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A comparison of large-scale spatial vegetation patterns following clearcuts and fires in Ontario's boreal forests

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Abstract

The role of wildfires as the most significant source of disturbance in boreal forests has been equaled by clearcuts during the past five decades. Post-disturbance revegetation patterns are important because they have a direct influence on many ecological processes. However, the knowledge of post-disturbance changes in spatial patterns of forest cover is scarce, especially at large scales.

We examined spatial patterns of forest cover in a four decade series of post-fire and post-clearcut landscapes in boreal Canada. A suite of indices was used to quantify spatial patterns of post-disturbance vegetation, based on Landsat TM imagery, and edaphic conditions. Indices were grouped in terms of patch geometry, contagion and composition. We used a general linear model to compare the effects of disturbance type, time since disturbance, edaphic conditions, and their interactions on these indices.

Clearcuts produced more heterogeneous landscapes after disturbances in comparison to fires. Time since disturbance also had a significant effect on spatial patterns of vegetation: the older disturbances had more landcover types with higher interspersion. Edaphic conditions also significantly affected spatial patterns of vegetation. Landscapes with complex spatial patterns of edaphic conditions also had complex spatial patterns of vegetation.

Keywords: Boreal forests; Spatial vegetation patterns; Fire; Clearcut

1. Introduction

Large-scale spatial patterns of vegetation are related to important ecological processes (Forman and Godron, 1986). For example, vegetation types are variably susceptible to fire (e.g., Foster, 1982); therefore, the resulting spatial patterns caused by fires can be influenced by spatial vegetation patterns (Turner et al., 1989a; Turner and Romme, 1994). Spatial patterns of vegetation also affect wildlife. For example, core areas of specific landcover polygons may provide critical habitat for some species (Wallin et al., 1994). Biomass accumulation may also be influenced by spatial vegetation patterns (Band, 1993). Since ecological processes are influenced by spatial patterns of vegetation, studies of the factors which form these patterns are warranted.

The formation of large-scale spatial patterns of vegetation is influenced by associations between vegetation communities and edaphic factors (e.g., Yarie, 1983; Bonan and Shugart, 1989), and the spatial

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patterns of edaphic factors (Krummel et al., 1987; Mladenoff et al., 1993). Associations between edaphic factors and composition of boreal forest communities have been demonstrated (Jones et al., 1983; Pastor and Broschart, 1990; Sims et al., 1996). For example, hydric sites with organic soils are strongly associated with a dense conifer (mainly black spruce (*Picea mariana* [Mill.] BSP)) overstory, and jack pine (*Pinus banksiana* Lamb.) is associated with xeric sites and sandy soils (Sims et al., 1997). Edaphic factors in boreal regions are spatially heterogeneous (Sims and Baldwin, 1991); therefore, the spatial pattern of boreal vegetation is expected to reflect the heterogeneity of edaphic factors.

Disturbances periodically change the influence of edaphic factors on spatial patterns of vegetation in boreal regions. Crown fires are a major disturbance agent in boreal forests, and cause an abrupt change to existing spatial vegetation patterns by destroying overstory vegetation. In the aftermath of fire, landscapes are characterized by large patches devoid of overstory vegetation, intermixed with remnant patches of pre-fire vegetation (Heinselman, 1973; Eberhart and Woodard, 1987). Eventually, the disturbed landscape may become revegetated, influenced in part by edaphic factors. Because vegetation composition is temporally dynamic, spatial patterns of vegetation also change over time. In a model using a northern Wisconsin landscape, He and Mladenoff (1999) found that spatial patterns of vegetation changed over time, due to succession. In boreal forests, post-fire jack pine stands can eventually transform to black spruce stands (Frelich and Reich, 1995; Kenkel et al., 1998). Similarly, stands immediately revegetated with deciduous species after disturbance may convert to boreal mixedwoods as understory conifers mature (Bergeron and Dansereau, 1993).

Fire has historically been the dominant disturbance agent in boreal forests (Heinselman, 1973); however, during the past five decades, clearcuts have become another important source of disturbance in this biome. For example, the total clearcut area within the managed forest area of Ontario increased from 0.5 million hectares between 1951 and 1960 to over 2 million hectares between 1981 and 1990 (Perera and Baldwin, 2000). In contrast, the area burned within this region remained constant at approximately 0.5 million hectares per decade from 1951 to 1990 (Perera and Baldwin, 2000). The managed forest area of Ontario totals 45 million hectares, and is dominated by boreal forests (approximately 30 million hectares).

Displacement of fires by clearcuts in boreal forests has resulted in concern that ecosystem processes may be altered so that forests will become unsustainable (Kimmins, 1997). A strategy to address this concern is to modify harvesting practices so they emulate natural disturbances (Hunter, 1993; Cissel et al., 1999). Clearcuts may be thought to emulate fires because both types of disturbances result in the removal of overstory vegetation resulting in large contiguous patches. However, the knowledge needed to emulate fires using clearcuts is incomplete. For example, fires have greater variability in frequency, severity, and intensity than clearcuts (Hunter, 1993; DeLong and Tanner, 1996). Therefore, clearcut-dominated landscapes result in different vegetation mosaics than fire-dominated landscapes. Clearcuts can be made to more closely emulate fires by using spatial databases of historical fires as reference conditions for clearcut patterns (Hessburg et al., 1999). Using this approach, Gluck and Rempel (1996) found that heterogeneity among boreal landcover types was lower within post-clearcut polygons compared to post-fire polygons, in one of the few studies of spatial patterns of vegetation within post-clearcut and post-wildfire disturbances. However, their study compared only two individual disturbances, and did not account for edaphic factors or the dynamic nature of spatial patterns of vegetation.

