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Fractal analysis of spatio-temporal dynamics in boreal forest landscapes

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Abstract. Remotely sensed data (LANDSAT) were used to investigate landscape-scale spatial and temporal dynamics in the boreal forests of Riding Mountain National Park, Canada. The analysis of temporal dynamics involved comparing the forest structure of regenerating post-fire sites (11 and 30 years old) to late-successional ones (> 95 years old), while the spatial analysis involved comparing sites of differing physiographic complexity (well-drained vs. impeded drainage). To facilitate the analysis, all images were simplified to $K= 10$ land-cover classes using K-means clustering. Fractal dimensions (computed using the probability-density function) were used to quantify landscape-scale spatial patterning. In addition, randomization tests (observed vs. randomized patterns) were used to compare spatio-temporal trends in landscape pattern. Without exception, observed landscapes were significantly more contagious (clumped) than random (maximally entropic) landscapes. The temporal analysis revealed that landscape-level spatial patterning becomes increasingly entropic during succession: regenerating (post-burn) sites showed greater spatial contagion than late-successional ones. Also, the equitability of land-cover classes declines as succession proceeds. In the spatial analysis, it was found that simple physiographies (well-drained sites) were characterized by a few dominant, overdispersed land-cover classes; less frequent classes showed high contagion. By contrast, sites of complex physiography (impeded drainage) had greater equitability of land-cover classes, and all classes had similar degrees of contagion. The implications of these findings to understanding ecosystem processes and management practices of boreal forests are briefly discussed.

Introduction

The boreal forest is subject to repeated large-scale disturbances such as crown fires, which produce vegetation patches of various successional ages on the landscape (Ritchie 1956; Rowe 1956; Dix & Swan 1971; De Grandpré et al. 1993). Natural fire cycles in the boreal forest range from less than 50 years to 200 years or more (Hirsch 1991; Payette 1992). In North America, large catastrophic burns are initially colonized by fire-adapted species such as jack pine and trembling aspen, producing localized uniform monocultures (Carleton & Maycock 1978). As these stands age, smaller-scale disturbances such as lightning ignitions (Granström 1993), windthrows (Dyer & Baird 1997), ungulate herbivory (Pickett et al. 1987), budworm infestations (Holling 1992; Morin 1994; Bergeron et al. 1995) and beaver flooding (Naiman 1988) gradually 'chip away' at the uniform early succession canopy (Frelich & Reich 1995). These smaller-scale gap disturbances are important in determining local successional pathways and biodiversity in boreal forests (Kenkel et al. 1997).

Underlying environmental gradients are also important in determining vegetation pattern, community composition and biodiversity (Watt 1947; Whittaker 1953; Noble & Slatyer 1980). Gradients in soil moisture are spatially complex over a wide range of scales (Smith & Huston 1989). In areas of impeded drainage, water movement and depth to water table are critical determinants of vegetation composition and patch dynamics (Mitsch & Gosselink 1993; Helm & Collins 1997). Intersection of the water table with an undulating topography creates a spatially complex 'ridge-swale' topography (Walker 1994). Such landscapes are characterized by discrete, oriented patches of vegetation that are sculpted by the movement and impoundment of water (Forman 1995).

Patchiness in boreal landscapes results in the exchange of species, energy and nutrients across ecotones and along interconnecting corridors. Disturbances and strong spatial gradients determine both the creation of new patches and the dynamics of existing patches (Dearden & Rollins 1993). Studies of the relationship between patch size and shape suggest that large contiguous habitat patches have a lower spontaneous extinction rate and are more biologically diverse (Frankel et al. 1995). In addition, biodiversity may decline when habitat patches are fragmented by natural or human disturbances (Dearden & Rollins 1993). Parks and ecological reserves, which are often preserved fragments of a once much larger landscape patch, are often too small to support viable populations of some species (Frankel et al. 1995; Glenn & Nudds 1989). An understanding of the role of natural fragmentation and spatial complexity is therefore critical to developing recommendations and protocols for habitat management at the landscape scale.

Fractal analysis is well-suited to the study of vegetation pattern, since fractals quantify spatial heterogeneity over multiple scales on the landscape (Lavorel et al. 1993; Loehle & Wein 1994; Kenkel & Walker 1996). The term 'fractal' (Mandelbrot 1983) was introduced to characterize scale-invariant phenomena, such as the repeating pattern of a forest canopy (Zeide 1991). Mathematical fractals are 'self-similar' in the sense that the same basic structure is repeated over all spatial scales. The following power-law relationship holds for natural fractal objects:

$$L_\delta \propto \delta^{(1-D)} \qquad [1]$$

where L is the length of the object at measuring scale δ, and D is the fractal dimension (Mandelbrot 1983).

Fractal analysis of remotely-sensed images has been used to quantify landscape patterns (Lam 1990; De Cola 1989), to characterize the spatial structure in forest stands (Ravan & Roy 1997), and to model forest succession (Hall et al. 1991; Fiorella & Ripple 1993). Of the currently available technologies, Landsat is well-suited for terrestrial vegetation studies (Treitz et al. 1992; Wickland 1991), and is particularly useful in investigating landscape-level patterns and processes in boreal forest (Hall et al 1991). The Landsat-5 Thematic Mapper samples seven spectral bands at 30 × 30 m ground resolution (Richards 1993). Vegetation produces a distinctive reflectance spectrum that is a complex function of physiognomy, canopy surface complexity and species composition (Markon 1992; Thomson et al. 1985; Rencz 1985; Hall et al. 1991).

Spatial statistics in landscape ecology have been used mainly for descriptive purposes, and most studies have examined the effects of human-induced habitat fragmentation (e.g. Tinker et al 1998; Ravan & Roy 1997; Rignot et al 1997; Tang et al 1997; Miller et al 1996; Baskent & Jordan 1995; Krummel et al. 1987). In many studies, remotely-sensed images are simplified into a series of binary representations prior to analysis (Milne 1992; Loehle & Wein 1994). Wiens (1995) argues that concepts of spatial 'complexity' must be modelled in terms of both spatial and temporal processes. He also notes that formal theories of landscape spatial patterning lag far behind their description. A consensus is emerging of a strong relationship between spatial pattern and vegetation dynamics (e.g. Jakubauskas 1997; Milne 1992; Hastings et al 1982; Frelich & Reich 1995), but specific hypotheses regarding spatio-temporal processes are still in the formative stages.

The objective of this study is to examine temporal changes in spatial dispersion within boreal forest landscapes, and to examine how spatial dispersion is affected by physiographic complexity. We hypothesize that in the absence of a controlling mechanism such as fire, landscape-level patterns in the boreal forest become increasingly spatially entropic over time. We also hypothesize that more spatially complex physiographic landscapes maintain a 'coarser' grained (less spatially entropic) spatial structure.

Study Area

Riding Mountain National Park (RMNP) is found in the southwestern portion of the province of Manitoba, Canada (Fig. 1). It is 2974 km^2 in size, extending approximately 115 km from east to west and 60 km from north to south at its greatest width (Parks Canada 1977). Most of the RMNP forests are classified as boreal mixed wood (Rowe 1972). This forest type, which reaches its southern and eastern limit in Manitoba, extends westward into central Saskatchewan and Alberta. Most of the Park is surrounded by a band of closed deciduous forest dominated by trembling aspen and bur oak. Further south, these stands give way to trembling aspen 'parkland', which is characterized by groves of aspen intermixed with grasslands.

