Vegetation limits the impact of a warm climate on boreal wildfires

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Summary

- Strategic introduction of less flammable broadleaf vegetation into landscapes was suggested as a management strategy for decreasing the risk of boreal wildfires projected under climatic change. However, the realization and strength of this offsetting effect in an actual environment remain to be demonstrated.
- Here we combined paleoecological data, global climate models and wildfire modelling to assess regional fire frequency (RegFF, i.e. the number of fires through time) in boreal forests as it relates to tree species composition and climate over millennial time-scales.
- Lacustrine charcoals from northern landscapes of eastern boreal Canada indicate that RegFF during the mid-Holocene (6000–3000 yr ago) was significantly higher than pre-industrial RegFF (AD *c.* 1750). In southern landscapes, RegFF was not significantly higher than the pre-industrial RegFF in spite of the declining drought severity. The modelling experiment indicates that the high fire risk brought about by a warmer and drier climate in the south during the mid-Holocene was offset by a higher broadleaf component.
- Our data highlight an important function for broadleaf vegetation in determining boreal RegFF in a warmer climate. We estimate that its feedback may be large enough to offset the projected climate change impacts on drought conditions.

Introduction

The patterns of and controls on wildfire behaviour have interested ecologists and geophysical scientists for more than a century (Bell, 1889), and extensive bodies of work have been produced about the climatic controls on wildfire ignition, propagation and severity (Campbell & Flannigan, 2000; Turetsky *et al.*, 2011; Zumbrunnen *et al.*, 2011). The processes governing wildfire behaviour operate at several time-scales (e.g. days, seasons and decades) and are influenced by weather, climate and other environmental factors such as temperature, precipitation, wind, and the structure and composition of forests. The concentrated activity in wildfire science is worthy of its importance – the anticipated increase in global wildfire activity resulting from human-caused climatic change is a threat to communities living at wildland–urban interfaces world-wide and to the equilibrium of the global carbon cycle (Kurz *et al.*, 2008; Flannigan *et al.*, 2009; Westerling *et al.*, 2011). In circumboreal forests, climatic change will probably act upon fuels through long-term increases in summer evapotranspiration and increased frequency of extreme drought years as a result of more persistent and frequent blocking high-pressure systems. Earlier arrival of spring, longer summer droughts and more frequent ignitions could also expose forests to higher wildfire activity (Wotton *et al.*, 2010).

Manipulation of vegetation composition and stand structure has been proposed as a strategy for offsetting climatic change impacts on wildfires (Hirsch *et al.*, 2004; Krawchuk & Cumming, 2011; Terrier *et al.*, 2013). Broadleaf deciduous stands are characterized by higher leaf moisture loading and lower flammability and rate of wildfire ignition and initiation than needleleaf evergreen stands (Päätalo, 1998; Campbell & Flannigan, 2000; Hély *et al.*, 2001). Therefore, their introduction into dense needleleaf evergreen landscapes as strategic barriers could decrease the intensity and rate of spread of wildfires, improving suppression effectiveness, and reducing wildfire impacts (Amiro *et al.*, 2001; Hirsch *et al.*, 2004). Considerable portions of boreal

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forests are currently being harvested and there may be opportunities for using planned manipulation of vegetation for management of future wildfire risks (Hirsch *et al.*, 2004). The concept has a long history, and its potential effect has been demonstrated through model simulation experiments (Hirsch *et al.*, 2004; Krawchuk & Cumming, 2011). Nevertheless, determining the efficiency of planned manipulation of vegetation with respect to wildfire behaviour at the landscape scale is a daunting task because ecological processes resulting from stand dynamics (e.g. canopy closure, mortality and species turnover) succeed one another over many decades, and the biotic feedback from these could be confounded by other factors that influence wildfire activity, namely increasing land uses and human ignition (Niklasson & Granström, 2000; Zumbrunnen *et al.*, 2011), active wildfire suppression efforts (Woolford *et al.*, 2010), and episodic shifts in drought regimes as a result of oceanic forcing (Shabbar *et al.*, 2011). Analyses of ecological features and feedback processes (climate and vegetation) in paleoecological records may provide significant insights for future wildfire management policies, particularly in terms of the magnitude of treatments required for an effect on wildfires over time (Willis & Birks, 2006; Gavin *et al.*, 2007; Higuera *et al.*, 2009; Marlon *et al.*, 2012).

Here we provide an assessment of the response of boreal wildfire activity to changes in vegetation as well as the strength of vegetation feedback to limit or amplify climatic change impacts on wildfires. This assessment was carried out by integrating into a wildfire modelling scheme information about millennial-scale changes in wildfire activity reconstructed from analysis of charred particles accumulated in lake sediments, climate simulated by general circulation models (GCMs), and vegetation changes inferred from pollen analysis. We tested the hypothesis that increasing wildfire risks in needleleaf boreal forests brought about by more wildfire-prone climatic conditions may be offset by an increasing broadleaf component in landscapes.

Materials and Methods

Reconstruction of regional fire frequencies

Variations in charcoal accumulation rate or influx (sedimentary charcoal load per time unit; e.g. $mm^{-2}\,cm^{-2}\,yr^{-1}$) provide a continuous record of local wildfire frequency in a point-based manner (i.e. average fire number per time unit at a given point) within the sampling resolution of the sediment record (Clark, 1990) that may be used in cross-comparison with, for instance, model simulations of past climate and pollen-based vegetation reconstructions. Here, fire events that occurred during the Holocene were reconstructed using charred particles extracted from the sediments of 11 small lakes from the transition zone of the boreal mixedwood and the dense needleleaf forests of eastern boreal Canada (Fig. 1, Table 1). At all sites it was possible to reconstruct wildfire frequency since the onset of sediments that followed the retreat of the Laurentide Ice Sheet in eastern North America. The investigated forests remained largely unaffected by humans until European settlement in the early 20th Century. Before that time, there is no record of the specific influence of Amerindian practices on fire activity for the region under study, but it is generally assumed that, in the boreal forest, Amerindians were using fire for clearing land around campsites and trails (Patterson & Sassaman, 1988). Fires were generally set during periods of low fire susceptibility and consequently were of low intensity and small in size (Lewis, 1982). All sampled lakes are located within the Central Canadian Shield Forest ecoregion (Olson *et al.*, 2001).

