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Large fires as agents of ecological diversity in the North American boreal forest

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Abstract. The present study undertook a hierarchical analysis of the variability within and among some individual fire events in the boreal ecozones of Canada and Alaska. When stratified by ecozone, differences in the spatial and temporal distribution of wildfires were observed in the Canadian Large Fire Data Base that reflect climatic, terrain and land-use differences across the country. Remote-sensing data collected before and after boreal forest fires permitted a rigorous analysis of the variability in burn severity within individual fire events, and the identification of certain fire-prone and more fire-resistant land-cover types. The occurrence of fire skips or islands was related to the distribution of those cover types, resulting in proportionally more unburned area within the perimeter of a burn for larger fires. Differences in burn severity led to differences in post-burn vegetation response of tree, shrub and moss layers that can persist for decades or even centuries. As a result, there can be considerable variability in the survival, density and distribution of residual biota and organic materials. This variability creates a range of post-fire vegetation patterns and contributes much to the habitat diversity of boreal landscapes.

Introduction

The circumboreal forest is the most extensive terrestrial biome on the planet, covering 14 million km^2 and making up 32% of the earth's forest cover (Burton *et al*. 2003). The North American boreal forest constitutes the largest biome in most Canadian provinces and territories, and in the USA state of Alaska. Unlike many tropical and temperate forests, boreal regions have a history of repeated glaciation and glacial displacement, with relatively few tree or other vascular plant species re-establishing in their wake. There is little species endemism in these northern forests, and no 'biodiversity hotspots' when considered on a global scale (Myers *et al*. 2000), all suggesting a relatively homogeneous ecological arena.

Yet that glacial history and the last 10 000 years of post-glacial recovery have generated a forested landscape developed on a mosaic of bedrock outcrops, glacial till, lacustrine deposits, and peaty organic soils in poorly drained depressions, interspersed with crystal-clear lakes, sedge fens and sphagnum bogs. A surprising diversity of such site types can be encountered over relatively short distances. This landscape-scale variability is enhanced by the impacts of relatively frequent wildfire, as the boreal forest is fire-prone (Rowe and Scotter 1973; Johnson 1992). This combination of an active wildfire regime and an underlying mosaic of terrain differences has generated the diversity of ecosystem composition, structure, productivity and habitat values characteristic of the boreal biome (Johnson *et al*. 1998; Weir *et al*. 2000; Bergeron *et al*. 2004).

Coupled with relatively little precipitation and concentrated thunderstorm activity in certain continental portions of the Sub-arctic, plus historic and contemporary human activity in some areas, the Canadian boreal regions experience an average of some 5000 reported ignitions per year (Canadian Forest Service, unpubl. data). In the spring, after the snow is gone but before the vegetation is physiologically active, many fuel types are highly flammable, as deciduous trees have not yet flushed and herbaceous ground cover and conifer foliage often has low moisture content, resulting in an active if short-lived 'spring fire season' (Lewis and Ferguson 1988; Forestry Canada Fire Danger Group 1992). Long-crowned conifers such as black spruce (*Picea mariana* (Mill.) B.S.P.) are interspersed with deep moss layers and peaty soils that often become dry and flammable during summer droughts and during the early fall as vegetation becomes dormant. Despite the large number of fires that occur annually, only ~3% of these fires burn an area ≥200 ha (Stocks *et al*. 2002). However, these large fires account for virtually all of the large-scale impacts in the boreal forest, as they are responsible for over 97% of the area burned (Weber and Stocks 1998).

The lack of fine-scale endemism, combined with a long history of evolutionary adaptation to forest fire, means that large fires in the boreal forest are not usually considered a threat to the

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Fig. 1. Slight differences in terrain, site moisture, fire behaviour and fire return interval can leave behind a complex patchwork of biological legacies and habitats after large fires in northern coniferous forests (Coffee Fire, 1980, northern Saskatchewan; photo by Bill de Groot, used with permission).

persistence of rare species or ecological integrity. In fact, large wildfires in the boreal forest usually promote diversity, and do so at multiple spatial scales (Suffling *et al*. 1988; Angelstam 1998; Bergeron *et al*. 2002). Indeed, as Rowe (1961) concluded, 'The boreal forest is a disturbance forest, usually maintained in youth and health by frequent fires...' Our paper builds on the observation that large fires in boreal North America accentuate climatic and terrain differences (Chapin *et al*. 2006) to generate important ecological diversity (Fig. 1). Here, diversity is broadly defined as the degree of heterogeneity in ecosystem structure and composition. As such, diversity can be variously measured at multiple scales, from microsites and forest stands to the entire boreal forest region.

The goal of the present paper is to examine how large fires generate landscape heterogeneity in the North American boreal forest. This is explored by examining patterns of large fires at multiple spatial scales: across the boreal region from Alaska to Quebec; within large ecological units (ecozones); and within individual fires. Specific objectives entailed evaluating: (1) the rates and variability in burning by large fires among the boreal ecozones of Canada; (2) the relationship between fire size and fire shape complexity; (3) the broad changes in vegetation within very large fires (>100 000 ha) spanning different regions of boreal North America; (4) fine-scale variations in burn severity; and (5) the land-cover composition of burned areas and unburned islands. We synthesised data already described in existing publications and undertook some novel analyses. For the purposes of the present paper, 'burn severity' refers to the full range of on-site ecological impacts within a fire event, from zero severity or fire 'skips' through to different degrees of forest canopy mortality and different degrees of understorey and forest-floor consumption. The importance of such post-fire heterogeneity for the generation and maintenance of ecological diversity is discussed.

Methods

Spatial variation in fire regimes across boreal Canada

Variation in large-fire patterns across Canada from 1959 to 1999 was examined by comparing fire statistics summarised for all boreal ecozones, which are ecological classification units consisting of fairly uniform climate, topography, and vegetation (Ecological Stratification Working Group 1995; Fig. 2). The nine boreal ecozones of Canada vary considerably in terms of topography, fire weather, forest fuels (i.e. vegetation), and human influence (Table 1) (Parisien *et al*. 2006).

Consisting of mapped fires reported by all Canadian provincial and federal fire management agencies, the Canadian Large-Fire Database (LFDB) is a compilation of fires ≥200 ha.

