site inference of spatial analyses is still in its infancy (requiring meta-analytical approaches) (McIntire 2004), so replicate sampling was not a priority of this study. More importantly, the spatial patterns and inferred mechanisms that we have posited are likely to be well-conserved across sites, unlike more variable phenomena such as stand density or species diversity. Harvest strategies regulated by norms are likely to produce low variation in spatial patterns among sites and, thus, our predictions are more precise. Natural disturbance sites are likely to be more variable and, hence, our predictions are not constrained (though precise in spatial form: spherical).

#### Field sampling

We measured soil properties and shrub cover on a 90 m long×40 m wide study plot established in each of the four sites, with 1-m and 5-m grid spacing (open circles in Fig. 1) with ( $n=227$ ) sampling locations per site (identified using permanent flags). Sampling was conducted during the summers of 2003 and 2004. Forest floor blocks (10 cm×10 cm×10–15 cm deep) were cut at each sampling point. Organic layer thickness (cm) was measured ( $\pm 5$  mm) and used to calculate O-layer bulk density. Samples were transported on ice packs to the laboratory and stored at 5 °C prior to analysis. Percent ericaceous shrub cover was estimated for the three dominant genera (*Kalmia*, *Rhododendron*, *Vaccinium*) within 25 cm×25 cm quadrats established at each sampling point. We measured diameter at breast height (DBH, 1.37 m) of spruce trees (DBH>1 cm) on each site. Diameter and position of trees were measured within a plot (60 m×12 m, old disturbed sites; 90 m×40 m, recently disturbed sites). Stem coordinates (i.e., grey triangles in Fig. 1) were estimated relative to one plot corner using 100-metre tapes ( $\pm 100$  mm). Tree density was estimated at each sampling point (i.e., open circles in Fig. 1) within 60 m×40 m plots on each site, using plotless-point sampling (Cottam and Curtis 1956). Regeneration density (DBH≤1 cm, trees m<sup>-2</sup>) and

its annual height growth (cm) were estimated within 1-m<sup>2</sup> quadrats established at each sampling point within 60 m×40 m plots on both recently disturbed sites.

#### Laboratory analyses

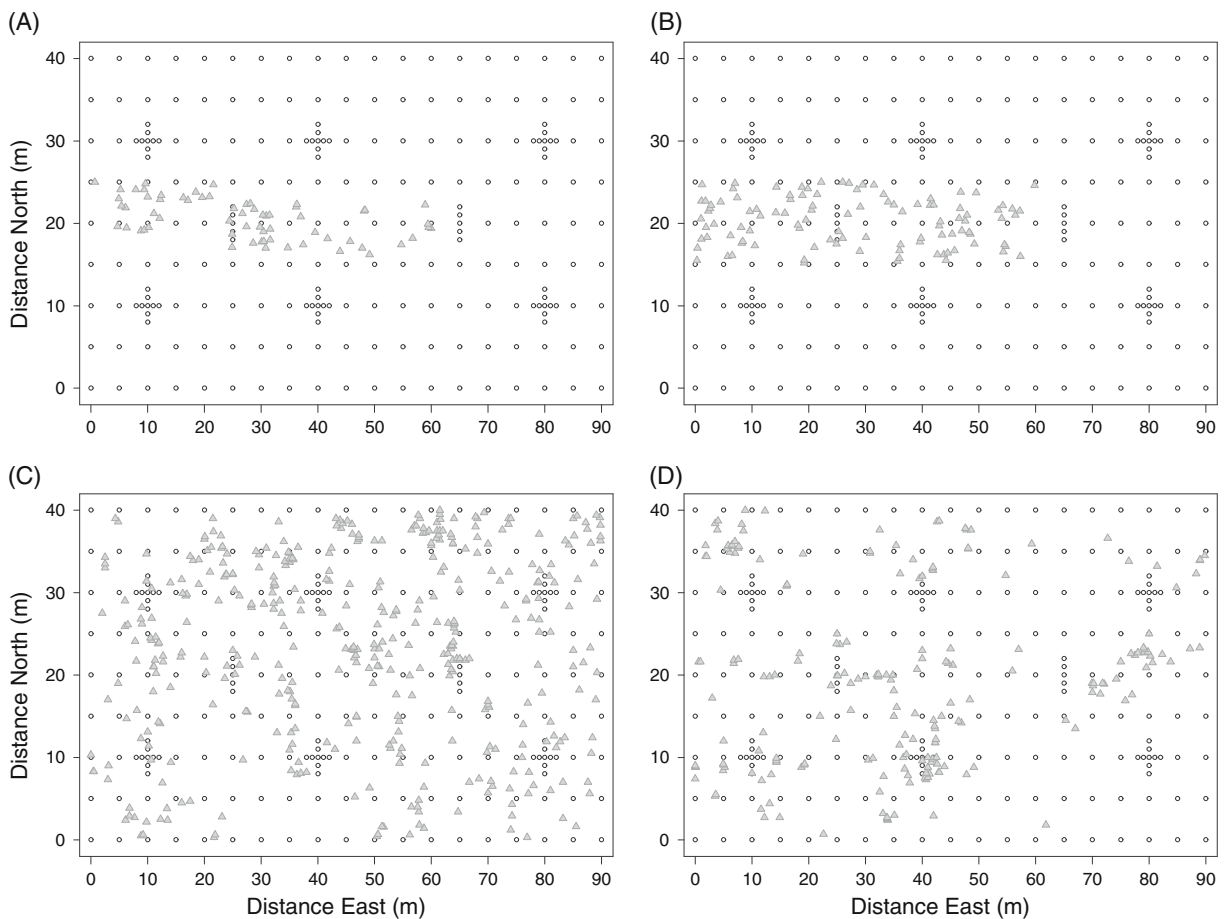
The forest humus was sieved to pass through a 5-mm mesh. Moisture content was calculated gravimetrically after oven-drying (65 °C, 48 h). Carbon content was determined following loss-on-ignition (600 °C, 6 h). Kjeldahl nitrogen was determined (Lachat Quickchem 800 FIA, Zwellger Instruments, Milwaukee, WI, Method No. 13-107-06-2-C), following sample digestion (boiling H<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>O<sub>2</sub>-Se). O-layer pH was estimated electrometrically (2 g air-dry organic soil:20 ml deionized water). N-mineralization potential was evaluated using anaerobic incubations (Waring and Bremner 1964). Mineralized N (g N kg<sup>-1</sup> 10 days<sup>-1</sup>) was calculated as the difference between soil NH<sub>4</sub><sup>+</sup> pools extracted before and after 10 d incubation at 30 °C.