Standard methods were used for charred particle extraction, dating procedures, and reconstruction of fire events (Higuera *et al.*, 2008). Briefly, charred areas (CHARa, in cm^2) were interpolated to constant time steps ($C_{interpolated}$), corresponding to the median temporal resolution of each record (Table 1). Low-frequency variations in $CHAR_a$, namely $C_{background}$, represent changes in charcoal production, transport, sedimentation, mixing, and sampling. We therefore decomposed $CHAR_a$ into

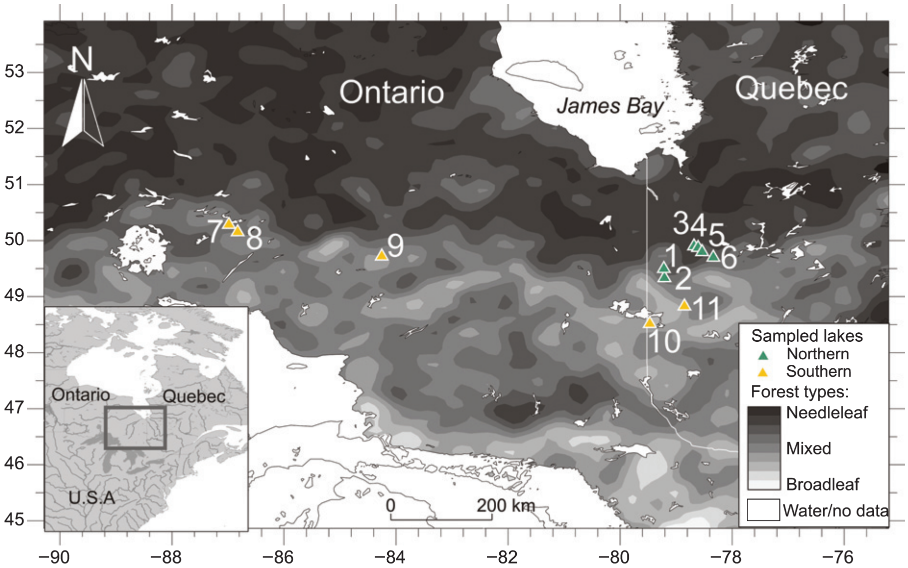

Fig. 1 Location of the 11 sampled lakes in Canada. Sampled lakes located north of the modern transition zone of the boreal mixedwood and dense needleleaf forests are: 1, Lac Pessière; 2, Lac aux Cèdres; 3, Lac aux Geais; 4, Lac Profond; 5, Lac Raynald; and 6, Lac à la Loutre; sampled lakes located south of the transition zone are: 7, Lake Jack Pine; 8, Lac Huard; 9, Lac Christelle; 10, Lac Francis; and 11, Lac Pas-de-Fond. Also shown are forest cover types obtained from Natural Resources Canada (2008) 250-m resolution land cover classes. The information relating to vegetation openness was discarded. The dimensionless scale ranges from needleleaf dominance (dark grey) to broadleaf dominance (light grey).

Table 1 Main features of studied lakes

Lake name	Lac Pessière	Lac aux Cèdres	Lac aux Geais	Lac Profond	Lac Raynald	Lac à la Loutre
Vegetation zone	Needleleaf	Needleleaf	Needleleaf	Needleleaf	Needleleaf	Needleleaf
Data	Charcoal and pollen	Charcoal and pollen	Charcoal	Charcoal	Charcoal	Charcoal
Latitude	49°30′33″N	49°20′45″N	49°53′32″N	49°51′41″N	49°48′33″N	49°42′43″N
Longitude	79°14′23″W	79°12′30″W	78°39′18″W	78°36′45″W	78°32′09″W	78°20′09″W
Elevation (m asl)	283	307	278	274	279	270
Hillslopes	Flat	Flat	Flat	Flat	Moderate	Flat
Lake surface (ha)	4.5	7.5	1.4	0.6	2.4	1.6
Water depth (m)	10.15	16	10.15	> 20	10.28	10.63
Length of organic core (cm)	603	573	603	223	472	227
Median deposition time (yr cm^{-1})	14	13.0	12.0	11.0	12.0	16.0
Reference	Carcaillet *et al.* (2001)	Carcaillet *et al.* (2006)	Ali *et al.* (2009)	Ali *et al.* (2009)	Ali *et al.* (2009)	Ali *et al.* (2009)

Lake name	Lac Jack Pine	Lac Huard	Lac Christelle	Lac Francis	Lac Pas-de-Fond
Vegetation zone	Boreal mixedwood	Boreal mixedwood	Boreal mixedwood	Boreal mixedwood	Boreal mixedwood
Data	Charcoal	Charcoal and pollen	Charcoal and pollen	Charcoal and pollen	Charcoal and pollen
Latitude	50°16′14″N	50°09′52″N	49°43′55″N	48°31′35.0″N	48°48′38″N
Longitude	86°57′46″W	86°49′36″W	84°15′16″W	79°28′20.0″W	78°49′55.0″W
Elevation (m asl)	341	346	265	305	290
Hillslopes	Moderate	Flat	Flat	Flat	Flat
Lake surface (ha)	2.8	2.9	1.8	0.9	1.9
Water depth (m)	12.8	8.3	7.0	6	11
Length of organic core (cm)	338	712	427	302	368
Median deposition time (yr cm^{-1})	25.0	10.0	16.9	26.0	23.0
Reference	A. A. Ali (unpublished)	Genries *et al.* (2012)	Genries *et al.* (2012)	Carcaillet *et al.* (2001)	Carcaillet *et al.* (2001)

background ($C_{background}$) and peak (C_{peak}) components using a locally defined threshold that identifies charcoal peaks probably related to the occurrence of one or more local fires (i.e. 'fire events' within *c.* 1 km). The locally weighted regression was applied with a 500-yr-wide window that maximized a signal-to-noise (peak-to-background) index and the goodness of fit between the empirical and modelled $C_{background}$ distributions (Kelly *et al.*, 2011). The residual series related to peaks was obtained by subtraction (i.e. $C_{peak} = C_{interpolated} - C_{background}$).