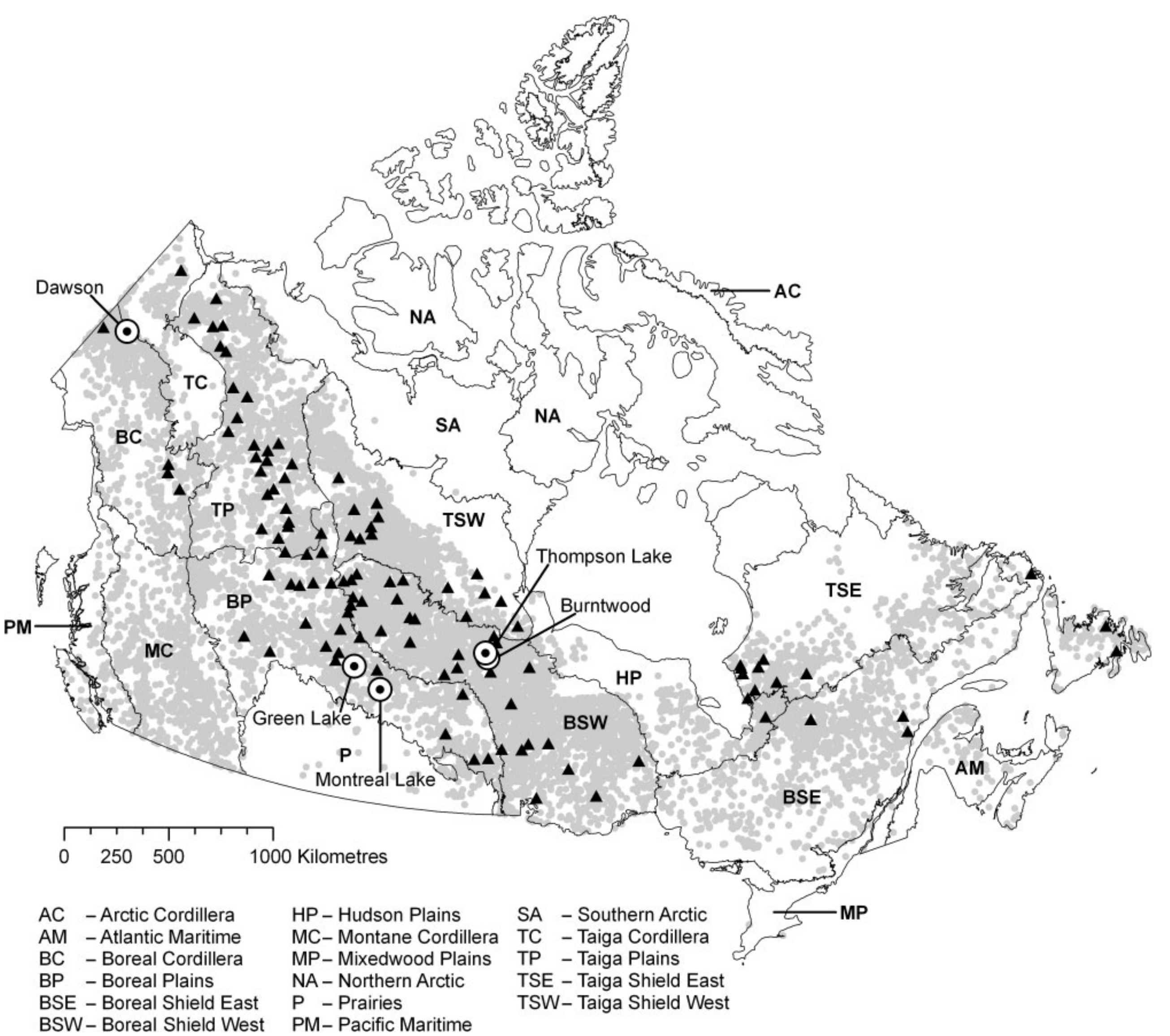

Fig. 2. The ecozones of Canada and the Canadian Forest Service Large Fire Database-Point fires (in grey), 1959–99. The triangles represent those Canadian fires ≥100 000 ha assessed for estimated net primary productivity (NPP) differences, and labelled circles designate the five large fires assessed for differenced Normalized Burn Ratio (dNBR).

There are two versions of the LFDB, the 'LFDB-Point' and the 'LFDB-Polygon'. The former consists of a point database of presumed points of ignition for large fires spanning the 1959–99 period and contains several attributes, such as ignition date and fire suppression actions (Stocks *et al.* 2002; available at http://fire.cfs.nrcan.gc.ca/research/climate_change/lfdb/lfdb_download_e.htm, accessed 13 November 2004). The LFDB-Polygon consists of the mapped perimeter of large fires from 1980 to 1999 (Parisien *et al.* 2006), for which the only non-spatial attribute is the year of burning.

The fire statistics we investigated include the median and the coefficient of dispersion (CD) in the number of large fires per year, the area burned per year, and the size of individual fires; CD is a distribution-free description of data spread defined as the average absolute deviation (of individual observations from the median) divided by the median (Bonett and Seier 2006). For purposes of comparison and to illustrate the skewness generated by a few very large fires, we also provide the mean and coefficient of variation (CV). These descriptive statistics were computed from the 'point version' (LFDB-Point) of the Canadian Forest Service LFDB (Stocks *et al.* 2002), aggregated by ecozone and zero-filled for regions (subsets of ecozones) or years that had no large fires recorded. Bootstrap 95% confidence intervals were computed using the 'boot' and 'boot.ci' functions in *R* (R Development Core Team 2008) for each measure using the bias-corrected percentiles, with non-overlapping confidence intervals interpreted as significant differences. Because of strong departures from normality, these were computed on log-transformed data, although non-transformed values are reported for ease of interpretation. Differences in the number of fires and

Table 1. Topography, climate, fuels (i.e. vegetation), and anthropogenic factors characterising the nine ecozones of the boreal forest of Canada (modified from Parisien *et al.* 2006)

Temp, temperature; precip, precipitation; WS, wind speed; SSR, Seasonal Severity Rating; con:other, coniferous-to-non-coniferous fuels ratio; hum:ltg, human-to-lightning-caused ignitions ratio. Topography information was taken from Ecological Stratification Working Group (1995). Fire weather information was compiled for the fire season (15 April to 30 September); climate data for Taiga Cordillera and Boreal Cordillera are the same. For anthropogenic factors, fire suppression represents the area (%) of the intensive suppression zones, and land use represents the cover (%) of 5-km buffers of the roads

Ecozone	Topography	Fire weather				Fuels		Anthropogenic factors		
		Mean temp (°C)	Mean total precip (mm)	Mean WS ($km\,h^{-1}$)	SSR	Con:other	Lakes, non-fuels (%)	Fire suppression (%)	Land use (%)	Hum:ltg ignitions
Taiga Cordillera (TC)	Mountainous with narrow valleys	14.4	192	7.6	1.7	0.38	55.1	0	14	0.09
Boreal Cordillera (BC)	Mountainous with extensive plateaus and wide valleys	14.4	192	7.6	1.7	2.88	32.2	41	19	1.02
Taiga Plains (TP)	Flat plain with broad lowlands and plateaus	13.8	187	15.6	2.5	1.21	23.0	20	22	0.23
Boreal Plains (BP)	Nearly level to rolling plain	16.1	283	16.1	3.7	1.27	25.6	90	56	1.17
Taiga Shield West (TSW)	Broadly rolling with numerous lakes	14.2	265	17.0	2.8	3.32	47.1	2	2	0.26
Boreal Shield West (BSW)	Broadly rolling with numerous lakes	16.0	398	16.5	1.9	5.06	25.3	54	21	0.61
Hudson Plains (HP)	Low-lying with extensive wetlands	14.4	374	15.8	1.1	1.77	11.6	0	3	0.35
Taiga Shield East (TSE)	Broadly rolling with numerous lakes	12.2	422	18.2	0.7	4.05	33.3	0	3	0.27
Boreal Shield East (BSE)	Broadly rolling with numerous lakes	16.1	473	18.4	1.5	1.69	11.3	70	46	2.22

area burned per year are inferred after being corrected for the area of each ecozone.

The relationship between fire size and fire shape complexity

The idea that large fires have a generally more complex shape than small ones is not new (Eberhart and Woodard 1987; Haydon *et al*. 2000; Parisien *et al*. 2006), but the functional form of this relationship and its applicability across the Canadian boreal forest remains unclear.

