A Comparison of Spatial Vegetation Patterns Following Clearcuts and Fires in Ontario's Boreal Forests

by

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A Graduate Thesis Submitted

In Partial Fulfillment of the Requirements

for the Degree of Master of Science in Forestry

Faculty of Forestry and the Forest Environment

Lakehead University

June 2000

ABSTRACT

Schroeder, D.H. 2000. A Comparison of Spatial Vegetation Patterns Following Clearcuts and Fires in Ontario's Boreal Forests. M.Sc.F. Thesis. Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario, Canada. 82 pp.

Key words: boreal forests, spatial vegetation patterns, fire, clearcut

The goal of this study was to compare spatial vegetation patterns, based on Landsat TM data, within post-clearcut and post-fire disturbances. Landscapes disturbed during the four decades prior to the collection date of the Landsat data were used for comparison. The disturbed landscapes were clustered according to their spatial edaphic factor patterns. A suite of indices representing patch geometry, contagion, and composition were used to describe spatial vegetation and edaphic factor patterns. A general linear model was used to compare the effects of disturbance type, time since disturbance, and edaphic factors (clusters) on seven indices of spatial vegetation patterns.

Patch size and patch density differed following clearcuts and fires. It appears that clearcuts may result in greater spatial heterogeneity among landcover types compared to fires. I propose that fires were more severe than clearcuts; thus, creating larger and fewer patches. Time since disturbance had the greatest effect on spatial vegetation patterns. One decade old disturbances had larger patches, higher contagion and fewer landcover types than older disturbances. I suggest that spatial vegetation patterns reflected the destruction of overstory vegetation in one decade old disturbances, and revegetation in the form of small patches in older disturbances. It appears that the effects of disturbance on spatial vegetation patterns are temporary. Edaphic factor patch shapes may influence the shape of vegetation patches.

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ACKNOWLEDGEMENTS

I wish to thank my advisor Dr. Ajith Perera, (Program Leader, Forest Landscape Ecology, Ontario Forest Research Institute (OFRI)), for providing an excellent learning experience as well as funding through a grant from the Ontario Ministry of Natural Resources. I also thank my committee, Dr. David Euler (Dean, Faculty of Forestry and the Forest Environment, Lakehead University) and Dr. Rob Rempel (Research Scientist, Centre for Northern Forest Ecosystem Research), and Dr. Tom Crow (Professor of Ecosystem Management, University of Michigan) for being the external examiner. Dr. Euler's help with many adminstrative details is also appreciated.

Many thanks to my colleagues at the Forest Landscape Ecology Program at OFRI for their camaraderie, and technical and editorial help. They are: Tarmo Remmel, Dennis Yemshanov, Kevin Weaver, Zbigniew Brodzik, Frank Schnekenburger, and Dave Baldwin. I also thank everyone else at OFRI who helped me with my thesis, especially Lisa Buse for editorial feedback.

Finally I wish to thank my family and friends for support throughout this time, and most importantly thanks to Dawn Clelland.

CHAPTER 1 – INTRODUCTION

Boreal forests have historically been subjected to frequent, severe wild fires. However, clearcutting presently disturbs more area than fire in Ontario's managed forest regions (Ward and Tithecott 1993). As a result, there is concern that clearcutting may alter ecosystem processes in such a way that forests become unsustainable (Booth *et al.* 1993; Bondrup 1995; Kimmins 1997). In the absence of complete knowledge of ecosystems, emulating natural disturbance patterns is advocated as a strategy for sustainable forest management (Cissel *et al.* 1999; Hunter 1999). The effects of natural disturbances on ecological phenomena, such as spatial patterns of disturbances, can serve as reference conditions to compare the effects of human activities (Hunter 1993; Hessburg *et al.* 1999).

Ecosystems can be described as having three basic attributes: composition, function, and structure. Composition, deals with the inventory of species, including genetic diversity. For example, broad climatic factors of the boreal biome favour vegetation tolerant of cold, dry conditions (Bonan and Shugart 1989). At smaller scales, boreal species are adapted to local climatic and edaphic conditions (Parker *et al.* 1996; Sims *et al.* 1996). Function deals with ecological processes such as disturbance and nutrient cycling. For example, the effect of climate change on disturbance frequency is an important area of research (Bonan *et al.* 1990; Bergeron and Flannigan 1995; Thompson *et al.* 1998). The third attribute, structure, focuses on the physical organization of ecosystems. For example, Van Wagner (1978) described a hypothetical age class distribution of forests based on estimates of fire return intervals. The structure of forests can also be quantified by measuring the spatial pattern of forest patches, where attributes of patches are defined by the observer, for example landcover types of forests and agricultural.

There have been only few studies of spatial vegetation patterns in Ontario's boreal forests; an example is Gluck and Rempel's (1996) work comparing landscape structure following fire and clearcuts. However, there is evidence that spatial vegetation patterns can affect ecological processes in boreal forests at coarse scales. For example, because vegetation types are variably susceptible to fire, patterns of fires can be influenced by spatial vegetation patterns (Turner *et al.* 1989a; Turner and Romme 1994). Wildlife habitat is also affected by spatial vegetation patterns. Bush (1999) found that pileated woodpecker (*Dryocopus pileatus*) presence/absence was significantly correlated to core area. Spatial vegetation patterns can also influence biomass accumulation (Band 1993). Our current understanding of interactions among landscape patterns and ecological processes is incomplete (Baskent and Jordan 1995; Schumaker 1996). Additional research toward understanding spatial vegetation patterns and processes that affect their formation is warranted.

Hierarchy theory can provide guidance toward studying ecological processes (O'Neill *et al.* 1986), such as those influencing spatial vegetation patterns in Ontario's boreal forests. Following hierarchy theory, ecological processes can be observed at different levels where higher levels act as constraints on lower levels (O'Neill *et al.* 1986), and lower levels can provide mechanistic explanations for trends observed at higher levels. Higher levels are typically observed at coarse scales and change over longer periods than lower levels (Allen and Hoekstra 1992). A top-down approach, using observations at coarse scales, can determine general trends in ecological processes (Walters and Holling 1990). Since there is little knowledge of spatial vegetation patterns in Ontario's boreal forests, coarse scale studies are warranted.

The formation of coarse scale spatial vegetation patterns in the boreal forests of Ontario is influenced by several edaphic factors including soil parent material (Thompson 2000). Associations between edaphic factors and composition of boreal forest communities have been demonstrated in boreal forests of the northern United States (Pastor and Broschart 1990). The spatial patterns of these edaphic factors are heterogeneous across the boreal biome (Sims and Baldwin 1991). For example, according to Sims *et al.* (1997) , hydric sites with organic soils are strongly associated with black spruce (*Picea mariana* [Mill.] BSP), whereas xeric sites and sandy soils are associated with jack pine (*Pinus banksiana* Lamb.).

Disturbances can alter spatial vegetation patterns by destroying overstory vegetation. Landscapes in the aftermath of fire are characterized by large patches devoid of overstory vegetation, intermixed with remnant patches (Heinselman 1973; Eberhart and Woodard 1987). Eventually the disturbed landscape becomes revegetated, influenced in part by edaphic factors. For example, in the boreal forest, dry, sandy patches subject to frequent fire typically support large patches of even-aged jack pine (Frelich and Reich 1995). Mesic sites with rich soils support a variety of boreal tree species (Sims *et al.* 1997) and, compared to dry, sandy patches, may have more heterogeneous spatial vegetation patterns. Clearcuts are also devoid of overstory vegetation in the immediate aftermath of disturbance; however, remnant patches are less frequent compared to fires

(DeLong and Tanner 1996). A general pattern for vegetation recovery following clearcuts appears to be a shift from coniferous forest cover to mixedwood and deciduous forest cover (e.g., Carleton 2000). Also, Perera and Baldwin (2000) found that the frequency of occurrence of fires and clearcuts differed among surficial geology types. Therefore, spatial vegetation patterns may differ between fires and clearcuts due to differences in surficial geology.

In addition to edaphic factors, time since disturbance can also affect spatial vegetation patterns. For example, Turner *et al.* (1997) found that revegetation was patchy in the immediate aftermath of fires in Yellowstone Park. In boreal forests, poor sites may not be revegetated for several decades following fire (Frelich and Reich 1995). Over longer periods, pioneer species common in the immediate aftermath of fires may be replaced by shade tolerant species (Heinselman 1973; Bergeron and Dubuc 1989; Kenkel *et al.* 1998). However, there is little knowledge of how spatial patterns of vegetation in boreal forests change through time (e.g., Hall *et al.* 1991).

The goal of this research is to compare the relative effects of clearcuts and fires on subsequent spatial vegetation patterns in boreal Ontario, under similar edaphic factors, and at multiple time periods after disturbance. For the purpose of this work, the term "landscape" is defined as the area bounded by a clearcut or fire disturbance. For this comparison, I chose coarse-scale, classified satellite imagery of Ontario's managed boreal forests, covering a four decade disturbance history, to compare vegetation recovery following clearcuts and fires. The null hypothesis tested is that there are no differences between spatial vegetation patterns within post-clearcut and post-fire disturbances over the same chronosequence given similar edaphic conditions.

CHAPTER 2 – LITERATURE REVIEW

2.1 BOREAL FOREST DISTURBANCES

Fires and clearcuts are two major agents of disturbance in Ontario (Ward and Tithecott 1993). The area burned within the managed forest area of Ontario was approximately 0.5 million ha per decade from 1951 to 1990 (Perera and Baldwin 2000). In contrast the total clearcut area within the same area increased from 0.5 million ha during 1951 to 1960 to over 2 million ha during 1981 to 1990 (Perera and Baldwin 2000). Clearcutting is the primary method of harvesting used in Ontario's boreal forests (Wedeles *et al.* 1995).

2.2 VEGETATION RESPONSE TO DISTURBANCE

2.2.1 Post-Fire Vegetation Dynamics

Interaction among vegetation, disturbance frequency and intensity, and heterogeneous site factors has resulted in a variety of possible successional pathways in boreal forests (Day and Harvey 1981; Zoladeski and Maycock 1990). These pathways are largely based on species ability to re-occupy a site after disturbance. Common post-fire pioneer species of boreal forests are birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), jack pine, and black spruce (Foster and King 1986; Sims *et al.* 1990). Recruitment of most species occurs within 30 to 50 years following disturbance (Bergeron and Dubuc 1989; Cogbill 1985). Frequent fires, common in boreal forests, often reset successional pathways before long-term compositional changes can take place (Zoladeski and Maycock 1990). However, in the absence of fire, successional pathways are predictable. Bergeron and Dubuc (1989) found that boreal forests in northwestern Québec could converge towards balsam fir (*Abies balsamea* [L.] Mill.) and cedar (*Thuja occidentalis* L.) on mesic sites, and black spruce and cedar on xeric sites. Dominance of balsam fir is possible in northwestern Ontario (Zoladeski and Maycock 1990). Frelich and Reich (1995) used a chronosequence to study succession of boreal species in northern Minnesota. They found that young post-fire stands (< 40 years) were characterized by aspen and jack pine monocultures, which eventually changed into mixed stands of black spruce, birch, cedar and balsam fir. Frelich and Reich (1995) asserted that species recruitment could occur after even 50 years, contrary to Bergeron and Dubuc (1989). A simplified hypothesis describing common forest successional pathways in northwestern Ontario is shown in Figure 1.