Our goal was to compare large-scale spatial patterns of vegetation following clearcuts and fires across a large sub-region of the boreal biome, and to account for the effects of edaphic factors and time since disturbance on resulting spatial patterns of vegetation. We tested the hypothesis that spatial vegetation patterns within post-clearcut and post-fire disturbances are not different over the same chronosequence given similar edaphic conditions. For the purposes of this study, the term ‘‘landscape’’ was used to define the area within an individual disturbance.

2. Methods

2.1. Study area

The study area is approximately 30 million hectares in extent and falls within the managed boreal forest

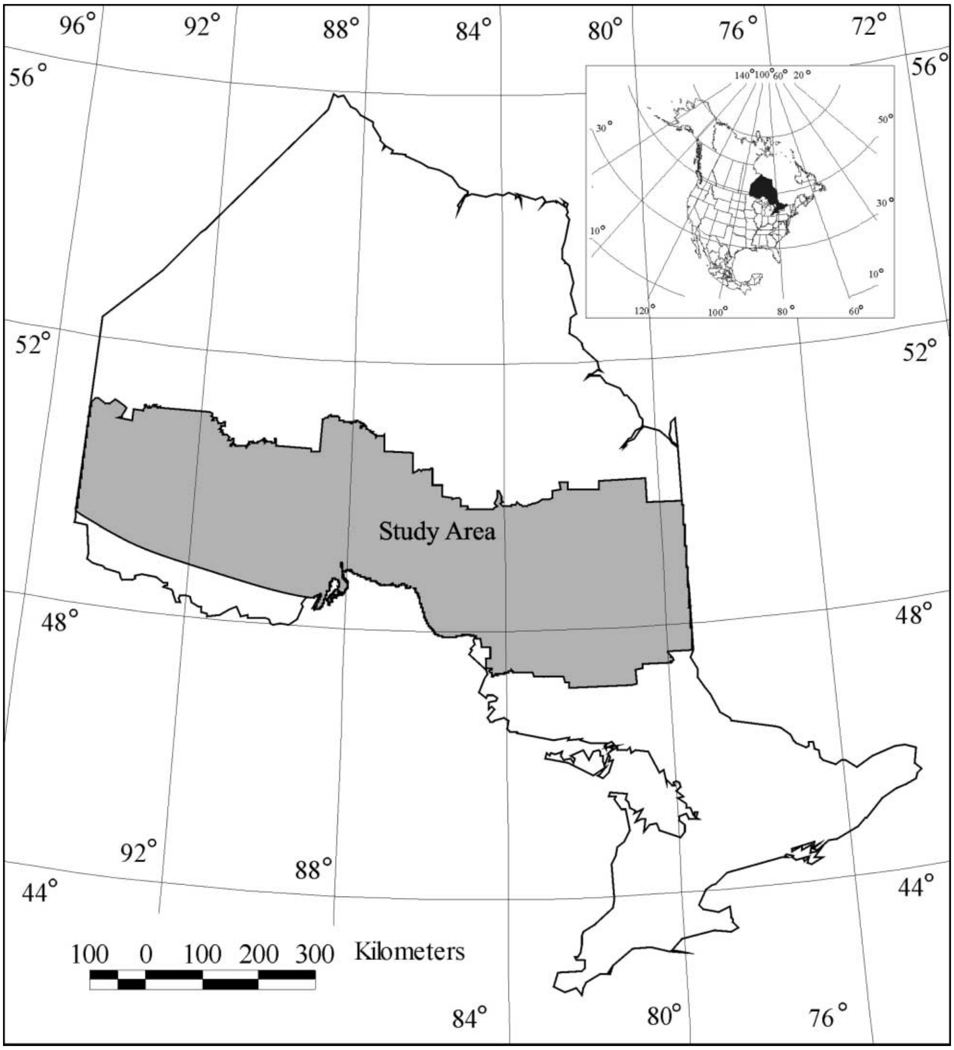

Fig. 1. Location of the study area in Ontario.

region of Ontario (Fig. 1). The climate of the study area is characterized by long cold winters, and cool to moderately warm summers. Mean annual temperature ranges from 4 °C in south to 0 °C in north (Rowe, 1972). Mean annual precipitation ranges from 61 cm in the northwest to 97 cm along the eastern shore of Lake Superior (Rowe, 1972).

Sims and Baldwin (1991) described the landforms of the boreal forests of Ontario. They indicated that influence of the most recent glacial period, and subsequent glacial retreat, was responsible for the spatial arrangement and types of edaphic conditions in the area. Glacial deposits, lacustrine deposits, and aeolian deposits dominate the landforms with limited occurrence of organic landforms. Soil textures include sand, gravel, loam, silt, and clay. Soil moisture regime (moisture availability during the growing season) ranges from dry to saturated and is influenced by landform and texture.

Dense forest cover types consist of conifer, deciduous and mixedwood forests (Spectranalysis, 1997). Black spruce and jack pine dominate coniferous stands, whereas trembling aspen (*Populus tremuloides* Michx.) and birch (*Betula papyrifera Marsh*) form deciduous stands. Mixedwood forests include combinations of the above as well as white spruce (Picea glauca (Moench) A.Voss) and balsam fir (Abies balsamea (L.) Mill.). Sparse coniferous, sparse deciduous, and poorly vegetated areas with shrub cover also occur within the study area (Spectranalysis, 1997).

2.2. Source data

2.2.1. Spatial/historical disturbance database

All previously mapped clearcut and fire disturbances larger than 200 ha within the study area, from the period 1951–1990, were sampled. Spatial boundaries of fires were derived from Landsat TM and MSS images (Fig. 2). Fires were dated based on photo interpretation, aerial reconnaissance, and ground truth records of the Ontario Ministry of Natural Resources (Perera et al., 1998). Only fires that destroyed the overstory were included. The clearcut database was created from Landsat TM images (Perera and Bae, 1996) as shown in Fig. 3. Clearcut boundaries and time of occurrence were checked with hardcopy maps produced from Landsat MSS images collected in 1977 and 1978 (Spectranalysis, 1993).