The analysis of the relationship between the size of large wildfires and the length (hence shape complexity) of their fire perimeter was explored using 5170 fire polygons from 1980 to 1999 from the LFDB-Polygon dataset. If the wildfire polygons consisted of more than one part, only the largest one was considered. The measure of complexity computed was the shape index (Rempel and Carr 2003), which is the ratio of the measured perimeter length to that of the perimeter length required for a circle of the same area. A circle thus has a shape index of 1 and complex shapes have an index >1 (unbounded). The magnitude of the relationship between the shape index (dependent variable) and log of fire size (independent variable) was calculated using correlation analysis, with its functional form described with a generalised additive model (GAM) with a loess smoother using the 'gam' function in *R*.

Variability in severity within fire events

Variability of burn severity observed within individual boreal fires was quantified at two spatial scales with two sources of satellite data that differed in resolution and in processing methods. First, we assessed the variability in burn severity inferred from the difference between pre-burn and post-burn estimates of net primary productivity (NPP) within 57 very large fires (101 000 to 797 000 ha) that occurred from Alaska to Newfoundland between 1982 and 1998. These NPP estimates were derived from National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) observations of corrected normalised difference vegetation index (NDVI) (Los *et al*. 2000; Tucker *et al.* 2001) and the Carnegie–Ames–Stanford Approach (CASA) light-use efficiency model (Potter *et al*. 1993) as described by Hicke *et al*. (2002). Hicke *et al*. (2003) used these NPP and large fire datasets to estimate post-fire recovery rates, concentrating on the greatest within-fire difference between pre- and post-fire NPP. In contrast, we were interested in the trends of all the 8×8 km (6400-ha) pixels within each fire, and especially the within-fire variability of those pixels. The difference in NPP estimates was based on calculations for pixel-based NPP from the year before a fire minus NPP for the same pixel immediately after the fire (same year, or fire year + 1). These differences primarily indicate the extent of vegetation surviving the fire. Overall means and standard errors in pixel-level pre-minus-post NPP differences were also computed by ecozone, and non-overlapping 95% bootstrap confidence intervals were used to test for significant ecozone differences within the boreal biome. Each individual fire was also individually assessed for the frequency of all pixels that exhibited NPP differences in 10% bins, allowing a quantitative and visual portrayal of within-fire variability; ecozone-level means and medians of this within-fire variability are presented.

Table 2. Characteristics of the five large fires used in the analysis of burn severity and land-cover composition of burned areas and unburned islands
Locations are given in longitude and latitude

Fire name	Location	Area (ha)	Number of islands	Island size (ha) (mean ± s.d.)	Year of burning	Pre-fire image (month–year)	Post-fire image (month–year)
Green Lake, SK	−107.86, 54.72	4961	141	4.1 ± 23.4	2003	08–2001	07–2004
Montreal Lake, SK	−105.64, 53.92	21 653	707	3.4 ± 20.0	2003	08–2001	08–2004
Burntwood, MB	−97.74, 55.80	2328	98	1.3 ± 4.5	2003	07–2001	08–2003
Thompson Lake, MB	−97.93, 56.01	30 401	1914	2.7 ± 15.7	2003	07–2001	08–2003
Dawson, YK	−138.36, 64.05	17 376	29	24.2 ± 42.1	2004	08–2003	07–2005

Second, a more detailed analysis of internal variability was conducted on five large boreal wildfires using Landsat (30×30 m pixel) data. The variation in burn severity was investigated using spectral information represented by the near-infrared and shortwave infrared portions of the electromagnetic spectrum using Landsat Thematic Mapper bands 4 (0.8 μm) and 7 (2.2 μm), respectively. The difference over sum of these two image bands from pre- and post-fire time periods has been referred to as the differenced Normalized Burn Ratio (dNBR) (Key and Benson 2006). A negative or small (<100) value of dNBR indicates regrowth or no appreciable change in vegetation, whereas positive values of dNBR increase with burn severity. The dNBR has been used to evaluate burn severity in the Canadian boreal (Hall *et al.* 2008), Alaskan boreal (Epting *et al.* 2005), and Sierra Nevada regions (van Wagtendonk *et al.* 2004; Collins *et al.* 2007) and elsewhere (French *et al.* 2008). Values of dNBR have typically been used as thresholds to define thematic classes of burn severity from continuous dNBR images (Epting *et al.* 2005; Key and Benson 2006). *In situ* measurements of burn severity using the composite burn index (CBI; Key and Benson 2006) were collected from all five fires from which locally meaningful dNBR thresholds for light, moderate and severe classes were derived from functional models of CBI = *f*(dNBR) for each fire (Hall *et al.* 2008). From these thresholds, the frequency distributions of dNBR values were produced to illustrate the variability within and among each of five sampled wildfires that were selected to illustrate the variability of burn severity within the boreal region. Basic information on fire location, size, timing, and Landsat image acquisition dates is provided in Table 2.

Land-cover composition of burned areas and unburned islands

The post-burn land-cover composition within the fire perimeter and within unburned islands was compared in the five large boreal wildfires analysed above (Table 2) using the Earth Observation for Sustainable Development of Forests (EOSD) land-cover data (Wulder *et al.* 2003). These 25-m resolution raster-based data were derived from fused Landsat and orthophoto images and are available for the forested areas of Canada. The land-cover types are broadly classified in terms of vegetation and openness (e.g. coniferous–dense, broadleaf–open), as well as non-fuel features such as snow or ice, rock, and open water. The cell-based information was sampled for each fire to characterise burned areas and unburned islands that were completely surrounded by burned areas. The mean percentage of each land-cover type was then tallied for each of these categories. Although it is understood that there were directional effects related to wind and fire growth, it is assumed that the entire area within the burn perimeter had an equal chance of being burned, so that the ratio of proportional burned to unburned areas in each cover type was interpreted as the tendency for each cover type to burn or not.

Results

Spatial variation in fire regimes across boreal Canada

The mean number of large fires per year, standardised per unit area, ranged from 0.24 fires per 10 000 km^2 (or a median of 0.12 fires per year per 10 000 km^2) in the Hudson Plains to 1.12 (median 0.89) large fires per 10 000 km^2 in the Boreal Shield West (Table 3). The Shield and Plains ecozones of western Canada have significantly more frequent large fires than those of eastern Canada (Table 3). The coefficient of dispersion in the number of large fires from year to year ranged from 60% (in the Taiga Plains) to 159% (in the Hudson Plains). The annual area burned, when expressed relative to the area of forest available in each ecozone, also varied significantly among ecozones, with the Boreal Shield West (mean 0.77, median 0.50% year^{-1}), Taiga Plains (mean 0.72, median 0.36% year^{-1}) and Taiga Shield West (mean 0.83, median 0.30% year^{-1}) experiencing higher rates of burn than the Taiga Cordillera (mean 0.20, median 0.06% year^{-1}), Taiga Shield East (mean 0.25, median 0.05% year^{-1}), Boreal Shield East (mean 0.14, median 0.05% year^{-1}) and the Hudson Plains (mean 0.13, median 0.02% year^{-1}; Table 3). Interannual variability in the area burned was much greater than variability in the number of fires, with CD values among years ranging from 104 to 532% within ecozones. Furthermore, ecozones with proportionally more area disturbed by fire appear to have lower interannual variability in the area burned ($r = -0.759$, $P = 0.018$, $n = 9$ for CD *v.* the median of area-adjusted area burned).

