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Fire and the relative roles of weather, climate and landscape characteristics in the Great Lakes-St. Lawrence forest of Canada

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Abstract

Question: In deciduous-dominated forest landscapes, what are the relative roles of fire weather, climate, human and biophysical landscape characteristics for explaining variation in large fire occurrence and area burned?
Location: The Great Lakes-St. Lawrence forest of Canada.
Methods: We characterized the recent (1959-1999) regime of large (≥ 200 ha) fires in 26 deciduous-dominated landscapes and analysed these data in an information-theoretic framework to compare six hypotheses that related fire occurrence and area burned to fire weather severity, climate normals, population and road densities, and enduring landscape characteristics such as surficial deposits and large lakes.
Results: 392 large fires burned 833 698 ha during the study period, annually burning on average 0.07% ± 0.42% of forested area in each landscape. Fire activity was strongly seasonal, with most fires and area burned occurring in May and June. A combination of antecedent-winter precipitation, fire season precipitation deficit/surplus and percent of landscape covered by well-drained surficial deposits best explained fire occurrence and area burned. Fire occurrence varied only as a function of fire weather and climate variables, whereas area burned was also explained by percent cover of aspen and pine stands, human population density and two enduring characteristics: percent cover of large water bodies and glaciofluvial deposits.
Conclusion: Understanding the relative role of these variables may help design adaptation strategies for forecasted increases in fire weather severity by allowing (1) prioritization of landscapes according to enduring characteristics and (2) management of their composition so that substantially increased fire activity would be necessary to transform landscape structure and composition.

Keywords: Area burned; Canadian Drought Code; Deciduous; Enduring landscape characteristics; Fire occurrence; Mixed-distribution; Mixed-effects modeling; Precipitation.

Abbreviations: AAB = Annual area burned; DC = Canadian Drought Code; PAAB = Proportion annual area burned.

Introduction

Extreme weather conditions conducive to fire ignition and spread are paramount in determining the occurrence and final size of large fires (Johnson & Larsen 1991; Diez et al. 1993). For example, drought is associated with both large fire incidence and annual area burned (AAB) in several different forest types (Balling et al. 1992; Girardin et al. 2004; Pereira et al. 2005). Other critical weather variables affecting AAB include temperature, wind speed, and relative humidity (Flannigan & Harrington 1988; Bessie & Johnson 1995; Taylor et al. 2004).

However, fire weather is not the only determinant of fire frequency or area burned. Over the course of one or several fire seasons, area burned can depend on a variety of landscape characteristics, including the arrangement and type of forest fuels, ignitions, topography, suppression effort, and abundance and distribution of firebreaks such as lakes or agricultural land (Hély et al. 2001; Ryan 2002; Lefort et al. 2003). While these variables have been the focus of much boreal forest ecology, we found no studies examining the roles of weather and landscape characteristics in influencing fire in the northern hardwood forests of eastern North America, where these fires do occur (Whitney 1987; Drever et al. 2006).

Our study goals were (1) to characterize the recent history of fires and (2) evaluate competing hypotheses regarding the relative importance of fire weather, climate and biophysical characteristics in explaining variation of fire occurrence and AAB in the Great Lakes-St. Lawrence forest region. Our hypotheses were:
1. Re-charge hypothesis. Fire occurrence and AAB depend on the input and retention of moisture in a given landscape, as a function of precipitation accumulated during the winter before the fire season, precipitation deficit/surplus (total precipitation – potential evapotranspiration) during the fire season, and the percent-

age of the landscape covered by sorted, well-drained glaciofluvial or undivided surficial deposits.

2. *Fire break hypothesis*. Fire occurrence and AAB depend on the amount and type of landscape features that have low flammability and reduce fire spread, i.e. aspen (*Populus* spp.) stands, large lakes and rivers, urban spaces, cropland or other non-burnable surfaces, and the percentage of the landscape covered by wetlands and ridged landforms.

3. *Human influence and access hypothesis*. Fire occurrence and AAB vary as a function of population and road densities. In landscapes with high human and road densities, increased human health and property concerns as well as increased detection, access and prioritization by fire fighting personnel result in lower AAB by large fires than in landscapes where road and human densities are relatively small.

4. *Fuels hypothesis*. Fire occurrence and AAB depend on the relative coverage of flammable fuel types such as boreal spruce stands vs. that of less-flammable fuel types such as aspen stands, agricultural matrix, and urban centres.

5. *Fire weather hypothesis*. Fire occurrence and AAB are a function of maximum fire weather severity as estimated by the yearly maximum value of the Canadian Drought Code (Turner 1972). Larger and more frequent fires burn during years when fire weather is severe.

6. *Amenable climate hypothesis*. Fire occurrence and AAB vary as a function of climatic conditions amenable to growth of the deciduous component in the mixed forests of our region: growing season length (landscapes with growing seasons that begin early in the spring allow the development of relatively less-flammable deciduous canopies), precipitation and potential evapotranspiration, and lightning density during the fire season.

Contrasting the roles of enduring landscape characteristics such as surficial deposits relative to ephemeral severe weather events in explaining variation in fire occurrence and area burned can shed light on which landscapes have a fire regime most intimately tied to weather and thereby may be most susceptible to climate change-related alterations in fire activity e.g. Bergeron et al. (2006).

Methods

Study area: Great Lakes-St. Lawrence forest region

The Great Lakes-St. Lawrence forest region (Fig. 1; modified from Rowe 1972) is transitional between the boreal forest to the north and Carolinian forests to the south. The region has generally low relief with rolling and forested hills, many lakes, wetlands, outwash plains and other glacial features. Elevation ranges from zero to approximately 1120 m above sea level, with a mean of 361 m. It is variously classified as the Mixedwood Shield (Anon. 1997), the western Sugar maple-Yellow birch bioclimatic domain in Québec (Robitaille & Saucier 1998) and the Laurentian Mixed Forest Province in the United States (Bailey 1995). *Acer saccharum* and *Betula alleghaniensis* typically dominate mesic, mid-slope sites. Other common tree species include *Tsuga canadensis*, *B. papyrifera*, *Populus tremuloides*, *Picea glauca*, *Abies balsamea*, *Pinus resinosa* and *P. strobus*. Forests cover 98% of the land area of this 40.5 million ha region.

Units of observation

We used ecodistrict-year as the observational unit i.e. a given year in each of 26 ecodistricts we examined.