2.2.2. Vegetation/landcover data

A mosaic of classified Landsat TM images was used to derive the vegetation data layer (Spectranalysis, 1997). We aggregated the original landcover data to 1 ha grain size using the ARC/Info (ESRI, 1997) RESAMPLE command with the NEAREST NEIGHBOR option. Turner and Ruscher (1988) and Mladenoff et al. (1993) also used a 1 ha grain size to determine coarse scale vegetation patterns. Observation of the data revealed many small patches (1–10 ha). We used a majority filter (3×3), following Gluck and Rempel (1996), and then removed all patches less than 10 ha, using ARCView (ESRI, 1998) software. Gaps left by the patches were filled using the ARCView NIBBLE command, using surrounding landcover types as reference.

2.2.3. Edaphic factors

The attributes used to define edaphic factor polygons were soil parent material, soil texture, and soil moisture. A vector database of the Ontario land inventory (OMNR, 1977) was used to derive edaphic factor polygons. The Ontario land inventory data contained the following parent material/soil

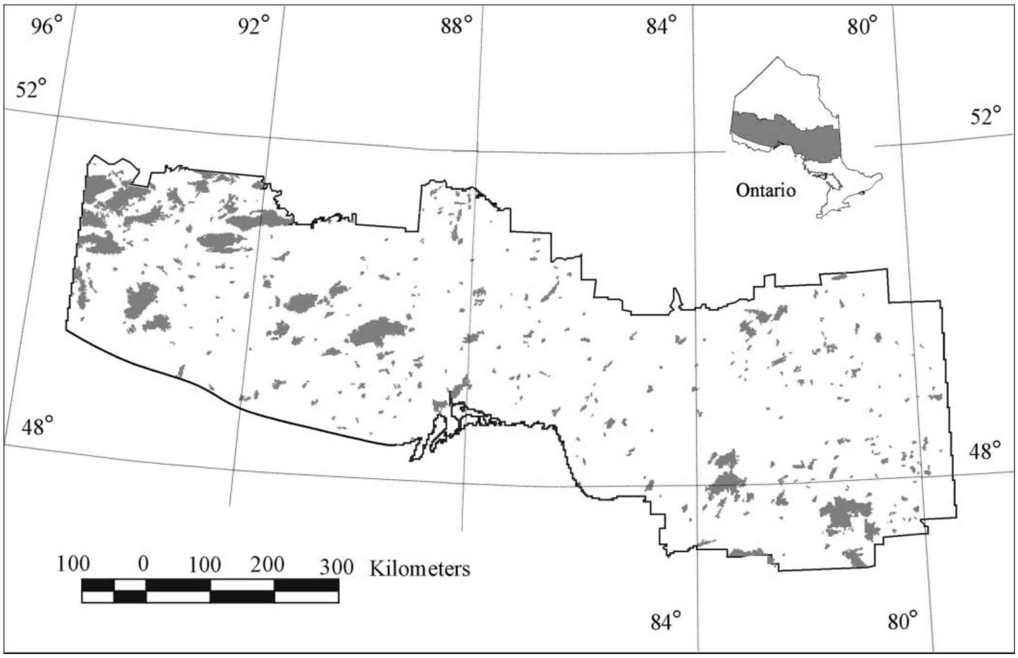

Fig. 2. Fires greater than 200 ha from 1951 to 1990 within the study area (Perera et al., 1998), $n = 386$.

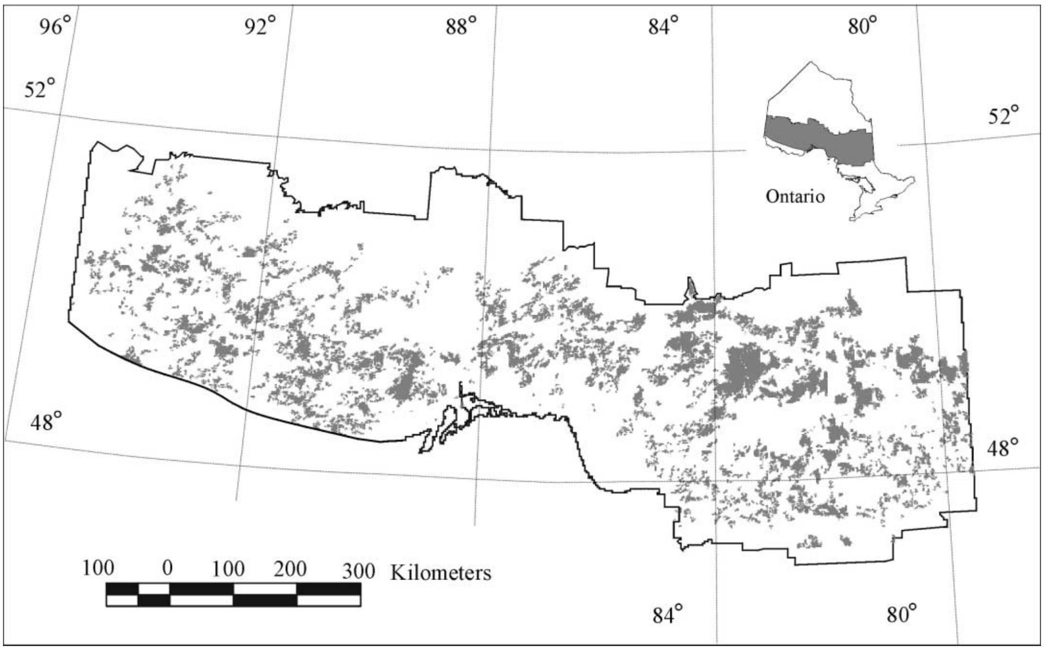

Fig. 3. Clearcuts greater than 200 ha from 1951 to 1990 within the study area (Perera and Bae, 1996), $n = 2432$.