Physiography and Soils

The most prominent physiographic feature of the study area is the Manitoba Escarpment, which rises approximately 300 m from the eastern Manitoba lowlands (first prairie level, mean elevation of 320 m) to the western Saskatchewan plain (second prairie level, mean elevation 610 m). The eastern border of RMNP parallels the base of this Escarpment. Regosolic soils are characteristic of alluvial fans and terraces along the base of the Escarpment. The uplands of the Saskatchewan Plain, which make up most of RMNP, are characterized by hummocky stagnation moraine deposits of calcareous glacial till (Ritchie 1964; Weir 1983). Soils in these areas vary considerably in drainage, texture and nutrient status (Ritchie 1964). Luvisolic soils predominate, but shallow peat deposits occur in poorly-drained areas throughout the Park (Cody 1988).

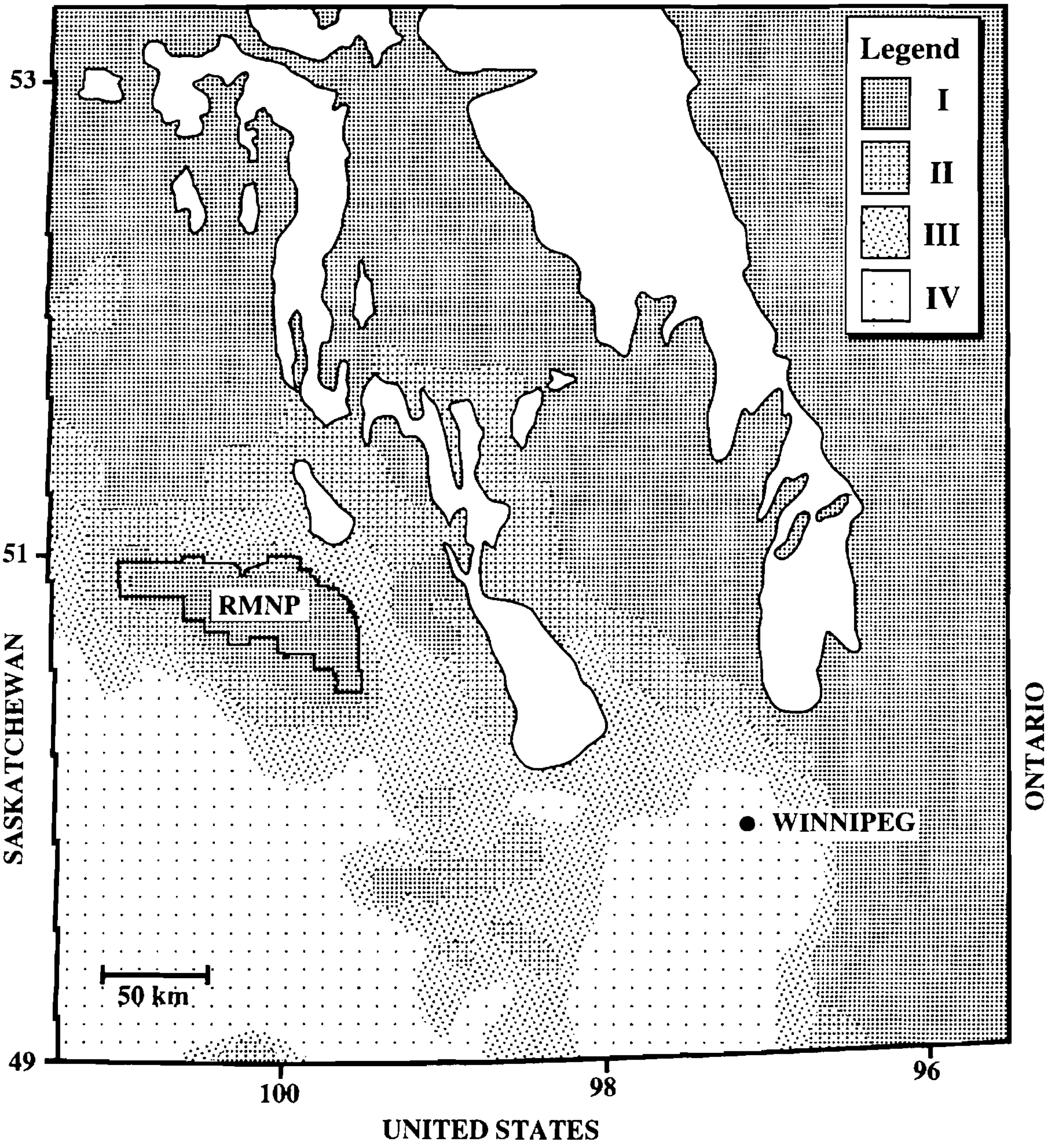


Figure 1. Map of southern Manitoba, Canada showing the location of Riding Mountain National Park. The various shadings are major vegetation zones: I = Boreal Forest (aspen, spruce, fire, pine) ; II = Deciduous Forest (aspen, oak, elm, maple); III = Aspen Parkland (aspen, grasses); IV = Grassland.

Climate

The study area falls within the Humid Microthermal climatic zone (Köppen-Geiger classification), which is characterized by a rain-snow climate of cold winters and warm summers (Waldron 1966). Marked differences in microclimatic conditions occur within RMNP. Total summer precipitation and maximum temperatures are lower on the Saskatchewan Plain, and higher at the base of the Manitoba Escarpment (Ritchie 1964; Bailey 1968). Mean annual total precipitation for the study area ranges from 40-55 cm, about two-thirds of which occurs as rain during the short growing season (Environment Canada 1990). The study area has a mean annual growing season of 160-180 days, and an average of 100-110 frost-free days (Weir 1983).

Vegetation

While mixed wood boreal forest is the predominant vegetation in RMNP (Rowe 1972; Bailey 1968), aspen parkland, bur oak savannah, grassland, and eastern deciduous forest are also encountered (Cody 1988). Post-glacial climatic variation, physiography, edaphic factors, natural and human disturbance, and herbivory have all influenced the structure and development of the natural vegetation. Moderately to well-drained uplands are characterized by semi-open to closed stands of trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*) and/or white spruce (*Picea glauca*). White birch (*Betula papyrifera*) and balsam fir (*Abies balsamea*) are occasionally encountered, usually in the northeast corner of the Park. The sandy soils east of Clear Lake are dominated by jack pine (*Pinus banksiana*) and/or black spruce (*Picea mariana*), in both mature and fire-regenerating stands. Black spruce and eastern larch (*Larix laricina*) are generally encountered in poorly-drained boggy lowlands. Eastern hardwood forest dominated by white elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica* var. *subintegrrima*) and Manitoba maple (*Acer negundo*) is restricted to rich soils at the base of the Manitoba Escarpment. Bur oak (*Quercus macrocarpa*) 'savannah' occurs on steep, exposed slopes and coarse-textured outwash deposits in the extreme north-east corner of the Park. Grasslands form a very minor component of vegetation of RMNP, and include both plains rough fescue and mixed-grass prairie elements (Cody 1988).

