

Landscape complexity in space and time

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Abstract. Landscape complexity in the boreal forest is a function of physiographic complexity (spatial processes) and post-fire successional (temporal) processes operating across scales. In this study we examine the role of succession and topographic complexity in determining the landscape complexity of Riding Mountain National Park, Manitoba, Canada. Landscape complexity is assessed by using multifractal analysis to quantify landscape patterns from Landsat TM imagery. To determine whether complexity changes with age, "young" sites (post-fire stand ages = 11 and 30 years) were matched with adjacent "old" sites (post-fire stand ages > 95 years). The influence of physiography on landscape complexity is examined by comparing sites having "simple" and "complex" physiographies (as determined by fractal surface analysis). The scaling properties of landscape complexity are determined by calculating the multifractal spectrum (D_q) for each site. Landscape complexity increases during early succession; multifractal profiles of 11 year old sites are lower than those of adjacent older stands. However, the multifractal profiles of 30 year old and adjacent older stands are indistinguishable, suggesting that change in landscape complexity occurs within 30 years following fire. Physiographically "complex" sites have consistently greater landscape complexity than adjacent "simple" sites. We conclude that landscape complexity increases over time as succession proceeds, and in space along a gradient from "simple" to "complex" physiographies. It follows that landscape complexity is lowest in early-successional, physiographically "simple" sites and highest in late-successional, physiographically "complex" sites.

Abbreviations: DEM - Digital Elevation Map; RMNP - Riding Mountain National Park; PCA - Principal Component Analysis.

Introduction

Landscape complexity of forested ecosystems is a function of both successional processes (post-disturbance colonization, and subsequent canopy development) and structural aspects of the underlying physiography (Frelich et al. 1998, Gosz 1993, Bonan and Shugart 1989). Catastrophic wildfire is the predominant large-scale disturbance in boreal forest ecosystems, with fire cycles ranging from less than 50 years to over 200 years (Hirsch 1991, Payette 1992). Post-fire colonization occurs as large, relatively uniform patches dominated by early-successional species such as jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*). These species are well adapted to regeneration following fire and form extensive, dense, uniform post-fire stands. As succession proceeds, the canopy structural properties of these early-successional stands are modified by various processes, including differential tree growth and the superimposition of smaller-scale stochastic disturbances. Small-scale disturbances in boreal forest ecosystems include individual tree mortality resulting from lightning strikes (Granström 1993) and windthrow (Dyer and Baird 1997), spruce budworm infestations (Holling 1992), and beaver flooding (Naiman 1988). The cumulative effect of small-scale dis-

turbances is to "chip away" at what was initially a relatively uniform canopy structure. The "gaps" created by these stochastic disturbances produce a forested landscape characterized by fine-scale patchiness. The creation of forest gaps also drives late-successional processes, favouring advanced regeneration of more shade-tolerant species and thus altering stand composition and structure (Frelich and Reich 1995, Kneeshaw and Bergeron 1998).

Physiography, which incorporates surficial topography and drainage, is also an important determinant of landscape complexity (Foster and King 1986). Gradients in soil moisture strongly influence species distributions (Bonan and Shugart 1989, Naiman et al. 1993, Helm and Collins 1997, Frelich et al. 1998), and in doing so affect the size, structure and diversity of forest patches (Foster and King 1986, Host et al. 1987). The interaction between vegetation and physiography produces complex, interdigitated and ecotonal landscape patterns that reflect underlying environmental trends (Gosz 1993).

The combined influences of disturbance (a temporal process) and physiography (a spatial process) on the landscape complexity of forested ecosystems has received surprisingly little attention (but see Foster and King 1986,

Frelich and Reich 1999). Studying the effect of spatio-temporal processes on landscape complexity requires examination of spatially-explicit data across many scales. Unfortunately, such data are very difficult to obtain using traditional ground-survey methods (Rey-Benayas and Pope 1995). Remote sensing is therefore the preferred technology for quantifying landscape complexity. Complexity of a remotely sensed image is normally assessed by examining the spatial patterns of spectral reflectance (De Cola 1994, Jakubauskas 1997). Pattern-based methods use the interdigitation and juxtaposition of landscape elements (e.g., pixels or patches) to measure landscape complexity (Rey-Benayas and Pope 1995). In remotely-sensed images of forest landscapes, variations in canopy composition and structure produce complex patterns of pixel spectral reflectances that define the landscape "texture" (Colwell 1974, Ravan and Roy 1997). Jakubauskas (1997) used this approach to examine changes in landscape pattern across a successional sere, based on Landsat imagery. The changes observed were consistent with known successional trends at the stand level, suggesting a commonality across scales.

Although the influence of temporal (successional) and spatial (physiographic) processes on forest canopy structure has been examined at both stand and landscape scales, there is a lack of integration across scales. Fractal theory (Mandelbrot 1983) provides a scale-invariant approach to measuring landscape complexity. In "classic" fractal systems, pattern complexity is characterized as a single scaling exponent, the fractal dimension (D). However, it has been argued that landscapes cannot be characterized by a single scaling exponent, since a number of

generating processes operating at different scales determine landscape complexity (Loehle and Wein 1994). Patterns resulting from multiple underlying processes are best studied using a multifractal approach (Scheuring and Riedi 1994). A multifractal system is characterized by a continuous "spectrum" of scaling exponents (Schroeder 1991). Many natural systems have multifractals characteristics, including geophysical phenomenon (Turcotte 1997), species patterns (Loehle and Wein 1994), and landscape patterns (De Cola 1994).