texture classes: (1) bedrock, (2) ground moraine with undifferentiated soil texture, (3) ground moraine with silt or sandy till, (4) ground moraine with clayey till, (5) end moraine, (6) esker/kame complex, (7) outwash deposits, (8) lacustrine deposits with undifferentiated soil texture, (9) lacustrine deposits with sandy soils, (10) lacustrine deposits with clayey soils, and (11) aeolian deposits. Soil moisture (based on moisture availability to plants during the growing season) was classed as: (1) dry, (2) fresh, (3) moist, (4) wet, or (5) saturated. To create the edaphic factor polygons, the DISSOLVE command in ARC/Info was used. The layer was converted to raster format using the POLYGRID command in ARC/Info with a 1 ha grain size.

2.3. Indices of spatial patterns

We chose a suite of indices based on McGarigal and Marks (1995) to measure spatial patterns of edaphic factors and vegetation. Multiple indices were used as no single index capable of differentiating landscapes has been developed (Li and Reynolds, 1994). The indices were chosen based on their ability to collectively differentiate spatial patterns within landscapes (Li and Reynolds, 1994).

Four indices were selected to describe spatial patterns of edaphic factors. They were:

1. Area weighted mean edge contrast index (AWMECI) is a measure of the total boundary length between landcover types with emphasis given to large patches and high contrast between landcover types. Contrast weights are set by the user to emphasize differences between landcover types with large contrasts versus boundaries between landcover types with low contrast. We deemed that boundaries between wet and dry soils would have greater influence on spatial patterns of vegetation relative to boundaries between fresh and moist soils (Table 1). Therefore, the contrast weight between wet and dry soil polygons was set at the maximum value, while the contrast weight between fresh and moist soil polygons was set at the minimum value.

$$\mathrm{AWMECI} = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\frac{\sum_{k=1}^{m} p_{ijk} d_{ik}}{p_{ij}}\right)\frac{a_{ij}}{A}\right] \times 100 \tag{1}$$

Table 1
Contrast weights used to emphasize differences in soil moisture for edaphic factors. Moisture levels were taken from Ontario land inventory soil attributes (OMNR, 1977)

	Dry	Fresh	Moist	Wet	Saturated
Dry	0.0	0.5	0.5	1.0	1.0
Fresh		0.0	0.0	0.5	0.5
Moist			0.0	0.5	0.5
Wet				0.0	0.0
Saturated					0.0

where AWMECI is the area weighted mean edge contrast index, m the number of landcover types, n the number of patches of landcover type j, p the perimeter of patch ij adjacent to patch k, d the contrast weight between landcover types i and k, P the perimeter of patch ij, a the area of patch ij, and A the total landscape area.

2. Area weighted mean patch fractal dimension (AWMPFD) is a measure of patch shape complexity. The value for AWMPFD ranges between 1 and 2, where 1 represents landscapes with simple patch shapes and 2 represents landscapes with more complex patch shapes.

$$\text{AWMPFD} = \sum_{i=1}^{m}\sum_{j=1}^{n}\left[\left(\frac{2\ln(0.25p_{ij})}{\ln a_{ij}}\right)\left(\frac{a_{ij}}{A}\right)\right] \tag{2}$$

where AWMPFD is the area weighted mean patch fractal dimension index, m the number of landcover types, n the number of patches of landcover type i, p the perimeter of patch ij, a the area of patch ij, and A the total landscape area.

3. Contagion is a measure of interspersion and dispersion among cell types within a grid. In this application, cell types represent different types of landcover. High contagion indicates that cells of the same landcover types are clumped together.

$$\text{Contagion} = \left[1 + \frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[P_i\left(g_{ik}/\sum_{k=1}^{m}g_{ik}\right)\right]\left[\ln(P_i)\left(g_{ik}/\sum_{k=1}^{m}g_{ik}\right)\right]}{2\ln m}\right] \times 100 \tag{3}$$

where contagion is a measure of cell aggregation, m the number of landcover types, P the proportion of the landscape occupied by landcover type i, g the number of cell adjacencies between landcover types i and k, and m the number of landcover types in the landscape.

4. Evenness is the opposite of dominance; therefore, single landcover types do not dominate landscapes with high evenness, whereas landscapes with low evenness are dominated by at least one landcover type.

$$E = \frac{-\sum_{i=1}^{m}P_i \ln P_i}{\ln m} \tag{4}$$

E is Shannon's measure of evenness, m the number of landcover types, P the proportion of the landscape occupied by landcover type i, and m the total number of landcover types.

We chose seven indices to describe spatial patterns of vegetation in terms of patch geometry, aggregation of landcover types, and composition. Indices describing geometry were AWMPFD (Eq. (2)), mean patch size, and edge density. Aggregation was measured by contagion (Eq. (3)). Composition was measured by patch density, patch richness, and evenness (Eq. (4)).

2.4. Data preparation

A geographic information system (GIS) was used to extract data. The vegetation and edaphic databases were masked to disturbance polygons using ARC/Info (ESRI, 1997). This step created two GIS layers, one with vegetation within disturbed landscapes, and the other with edaphic factors within disturbed landscapes. Next, spatial pattern indices were calculated for vegetation and edaphic factors within each disturbance polygon using FRAGSTATS (McGarigal and Marks, 1995).

Disturbances were then clustered based on the spatial patterns of their underlying edaphic factors. Exploratory multivariate clustering using a hierarchical technique showed 4–5 possible groups. k-Means clustering ($k = 5$) was used to assign disturbances to final cluster memberships (Everitt, 1980). Fires and clearcuts were further sub-divided by decade of occurrence, where decade 1 (1981–1990) was the first decade since disturbance and decade 4 (1951–1960) was the fourth decade since disturbance.