Consistent with theoretical evidence (Higuera *et al.*, 2007) and empirical studies (Whitlock & Millspaugh, 1996; Carcaillet *et al.*, 2001; Higuera *et al.*, 2009), we assumed in a second step that C_{peak} was composed of two subpopulations, namely C_{noise}, representing variability in sediment mixing, sampling, and analytical and naturally occurring noise, and C_{fire}, representing significant peaks of charcoal input from local fires. For each peak, we used a Gaussian mixture model to identify the C_{noise} distribution. We considered the 99th percentile of the C_{noise} distribution as a possible threshold separating samples into 'fire' and 'nonfire' events; between-record differences were similar using other threshold criteria. We did not screen peaks based on the original charcoal counts of each peak, as in Higuera *et al.* (2009). All charcoal time-series analyses were performed using the program CharAnalysis (P.E. Higuera; freely available at http://CharAnalysis.googlepages.com).

To document past millennial to centennial time-scale fluctuations in regional wildfire activity, sites were grouped into northern (hereafter 'North') and southern ('South') landscapes with respect to their location along the gradient of transition from boreal mixedwood to dense needleleaf vegetation zones (Fig. 1). This grouping was historically supported by pollen grain concentrations of major tree species and plant macroremain data (Terasmae & Anderson, 1970; Vincent, 1973; Richard, 1980; Liu, 1990; Gajewski *et al.*, 1993; Ali *et al.*, 2008; Genries *et al.*, 2012). The vegetation composition in the northern landscapes did not change significantly over the last 6000 yr. In southern landscapes, a reduction in the proportion of broadleaf taxa since 1200 calibrated years before present (hereafter BP) tended to reduce the differences between the boreal mixedwood and needleleaf forests (Carcaillet *et al.*, 2010). From fire event dates extracted from C_{fire} over past millennia, we computed regional fire frequencies (RegFFs) using a kernel-density function (Mudelsee, 2002) that allowed a detailed inspection of time-dependent event frequencies (Mudelsee *et al.*, 2004). RegFF can be viewed as an arithmetic average of all fire frequencies determined in a designated area during a specified time period, and is herein expressed in *n* fires 1000 yr^{-1}. We used a Gaussian kernel, *K*, to weigh observed fire event dates, $T_{(i)}$, $i, \ldots, N$ (where N is the total number of events), and calculated the regional frequency, RegFF, at each time t as:

$$\mathrm{RegFF}_{(t)} = \left(\sum_i K((t - T_{(i)})/h)/h\right)/n_{(t)} \quad \text{Eqn 1}$$

($n_{(t)}$, the total number of sampled cores at time t.) Selection of the bandwidth ($h = 500$ yr) was guided by cross-validation aimed at finding a compromise between large variance and small bias (which occurs under shorter h) and small variance and large bias (longer h). We assessed the significance of changes with the help of bootstrap confidence intervals (CIs) computed from confidence bands (90%) around RegFF (Mudelsee *et al.*, 2004).

Drought severity

We used paleoclimatic simulations provided by the UK Universities Global Atmospheric Modelling Programme to develop a mechanistic understanding of the climatic variations associated with the reconstructed paleofire regime. These simulations were performed with the Hadley Centre climate model (HadCM3; Singarayer & Valdes, 2010), which is a state-of-the-art global climate model (GCM) used in both the third and fourth assessment reports of the Intergovernmental Panel on Climate Change (2001, 2007). The GCM is a three-dimensional time-dependent numerical representation of the atmosphere, oceans and sea ice and their phenomena over the entire Earth, using the equations of motion and including radiation, photochemistry, and the transfer of heat and water vapour. The HadCM3 GCM simulations used in the present study consist of climatic averages at 1000-yr intervals (i.e. maximum temporal resolution available) covering the last 120 000 yr at a spatial resolution of 2.5° in latitude by 3.75° in longitude. These simulations include forcing from a prolonged presence of the residual Laurentide Ice Sheet in eastern North America and an improved way of handling the isostatic rebound that was previously less effective (Singarayer & Valdes, 2010). For each millennium interval, anomalies for air temperature (the difference between a given millennia and the pre-industrial (AD *c.* 1750) period) and precipitation (the percentage of change between a given millennia and the pre-industrial period) were computed. A downscaling method was used in which means of HadCM3 GCM anomalies of temperature and precipitation were applied to Climate Research Unit spatial grids TS 3.1 (period AD 1901–2008; Mitchell & Jones, 2005) over an area compatible for comparison with our RegFF reconstructions (48.5°–51.5°N and 86.5°–78.0°W, for a total of 126 CRU pixels encompassing nine HadCM3 pixels). The produced time-series of monthly temperature and precipitation (108-yr monthly time-series for each millennium) were then used to compute the monthly Drought Code, which is a monthly adaptation of the daily Drought Code (DC) index of the Canadian Forest Fire Weather Index System (Girardin & Wotton, 2009). The DC is used in several countries by fire agencies to predict the risk of fire ignition based on weather conditions (de Groot *et al.*, 2007). It represents the net effect of changes in evapotranspiration and precipitation on cumulative moisture depletion in the organic matter of the deep humus layer (18 cm thick, 25 kg m^{-2} dry weight, and 138.9 kg m^{-3} bulk density). The DC (and its monthly version) is significantly correlated with wildfire activity in our study area (Balshi *et al.*, 2009; Girardin *et al.*, 2009). We nonetheless feel the need to specify that the DC might not apply to locations where there is a distinctly thin or absent deep duff layer. Calculation started every simulated year in April and ended in October (Van Wagner, 1987; Terrier *et al.*, 2013). An overwintering adjustment was included in the calculation, such that the starting values in spring depend on antecedent autumn drought severity and winter precipitation (Girardin & Wotton, 2009). Medians of April to October monthly Drought Code values were computed for each year, and then across the 108 yr and 126 CRU pixels, and at each millennium, to produce a multi-millennia seasonal Drought Code (SDC) severity time-series. Confidence intervals (90%) for uncertainty in the regional climate history were built by bootstrap resampling of single-HadCM3 pixel SDC anomaly time-series.