In this study, we use multifractal analysis of remotely-sensed imagery (Landsat thematic mapper data) to examine how spatial and temporal phenomena affect scale-invariant landscape complexity. Specifically, we assess how successional change and physiographic complexity influence landscape pattern by addressing the following questions:

1. Does landscape complexity change predictably during succession?
2. To what extent is landscape complexity influenced by underlying physiography?
3. How do spatial and temporal processes interact in determining scale-invariant landscape complexity?

Study area

Location and physiography

Riding Mountain National Park (RMNP) is a 2974 km² forest reserve in south-western Manitoba, Canada (Fig. 1). The Park is roughly rectangular in shape, with a

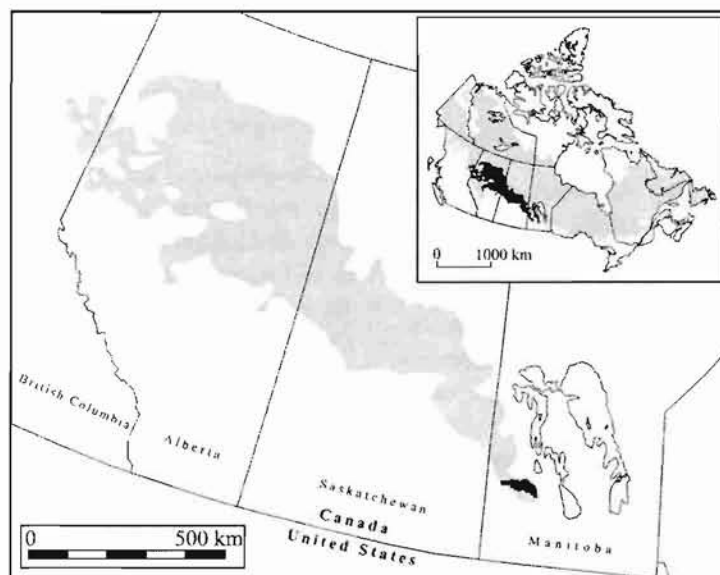


Figure 1. Distribution of the boreal forest in Canada (top inset) and the boreal mixedwood section (main figure). The location of RMNP is indicated (bold dot).

main east-west axis of approximately 115 km and a north-south axis of approximately 60 km (Canada 1979). Most of RMNP occurs on the Saskatchewan Plain or "second prairie level" (mean elevation 610 m). The Manitoba Escarpment parallels the eastern border of the Park, dropping approximately 300 m to the Manitoba lowlands or "first prairie level" (mean elevation of 320 m). The central region of RMNP is characterized by a complex physiography of glacial till ridges interspersed with wetlands. By contrast, the northern region has a more uniform slope, resulting in good drainage and a comparatively simple physiography (Canada 1979).

Climate

RMNP falls within the Humid Microthermal climatic zone (Köppen-Geiger classification), characterized by short, warm summers and long, cold winters. Mean annual temperature is approximately 2°C. Mean annual total precipitation is approximately 55 cm, approximately two-thirds of which falls as rain during the 160-180 day growing season (Environment Canada 1993).

Vegetation

Boreal "mixed-wood" forest is the predominant vegetation type of RMNP (Rowe 1956). These forests typically consist of a mixture of hardwoods (trembling aspen, *Populus tremuloides*; balsam poplar, *P. balsamifera*; and/or white birch, *Betula papyrifera*) and the softwood white spruce (*Picea glauca*). Stands of jack pine (*Pinus banksiana*) occur on sandy soils in the south-eastern region of the Park. Black spruce (*Picea mariana*) stands are restricted to poorly-drained and nutrient-deficient substrates.

Disturbance history

Historically, catastrophic crown fires have had a major impact on the composition, structure and development of forest stands in RMNP. Historical accounts, fire scars and stand age data indicate that large fires occurred in 1822, 1853-1855, 1889-1891, and 1918-1919 (Rowe 1956). Fires were most prevalent during the early years of European settlement (1885-1895) as land was cleared for farming. Two "back-to-back" catastrophic fires in the early 1890's burned over 70% of the western half of RMNP, considerably reducing the abundance of white spruce (Rowe 1956). As a result, the western half of RMNP is dominated by the clonal hardwoods trembling aspen and balsam poplar. Jack pine stands in the south-eastern portion of RMNP have burned repeatedly since fire records began. While fire-fighting efforts since the 1930's have dramatically reduced the incidence and ex-

tent of forest fires in RMNP, major burns occurred in 1961 at Gunn Lake and in 1980 at Rolling River (Fig. 2a). By contrast, the north-east region of RMNP has not burned for at least 125 years (Sentar 1992).