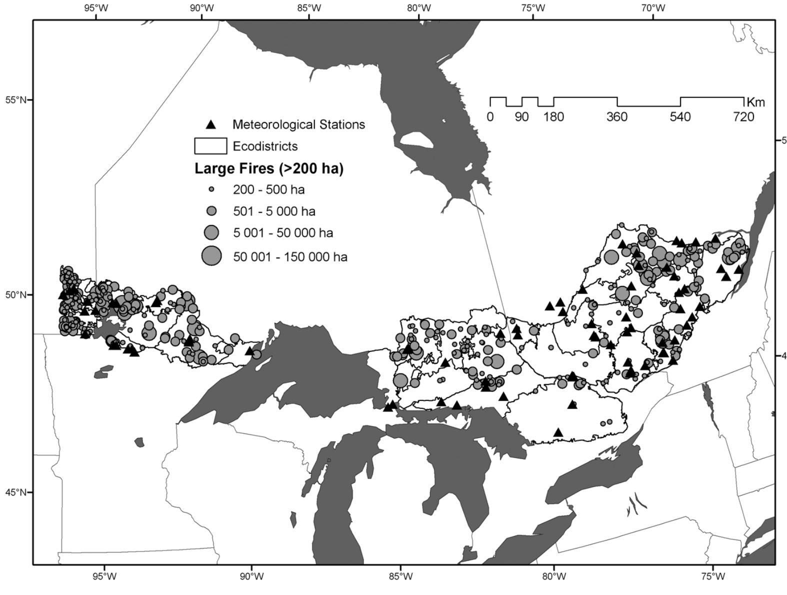

Fig. 1. The Great Lakes-St. Lawrence forest region, location of meteorological stations used, and distribution of large fires analyzed.

Ecodistricts (Fig. 1) are landscape units characterized by distinctive assemblages of relief, geology, landforms and soils, vegetation, water, fauna, and land use (Anon. 1996a). Ecodistrict size varied from 138 417 to 4 808 038 ha (± SD). The fire season consisted of the months between April and October, inclusive.

Proportion annual area burned (PAAB)

Annual area burned for each ecodistrict was calculated from the Canadian Large Fire Database (LFDB). The LFDB is a compilation of all large forest fires in Canada (1959-1999) as reported by provincial and territorial agencies as well as Parks Canada (Canadian Forest Service 2002 URL: http://www.nofc.forestry.ca/fire/research/climate_change/lfdb_e.htm). Although the LFDB includes only fires > 200 ha, these fires account for approximately 97 % of area burned in Canada (Stocks et al. 2002). Our analysis included both human and lightning-caused fires as well as fires of unknown origin. We modeled proportion of total forested area burned each year in each ecodistrict (PAAB) as the dependent variable to account for size differences among ecodistricts. Using only large fires reduced the effect of increasing efficiency in fire detection and suppression during the period of record, as well as the confounding influence on the relationships between the explanatory and fire variables arising from very small, localized fires that do not respond to environmental conditions (Lefort et al. 2004).

Explanatory variables

We examined four types of explanatory variables: human, biophysical, climate and fire weather (see App. 1 for variable descriptions and data sources). While these variables are interrelated and some are included in more than one model, correlations among the explanatory variables were below levels high enough to cause collinearity problems (Burnham & Anderson 2002). The human variables were population and road density. We estimated temporal variability in population density by adjusting the 1991 estimates (Marshall et al. 1999 URL: http://sis.agr.gc.ca/cansis/nsdb/ecostrat/data_files. html) according to trends in rural population growth (as provided by Statistics Canada 2006) in the provinces where ecodistricts occur. Road density was determined by the 2001 Road Network file (Anon. 2001b) and captures only the spatial variation among ecodistricts. This database is the earliest available spatial information that provides coverage of both rural and urban areas for the three provinces in the study area. The biophysical variables related to forest fuel types, as determined from Nadeau et al. (2005), as well as surficial geology and local surface forms, as determined from Marshall et al. (1999). We lumped the three pine classes of forest fuels (red and white pine, mature jack pine, and immature jack pine) into a general pine type as each class represented only a small fraction of each ecodistrict.

The climate and fire weather variables were based on 1961-1990 climate normals and yearly-aggregated data, respectively. To estimate yearly precipitation and the severity of fire weather, we compiled daily total precipitation and maximum temperature data from April to October for 1959 to 1999 from Environment Canada meteorological stations across the study area (Fig. 1). Variables for each ecodistrict were based on stations within a 50-km radius of the ecodistrict centroid, as estimated with ARCVIEW 3.2a (Anon. 1996b), using the station closest to the centroid first and then filling in missing data with more distant stations. Three ecodistricts (407, 409, 412) were not included in this analysis because no stations exist within 50 km of their centroids. We screened and corrected the temperature and precipitation data sets for missing daily values.

We estimated severity of fire weather using the Canadian Drought Code (DC). The DC provides a daily numerical estimate of the weather conditions conducive to fire involving deep, organic, duff layers of forest soil or heavy forest fuels (Turner 1972). This index is calculated on a day-to-day cumulative basis to maintain a ledger of stored moisture by accounting for daily losses through evapotranspiration and gains from precipitation. See Turner (1972), Van Wagner (1987) and Girardin et al. (2004) for computational details. The DC is a significant predictor of fire frequency and area burned in the southern boreal forest of Canada (Girardin et al. 2004). Since the DC is especially responsive to daily precipitation (i.e. one rainfall event can influence the index calculation for several days afterwards; Girardin et al. 2004), any years with more than five days of missing precipitation data were excluded from the analysis.

Model fitting and selection

Our data on fire occurrence and size were markedly non-normal, exhibiting a large clump of values at zero and skewed non-zero values. To deal with this structure, we used a mixed-distribution, mixed-effects model for repeated measures data with clumping at zero and correlated random effects (Tooze et al. 2002; Martin et al. 2005). The mixed-distribution approach combines a model of the occurrence probability of non-zero values (the ‘occurrence model’, based on logistic regression using all ecodistrict-years) with the probability distribution of non-zero values (the ‘area burned’ model, based on lognormal regression using ecodistrict-years where PAAB > zero). Using this modeling approach allowed the simultaneous assessment of how different explanatory variables affected both the occurrence probability of fire and area burned given that a fire was observed. Mixed-effects models incorporate fixed effects of standard explanatory variables with random effects (correlation and non-constant variability) resulting from repeated, random unit observations (different years) on the same unit (ecodistrict). This mixed-effects approach accounts for the sampling replication and lack of independence inherent in repeated measures data (Tooze et al. 2002). Both the occurrence and area burned model components incorporated ecodistrict as a random effect.