2.2.2 Post-Clearcut Vegetation Dynamics

Knowledge of vegetation dynamics following clearcuts is largely limited to initial vegetation composition after disturbance because clearcuts have a shorter history in Ontario than fires. For example, clearcuts did not occur until the early twentieth century in northeastern Ontario (Carleton and MacLellan 1994). In some conifer-dominated stands natural revegetation following clearcuts appears to shift to pure-deciduous and deciduous dominated mixedwood stands (Jeglum 1983; Harvey and Bergeron 1989; Carleton and MacLellan 1994). Twolan-Strutt and Welsh (1997) concluded that post-clearcut stands in boreal mixedwoods had little conifer regeneration. Moore (1973) found that in northeastern Ontario, black spruce revegetated lowland black spruce sites and balsam fir replaced black spruce on mixedwood sites after harvesting. Jack pine may regenerate naturally after clearcutting if the logging method leaves cones in the cutover and creates exposed mineral soil (OMNR 1986). Trembling aspen replaces

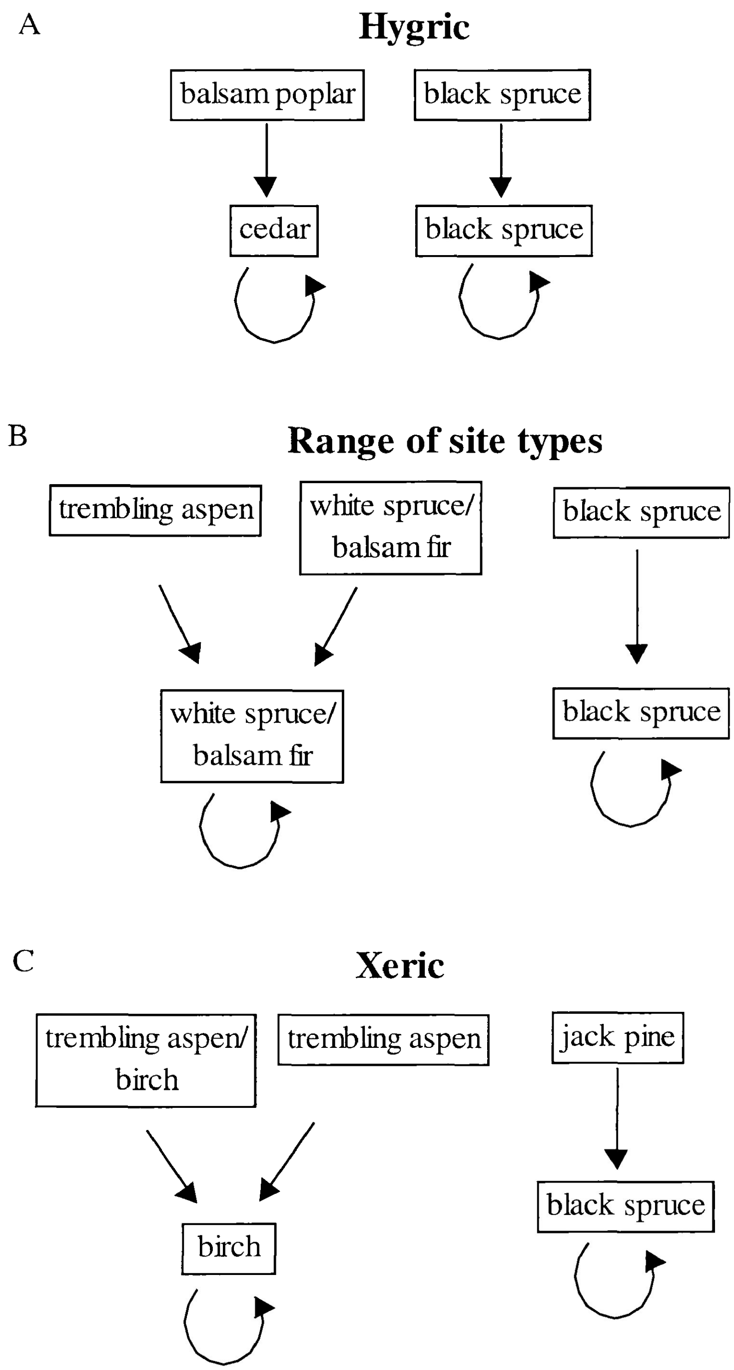

Figure 1. Potential boreal forest succession pathways occurring on different site types: A) Hygric sites B) Range of site types C) Xeric sites (Kenkel *et al.* 1998). Botanical names are: balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* [Moench] Voss).

itself after clearcutting, however the logging method and season of harvest may affect revegetation density (Davidson *et al.* 1988; Bates *et al.* 1993).

Artificial regeneration of clearcuts is common in Ontario. For example, in 1994 over 100 000 ha were seeded or planted, primarily with coniferous species (NRC 1996). However, coniferous plantations may change to mixedwood or deciduous forest cover types if naturally regenerated deciduous species are not eliminated through silvicultural treatments (Morris *et al.* 1988; Wedeles *et al.* 1995).

There have been few comparisons of post-disturbance vegetation composition between clearcuts and fires in boreal forests. In one study, Noble *et al.* (1977) compared the composition of jack pine – black spruce forests following logging and fire. They found that post-harvest sites with and without slash burning were more similar to undisturbed sites that post-wildfire sites. Logging followed by rock raking also resulted in compositional differences compared to post-wildfire sites. In another study, Carleton and MacLellan (1994) found that clearcut black spruce stands had a significantly greater deciduous component compared to post-fire spruce stands.

2.3 VEGETATION – ENVIRONMENT RELATIONSHIPS

Environmental factors and vegetation interact at different scales and can be organized into different levels, following hierarchy theory (O'Neill *et al.* 1986). As such, factors at higher levels act as constraints on lower levels. Ohmann and Spies (1998) found that coarse climatic differences across Oregon were the primary controls on regional species gradients. Tree species of the boreal biome are favoured by adaptation to a cold, dry climate, and nutritionally poor soils (Bonan and Shugart 1989). One factor may influence vegetation at different hierarchical levels. Using temperature as an example, species adapted to cold winters are favoured in the boreal biome; however, at a micro scale, a late frost may favour one species over another.

At smaller scales, heterogeneous edaphic factors within biomes may influence the composition of vegetation communities. Nichols *et al.* (1998) studied the influence of edaphic factors on vegetation in the northeastern United States, and found that plant species richness was highly related to geomorphological heterogeneity. Yarie (1983) found that in the Alaskan interior, black spruce dominated low productivity sites and mixedwoods occupied more productive sites. In northwestern Ontario, boreal forest communities have been classified based on occurrence of soil moisture and texture gradients (Sims *et al.* 1996; Kenkel *et al.* 1998). In a similar study in northeastern Ontario, Jones *et al.* (1983) integrated 23 vegetation types and 14 soil types using multivariate ordination. They created 14 groups, where each group was identified by a range of mature forest cover types, and associated soil texture and moisture conditions. Since edaphic factors are spatially heterogeneous (Sims and Baldwin 1991), the spatial patterns of these soils are expected to influence spatial patterns of vegetation.

Fine-scale edaphic factors may also affect establishment of individual species. For example, Galipeau *et al.* (1997) found that white spruce establishment after fires was more successful on sandy and loamy soils compared to heavy clays. Conversely, balsam fir establishment was not affected by soil texture (Harvey and Bergeron 1989). Sims *et al.* (1990) provided a summary of microsite requirements for boreal tree species establishment. Other studies have also shown correlation between moisture/texture soil classes and overstory vegetation. Pastor and Broschart (1990) found that edaphic factors influenced the spatial pattern of northern hardwood and conifer forests of the Great Lakes region in the United States. Leduc *et al.* (1992) showed that hardwood species in southern Québec were strongly associated with edaphic factors.

2.4 SPATIAL PATTERNS

2.4.1 Interaction Between Vegetation and Fire Dispersal

Spatial vegetation patterns can affect spatial characteristics of fire. Turner *et al.* (1989a) modelled disturbance propagation as a factor of landscape patterns and disturbance frequency and intensity. In a simulation, Roberts (1996) found complex interactions between fire return interval and environmental heterogeneity on indices of spatial vegetation patterns.

Fire dispersal is influenced by weather conditions, fuel availability, forest age class, and topography (Turner and Romme 1994). Fuel availability in boreal forests has been classified according to different vegetation communities, based on composition and age class (Alexander *et al.* 1984). The spatial arrangement of vegetation communities can affect the spread of fire due to differences in fuel availability across landscapes (Stocks 1974; Turner and Romme 1994). A study in Labrador by Foster (1982) found that deciduous forests dominated by birch could act as fire breaks, whereas surrounding conifer stands were more susceptible to fire. He also found that many fires in open lichen woodlands did not expand into mature lowland black spruce – balsam fir stands.

2.4.2 Quantifying Spatial Patterns

Many indices can be used to describe landscape patterns for categorical spatial data (McGarigal and Marks 1995; Haines-Young and Chopping 1996). Landscape pattern indices can be indicators of functional or structural heterogeneity of landscape patterns (Li and Reynolds 1995). Indices of functional heterogeneity are linked to specific ecological processes. For example, Wallin *et al.* (1994) considered edge density and patch core area to be important measures of functional heterogeneity. Indices of structural heterogeneity are able to differentiate landscapes based on their spatial patterns. Li and Reynolds (1994) listed five components of landscape heterogeneity needed to differentiate landscape patterns: number of patch types, proportion of landscape occupied by each patch type, spatial arrangement of patches, patch shape, and contrast between neighbouring patches. This study will emphasize will structural heterogeneity.

A suite of indices is useful to describe landscape structure, as no single index capable of characterizing all landscape features has been developed (Li and Reynolds 1994; O'Neill *et al.* 1988). Riitters *et al.* (1995) advocated that only five indices are needed to describe most variation in landscape patterns: average patch perimeter to area ratio, Shannon contagion, average patch area (normalized to the area of a square with the same perimeter), patch perimeter-area scaling, and the number of attribute classes. Sachs *et al.* (1998) used these indices to describe changes in forest structure over time. Mladenoff *et al.* (1993) compared disturbed and undisturbed landscapes using landscape diversity and patch attributes including type, area, number, size class distribution, fractal dimension, and importance value. Gluck and Rempel (1996) compared patch composition, patch size, patch shape, and interspersion between clearcut and burned landscapes. Techniques using fractal dimension can differentiate anthropogenically and naturally influenced landscapes (Krummel *et al.* 1987; Elkie 1998).

2.4.3 Spatial Patterns and Ecological Scale

Spatial scale refers to extent and grain size (smallest resolvable unit) of spatial data (Turner 1990). Indices used to describe spatial patterns are sensitive to scale (Turner *et al.* 1989b; Benson and MacKenzie 1995; O'Neill *et al.* 1996). Baker (1993) demonstrated the effects of scale on landscape indices in a study of spatial patterns following disturbance in Minnesota. He found that landscape indices responded differently over time depending on grain size. Turner *et al.* (1989b) found that landscape indices did not change linearly with scale. They cautioned against direct comparison of landscape indices calculated at different extents or grain sizes.

2.4.4 Vegetation Patterns and Disturbance

Components of disturbance that influence subsequent revegetation are intensity, frequency, and shape of disturbances (Turner *et al.* 1997). Over long temporal scales, frequent, high intensity fires can result in less heterogeneous spatial vegetation patterns compared to intermittent, low intensity fires (Frelich and Reich 1995). At fine spatial scales, disturbance shape influences seed distribution (Johnson 1992); however, the effect of seed rain on subsequent spatial patterns may not be a factor in determining coarse scale spatial patterns (Spies and Turner 1999). DeLong and Tanner (1996) asserted that spatial patterns (disturbance shape and size) of fires are more variable than clearcuts in boreal forests of British Columbia. Fire size may also be a factor in determining the shape of disturbed landscapes. Eberhart and Woodard (1987) found that disturbance shape complexity increased with fire size in Alberta's boreal forests.

Disturbance type can affect the formation of subsequent spatial vegetation patterns within a disturbed landscape. Mladenoff *et al.* (1993) compared the spatial patterns of an unaltered old-growth landscape to an anthropogenically disturbed landscape occurring on similar edaphic factors in the Great Lakes region of the United States. Their study showed that mean patch size was lower, and the complexity of patch shapes was simpler in the disturbed landscape. Gluck and Rempel (1996) compared spatial patterns within a clearcut landscape and a burned landscape at multiple scales in northwestern Ontario. They found that patches within the clearcut landscape were larger, more irregular in shape, and had a larger core area in comparison with post-fire patches.

Spatial vegetation patterns may change due to vegetation dynamics in the absence of disturbance. Modelling change in a northern Wisconsin landscape, He and Mladenoff (1999) found that patch structure changed over time due to succession. In boreal forests, jack pine stands can eventually transform to black spruce stands (Frelich and Reich 1995). Therefore, a jack pine stand adjacent to a black spruce stand may eventually merge. Similarly, stands which are revegetated with deciduous species immediately after disturbance may convert to mixedwoods as understory conifers mature (Bergeron and Dansereau 1993).

CHAPTER 3 – METHODS

3.1 STUDY AREA

The study area is approximately 30 million hectares in extent and falls within the managed boreal forest region of Ontario (Figure 2). 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 the 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 study area. They indicate that 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. Organic landforms have limited occurrence, and are more common north of the study area. Soil textures include sand, gravel, loam, silt, and clay. Soil moisture regimes (moisture availability during the growing season) range from dry to saturated, and are influenced by landform and texture.