#### Model fitting

##### Variograms

Spatial trends in the measured properties were removed prior to further analysis. Data for each variable had a moderate negatively skewed distribution and, consequently, they were square-root-transformed to meet normality assumptions. We then estimated one isotropic (all directions on burned stands) and two anisotropic (parallel or perpendicular to the trails on harvested stands) experimental variograms. Only distances less than half-maximum grid length were plotted to ensure robustness of the variograms.

We worked with four theoretical variograms (Fig. 2) that were chosen to represent different processes of interest. These variograms take different shapes, indicating that the patterns are different in quality and have different quantitative model parameters. In the “spherical” model, semivariance rises monotonically from ca. zero to a maximum (*sill*) as distances between paired points increase. The distance at which this maximum is reached (*range*) indicates the mean diameter of patches, which are arranged randomly across the plot. In the “wave” model, semivariance rises monotonically to



**Fig. 1** Sampling design on four disturbance types located in central Quebec: old harvest (1942; A), old burn (1906; B) recent harvest (1988; C), and recent burn (1986; D). Hypothesized harvest trails are located in N-S direction on harvested sites. Open circles represent locations ( $n=227$ ) where soil and shrub variables were sampled. Grey triangles represent black spruce point locations (old harvest,  $n=63$  stems; old burn,  $n=103$

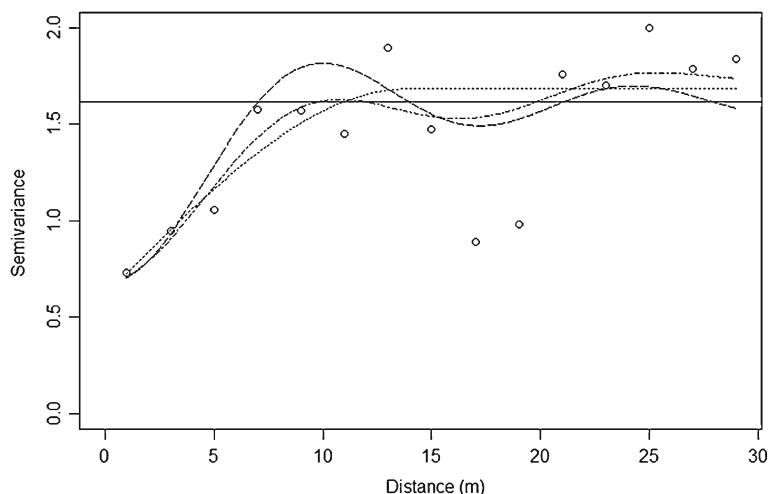
stems; recent harvest,  $n=411$  stems; recent burn,  $n=203$  stems). Stems were referenced (X, Y) and diameters at breast height for each stem were measured. Black spruce density (four sites) and black spruce regeneration density and its annual height growth (recent harvest and recent burn) were also measured on quadrats centred on each white circle within  $60\text{ m} \times 40\text{ m}$  plots ( $n=153$ )

a maximum and then decreases, thereby representing a repeating and dampened spatial signal. To understand the roles of complementary spatial processes, the fitting of “nested” model variograms can extract the separate patterns if they are quantitatively or qualitatively different (e.g., Fajardo and McIntire 2007). Nested models are multi-scale variograms, i.e., a combination of several variogram functions representing  $k$  spatial structures with different parameters (Journel and Huijbregts 1978). In our study, the nested model was originally conceived as a mixture of both wave and spherical models. Since the algorithm that mixed wave and spherical models had convergence problems, we used

exponential models instead, which had good stability during fitting. The “pure nugget effect model” (Legendre and Legendre 1998) (referred to as “nugget”) indicates random spatial structure or a lack of spatial dependence at the scales we measured (equivalent to a null hypothesis).