Monthly temperature and precipitation data collected from eight GCMs and four scenarios of greenhouse gas (GHG) emissions were used for projection of changes in SDC over the next century (Supporting Information Table S1). The objective was to assess whether the magnitude of past simulated drought conditions is analogue to plausible scenarios expected for the late 21st Century. GCM selections were made according to the availability of monthly means of daily maximum temperature outputs necessary for simulation of the SDC. For the present study, GCM data were collected from four to six cells, depending on model resolution, and for the interval 1961–2100. To account for differences between the CRU data and the GCM projections, the monthly simulations were adjusted relative to the absolute difference from the 1961–1999 monthly means of CRU data (Balshi *et al.*, 2009). A correction was also applied to the interannual variability by changing the width of the distributions so that mean monthly GCM projections and CRU data had equal standard deviations over their common period 1961–1999 (details in Bergeron *et al.*, 2010). These anomaly correction methods were intended to capture the future changes in the frequency of precipitation events that could cause the year-to-year variability in the SDC to also change significantly. These anomaly correction methods were not applied to the HadCM3 paleoclimatic projections because the necessary information was not available.

Flammability

Data on modern forest composition were extracted from a database of temporary sample plots established by the ministère des Ressources naturelles et de la Faune for the province of Quebec (third and fourth forest inventory programs). Aboveground biomass was estimated for each stem within a plot using measured diameter at breast height and the species-specific tree biomass equations of Lambert *et al.* (2005). Values were summed to obtain estimates of species plot-level aboveground biomass and averaged across the vegetation zones defined by Terrier *et al.* (2013).

Past changes in forest composition were documented by summarizing the timing and magnitude of palynological changes at six sampled lakes (two from the northern landscapes and four from the southern ones; Table 1 and Fig. 1), and by examining the differences between the sites through time. Pollen percentages were calculated for 100-yr time windows corresponding to the median resolution of the 11 pollen records. Average pollen percentages per flammable needleleaf species (*Pinus banksiana* Lamb. and *Picea mariana* (Miller) BSP) were compared with average percentages of less flammable broadleaf species (*Populus tremuloides* Michx. and *Betula* sp.) and a needleleaf index was computed, which is equivalent here to the needleleaf percentage. Our analysis of the pollen data deals mainly with qualitative interpretation. No attempt was made to calibrate the needleleaf index on numerical data sets of modern forest attributes because of the low pollen-site replication in the forests under study.

Fire modelling framework

To develop projections of past and future wildfires that take into account regional climate and tree composition changes, we used empirical models (Terrier *et al.*, 2013) describing the distribution of wildfire occurrences in eastern Canada as a function of sets of wildfire bioclimatic zones determined from modern fire weather (FW) and tree species composition (TreeComp). The wildfire occurrence models were formulated by Terrier *et al.* (2013) using piecewise regression models:

$$FireOcc_j = \sum \left(c_1 BF_1 \times FW_j + c_2 BF_2 \times TreeComp \right) \qquad \text{Eqn 2}$$

In Eqn 2, FireOcc is the number of lightning-caused fires above a specified size-threshold per year per 1000 km^2 for a period j, c_1 and c_2 correspond to constants, and BF_1 and BF_2 are basis functions for nonlinear interactions between FireOcc and FW and TreeComp variables. Lightning is the primary source of wildfire ignition in boreal North America and usually results in fires that account for the majority of the area burned (Stocks *et al.*, 2003). FW is defined using fuel moisture codes at different forest floor levels computed from April to October, and averaged over 10-yr periods. TreeComp takes the form of binary variables to indicate the presence of a given vegetation category. A parsimonious model for large fires (size > 200 ha; Stocks *et al.*, 2003) with mean SDC as a predictor variable is shown in Fig. 2 and used in this study. Therein, FireOcc of size > 200 ha in boreal mixedwood landscapes (i.e. with vegetation attributes described by Fig. 2b) progressively increases as mean SDC increases above 125 units (Fig. 2d). The presence of a tree composition dominated by needleleaf species *P. mariana* (Fig. 2a) contributes significantly to increasing the FireOcc quantity; a compositional group dominated by nonboreal broadleaf species (e.g. sugar maple, *Acer saccharum* Marshall; Fig. 2c) contributes significantly to lowering it (zero slope model; Fig. 2). An application of the FireOcc > 200 ha model to a gridded climatology data set suggested that the model was adequate for projecting patterns of wildfire occurrences across the boreal mixedwood and needleleaf forests under study (Fig. S1). In this work, we project past FireOcc > 200 ha using HadCM3 GCM median SDC simulations and pollen-based vegetation information based on the needleleaf index as input data for the model. For the future, projections were made using the multiple GCM simulations and scenarios with and without vegetation changes. For this analysis, 10-yr SDCs computed from the GCM simulations were used as inputs into the FireOcc model. The change from needleleaf (vegetation attributes described by Fig. 2a) to boreal mixedwood forests (vegetation attributes described by Fig. 2b) was arbitrarily set at AD 2040.