Forest cover types are described by Sims *et al.* (1997) and consist of conifer, deciduous and mixedwood forests. Coniferous stands may be formed by black spruce and jack pine, and deciduous stands by trembling aspen and birch. Mixedwood forests include combinations of the above as well as white spruce and balsam fir. Mixedwood forests are found across a variety of soil types in the boreal region. Black spruce stands are

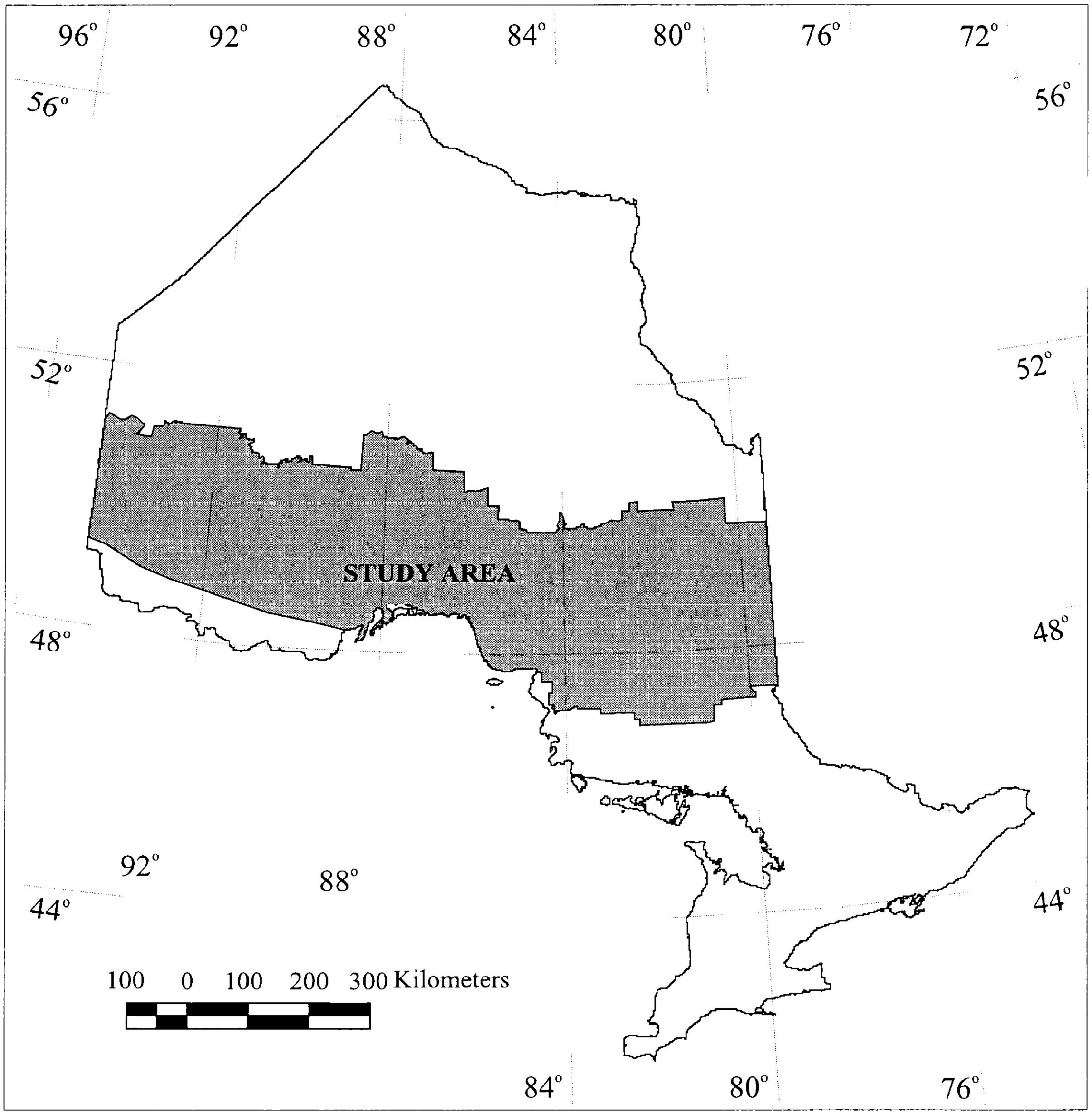

Figure 2. Location of the study area in Ontario.

associated with nutrient poor sites with wet, organic soils. Jack pine stands are also associated with nutrient poor sites; however, they are common on dry, sandy soils.

3.2 STUDY DESIGN

The premise of this study is that spatial vegetation patterns are a function of disturbance type, time since disturbance, and environmental factors. The following conceptual model was used to meet the research goal:

$$V = f\,(d, t, e)$$

Where:

V = spatial vegetation pattern

d = disturbance type

t = time since disturbance

e = spatial edaphic factor pattern

The dependent variable, V, was defined by a suite of seven indices used to describe patch geometry, contagion, and patch composition (Section 2.4.2) of landcover data within disturbances. The variable disturbance type was either a clearcut or fire, and disturbance perimeters were used to define landscape boundaries. The second variable was the time of disturbance, in decades, prior to the landcover data collection date. The third variable accounted for the effect of edaphic factors on spatial vegetation patterns. A suite of indices (Section 2.4.2) was used to define spatial edaphic factor patterns for each disturbance. Disturbances were then grouped according to their multivariate indices of edaphic factors.

3.3 SOURCE DATA

3.3.1 Edaphic Factors

Ontario Land Inventory data (OMNR 1977) was used to derive spatial edaphic factors. Defining attributes of edaphic factor polygons were soil parent material/texture and soil moisture. The following parent material/soil texture classes were used: 1) bedrock, 2) ground moraine with undifferentiated 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) classes were: 1) dry, 2) fresh, 3) moist, 4) wet, and 5) saturated. To create the edaphic factor polygons, the DISSOLVE command in ARC/Info (ESRI 1997) geographic information systems (GIS) software was used. The layer was converted to raster format using the ARC/Info POLYGRID command with a 1-ha grain size.

3.3.2 Vegetation/Landcover Data

A mosaic of classified Landsat Thematic Mapper (TM) images was used to derive the vegetation data layer (Spectranalysis 1997), shown in Figure 3. Spectranalysis used Landsat TM bands 2, 3, 4, 5, and 7 (green, red, and three infrared bands) to perform a supervised classification based on a maximum likelihood algorithm. Images were then manually edited to reduce errors due to landcover classes with similar reflectance values. For example, cutovers and agricultural land had similar signals but could be differentiated by adjacent landcover types such as dense forest or roads associated with

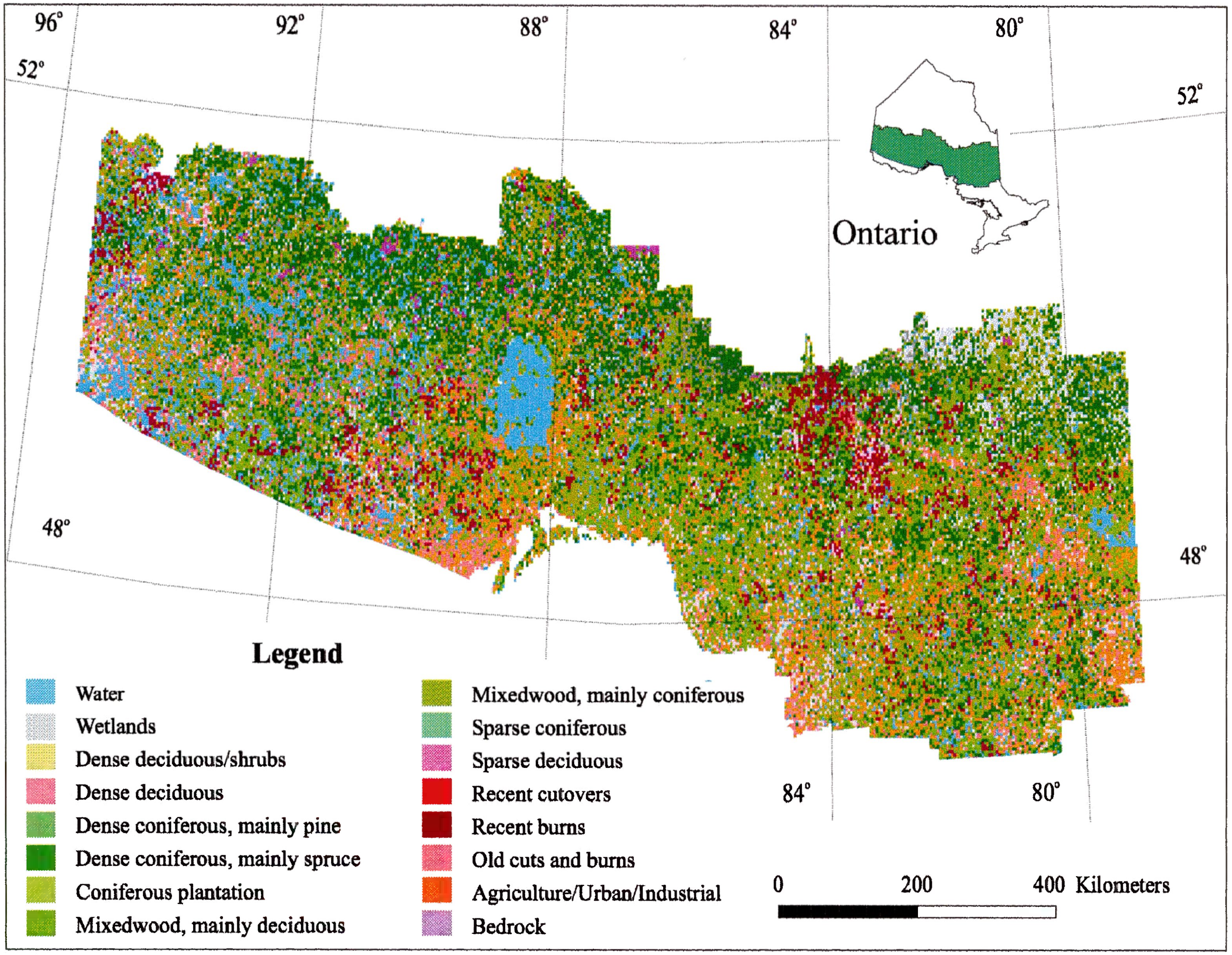

Figure 3. Landcover types as derived from Landsat TM data. Grain size = 1 ha (after Spectranalysis 1997).

settlements. Spectranalysis did not determine classification accuracy; however, comparisons with aerial photos were done. They showed good agreement (>75 %) for classes with distinct boundaries, but were weak for classes with subtle boundary differences (≈ 50%). Weak agreement does not indicate incorrect classification, but indicates differences between air photo and Landsat TM images.

I aggregated the original landcover data to 1-ha grain size using the ARC/Info 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). I used a majority filter (3 × 3), as was done by 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, by using surrounding landcover types as reference.

3.3.3 Spatial/Historical Disturbance Database

All known clearcuts and fires, larger than 200 ha, that occurred between 1951 and 1990 were sampled. Figures 4 and 5 show the clearcuts (Perera and Bae 1996) and fires (Perera *et al.* 1998). The clearcut database was created from Landsat TM images and a database derived from hardcopy maps (Landsat Multi-spectral scanner (MSS) collected in 1977 and 1978) of historical clearcuts (Spectranalysis 1993). Fire boundaries were derived from Landsat TM and MSS images (Perera *et al.* 1998), and dates were based on photo interpretation, aerial reconnaissance, and ground truth records of the Ontario Ministry of Natural Resources. Only those fires that destroyed the overstory were used.