The four theoretical variograms (Fig. 2) were simultaneously fitted by weighted least-squares (Cressie 1985) using the *geoR* package (Ribeiro and Diggle 2001). Formulae for the aforementioned models are available in this package. We used the Akaike Information Criterion with small-sample size adjustment ( $AIC_c$ ; Burnham and Anderson 2002) to rank

**Fig. 2** Experimental variograms (open circles) of a variable and the four theoretical variogram models used in this study: nugget (solid line), spherical (dotted line), wave (dashed line) and nested (dotted/dashed line)



variogram fits (i.e., without disregarding the worst fits). The best models had the lowest  $AIC_c$  values (Electronic Supplementary material, ESM 1).

#### PCNM analyses

Based on relationships among the closest sample points, PCNM analysis allows the modelling of spatial relationships at several scales (Borcard and Legendre 2002). PCNM is a form of spatial regression that constructs base functions from the singular value decomposition of a matrix of geographic distances among sample locations. Base functions are obtained by principal coordinate analysis of a truncated pairwise geographic distance matrix among sampling points (Borcard and Legendre 2002; Dray et al. 2006). The eigenvectors associated with successive eigenvalues represent sinusoidal functions of increasing periodicity that can be used as spatial predictors in multivariate regression. Each of the base functions is thus uncorrelated with the others; eigenvectors associated with larger and smaller eigenvalues represent broad- and fine-scale variation, respectively (Borcard and Legendre 2002). In our study, we worked only with positive eigenvalues (i.e., original PCNM approach; Borcard and Legendre 2002), since we were interested in globally induced structure and not in fine-scale autocorrelation generated by inherent biotic processes, such as intra-specific competition between trees.

To do our PCNM analyses, we required estimates of soil properties and shrub cover values (measured on open circles in Fig. 1) at each spruce location (i.e., grey triangles in Fig. 1). To obtain these, we interpolated

using ordinary kriging from the best isotropic variogram fits (*geoR* package, R). We calculated weighted estimates for the soil and shrub variables, if more than one model fit had an  $AIC_c < 2$  (Burnham and Anderson 2002).

We generated base functions using X-Y coordinates of spruce stem locations for each site (grey triangles in Fig. 1). PCNM yielded 38, 62, 230 and 95 base functions for the old harvest, old burn, recent harvest, and recent burn, respectively. We fitted spherical variograms to each base function to determine ranges of spatial dependency (Bellier et al. 2007). PCNM functions were then divided into the three aforementioned a priori models, based on similarity of scale: broad- (range >14 m), medium- (>6 and <14 m) and fine-scale (<6 m). We then performed two sets of multiple regressions. First, we used these three PCNM spatial models to verify whether patterns of spruce DBH are determined by the presence of abovementioned spatial structures, i.e., a) trails and b) shrub patches. Second, we verified if soil and shrub cover variables are related to the spatial structure of spruce DBH. As pointed out in the Introduction, shrubs may compete with spruce by modifying humus quality and by imposing potential allelopathy. We thus computed this second set of regressions to verify whether or not shrubs promote differences in soil properties and spruce presence that result in a long-term spatial signature perpetuating the trail and the shrub patterns.

For the first set of regressions, the fraction of total variance explained by each spatial model was determined by regressing spruce DBH against these three subsets of parsimonious spatial models. Forward

selection was performed using Monte Carlo tests (999 permutations), retaining variables with  $P < 0.05$ .  $R^2$ -values were adjusted ( $R^2_{adj}$ ) for the number of sampling locations and explanatory variables. Bonferroni corrections were obtained by dividing alpha ( $\alpha = 0.05$ ) by the number of base functions in each model. We only used selected base functions in subsequent multiple regressions. Second, we identified which soil and shrub variable (previously kriged to locations where spruce stems were situated) varied significantly at each spatial scale of DBH variation. Using the same criteria, we regressed each significant spatial model of spruce DBH against the kriged estimates.

We obtained base functions of spruce density on the four sites and regeneration density and growth on the recently disturbed sites via the same analyses (i.e., identification of significant scales and two subsequent sets of multiple regressions); kriging was not employed in these analyses, since spruce density and regeneration were measured at the same grid points (though within  $60 \text{ m} \times 40 \text{ m}$  plots,  $n = 153$ ) where we measured soil properties and ericad cover. This procedure yielded 36 PCNM variables for spruce density and regeneration. PCNM was performed in R (Version 2.7.1, R Development Core

Team 2004) using *spacemaker* (Dray 2006b); regressions were computed with *packfor* (Dray 2006a).

### Correlation analyses

In addition, we performed *t*-tests for Pearson correlations corrected for spatial autocorrelation, following Dutilleul (1993). Spatial autocorrelation may affect the classical tests of significance of correlation or regression coefficients by inflating rates of Type I error. Dutilleul's modified *t*-test corrects the variance of the test statistic as well as the degrees of freedom in the presence of spatial autocorrelation. These correlations were not a part of the a priori approach; hence, we did not have specific hypotheses tied to these analyses. The latter analyses were used to assess direct associations between shrub cover and spruce growth variables.

## Results

Soil and vegetation variables following natural or anthropogenic disturbance are summarized in Table 1.