Natural Disturbance

Catastrophic crown fires have had a major impact on forest stand composition, structure and development in RMNP. In boreal forests, the oldest stands tend to occur on hygric sites and in areas where physiographic features have afforded some protection from fire (Heinselman 1973). Historical accounts, fire scars and stand age data indicate that large fires occurred in 1822, 1853-1855, 1889-1891, and 1918-1919 (Rowe 1955). Fires were most prevalent during European settlement (1885-1895) as land was cleared for farming (Tunstell 1940; Sentar 1992). Two catastrophic fires in the early 1890's burned over 70% of the area west of the Strathclair trail (which divides RMNP in half), "...not leaving even a spruce seed-tree over large tracts" (Dickson 1909; Evans 1923). Most of the post-fire regeneration in the western region has been to trembling aspen and balsam poplar. Jack pine stands in the southeastern portion of the Park have burned repeatedly since the turn of the century (Sentar 1992). While fire-fighting efforts since the 1930's have dramatically reduced the incidence and extent of forest fires, major fires occurred in 1940 (Whitewater Lake), 1961 (Gunn Lake) and 1980 (Rolling River). A number of smaller fires during the 1930's and 1940's were thought to have been deliberately set by farmers (Bailey 1968). Most of the forests in the north-east portion of RMNP have not burned for at least 125 years (Sentar 1992).

Human Disturbance

Peak logging activity in RMNP coincided with settlement and railway construction at the turn of the century (Bailey 1968). Milling operations were concentrated near settlements along the base of the Manitoba Escarpment (Sentar 1992). Fires often accompanied timber harvesting, as loggers and settlers burned hay meadows and cleared land for farming. White spruce was the most heavily exploited species in RMNP, but jack pine, balsam fir, aspen, bur oak, green ash and black spruce were also taken (Bailey 1968). Sawmills operated within RMNP from the late 1880's until the mid-1940's. From the 1940's through the mid-1960's, high-grading (selective logging of white spruce) occurred on a very limited scale in more accessible areas of RMNP (Sentar 1992).

Materials and Methods

Image Preprocessing

All landscape analyses were performed on a LANDSAT-5 image of RMNP acquired on August 3, 1991. This image was selected for its high atmospheric transmittance and minimal cloud cover. The three reflectance bands most useful in distinguishing vegetation in boreal ecosystems (Bolstad & Lillesand 1992) were used: 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). Some image preprocessing was performed by Radarsat International (Vancouver), including a standard radiometric correction to eliminate variability in sensor response ('destriping', Richards 1993), and a bit error reduction in the geometric registration of the scene. The final raster product conformed to the NAD27 grid system at a pixel resolution of 30 x 30 m. Each of the three LANDSAT bands were centred at 5631.3 km N by 403.4 km E. Prior to classifying the image, a dark order subtraction was used to correct for residual atmospheric effects (Chavez 1988). Band reflectance histograms from the image indicated that a path irradiance model of λ^{-4} (corresponding to a clear atmosphere dominated by Rayleigh scattering, Richards 1993) was appropriate. Additional subtraction constants were then determined from standard path radiance tables (Chavez 1988).

Site Selection

*a) Temporal Analysis: Regenerating vs. Mature Sites.*Three square sites, 100 × 100 pixels (3 × 3 km) in size, were selected from each of two burned areas: (a) 1980 Rolling River fire, 11 years old; (b) 1961 Gunn Lake fire, 30 years old. Each burn site was paired ('matched') to a mature (> 95 year old) site (Fig. 2a, Table 1a). The 'match' sites were carefully selected using several criteria: (a) spatial adjacency to burned sites; (b) matching topography and elevation; (c) matching soil texture and drainage patterns (data from Canada 1979). Careful matching ensured minimal confounding between inherent spatial variation and temporal variation in landscape patterns (i.e. changes related to stand age). All sites occurred on the Saskatchewan Plain.

b) Spatial Analysis: Simple vs. Complex Physiographic Gradients. Six square sites, 100 × 100 pixels (3 × 3 km) in size, were selected from areas characterized by spatially complex physiographic gradients. Each of these 'complex' sites was paired ('matched') to a site having a spatially 'simple' physiographic gradient (Fig. 2b, Table 1b). Spatially 'complex' sites

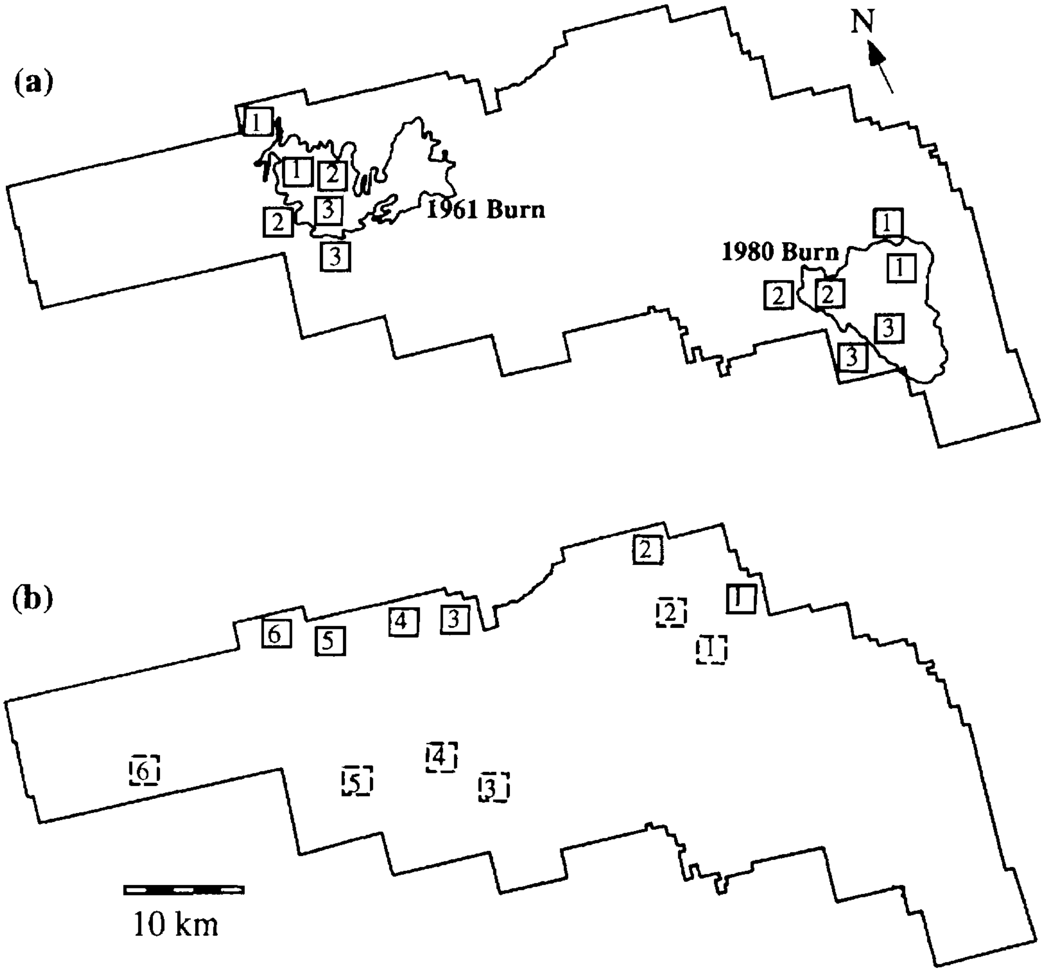


Figure 2. Locations of the 24 sample sites in Riding Mountain National Park: (a) 1961 and 1980 burn sites and their matches; (b) 'complex' physiography sites (dashed lines) and matched 'simple' physiography sites (solid lines).