2.5. Data analysis

A general linear model was used to test the effects of disturbance type, time since disturbance, and clustered edaphic factors on indices of spatial vegetation pattern. Disturbance size was used as a covariate because indices of landscape pattern are influenced by the size of landscapes, as was demonstrated by Turner et al. (1989b). Pairwise comparisons of treatment means were done in cases where significant differences due to main effects were found. The comparisons used estimated population marginal means of treatments, to account for the covariate, and were tested with a least significant difference test (Milliken and Johnson, 1984).

We calculated the amount of non-vegetated landcover type as a percent of total disturbance area for each period after disturbance. These values could help explain the anticipated differences of spatial patterns of vegetation due to time since disturbance. The non-vegetated landcover type comprised sparse forest, cutover, and burned landcover types because of difficulty in distinguishing these types with the Landsat TM imagery (Spectranalysis, 1992).

3. Results and discussion

A total of 2818 disturbance polygons were included in the analysis. The minimum and maximum number of replicates was 5 and 400, respectively. The number of fires varied over the four decades, and the number of clearcuts was highest in the first decade after disturbance, and decreased in each subsequent decade (Table 2). We defined edaphic clusters as having high contagion and complex patch shapes (cluster 1), high evenness (cluster 2), high evenness and edge contrast (cluster 3), high contagion and simple patch shapes (cluster 4), and non-descript (cluster 5) (Table 3).

Table 3
Cluster centers for disturbances based on spatial patterns of edaphic factors. Values represent the mean value for each index[a]

Pattern indices	Cluster[b]				
	1	2	3	4	5
AWMECI	0.01	0.08	*0.53*	0.01	0.15
AWMPFD	*0.62*	0.38	0.34	*0.28*	0.44
Evenness	0.03	*0.85*	*0.85*	0.02	0.49
Contagion	*0.97*	0.25	0.22	*0.98*	0.56

[a] Italicized values indicate the variables used to define clusters.

[b] $n\,(\text{cluster}\,1) = 590$; $n\,(\text{cluster}\,2) = 465$; $n\,(\text{cluster}\,3) = 370$; $n\,(\text{cluster}\,4) = 917$; $n\,(\text{cluster}\,5) = 476$.

There were no interactions among main effects; therefore, disturbance type, time since disturbance, and edaphic factors were interpreted independently (Table 4). The covariate, disturbance size, reduced error significantly ($p < 0.05$) for all response variables except edge density. Disturbance size did not affect edge density because it was calculated per unit area (m/100 ha). Of the main effects, disturbance type had a significant effect on mean patch size and patch density. Time since disturbance had a significant effect on all variables except AWMPFD. Edaphic clusters significantly affected AWMPFD and patch richness.

3.1. Effect of disturbance type

Mean patch size within fire disturbances (78.5 ha, S.E. ±2.4) was significantly larger than clearcuts

Table 2
Number of disturbances and mean disturbance size (ha) by time since disturbance, and disturbance type[a]

Time since disturbance (decades)	Number of disturbances		Mean disturbance size (ha)	
	Clearcut	Fire	Clearcut	Fire
D1	1312	91	1021 ± 41	4194 ± 1310
D2	616	139	1824 ± 108	3473 ± 1007
D3	389	61	2076 ± 148	4394 ± 1623
D4	115	95	3176 ± 487	3266 ± 553
Total	2432	386	1494 ± 50	3738 ± 556

[a] Values are means ± S.E.; $n = 2818$; D1: decade 1 (1981–1990); D2: decade 2 (1971–1980); D3: decade 3 (1961–1970); D4: decade 4 (1951–1960).

Table 4
Results of the ANOVA for indices of spatial vegetation patterns[a]

Source	Geometry				Contagion	Composition		
	d.f.	AWMPFD	Mean patch size	Edge density		Patch density	Patch richness	Evenness
Disturbance type	1	0.457	*0.003*	0.364	0.166	*<0.001*	0.187	0.069
Time since disturbance	3	0.053	*0.013*	*<0.001*	*<0.001*	*0.007*	*<0.001*	*<0.001*
Disturbance × time	3	0.971	0.382	0.530	0.240	0.997	0.344	0.091
Cluster (block)	4	*0.023*	0.915	0.344	0.323	0.345	*0.031*	0.440
Disturbance × cluster	4	0.181	0.295	0.149	0.132	0.350	0.256	0.077
Time × cluster	12	0.459	0.185	0.258	0.234	0.594	0.536	0.135
Disturbance × time × cluster	12	0.493	0.974	0.788	0.778	0.795	0.231	0.866
Covariate (disturbance size)	1	*<0.001*	*<0.001*	0.969	*<0.001*	*<0.001*	*<0.001*	*<0.001*

[a] Italicized values indicate a significant difference ($p < 0.05$); $n = 2818$.

(64.1 ha, S.E. ±1.1). Patch size was larger in fires compared to clearcuts in each decade after disturbance (Fig. 4a). This suggests that the effect of disturbance type on patch size and patch density can be observed for four decades after disturbance. Our results are contrary to the findings of Gluck and Rempel (1996). Patch size was expected to be smaller following fires because fires in boreal forests result in more remnant patches than clearcuts, as was found by DeLong and Tanner (1996). Two factors could have caused the contradiction between this study and that of Gluck and Rempel (1996). First, sample size was much larger in this study ($n = 2818$ versus $n = 2$). Second, there were two differences in ecological scale between the studies that may have affected the behavior of the spatial pattern indices. The first was minimum patch size. In this study, patches greater or equal to 10 ha were used, whereas Gluck and Rempel's study included smaller patches. Second, the number of landcover types in this study was 16 versus 14 and 9 used by Gluck and Rempel. In another study, changes in the number of landcover types were found to have a marked influence on indices of spatial pattern (Turner et al., 1989b). Despite the possibility that sample size and scale caused the differences between our results and those of Gluck and Rempel (1996), larger patches within post-fire disturbances compared to post-clearcut disturbances were unexpected.