We used the MIXCORR macro (Tooze et al. 2002) in SAS 8.2 (Anon. 2001a). This method relies on maximum likelihood methods for model fitting, estimating the effect of explanatory variables on the occurrence probability and mean of non-zero values, and estimating parameters for both model components. A lognormal probability distribution was used to characterize the error structure of the area burned model. The model components were combined when calculating the overall likelihood for mixed-distribution model, which is a product of the likelihoods of each component.
The model forms were:

$$\text{Occurrence: logit(Probability of Fire)} = a_1 + b_1{*}X_1 + c_1{*}X_2 + d_1{*}X_3 \ldots + i_1{*}X_j + u_1 \tag{1}$$

$$\text{Area burned: log(PAAB)} = a_2 + b_2{*}X_1 + c_2{*}X_2 + d_2{*}X_3 \ldots + i_2{*}X_j + u_2 + \sigma_2^2, \tag{2}$$

where a_1 and a_2 are intercept parameters; b_1 and b_2 are slope parameters for explanatory variable X_1; c_1 and c_2 are slope parameters for explanatory variable X_2, and so on; u_1 is the occurrence random unit effect; u_2 is the area burned random unit effect; and σ_2^2 is the variance of the residuals. In addition, the MIXCORR macro determines a parameter of covariance, ρ, of random effects between the occurrence and area burned components of the model mixture. We considered explanatory variables with slope estimates for which the 95% CI excluded zero as having strong support from the data for an effect on our dependent variable.

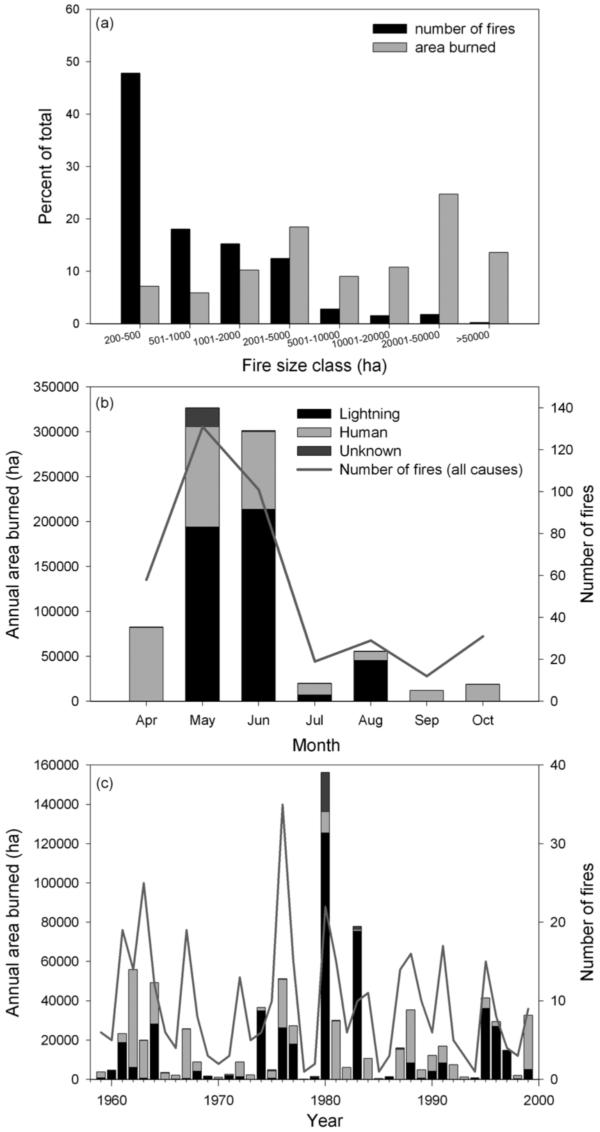

Fig. 2. Annual area burned and fire occurrence of fires > 200 ha (1959-1999) by size class as a percent of total (**a**) and by month (**b**) and year (**c**). The legend in (**b**) applies for (**c**).

We compared our hypotheses using an information-theoretic approach, where the goal is to make inferences from data that minimize information loss by selecting the most parsimonious models from a suite of candidate models (Burnham & Anderson 2002). This approach allowed elucidating what explanatory variables were essential for providing the most parsimonious fit. Akaike's Information Criterion modified for small samples (AICc) was calculated for each model, as well as the difference in AICc between each model and the model with the minimum AIC (ΔAICc) and the Akaike weight (*w*) (Burnham & Anderson 2002). The Akaike weights estimated the probability that each model is the best of the suite and provided the basis for computing the weighted averages of parameter estimates. Model averaging was performed to account for model selection uncertainty (Burnham & Anderson 2002).

Table 1. Results of model selection. Neg2LL indicates the negative 2 log likelihood; K, number of parameters; AIC_c, Akaike Information criterion corrected for small sample sizes; $DAIC_c$, AIC_c difference between a given model and the one for which the strength of evidence is highest; *w*, Akaike weight, the estimated probability a particular model of the set provides the most parsimonious data fit. Variables are described in App. 1.

Model	Hypothesis	Explanatory variables	Neg2LL	*n*	K	AIC_c	ΔAIC_c	*w*
1	*Re-charge*	WinterPpt, PptSurpDef, GlacioFlvComplexPerc, GlacioFlvPlainPerc,UndividedPerc	-922.91	904	16	-890.296	0	0.755
5	*Fire weather*	DC_max	-904.03	904	8	-887.869	2.427	0.224
6	*Amenable climate*	GSL, TotalP_FS,StrikeDen, PE_FS	-910.75	904	14	-882.275	8.022	0.0137
2	*Fire break*	AspenPerc, NonburnablePerc, WaterPerc, RidgedPerc WetlandPerc	-912.94	904	16	-880.326	9.970	0.005
3	*Human influence and access*	RoadDen, PopDen	-896.79	904	10	-876.547	13.749	0.001
4	*Fuels*	PinePerc, BorealSprucePerc, AspenPerc,GrassPerc, BorealMixPerc, NonburnablePerc	-912.53	904	18	-875.754	14.542	0.001

Results

Fire occurrence and area burned

During the fire seasons of 1959 to 1999, 392 large fires burned 833 698 ha in the Great Lakes-St. Lawrence forest of Canada. Fires ≤ 1 000 ha were the most frequent (66% of all fires) yet accounted for only 13% of the total area burned (Fig. 2a). Conversely, fires > 10 000 ha in size accounted for 49% of the total area burned; one fire over 113 514 ha in the western section of the region comprised 14% of the total area burned. Fires showed strong seasonality, with most fires and area burned occurring in May and June (Fig. 2b). Most (55%) of the area burned resulted from lightning-caused fires (Fig. 2b). Except for punctuated spells of high fire activity such as occurred in 1976, 1980 and 1984, fires were quite variable; generally, 6-8 fires burned less than 60 000 ha each year across the study region (Fig. 2c). Large fires burned a small fraction of ecodistrict forest area per year, with a mean of 0.07% (SD = 0.42%; range = 0-6.8%) of ecodistrict forest area per year. Lightning density across the study region showed a seasonal trend characterized by an abrupt increase in June, a maximum in July and a subsequent gradual decrease to October (Fig. 3). Mean monthly maximum Drought Code across the region increased to a peak in August with a slow decrease until October (Fig. 3).