Table 1. Summary of the physiographic variables and land-cover classes for the 24 study sites shown in Fig. 2.

(a)

		Elevation (m)			Slope*	Class Frequency				Hill's
		Mean	Min	Max	(degrees)	I	II	III	IV	Evenness
11 Year										
	1	720	685	749	.68	.248	.194	.141	.129	.71
	2	657	646	678	.26	.257	.239	.103	.095	.76
	3	666	644	686	.44	.287	.177	.132	.104	.76
>95 Year										
	1	682	604	736	.85	.283	.245	.187	.144	.58
	2	677	644	704	.63	.275	.262	.161	.105	.64
	3	666	640	680	.26	.382	.277	.134	.061	.53
30 Year										
	1	572	540	589	.44	.226	.190	.179	.125	.74
	2	585	564	604	.44	.246	.209	.147	.141	.72
	3	595	580	613	.26	.195	.171	.154	.142	.81
>95 Year										
	1	564	526	581	.57	.294	.292	.140	.073	.62
	2	598	548	615	.44	.337	.164	.162	.107	.68
	3	614	581	634	.36	.263	.240	.112	.110	.72

(b)

		Elevation (m)			Slope*	Class Frequency				Hill's
		Mean	Min	Max	(degrees)	I	II	III	IV	Evenness
Complex										
	1	684	643	722	.89	.187	.182	.146	.131	.77
	2	698	663	734	.57	.237	.202	.194	.138	.71
	3	600	592	617	.13	.213	.197	.136	.131	.83
	4	604	592	615	.26	.183	.172	.140	.109	.74
	5	622	593	638	.36	.248	.172	.169	.142	.82
	6	626	598	664	.51	.270	.241	.122	.114	.69
Simple										
	1	526	410	675	3.30	.407	.258	.170	.092	.46
	2	496	363	669	4.22	.474	.392	.054	.033	.33
	3	502	445	566	1.36	.492	.419	.035	.030	.30
	4	535	472	589	1.78	.561	.365	.037	.017	.27
	5	527	475	584	1.28	.434	.301	.086	.082	.43
	6	539	496	575	1.06	.403	.327	.190	.052	.38

* Slope determined from plane of best fit, using digital elevation data.

exhibited a ridge-swale topography and a stationary elevational profile indicative of restricted drainage, and had soils associated with a high water table (Canada 1979). Conversely, spatially 'simple' sites did not exhibit a ridge-swale topography, had a non-stationary (directional, sloping) elevation profile, and occurred on well-drained soils (Canada 1979). All selected sites had < 5% open water, to ensure that only terrestrial vegetation patterns were being compared. As in the temporal analysis, all sites occurred on the Saskatchewan Plain.

Image reduction

Because the landscape spatial analysis used in this study requires binary data, a simplification of the three-band LANDSAT scenes (24 bit pixels) was required. We used an unsupervised classification (Richards 1993) to reduce each three-band scene into a simplified image. Unsupervised classification is a 'neutral' data reduction strategy, since no prior assumptions are made regarding the floristic composition of pixels; instead, the classification group structure is based purely on spectral information (Richards 1993). The classification method used was non-hierarchical K-means clustering, in which an iterative algorithm is used to determine an optimal partitioning of variable space into K non-overlapping groups (Lillesand & Kiefer 1994). In this study, $K = 10$ 'land-cover' classes were determined for each image; preliminary analyses indicated that ten groups produced an optimal image reduction for our purposes.

To ensure that each landscape comparison was treated identically during the image reduction (classification) phase, each site was paired with its match to create a single image (100 x 200 pixels in size). Unsupervised classifications were performed on these 'paired' images. There were a total of six paired images for the temporal analysis (3 in the 1980 burn, 3 in the 1961 burn), and six paired images for the spatial analysis (Fig. 2).

Data Analysis

Probability-Density Function. Although this method was originally developed for point processes (Voss 1988), it can be used to estimate the fractal dimension of a binary (black/white) pixel image (e.g. Milne 1991). Unlike the better known area-perimeter fractal methods (Hastings & Sugihara 1993), discrete habitat 'islands' are not required. The probability-density function is obtained by successively centering a square (L x L) sampling 'window' on each occupied (black) pixel of the binary image. The number of occupied pixels (n) is counted in each sampling window. The frequencies of these counts are then expressed as probabilities:

$$\sum_{n=1}^{N(L)} \rho_L = 1 \qquad [2]$$

where $N(L) \leq L^2$. For a given value of L, the first moment of the probability distribution is:

$$M(L) = \sum_{n=1}^{N(L)} n\, \rho_L \qquad [3]$$

These computations are repeated for various values of L (L must be an odd number, since windows are centred on occupied pixels). Fractal images follow a power law relationship (Voss 1988: 66):

$$M(L) \propto L^D \qquad [4]$$

The fractal dimension D is thus determined as the log-log slope of the first moment $M(L)$ as a function of L (Milne 1992: 47). Using this method, the fractal dimension has a theoretical range from 1 (minimal dispersion, maximal contagion) to 2 (maximal dispersion or entropy). In practice, the upper limit of D for random landscapes is a function of the frequency of occupied pixels, with the result that dominance and contagion are potentially confounded (cf. Milne 1988; Hargis et al. 1998). To overcome this problem, a randomization technique (Manly 1991) was used to establish a statistical 'baseline' for determining deviations of the observed probability density D-values from random. For each site (binary image), occupied pixels were spatially randomized (maintaining the same pixel frequency on the landscape) and the probability density D recomputed. This step was repeated 19 times per site, to generate expected D-values for spatially random (maximally entropic) landscapes.

For each of the 24 sites (Fig. 2), probability density function D-values were determined separately for the four most frequent 'landscape classes' (96 analyses in total). For each of these 96 analyses, the probability density function was also determined for each of the 19 randomizations of the landscape (1824 randomizations in total). In all analyses, L ranged from 3 to 25 in steps of two (12 values in total). All log-log plots were linear ($r^2 = 0.996$ to 0.999, $p < 0.001$), indicating that the landscapes were statistically self-similar.