Fires in the Taiga Plains (with a mean size of 12 748 ha per fire, median 1850 ha), Taiga Shield West (mean 8780 ha, median 1814 ha) and Boreal Cordillera (mean 6297 ha, median 1728 ha) were significantly larger than those in the Boreal Shield East (mean 5182, median 806 ha) and the Boreal Plains (mean 6183, median 682 ha). Variability in median fire size among years (CD = 39 to 371%) was larger than the variability among ecoregions in all ecozones (CD = 10 to 214%) except the Boreal Plains (Table 3). Not only were there large differences among ecozones in the percentage annual area burned, but also in the size distribution of fires. For example, there is a notable paucity of extremely

Table 3. Variation among 41 years (1959–99) and 4 to 20 ecoregions in annual statistics on large wildfires in the nine boreal Canadian ecozones

Median values subtended by the same letter code have overlapping 95% bootstrap confidence intervals, and are thus inferred to be not significantly different

Attribute	Taiga Cordillera	Boreal Cordillera	Taiga Plains	Boreal Plains	Taiga Shield West	Boreal Shield West	Hudson Plains	Taiga Shield East	Boreal Shield East
Number of ecoregions	7	12	18	10	4	9	3	12	20
Forested area (km^2)[A]	117 994	275 581	522 075	580 877	316 568	670 929	328 553	458 375	928 072
Number of large fires (>200 ha) used in analysis	210	745	1215	1722	1229	3073	317	466	1058
Large fires, mean number per year ($n = 41$)	5.1	18.2	29.6	42.0	30.0	75.0	7.7	11.4	25.8
Large fires, mean number per year per 10 000 km^2	0.434	0.659	0.568	0.723	0.947	1.117	0.235	0.248	0.278
CV (%) among years in number per year	98.8	87.0	65.9	70.0	105.1	88.5	120.5	104.2	76.8
Large fires, median number per year ($n = 41$)	3	13	28	34	25	60	4	8	22
Large fires, median number per year per 10 000 km^2	0.254	0.472	0.536	0.585	0.790	0.894	0.122	0.175	0.237
	bc	ab	b	ab	ab	a	c	c	c
CD[B] (%) among years in number per year	122.8	93.4	60.4	66.0	76.1	75.2	159.1	114.0	65.6
Annual area burned, mean km^2 per year	237	1144	3778	2597	2632	5162	419	1126	1337
Annual area burned, mean % area per year	0.201	0.415	0.724	0.447	0.831	0.769	0.128	0.246	0.144
CV (%) among years in annual area burned	203.5	129.5	151.5	165.0	198.3	122.8	202.8	289.1	125.0
Annual area burned, median km^2 per year	66	482	1895	723	957	3374	75	209	501
Annual area burned, median % area per year	0.056	0.175	0.363	0.124	0.302	0.503	0.023	0.046	0.054
	bc	ab	a	ab	a	a	c	bc	b
CD[B] (%) among years in annual area burned	320.9	200.6	168.6	315.9	247.2	103.8	531.7	519.7	223.0
Mean large fire size[C] (ha)	4631	6297	12 748	6183	8780	6887	5423	9904	5182
Overall CV (%) of large fire size[C]	317.5	223.4	426.5	407.2	287.4	275.7	255.4	291.0	360.6
CV (%) among years of large fire size[C] (per ecoregion)	176.4	102.9	117.6	128.7	109.1	60.8	163.5	149.1	130.5
CV (%) among ecoregions of large fire size[C] (per year)	94.0	70.7	119.8	108.2	79.7	92.4	111.0	136.3	128.7
Median large fire size[C] (ha)	1279	1728	1850	682	1814	1296	1006	1567	806
	ab	a	a	c	a	b	bc	ab	c
Overall CD[B] (%) of large fire size[C]	314.7	324.9	650.9	351.7	445.3	489.0	495.2	591.4	594.4
CD[B] (%) among years of large fire size[C] (per ecoregion)	90.3	130.4	249.5	148.0	147.1	276.3	39.1	370.8	75.5
CD[B] (%) among ecoregions of large fire size[C] (per year)	30.0	19.5	137.5	239.5	80.6	213.5	9.8	66.8	15.6

[A] From Stocks *et al*. (2002).
[B] CD = coefficient of dispersion, average absolute deviation/median × 100.
[C] Caution: this refers to fires >200 ha only; mean or median size of all individual large fires recorded in each ecozone.

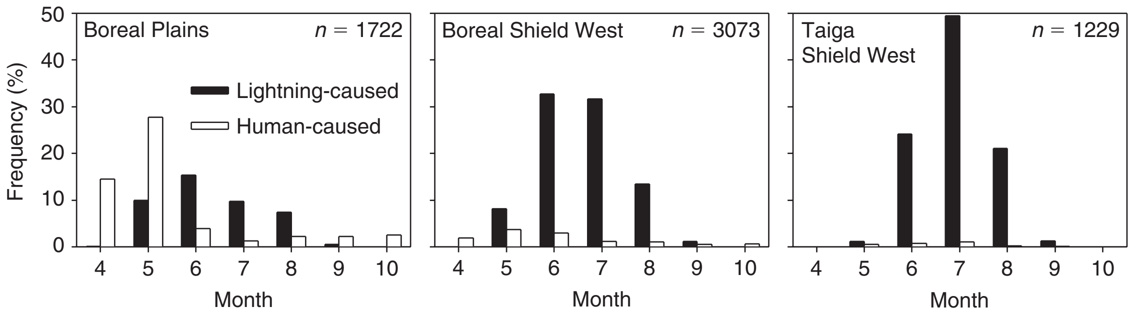

Fig. 3. Frequency of large fires (≥200 ha) originating in different months of the year in three western Canada ecozones spanning an increasing latitudinal gradient, showing the distinction between lightning-caused and human-caused fires.

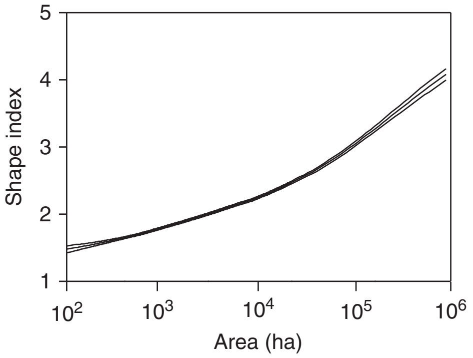

Fig. 4. The generalised additive model of shape index of wildfires ≥200 ha as a function of wildfire log-size using a loess smoother ($n = 5170$). The middle line represents the fitted function, whereas the lower and upper lines are the standard errors.

large fires (>50 000 ha) in the dissected Boreal Cordillera *v.* the dominant role of fires >100 000 ha in the more level (and fuel-continuous terrain of the) Taiga Plains, Boreal Plains, Taiga Shield (both West and East), and Boreal Shield East (Stocks *et al.* 2002; Fig. 2).

There were also distinct patterns with respect to the timing and cause of ignition of large fires in the three western boreal ecozones (Fig. 3). Of these, the southernmost ecozone, the Boreal Plains, had the most active spring fire season (April and May), where most of these spring fires were human-caused. Most of the summer (June to August) fires in the Boreal Plains were caused by lightning, whereas most of the few fall (September and October) fires were human-caused. In contrast, the peak in the number of large fires in the northernmost ecozone, the Taiga Shield West, was in the middle of summer, with very few human-caused large fires. Intermediate trends were observed in the middle ecozone, the Boreal Shield West, although most of the fires were lightning-caused.