Model selection and parameter estimation

The recharge hypothesis (model 1) received the highest relative support of all the hypotheses considered, having an Akaike weight of 0.75 (Table 1). The next best model was model 5, the fire weather hypothesis, which had an Akaike weight of 0.22, meaning that, based on the evidence ratio (evidence of best model: model of interest), the strength of evidence is 3.4 times greater for the recharge hypothesis than for the fire weather hypothesis. All other models had Akaike weights ≤ 0.01, and thus had relatively much lower support from the data.

Model-averaged parameter values suggested several variables had an effect on the probability of fire occurrence and on proportion of area burned yearly (Table 2) (see App. 2 for maps depicting the spatial variation in these explanatory variables). Of the four general classes of variables analyzed, only fire weather and climate variables affected fire occurrence. Growing season length (GSL) and seasonal precipitation deficit/surplus (PptSurpDef) had a negative effect on yearly proportion burned in both the occurrence and area burned components of the model. Positive effects for two other climate-related variables, maximum DC (DC_max) and total previous-winter precipitation (WinterPpt), were supported by the data for the occurrence but not area burned model component. All the landscape variables for which the data provided strong support related to area burned but not fire occurrence. Of these, human population density (PopDen) and percent of the landscape covered by aspen stands (AspenPerc), by large water bodies (WaterPerc), and by pine stands (PinePerc) showed a negative effect

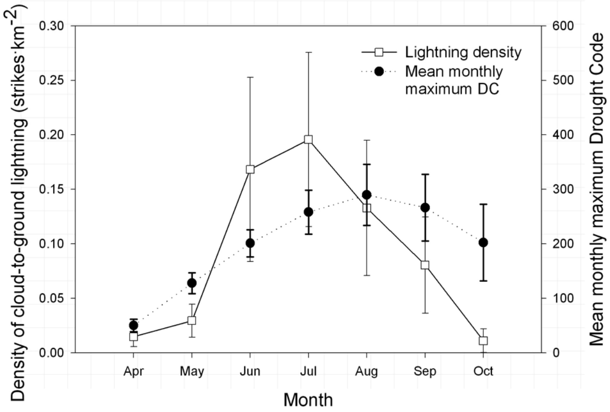

Fig. 3. Mean monthly density (± SD) of cloud-to-ground lightning and mean monthly maximum Drought Code (± SD) in the Great Lakes-St. Lawrence forest region.

on yearly proportion burned, while percent of landscape covered by glaciofluvial plains had a positive effect (GlacioFlvPlainPerc) (Table 2).

Discussion

Recent large fires in the Great Lakes-St. Lawrence forest

Fires greater than 200 ha burned ca. 2.5% of the region's forests over the 41-yr period of study. Annual fire activity represented a small fraction of individual landscapes across the region, on average affecting 0.07% of the forest area in each ecodistrict. This fraction is comparable to the annual burn rate reported since 1940 for the mixedwood (0.05%) and deciduous (0.04%) forests in the Québec portion of the study region (Bergeron et al. 2006). It also corresponds well to modern burn rates documented for the northern hardwood landscapes of Michigan, USA (0.03% between 1985-2000; Cleland et al. 2004) and northern New England (0.02% between 1961-1978; Fahey & Reiners 1981). In all these cases, burn rates are an order of magnitude less than the recent burn rates typically reported for boreal landscapes north of the region; for example, Bergeron et al. (2006) documented average yearly burn rates since 1940 for Québec

Table 2. Slope parameter estimates and standard error (SE) for explanatory variables as averaged over all the models. Variables are described in App. 1. A *t*-value > |1.96| (in **bold**) indicates a parameter has 95% confidence intervals that do not include zero. 'Occurrence' indicates the parameter estimate for the logistic model component while 'Area burned' indicates its estimate for the lognormal component. Random effects are standard deviation estimates related to ecodistricts.

Explanatory variable	Occurrence Estimate	SE	*t*	Area burned Estimate	SE	*t*
Human						
Population density (PopDen)	-0.022	0.088	-0.25	-0.216	0.082	**–2.65**
Road density (RoadDen)	-0.199	0.566	-0.35	0.295	0.478	0.62
Biophysical						
Aspen percent cover (AspenPerc)	–0.023	0.013	–1.78	–0.037	0.011	**–3.36**
Boreal Mixedwoods percent cover (BorealMixPerc)	–0.013	0.032	–0.42	–0.053	0.033	–1.61
Boreal Spruce percent cover (BorealSprucePerc)	–0.019	0.029	–0.63	–0.047	0.029	–1.59
Glaciofluvial Complexes percent cover (GlacioFlvComPerc)	0.017	0.040	0.42	0.071	0.038	1.85
Glaciofluvial Plains percent cover (GlacioFlvPlaPerc)	0.022	0.024	0.93	0.043	0.022	**1.97**
Grass percent cover (GrassPerc)	0.009	0.046	0.20	–0.056	0.045	–1.24
Nonburnable surfaces percent cover (NonburnablePerc)	0.006	0.016	0.35	0.023	0.014	1.63
Pine percent cover (PinePerc)	–0.027	0.031	–0.87	–0.054	0.027	**–2.01**
Ridged landforms percent cover (RidgedPerc)	0.031	0.037	0.84	–0.044	0.030	–1.49
Rock outcrop percent cover (UndividedPerc)	–0.009	0.017	–0.51	0.037	0.020	1.87
Water bodies percent cover (WaterPerc)	–0.022	0.013	–1.63	–0.032	0.013	**–2.39**
Wetlands percent cover (WetlandPerc)	0.000	0.009	0.02	–0.002	0.007	–0.30
Climate and fire weather						
Drought Code maximum (DC_Max)	0.003	0.001	**3.38**	0.002	0.001	1.66
Growing Season Length (GSL)	–0.082	0.029	**–2.77**	–0.084	0.032	**-2.61**
Potential evapotranspiration for fire season (PE_FS)	0.009	0.006	1.48	0.010	0.007	1.54
Precipitation surplus/deficit (PptSurpDef)	–0.003	0.001	**–3.62**	–0.002	0.001	**–2.65**
Strike density of cloud-to-ground lightning (StrikeDen)	0.458	0.823	0.56	–0.450	0.718	–0.63
Total fire season precipitation (TotalP_FS)	0.001	0.003	0.39	–0.005	0.003	–1.47
Winter precipitation (WinterPpt)	0.003	0.001	**1.98**	0.001	0.002	0.79
Regression						
Intercept (a_1, a_2)	–2.065	0.431	**–4.79**	–7.470	0.443	**–16.85**
Residual (σ_2^2)				1.590	0.190	**8.36**
Random effect(u_1, u_2)	0.386	0.187	**2.06**	0.294	0.174	1.68
Covariance (ρ)	0.288	0.152	**1.90**			

landscapes in Abitibi and central Québec of ca. 0.26%.