Statistical analyses

Relationships among RegFF, SDC and FireOcc were assessed using Pearson's r coefficient (von Storch & Zwiers, 1999; Systat Software Inc, 2004). For these analyses, RegFF reconstructions were downsampled to the time resolution of HadCM3 simulations (i.e. 1000-yr intervals). Linear relationships between two variables were visually inspected using scatter-plots. The statistical significance of correlations was determined using bootstrap resampling (von Storch & Zwiers, 1999). When the confidence

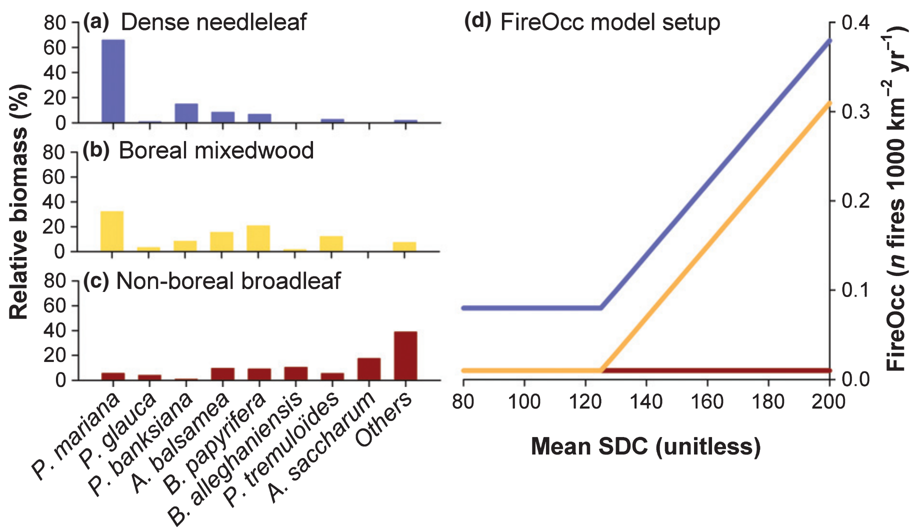

Fig. 2 Modern vegetation attributes in the studied forests and their modelled effect on wildfire activity. (a–c) Relative contribution of dominant tree species to total stand biomass in dense needleleaf, boreal mixedwood and nonboreal broadleaf forests in Canada; statistics were obtained from analysis of Quebec's temporary sample plots from the third and fourth inventories (n = 4665, 10 047 and 20 937 plots, respectively). (d) Empirical model for the occurrence of large wildfires (FireOcc) as a function of mean seasonal Drought Code (SDC) severity and vegetation composition (refer to Terrier *et al.*, 2013).

interval contains zero, the hypothesis of 'no correlation' cannot be rejected at the 90% level.

Significant differences in needleleaf index between pollen series of northern and southern landscapes were analysed using a moving two-sample Student's *t*-test (two-sided and equal variance; von Storch & Zwiers, 1999). Cubic smoothing splines were fitted to the individual series before conducting the Student's *t*-test analysis; the smoothing was automatically determined using a cross-validation procedure (AutoSignal, 1999). We are seeking to disprove the null hypothesis of equal means of the needleleaf index when the *P*-value is lower than 0.05.

The significance of changes in FireOcc projected using the multiple GCM simulations, and under scenarios with and without vegetation changes, was tested using the two-sample Student's *t*-test (one-sided) comparing the 1961–1999 and 2041–2100 intervals ($n=10$ decades). A Holm–Bonferroni correction was applied to counteract the problem of multiple comparisons (Holm, 1979). One seeks to disprove the null hypothesis asserting that 2041–2100 FireOcc is not greater than 1961–1999 FireOcc when the *P*-value is lower than $0.05/(m-1)$, where m is the number of *P*-values being tested at a given iteration.

Results and Discussion

Climate controls on boreal wildfires

Past millennial to centennial time-scale fluctuations in wildfire activity are herein documented by two composite reconstructions of RegFF (north and south) covering the mid-Holocene period to the late-Holocene pre-industrial period (Fig. 3a,b). Analysis of sensitivity to site selection and data treatment confirmed the robustness of the reconstructions for the period from 6000 BP to present (results not shown). Unstable RegFFs in both reconstructions before 6000 BP (particularly evident in the southern reconstruction) were mainly associated with the successive inclusion of sampling sites in association with the heterogeneous deglaciation in North America (Dyke, 2004, 2005). Therefore, the period before 6000 BP was discarded from further analyses. The two RegFF reconstructions were uncorrelated with one another during the period from 6000 BP to the pre-industrial era ($r=-0.15$; 90% bootstrap confidence interval (90% CI) -0.78, 0.59; $n=7$ millennia), implying different temporal wildfire trajectories and probably different controls on wildfires (Bremond *et al.*, 2010). In northern landscapes, wildfires were frequent *c.* 6000 and 2000 BP with a maximum of RegFF estimated at 7.2 wildfires per millennium at 2500 BP (Fig. 3a). The period around 2000 BP marked the onset of a gradual decline in North-RegFF towards a minimum value attained during the pre-industrial period at 3.5 wildfires per millennium (Fig. 3a). These changes between the mid-Holocene period and the pre-industrial period are significant according to the bootstrap resampling of wildfire event dates (with the exception of the period around 4000 BP which is not statistically different from the pre-industrial period). By contrast, the South-RegFF remained constant during the last 6000 yr, with values fluctuating at *c.* 4–6 wildfires per millennium (Fig. 3b).