Evenness. Changes in the relative frequency of the $K = 10$ land-cover classes was also determined for the spatial and temporal analyses. The Shannon-Weaver diversity index:

$$H = -\sum_{i=1}^{K} p_i \ln p_i \qquad [5]$$

measures the entropy of land-cover classes. The maximum value of $H = \ln K$, which occurs when all land-cover classes are equally frequent ($f_1 = f_2 = \ldots = f_{10} = 0.1$). Hill (1973) suggested a measure of 'effective' richness, $N = e^H$, that has an upper limit of K. Evenness is simply a relativized measure of class equitability (upper limit = 1), computed as:

$$E = N/K \qquad [6]$$

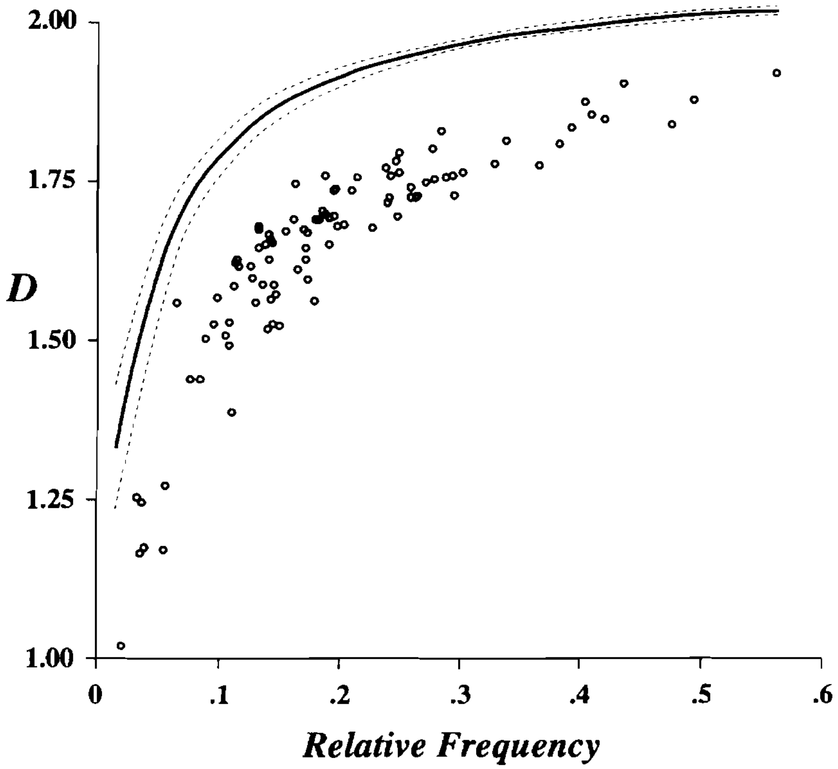
The number of pixels in each land-cover class from the unsupervised classifications were used in the evenness calculations.

Results

Observed vs. Random Landscapes

Fractal dimension (D) values of the four most frequent land-cover classes in each of the 24 sites are summarized in Fig. 3. Without exception, the observed

Figure 3. Probability density fractal dimension (D) as a function of relative class freqency. The confidence envelope for simulated random landscapes is shown (solid line = mean, dashed lines = upper and lower limits). Open circles are values from the 96 land-cover and site combinations used in this study (refer to text for details).



landscapes had significantly greater spatially contagion (lower fractal dimension) than random landscapes of the same frequency. A nonlinear relationship exists between relative frequency and $D$for random landscapes: for frequencies > 40% the expected D= 2, but for frequencies of 25% this declines to D= 1.9. D-values drop precipitously for frequencies < 10%.

Two observed landscapes, and corresponding random landscapes of the same relative frequency, are illustrated in Fig. 4. These examples are taken from the spatial analysis (i.e. comparison of simple vs. complex physiographic landscapes) discussed below. Note that the observed landscapes are considerably less spatially entropic (i.e. have greater spatial contagion) than their corresponding random landscapes.

Temporal Analysis

Comparisons of the 11 year old burns and their matched sites (> 95 years old) are summarized in Fig. 5a. D-values for the burn sites were generally lower than those of the matches sites, and showed greater deviation from the randomly generated landscapes (Fig. 6a). Similar results were obtained in the comparison of 30 year old burns and their matched sites, although trends were somewhat less clear (Fig. 5b). Compared to early-successional (11 year old) sites, mid-successional (30 years old) sites are spatially more similar to late-successional sites (Fig. 6b). Together, these results indicate that landscape-level spatial patterning in boreal forest becomes increasingly spatially entropic during succession: early successional (post-burn) sites are under-dispersed (i.e. greater spatial contagion) compared to late-successional ones.

Landscape evenness (unsupervised classifications, K= 10 land-cover classes) declines during succession, from 0.75 in early-succession (11 and 30 years old) to 0.63 for late-succession (> 95 year old) sites (Table 1). Land-cover class evenness was significantly greater in the 11 year old sites compared to late-succession matched sites (paired t-test, t = 5.02, p = 0.038). Similar results were obtained for the mid-succession (30 year old) sites (t = 3.95, p = 0.059). These results indicate that land-cover classes are more equitable in early-successional sites, but as succession proceeds sites become increasingly dominated by a few land-cover classes.

Spatial Analysis

The six physiographically 'simple' sites are located near the northern boundary of RMNP (Fig. 2) on gentle north-facing slopes (mean slope = 2.17°). By contrast, the six physiographically 'complex' sites are located on gently rolling terrain (mean slope = 0.43°, Table 1). Topographical contour maps for representative