**Table 1** Variation in soil physico-chemical properties, ericaceous shrub cover, and black spruce growth variables among four disturbance types

Variables	Abbreviation	Old harvest		Old burn		Recent harvest		Recent burn	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV
Organic layer thickness (cm)	OL	11.1	52.5	15.7	35.9	14.4	53.8	8.5	53.9
Soil water content (%)	WC	255.8	51.1	261.0	18.6	433.6	63.2	206.6	42.4
Carbon to nitrogen ratio	C/N	83.6	33.84	64.9	19.3	110.4	141.2	86.5	25.9
N-mineralization potential ( $\text{g N kg}^{-1} \text{ soil } 10 \text{ days}^{-1}$ )	NMIN	1.5	73.4	1.3	63.1	0.8	104.4	1.1	55.4
<i>Kalmia angustifolia</i> cover (%)	KAAN	17.7	83	5.7	136.8	13.3	65.6	24.3	78.5
<i>Rhododendron groenlandicum</i> cover (%)	RHGR	3.3	181.1	0.9	421.9	21.6	89.1	14.2	151.1
<i>Vaccinium</i> spp. cover (%)	VACC	1.9	208	3.1	126.4	12.0	95.5	22.6	49.9
Black spruce diameter at breast height (DBH > 1 cm) (cm)	DBH	11.7	20.9	16.1	29.7	2.6	53.0	3.3	45.5
Black spruce (DBH > 1 cm) density (trees $\text{m}^{-2}$ )	DENS	0.6	59.9	0.7	114.6	0.3	95.7	0.2	193.6
Black spruce regeneration (DBH $\leq$ 1 cm) density (trees $\text{m}^{-2}$ )	DENS <sub>REG</sub>	ND	ND	ND	ND	0.8	95.6	0.2	196.5
Black spruce regeneration annual height growth (cm)	GROWTH	ND	ND	ND	ND	0.7	72.9	0.4	197.2

CV Coefficient of variation (%); ND Not determined

## Wildfire-related patterns

Spatial patterns of soil and vegetation properties reflected complexity that was related to different burn intensities. Spherical models had the highest summed Akaike weights (Table 2, Fig. 3) for properties measured on both burns. For the spherical model, variogram range parameters (ESM 1) varied from 4.2 m to 29.8 m and from 4.8 m to 30 m on the old burn and recent burn, respectively.

Two PCNM models (broad-scale, >14 m; fine-scale, <6 m; Table 3) explained variation in spruce growth variables on the burns. The only exception was variation in spruce density on the recent burn, which was explained using the medium-scale model (>6 m and <14 m). The broad-scale model contributed to the largest fraction (8 % to 37 %) of explained variation in spruce growth variables, followed by the fine-scale (3 % to 11 %) and medium-scale (9 %) models on the burned sites.

The second set of multiple regressions (Table 4) showed that the three shrubs made marginal contributions in explaining spruce parameters on both burned sites ( $R_{adj}^2 = 0.01 - 0.04$ ), except for *Vaccinium* cover on the recent burn, which accounted for 13 % of the variation in spruce density at fine-scales. Soil properties also made contributions to the significant models for spruce growth variables ( $R_{adj}^2$  ranging from 0.02 to 0.42). Organic layer thickness accounted for a large fraction of spruce DBH variation on these burned sites; it represented respectively 42 % and 38 % of the

**Fig. 3** Experimental variograms (open circles) of (a) OL (Organic layer thickness, cm); (b) C/N (Carbon to nitrogen ratio), and (c) KAAN (*Kalmia angustifolia* cover, %) on four disturbance types in central Quebec: old harvest (1942; A), old burn (1906; B) recent harvest (1988; C), and recent burn (1986; D). Theoretical variograms (nugget, spherical, wave and nested) having statistical support, i.e., lowest Akaike Information Criterion ( $\Delta_i \leq 2$ ) are fitted to experimental variograms. The wave model has a constrained range (~6–10 m) for the four sites. Directional variograms were computed parallel or perpendicular to the hypothesized trails (harvested stands), or in all directions (burned stands)

variation in DBH for the broad- (old burn) and fine-scale (recent burn) models.

Correlations corrected for spatial autocorrelation indicated that only *Vaccinium* cover and spruce regeneration density were negatively associated on the recent burn (Table 5).

