Fire as the dominant driver of central Canadian boreal forest carbon balance

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Changes in climate, atmospheric carbon dioxide concentration and fire regimes have been occurring for decades in the global boreal forest^{1–3}, with future climate change likely to increase fire frequency⁴—the primary disturbance agent in most boreal forests^{3,5}. Previous attempts to assess quantitatively the effect of changing environmental conditions on the net boreal forest carbon balance have not taken into account the competition between different vegetation types on a large scale^{6–9}. Here we use a process model with three competing vascular and non-vascular vegetation types to examine the effects of climate, carbon dioxide concentrations and fire disturbance on net biome production, net primary production and vegetation dominance in 100 Mha of Canadian boreal forest. We find that the carbon balance of this region was driven by changes in fire disturbance from 1948 to 2005. Climate changes affected the variability, but not the mean, of the landscape carbon balance, with precipitation exerting a more significant effect than temperature. We show that more frequent and larger fires in the late twentieth century resulted in deciduous trees and mosses increasing production at the expense of coniferous trees. Our model did not however exhibit the increases in total forest net primary production that have been inferred from satellite data^{1,10}. We find that poor soil drainage decreased the variability of the landscape carbon balance, which suggests that increased climate and hydrological changes have the potential to affect disproportionately the carbon dynamics of these areas. Overall, we conclude that direct ecophysiological changes resulting from global climate change have not yet been felt in this large boreal region. Variations in the landscape carbon balance and vegetation dominance have so far been driven largely by increases in fire frequency.

We used the Biome-BGC process model^{11,12} to simulate the 1,000 km × 1,000 km Boreal Ecosystem-Atmosphere Study (BOREAS) region; at 15–20% of the North American boreal forest, it encompasses much of Manitoba and Saskatchewan as well as eastern Alberta, Canada. Species diversity is low, and the landscape is dominated by black spruce (*Picea mariana* (Mill.) BSP), trembling aspen (*Populus tremuloides* Michx.) and bryophytes. Regional climate changes over the past 60 years have been modest (Supplementary Information). We used a full-factorial design to examine the effects of climate (meteorology, 'M'), CO₂ ('C') and fire disturbance ('D') on net biome production (NBP, net ecosystem carbon balance integrated over time and space¹³), net primary production (NPP), and vegetation dominance. The model included interacting carbon, nitrogen and water cycles^{11,14}; a Farquhar photosynthesis model; dynamic and competing vegetation types, including coniferous trees, deciduous broad-leaf trees and mosses¹²; and explicit representation of non-vascular plants¹⁵, which constitute an important component of boreal biogeochemical cycling.

For the period 1948–2005, mean simulated NBP was $9.9 \pm 11.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($N = 579,395$ cells, excluding lakes, agricultural

areas, and so on; the error term is interannual variability), indicating the landscape was a small carbon sink until late in the twentieth century. Spatial variability (cell standard deviation) was $78.9 \text{ g C m}^{-2} \text{ yr}^{-1}$. The difference between this (the 'MDC' scenario) and what would have happened without any changes in climate, CO₂ or fire (the 'base' scenario), here denoted $\text{NBP}_{\text{MDC-base}}$, was -423 g C m^{-2} or $-8.0 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Fig. 1). Over the final ten years (1996–2005), $\text{NBP}_{\text{MDC-base}}$ was $-13.3 \text{ g C m}^{-2} \text{ yr}^{-1}$. In other words, the simulation indicated that the region lost on average 423 g C m^{-2} (or 245 Tg for the entire region, about 2% of soil carbon) over the past 58 years, relative to what would have happened if mid-century conditions had continued unaltered, with the difference increasing in recent years.

The CO₂ effect exerted, by itself, a positive effect on 58-yr mean NBP ($0.5 \text{ g C m}^{-2} \text{ yr}^{-1}$), while the disturbance and meteorology effects were negative (-8.5 and $-0.3 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively). In a sinusoidal model fitted to the NBP output data, the disturbance effect (that is, scenarios D, DC, MD, MDC) changed the wave's offset (mean) by $-0.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 1); the meteorology and disturbance effects both increased NBP wave amplitude by $\sim 0.2 \text{ g C m}^{-2} \text{ yr}^{-1}$. The CO₂ effect was not significant except interacting with disturbance, where it significantly affected wave period. This interactive effect emphasizes the limitations of extrapolating ecosystem-scale changes from studies on individual forcing effects.