Materials and methods

Remote sensing data

A Landsat-5 image of RMNP acquired on August 3, 1991 is used in this study, and all landscape ages cited are expressed relative to this date. The image has high atmospheric transmittance and minimal cloud cover. Our analyses utilized three spectral reflectance bands: band 3 (red, 0.63-0.69 μm), band 4 (near infrared, 0.76-0.90 μm), and band 5 (mid infrared, 1.55-1.75 μm). A standard radiometric correction (Radarsat International, Vancouver) was used to eliminate variability in sensor response. The final raster product conformed to the NAD27 grid system (Zone 14) at a pixel resolution of 30 x 30 m. Bands were centred at 5631.3 km N by 403.4 km E. A dark order subtraction based on a path irradiance model of λ^{-4} (corresponding to a clear atmosphere dominated by Rayleigh scattering, Richards 1993) was performed to correct for residual atmospheric effects (Chavez 1988).

An unsupervised K-means classification was performed on the three-band data to simplify the spectral image into ten discrete "classes" (Richards 1993). Unsuper-

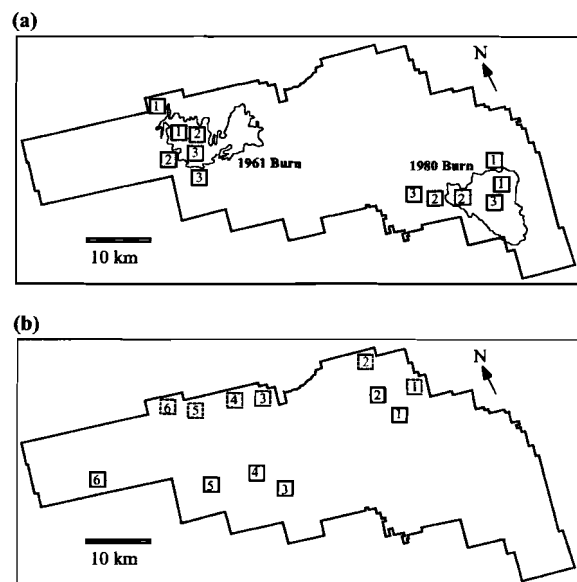


Figure 2. Locations of the 24 sample sites in Riding Mountain National Park: (a) "young" (11-30 year) sites mapped within the boundaries of the 1980 and 1961 burns and adjacent "old" (> 95 yr) sites; (b) "complex" (solid lines) and matching "simple" sites (broken lines).

vised classification is a “neutral” strategy that makes no prior assumptions regarding ground-based floristic composition. The classes are therefore defined purely on the basis of pixel-based spectral reflectance data.

Topographic complexity of our study sites was measured using a digital elevation map (DEM) based on orthophotography of RMNP. Resolution of the DEM was 120 x 120 m, and elevation was recorded as metres above sea level.

Site selection

“Young” vs. “old”. We selected three square study sites (2.88 x 2.88 km, or 96 x 96 pixels) from each of two recently burned areas: the 1980 Rolling River fire (11 years old), and the 1961 Gunn Lake fire (30 years old). Each “young” site was then paired (matched) with an “old” site, i.e., a region that has not burned for at least 95 years (Fig. 2a). We selected the “old” sites using several criteria: (a) adjacency to “young” sites; (b) similar topography and elevation to “young” sites; (c) similar soil texture and drainage patterns to “young” sites (data from Canada

1979). All twelve study sites occur on the Saskatchewan Plain and have less than 5% open water.

“Simple” vs. “complex”. We selected six square study sites (2.88 x 2.88 km, or 96 x 96 pixels) exhibiting a ridge-swale topography and a stationary elevational profile indicative of restricted drainage. These are referred to as “complex” physiographic sites. Each “complex” site was paired (matched) with an adjacent site having a non-stationary (directional or sloping) elevation profile, and occurring on well-drained soils (Canada 1979). These are referred to as “simple” physiographic sites. All twelve study sites occur on the Saskatchewan Plain and have less than 5% open water. Example digital terrain maps of a “simple” and “complex” site pair are shown in Fig. 3a.

Data analysis

Site physiography. Physiographic complexity was determined for each site to ensure that “young” and “old” sites are not confounded by differences in physiography, and that landscape physiographic complexity is greater for “complex” sites compared to “simple” ones. For all 24