## Forest harvest-related patterns

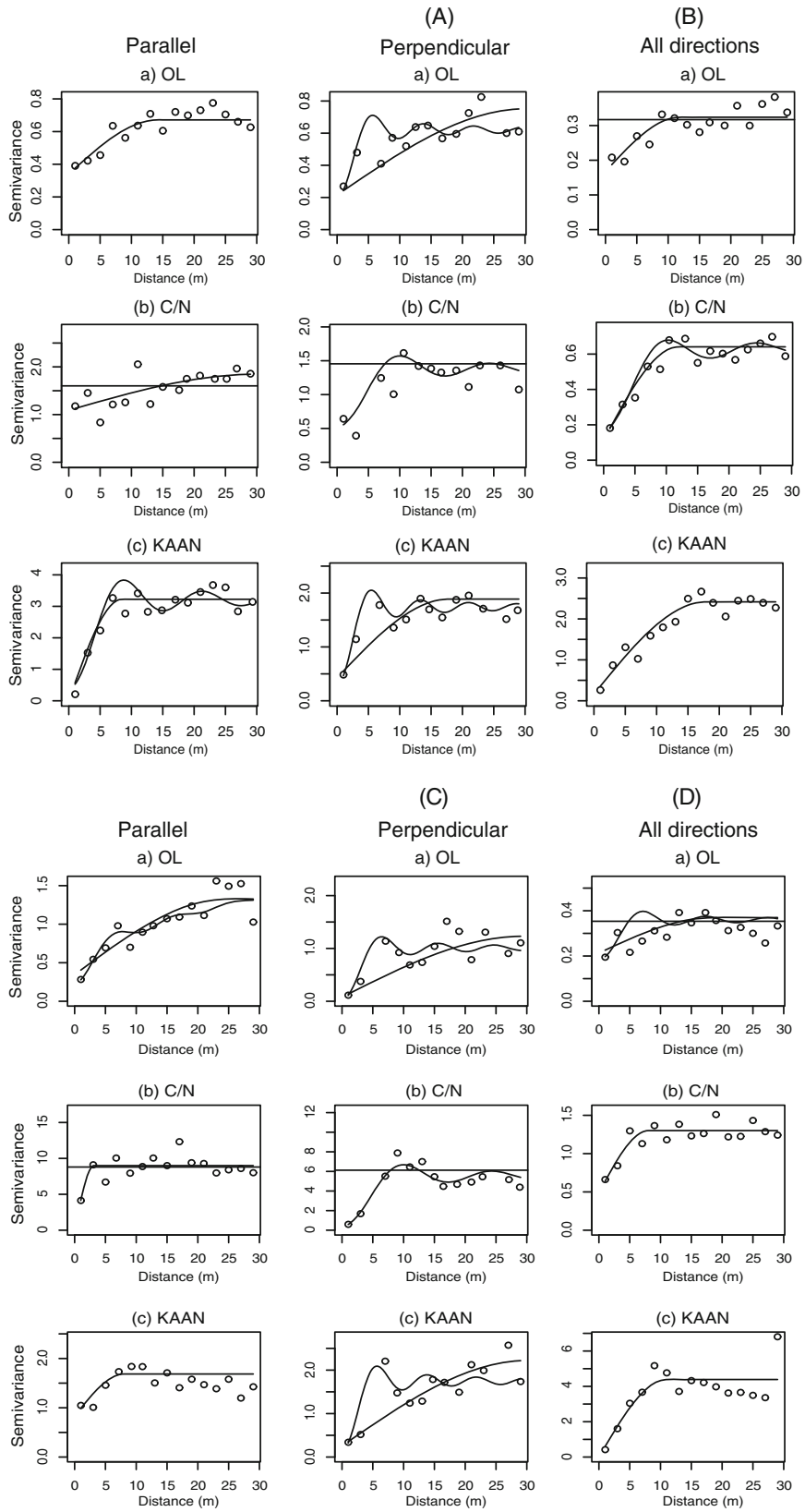
Spatial patterns of soil and vegetation showed a regular structure. Summed Akaike weights (Table 2, Fig. 3) for models having statistical support emphasized the importance of wave models for properties that were measured perpendicular to the trails on both harvested sites. The spherical model had the highest summed Akaike weights for variograms computed parallel to trails. Range estimates (ESM 1) for properties fitted to spherical variograms varied from 4.9 m to 26.5 m on the old harvest, and from 4 m to 25.8 m on the recent harvest.

**Table 2** Sum of Akaike weights ( $w_i$ ) for the 11 variables (Table 1) for which variogram models (spherical, wave, nested, nugget) have statistical support ( $\Delta_i \leq 2$ ) at each site. Summed weights are shown for each of the four models in each of the four sites (old harvest, 1942; old burn, 1906; recent harvest,

1988; recent burn, 1986). Values in bold indicate variogram models having the highest summed Akaike weights for the variables measured. Supported models for the 11 variables are shown in ESM 1; graphical examples are shown for three variables in Fig. 3

Models	Old harvest		Old burn All directions	Recent harvest		Recent burn All directions
	Parallel	Perpendicular		Parallel	Perpendicular	
Spherical	<b>4.15</b>	1.76	<b>4.02</b>	<b>5.53</b>	3.27	<b>7.16</b>
Wave	1.74	<b>3.75</b>	0.97	1.40	<b>4.36</b>	0.96
Nested	0.48	0.29	0.94	1.60	0.62	0.79
Nugget	2.66	3.18	3.04	2.44	2.75	2.12





**Table 3** Relationships between black spruce growth variables and three models describing spatial distribution of spruce over broad-scales (>14 m), medium scales (>6 and <14 m), and fine-

scales (&lt; 6 m) on four disturbance types. Only forward-selected significant variables after 999 random permutations with Bonferroni corrections are included in each model