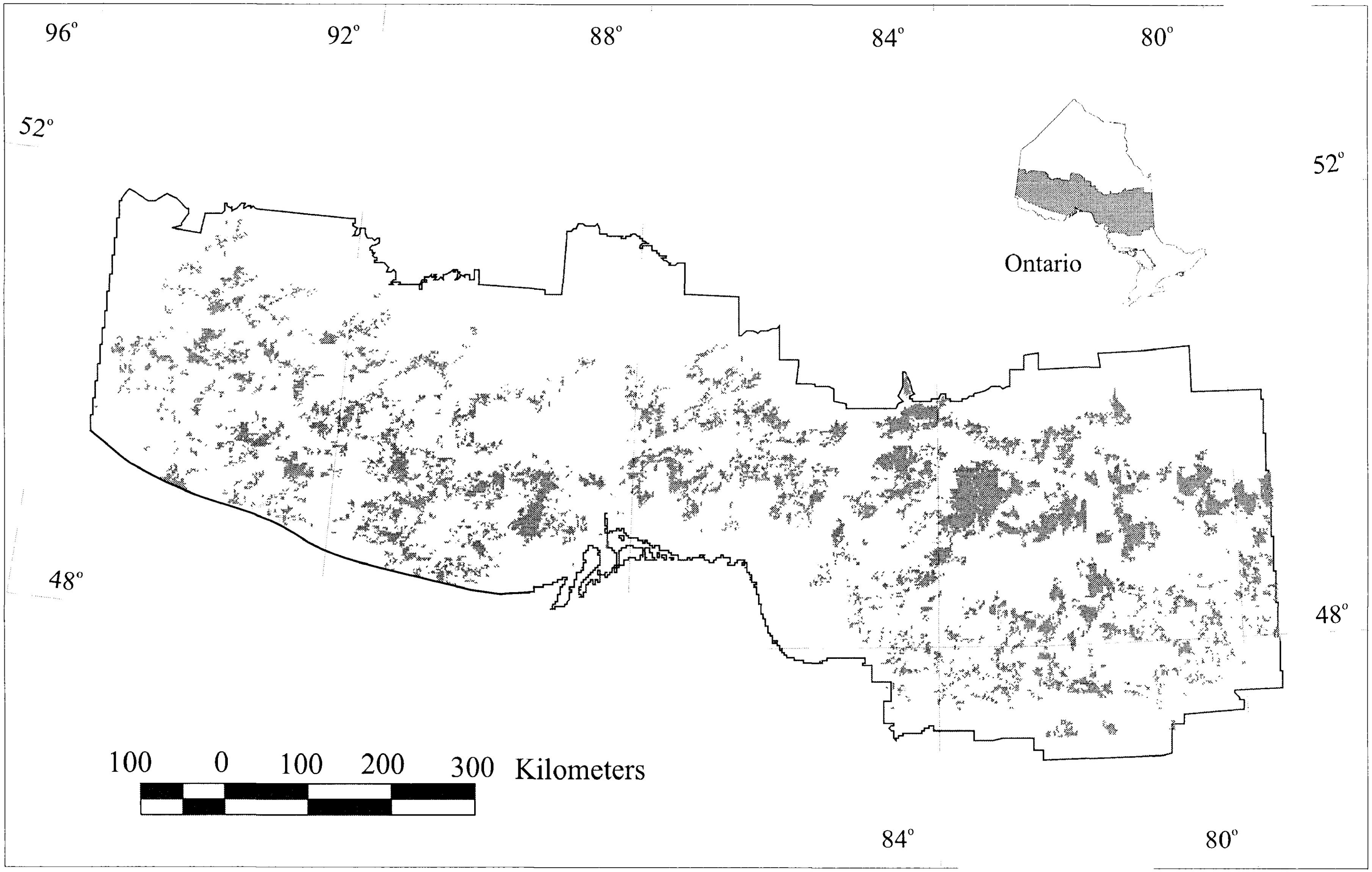

Figure 4. Clearcuts greater than 200 ha between 1951 and 1990 within the study area (Perera and Bae 1996). $n = 2432$.

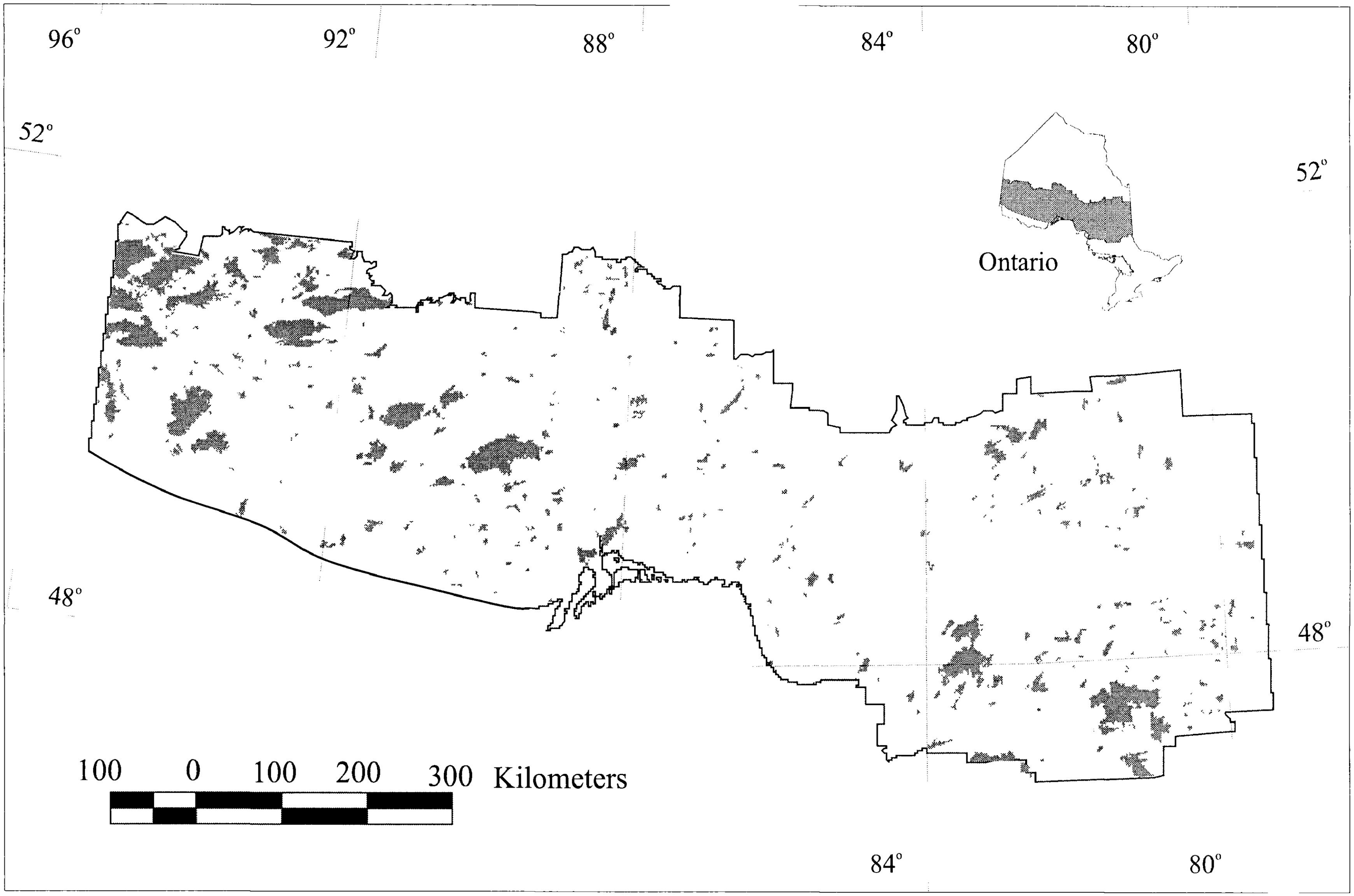

Figure 5. Fires greater than 200 ha between 1951 and 1990 within the study area (Perera *et al.* 1998). $n = 386$.

3.4 INDICES OF SPATIAL PATTERNS

Spatial pattern indices representing measures of patch geometry, contagion, and composition were chosen to describe vegetation and environmental factor patterns. The vegetation and edaphic factor databases were in raster format. Attributes for pixels (the smallest resolvable elements in a raster database) were based on landcover type for the vegetation data, and soil moisture and texture for the edaphic factor data. Patches within raster databases were defined by clumps of adjacent pixels with the same attribute value.

The following descriptions of spatial pattern indices were taken from McGarigal and Marks (1995). Measures of patch geometry include *area weighted mean edge contrast index* (AWMECI), *area weighted mean patch fractal dimension* (AWMPFD), *mean patch size*, and *edge density.* Edge contrast estimates patch dissimilarity using assigned contrast weights. For example, two adjacent forest types may have low contrast weights compared to adjacent forest and non-forest patches. AWMPFD is a measure of the complexity of patch shapes. Simple shapes such as a circle or square have low values. Higher values indicate that patch shapes are more complex. *Edge density* measures total edge of all patch types, standardized to the number of patches per 100 ha.

Contagion measures pixel adjacency. High values indicate that similar pixels are highly aggregated. Contagion is considered a measure of pixel dispersion and interspersion (McGarigal and Marks 1995).

Composition indices measure the number of landcover types and their relative abundance. For example, *patch density* (number of patches per 100 ha), *patch richness* (number of landcover types), and *evenness* are measures of composition. *Evenness* is a measure of areal distribution among patches, a high value indicates area is evenly distributed among patch types. Shannon's measure of evenness was used in this study (McGarigal and Marks 1995).

Four indices were chosen to differentiate edaphic factor patterns, based on Li and Reynolds (1994). They were AWMECI, AWMPFD, contagion, and evenness. I chose contrast weights, needed to calculate AWMECI, to emphasize differences in soil moisture among edaphic factors (Table 1).

I chose seven indices to describe vegetation patterns in terms of patch geometry, contagion, and composition. Indices describing geometry were AWMPFD, mean patch size, and edge density. Composition was measured by patch density, patch richness, and evenness.

3.5 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. I wrote a script using ARCView's Avenue language to automate this procedure. The script extracted edaphic factors or vegetation associated with each disturbance

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

individually from the masked GIS layers, and saved them as a temporary ARCView theme. The temporary theme was converted to an image, and then a subroutine from LEAP II (Perera *et al.* 1997) was used to convert the ARCView-generated image from 32-bit to 8-bit format for use in FRAGSTATS (McGarigal and Marks 1995). The script then launched FRAGSTATS, which calculated the spatial pattern indices.

Disturbances were then clustered according to the spatial patterns of their edaphic factors. Exploratory multivariate clustering using a hierarchical technique showed four to five possible groups. K-means clustering (k = 5) was used to assign disturbances to final cluster memberships (Everitt 1980). To organize the data for statistical analysis the clusters were sub-divided according to time since disturbance (by decade) and disturbance type. Decade one refers to disturbances which occurred in the 10 years prior to the landcover data collection date (i.e., 1981 to 1990). Disturbances in decade 2 occurred between 1971 and 1980, in decade 3 between 1961 and 1970, and in decade 4 between 1951 and 1960.

3.6 DATA ANALYSIS

A randomized complete block design was used to test the general hypotheses. Response variables were the indices of spatial vegetation patterns (area weighted mean patch fractal dimension, mean patch size, edge density, contagion, patch density, patch richness, and evenness). Edaphic factor clusters were considered as blocks due to their ability to differentiate disturbances based on their spatial patterns. Size of disturbance polygons was significantly ($p < 0.05$) correlated with the indices of spatial vegetation patterns; therefore, disturbance size was used as a covariate in the analysis. The covariate adjusted the response variables so that the effect of disturbance size was eliminated. Adjustment of response variables was based on linear regression, and the procedure was integrated into the general linear model. Appendix I lists the correlations between disturbance size and the response variables. Analysis was run using SPSS (1997) software.

The following general linear model was used for statistical analysis:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \delta_k + (\alpha\delta)_{ik} + (\beta\delta)_{jk} + (\alpha\beta\delta)_{ijk} + \gamma(x_{ijk} - \bar{x}_{..}) + \in_{ijkl}$$

where:

Y_{ijkl}	=	Response variable (7 vegetation pattern indices)
α_i	=	Disturbance type, i = 1–2 (fixed effect)
β_j	=	Time since disturbance in decades, j = 1–4 (fixed effect)
$(\alpha\beta)_{ij}$	=	Time – disturbance type interaction (fixed effects)
δ_k	=	Clusters (blocks), k = 1–5 (random effect)
$(\alpha\delta)_{ik}$	=	Disturbance type – block interaction (random effect)
$(\beta\delta)_{jk}$	=	Time since disturbance – block interaction (random effect)
$(\alpha\beta\delta)_{ijk}$	=	Disturbance type – time – block interaction (random effect)
γ	=	Linear regression coefficient indicating dependence of the response variable on covariate *x*
x_{ijk}	=	Covariate (disturbance area)
$\in_{ijkl}$	=	Experimental error

Specific hypotheses for each response variable were:

<u>Disturbance type</u>
Ho_1: $\alpha_1 = \alpha_2 = 0$
Ha_1: at least one $\alpha_i \neq 0$

<u>Time since disturbance</u>
Ho_2: $\beta_1 = \beta_2 = \beta_3 = \beta_4 = 0$
Ha_2: at least one $\beta_j \neq 0$

Clusters
Ho$_3$: $\delta_1 = \delta_2 = \delta_3 = \delta_4 = \delta_5 = 0$
Ha$_3$: at least one $\delta_k \neq 0$

The interaction effects test the hypotheses:

Disturbance type and time since disturbance
Ho$_4$: $(\alpha\beta)_{ij} = 0$ for all i,j
Ha$_4$: at least one $(\alpha\beta)_{ij} \neq 0$

Disturbance type and clusters
Ho$_5$: $(\alpha\delta)_{ik} = 0$ for all i,k
Ha$_5$: at least one $(\alpha\beta)_{ik} \neq 0$

Time since disturbance and clusters
Ho$_6$: $(\beta\delta)_{jk} = 0$ for all j,k
Ha$_6$: at least one $(\beta\delta)_{jk} \neq 0$

Disturbance type, time since disturbance, and clusters
Ho$_7$: $(\alpha\beta\delta)_{ijk} = 0$ for all i,j,k
Ha$_7$: at least one $(\alpha\beta\delta)_{ijk} \neq 0$

The covariate tests the hypothesis:

Ho$_8$: $\gamma = 0$
Ha$_8$: $\gamma \neq 0$

Pairwise comparisons of treatment means were done for all significant main effects and corresponding response variables. The comparisons used the estimated population marginal means, to account for the covariate, and were tested using a Least Significant Differences (Milliken and Johnson 1984).