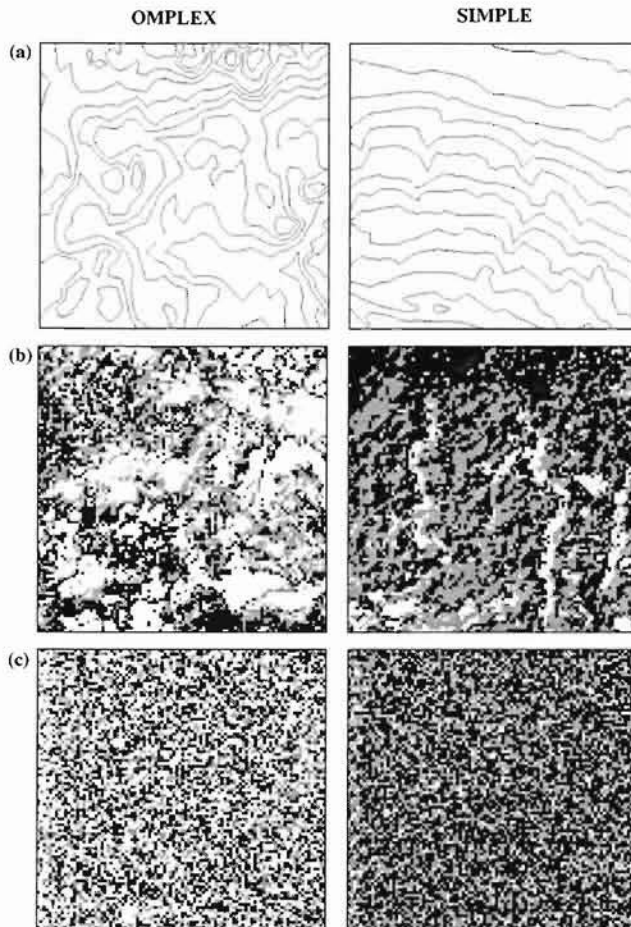


Figure 3. “Complex” site with a pair-matched “simple” site: (a) elevation contours; (b) patterns of the 3 most frequent land-cover classes (black and grey shades - the remaining 7 classes are combined as white); (c) random landscapes generated from above.

study sites, both slope and topographic variation (based on DEM data) are used as measures of physiographic complexity.

We performed principal component analysis (PCA) on the DEM for each site to obtain a “plane of best fit”. We then determined site slope from the direction cosines of the principal axis. Slope values are compared across sites using paired t-tests.

To quantify topographic variation, we analyzed the DEM for each sample site using the surface algorithm described by Polidori et al. (1991). This method calculates a persistence exponent (η) for sequential values in a spatial (or temporal) series. Persistence measures the degree of autocorrelation of adjacencies in a series; if $\eta < 0.5$ the series is negatively autocorrelated, whereas $\eta > 0.5$ indicates positive autocorrelation. Persistence η is computed from the power-law relationship:

$$\log |e| = \log k + \eta \log d \quad [1]$$

where $|e|$ is the mean absolute difference between values in a spatial series separated by lag distance d . We implemented the surface algorithm using a “rook” sampling technique. The fractal dimension (D) of the surface is calculated as:

$$D = 2 - \eta \quad [2]$$

We compared fractal surface complexity values across sites using paired t-tests.

Landscape complexity. We used multifractal analysis to measure landscape complexity for each of the 24 study sites. Each study site consists of a 96 x 96 grid of pixels, with each pixel assigned to one of $s = 10$ “classes”. To characterize the scaling properties of landscape pattern, study sites were gridded into square units of side length δ , ranging from $\delta = 2$ (2 x 2 pixels, or 0.36 ha) to $\delta = 48$ (48 x 48 pixels, or 207 ha) and using all whole number factors of 96. For a given side length δ , the “local diversity” H_i of the i th unit is computed as Shannon’s entropy:

$$H_i(\delta) = \sum_{k=1}^s (f_k / \delta^2) \ln (f_k / \delta^2) \quad [3]$$

where f_k is the frequency of k th class in the i th unit. The relative entropy contributed by each unit to the entire site is then determined as:

$$p_i = H_i(\delta) / \sum_{j=1}^{(96/\delta)^2} H_j(\delta). \quad [4]$$

Using these proportional values, the generalized entropy (q^{th} moment of a multifractal) is determined from the function (Rényi 1970; Scheuring and Riedi 1994):

$$I_q(\delta) = 1/(1-q) \ln \sum_{i=1}^{N_\delta} p_i^q \quad [5]$$

From this, the generalized dimension D_q for the q^{th} fractal moment is given by:

$$D_q = -\lim \left[\frac{I_q(\delta)}{\ln(\delta)} \right] \quad [6]$$

In practice, a plot of generalized entropy $I_q(\delta)$ against $\log \delta$ is used to estimate D_q (Hentschel and Procaccia 1983). If a straight line is obtained over the range of δ , D_q is given by the negative of the gradient.

A “family” of generalized dimensions is obtained by varying q . By measuring dimension as a function of q , the multifractal nature of a spatial pattern is revealed (Scheuring and Riedi 1994). As the value of q increases, greater weight is given to grid units with high “local diversity” in calculating D_q . While q can in theory range from $-\infty$ to $+\infty$ (Schroeder 1991), it is generally recommended that $0 \leq q \leq 3$ when analyzing statistical fractals (Appleby 1996). In this study, we characterized the multifractal spectrum of landscape complexity for each study site by plotting D_q against q , with q ranging from 0 to 3 in increments of 0.5. For “classic” fractal objects D_q is a simple linear function of q ; no additional information is obtained by examining higher moments. For multifractal objects, D_q is a non-linear function of q (Schroeder 1991).