In terms of seasonality, the peak of fire activity in the Great Lakes-St. Lawrence forest preceded the July peak in lightning density, occurring during May and June (Fig. 2b). A similar seasonal fire trend was observed for recent natural fires in the deciduous forests of the central Appalachian mountains of the United States (Lafon et al. 2005). This situation contrasts what typically occurs in the Canadian boreal forest (Stocks et al. 2002) and western United States (Westerling et al. 2003), where fire frequency and area burned are highest during the hottest and driest period of the annual climatological cycle in July and August.

Fire hazard in our study region thus seems strongly negatively associated with deciduousness, as evidenced by how fires in the study region differ both in their extent and seasonality from adjacent boreal landscapes, despite having similar trends in fire weather severity (Girardin et al. 2004). This association has a temporal dimension related to the onset of broadleaf emergence and growth as well as a spatial dimension related to the relative abundance of deciduous stands in a given landscape. As compared to conifers, deciduous trees and stands possess structural and fuel attributes that impart low flammability, including low bulk density of the canopy, leaves with high moisture content, low concentrations of flammable resins and oils, discontinuity of fuels between the forest floor and tree crowns, high rates of decomposition for coarse woody debris, and relatively fire-retardant fine fuels and litter (Philpot 1970; Van Wagner 1977; Hély et al. 2000; Frelich 2002). The development of a deciduous canopy decreases wind speeds and penetration of solar irradiance to the forest floor, limiting desiccation of forest fuels (Schroeder & Buck 1970; Lafon et al. 2005). Moreover, deciduous stands can limit the intensity and spread of large fires (Hély et al. 2001; Vazquez et al. 2002; Wang 2002).

Hypotheses selection

The recharge hypothesis, where fire occurrence and area burned are a function of precipitation surplus/deficit, glaciofluvial deposits, and total precipitation accumulated during the antecedent winter, had the highest level of data support. The recharge hypothesis was the only model that captured spatial variation related to fuel type and landscape moisture retention (as determined by surficial deposits) with spatial and temporal variation in the climatic conditions that affect when fires burn and how large they become during a given fire season. Moreover, including antecedent precipitation allowed capturing variation of fire hazard attributable to lagged weather effects, effects increasingly recognized as important to long-lead forecasting of fire activity (Westerling et al. 2002; Crimmins & Comrie 2004).

Relative role of explanatory variables

Only fire weather/climate variables influenced whether fires occurred in a given ecodistrict-year, whereas these variables along landscape characteristics explained proportion of area burned. Our data suggest precipitation deficit/surplus was the most important variable of our set in explaining fire occurrence and proportion burned (Table 2). Precipitation deficit/surplus integrates variation in fuel moisture and seasonal water paucity. When precipitation exceeds potential evapotranspiration (PET), precipitation deficit/surplus indicates the amount of moisture available for storage in forest fuels and the seasonal conditions that maintain an attenuated fire threat. When precipitation is lower than PET, actual evapotranspiration is equal to precipitation and precipitation deficit/surplus reflects the variation in fire hazard attributable to forest fuel dryness as well as the seasonal water paucity. Last, since actual and potential evapotranspiration are indicators of environmental energy available for tree growth and for sustaining high tree species diversity (Currie & Paquin 1987), precipitation deficit/surplus may also reflect regional variation in the relative abundance of deciduous versus coniferous species related to evapotranspiration.

Growing season length (GSL) was inversely related to both fire occurrence and area burned (Table 2). As with precipitation deficit/surplus, GSL integrates climatic and fuel conditions. Relative to landscapes where the growing season is shorter, a longer growing season allows the earlier development of the deciduous component of stands and landscapes (Richardson et al. 2006) and a concurrent decrease in fire hazard. Many southern deciduous tree species have their northern limit within the Great Lakes-St. Lawrence forest region (Burns & Honkala 1990). Longer growing seasons favour the growth of these species and allow them to form the secondary component of the species mix across stands at the competitive exclusion of white spruce, balsam fir and conifers prevalent in more mixed forests to the north (Nichols 1935; Rowe 1972).

Drought code and antecedent winter precipitation influenced only fire occurrence. Our finding that yearly maximum DC values are positively related to fire occurrence corroborates work in the southern Canadian boreal forest demonstrating the relationship between the condition of deep forest fuels, area burned and fire frequency (Girardin et al. 2004). Contrary to what we observed, we had expected high pre-fire season winter precipitation would more fully charge the landscape with moisture and thereby decrease fire occurrence, as has been shown across a variety of forest types in the western United States (Westerling et al. 2002). In the Great Lakes-St. Lawrence forests, above-average precipitation during the antecedent winter may mean large snow loads or ice accumulation increase branch ablation and tree fall of winter damage-susceptible species such as sugar maple or yellow birch (Croxton 1939), thereby increasing dead vegetation during the following fire season. Alternatively, high winter precipitation may cause higher-than-average moisture retention in mineral soil layers, thereby increasing production in the following fire season of the fine fuels necessary to support large fires, as has been shown in some fuel-limited western forests (Kipfmueller & Swetnam 2000; Westerling et al. 2002).

Other variables – aspen stands, large water bodies, glaciofluvial deposits and human population density – for which our data provided evidence for an effect on area burned are well documented as influencing fire size and spread (Howard 1996; Grimm 1984; Whitney 1986; Zhang et al. 1999; Cumming 2001; Drever et al. 2006). Our finding that population density negatively affected percent area burned is incongruent with the pattern observed in the deciduous-dominated forests of northern New England, USA, where percent area burned between 1909 and 1959 either remained roughly constant or increased with population density (Fahey & Reiners 1981). In our study region, observed decreases in area burned with increasing population density may be related to the presence of agricultural areas and other firebreaks as well as to better access and more active fire suppression effort.

Our fuel map captured only spatial variation of forest fuels and represented the end state of changes occurring over the period of study, thereby precluding analyses of potential feedbacks between fuels and fire that can drive fire regime in decadal time scales (Ryan 2002). This lack of temporal dynamism may be behind the unexpected result that percent pine cover of each ecodistrict (PinePerc) showed a negative relationship with PAAB (Table 2). However, our finding may also reflect the decrease in abundance of white and red pine communities that has been documented throughout their range (Zhang et al. 1999; Radeloff et al. 1999; Thompson et al. 2006). Thus, many pine-dominated stands may have burned but failed to regenerate to pine dominance. Moreover, given the low amount of each landscape burned per year and that our study focused only on a 41-year period, temporal variation in fuel types within ecodistricts was arguably less important than the relative coverage of different fuel types in explaining fire occurrence and area burned.

Characterizing the relative roles of climatic and landscape variables may help design strategies for dealing with the forecasted increase in fire weather severity, increased area burned, and a longer fire season across Canada (Flannigan et al. 2005). These strategies could involve silvicultural practices that influence the abundance and distribution of deciduous fuel types. Indeed, such 'fire smart' strategies already inform planning of fire risk abatement in different jurisdictions, principally through the management of aspen stands in time and space (Hirsch et al. 2001; Le Goff et al. 2005). Prioritization of landscapes in which to implement such strategies could be based on prevalence of the various enduring landscape attributes identified here as important influences on area burned e.g. landscapes with few large water bodies and high percent cover of glaciofluvial deposits. This approach would mean that, compared to the present, substantially longer or more severe fire seasons and increased fire activity would be necessary to transform landscape structure and composition into alternate configurations, thereby affording increased ecological resilience (Holling 1973).