We suggest that severity is higher in large fires compared to large clearcuts, which resulted in our observation of larger patches following fires relative to clearcuts. A measure of disturbance severity is the areal extent of the disturbance; therefore, a disturbance resulting in many remnant patches is less severe than a disturbance with few remnant patches. Based on this definition of severity, Eberhart and Woodard (1987) suggested that large fires were more severe than small fires after they observed that large fires had fewer remnants than small fires in boreal Alberta. They also suggested that large fires occurred during drought periods, and as a result, fewer potential remnant patches would escape disturbance. We made the assumption that only severe fires were included in our data, since small disturbances were not a part of this study. Since patch size was larger following fires compared to clearcuts, we suggest that large fires are more severe than large clearcuts.

Patch density within clearcuts (2.15 patches/100 ha, S.E. ±0.02) was higher than fires (1.61 patches/100 ha, S.E. ±0.04). Patch density was lower in fires compared to clearcuts in each decade after disturbance (Fig. 4c). This suggests that the effect of disturbance type on patch size and the number of patches can be observed for four decades after disturbance. Fewer patches within post-fire disturbances were surprising, because fires were expected to result in more remnant patches than clearcuts, as discussed above. Logically, disturbances with a greater number of remnant patches will have a higher patch density than disturbances with fewer remnant patches. However, patch density could be expected to have the inverse behavior to mean patch size if extent is kept constant (Hargis et al., 1998). In this study, extent was standardized by the covariate (disturbance size); therefore, the explanation for differences in mean patch size between fires and clearcuts could be extended to explain patch density.

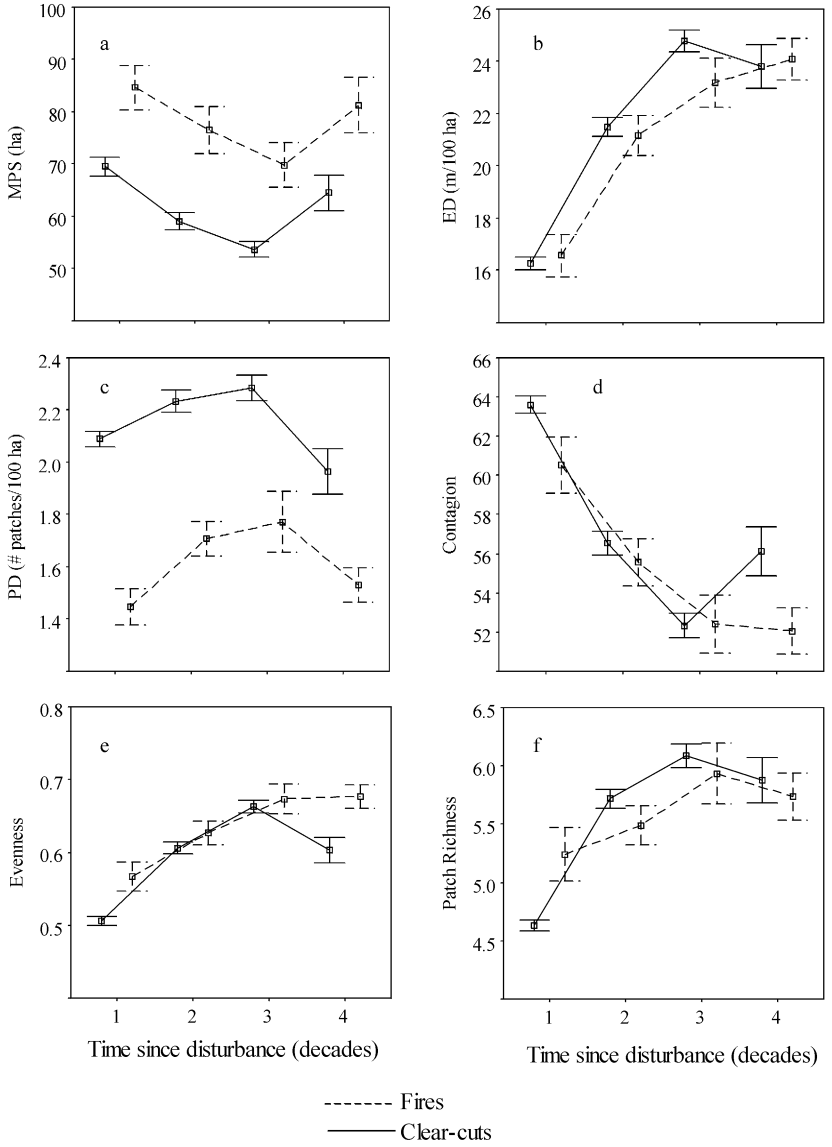

Fig. 4. Effect of time since disturbance on vegetation pattern indices. Error bars show means ± S.E.; $n = 2818$; MPS: mean patch size; ED: edge density; PD: patch density.

3.2. Effect of time since disturbance

Mean patch size and contagion were higher in decade 1 compared to older decades (Table 5, Fig. 4a and d), and edge density, patch density, evenness, and patch richness were lower in decade 1 compared to older decades (Table 5, Fig. 4b, c, e and f). Patch density was lower in decade 4 compared to decades 2 and 3 (Table 5). These results followed the expected trend where clearcuts and fires both cause abrupt change to patterns of spatial vegetation due to overstory destruction. The patterns of spatial vegetation were expected to change over time because of revegetation.