Landscape complexity is also a function of class frequency, since the number of possible adjacencies is determined by the frequency distribution of classes (Turner 1989). It is therefore important to determine the degree to which the observed landscape pattern deviates from a random one (Harvey et al. 1983). For each study site, we generated random (null model) landscapes by randomizing pixel positions while maintaining the observed class frequency distribution. Examples of observed and randomized study site landscapes are shown in Fig. 3b, c. Randomized landscapes were analysed using the same multifractal method described above. We use a Monte Carlo procedure (Manly 1991) to test the null hypothesis that the observed landscape patterns are statistically random. Specifically, we compared the D_q profile for each site with those obtained from 100 randomized landscapes.

Multifractal response profiles (plot of D_q vs. q) are analogous to other continuous, highly autocorrelated

processes in biology. We used profile analysis (Morrison 1990) to test for differences in the profiles of "simple" and "complex" sites.

Results

Site physiography

There were no significant differences in physiographic characteristics between "young" (11 - 30 years) and "old" (> 95 years) sites (Table 1a). Terrain slopes were similar (paired $t = 0.46$, $P = 0.67$) and ranged from 0.26° to 0.85° . Topographic fractal dimension ranged from $D = 1.07 - 1.41$, but differences between site pairs were not significant (paired $t = 0.81$, $P = 0.46$).

As anticipated, significant differences were found between the physiography of "simple" and "complex" sites (Table 1b). The "simple" sites have a moderate terrain slope (mean = 2.16°), whereas "complex" sites are almost flat (mean = 0.45° ; paired $t = 3.67$, $P = 0.014$). Topographic fractal dimension of "simple" sites is significantly lower than for "complex" sites (mean $D = 1.09$ vs. 1.34 ; paired $t = 10.03$, $P < 0.001$).

Table 1. Physiographic characteristics (terrain slope and topographic fractal dimension) for the 24 sample sites (site numbering follows Fig 2.): (a) "young" (11-30 year post-burn) and "old" (> 95 years) sites; (b) physiographically "simple" and "complex" sites.

(a)				
	Young		Old	
Site	Slope (degrees)	Surface Fractal	Slope (degrees)	Surface Fractal
11 year				
1	.68	1.23	.85	1.41
2	.26	1.35	.63	1.23
3	.48	1.25	.67	1.24
Mean	.47	1.28	.72	1.29
30 year				
1	.44	1.14	.57	1.16
2	.44	1.07	.44	1.27
3	.26	1.31	.36	1.28
Mean	.38	1.17	.46	1.24
(b)				
	Simple		Complex	
Site	Slope (degrees)	Surface Fractal	Slope (degrees)	Surface Fractal
1	3.30	1.03	.89	1.29
2	4.22	1.07	.57	1.30
3	1.36	1.11	.13	1.44
4	1.78	1.07	.26	1.22
5	1.28	1.04	.36	1.34
6	1.06	1.21	.51	1.47
Mean	2.16	1.09	.45	1.34

Landscape complexity

Observed values of D_q for all sites approached the maximum value of the function ($D \rightarrow 2$), indicating that boreal forests in RMNP have high landscape complexity at all successional stages (Figs. 4, 5). However, the multifractal profiles of all sites deviated significantly from random (Monte Carlo confidence limits, Figs. 4, 5), indicating some degree of "spatial organization" at all successional stages. The multifractal profiles of all sites are broadly linear over the observed scale range (30 to 3000 m), suggesting that landscape complexity can be characterized using a single scaling exponent.

The earliest successional landscapes (Rolling River fire, 11 years) have lower landscape complexity than paired "old" sites (Fig. 4a; $D_0 \approx 1.96$ for "young" sites, vs. $D_0 \approx 1.98$ for "old" sites). However, the multifractal profiles of 30-year old sites (Gunn Lake fire) and paired "old" sites are indistinguishable ($D_0 \approx 1.98$; Fig. 4b). This indicates that changes in landscape complexity attributable to successional processes occur within the first few decades of stand development.

Sites characterized by greater physiographic complexity had higher landscape complexity than physiographically simple sites (Fig. 5; $D_0 \approx 1.94$ for "simple" sites, vs. $D_0 \approx 1.98$ for "complex" sites). Profile analysis confirmed that these differences in landscape complexity are statistically significant (Fig. 5c; $t = 4.57$, $P = 0.001$).

Discussion

This study makes extensive use of simplified (through unsupervised classification) Landsat TM imagery to examine changes in landscape complexity in space and time. By using an unsupervised classification approach, spatial patterns can be characterized without having to resort to an *a priori* delineation of floristic groupings. Previous studies have generally relied on spatially explicit polygon mapping techniques, photographic interpretation, or supervised classification to delineate floristic groupings prior to spatial analysis (e.g., Hall et al. 1991, Frelich and Reich 1995, Ravan and Roy 1997). Such an approach is scale-specific and requires a detailed knowledge of vegetation classes on the ground. Furthermore, the interpretation of results is restricted to the vegetation classes specified. The delineation of vegetation classes is also problematic, as it necessarily results in oversimplification of inherently complex, heterogeneous landscapes (Bettinger et al. 1996).