The relationship between fire size and fire shape complexity

A fairly strong correlation ($r = 0.490$, $P < 0.001$, $n = 5170$) was observed between the shape index and the logarithm of size for individual large wildfires from 1980 to 1999. The magnitude of this relationship varied among ecozones, from $r = 0.350$ ($P < 0.001$, $n = 245$) in the Hudson Plains to $r = 0.585$ ($P < 0.001$, $n = 649$) in the Taiga Plains ecozone. The shape index varies nearly linearly as a function of log-size for all the pooled fires (Fig. 4), with similar functional forms of the relationship observed in individual ecozones (not shown).

Variability in severity within fire events

Based on the analysis of AVHRR data and estimated pre- and post-fire NPP differences in 57 very large fires across the North American boreal zone, we observed that fires in the Taiga Plains and Taiga Shield West have experienced the greatest NPP changes, more so than the average pre–post differences encountered in Alaska or Boreal Plains fires (Fig. 5). Note that this comparison of populations of pixels came from as few as two, three, or four fires in some ecoregions, with great variability in the Boreal Cordillera.

Average NPP difference values within fires were more or less normally distributed in all ecozones (Fig. 6), but more homogeneous fires (as indicated by narrower distributions) were found in the Hudson Plains, in contrast with other ecozones that have more heterogeneous fires (broader distributions). In addition, ecozones such as the Alaska Boreal Interior and Hudson Plains have median NPP differences lower than other ecozones in which more pixels burn more severely (e.g. the Boreal Shield East). The breadth of these curves at their base may be a direct measure (or at least an indicator) of the degree to which fires have generated diversity in forest structure and function. Some negative values in estimated pre-minus-post fire NPP are probably due to vigorous post-fire recovery (e.g. by fireweed, *Epilobium angustifolium* L., or fast-growing shrubs such as willow, *Salix* spp., or alder, *Alnus* spp.). We note that very large forest fires generate a range of within-fire NPP responses following fire, with mean or median severity (NPP differences) and variance in severity varying among ecozones. These differences in NPP following fire, both within fires and among ecozones, indicate substantial heterogeneity in post-fire vegetation characteristics.

Similar patterns of burn severity were found when individual fires were sampled at a finer resolution. The mapped burn severity classes of the Montreal Lake fire exemplify the level of variation in burn severity experienced by large boreal fires (Fig. 7). The Montreal Lake fire has also been used to illustrate how satellite data can be used in estimating carbon emissions across the mosaic of fuel types and burn severities (de Groot *et al.* 2007). There was a general similarity in the frequency

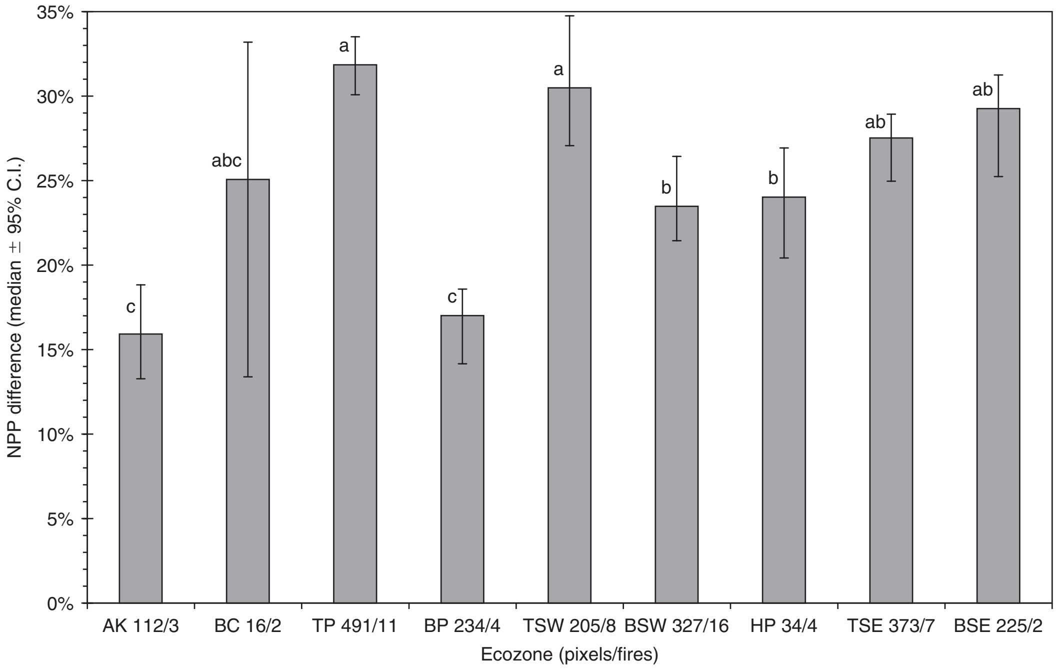

Fig. 5. Median estimated net primary productivity (NPP) differences before and after large forest fires in North American boreal ecozones. Large values denote a greater degree of biomass consumption and burn severity. The number of 6400-ha pixels and the number of individual fires included in each ecozone assessment are given beneath ecozone codes (AK, Alaska Boreal Interior; others are defined in Table 1). Bars sharing the same lower-case letter code have overlapping 95% bootstrap confidence intervals (C.I.), and are not significantly different from each other.

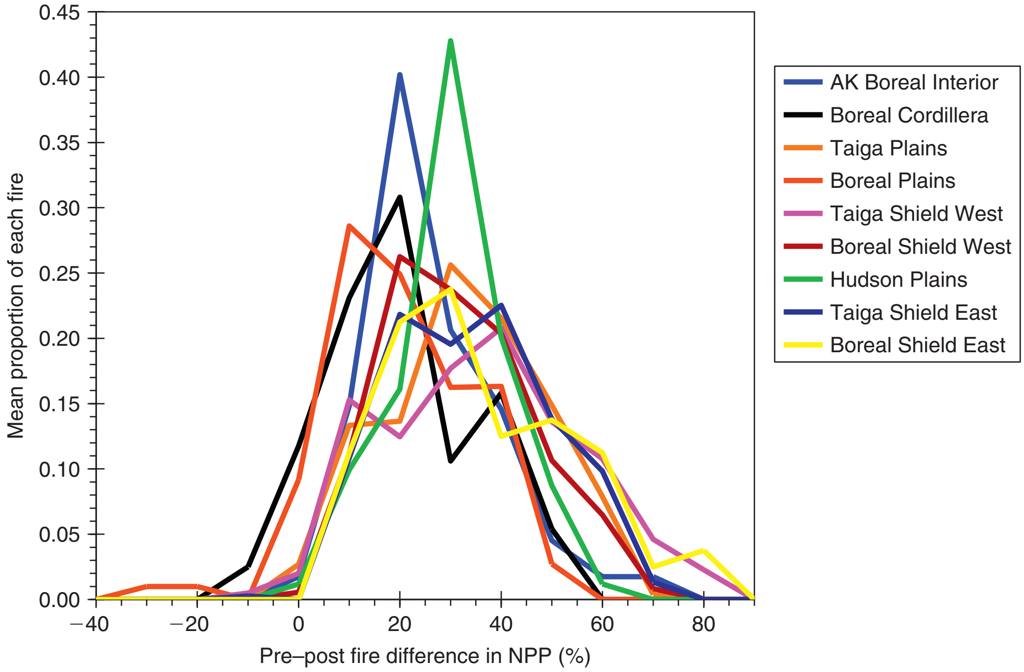

Fig. 6. Frequency distributions of pre- minus post-fire differences in net primary productivity (NPP) within individual large forest fires, averaged for different ecozones in boreal North America. The higher the NPP difference value, the greater the level of biomass consumption; negative values denote some post-burn pixels with NPP estimated to be greater than under pre-burn conditions.