It appears that revegetation may occur by means of small patches. Homogeneous patches can be formed by emerging boreal species such as jack pine, black

Table 5
Pairwise comparisons of time since disturbance means (adjusted for covariate) for spatial vegetation pattern indices[a]

Comparisons between decades	Geometry		Contagion	Composition		
	Mean patch size (ha)	Edge density (m/100 ha)		Patch density (No. of patches/100 ha)	Patch richness	Evenness
D1	n.d.	16.58 ± 0.5	61.77 ± 0.9	n.d.	4.92 ± 0.1	0.54 ± <0.0
D2	n.d.	21.09 ± 0.5	56.61 ± 0.8	n.d.	5.66 ± 0.1	0.61 ± <0.0
D1	74.55 ± 3.2	16.58 ± 0.5	61.77 ± 0.9	1.81 ± 0.1	4.92 ± 0.1	0.54 ± <0.0
D3	58.74 ± 4.0	24.02 ± 0.7	51.98 ± 1.1	2.05 ± 0.1	5.92 ± 0.1	0.67 ± <0.0
D1	n.d.	16.58 ± 0.5	61.77 ± 0.9	n.d.	4.92 ± 0.1	0.54 ± <0.0
D4	n.d.	24.09 ± 0.7	54.51 ± 1.2	n.d.	5.84 ± 0.1	0.63 ± <0.0
D2	n.d.	21.09 ± 0.6	56.61 ± 0.8	n.d.	n.d.	0.61 ± <0.0
D3	n.d.	24.02 ± 0.7	51.98 ± 1.1	n.d.	n.d.	0.67 ± <0.0
D2	n.d.	n.d.	n.d.	1.97 ± 0.1	n.d.	n.d.
D4	n.d.	n.d.	n.d.	1.77 ± 0.1	n.d.	n.d.
D3	n.d.	n.d.	n.d.	2.05 ± 0.1	n.d.	n.d.
D4	n.d.	n.d.	n.d.	1.77 ± 0.1	n.d.	n.d.

[a] Values shown are significantly different ($p < 0.05$) between decades listed in the left column; values are means ± S.E.; n.d.: no difference; $n = 2818$; D1: decade 1 (1981–1990); D2: decade 2 (1971–1980); D3: decade 3 (1961–1970); D4: decade 4 (1951–1960).

spruce, and aspen (Sims et al., 1990). However, these patches may be influenced by fine-scale environmental factors (Vassov and Baker, 1988; Sims et al., 1990) that were not detected in our study. At fine scales, sites with optimal seedbeds and soil conditions are revegetated more quickly than poor sites (Frelich and Reich, 1995). For example, exposed mineral soil on well-drained loam provides more opportunities for seed germination than a site defined by shallow soils and rock outcrops (Sutherland and Foreman, 1995). We also found the proportion of non-vegetated landcover types was successively lower from decade 1 to 4 (79%, decade 1; 69%, decade 2; 44%, decade 3; 31%, decade 4). This may indicate that dense forest landcover types replaced non-vegetated landcover types. The above arguments may be used to explain the effect of time since disturbance on spatial vegetation pattern indices as follows:

Patch richness. Boreal forest species may not revegetate disturbed sites during the same period after disturbance (Ellice and Mattice, 1974; Galipeau et al., 1997). As a result, revegetation by different species at different times since disturbance could have resulted in more landcover types, or greater patch richness, in decades 2–4 compared to decade 1.

Patch density. Logically landscapes with few small patches will have lower patch density than landscapes with many small patches. Therefore, revegetation by means of small patches resulted in higher patch density in decade 2 compared to decade 1. Lower patch density in decade 4 compared to decades 2 and 3 may be due to displacement of non-vegetated landcover types by dense forest cover types as a result of revegetation.

Evenness. The number of landcover types and distribution of area among landcover types influence evenness (McGarigal and Marks, 1995). In decade 1, large patches of non-vegetated landcover types dominated disturbed landscapes, resulting in low evenness. Revegetation in older decades resulted in a greater number of landcover types, and by displacing non-vegetated landcover, more even distribution of area among landcover types.

Mean patch size. Logically, a landscape with few large patches, as in decade 1, will have a larger mean patch size than a landscape with numerous small patches as in decade 3. Since revegetation appears to have occurred in the form of small patches, it explains the difference in mean patch size.

Edge density. Patch density and patch richness may influence edge density (McGarigal and Marks, 1995) and both indices were lower in decade 1 compared to older disturbances. Consequently, the boundary length, or edge density, between landcover types was lower in decade 1 compared to older disturbances. Patch shape could also have affected edge density. However, AWMPFD was used to measure patch shape and was not affected by time since disturbance; therefore, it appears that edge density was not influenced by patch shape.

Contagion. High contagion values in decade 1 compared to decade 3 indicate that cells with similar landcover types were clumped together in recent disturbances and dispersed in older decades. Contagion is sensitive to the number of landcover types (McGarigal and Marks, 1995) and may be influenced by patch size (Hargis et al., 1998). It appears that contagion was sensitive to changes in spatial vegetation pattern; however, it may be influenced by more than one component of landscape heterogeneity.

In this study, individual disturbances were not repeatedly observed over four decades. However, based on our observation of many disturbances representing four decades since disturbance, we propose the following trend for spatial patterns of vegetation (Fig. 5):

1. Recent disturbances have large, contagious patches and few landcover types due to the destruction of overstory vegetation.
2. Over time, spatial patterns of vegetation change to smaller, less contagious patches, and more landcover types due to revegetation.