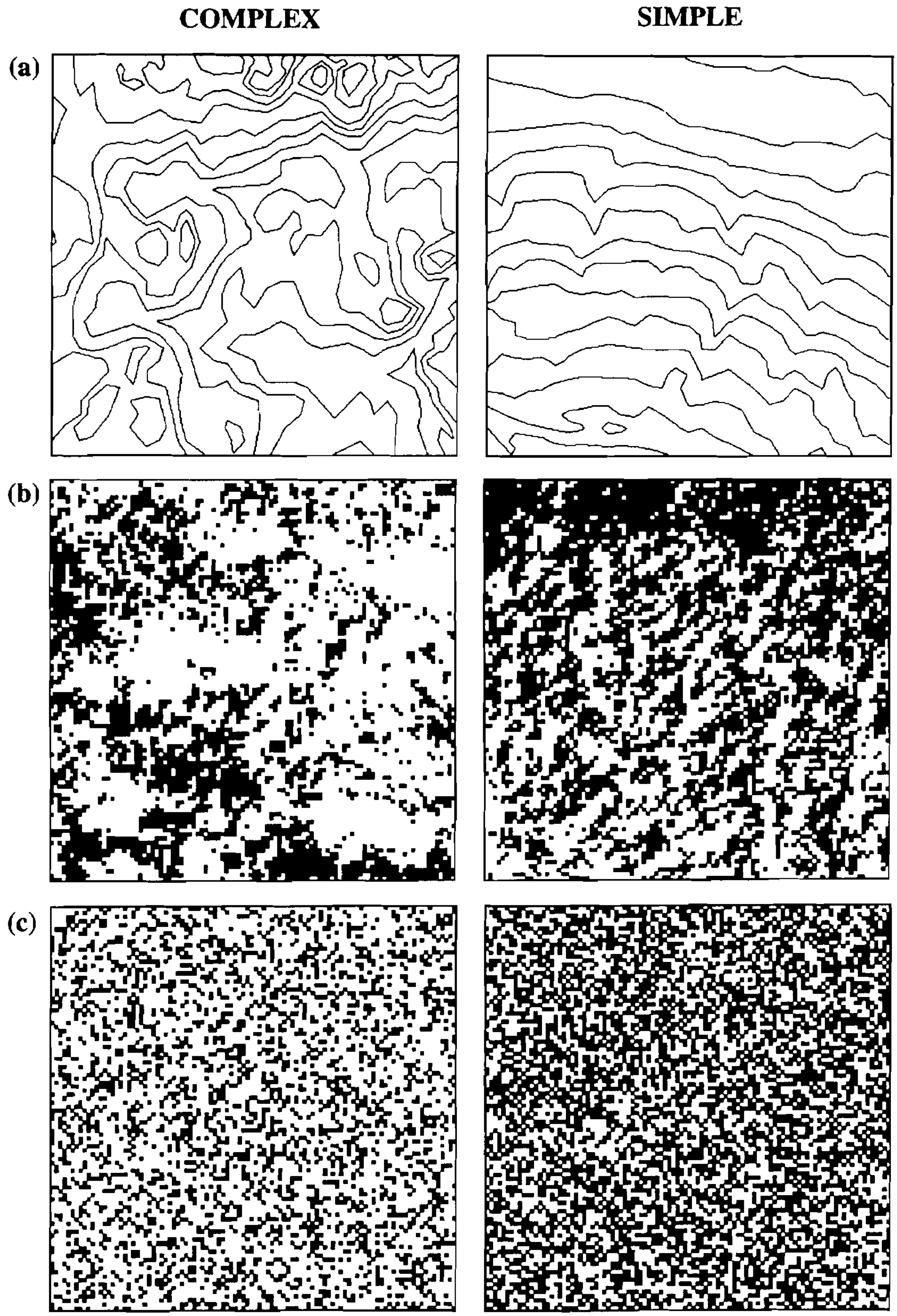


Figure 4. Examples of sites used in comparing complex and simple physiographies: (a) elevation contours; (b) patterns of the most frequent land-cover class: complex $f = 0.3$, $D = 1.75$, and simple $f = 0.5$, $D = 1.83$; (c) simulated random landscapes: $f = 0.3$, $D = 1.89$, and $f = 0.5$, $D = 1.95$.

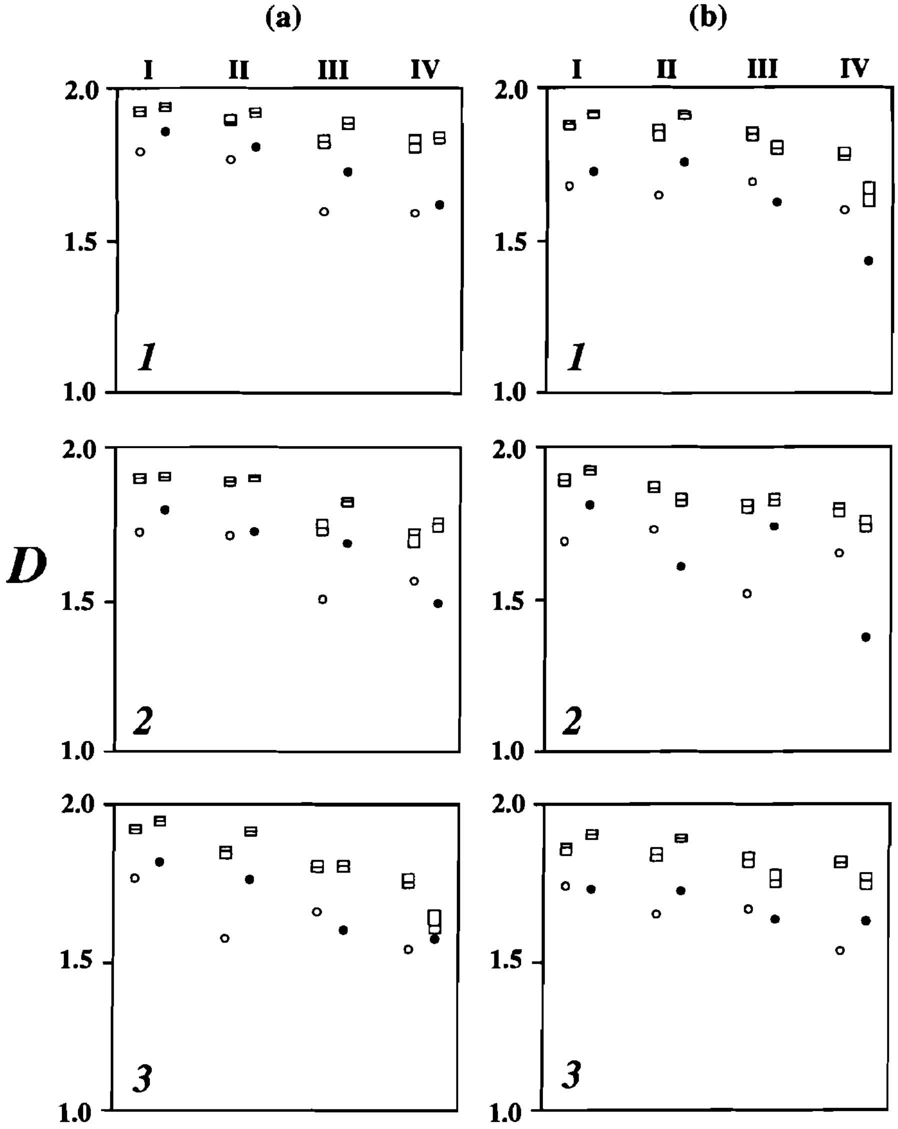


Figure 5. Temporal analysis, showing deviations of probability-density function *D*-values (circles) from random (boxes, showing mean and range) for the four most frequency land-cover classes I - IV: (a) three 11-year old sites (open circles) and matched mature sites (filled circles); (b) three 30-year old sites (open circles) and matched mature sites (filled circles).

'simple' and 'complex' physiographic landscapes are illustrated in Fig. 4. The simple physiographic landscape displays a strongly directional (south to north) drainage pattern, whereas more circuitous drainage patterns characterize the complex landscape.

For complex sites, approximately 75% of the total landscape cover was accounted for by the first four classes, while over 90% was accounted for in physiographically simple sites (Table 1). For the two most frequent land-cover classes I and II, fractal dimensions (*D*) for simple sites were greater than those of complex sites. However, the reverse was generally true for the less frequent land-cover classes III and IV (Fig. 7). Similarly, classes I and II of the simple sites deviated less from random landscapes, but classes III and IV showed a greater deviation (Fig. 8). Landscape evenness was significantly lower in simple sites (0.36 vs. 0.76 for complex sites; $t = 11.03$, $p < 0.001$). These results indicate that simple physiographies are characterized by a few dominant, overdispersed land-cover classes, with the less frequent classes being highly under-dispersed (i.e. high contagion) on the landscape. By contrast, complex physiographies show greater equitability of land-cover classes, and classes have similar degrees of dispersion (deviation from random landscapes) irrespective of their absolute frequency (Fig. 8).