The amount of non-vegetated landcover type as a percent of total disturbance area was also calculated. Spectranalysis (1992) reported difficulty in distinguishing sparse forest from recent and old disturbances. I combined all sparse forest, cutover, and burned patch types for this calculation. This data was used to illustrate the proportion of non-vegetated and partially vegetated landcover types within disturbances at different times after disturbance.

CHAPTER 4 – RESULTS

A total of 2818 disturbance polygons were included in the analysis. Table 2 shows the number of disturbances by clusters, time since disturbance, and disturbance type. 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 decreased from decade 1 to decade 4. I defined clusters (Tables 2 and 3) 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). Distribution of disturbances among clusters varied for both disturbance types, with one cluster having substantially more disturbances. The total number of clearcuts and fires for each cluster, as a percentage of the total number of clearcuts and fires respectively, was similar in clusters 2, 3, and 5.

Table 4 lists mean disturbance size by time since disturbance, disturbance type, and clusters. Disturbance size and standard error of the mean were lowest in cluster 4 for all of the time periods and disturbance types. Mean fire size and standard error were higher than clearcuts for all time periods. Mean fire size varied over the four decades while clearcut size decreased.

Table 2. Number of disturbance polygons by edaphic factors, time since disturbance, and disturbance type. Clusters represent disturbances with different spatial patterns of edaphic factors. Values in parentheses represent the number of disturbances for each cluster as a percentage of the total number of disturbances for each disturbance type.

Cluster	Time Since Disturbance (Decades) 1		2		3		4		Totals	
	Clearcut	Fire	Clearcut	Fire	Clearcut	Fire	Clearcut	Fire	Clearcut	Fire
1	347	18	116	16	65	11	12	5	540 (22%)	50 (13%)
2	218	17	103	20	69	7	14	17	404 (17%)	61 (16%)
3	143	8	97	15	62	10	20	15	322 (13%)	48 (12%)
4	400	37	181	67	122	25	44	41	747 (31%)	170 (44%)
5	204	11	119	21	71	8	25	17	419 (17%)	57 (15%)
Total	1312	91	616	139	389	61	115	95	2432	386

Table 3. Cluster centres for disturbances based on spatial patterns of edaphic factors. Values represent the mean value for each index. Bold values indicate the variables used to define clusters.

Pattern indices	Cluster				
	1	2	3	4	5
Area Weighted Mean Edge Contrast Index	0.01	0.08	**0.53**	0.01	0.15
Area Weighted Mean Patch Fractal Dimension	**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

Table 4. Mean disturbance size (ha) by edaphic factors, time since disturbance, and disturbance type. Clusters represent disturbances with different spatial patterns of edaphic factors. Data are mean ± SE. Sample size ranged from 5 to 400.

	Time Since Disturbance (Decades)							
	1		2		3		4	
Cluster	Clearcut	Fire	Clearcut	Fire	Clearcut	Fire	Clearcut	Fire
1	1012 ± 57	5049 ± 3080	1825 ± 216	3281 ± 1278	2216 ± 433	7404 ± 1824	3678 ± 1671	4939 ± 1540
2	1331 ± 118	7052 ± 5092	1914 ± 262	6650 ± 3076	2836 ± 437	17572 ± 13302	3699 ± 1124	5529 ± 1789
3	1356 ± 200	1300 ± 282	2648 ± 303	2462 ± 812	2795 ± 422	3203 ± 1064	5693 ± 1783	4859 ± 2371
4	510 ± 27	948 ± 130	682 ± 58	658 ± 61	835 ± 69	841 ± 144	1345 ± 502	1779 ± 456
5	1457 ± 131	10781 ± 5184	2800 ± 345	10279 ±5 692	2714 ± 351	1315 ± 301	3853 ± 944	2690 ± 462
Total	1028 ± 41	4194 ± 1310	1825 ± 108	3473 ± 1007	2076 ± 148	4394 ± 1623	3176 ± 487	3266 ± 533

4.1 RESULTS OF ANOVA

The ANOVA results are shown in Table 5. As there were no interactions among main effects, each main effect could be interpreted independently. Type of disturbance had a significant effect on mean patch size and patch density. Mean patch size within fire disturbances (78.5 ha, S.E. ± 2.4) was larger than within clearcuts (64.1 ha, S.E. ± 1.1). Patch density within clearcuts (2.15 patches/100 ha, S.E. ± 0.02) was larger than within fires (1.61 patches/100 ha, S.E. ± 0.04). Time since disturbance had a significant effect on all variables except area weighted mean patch fractal dimension (AWMPFD). Clusters based on spatial patterns of edaphic factors had a significant effect on AWMPFD and patch richness. There were no apparent trends among patch geometry, contagion, and composition variables. The covariate (disturbance size) was effective in reducing error for all response variables except edge density. Complete ANOVA results and pairwise comparisons of treatment means are presented in Appendix II.

4.2 EFFECT OF TIME SINCE DISTURBANCE ON RESPONSE VARIABLES

Pairwise comparisons of time since disturbance means for spatial vegetation patterns indicate significant differences between decades 1 (<10 years since disturbance) and 3 (21 to 30 years since disturbance) (Table 6). The response variables, with the exception of mean patch size and patch density, were also significantly different between decades 1 and 2 (11 to 20 years since disturbance). Only patch density was significantly different between decades 3 and 4 (31 to 40 years since disturbance). Three indices, edge density, contagion and evenness were significantly different between decade 1 and all other decades, and between decades 2 and 3. Figure 6 illustrates differences in response variables due to the influence of time since disturbance. Contagion and mean

Table 5. Results of the ANOVA for indices of spatial vegetation patterns.

Source		Geometry			Contagion	Composition		
	df	AWMPFD	MPS	ED	Contagion	PD	PR	Evenness
disturbance type	1	ns	***s***	ns	ns	***s***	ns	ns
time since disturbance	3	ns	***s***	***s***	***s***	***s***	***s***	***s***
disturbance × time	3	ns	ns	ns	ns	ns	ns	ns
cluster (block)	4	***s***	ns	ns	ns	ns	***s***	ns
disturbance × cluster	4	ns	ns	ns	ns	ns	ns	ns
time × cluster	12	ns	ns	ns	ns	ns	ns	ns
disturbance × time × cluster	12	ns	ns	ns	ns	ns	ns	ns
covariate (disturbance size)	1	***s***	***s***	ns	***s***	***s***	***s***	***s***

Notes: s = significant difference ($p < 0.05$); ns = no significant difference; $n = 2818$; AWMPFD = area weighted mean patch fractal dimension; MPS = mean patch size; ED = edge density; PD = patch density; PR = patch richness.

Table 6. Results of pairwise comparisons of time since disturbance means for spatial vegetation pattern indices.

Comparisons between decades	Geometry		Contagion	Composition		
	MPS	ED	Contagion	PD	PR	Evenness
D1 – D2	ns	*s*	*s*	ns	*s*	*s*
D1 – D3	*s*	*s*	*s*	*s*	*s*	*s*
D1 – D4	ns	*s*	*s*	ns	*s*	*s*
D2 – D3	ns	*s*	*s*	ns	ns	*s*
D2 – D4	ns	ns	ns	*s*	ns	ns
D3 – D4	ns	ns	ns	*s*	ns	ns

Notes: s = significant difference ($p < 0.05$); ns = no significant difference; $n = 2818$; D1 = decade 1 (< 10 years since disturbance); D2 = decade 2 (11 to 20 years since disturbance); D3 = decade 3 (21 to 30 years since disturbance); D4 = decade 4 (31 to 40 years since disturbance); MPS = mean patch size; ED = edge density; PD = patch density; PR = patch richness.

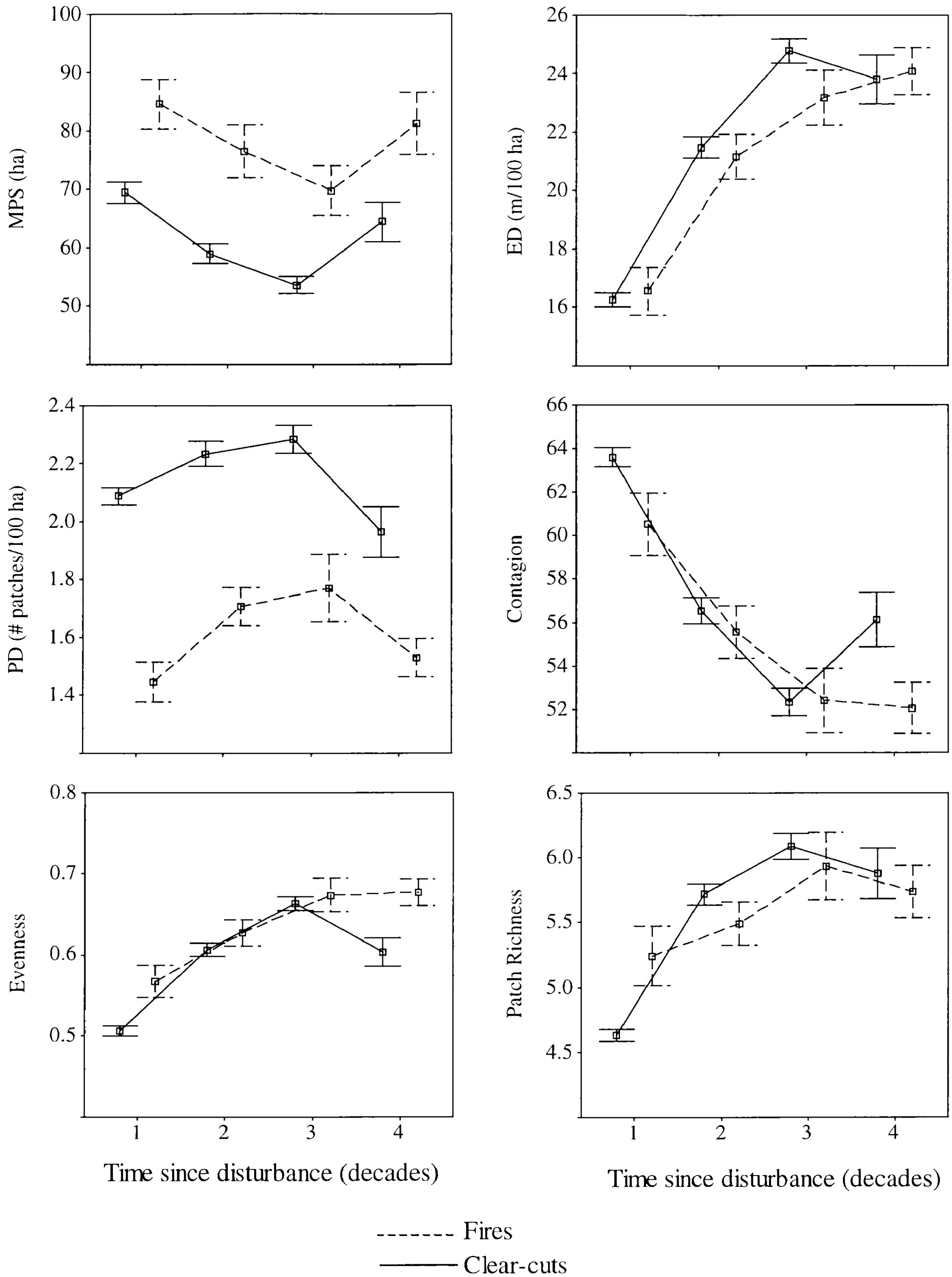

Figure 6. Effect of time since disturbance on vegetation pattern indices. Error bars show means ± SE; $n = 2818$; MPS = mean patch size; ED = edge density; PD = patch density.

patch size values were higher in decade 1 compared to decade 3. Conversely edge density, patch density, patch richness, and evenness were lower in decade 1 compared to decade 3. Patch density was lower in decade 4 compared to decade 3.

4.3 EFFECT OF CLUSTERS ON RESPONSE VARIABLES

Pairwise comparisons of cluster means showed a significant influence by cluster 4 (high contagion and simple patch shape) on AWMPFD and patch richness and by cluster 1 (high contagion and complex patch shape) on AWMPFD (Table 7). AWMPFD and PR were significantly lower in cluster 4 compared to other clusters (Figure 7). AWMPFD was significantly higher in cluster 1 (Figure 7).

4.4 EFFECT OF TIME SINCE DISTURBANCE ON NON-VEGETATED LANDCOVER

The proportion of non-vegetated landcover type within disturbed landscapes at different times since disturbance is shown in Table 8. For clearcuts and fires, the proportion of non-vegetated landcover type was highest in the first decade after disturbance and successively lower for decades 2 to 4.