Response variable	Old harvest			Old burn			Recent harvest			Recent burn		
	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$
DBH	0.28**	Med-sc	0.15**	0.14**	Br-sc	0.08**	0.17**	Med-sc	0.09**	0.13**	Br-sc	0.10***
		Fine-sc	0.13**		Fine-sc	0.06**		Fine-sc	0.08*		Fine-sc	0.03**
DENS	0.55***	Med-sc	0.22**	0.44***	Br-sc	0.37**	0.48***	Fine-sc	0.48***	0.35***	Br-sc	0.15**
		Fine-sc	0.21**		Fine-sc	0.07*		Fine-sc	0.11**			
		Br-sc	0.12*		Med-sc	0.09**						
DENS <sub>REG</sub>	ND			ND			0.32***	Med-sc	0.17***	0.46***	Br-sc	0.35**
								Fine-sc	0.15**		Fine-sc	0.11**
GROWTH	ND			ND			0.24***	Med-sc	0.14***			
								Fine-sc	0.10**			

\*\*\*\*  $P \leq 0.0001$ , \*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$ . Abbreviations are defined in Table 1. *Br-sc* broad-scale; *Med-sc* medium-scale; *Fine-sc* fine-scale; *ND* Not determined

The first set of multiple regressions (Table 3) indicated that variation in all spruce growth variables could be explained on the old harvest using medium- and fine-scale models. In the recent harvest, variation in spruce density was uniquely explained at fine-scales. A significant proportion of variation in spruce density on the old harvest was also related to its broad-scale spatial model. Each model accounted for 8 % to 48 % of among-location variability in spruce growth variables.

Shrub cover was associated with significant spatial models of spruce growth variables on both harvested sites (Table 4;  $R^2_{adj} = 0.03 - 0.27$ ), while soil properties made slight contributions to these significant models ( $R^2_{adj} = 0.01 - 0.15$ ). *Rhododendron* cover accounted for a large proportion of variation in spruce DBH and spruce regeneration density on harvested sites. Cover of this shrub accounted for 25 % and 27 % of the variation at the medium-scale model in DBH (old harvest) and spruce regeneration density (recent burn), respectively.

Moreover, shrubs and spruce growth were negatively correlated on both harvested sites (Table 5). DBH of mature spruce, together with regeneration density and growth, was negatively associated with *Kalmia* cover on the recent harvest. Spruce DBH and density (old harvest) and regeneration density and growth (recent harvest) declined with increasing

*Rhododendron* cover. Spruce DBH (both harvested sites) declined as *Vaccinium* cover increased.

## Discussion

### Wildfire vs forest harvest

Our results suggest that the spatial signatures in soil and vegetation properties associated with wildfire and forest harvest did not converge over short- or long-term scales. Discrimination of natural and harvest structure signatures could only be inferred with precise spatial predictions. Despite the lack of replication, our precise spatial predictions were non-trivial and were largely supported over recent (16–18 years) and long-term (62–98 years) scales. Anthropogenic disturbance simplified spatial signatures to characteristic management dimensions (e.g., harvest trails) that persisted with succession (~60 years). On the recent harvest (i.e., careful logging), machine trails are restricted to about 4–5 m in width and the harvested strip between trails occupies about twice the operable reach of a harvester (about 10–12 m in width). On the old-harvest, horse-logging techniques necessitated that trails be as straight as possible and wide enough to allow free passage of the horses used to haul out the logs. Trees were felled so that the logs could be placed

**Table 4** Relationships between significant models describing spatial variation of spruce growth and soil and shrub variables (physico-chemical soil organic layer properties and ericaceous shrub cover) over broad-scales ( $\geq 14$  m), medium scales ( $> 6$  and  $< 14$  m) and fine-scales ( $< 6$  m) on four disturbance types. Only forward-selected significant variables after 999 random permutations with Bonferroni corrections are included in each model

Response variable	Old burn			Recent harvest			Recent burn				
	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$	$R^2_{adj}$	Predictor variables	Partial $R^2_{adj}$
DBH br-sc			0.61****	OL	0.42****			0.09**	OL	0.05**	
				NMIN	0.13****				C/N	0.02**	
				WC	0.05**				NMIN	0.02**	
				C/N	0.02****						
				VACC	0.01**						
DBH med- sc	0.63****	RHGR	0.25****			0.19**	KAAN	0.07****			
		VACC	0.18****				NMIN	0.04****			
		WC	0.10****				VACC	0.03****			
		OL	0.08****				RHGR	0.02****			
		NMIN	0.02**				C/N	0.02****			
DBH fine- sc	0.47****	VACC	0.14****			0.43****	VACC	0.13****	0.46****	OL	0.38****
		RHGR	0.14****				RHGR	0.11****		C/N	0.05****
		KAAN	0.08**				NMIN	0.09****		VACC	0.03****
		C/N	0.06**				KAAN	0.05****			
		NMIN	0.05**				WC	0.05**			
DENS br- sc			0.19*	WC	0.10*						
				C/N	0.09**						
DENS med- sc	0.08*	VACC	0.08**						0.08**	WC	0.08**
DENS fine-sc	0.09**	RHGR	0.07**			0.12**	KAAN	0.08****	0.13**	VACC	0.13**
		NMIN	0.02*				WC	0.02**			
DENS <sub>REG</sub> br-sc	ND		ND				C/N	0.02**	0.29**	C/N	0.21*
DENS <sub>REG</sub> med-sc	ND		ND			0.46****	RHGR	0.27**		WC	0.08*
							WC	0.15**			
							OL	0.04**			
DENS <sub>REG</sub> fine-sc						0.15**	KAAN	0.11****	0.04*	VACC	0.04*
GROWTH med-sc	ND		ND								