Discussion

The influential theory of vegetation dynamics proposed by Clements (1936) states that self-replacing 'climax' communities are characteristic of specific climatic zones. However, in disturbance-driven ecosystems such as the boreal forest (where catastrophic fire cycles are often < 100 yrs), the development of a Clementsian climax is not expected (Pickett et al. 1987; Horn 1976; Rowe 1961). Our results demonstrate that late-successional stands, as well as physiographically simple landscapes, are spatially dominated by one or two land-cover classes. This should not be interpreted as a validation of Clements' climax model, since few boreal trees are able to regenerate beneath their own canopy as required of a Clementsian 'climax' species (Dix & Swan 1971). The dominance of trembling aspen in RMNP is attributable to the cumulative effects of past disturbances, the ability of the species to root sucker, and its persistence in the canopy of post-fire stands for 100 years or more (Heinselman 1973; Kneeshaw & Bergeron 1996). Rare land-cover classes in late-successional stands may be attributable to gap dynamic processes. Kneeshaw & Bergeron (1998) found that canopy gaps increase from 7% in early succession stands to 40% in old-growth (> 200 year old) boreal forests. Colonization of canopy gaps may reflect a lottery model, in which the first species to establish in a gap usurps the space to the exclusion of other species (Hurtt & Pacala 1995).

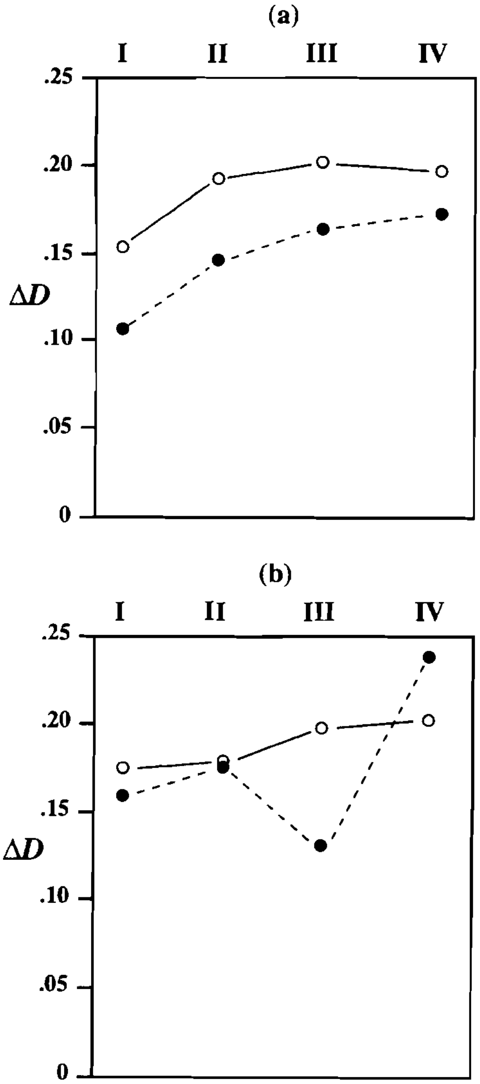


Figure 6. Temporal analysis, mean deviations of observed probability-density function *D*-values from random. (a) 11-year old sites (open circles) and matched mature sites (filled circles); (b) 30-year old sites (open circles) and matched mature sites (filled circles).

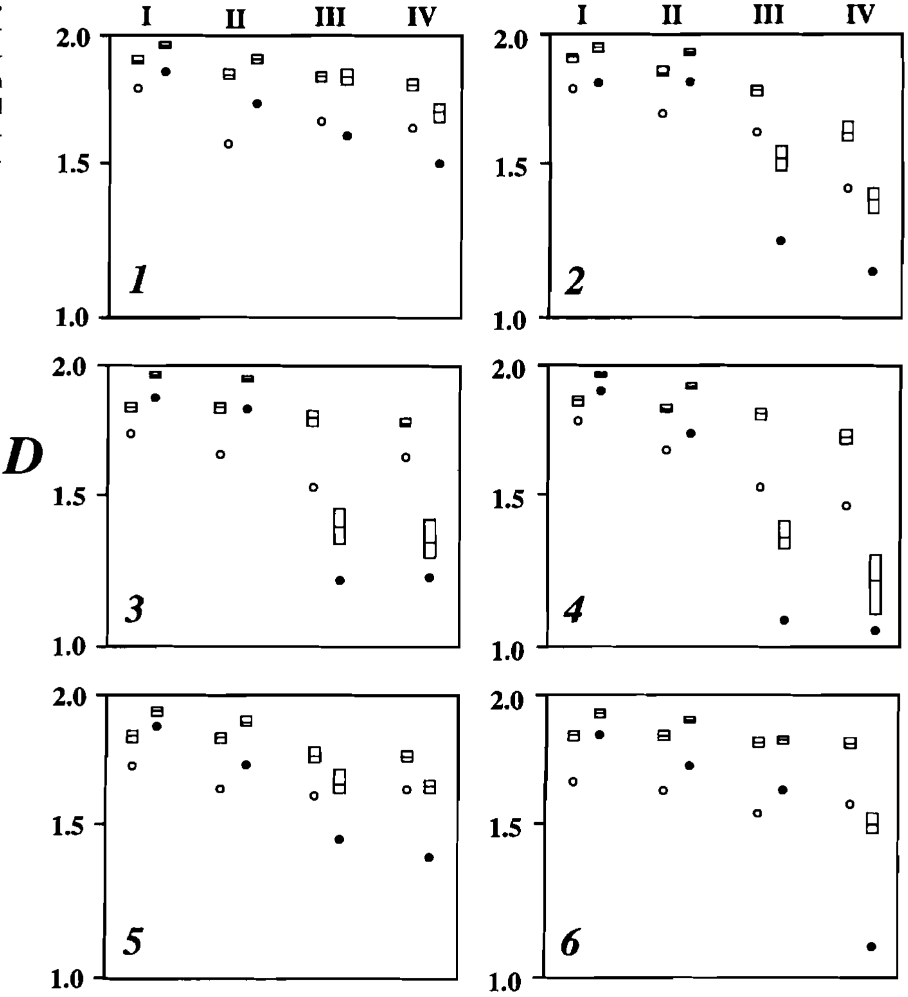
Temporal Dynamics

Our results indicate that early successional sites are under-dispersed (greater contagion) relative to late-successional ones (cf. Frelich & Reich 1995), and that sites become increasingly dominated by a few land-cover classes as succession proceeds (cf. Tinker et al. 1998; Ravan & Roy 1997). These findings are consistent with a three-phase dynamic model of landscape-level structural succession:

1. Colonization Phase. Following a catastrophic fire, boreal forest sites are rapidly recolonized by invasive, opportunistic species (Shafi & Yarranton 1973). High diversity of land-cover classes in early succession is attributable to the combined effects of differential propagule availability (cf. Egler 1954), variation in fire severity, and environmental heterogeneity. In recently disturbed habitats, limited propagule dispersal and differences in the colonization strategies of species result in complex patterns of establishment that promote high contagion of vegetation classes (Holt et al. 1995). In addition, pyric ecosystems are characterized by complex patterns of fire intensity that reflect physiographic variation on the landscape (Turner & Romme 1994; Kushla & Ripple 1997). Considerable variation in fire intensity was also noted in our study sites, from severe fires on well-drained uplands to much lighter fires in moist depressions. Together, these factors result in a floristic landscape that is characterized by discrete, early-successional vegetation patches of simple horizontal and vertical structure. No single land-cover class predominates at this stage of vegetation development.