Table 7. Results of pairwise comparisons of treatment means for spatial vegetation pattern indices with clusters.

Comparisons between clusters	AWMPFD	PR
C1 – C2	*s*	ns
C1 – C3	*s*	ns
C1 – C4	*s*	*s*
C1 – C5	*s*	ns
C2 – C3	ns	ns
C 2– C4	*s*	*s*
C2 – C5	ns	ns
C3 – C4	*s*	*s*
C3 – C5	ns	ns
C4 – C5	*s*	*s*

Notes: s = significant difference ($p < 0.05$); ns = no significant difference; n = 2818; 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); AWMPFD = area weighted mean patch fractal dimension; PR = patch richness.

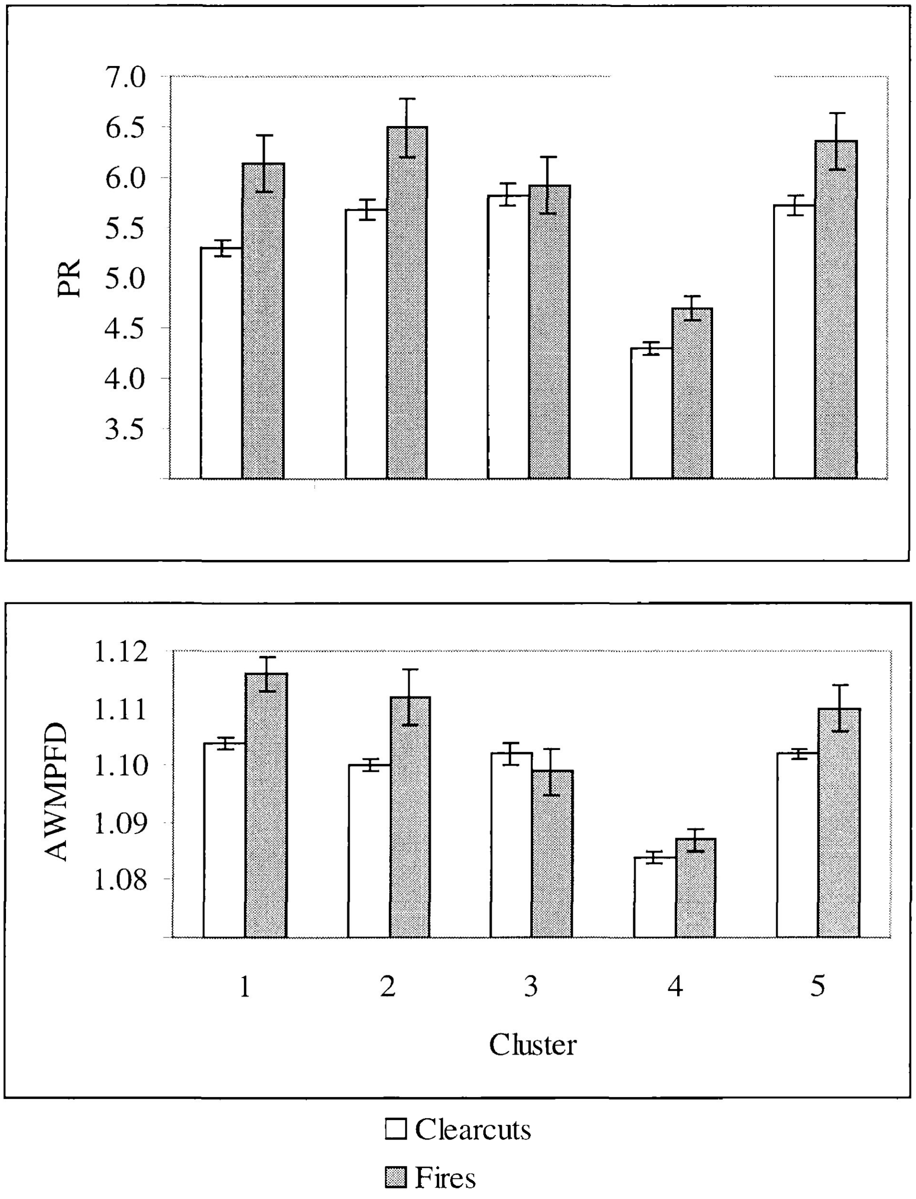

Figure 7. Effect of clusters on vegetation pattern indices. Data show means ± SE; n = 2818; PR = Patch Richness; AWMPFD = Area Weighted Mean Patch Fractal Dimension.

Table 8. Proportion of disturbed landscapes occupied by non-vegetated forest at different times since disturbance.

Time since disturbance (decades)	Disturbance type	
	clearcuts	fires
1	88%	70%
2	76%	62%
3	49%	38%
4	37%	24%

Notes: Values represent the mean amount of non-vegetated landcover type as a percent of disturbance area ($n = 2818$).

CHAPTER 5 – DISCUSSION

5.1 EFFECT OF DISTURBANCE TYPE

DeLong and Tanner (1996) stated that in the boreal forests of British Columbia, remnant patches occur frequently following fires, but not following clearcuts. A disturbance with many small remnant patches will have a smaller mean patch size than a disturbance with few remnant patches. Therefore, patch size is expected to be smaller following fire compared to clearcuts. However, in this study, mean patch size was significantly larger following fires. I suggest that the effect of disturbance type on mean patch size was due to differences in disturbance severity. In a study of boreal forests in Alberta, Eberhart and Woodard (1987) found that large fires had fewer remnants than small fires. They suggested that larger fires occurred during drought periods resulting in higher fire severity. Because of this, fewer potential remnant patches would escape disturbance. Since small fires were not a part of this study, I made the assumption that all the fires were severe. Also, Ward and Tithecott (1993) showed that fuel loading has increased due to fire suppression in Ontario. The effect of increased fuels can result in greater fire severity, creating the potential for larger burned patches. Unlike fire, clearcut severity is less likely to be affected by disturbance size (Lertzman and Fall 1998).

Disturbance size may have also affected mean patch size. Logically, patch size is bounded by disturbance size; therefore, small disturbances should result in lower values for mean patch size compared to large disturbances (Table 5). However, disturbance size was taken into account as a covariate in the General Linear Model (Section 3.6). Therefore, differences in severity between clearcuts and fires as discussed above, are likely the cause for larger patch size following fires.

Patch density was higher in post-clearcut than post-fire disturbances. It was suggested above that high disturbance severity due to large fires caused greater mean patch size in fires than in clearcuts. The same argument may be extended to explain why patch density was lower following fires compared to clearcuts. Hargis *et al.* (1998) stated that the behaviour of patch density is inverse to that of mean patch size in landscapes with the same extent. In this study, extent was defined by the size of disturbed landscapes. As previously discussed, disturbance extent was standardized by the covariate. Therefore, the behaviour of patch density was expected to be the inverse of mean patch size. In the previous discussion I hypothesized that disturbance severity due to large fires may have caused a larger mean patch size following fires. This argument could also explain why patch density was lower following fires than clearcuts.

5.2 EFFECT OF TIME SINCE DISTURBANCE

5.2.1 Time Since Disturbance and Landscape Composition

5.2.1.1 Effect of time on patch richness

Patch richness was significantly lower in decade 1 compared to decades 2, 3, and 4. This indicates that older disturbances had more landcover types than recent disturbances. The difference in patch richness may be due to revegetation by different forest cover types. In boreal forests there are several species that can become reestablished in the aftermath of disturbance. Species such as jack pine, black spruce, and aspen are common pioneer species, and are capable of forming heterogeneous patches after disturbance (Sims *et al.* 1990). However, all species may not revegetate disturbed sites during the same time period after disturbance (Ellice and Mattice 1974; Galipeau *et al.* 1997). Therefore, higher patch richness in older disturbances could be due to the emergence of forest cover types at different times after disturbance.

5.2.1.2 Effect of time on patch density

Patch density was significantly higher in decade 3 than decades 1 and 4 (i.e., decade 1 < decade 3 > decade 4). I hypothesize that higher patch density in decade 3 compared to decade 1 was a result of revegetation in the form of small patches. Reestablishment of boreal tree species can be patchy due to fine-scale environmental factors (Vassov and Baker 1988; Sims *et al.* 1990), with sites having optimal seed beds and soil conditions 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). Harvey and Bergeron (1989) reported variable stocking levels one decade after clearcutting, largely due to edaphic factors. Thus, the initial establishment of vegetation after disturbance appears to occur in small patches. To test this argument, I examined the proportion of disturbed landscapes occupied by non-vegetated landcover types (Table 8). These landcover types occupied a large proportion of disturbed landscapes in decade 1 (88% for clearcuts, and 70% for fires) but smaller proportions in subsequent decades. It is possible that non-vegetated landcover types were displaced by dense forest cover types due to revegetation over four decades, which is consistent with Bergeron and Dubuc (1989) and Frelich and Reich (1995).

Patch density was lower in decade 4 compared to decade 3. To explain this difference I return to the hypothesis that patch density had a high value in decade 3 due to revegetation by means of small patches. I further hypothesize that in decade 4, vegetation patches were fewer, and total area under dense forest cover types was higher. The proportion of landscapes occupied by non-vegetated landcover types was lower in decade 4 compared to decade 3. Dense forest cover types, due to revegetation, may have displaced non-vegetated landcover types. A greater proportion of dense forest cover types in decade 4 compared to decade 3 could have caused lower patch density.

Figure 6 shows that post-fire patch density was lower than post-clearcut patch density in each decade after disturbance. Thus, the effect of disturbance type on patch density can be observed for 4 decades after disturbance.

5.2.1.3 Effect of time on evenness

Evenness is an indicator of the proportion of each landcover type within a landscape, and is influenced by patch richness (McGarigal and Marks 1995). High evenness indicates that area is evenly distributed among landcover types (McGarigal and Marks 1995). Evenness was significantly lower in decade 1 compared to older decades, and decade 2 was significantly lower than decade 3. Disturbances in decade 1 were occupied by a large proportion of non-vegetated landcover types (Table 8). Therefore, I hypothesize that evenness had low values in decade 1 due to the dominance of non-vegetated landcover types. Both patch richness and evenness were higher in decades 2, 3, and 4 compared to decade 1. Higher values for evenness in older decades may have been due to a greater proportion of dense forest cover types within disturbances, due to revegetation.

5.2.2 Time Since Disturbance and Patch Geometry

5.2.2.1 Effect of time on mean patch size

Mean patch size of vegetation in decade 1 was significantly larger than decade 3 (Table 6). Previously, I hypothesized that disturbed landscapes had large patches of non-vegetated landcover types in decade 1. I also hypothesized that in decade 3 revegetation had occurred by means of small vegetation patches. Logically, a landscape with few large patches will have a larger mean patch size than a landscape with numerous small patches. Therefore, the decrease in mean patch size between decade 1 and decade 3 appears to be due to the emergence of small vegetation patches.

Figure 6 shows that mean patch size following fires was larger than following clearcuts in each decade after disturbance. Thus the effect of disturbance type on mean patch size can be observed for 4 decades after disturbance.

5.2.2.2 Effect of time on edge density

Edge density is a measure of boundary length between different landcover types and may be influenced by the number and size of patches, and patch shape (McGarigal and Marks 1995). Edge density was significantly lower in decade 1 than decades 2, 3, and 4. Patch density and patch richness were also lower in decade 1 compared to older disturbances. As a result, the boundary length, or edge density, between landcover types was also lower in decade 1. Patch shape could also have affected edge density. In this study, area weighted mean patch fractal dimension was used to measure patch shape. It was not affected by time since disturbance; therefore, it appears that edge density was influenced by patch density and patch richness, but not by patch shape.

5.2.3 Time Since Disturbance and Contagion

Contagion is a useful index to monitor landscape patterns because it has a true spatial component (Li and Reynolds 1994). McGarigal and Marks (1995) describe contagion as a measure of the spatial arrangement of pixels (the smallest resolvable elements in a raster database) within a landscape. High values of contagion indicate that pixels of the same type are clumped together (McGarigal and Marks 1995). Contagion is also sensitive to the number of landcover types (McGarigal and Marks 1995). In this study, contagion was significantly higher in decade 1 than decades 2, 3 and, 4. Hargis *et al.* (1998) found that contagion was higher in landscapes with large patches. In this study, mean patch size was larger in decade 1 compared to decade 3, but patch richness was the inverse. Therefore, the difference in contagion in different decades could be to due to the influence of mean patch size and patch richness. In another study Li and Reynolds (1993) found that, in simulated landscapes, contagion decreased as small patches with different attributes were added to landscapes.