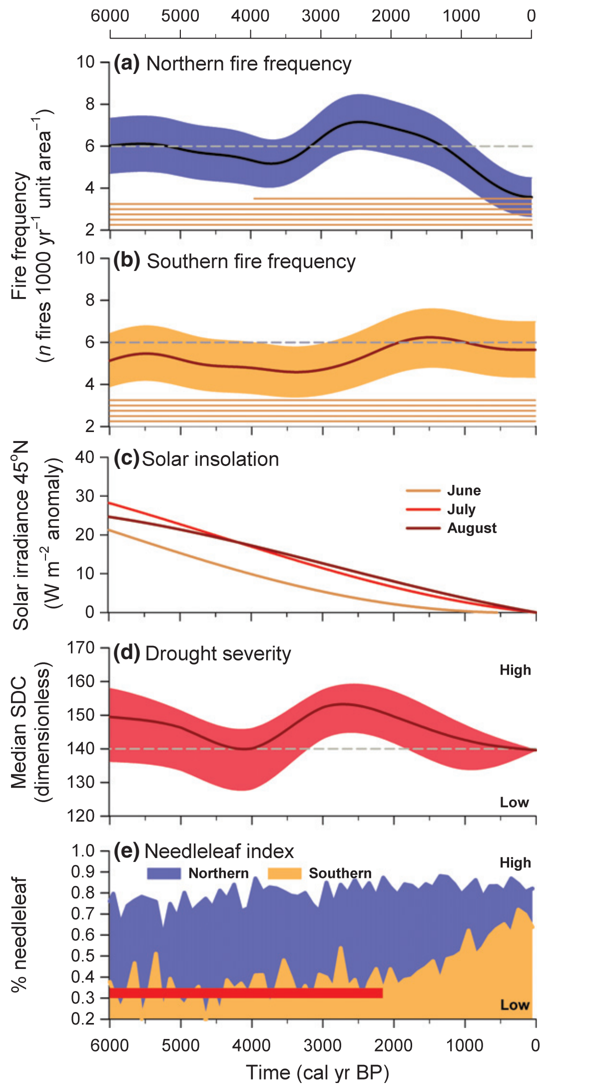

Fig. 3 Past fluctuations in wildfire activity in the transition zone of the dense needleleaf and boreal mixedwood forests of eastern Canada, and their associated forcings. (a, b) Northern and southern regions' fire frequencies. Shaded areas denote 90% bootstrap confidence intervals (CIs) for uncertainty in fire frequencies. Horizontal bars: the period covered by fire data for each individual sampled lake. (c) June–August solar insolation computed at 45°N (Berger & Loutre, 1991). (d) Median seasonal Drought Code (SDC) severity computed from simulated climate outputs of the Hadley Centre climate model (HadCM3) with 90% CI. A high value indicates a high seasonal fire danger. (e) Needleleaf index inferred from the mean proportions of total pollen counts of black spruce and jack pine. A high percentage indicates a dominance of needleleaf over broadleaf species. Significant differences ($P<0.05$) in the needleleaf index between northern and southern landscapes are indicated by the thick horizontal red line. By definition, the period of 0 calibrated years before present (cal yr BP) is equivalent to the pre-industrial period (AD *c.* 1750).

Estimates of pre-industrial RegFFs are equal in both reconstructions, as can be judged from the overlapping 90% CIs around RegFF (Fig. 3a,b). They are also in the range of plausible values in these forests, as documented by the stand-replacing fire history studies (Fig. S2).

Changes in regional wildfire frequencies can reflect a millennial-scale climatic control on wildfire danger. In high latitudes of the Northern Hemisphere, the input of summer solar irradiance has declined over the last 6000 yr as a result of changes in the Earth's axial tilt (Berger & Loutre, 1991). The period *c.* 4000 BP was a millennial-scale transitional period between the mid-Holocene, characterized by very high positive anomalies in summer solar irradiance, and the late-Holocene, marked by an ongoing decrease in solar irradiance up until today (Fig. 3c). Model simulations and reconstructions of past temperature changes indicate a millennial-scale summer cooling over the last 2000 yr as a direct response to the solar forcing (Kaufman *et al.*, 2009; Viau & Gajewski, 2009; Marcott *et al.*, 2013). Recent studies suggested that declining incoming solar irradiance has had an impact on boreal wildfire danger and activity (Hély *et al.*, 2010; de Lafontaine & Payette, 2011). Accordingly, the Holocene median SDC severity assessed from HadCM3 GCM simulations decreased through the last 2000 yr, falling from 152 units at 3000 BP to 139 units during the pre-industrial period (Fig. 3d). Low North-RegFFs recorded during the mid- and the late-Holocene correspond to low wildfire season severities and vice versa. Altogether, the North-RegFF reconstruction is correlated with simulated median SDC from 6000 to 0 BP ($r = 0.83$ with 90% CI 0.74, 0.98; $n = 7$). Such close similarities between climate controls and RegFF are not distinguished when analysing the South-RegFF ($r = -0.23$ with 90% CI -0.86, 0.52; $n = 7$), suggesting another controlling factor for wildfire activity in southern landscapes over recent millennia. Below, we provide an explanation for the diverging North- and South-RegFF trajectories from the mid- to the late-Holocene that involves an offsetting effect on the climate forcing brought on by regional vegetation changes.

Vegetation feedback

Important vegetation modifications in eastern North America marked the transition from the mid- to the late-Holocene. Noticeable through investigations of pollen records was a southerly displacement of the transition zone of the mixedwood and needleleaf forests in association with cooler climatic conditions (Liu, 1990; Dyke, 2005; Carcaillet *et al.*, 2010). We examined the potential links between changes in RegFF and vegetation inferred from published sedimentary pollen data sets (Table 1). Pollen assemblages vary according to the vegetation composition and structure surrounding the study sites (Jackson & Lyford, 1999; Broström *et al.*, 2005), and modification of these assemblages can occur with canopy disturbances and climatic changes (Richard, 1980; Koff *et al.*, 2000). In eastern boreal North America, a post-disturbance transition from broadleaf to needleleaf species can occur under abundant needleleaf regeneration. The relative dominance of needleleaf species can be greater in stands under long fire-return intervals, or lower under dry climatic conditions (Bergeron *et al.*, in press). Given that the 11 sites are within a transition zone of two forest types and that species' abundance at each site is dynamically related to the changing climate (Carcaillet *et al.*, 2001), we expected some changes in sites belonging to forest types over past millennia. This was seemingly the case. Modern vegetation composition in northern landscapes is dominated by black spruce (*P. mariana*; Fig. 2). This dominance was already set some 6000 yr ago according to pollen analysis and persisted throughout the intervening millennia (Fig. 3e). By contrast, a gradual development towards flammable needleleaf species such as black spruce and jack pine (*P. banksiana*) was recorded in southern landscapes *c.* 2000 BP (Fig. 3e). This change came at the cost of a decrease in the abundance of broadleaf species, that is, birches (*Betula papyrifera* and *B. alleghaniensis*), grey alder (*Alnus incana*) and aspen (*P. tremuloides*; Fig. 3e). Therefore, the pre-industrial composition of the southern sites is much closer to the dense needleleaf forest type than it was some 6000–3000 yr ago (Fig. 3e; Carcaillet *et al.*, 2010).