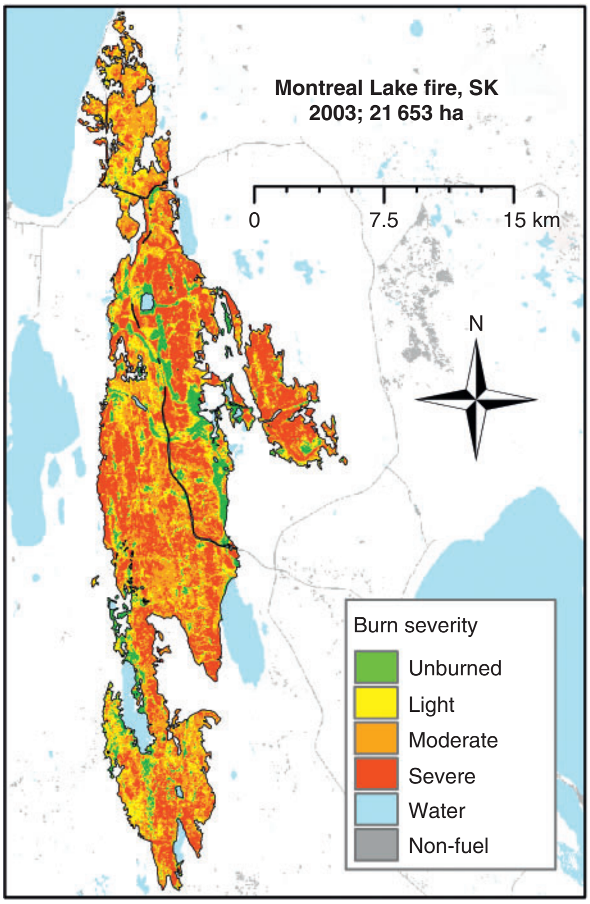

Fig. 7. Differenced Normalized Burn Ratio (dNBR) mapped in 25-ha pixels for the Montreal Lake fire of northern Saskatchewan, with dNBR values themed in classes defined by Hall *et al.* (2008).

distributions of dNBR values across the five fires studied (Fig. 8), whereby most of each fire's area can be described as moderately or severely burned. There was some skewing in the distributions, but a range of burn severities was observed in all fires. That the distribution of dNBR values of the two Manitoba fires had generally a greater number of higher burn severity values is partly attributable to the use of post-burn imagery being acquired in the same year. Burn severity is more apparent at the conclusion of the burn than it is 1 year afterwards because, in the latter case, vegetation response has had an opportunity to occur. However, the adjusted burn severity class derived from the dNBR–CBI relationship (Hall *et al.* 2008) appears to have effectively addressed this bias.

Land-cover composition of burned areas and unburned islands

Although each fire exhibits some individualistic tendencies with respect to the proportion of land-cover composition found burned or in unburned islands, some trends appeared to emerge (Table 4). As highlighted in the burn ratio (of proportional burned and unburned areas by cover type), herbaceous communities (grassland and sedge cover) and coniferous forest tended to burn more than would be expected by their abundance alone, whereas wetland-herb, broadleaf types, and dense mixedwood cover types appear to be more resistant to fires. Despite the high variability in the prevalence of different land-cover types among fires, as evidenced in the coefficient of variation of island land-cover types, the high burn ratios of coniferous cover types was particularly consistent across all fires (Table 4). Through these distinctive probabilities of different cover types burning or remaining unburned, each fire leaves a combination of habitats that differs from that found in the unburned forest.

Discussion

Fire and landscape heterogeneity

Patterns in weather, fuels and landform clearly set the stage for variability in the fire regime and its impacts at different locations in the boreal forests of North America. Large fires are drivers of diversity in boreal forest across a hierarchy of scales. That is: (1) there is diversity within the entire boreal forest of North America as a function of climatic and topographic effects on the rates of burning and the configuration of these areas burned (inter-regional or inter-landscape differences); (2) there are differences within a given landscape mosaic caused by landscape environmental attributes and stochasticity; and (3) there is a diversity within a fire that can be described in terms of burn severity. All of these differences influence the array of habitat available to different species of animals, plants, fungi and microbes, and influence the rate and trajectory of ecosystem processes such as carbon fixation, nutrient cycling and succession. For example, it is well documented that the fire regime has a strong influence on a region's vertebrate fauna (Bunnell 1995), and the return interval and severity of fire can constrain populations of ungulates through their influence on forage availability (Larsen 1980; Thomas *et al.* 1996).

Although all parts of the boreal forest can experience large fires, the spatial distribution of these fires within the biome is far from uniform (Amiro *et al.* 2001; Stocks *et al.* 2002; Kasischke and Turetsky 2006; Parisien *et al.* 2006), thereby creating variability from region to region. Kasischke *et al.* (2002) have noted significant relationships between annual area burned and elevation, aspect, and climatic indicators in the boreal forests of Alaska. Such variability is expressed not only in the rate of burning, but also in the fire size distribution, both factors that may promote heterogeneity (Lertzman *et al.* 1998). The number of annual fires (even large fires) per unit area is surprisingly uniform, in comparison with the much greater year-to-year variability in area burned (Table 3). Fire size too seems to vary more over time than among ecoregions, again emphasising the influence of weather patterns on the overall impact of fire in each ecozone from one year to the next. Organism dispersal into large burns (especially central portions of intensely burned forest) can be limited, with the biological legacies left behind by fire skips or lightly burned areas assuming a greater role in ecosystem recovery (Turner *et al.* 1998; Franklin *et al.* 2000).