5.3 EFFECT OF CLUSTERS

Clusters 4 and 1 had a significant effect on area weighted mean patch fractal dimension (AWMPFD) (Table 7). Mean AWMPFD for edaphic factors was lowest in cluster four and highest in cluster 1. AWMPFD for vegetation patterns was also lowest in cluster 4 and highest in cluster 1 (Figure 7). This suggests that patch shape of edaphic factors had a strong effect on the shape of vegetation patches. In another study Krummel *et al.* (1987) found that patch shape of deciduous forests in the southern United States had a higher fractal dimension in a floodplain compared to adjacent agricultural areas. They concluded that environmental factors were the driving force behind the deciduous forest patch shapes in the floodplain.

Patch richness was significantly lower in cluster 4 than the other clusters. The edaphic factors in cluster 4 were defined by high contagion and low AWMPFD. Cluster 1 also had high contagion but AWMPFD was high. It appears that low AWMPFD of edaphic factors influenced patch richness in cluster 4. Intuitively, a relationship between low AWMPFD and patch richness could not be made. Cluster 4 had the smallest mean disturbance size (Table 4), which may have limited the potential number of different landcover types. However, patch richness was standardized by the covariate. Other fine-scale effects not detected in the results may have affected patch richness. For example, Nichols *et al.* (1998) used a fine-scale approach in the eastern United States, and found significant relationships between plant species richness and spatial variation in slope, aspect, and soil drainage.

I suggested in the introduction that spatial edaphic factor patterns influence vegetation patterns. However, a significant effect only occurred for AWMPFD. The failure of clusters to have a significant effect on spatial vegetation pattern indices may be due to scale. The Ontario Land Inventory (OLI) database used to quantify edaphic factors was originally mapped at a scale of 1:250,000 (OMNR 1977), which may be too coarse to affect vegetation data at the scale used in this study. Efforts are being made to combine OLI with topographic, surficial geology, and satellite imagery databases to improve forest soils mapping (Wickware *et al.* 1997).

5.4 EFFECT OF COVARIATE

The covariate, disturbance size, was significant in reducing error for all response variables except edge density. Edge density was not affected because it was calculated per unit area (m/100ha). Other studies have also found that changing landscape extent significantly affects landscape pattern indices (Turner *et al.* 1989b, Weaver *et al.* 2000).

5.5 GENERAL DISCUSSION

Some indices appeared to be correlated (Figure 6). For example, patch richness, evenness, and edge density increased between decade 1 and decade 3, whereas contagion decreased. Number of landcover types is used in the mathematical formulae for all of these indices (McGarigal and Marks 1995); thus, changes in patch richness may have caused the correlation. Correlation among spatial pattern indices has been found in other studies (e.g., Turner *et al.* 1989b; Li and Reynolds 1994; Hargis *et al.* 1998).

Coarse grain size used for the vegetation data may have caused a difference in the time that vegetation was detected in my results and the actual time of revegetation. Table 8 indicates that, in decades 1 and 2, disturbances were largely non-vegetated or sparsely vegetated. This was unexpected because pioneer species can repopulate a disturbance at high densities within one decade (e.g., Sims *et al.* 1990; Turner *et al.* 1997). However, assigning emerging vegetation to forest cover classes was confounded by canopy openings (Spectranalysis 1992). A patch with 100% crown closure means that all reflected light is due to vegetation. If canopy openings exist, then reflected light is due to vegetation and soils. Soils reflect light at different wavelengths than vegetation and can confound attempts to differentiate sparse vegetation and emerging vegetation following disturbance (White *et al.* 1996). Therefore, the capability of the Landsat TM sensor to detect new vegetation is a factor of vegetation density and crown closure. As such, some patches may have been classified as non-vegetated or sparse forest landcover types using remote sensing, while a field survey may have concluded otherwise.

Aggregation of spatial data may also have caused a loss of information. Turner *et al.* (1989b) found that small patches and rare patch types were most likely to disappear during aggregation. Previously, I suggested that revegetation occurred by means of small patches, some of which could have been lost due to aggregation.

CHAPTER 6 – CONCLUSION

6.1 SUMMARY OF FINDINGS

The premise of this study was that vegetation patterns within disturbed landscapes are a result of disturbance type, time since disturbance, and spatial patterns of edaphic factors. A relative comparison was done to test the effects of clearcuts and fires on vegetation patterns over the same chronosequence, and under similar spatial edaphic factor patterns. The null hypothesis that spatial vegetation patterns do not differ following clearcuts and fires was rejected. Since interactions among main effects were not significant, the main effects (disturbance type, time since disturbance, and edaphic factors) were interpreted independently.

Fires had larger patches and lower patch density than clearcuts in all four decades following disturbance. This was surprising given the expectation of a greater number of remnant patches within fires compared to clearcuts. However, it is possible that fire size is related to the number of remnant patches. Conditions which cause large fires may also make fires more severe, resulting in fewer remnant patches compared to small (less severe) fires. Since I studied only large disturbances, fire severity could have caused larger and fewer patches within post-fire disturbances compared to post-clearcut disturbances.

Time since disturbance influenced all indices of spatial vegetation pattern except patch shape. One-decade-old disturbances had larger patches, fewer landcover types, and higher contagion compared to three-decade-old disturbances. Clearcuts and fires were expected to result in large patches devoid of vegetation initially, and over time the spatial patterns caused by these disturbances would change due to revegetation. In this study, individual disturbances were not observed repeatedly through all four decades following disturbance. However, observation of many disturbances representing all four decades revealed the expected trend for spatial vegetation patterns. Spatial vegetation patterns within one-decade-old disturbances appear to be the result of overstory destruction, and spatial vegetation patterns within older disturbances appear to be due to revegetation by means of small patches. The emergence of vegetation in the form of small patches may be due to fine-scale edaphic factors not detected in this study. Revegetation by multiple types of forest cover may explain why the number of landcover types was higher in older disturbances compared to one-decade-old disturbances. The above trends are based on observations of spatial vegetation patterns within disturbances of different ages.

Clusters of edaphic factors had a significant effect on patch shape and the number of landcover types. The results of this study suggest that disturbances with complex edaphic factor patch shapes also have complex landcover patch shapes, and indicate that the spatial position of edaphic factors influences the spatial position of landcover types.

Some spatial vegetation pattern indices showed correlations with more than one other index. Edge density, contagion, and evenness appeared to be influenced by the number of landcover types, and the number and size of patches. The continued use of correlated 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.

My results reveal specific dynamics of spatial vegetation patterns following clearcuts and fire. Spatial vegetation patterns following both types of disturbance appear to change from large, contagious patches to smaller more evenly dispersed patches. However, patches within fires were larger and fewer in comparison to clearcuts. Differences between post-clearcut and post-fire landscapes, and mechanisms of spatial vegetation pattern dynamics present specific goals for future research.

6.2 FUTURE CONSIDERATIONS

In this study, disturbance size had a significant effect on indices of spatial pattern and was standardized for the statistical analysis. For example, the size of a landscape sets an upper limit on patch size. It follows that large landscapes can have larger patches than small landscapes. Therefore, studies using indices of landscape pattern should account for landscape extent.

A hypothesis generated by this study is that disturbance severity affects subsequent spatial vegetation patterns, and that severity, in turn, is a result of the type and size of disturbances. I predict that large fires are more severe than large clearcuts, resulting in larger patches and lower patch density. Therefore, studies of large-scale disturbances should include disturbance severity as well as spatial patterns.

I propose three hypotheses based on the results of the effect of time since disturbance and the effect of edaphic factors on spatial vegetation patterns. They are:

1) Spatial patterns observed over time, within the same disturbed landscape, will progress from large, clumped patches, to finer spatial patterns because of revegetation in the form of small patches.
2) The number of forest cover types increases with time since disturbance because of the emergence of different types of forest cover.
3) The geometric and spatial placement of edaphic factor patches influences the geometric and spatial placement of vegetation patches.

Interpretation of spatial vegetation patterns in future studies should not be done without accounting for temporal and edaphic factors.

This study is one of 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 understand the effects of harvesting and fires on post-disturbance vegetation dynamics.

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APPENDICES

APPENDIX I

CORRELLATION BETWEEN VEGETATION PATTERN INDICES AND DISTURBANCE SIZE

Vegetation Pattern Index	Pearson Correlation Coefficient	*P*
Patch Density	-0.202	0.000
Edge Density	0.052	0.006
Area Weighted Mean Patch Fractal Dimension	0.425	0.000
Patch Richness	0.408	0.000
Evenness	-0.028	0.139
Contagion	0.047	0.013
Mean Patch Size	0.184	0.000

Note: P values based on 2-tailed tests.

APPENDIX II

ANOVA TABLES AND PAIRWISE COMPARISONS OF TREATMENT MEANS FOR RESPONSE VARIABLES

Appendix II-1. ANOVA table for mean patch fractal dimension.

Source	Type III SS	df	Mean Square	F	*P*
INTERCEPT	8.36E+02	1	8.356E+02	95926.44	***0.000***
Error	3.60E-02	4	8.711E-03 [a]		
DIST	6.00E-04	1	6.001E-04	0.66	0.457
Error	4.30E-03	5	9.134E-04 [b]		
TIME	5.37E-03	3	1.788E-03	3.16	0.053
Error	9.11E-03	16	5.659E-04 [c]		
DIST * TIME	1.26E-04	3	4.184E-05	0.08	0.971
Error	8.82E-03	16	5.374E-04 [d]		
CLUSTER	4.53E-02	4	1.133E-02	11.47	***0.023***
Error	3.64E-03	4	9.881E-04 [e]		
DIST * CLUSTER	3.86E-03	4	9.652E-04	1.80	0.181
Error	8.15E-03	15	5.365E-04 [f]		
CLUSTER * TIME	6.80E-03	12	5.668E-04	1.06	0.459
Error	6.41E-03	12	5.337E-04 [g]		
DIST * CLUSTER * TIME	6.40E-03	12	5.337E-04	0.95	0.493
Error	1.56E+00	2777	5.605E-04 [h]		
DISTURBANCE SIZE	2.83E-01	1	2.830E-01	504.17	***0.000***
Error	1.56E+00	2777	5.605E-04 [h]		

Notes: DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-1. Pairwise comparisons between cluster means for area weighted mean patch fractal dimension.

(I) CLUSTER	(J) CLUSTER	Mean Difference (I-J)	*P*
1	2	1.086E-02	0.000
	3	9.406E-03	0.001
	4	1.984E-02	0.000
	5	8.882E-03	0.002
	1	-1.086E-02	0.000
	3	-1.458E-03	0.596
	4	8.981E-03	0.000
	5	-1.982E-03	0.455
	1	-9.406E-03	0.001
	2	1.458E-03	0.596
	4	1.044E-02	0.000
	5	-5.240E-04	0.846
	1	-1.984E-02	0.000
	2	-8.981E-03	0.000
	3	-1.044E-02	0.000
	5	-1.096E-02	0.000
	1	-8.882E-03	0.002
	2	1.982E-03	0.455
	3	5.240E-04	0.846
	4	1.096E-02	0.000

Note : Pairwise comparisons are based on estimated marginal means.

Appendix II-2. ANOVA table for mean patch size.

Source	Type III SS	df	Mean Square	F	*P*
Intercept	2.82E+06	1	2.818E+06	2675.14	***0.000***
Error	3.21E+04	30	1.053E+03 [a]		
DIST	3.89E+04	1	3.892E+04	22.30	***0.003***
Error	1.10E+04	6	1.745E+03 [b]		
TIME	2.66E+04	3	8.872E+03	4.71	***0.013***
Error	3.55E+04	19	1.882E+03 [c]		
DIST * TIME	4.04E+03	3	1.347E+03	1.07	0.382
Error	3.13E+04	25	1.265E+03 [d]		
CLUSTER	2.01E+03	4	5.032E+02	0.22	0.915
Error	1.29E+04	6	2.244E+03 [e]		
DIST * CLUSTER	6.38E+03	4	1.595E+03	1.32	0.295
Error	2.53E+04	21	1.209E+03 [f]		
CLUSTER * TIME	2.09E+04	12	1.741E+03	1.70	0.185
Error	1.23E+04	12	1.023E+03 [g]		
DIST * CLUSTER * TIME	1.23E+04	12	1.023E+03	0.37	0.974
Error	7.68E+06	2777	2.764E+03 [h]		
DISTURBANCE SIZE	2.57E+05	1	2.573E+05	93.07	***0.000***
Error	7.68E+06	2777	2.764E+03 [h]		

Notes: DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-2. Pairwise comparisons between decades for mean patch size.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	1.042E+01	0.076
	Decade 2	1.549E+00	0.764
	Decade 1	-5.391E+00	0.319
Decade 3	Decade 4	-1.042E+01	0.076
	Decade 2	-8.869E+00	0.068
	Decade 1	-1.581E+01	0.002
Decade 2	Decade 4	-1.549E+00	0.764
	Decade 3	8.869E+00	0.068
	Decade 1	-6.940E+00	0.105
Decade 1	Decade 4	5.391E+00	0.319
	Decade 3	1.581E+01	0.002
	Decade 2	6.940E+00	0.105

Note : Pairwise comparisons are based on estimated marginal means.