2. Competition Phase. As succession proceeds, the increasing girth and stature of colonizing tree species has two important consequences at the landscape scale: (a) the development of a more variable and structurally heterogeneous vertical physiognomy; (b) the development of closed-canopy forest stands, leading to greater resource competition and the local extirpation of opportunistic species assemblages. During the competition phase, species are 'sorted' along important environmental gradients (Czárán 1989), with some

Figure 7. Spatial analysis, showing deviations of probability-density function *D*-values (circles) from random (boxes, showing mean and range) for the four most frequency land-cover classes I - IV in each of six sites.



species assemblages being restricted to localized landscape patches where specific environmental conditions prevail (e.g. small wetlands in an upland landscape). Land-cover class evenness declines as fast-growing pioneer trees consolidate their dominance of the landscape (cf. Carleton & Maycock 1978). During this phase, the landscape consists of a matrix of one or two dominant land-cover classes, interspersed with localized environmentally distinct patches (e.g. wetlands), remnant unburned patches (De Grandpré et al 1993), and patches into which pioneer trees have not yet dispersed. As a result, the predominant land-cover classes become increasingly over-dispersed (more spatially entropic) on the landscape.

3. Gap Dynamic Phase. Once the pioneer trees have consolidated their dominance on the landscape, subsequent colonization is largely restricted to canopy gaps created by various small-scale disturbances (Galipeau et al. 1997). Restrictions imposed by dispersal mechanisms will limit the ability of late-successional species (e.g. white spruce, balsam fir) to dominate late-successional stands. Small-scale canopy gaps gradually break up the contiguous forest canopy (cf. Frelich & Reich 1995), creating a distinctive 'peppering' effect in the predominant land-cover classes. This results in a further increase in spatial entropy at the landscape scale (cf. Baker 1992).

Spatial Dynamics

Our results reveal that physiographically 'complex' sites have a greater equitability of land-cover classes than 'simple' ones. In addition, land-cover classes in 'complex' sites have similar degrees of dispersion on the landscape, whereas 'simple' sites are characterized by over-dispersed dominant land-cover classes and under-dispersed (strong contagion) subordinate classes. In 'complex' sites, dominance of a single land-

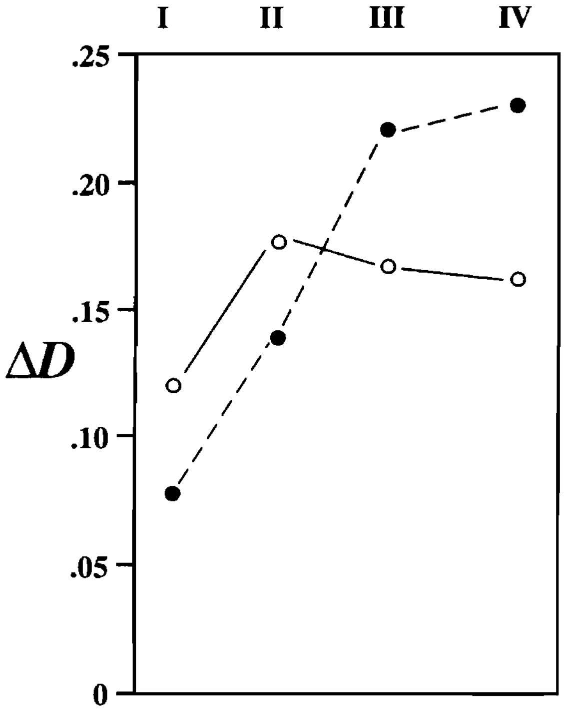


Figure 8. Spatial analysis, mean deviations of observed probability-density function *D*-values (open circles) from random (filled circles).

cover class is precluded by the physiological constraints imposed on the system by strong environmental gradients (Host et al. 1987). Environmental heterogeneity, particularly variations in water table depth in poorly drained landscapes, produces complex scale-dependent patterns of vegetation composition and physiognomy (Palmer & Dixon 1990; Sjörs 1980). As a result, high evenness of land-cover classes is expected in sites where strong and spatially complex environmental gradients prevail. In addition, the most common land-cover classes in 'complex' sites are more contagious than those in 'simple' sites (Figs. 7 and 8); strong environmental gradients result in a highly 'ecotonal' landscape (Forman 1995).

The persistence of long-lived species, which we argue results in land-cover class dominance in physiognomically 'simple' sites, also enhances evenness and contagion in 'complex' sites. Mechanisms promoting spatial patchiness in physiographically 'complex' sites include: (a) interspecific competition: species become distributed along one or more environmental gradients in accordance to their adaptive physiologies (cf. Czárán 1989); (b) patch isolation: land-cover classes below a critical proportion on the landscape (the percolation threshold, = 0.59) become disconnected, greatly diminishing propagule immigration (Lavorel et al. 1993; With & Crist 1995); (c) patch size: species richness may decline by up to 50% for each 10% reduction in optimal habitat (Hansson 1992; May 1975). Together, these mechanisms enhance the influence of long-lived species on the 'local' character of 'complex' landscapes.

To summarize, in complex physiographies (i.e. strong environmental gradients present) the physiological requirements of species assemblages closely match the spatial complexity of the environment, thus maintaining high biodiversity on the landscape (i.e. high evenness of land-cover classes) and a high degree of contagion or patchiness. By contrast, 'simple' physiographies become increasingly dominated by a few land-cover classes, with subordinate classes persisting only as small, highly contagious patches where suitable environmental conditions prevail (e.g. wetlands, areas of excessive drainage). During late succession, gap dynamic processes will "chip away" at the dominant land-cover classes (cf. Frelich & Reich 1995), producing a 'peppering' effect (increased spatial entropy) in simple physiographic landscapes.

Conclusions

We hypothesize that early-successional and 'complex' physiographic landscapes are entropic *between* contagious patches, whereas late successional and 'simple' landscapes are characterized by high levels of entropy *within* patches (Fig. 4b). During succession, there is a 'paradigm shift' from discrete, contagious patches toward 'peppered', highly entropic landscapes (Frelich & Reich 1995; Kenkel et al. 1997). As an analogy, consider changes in the entropy of a gaseous system. Initially, two gases are separated by a simple divider; this is analogous to a landscape in which propagule availability and dispersal are limited. When the divider is removed, the gases are free to disperse and eventually becoming completely intermixed. Analogously, forest stands becomes both a source and sink for dispersing propagules once reproductive age is achieved. Stochastic small-scale disturbances create gaps that are available for colonization, eventually creating a uniformly heterogeneous landscape (i.e. high within-patch entropy). This analogy can of course only be taken so far: the mixing of gases is completely stochastic, whereas in natural landscapes competition, physiological constraints and spatially-varying environmental conditions will maintain some degree of 'order' on the landscape (Fig. 3). For example, strong environmental gradients will prevent the complete mixing of land-cover classes. Thus maximal landscape-scale spatial entropy is expected in late-successional stands on simple physiographic sites, whereas early succession stands and complex physiographic landscapes are expected to be less spatially entropic.

A boreal landscape is a complex mosaic of habitat patches, the spatial juxtaposition of which affects various ecological processes. The movements of species, energy and material between these patches are critical determinants of ecosystem function (Wiens et al. 1985). The population dynamics of both plant and animal species are affected by landscape complexity, since organisms perceive their environment at various spatial scales (Pulliam et al. 1992). Our results indicate that natural landscapes are structurally complex, and that landscape patterning is highly dynamic in space and time. Management of natural habitats must therefore consider more than biodiversity; maintaining variation in landscape structural complexity is also of critical importance.

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