Figure 1 | Difference in net biome production (NBP) between simulation scenarios, over length of simulation. A negative value indicates a relative carbon source to the atmosphere. Scenario labels indicate main effects applied to base case (mid-century conditions): climate (meteorology, 'M'), CO₂ ('C'), disturbance ('D') and their combination ('MDC'). Data are smoothed using a 5-yr running mean. Bar graph, on right-hand axis, shows annual area burned in the study area.

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Table 1 | Significant parameters in sinusoidal model of net biome production

Parameter	Description	Estimate	s.e.	T	P
β_{1D}	Disturbance effect on β_0 (offset) trend	-0.29	0.02	-12.78	<0.0001
β_2	Wave amplitude	-11.04	1.02	-10.78	<0.0001
β_{3M}	Meteorology effect on β_2 trend	0.25	0.04	6.18	<0.0001
β_{3D}	Disturbance effect on β_2 trend	0.19	0.04	4.79	<0.0001
β_4	Wave period	18.88	0.34	55.87	<0.0001
β_{5M}	Meteorology effect on β_4 trend	0.04	0.01	4.60	<0.0001
β_{5MDC}	D×C interaction effect on β_4 trend	0.31	0.02	14.71	<0.0001
ϕ	Initial wave phase	6.07	0.55	11.07	<0.0001

See equation (1) in Methods. Estimate (in g C m^{-2} for β_2 ; in $\text{g C m}^{-2} \text{yr}^{-1}$ for β_{1D} , β_{3M} , β_{3D} ; in yr for β_4 , ϕ ; in yr yr^{-1} for β_{5M} , β_{5DC}), standard error (s.e.), T statistic and P value are given. D×C refers to two-way interaction of disturbance and CO_2 . Model residual s.e. was 10.73 on 456 degrees of freedom.

The major and consistent driver of NBP was thus fire disturbance. For the entire grid, mean loss to fire in the base scenario was $2.7 \pm 0.6 \text{ g C m}^{-2} \text{yr}^{-1}$, increasing in the real-world MDC scenario to $6.8 \pm 1.0 \text{ g C m}^{-2} \text{yr}^{-1}$ (spatial variability was respectively 98.7 and $108.9 \text{ g C m}^{-2} \text{yr}^{-1}$). The southwest grid quadrant's NBP was the most variable in time and space (23.2 and $100.9 \text{ g C m}^{-2} \text{yr}^{-1}$, respectively) and the northeast the lowest (8.9 and $46.9 \text{ g C m}^{-2} \text{yr}^{-1}$, respectively). For the final 30 yr of the simulation, the northwest grid quadrant was a C source ($-15.1 \text{ g C m}^{-2} \text{yr}^{-1}$) while the other three quadrants were small sinks (3.9 – $11.6 \text{ g C m}^{-2} \text{yr}^{-1}$). Soil drainage also significantly affected carbon dynamics. NBP was more spatially variable in well drained than in poorly drained areas, and over the final 30 yr of the simulation more variable in time as well (year-to-year standard deviation of 12.2 versus $11.4 \text{ g C m}^{-2} \text{yr}^{-1}$, respectively). Thus during this period poorly drained areas damped regional NBP swings (although early in the simulation these areas exhibited

more variability). NBP was positively affected by temperature ($T_{111} = 4.96$, $P < 0.0001$); poorly drained NBP was positively and extremely strongly affected by precipitation, while well drained areas were negatively affected ($P < 0.0001$ for each).

Mean total NPP ($186.1 \text{ g C m}^{-2} \text{yr}^{-1}$) was dominated by evergreen needle-leaf trees ($141.4 \text{ g C m}^{-2} \text{yr}^{-1}$). Conifer NPP declined by $0.5 \text{ g C m}^{-2} \text{yr}^{-2}$ ($T_{113} = -7.28$, $P < 0.0001$) in the MDC scenario, relative to the base case, and its share of total NPP dropped from 80% at the beginning of the simulation to 73% at its end as fire converted mature coniferous stands to young deciduous ones (Fig. 2a). The distribution of NPP among grid cells was skewed, particularly for deciduous broadleaf trees, which did not occur in 77% of the forest cells; coniferous trees were much more evenly distributed (Fig. 2b). Mean NPP_{MDC} for deciduous broadleaf trees was thus low, $17.7 \text{ g C m}^{-2} \text{yr}^{-1}$, and rose by $0.2 \text{ g C m}^{-2} \text{yr}^{-2}$ between the base and MDC scenarios. Bryophyte NPP averaged $29.2 \text{ g C m}^{-2} \text{yr}^{-1}$ and increased between scenarios by $0.1 \text{ g C m}^{-2} \text{yr}^{-2}$. Mean stem and leaf carbon were respectively 1,785 and 284 g m^{-2} in the MDC scenario, while mean deep soil carbon was 19.8 kg m^{-2} (12.7 and 31.6 kg m^{-2} in the well and poorly drained areas, respectively).