Appendix II-3. ANOVA table for edge density.

Source	Type III SS	df	Mean Square	F	*P*
INTERCEPT	3.21E+05	1	3.207E+05	2144.26	***0.000***
Error	7.72E+02	5	1.496E+02 [a]		
DIST	9.70E+01	1	9.701E+01	1.00	0.364
Error	4.76E+02	5	9.700E+01 [b]		
TIME	8.14E+03	3	2.712E+03	37.67	***0.000***
Error	1.17E+03	16	7.200E+01 [c]		
DIST * TIME	1.19E+02	3	3.981E+01	0.76	0.530
Error	9.71E+02	19	5.233E+01 [d]		
CLUSTER	6.96E+02	4	1.739E+02	1.45	0.344
Error	5.91E+02	5	1.201E+02 [e]		
DIST * CLUSTER	4.02E+02	4	1.004E+02	1.95	0.149
Error	8.61E+02	17	5.153E+01 [f]		
CLUSTER * TIME	8.61E+02	12	7.172E+01	1.47	0.258
Error	5.87E+02	12	4.888E+01 [g]		
DIST * CLUSTER * TIME	5.87E+02	12	4.888E+01	0.66	0.788
Error	2.05E+05	2777	7.374E+01 [h]		
DISTURBANCE SIZE	1.10E-01	1	1.100E-01	0.00	0.969
Error	2.05E+05	2777	7.374E+01 [h]		

Notes : DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appenix II-3. Pairwise comparisons between decades for edge density.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	6.984E-02	0.942
	Decade 2	3.005E+00	0.763
	Decade 1	7.510E+00	0.000
Decade 3	Decade 4	-6.984E-02	0.942
	Decade 2	2.936E+00	0.000
	Decade 1	7.440E+00	0.000
Decade 2	Decade 4	-3.005E+00	0.763
	Decade 3	-2.936E+00	0.000
	Decade 1	4.505E+00	0.000
Decade 1	Decade 4	-7.510E+00	0.000
	Decade 3	-7.440E+00	0.000
	Decade 2	-4.505E+00	0.000

Note : Pairwise comparisons are based on estimated marginal means.

Appendix II-4. ANOVA table for contagion.

Source	Type III SS	df	Mean Square	F	*P*
INTERCEPT	2.16E+06	1	2.163E+06	4384.41	***0.000***
Error	2.47E+03	5	4.934E+02 [a]		
DIST	8.04E+02	1	8.043E+02	2.65	0.166
Error	1.47E+03	5	3.037E+02 [b]		
TIME	1.14E+04	3	3.795E+03	17.01	***0.000***
Error	3.57E+03	16	2.232E+02 [c]		
DIST * TIME	7.14E+02	3	2.382E+02	1.53	0.240
Error	2.87E+03	18	1.557E+02 [d]		
CLUSTER	2.33E+03	4	5.825E+02	1.52	0.323
Error	1.96E+03	5	3.839E+02 [e]		
DIST * CLUSTER	1.27E+03	4	3.166E+02	2.06	0.132
Error	2.55E+03	17	1.534E+02 [f]		
CLUSTER * TIME	2.69E+03	12	2.242E+02	1.54	0.234
Error	1.75E+03	12	1.459E+02 [g]		
DIST * CLUSTER * TIME	1.75E+03	12	1.459E+02	0.67	0.778
Error	6.01E+05	2777	2.165E+02 [h]		
DISTURBANCE SIZE	4.41E+03	1	4.414E+03	20.38	***0.000***
Error	6.01E+05	2777	2.165E+02 [h]		

Notes : DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-4. Pairwise comparisons between decades for contagion.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	2.529E+00	0.123
	Decade 2	-2.100E+00	0.146
	Decade 1	-7.266E+00	0.000
Decade 3	Decade 4	-2.529E+00	0.123
	Decade 2	-4.629E+00	0.001
	Decade 1	-9.795E+00	0.000
Decade 2	Decade 4	2.100E+00	0.146
	Decade 3	4.629E+00	0.001
	Decade 1	-5.166E+00	0.000
Decade 1	Decade 4	7.266E+00	0.000
	Decade 3	9.795E+00	0.000
	Decade 2	5.166E+00	0.000

Note : Pairwise comparisons are based on estimated marginal means.

Appendix II-5. ANOVA table for patch density.

Source	Type III SS	df	Mean Square	F	*P*
INTERCEPT	2.72E+03	1	2.717E+03	2130.53	***0.000***
Error	7.80E+00	6	1.275E+00 [a]		
DIST	5.11E+01	1	5.109E+01	60.04	***0.000***
Error	4.72E+00	6	8.510E-01 [b]		
TIME	1.01E+01	3	3.380E+00	5.36	***0.007***
Error	1.24E+01	19	6.310E-01 [c]		
DIST * TIME	3.55E-02	3	1.184E-02	0.02	0.997
Error	1.31E+01	19	7.050E-01 [d]		
CLUSTER	5.45E+00	4	1.363E+00	1.80	0.345
Error	2.00E+00	3	7.560E-01 [e]		
DIST * CLUSTER	3.32E+00	4	8.290E-01	1.19	0.350
Error	1.16E+01	17	6.940E-01 [f]		
CLUSTER * TIME	6.86E+00	12	5.710E-01	0.87	0.594
Error	7.89E+00	12	6.570E-01 [g]		
DIST * CLUSTER * TIME	7.89E+00	12	6.570E-01	0.66	0.795
Error	2.78E+03	2777	1.002E+00 [h]		
DISTURBANCE SIZE	8.75E+01	1	8.746E+01	87.30	***0.000***
Error	2.78E+03	2777	1.002E+00 [h]		

Notes : DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-5. Pairwise comparisons between decades for patch density.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	-2.780E-01	0.013
	Decade 2	-1.990E-01	0.043
	Decade 1	-3.903E-02	0.704
Decade 3	Decade 4	2.780E-01	0.013
	Decade 2	7.932E-02	0.391
	Decade 1	2.390E-01	0.014
Decade 2	Decade 4	1.990E-01	0.043
	Decade 3	-7.932E-02	0.391
	Decade 1	1.600E-01	0.05
Decade 1	Decade 4	3.903E-02	0.704
	Decade 3	-2.390E-01	0.014
	Decade 2	-1.600E-01	0.05

Note : Pairwise comparisons are based on estimated marginal means.

Appendix II-6. ANOVA table for patch richness.

Source	Type III SS	df	Mean Square	F	*P*
Intercept	1.97E+04	1	1.973E+04	407.24	***0.000***
Error	2.00E+02	4	4.845E+01 [a]		
DIST	1.19E+01	1	1.192E+01	2.39	0.187
Error	2.33E+01	5	4.999E+00 [b]		
TIME	1.44E+02	3	4.816E+01	14.27	***0.000***
Error	5.20E+01	15	3.375E+00 [c]		
DIST * TIME	1.27E+01	3	4.229E+00	1.20	0.344
Error	5.39E+01	15	3.536E+00 [d]		
CLUSTER	2.52E+02	4	6.311E+01	12.35	***0.031***
Error	1.58E+01	3	5.108E+00 [e]		
DIST * CLUSTER	2.12E+01	4	5.311E+00	1.49	0.256
Error	5.12E+01	14	3.561E+00 [f]		
CLUSTER * TIME	4.15E+01	12	3.455E+00	0.95	0.536
Error	4.37E+01	12	3.642E+00 [g]		
DIST * CLUSTER * TIME	4.37E+01	12	3.643E+00	1.27	0.231
Error	7.99E+03	2777	2.875E+00 [h]		
DISTURBANCE SIZE	1.18E+03	1	1.176E+03	408.99	***0.000***
Error	7.99E+03	2777	2.875E+00 [h]		

Notes : DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-6. Pairwise comparisons between decades for patch richness.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	-8.047E-02	0.670
	Decade 2	1.830E-01	0.271
	Decade 1	9.190E-01	0.000
Decade 3	Decade 4	8.047E-02	0.670
	Decade 2	2.630E-01	0.093
	Decade 1	1.000E+00	0.000
Decade 2	Decade 4	-1.830E-01	0.271
	Decade 3	-2.630E-01	0.093
	Decade 1	7.370E-01	0.000
Decade 1	Decade 4	-9.190E-01	0.000
	Decade 3	-1.000E+00	0.000
	Decade 2	-7.370E-01	0.000

Notes : Pairwise comparisons are based on estimated marginal means.

Appendix II-6. Pairwise comparisons between clusters for patch richness.

(I) CLUSTER	(J) CLUSTER	Mean Difference (I-J)	*P*
1	2	1.053E-03	0.996
	3	-1.370E-01	0.509
	4	9.760E-01	0.000
	5	-4.526E-02	0.823
	1	-1.053E-03	0.996
	3	-1.380E-01	0.482
	4	9.750E-01	0.000
	5	-4.631E-02	0.807
	1	1.370E-01	0.509
	2	1.380E-01	0.482
	4	1.113E+00	0.000
	5	9.206E-02	0.634
	1	-9.760E-01	0.000
	2	-9.750E-01	0.000
	3	-1.113E+00	0.000
	5	-1.021E+00	0.000
	1	4.526E-02	0.823
	2	4.631E-02	0.807
	3	-9.206E-02	0.634
	4	1.021E+00	0.000

Notes : Pairwise comparisons are based on estimated marginal means.

Appendix II-7. ANOVA table for evenness.

Source	Type III SS	df	Mean Square	F	*P*
Intercept	2.69E+02	1	2.688E+02	3333.01	***0.000***
Error	4.23E-01	5	8.064E-02 [a]		
DIST	3.42E-01	1	3.420E-01	5.43	0.069
Error	3.01E-01	5	6.292E-02 [b]		
TIME	2.02E+00	3	6.730E-01	14.71	***0.000***
Error	7.20E-01	16	4.577E-02 [c]		
DIST * TIME	1.98E-01	3	6.603E-02	2.49	0.091
Error	5.23E-01	20	2.656E-02 [d]		
CLUSTER	3.72E-01	4	9.306E-02	1.09	0.440
Error	5.03E-01	6	8.525E-02 [e]		
DIST * CLUSTER	2.64E-01	4	6.600E-02	2.54	0.077
Error	4.55E-01	18	2.598E-02 [f]		
CLUSTER * TIME	5.56E-01	12	4.637E-02	1.93	0.135
Error	2.89E-01	12	2.407E-02 [g]		
DIST * CLUSTER * TIME	2.89E-01	12	2.406E-02	0.57	0.866
Error	1.17E+02	2777	4.201E-02 [h]		
DISTURBANCE SIZE	6.01E-01	1	6.010E-01	14.30	***0.000***
Error	1.17E+02	2777	4.201E-02 [h]		

Notes: DIST= Disturbance type, TIME = Time since disturbance (decades)

a $0.757(MS_{CLUSTER}) - 8.586E\text{-}14(MS_{DIST*CLUSTER}) + 7.264E\text{-}14(MS_{DIST*CLUSTER*TIME}) + 0.243(MS_{ERROR})$

b $0.872(MS_{DIST*CLUSTER}) + 0.128(MS_{ERROR})$

c $0.862(MS_{CLUSTER*TIME}) + 0.138(MS_{ERROR})$

d $0.861(MS_{DIST*CLUSTER*TIME}) + 0.139(MS_{ERROR})$

e $0.985(MS_{DIST*CLUSTER}) + 0.880(MS_{CLUSTER*TIME}) - 0.880(MS_{DIST*CLUSTER*TIME}) + 1.537E\text{-}02(MS_{ERROR})$

f $0.893(MS_{DIST*CLUSTER*TIME}) + 0.107(MS_{ERROR})$

g $1.000(MS_{DIST*CLUSTER*TIME}) + 1.198E\text{-}04(MS_{ERROR})$

h MS_{ERROR}

Appendix II-7. Pairwise comparisons between decades for evenness.

(I) TIME	(J) TIME	Mean Difference (I-J)	*P*
Decade 4	Decade 3	-4.106E-02	0.073
	Decade 2	2.425E-02	0.228
	Decade 1	9.148E-02	0.000
Decade 3	Decade 4	4.106E-02	0.073
	Decade 2	6.531E-02	0.001
	Decade 1	1.330E-01	0.000
Decade 2	Decade 4	-2.425E-02	0.228
	Decade 3	-6.531E-02	0.001
	Decade 1	6.723E-02	0.000
Decade 1	Decade 4	-9.148E-02	0.000
	Decade 3	-1.330E-01	0.000
	Decade 2	-6.723E-02	0.000

Note : Pairwise comparisons are based on estimated marginal means.