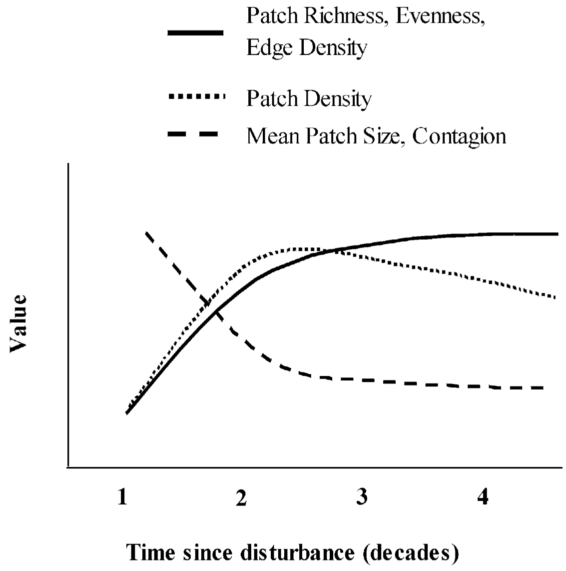

Fig. 5. Proposed trends for spatial patterns of vegetation following disturbance.

Some spatial vegetation pattern indices followed similar trends at different times since disturbance (Fig. 4). Similar trends among indices may occur because of the influence of one factor on several indices. For example, evenness, contagion, and edge density are all affected by the number of landcover types. The use of indices may seem redundant, but each can provide unique information about spatial vegetation patterns. For example, evenness is a measure of the areal distribution among landcover types, whereas contagion is a measure of interspersion and dispersion of landcover types.

3.3. *Effect of edaphic clusters*

AWMPFD for cluster 1 (complex patch shapes) was significantly higher than all other clusters (Table 6). For cluster 4 (simple patch shapes), AWMPFD was significantly lower than all other clusters (Table 6). This may suggest that patch shape of edaphic factors had a strong effect on the shape of vegetation patches as concluded by Krummel et al. (1987) after studying deciduous forest patch shapes in the floodplain forests in the southern United States.

Patch richness was significantly lower in cluster 4 (simple patch shapes) than all other clusters (Table 6). An explanation for the effect of edaphic factors on patch richness was not apparent. However, using a finer scale than this study, Nichols et al. (1998) found

Table 6
Results of pairwise comparisons for edaphic cluster means (adjusted for covariate) for indices of spatial vegetation pattern[a]

Cluster	AWMPFD	Patch richness
C1[b]	*1.105 ± 1.058E−3*	5.34 ± 0.08
C2	1.102 ± 1.402E−3	5.79 ± 0.10
C3	1.102 ± 1.448E−3	5.84 ± 0.11
C4[c]	*1.084 ± 7.090E−4*	*4.38 ± 0.05*
C5	1.103 ± 1.286E−3	5.79 ± 0.10

[a] C1: cluster 1 (high contagion and complex patch shapes), C2: cluster 2 (high evenness), C3: cluster 3 (high evenness and edge contrast), C4: cluster 4 (high contagion and simple patch shapes), C5: cluster 5 (non-descript); $n = 2818$.

[b] C1 > C2, C3, C4, C5 for AWMPFD.

[c] C4 < C1, C2, C3, C5 for AWMPFD and patch richness.

significant relationships between plant species richness and spatial variation in slope, aspect, and soil drainage in the eastern United States. Their study suggests that fine-scale edaphic factors not observed in this study might have influenced patch richness.

4. Conclusions

Spatial patterns of vegetation were different following clearcuts and fires; therefore, we rejected the null hypothesis that there is no difference between post-fire and post-clearcut spatial patterns of vegetation. Post-fire landscapes had larger and less numerous patches than post-clearcut landscapes. It appears that clearcuts may result in greater heterogeneity among landcover types relative to fires. To explain the influence of disturbance type on spatial patterns of vegetation, we suggest that severity of large fires is higher than severity of large clearcuts; consequently, fires result in larger and fewer patches than clearcuts.

Time since disturbance had a significant effect on spatial patterns of vegetation. Recent disturbances had fewer and more aggregated landcover types, and larger and less numerous patches compared to older disturbances. Spatial patterns of vegetation within recent disturbances appear to reflect the sudden destruction of overstory vegetation, which was expected to cause large patches. In older disturbances, the spatial patterns of vegetation seem to be a result of revegetation in the form of small patches. Revegetation by multiple types of forest cover at different times since disturbance may explain why the number of landcover types was higher in older disturbances compared to one-decade-old disturbances.

Edaphic factors were expected to influence spatial vegetation patterns because of their association with vegetation communities. Disturbances defined by complex edaphic factor patch shapes had complex vegetation patch shapes, and disturbances with simple edaphic factor patch shapes had simple vegetation patch shapes, suggesting that edaphic factors may affect vegetation patch shape. We suggest that the spatial position of edaphic factor polygons influences the spatial position of landcover types.

Our results reveal specific dynamics of large-scale spatial patterns of vegetation following clearcuts and fire. Spatial patterns of vegetation following both types of disturbance appear to change from large, contagious patches to smaller more evenly dispersed patches. However, clearcuts may result in greater heterogeneity among landcover types. Differences between post-clearcut and post-fire landscapes, and mechanisms of spatial vegetation pattern dynamics present specific goals for future research.

The results of this study generated the following four hypotheses for future research:

1. The severity of large fires results in larger and less numerous patches than are created by clearcuts.
2. The trend for spatial patterns of vegetation is for numerous, large, contagious patches within recent disturbances to few, small, less contagious patches within older disturbances.
3. Spatial patterns of vegetation within older disturbances are due to revegetation in the form of small patches.
4. The geometric and spatial placement of edaphic factor patches influences the geometric and spatial placement of vegetation patches.

This study is one of the few to date to examine the dynamics and mechanisms of large-scale spatial vegetation patterns within the boreal biome. More studies at large ecological scales, such as those suggested above, are needed to better understand the effects of harvesting and fires on post-disturbance vegetation dynamics.

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