A potential explanation for the divergence between the two RegFF trajectories may lie in the changing vegetation. The declining risks brought about by less wildfire-prone climatic conditions (Fig. 3d) may well have been offset by an increasing needleleaf component in southern landscapes some 2000 yr ago (Fig. 3e). We tested this hypothesis by integrating the HadCM3 GCM median SDC simulations and pollen-based vegetation

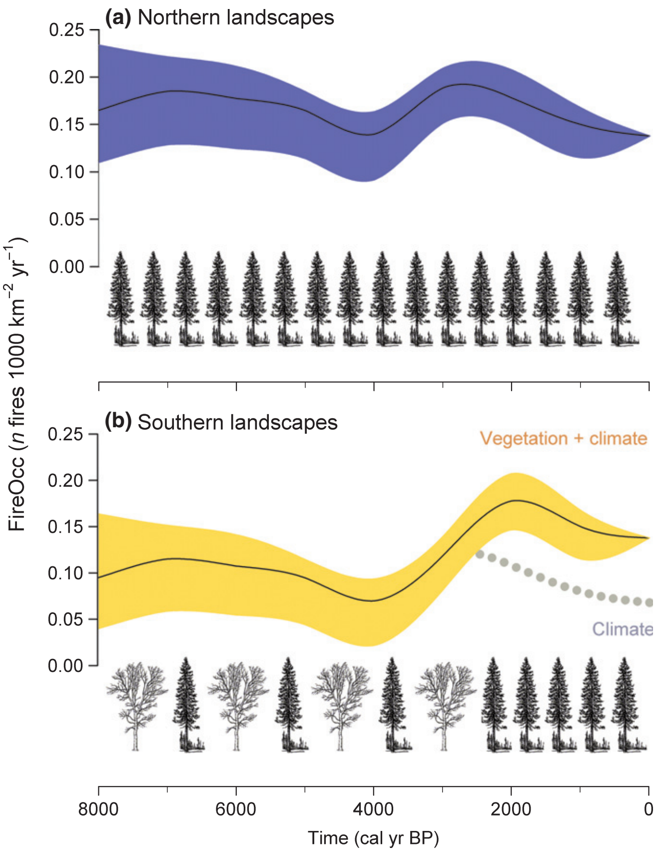

Fig. 4 Projected changes in the occurrence of large wildfires (FireOcc) in (a) northern and (b) southern landscapes from 6000 to 0 BP (calibrated years before present) simulated using climatic data from the HadCM3 general circulation model (GCM) and vegetation changes deduced from pollen analyses (see Fig. 3d–e). The shaded area is the 90% CI. In (a), a fixed vegetation composition dominated by needleleaf forests was set throughout the entire period. In (b), vegetation was manipulated (*Vegetation + climate*) with a shift from a boreal mixedwood to a needleleaf-dominated forest at 2000 BP. The status quo scenario of no vegetation change (*Climate*) is also shown in (b).

information into the fire model for projection of FireOcc of size > 200 ha. Model projections for northern landscapes suggest a decline in FireOcc > 200 ha, with the median FireOcc of the last two millennia being *c.* 20% lower than the median of 6000–2000 BP (Fig. 4). This difference closely matches the decline of *c.* 25% seen in North-RegFF over the same periods (Fig. 3a). The opposite pattern is found in southern landscapes. Therein model projections indicate higher levels of FireOcc during the last 2000 yr relative to the mid-Holocene period (Fig. 5b), which is coherent with the wildfire trajectory deduced from the South-RegFF observations (Fig. 3b; $r = 0.80$ with 90% CI 0.50, 0.99; $n = 7$). This stable state in FireOcc occurs because the induced shift in vegetation from boreal mixedwood to dense needleleaf landscapes at 2000 BP was sufficient for offsetting the FireOcc decline brought on by a lowering of the median SDC (Fig. 3d). If these landscapes had remained in a boreal mixedwood state as they were some 5000 yr ago, they would have undergone a significant decline in large wildfires towards levels approximating 0.07 fires per year per 1000 km (Fig. 4b). But, as seen with the South-RegFF (Fig. 3b), this was not observed. Hence, the modelling results suggest that biotic feedback arising from vegetation changes was strong enough to modulate past climatic change influences on large wildfire activity.

Our results indicate that modification of vegetation composition has contributed to a lower wildfire probability in a warmer climate. Nonetheless, uncertainty remains about the efficiency of such effects in the 21st Century if GHG levels and climate conditions become significantly different from historical levels. Under excessive droughts, the biotic feedback might not be strong enough to limit future wildfire activity. To address this question, we used projected drought from an ensemble of eight global climate models forced by various scenarios of GHG emissions (Table S1) as input into the FireOcc model. For this experiment, we induced a vegetation shift from dense needleleaf to boreal mixedwood landscapes at AD 2040 and compared the results with a status quo scenario (Fig. 5). Results indicated that median SDC at the end of the 21st Century could reach levels similar to those simulated from the HadCM3 GCM during the mid-Holocene (i.e. *c.* 30 SDC units above the AD 1961–1999 baseline). Keeping vegetation composition in a needleleaf state produced a doubling in FireOcc for the late 21st Century compared with AD 1961–1999 levels (ensemble median; Fig. 5a). Increases in FireOcc were significant in seven out of 21 experiments (one-sided Student's *t*-test with correction for multiple comparisons). Inducing a vegetation change to boreal mixedwood landscapes (Fig. 5b) was effective in offsetting climatic change impacts on FireOcc in six out of these seven experiments (the effect failed for MIROC3.2 medres A1B). Altogether, the negative vegetation feedback was sufficient to limit the rise in FireOcc calculated over the interval 2041–2100 to 30% of the level projected for the baseline period (ensemble median; Fig. 5b) and well within the range of historical variations (i.e. < 0.20 fires 1000 km^{-2} yr^{-1}; Fig. 4b).