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References

Anon. 1996a. *A national ecological framework for Canada*. Ecological Stratification Working Group. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of Environment Directorate, Ottawa/Hull, ON, CA.

Anon. 1996b. *ArcView GIS: The Geographic Information System for everyone*. Environmental Systems Research Institute Inc. (ESRI), Redlands, CA, US.

Anon. 1997. *Ecological regions of North America: Toward a common perspective*. Commission for Environmental Cooperation (CEC), Montréal, QC, CA.

Anon. 2001a. *The SAS System for Windows Version 8.02*. SAS Institute Inc., Cary, NC, US.

Anon. 2001b. *Road Network Files 2001 Census reference guide*. Ministry of Industry, Statistics Canada, Ottawa, ON, CA.

Anon. 2006. *Censuses of Population, 1851-2001*. Ministry of Industry, Statistics Canada, Ottawa, ON, CA.

Bailey, R.G. 1995. *Description of the ecoregions of the United States*. Miscellaneous Publication No. 1391, USDA Forest Service, Washington, DC, US.

Balling, Jr., R.C., Meyer, G.A. & Wells, S.G. 1992. Relation of surface climate and burned area in Yellowstone National Park. *Agricultural and Forest Meteorology* 60: 285-293.

Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M.D., Gauthier, S., Kneeshaw, D.D., Lauzon, É., Leduc, A., Le Goff, H., Lesieur, D. & Logan, K. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. *Canadian Journal of Forest Research* 36: 2737-2744.

Bessie, W.C. & Johnson, E.A. 1995. The relative importance of fuels and weather on fire behavior in sub-alpine forests. *Ecology* 76: 747-762.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag, New York, NY, US.

Burns, R.M. & Honkala, B.H. (eds.) 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654, USDA Forest Service, Washington, DC, US.

Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, J.K., Watson, R.L., Sloan, A.M. & Brosofske, K.D. 2004. Characterizing historical and modern fire regimes in Michigan (USA): a Landscape ecosystem approach. *Landscape Ecology* 19: 311-325.

Crimmins, M.A. & Comrie, A.C. 2004. Interactions between antecedent climate and wildfire variability across southeastern Arizona. *International Journal of Wildland Fire* 13: 455-466.

Croxton, W.C. 1939. A study of the tolerance of trees to breakage by ice accumulation. *Ecology* 20: 71-73.

Cumming, S.G. 2001. Forest type and wildfire in the Alberta boreal mixedwood: What do fires burn? *Ecological Applications* 11: 97-110.

Currie, D.J. & Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329: 326-327.

Diez, E.L.G., Salazar, J.L.L. & Davila, F.D. 1993. Some meteorological conditions associated with forest-fires in Galicia (Spain). *International Journal of Biometeorology* 37: 194-199.

Drever, C.R., Messier, C., Bergeron, Y. & Doyon, F. 2006. Fire and canopy species composition in the Great Lakes-St. Lawrence forest of Temiscamingue, Québec. *Forest Ecology and Management* 231: 27-37.

Fahey, T. & Reiners, W.A. 1981. Fire in the forests of Maine and New Hampshire. *Bulletin of the Torrey Botanical Club* 108: 362-373.

Flannigan, M.D. & Harrington, J.B. 1988. A study of the relation of meteorological variables to monthly provincial area burned by wildfire (1953-1980). *Journal of Applied Meteorology* 27: 441-452.

Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R. & Stocks, B.J. 2005. Future area burned in Canada. *Climate Change* 72: 1-16.

Frelich, L.E. 2002. *Forest dynamics and disturbance dynamics: studies from temperate evergreen-deciduous forests*. Cambridge University Press, Cambridge, UK.

Girardin, M.P., Tardif, J., Flannigan, M.D., Wotton, B.M. & Bergeron, Y. 2004. Trends and periodicities in the Canadian Drought Code and their Relationships with atmospheric circulation for the southern Canadian boreal forest. *Canadian Journal of Forestry Research* 34: 103-119.

Grimm, E.C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecological Monographs* 54: 291-311.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3: 329-382.

Hély, C., Bergeron, Y. & Flannigan, M.D. 2000. Effects of stand composition on fire hazard in mixed-wood Canadian boreal forest. *Journal of Vegetation Science* 11: 813-824.

Hély, C., Flannigan, M., Bergeron, Y. & Mcrae, D. 2001. Role of vegetation and weather on fire behavior in the Canadian mixedwood boreal forest using two fire behavior prediction systems. *Canadian Journal of Forestry Research* 31: 430-441.

Hirsch, K., Kafka, V., Tymstra, C., Mcalpine, R., Hawkes, B., Stegehuis, H., Quintilio, S., Gauthier, S. & Peck, K. 2001. Fire-smart forest management: a pragmatic approach to sustainable forest management in fire-dominated ecosystems. *The Forestry Chronicle* 77: 357-363.

Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4: 2-23.

Johnson, E.A. & Larsen, C.P.S. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72: 194-201.

Kipfmueller, K.F. & Swetnam, T.W. 2000. Fire-climate interactions in the Selway-Bitterroot Wilderness Area. In: Cole, D.N. & McCool, S.F. (eds.) *Proceedings: Wilderness science in a time of change, Missoula, MT May 23-27, 1999*, pp. 270-275. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, US.

Lafon, C.W., Hoss, J.A. & Grissino-Mayer, H.D. 2005. The contemporary fire regime of the Central Appalachian mountains and its relation to climate. *Physical Geography* 26: 126-146.

Le Goff, H., Leduc, A., Bergeron, Y. & Flannigan, M. 2005. The adaptive capacity of forest management to changing fire regimes in the boreal forest of Quebec. *The Forestry Chronicle* 81: 582-592.

Lefort, P., Gauthier, S. & Bergeron, Y. 2003. The influence of fire weather and land use on the fire activity of the Lake Abitibi Area, eastern Canada. *Forest Science* 49: 509-521.

Lefort, P., Leduc, A., Gauthier, S. & Bergeron, Y. 2004. Recent fire regime (1945-1998) in the boreal forest of western Quebec. *Ecoscience* 11: 433-445.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, S.J., Tyre, A.J. & Possingham, H.P. 2005. Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8: 1235-1246.

Nadeau, L.B., McRae, D.J. & Jin, J. 2005. *Development of a national fuel-type map for Canada using fuzzy logic*. Information Report NOR-X-406, Canadian Forest Service, Northern Forestry Centre, Edmonton, AB, CA.