The Biome-BGC model has been extensively validated in North American boreal ecosystems at the stand level (for example, in simulating post-disturbance forest dynamics^{15,16}) and in comparison to eddy covariance data¹⁷. Figure 3 shows how model output compared to results from several chronosequence studies performed at the BOREAS northern and southern study areas in Thompson, Manitoba, and Candle Lake, Saskatchewan, respectively. (We note however that these studies do not constitute a random sample—on the contrary, many were performed in ‘end-member’ stands that constitute a small fraction of the landscape at any given time¹⁸.)

Comparisons at the biome level, particularly with studies using complementary methods at large temporal and spatial scales, are more appropriate here. The steady-state biomass and soil C values reported above are close to those inferred from inventory and mass-balance modelling¹⁸. Such inventory approaches have yielded net ecosystem production and NPP estimates of -14 to 98 and 215 to $330 \text{ g C m}^{-2} \text{yr}^{-1}$, respectively, for western boreal Canada, and emphasized the role of natural disturbances^{18,19}. Mean carbon lost in each fire event in this study was $1.5 \pm 1.1 \text{ kg C m}^{-2}$, comparable to observed data^{18,20}, long-term mass balance results²¹ and previous modelling efforts^{9,22}. We assumed that the boreal landscape was a small C sink in 1948, the beginning of the simulation; inventory models support this assumption¹⁸, and poorly drained areas in

Figure 2 | Temporal and spatial distribution of simulated net primary production (NPP). **a**, Difference in NPP between real-world ‘MDC’ scenario and the mid-century base case, by vegetation type (evergreen needle-leaf trees, ENF; deciduous broadleaf trees, DBF; and bryophytes, BRY) over the simulation. Data are smoothed using a 5-yr running mean. **b**, Histogram of simulated NPP for MDC scenario, all grid cells, year 2005.

Figure 3 | Comparison of model output with observed data from a variety of studies. (Studies are listed in Supplementary Information.) Contour plot shows number of grid cells from real-world ‘MDC’ scenario, year 2005, for each combination of net primary production (NPP) and net ecosystem production (NEP). Scatter plot points are published data: circles, data from the BOREAS Northern Study Area; squares, Southern Study Area data. Red symbols are the main BOREAS flux tower sites.

particular had probably not achieved a postglacial steady state²³. This mean NBP was higher than the long-term sequestration mean implied by soil stocks²¹, but lower than values implied by inverse modelling efforts²⁴. Our simulations did not show the strong trend in boreal photosynthetic and total NPP activity inferred from satellite data^{1,25,26}: here deciduous broadleaf and bryophyte NPP increased, while evergreen NPP (and total NPP) declined as older stands burned with increasing frequency. Because 5% or more of the landscape can burn in high-fire years, and because many such years have occurred in the last two decades, at regional scales satellites may be recording high post-fire growth, rather than growth directly caused by CO₂ or climate change²⁷.

Several sources of uncertainty are worth noting. First, the possible current damping role of poorly drained areas, their large carbon storage, and the control of soil drainage on fire emissions²¹ all argue for a better understanding of such systems, but they are poorly modelled by most terrestrial models, including, despite significant improvements¹⁵, Biome-BGC. We believe this is the largest area of uncertainty with regard to the results presented here. Second, the 58-yr period simulated here is considerably shorter than fire return intervals of the North American boreal forest, and the long-term effects of increased fire may be different from the short-term ones portrayed here. The effects of increased fire will be felt over multiple timescales: short (increased C volatilization), medium (the large areas burned in 1989–95 are only now, 12–18 yr later, turning from C sources to sinks²⁸), and long, with shifts in soil carbon stocks, forest age structure, and species dominance.

Fire activity is driven by local and regional climate^{2,3}, even if in this study they are treated as separate effects in order to understand quantitatively the contribution of different climate-driven ecosystem processes to forest carbon balance. Fuel loads are a function of long-term climate, while daily weather determines fire activity by drying out the forest fuels, igniting these fuels, and controlling fire spread. Thus climate is indirectly but ultimately responsible for determining the twentieth-century boreal forest carbon dynamics in central Canada. Our results suggest, however, that the ecophysiological changes from global climate change have not yet been felt in this large boreal region; rather, variations in landscape carbon balance and vegetation dominance have so far been largely driven by increases in fire frequency. This implies that fire management may have underappreciated benefits, even if practiced selectively, in affecting decadal boreal carbon balance; currently some degree of fire suppression is attempted on ~50% of large Canadian fires³. Our results only apply, however, to systems dominated by stand-replacing fires such as the North American boreal forest. Other regional disturbance agents such as insects and logging are growing in importance^{18,29}, and should be considered in future management and modelling efforts.