Conclusions

With the urgent necessity for strategic decisions to cope with the increasing threat future wildfires pose, there is a requirement for sound assessments of the costs and benefits of planned manipulation of vegetation in wildland–urban interfaces of global boreal forests. The use of paleoecological data and GCM simulations in a wildfire model for testing the sensitivity of biotic feedback is a significant contribution to this objective. Manipulative vegetation treatments have been suggested as potential climate-change adaptation strategies in boreal forests, mostly on the basis of simulation experiments (Hirsch *et al.*, 2004; Krawchuk & Cumming, 2011; Terrier *et al.*, 2013). Our assessment of millennial-scale variations of seasonal wildfire danger, vegetation flammability, and fire activity suggests that feedback effects arising from vegetation changes are large enough to offset climatic change impacts on fire danger. Our quantitative results are subject to uncertainties, including those associated with the increasing impact of human ignitions and differences in fire seasonality (Wotton *et al.*, 2010). However, our main finding is robust: in spite of the warm climate some 6000–3000 yr ago in eastern Canada, RegFF in

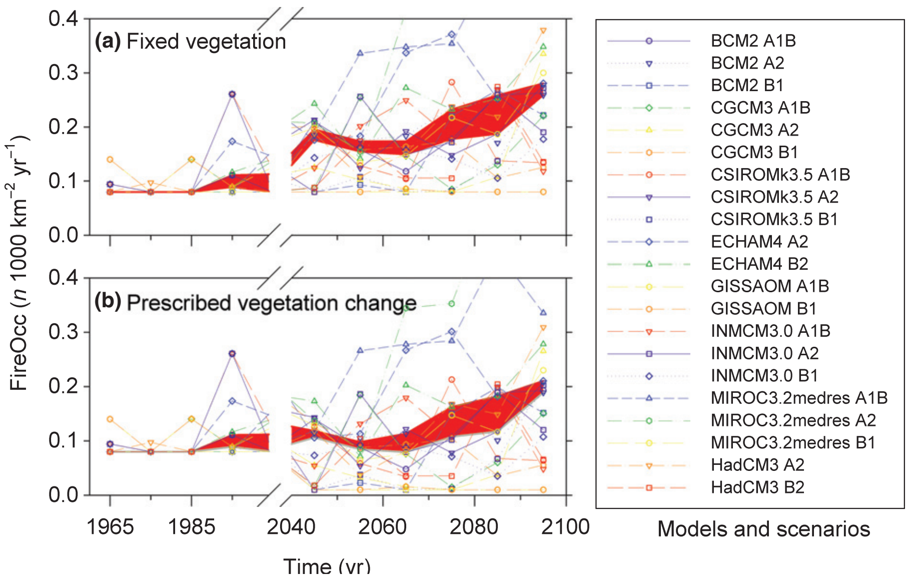

Fig. 5 Projected changes in the occurrence of large wildfires (FireOcc) in the modern northern needleleaf landscape over the 21st Century simulated from an ensemble of eight global climate models forced by various scenarios for greenhouse gas emissions. A 90% bootstrap confidence interval (CI) for the ensemble median is shown (red shading). In scenario (a), vegetation was set with a fixed needleleaf forest throughout all periods. In scenario (b), vegetation was manipulated with a shift from a needleleaf to a boreal mixedwood forest at AD 2040. In scenario (a), mean FireOcc calculated over the interval 2041–2100 is significantly greater than mean FireOcc calculated over the interval 1961–1999 (one-sided Student's *t*-test $P < 0.05$). In scenario (b), 2041–2100 FireOcc is not significantly greater than 1961–1999 FireOcc.

southern landscapes was not significantly higher than the pre-industrial RegFF and this was a result of the lower landscape proportion of flammable needleleaf species. Future climate warming will lead to increases in the proportion of hardwood forests in both southern and northern boreal landscapes (McKenney *et al.*, 2011; Terrier *et al.*, 2013). However, this effect will spread over long periods because of low species migration and dispersal rates. If lower proportions of flammable needleleaf species in landscapes are a natural feature of a warmer climate (Carcaillet *et al.*, 2010; Terrier *et al.*, 2013), then in the short term forest management should gradually provide more space for approaches promoting broadleaf and boreal mixedwood forests. This would be a way to reduce wildfire risk during the transition to a new vegetation equilibrium. This consideration is important as it could make vegetation changes socially and environmentally acceptable. There are also many other benefits brought about by the increasing dominance of broadleaf species in landscapes. This may include the higher albedo and summer evapotranspiration from deciduous trees, which would cool and counteract regional warming (Rogers *et al.*, 2013), and the increase in the resilience of forests to climatic changes (Drobyshev *et al.*, 2013). Further studies should address questions dealing with the magnitude of vegetation composition changes needed to attain the wildfire management objectives (e.g. relative abundance of species and size of the managed areas), the existence of potential constraints on the success of species establishment (e.g. nutrient limitations), and how the treatments would interfere with other values and concerns of the forest sectors (e.g. forest conservation and timber supply).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Observed versus projected number of forest fires of size > 200 ha yr^{-1} per 1000 km^2 in the province of Quebec (Canada).

Fig. S2 Verification of RegFF against independent fire history studies from needleleaf and boreal mixedwood landscapes.

Table S1 General circulation models and their greenhouse gas forcing scenarios

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