We used multifractal analysis to characterize spatio-temporal changes in landscape complexity. A number of Landsat-based studies have used band-ratioing tech-

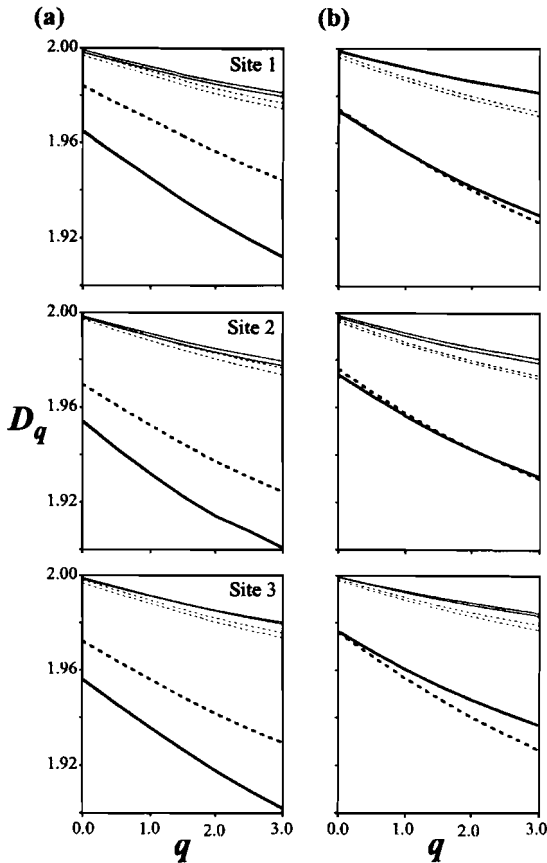


Figure 4. Multi-fractal profiles for “young” (solid thick lines: —) and “old” (broken thick lines: - -) sites: (a) 11-year post-burn “young” sites and paired “old” sites; (b) 30-year post-burn “young” sites and paired “old” sites. Upper and lower bounds for the random landscapes are shown: “young” sites (solid fine lines: —) and “old” sites (broken fine lines: - -).

niques to estimate biophysical parameters of forest stands along successional gradients (e.g., Fiorella and Ripple 1993). Such an approach ignores the complex spatio-structural patterns of spectral reflectance characteristic of forested landscapes. Structural properties of tree canopies (e.g., branching patterns, leaf arrangement and shadowing) are often more important than floristic composition in determining the reflectance properties of forested landscapes (Colwell 1974, Jakubauskas 1996). Surface albedo is affected by the presence of small canopy gaps (Rowe 1993), and may be an expression of emergent properties of canopy architecture (Walker and Kenkel 2000). Local variations in canopy structure, even at the scale of a few metres, produce complex patterns of spectral reflectance in Landsat images (Jakubauskas 1997). A multi-fractal approach is thus well suited to detecting spatio-temporal changes in landscape complexity and structure (De Cola 1994).

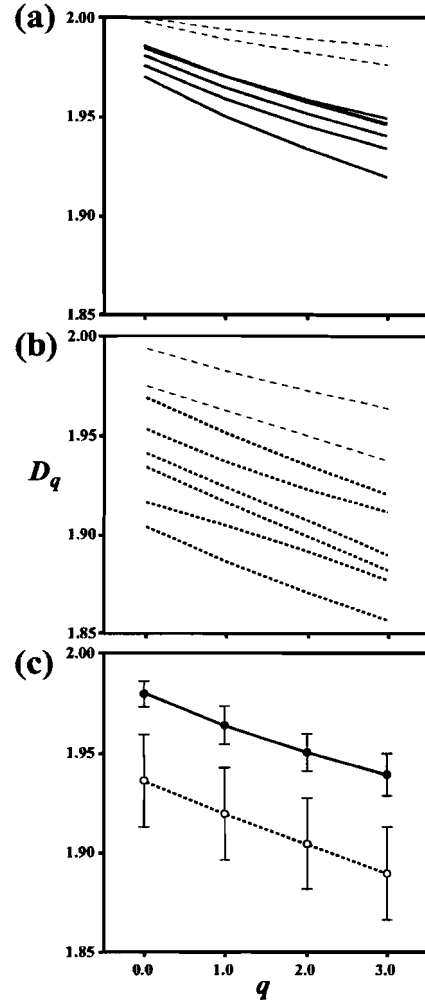


Figure 5. Multi-fractal profiles for “complex” and “simple” sites: (a) “complex” sites (solid thick lines: —) with the upper and lower bounds of the random landscapes (fine broken lines: - - -); (b) “simple” sites (broken thick lines: - -) and envelopes for the random landscapes (fine broken lines: - - -); (c) mean values for the “complex” sites (solid circles and thick line: —) and “simple” sites (open circles and broken thick line: - -), bars indicate the standard deviation.