Nichols, G.E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology* 16: 403-422.

Pereira, M.G., Trigo, R.M., Da Camara, C.C., Pereira, J.M.C. & Leite, S.M. 2005. Synoptic patterns associated with large summer forest fires in Portugal. *Agricultural and Forest*

Meteorology 129: 11-25.

Philpot, C.W. 1970. Influence of mineral content on the pyrolysis of plant materials. *Forest Science* 16: 461-471.

Radeloff, V.C., Mladenoff, D.J., He, H.S. & Boyce, M.S. 1999. Forest landscape change in the northwestern Wisconsin pine barrens from pre-European settlement to the present. *Canadian Journal of Forest Research* 29: 1649-1659.

Richardson, A.D., Bailey, A.S., Denny, E.G., Martin, C.W. & O'Keefe, J. 2006. Phenology of a northern hardwood forest canopy. *Global Change Biology* 12: 1174-1188.

Robitaille, A. & Saucier, J.P. 1998. *Paysages régionaux du Québec méridional*. Les publications du Québec, Sainte-Foy, QC, CA.

Rowe, J.S. 1972. *Forest regions of Canada*. Canadian Forestry Service Publication 1300, Department of the Environment, Ottawa, ON, CA.

Ryan, K.C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* 36: 13-39.

Schroeder, M.J. & Buck, C.C. 1970. *Fire weather: A guide for application of meteorological information to forest fire control operations*. Agriculture Handbook 360, USDA Forest Service, Washington, DC, US.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L. & Skinner, W.R. 2002. Large forest fires in Canada, 1959-1997. *Journal of Geophysical Research* 107: 8149.

Taylor, S.W., Wotton, B.M., Alexander, M.E. & Dalrymple, G.N. 2004. Variation in wind and crown fire behaviour in a northern jack pine-black spruce forest. *Canadian Journal of Forest Research* 34: 1561-1576.

Thompson, I.D., Simard, J.H. & Titman, R.D. 2006. Historical changes in white pine (*Pinus strobus* L.) density in Algonquin Park, Ontario, during the 19th Century. *Natural Areas Journal* 26: 61-71.

Tooze, J.A., Grunwald, G.K. & Jones, R.H. 2002. Analysis of repeated measures data with clumping at zero. *Statistical Methods in Medical Research* 11: 341-355.

Turner, J.A. 1972. *The Drought Code component of the Canadian Forest Fire Behavior System*. Canadian Forest Service Publication No. 1316, Department of the Environment, Ottawa, ON, CA.

Van Wagner, C.E. 1977. Conditions for the start and spread of crownfire. *Canadian Journal of Forest Research* 7: 23-24.

Van Wagner, C.E. 1987. *Development and structure of the Canadian forest weather index*. Forestry Technical Report 35, Canadian Forest Service, Ottawa, ON, CA.

Vazquez, A., Perez, B., Fernandez-Gonzalez, F. & Moreno, J.M. 2002. Recent fire regime characteristics and potential natural vegetation relationships in Spain. *Journal of Vegetation Science* 13: 663-676.

Wang, G.G. 2002. Fire severity in relation to canopy composition within burned boreal mixedwood stands. *Forest Ecology and Management* 163: 85-92.

Westerling, A.L., Gershunov, A., Brown, T.J., Cayan, D.R. & Dettinger, M.D. 2003. Climate and wildfire in the western United States. *Bulletin of the American Meteorological Society* 84: 595-604.

Westerling, A.L., Gershunov, A., Cayan, D.R. & Barnett, T.P. 2002. Long lead statistical forecasts of area burned in western US wildfires by ecosystem province. *International Journal of Wildland Fire* 11: 257-266.

Whitney, C.G. 1986. Relation of Michigan's pre-settlement pine forests to substrate and disturbance history. *Ecology* 67: 1548-1559.

Whitney, G.G. 1987. An ecological history of the Great Lakes forest of Michigan. *Journal of Ecology* 75: 667-684.

Zhang, Q., Pregitzer, K.S. & Reed, D.D. 1999. Catastrophic disturbance in the presettlement forests of the Upper Peninsula of Michigan. *Canadian Journal of Forest Research* 29: 106-114.

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For App. 1-2, see also JVS/AVS Electronic Archives; www.opuluspress.se/

App. 1. Descriptions and data sources of explanatory variables for each ecodistrict.

Variable name	Description	Reference(s)
Human		
PopDen	Population density (people per km^2).	Population database of the National Ecological Framework for Canada (Marshall et al. 1999; Anon. 2006)
RoadDen	Density (km per km^2 of land area) of all primary, secondary and tertiary roads, as derived from 2001 Road Network File.	(Anon. 2001)
Biophysical		
AspenPerc	Percent of ecodistrict covered by Aspen fuel type.	(Nadeau et al. 2005)
BorealMixPerc	Percent of ecodistrict covered by Boreal Mixedwood fuel type.	(Nadeau et al. 2005)
BorealSprucePerc	Percent of ecodistrict covered by Boreal Spruce fuel type.	(Nadeau et al. 2005)
GlacioFlvComplexPerc	Percent of ecodistrict covered by Glaciofluvial Complexes, i.e. sand, gravel and locally diamicton deposited by glacial meltwaters as undifferentiated ice contact stratified drift and outwash.	Surficial geology database of the National Ecological Framework for Canada (Marshall et al. 1999)
GlacioFlvPlainPerc	Percent of ecodistrict covered by Glaciofluvial Plains, i.e. sand and gravel deposited by glacial meltwaters as outwash sheets, valley trains, and terrace deposits.	Surficial geology database of the National Ecological Framework for Canada (Marshall et al. 1999)
GrassPerc	Percent of ecodistrict covered by Grass fuel type.	(Nadeau et al. 2005)
NonburnablePerc	Percent of ecodistrict covered by nonburnable surfaces, including urban developments, agricultural fields, and water.	(Nadeau et al. 2005)
PinePerc	Percent of ecodistrict covered by immature, mature as well as red and white pine stands.	(Nadeau et al. 2005)
RidgedPerc	Percent of ecodistrict covered by long, narrow elevations of the surface, usually sharp crested with steep sides; ridges may be parallel, subparallel, or intersecting.	Local surface form database of the National Ecological Framework for Canada (Marshall et al. 1999)
UndividedPerc	Percent of ecodistrict covered by areas composed of > 75% rock outcrops.	Surficial geology database of the National Ecological Framework for Canada (Marshall et al. 1999)
WaterPerc	Percent of ecodistrict covered by large lakes and other water bodies (> ca. 1 km^2).	Land and Water Areas database of the National Ecological Framework for Canada (Marshall et al. 1999)
WetlandPerc	Percent of ecodistrict covered by swamps, bogs or fens.	Local surface form database of the National Ecological Framework for Canada (Marshall et al. 1999)
Climate and fire weather		
DC_max	Maximum value for Drought Code (unitless) during fire season.	Derived from station data (see Methods) and calculated as per (Turner 1972)
GSL	Growing season length (days), as determined by the number of days between the first and last day of the year when mean daily air temperature ≥ 5 ºC.	Canadian Ecodistrict Climate Normals 1961-1990 database of the National Ecological Framework for Canada (Marshall et al. 1999)
PE_FS	Potential evapotranspiration (mm) for the fire season (April to October), as calculated using the Penman method for a standard crop i.e. a continuous cover of short green plants exhibiting growth unlimited by nutrients, that shades the ground completely and has a negligible effect on evaporative water loss	Canadian Ecodistrict Climate Normals 1961-1990 database of the National Ecological Framework for Canada (Marshall et al. 1999)