Yet another factor that may differentiate fire regimes among ecozones is the time of year at which large fires tend to burn. Ecozones exhibit different temporal patterns of fire within the year (Fig. 3). Two trends are noteworthy: (1) the fire season peaks later for the more northerly taiga zones; and (2) where human populations are more abundant, human-caused ignitions

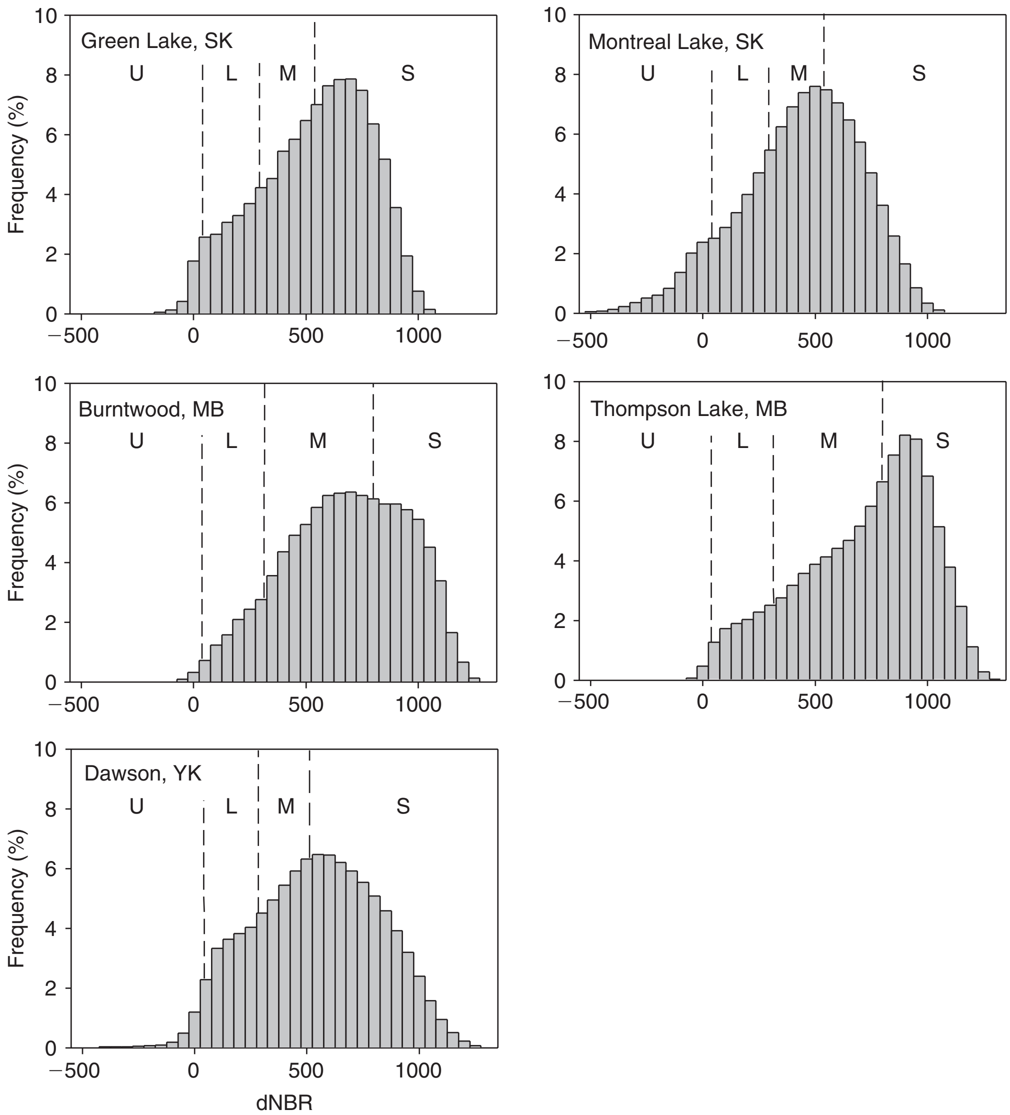

Fig. 8. Frequency distributions of the differenced Normalized Burn Ratio (dNBR) values in 50-unit classes for five large fires of the boreal forest, and their overall mean. The burn severity classes, based on Hall *et al.* (2008) are: U, unburned; L, light; M, moderate; and S, severe.

take on a greater importance and shift the fire regime to having more spring fires. The seasonal distribution of fires is also an important generator of diversity in boreal forests, as their impacts on trees, understorey vegetation and the forest floor can be very different (Weber and Flannigan 1997). In general, spring fires can spread quickly because of high winds, whereas summer fires can be much hotter and deep-burning (Amiro *et al.* 2001, 2004; Parisien *et al.* 2004).

Our results suggest that not only does the number of large fires and their area burned vary among ecozones, but very large fires (≥100 000 ha) may also be categorically different on average. For example, the legacy of fire (as measured by effect on NPP) appears much more variable in the Taiga Shield East. This may reflect a combination of less extreme fire weather (Amiro *et al.* 2004), more fuel discontinuity and no fire suppression (Parisien *et al.* 2006). However, differences among ecozones and their reasons require further examination, as this analysis was based on a somewhat limited number of fires and a very coarse resolution.

Depending on fire intensity, rate of spread, and other aspects of fire behaviour, there can be a large amount of point-to-point variability in burn severity, with consequent impacts on other aspects of the ecosystem (Turner and Romme 1994; Weber and Flannigan 1997). Whether assessed on the ground or at different scales of aerial detection, every forest fire represents a unique combination of fire skips, crown fire, surface fire and ground fire that affect the species and habitat features found in the canopy, the understorey, and in the forest floor. This variation often results in a mosaic of differential tree mortality, forest floor consumption, fire size, fire shape, habitat attributes, and post-fire recovery trajectories. In particular, the combined effects

Table 4. The percentage land cover by EOSD (Earth Observation for Sustainable Development of Forests) land-cover type class within the areas burned and unburned islands for five large boreal fires in western Canada

Land-cover types with burned or unburned areas that never exceeded 1% are not included

Cover type	Green Lake, SK		Montreal Lake, SK		Burntwood, MB		Thompson Lake, MB		Dawson, YK		Mean of five fires			CV of island proportions[B]
	Fire	Islands	Fire	Islands	Fire	Islands	Fire	Islands	Fire	Islands	Fire	Islands	Burn ratio[A]	
Water	0.5	0.4	0.2	7.2	1.7	3.1	0.5	3.5	0	0.9	0.58	3.02	0.192	89.26
Exposed land	1.5	0.3	0.7	1.2	0.7	4.2	0	0	0.9	2.1	0.76	1.56	0.487	108.27
Tall shrubs	0	0	2	0.2	0	0	0.2	0	5.4	16.8	1.52	3.40	0.447	220.33
Low shrubs	0	0	2.7	6.9	0	0	0	0	28.8	41.7	6.30	9.72	0.648	186.47
Wetland – treed	14.2	6.3	15.5	27.1	0.1	0	4.8	3.5	0	0	6.92	7.38	0.938	153.61
Wetland – shrub	3.1	0.7	4.6	12	3.9	12.9	17.2	26.6	0.1	0.1	5.78	10.46	0.553	103.79
Wetland – herb	0.2	0	0.6	2.9	1.5	5.3	1.3	3.9	0	1.1	0.72	2.64	0.273	80.51
Herb	0.9	2.8	0	0	0	0	0	0	5.2	1.9	1.22	0.94	**1.298**	141.05
Dense coniferous	18.9	3.4	22.3	10.9	44.4	4.5	33.4	22	0	0	23.80	8.16	**2.917**	106.43
Open coniferous	19.7	3	32.2	18.9	42.7	17.4	42	22.2	20.5	9.8	31.42	14.26	**2.203**	54.45
Sparse coniferous	0	0	0	0	0	0	0	0	36	14	7.20	2.80	**2.571**	223.61
Dense broadleaf	6.9	31.7	0.2	1.7	5	26.4	0.7	3.4	0.9	6.4	2.74	13.92	0.197	100.86
Open broadleaf	4.4	4.5	1.5	10.9	0	0	0	0	0.1	0.4	1.20	3.16	0.380	149.52
Dense mixedwood	0	0	0	0	0	26.2	0	14.8	0	0	0.00	8.20	0.000	145.49
Open mixedwood	29.5	47	17.4	0	0	0	0	0	1.8	3.5	9.74	10.10	0.964	204.79

[A] Ratio of the mean proportion of burned area to the mean proportion in unburned islands; values >1.0 are highlighted in bold, indicative of more fire-prone cover types.
[B] Standard deviation of the proportional area in unburned islands in five individual fires, divided by the mean proportional area in unburned islands × 100.

of overstorey removal, competition reduction, and forest floor consumption determine the regeneration patterns of tree species after fire in the boreal forest (Zasada *et al.* 1992; Greene *et al.* 1999; Johnstone and Chapin 2006). Researchers in Alaska have recognised five levels of surface fire severity (Dyrness *et al.* 1986) and 30 post-fire successional trajectories (Chapin *et al.* 2006).