We found that landscape complexity of “young” (11 year old) forest stands was lower than that of adjacent “old” (> 95 year old) stands. Spatial variation in fire intensity (Turner and Romme 1994) and rapid post-fire recolonization (Pickett et al. 1987; Walker and Kenkel 1998) result in “young” landscapes characterized by compositionally and structurally homogeneous forest patches of relatively uniform size (Frelich and Reich 1995; Fig 6). Over time, these homogenous patches begin to “disaggregate” (He and Mladenoff 1999) as small (10-30 m in diameter) gaps accumulate and progressively “chip away” at the canopy (Frelich and Reich 1995). Both biotic and

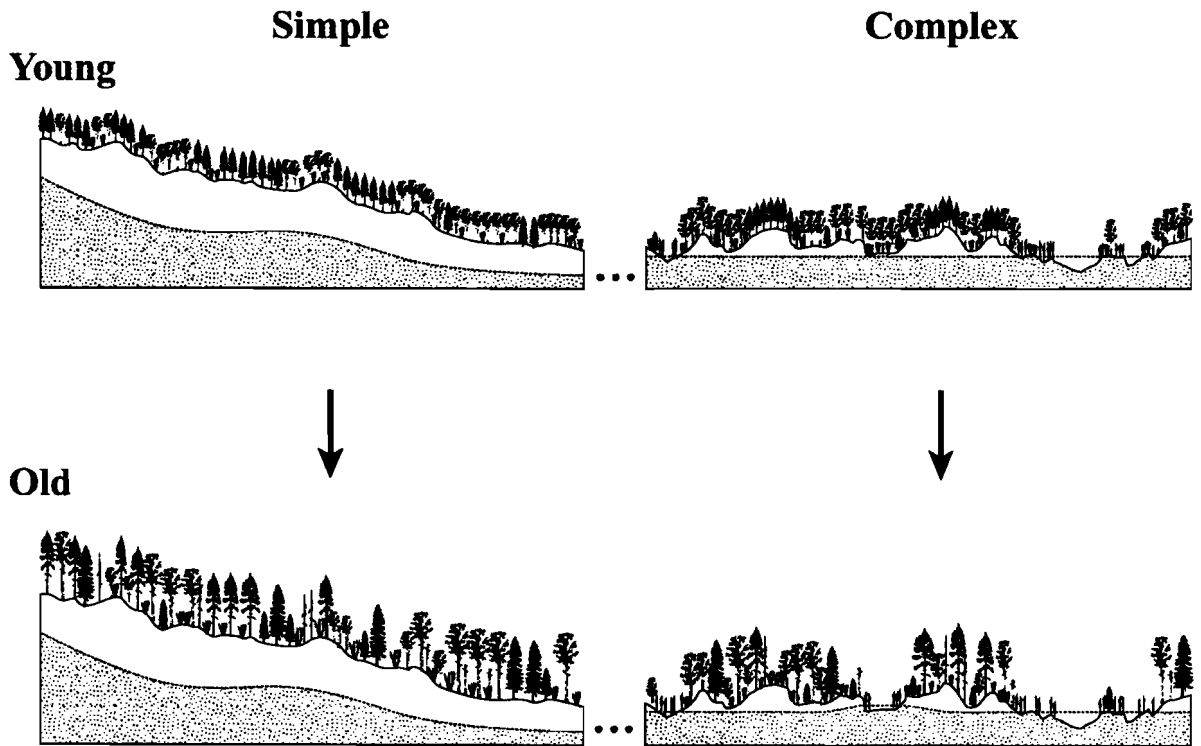


Figure 6. Landscape cross section showing change in canopy structure over time (“young” to “old” sites) and space (“complex” and “simple” sites). The upper limit of the watertable is indicated by a dotted line.

abiotic processes are involved in forest canopy “breakup”. Abiotic processes such as windthrow and lightning damage are stochastic in origin and produce gaps ranging in size from a single large tree branch to an entire stand (Ganström 1993, Dyer and Baird 1997). Biotic processes such as insect damage, ungulate herbivory and beaver activity are also stochastic in nature and variable in spatial extent (Naiman 1988, Holling 1992). Biotic and abiotic disturbances accumulate on the landscape over time, with smaller-scaled events occurring more frequently than larger-scaled ones (He and Mladenoff 1999). The canopy gaps created by such disturbances favour the release of suppressed understory trees, driving succession and producing more diverse, multi-aged and structurally complex forest canopies (Pickett et al. 1987, Frelich and Reich 1995). In 200 year old boreal stands, canopy gap processes may account for over 40% of total forest cover (Kneeshaw and Bergeron 1998). On a Landsat image, these canopy gap processes result in spectral reflectance features that become progressively finer-grained and stochastic as stands age (Rey-Benayas and Pope 1995, Jakubauskas 1997). Over time, canopy gap processes can

produce landscape patterns that are entirely stochastic (De Cola 1994).

Our results indicate that the time required for post-fire boreal landscapes to achieve a high level of spatial complexity is short; by 30 years post-fire, landscape complexity is not discernibly different from that of older (> 95 years) stands (Fig. 4). By contrast, other researchers have concluded that more than a century of cumulative gap-disturbance events are required to appreciably alter landscape complexity (Frelich and Reich 1995, He and Mladenoff 1999). However, these studies specifically focussed on changes resulting from canopy gap formation (tree senescence); changes in the structural properties of the canopy prior to gap formation were not considered. Our approach was to use Landsat imagery to examine all aspects of canopy structure, not just gap formation. Changes in canopy structural properties attributable to differential growth rates, self-thinning, shadowing and differences in leaf distribution and branching patterns all contribute to variation in spectral reflectance values (Colwell 1974, Rey-Benayas and Pope 1995, Jakubauskas 1996). As a result, Landsat imagery is able to detect changes in landscape complexity long before canopy tree

senescence and gap formation occur (Hall et al. 1991, Jakubauskas 1997).