App. 1-2. Internet supplement to: Drever, C.R.; Drever, M.C.; Messier, C.; Bergeron, Y. & Flannigan, M. 2008. Fire and the relative roles of weather, climate and landscape characteristics in the Great Lakes-St. Lawrence forest of Canada
J. Veg. Sci. 19: 57-66. doi : 10.3170/2007-8-18313.

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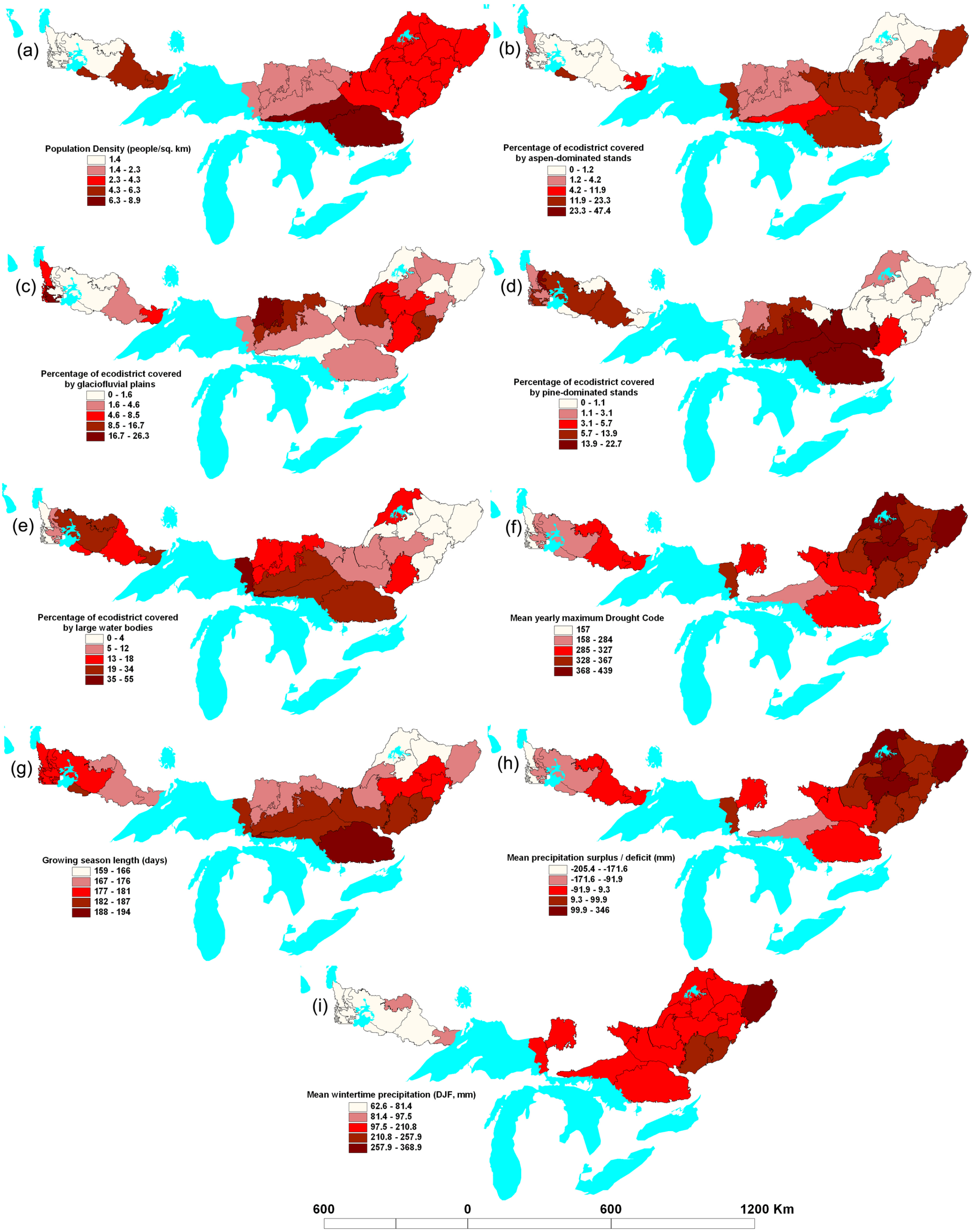
App. 1. ***Cont.***

Variable name	Description	Reference(s)
PptSurpDef	Difference between total precipitation between April to October (as determined from meteorological stations) and PE_FS (mm).	Total precipitation derived from station data (see Methods); PE_FS derived from Canadian Ecodistrict Climate Normals 1961-1990 database of the National Ecological Framework for Canada (Marshall et al. 1999)
StrikeDen	Density of cloud-to-ground lightning (number of strikes per km^2 during April to October) averaged from seven years (1999-2005) of occurrence data gathered from a network of ground-based sensors by the Meteorological Service of Canada. Detection efficiency > 90%, with a location accuracy of 0.5 km.	Pers. comm., William Burrows, Environment Canada
TotalP_FS	Total seasonal precipitation (mm) during April to October, as determined from 1961-1990 climate normals derived by interpolation from all available meteorological stations.	Canadian Ecodistrict Climate Normals 1961-1990 database of the National Ecological Framework for Canada (Marshall et al. 1999)
WinterPpt	Total precipitation (mm) during December, January, and February before each fire season.	Derived from meteorological station data (see Methods).



App. 2. Variation among ecodistricts of key explanatory variables: (a) 1991 population density (PopDen); (b) percent cover by aspen-dominated stands (AspenPerc); (c) percent cover by glaciofluvial plains (GlacioFlvPlainPrec); (d) percent cover by pine-dominated stands (PinePerc); (e) percent cover by large water bodies (WaterPerc); (f) 41-yr mean (1959-1999) of yearly maximum Drought Code (DC_max); (g) growing season length (GSL); (h) 41-yr mean (1959-1999) of precipitation surplus/deficit during the fire season (PptSurpDef): and (i) 41-yr mean (1959-1999) of antecendent winter precipitation (WinterPpt). See App. 1 for full variable descriptions and data sources.

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