Our analysis of large fires from across boreal North America is also consistent with the idea – long recognised by field-based fire behaviour specialists – that the burn severity in large boreal fires is extremely variable. Hall *et al.* (2008) found relationships between dNBR and fuel type and with fire weather, but much remains to be learned about the drivers of spatial heterogeneity in burn severity because the high-resolution data required for these analyses are only starting to be developed. The relationship between burn severity and the fire environment may not be straightforward and, in addition, may vary from one fire to the next, as suggested by Collins *et al.* (2007) in the Sierra Nevada of California. The fact that such broad variability in fire impacts is found in all large fires investigated further emphasises the need to develop these mapping tools and to avoid simplistic descriptions of impacts within a fire perimeter.

With regard to patterns in burn severity, particular attention has been paid to unburned islands, because of their potential importance as seed sources and 'lifeboats' promoting ecosystem recovery after fire (Viedma *et al.* 1997; Charron and Greene 2002; Schmiegelow *et al.* 2006). In fact, in many parts of the Canadian boreal forest, harvesting patterns are now required to include uncut areas that mimic spatial patterns of unburned islands (Bergeron *et al.* 2002; Burton *et al.* 2003; Perera *et al.* 2004). However, given the extreme natural variability in large fires, there cannot be a single prescription for how large or how much area should be kept free of managed disturbance. For example, the five large fires of the present study showed substantial differences in the mean size and number of unburned islands as well as differences among land-cover classes (Table 2).

Virtually all large fires leave some unburned islands (Bergeron *et al.* 2002), but we are only beginning to understand the degree to which, and the reasons why, some land-cover types burn preferentially. Even though these large fires undoubtedly exhibit extreme fire behaviour and consume some area of almost all cover types (Hély *et al.* 2001), our results provide support for landscape-scale interpretations that deciduous forest is less likely to burn in the boreal mixedwood region (Cumming 2001). Kafka *et al.* (2001) likewise concluded, from analysis of patterns within a single large fire in Quebec, that unburned areas were positively associated with deciduous or mixed stands, and negatively associated with conifer stands, whereas severely burned spots were positively associated with conifers and negatively associated with the deciduous stands.

Landscape heterogeneity and ecological diversity

Large fires in the boreal forest not only promote landscape heterogeneity through their variable burn severity and patterns of unburned islands, but also by generating complex edges at their perimeter (Andison 2006). This greater edge and shape complexity is an important template for the ecological diversity of the boreal forest. It is widely recognised that complex edges provide important habitat for wildlife and exhibit distinctive ecosystem processes (Lidicker 1999; Harper *et al*. 2005). The relationship between wildfire perimeter complexity and fire size was consistent with that reported by Eberhart and Woodard (1987) in the boreal forest of Alberta, but our analysis (Fig. 4) extends well beyond the upper range of fire sizes (maximum only 17 770 ha) in their study. This relationship is not unique to the boreal forest, as it also has been observed in Australia (Haydon *et al*. 2000) and Spain (Díaz-Delgado *et al*. 2004); the relationship may be universal, but this remains to be determined. Foster (1983) claims that the increased complexity is largely an effect of wildfires being exposed to different weather conditions. It is also certain that fire growth and spread are influenced by the landscape heterogeneity caused by the mosaic of vegetation types, landforms, and non-fuels (e.g. lakes, exposed rock, anthropogenic features). These are likely to be the same variables that promote variability in burn severity and residual vegetation.

The severity of fire that occurred decades or even centuries ago affects forest productivity and floristics today. Differences in forest fire severity have resulted in documented differences in vascular vegetation (Schimmel and Granström 1996; Chapin *et al*. 2006), mycorrhizal fungi (Dahlberg *et al*. 2001), and soil insects (Wikars and Schimmel 2001) in Swedish boreal forests. Rees and Juday (2002) observed greater floristic richness in burned stands than in logged stands at comparable stand development stages in upland boreal forests in Alaska. Stand structures and community compositions eventually converge and stabilise over the course of stand development and succession in the boreal forest, but clearly the presence of fire, and the variation in burn severity, generates much of the observed diversity in boreal plant communities (Larsen 1980; Chapin *et al*. 2006; Lecomte *et al*. 2006*a*).

In western Quebec, Fenton *et al*. (2005) and Lecomte *et al*. (2006*b*) found that high-severity fires offset the paludification effects (characterised by nutrient unavailability and sometimes extremes of moisture availability) of sphagnum moss build-up over time. Severe fires also reduced the ericaceous cover that appears to constrain tree growth and facilitate sphagnum growth. Stands originating after high-severity or low-severity fires both had an average age of 187 years, but still exhibited marked differences in forest floor thickness, basal area (primarily of black spruce), canopy openness, and cover by sphagnum moss and ericaceous shrub species (Fenton *et al*. 2005). These differences are clearly legacies of variation in burn severity, and, as illustrated in the cases above, that variation is especially pronounced in large fires.

Conclusions

The severity characteristics of large fires vary across boreal North America, in part reflecting climatic differences in vegetation and fuels, and the range of fire weather experienced during lengthy fires. Thus fires often amplify underlying differences in site and climate. The local effects of site and stand attributes on fire severity can generate further diversity in the density and configuration of biological legacies left after a fire. The more we look, the more we find residual structure and uneven burn severity in large boreal forest fires: islands of green and partially burned trees, evidence of surface fire and mixed surface–crown fires, microsite variability in the extent of smouldering combustion (Miyanishi 2001) and the depth of burn. More research is needed to explore the concordance of canopy, understorey, and forest floor impacts, and their spatial dispersion. Residual structure and its effects persist over decades and centuries, with important implications to stand and landscape diversity, productivity, and habitat value (Franklin *et al*. 2000).

There is essentially a natural fire regime prevailing in many parts of the boreal region, and there is much that remains to be learned about boreal forest fires and their ecological role. The world's boreal forests are important reservoirs of carbon, especially in organic soils (Turetsky *et al*. 2002). The intact food webs, hydrological systems, unroaded wilderness and natural disturbance regimes of boreal regions constitute an important resource for biodiversity conservation (Kareiva and Marvier 2003; Leroux and Schmiegelow 2007). Much of the diversity in mortality, residual structure, and biological legacies associated with variability in the fire regime and burn severity found in boreal regions is lost when burned areas are logged to salvage timber value (Lindenmayer *et al*. 2004). Although there may be good reasons to reallocate harvesting quotas to disturbed areas, inadequate retention of naturally burned stands and within-stand structures will result in the loss of important fire-generated habitat and associated biological diversity (Schmiegelow *et al*. 2006).

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