We found that physiographically "complex" sites have greater landscape complexity than "simple" ones. In our study area, physiographic complexity is positively correlated with landscape-scale variation in soil moisture availability. It is this coupling of physiography and resource availability that determines landscape complexity. The spatial pattern of "islands" created by "flooding" a fractal landscape reflects underlying surface complexity (Mandelbrot 1983: Chapter 28). Similarly, a complex physiographic landscape intersected by the water table produces heterogeneous patterns of soil moisture availability (Fig. 6). Because competitive success is often determined by the relative availability of soil resources (Palmer and Dixon 1990, Zobel et al. 1993, Frelich and Reich 1998), vegetation (i.e., landscape) complexity will mimic physiographic complexity.

We conclude that succession (temporal processes) and physiography (spatial processes) interact to determine scale-invariant landscape complexity (Fig. 7). The spatial complexity of early-successional "simple" landscapes is primarily a reflection of post-fire colonization

patterns that produce relatively large and structurally homogeneous forest patches. By contrast, "complex" physiographic landscapes have greater microsite variation, resulting in smaller, more structurally heterogeneous patches. Over time all landscapes develop greater canopy structure complexity, and accumulate stochastic disturbances that "chip away" at the forest patches. As these processes accumulate, the landscape takes on an increasingly finer-grained texture. In physiographically "simple" sites only one or a few landcover-types dominate. Gaps therefore create structural discontinuities in a relatively simple canopy. By contrast, in "complex" physiographic sites stochastic disturbance events accumulate on what was initially a more fine-grained landscape pattern. Our model thus predicts that landscape complexity is lowest in early-successional "simple" sites and highest in late-successional "complex" sites (Fig. 7).

The recognition that physiographic complexity strongly influences forest landscape complexity has potential application in predicting trends in biodiversity. Numerous models predict that complex fractal habitats will have greater overall species richness than simple ones (e.g., Scheuring 1991, Palmer 1992). Complex physiographic surfaces promote the "coexistence" of a

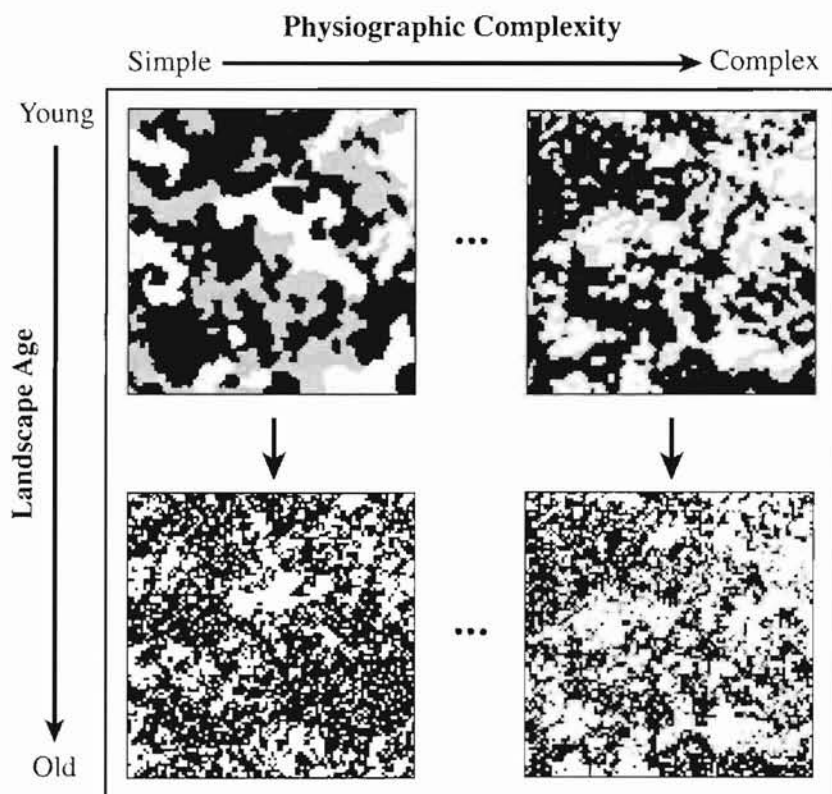


Figure 7. Landscape complexity resulting from canopy structural change in the boreal forest in space and time (see Fig. 6). Landscape complexity and patch heterogeneity is greatest for "old" physiographically "complex" sites.

larger number of habitats. Because landscape (and thus habitat) complexity is scale-invariant, complex landscapes are also expected to support a larger number of species. Recent research supports this view: complex landscapes have been shown to be more biologically diverse than simple ones (Zobel et al. 1993, Rey-Benayas and Pope 1995). The measurement of scale-invariant landscape complexity may therefore have direct application to biodiversity and ecosystem monitoring studies.

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