\*\*\*\*  $P \leq 0.0001$ , \*\*\*  $P \leq 0.001$ , \*\*  $P \leq 0.01$ , \*  $P \leq 0.05$ . Abbreviations are defined in Table 1. ND Not determined

**Table 5** Correlations corrected for spatial autocorrelation between cover (%) of shrubs (*Kalmia angustifolia*, *Rhododendron groenlandicum* and *Vaccinium* spp.) and black spruce diameter at breast height (DBH>1 cm; cm), density (trees m<sup>-2</sup>),

regeneration (DBH≤1 cm) density (trees m<sup>-2</sup>) and regeneration annual height growth (cm) obtained across grids (Fig. 1) established on four disturbance types

Spruce parameters	Old harvest			Old burn			Recent harvest			Recent burn		
	KAAN	RHGR	VACC	KAAN	RHGR	VACC	KAAN	RHGR	VACC	KAAN	RHGR	VACC
DBH	-0.187	-0.256 *	-0.284*	0.030	-0.046	-0.031	-0.263*	0.043	-0.291*	0.006	-0.097	-0.081
DENS	-0.173	-0.349**	-0.058	-0.177	-0.065	-0.157	0.023	0.178	-0.336*	-0.037	-0.159	0.249
DENS <sub>REG</sub>	ND	ND	ND	ND	ND	ND	0.056	-0.399**	-0.048	-0.023	-0.221	-0.438**
GROWTH	ND	ND	ND	ND	ND	ND	-0.253*	-0.312*	0.106	0.004	-0.065	-0.051

\*\*  $P \leq 0.01$ , \*  $P \leq 0.05$ . Abbreviations are defined in Table 1. ND Not determined.

along or in the trails with a minimum of effort (Walker and Stevens 1947). By following this technique, trails would have been 2 to 3 m wide. In felling mature spruce 20 m in height, the distance between trails would have been about 14 m. The fact that the old harvest also created a regular structure of parallel trails with similar dimensions as those created by careful logging, allowed us to verify if this structure was still evident 60 years after disturbance. Our spatial predictions for the harvested sites (careful logging) thus integrated these dimensions as a priori constrained parameters. These predictions were supported even in the longer term on the harvested site, despite the fact that horse-logging is a technique that imposes lower levels of disturbance compared to modern careful logging practice. Thus, the persistence of the harvest signatures over multiple decades is real.

Wildfire generated a wide spectrum of responses in soil and vegetation properties at different scales (Table 2, Fig. 3, ESM 1). Behaviour conforming to spherical variogram models has been commonly observed for soil variability, such as nutrient (Smithwick et al. 2005) and moisture conditions (Bond-Lamberty et al. 2006) in terrestrial ecosystems. The nugget model suggested the absence of spatial structure in the data, at least at the scale the observations were made (Legendre and Fortin 1989), which is consistent with fire behaviour. A fire may extend over large areas, resulting in large homogeneous areas and, at the same time, it can burn the ground cover and partially reduce forest floor depth (Eberhart and Woodward 1987) to varying degrees, from the scale of single trees or small clusters of trees to the entire landscape (Brown et al. 1999). We also found some support for constrained wave and nested models in both burns, but these were clearly different from harvest sites

since the former occurred in all directions and were not principally perpendicular to the trails, as was the case after harvest.

Sixty years after forest harvesting, the dominant driver of current patterns remains the ecological signature of the harvest trails (Table 2, Fig. 3). We hypothesized that the signature of harvest trails would be evident. As expected, the wave variogram was the most important model for inferring spatial variation of properties measured perpendicular to the trails on both harvested sites. This wave variogram was constrained (range ~6 to 10 m) to reflect the inter-trail distance. However, we anticipated that wave fits occurring parallel to the trails (e.g., not interrupted by trails) or at a different scale would not represent the signature of forest harvesting. Contrary to expectation, we also found some support for the wave model parallel to the trails. We attributed this behaviour to the fact that trails were not strictly straight, especially on the old harvest (i.e., horse-logged; Walker and Stevens 1947). Since the spherical fit usually models the spatial variation existing in most systems (Robertson et al. 1988; Fraterrigo et al 2005), it seems reasonable that behaviour conforming to a spherical model was found parallel to the trails on both harvested sites.

Wildfires showed no such regular, repeating structures such as those of the trails. Due to the pulsing propagation of the fire front and related variation in fire intensity and burn severity, fires can create a regular pattern. However, our wave model was constrained to specifically fit repetitive harvest patterns. Moreover, if other processes such as insect outbreaks, topographical features, or climate effects were responsible for the observed repeating patterns, we should have also observed these on fire-origin sites, which

were subject to the same local conditions. On harvested sites, vegetation and soil properties on trails and zones between trails did not converge with time since disturbance, contrary to the observations made by Harvey and Brais (2002) seven years after careful logging. They hypothesized that intra-site differences between trails and protection strips would gradually attenuate. Our results suggest that attenuation is unlikely to occur, since we found comparable differences sixty years after horse-logging, i.e., even with a technique that imposed lower levels of disturbance than careful logging.

### Spruce and ericaceous shrubs following disturbance

Our results show that spatial patterns in spruce regeneration, density and diameter differed markedly following wildfire or forest harvest disturbances. These patterns were consistent with the identified spatial signatures and the scale of the wildfire or logging effects, respectively (Table 3). Following forest harvest, black spruce spatial distribution and growth were associated with ericaceous shrub patches and by trails used for harvest. Spatial structures generated by wildfire were different and principally driven by abiotic properties (i.e., physico-chemical variables), while those generated by harvest were driven mainly by biotic properties (i.e., ericaceous shrub cover) (Table 4). Indeed, forest floor patches that were not completely burned likely had deeper organic layers, which contribute to higher moisture, colder temperatures and slower decomposition (Van Cleve and Viereck 1981). These conditions can affect subsequent seedling development (Greene et al. 1999) and tree growth rates (Simard et al. 2007). Otherwise, unburned or lightly burned areas may contain patches of trees that survive the fire (Eberhart and Woodward 1987). In turn, trees can modify environmental conditions under their canopies, such as light availability, soil nutrient and moisture conditions (Saetre 1999). The only exception to such physico-chemical drivers is the large contribution made by *Vaccinium* cover to spruce growth on the recent burn. Historical records (NRC 2008) indicated that wildfire on this site may not have been intense, since it occurred at the end of May (prior to fire season), when snowmelt was not complete and organic substrates likely remained moist. Low-intensity burns, which are likely very patchy in intensity and impacts, can favour rapid resprouting of *Vaccinium* (Yarborough et al. 1986). This would also explain the negative correlation found

between *Vaccinium* and spruce regeneration density (Table 5). Consequently, the pre-existing shrub cover may contribute to fine-scale structures related to the presence of shrub patches, as appeared to be the case after harvesting.

The strong significant association between spruce growth and the cover of the three shrubs on harvested sites (Table 4) is consistent with our predictions and visual observations, as well as with shrub inhibitory behaviour. Once established, ericaceous shrubs can take advantage of full-light conditions and further maintain differences between canopy openings and the surrounding forest. Within the New Jersey Pinelands, Ehrenfeld et al. (1995) suggested that the ericaceous shrubs *Vaccinium pallidum*, *V. angustifolium* and *Gaylussacia baccata* helped preserve differences between canopy gaps and the forest matrix by maintaining high fine-root biomass, trapping litter, and inhibiting decomposition. Our results suggest that the post-disturbance structure of dominant ericaceous shrub forms may contribute greatly to spatial patterning of spruce regeneration and growth, and thus play a major role in the absence of canopy closure.

Most studies in eastern Canada have focused on *Kalmia angustifolia* (e.g., Titus et al. 1995), and Damman (1971) reported permanent soil degradation following long-term site occupancy by this shrub. Interestingly, our results suggest the impacts of *Kalmia* are least important, except on the recent harvest, suggesting that the effects of *Kalmia* disappear with time. This behaviour may be related to competition among ericaceous shrubs, given the greater presence of *Rhododendron* on both harvested sites. In a recent study of these same three ericaceous shrubs in Quebec North Shore forests, Laberge-Pelletier (2007) also noted an early presence of *Kalmia* after disturbance, with a subsequent increase in *Rhododendron* during succession. *Rhododendron* may also be better-adapted to patches of deeper organic material that are found after forest harvest.

### Conclusions

Forest harvest attempts to reduce impacts on ecosystems to ensure long-term maintenance of ecosystem functions and to retain the social and economic benefits that they provide to society. One proposed means to limit the negative impacts of forestry activities on ecosystems requires the application of practices that are inspired by natural disturbances as an alternative to

traditional forest management (e.g., Gauthier et al. 2008). The rationale underlying this approach is that native species have evolved under natural disturbance regimes, such as wildfire. Our results suggest, however, that the spatial signatures in soil and vegetation properties associated with wildfire and forest harvest did not converge over short- or long-term scales. Wildfire resulted in distinctly different and more complex spatial signatures while forest harvest simplified patterns according to operational constraints (e.g., trails). Thus, the persistence of these spatial signatures associated with harvest over multiple decades is real. To ensure the resilience of these boreal black spruce forests and their continued benefits to society, the negative impacts of harvest on long-term structure and function should be minimized. One possible approach is the application of harvesting in such a way as to incorporate complexity in harvest patterns, to more closely emulate the natural disturbance of wildfire.

The present study not only provided a methodology to measure and compare spatial patterns after disturbance, but it also showed how we can use spatial patterns to understand dominant forces acting on ecosystems. Incorporation of particular spatial signatures into a priori hypotheses and the examination of their support using precise spatial analyses provided stronger inference for understanding processes structuring these ecological systems. This a priori approach linking processes and spatial patterns could be used in conjunction with other statistical tools, such as spectral analysis, wavelets, and local-pattern analyses, among others, and it may also be applied to spatial patterns generated by other processes or by temporal data patterns. This will enhance our understanding of the processes underlying pattern generation and shifts.

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