METHODS SUMMARY

The processes and logic of Biome-BGC have been described elsewhere^{11,12,14}; the version used here was extensively modified with regard to the effects of poor soil drainage¹⁵ and competing vegetation types, including bryophytes¹². All vegetation types were treated as potentially present in every cell, allowing for species composition changes during simulations. In each fire event, fixed percentages of stem, leaf, coarse root, fine root, litter, woody debris and shallow soil were volatilized, reflecting typical dynamics of a stand-replacing fire. Plant growth was restarted the year following fire. Basic land cover categories were assigned using the MODIS MOD12 data product; soil data were derived from the BOREAS regional soils data. A digital elevation model was obtained from the ORNL DAAC. Meteorological data were downloaded from the Climate Analysis Branch at NOAA for the years 1948–2005. Spatially and temporally explicit data from the Canadian Forest Service's Large Fire Database (LFDB) were used to drive the model; these data include 97% of the area burned in Canada³. Plant physiological parameters were standardized across the entire simulation grid and published previously¹⁵. Simulation cell size was 1 km²; each cell was self-initialized until just before its deep soil carbon stabilized (that is, leaving a small ongoing carbon sink). Eight 58-yr simulations, each a combination of the three main effects (meteorology, disturbance and CO₂) being tested, were then run. Mid-century meteorological and fire data consisted of the 1948–67

time period, cycled as necessary to fill out a 58-yr simulation; changed conditions consisted of the actual 1948–2005 record. Mid-century CO₂ was 310 p.p.m., while in changed conditions it rose from 310 to 380 p.p.m. The carbon balance output by the model was analysed in R 2.4.0 (ref. 30) using a nonlinear sinusoidal model.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Author Contributions S.T.G., B.B.-L. and D.E.A. designed the experiment. S.D.P. and D.E.A. assembled input data, and B.B.-L. and S.D.P. wrote code, ran the model, and analysed output data. B.B.-L. administered the experiment and wrote the manuscript.

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METHODS

Biome-BGC process model. The processes and logic of Biome-BGC have been described elsewhere^{11,12,14}; the version used here was extensively modified with regard to the effects of poor soil drainage¹⁵ and competing vegetation types, including bryophytes¹². All vegetation types were treated as potentially present in every cell, allowing for species composition changes during simulations. In each fire event, fixed percentages of stem, leaf, coarse root, fine root, litter, woody debris and shallow soil were volatilized, reflecting typical dynamics of a stand-replacing fire. Plant growth was restarted the year following fire.

Input data sources. Basic land cover categories were assigned using the MODIS MOD12 data product (<http://www.modis.bu.edu/landcover/userguide/lc.html>); the MODIS MCD43B product was used for albedo: a 16-day composite image from 28 July to 12 August 2003 was calibrated and resampled using bilinear interpolation, and the shortwave band extracted from the 20-band image. MODIS products were imported, subset and masked to include only the simulation grid using nearest neighbour resampling. Soil data were derived from data layers of the BOREAS regional soils data (http://www.daac.ornl.gov/BOREAS/guides/Region_Soils_Raster.html). A digital elevation model was obtained from the ORNL DAAC. All data were reprojected, if necessary, to BOREAS Albers Equal Area Conic.

Estimates of the sand, silt and clay percentages were obtained using the soil texture raster data and the Canadian Soil Information System (CanSIS) website (<http://sis.agr.gc.ca/cansis/>); these were applied to all other soils in the raster image that were similar to known soil textures. Thirty per cent of the BOREAS grid was coded as 'not applicable'. In order to increase the number of pixels with soil texture information, these 'not applicable' locations were filled in by association with land cover. The rooting depth data layer was used to calculate the Biome-BGC effective soil depth parameter, based on four categories (0.2, 0.75, 1.5 and 2.5 m). Values of 'not applicable' were replaced on the basis of soil texture associations.

Our revised version of Biome-BGC has water inflow and outflow rate parameters (inflow α_0 , surface outflow α_1 and subsurface outflow α_2)¹⁵. A soil drainage class raster image was used to compute these three BGC parameters based on the following criteria: excessively well drained ($\alpha_0 = 0.0$, $\alpha_1 = 1.0$, $\alpha_2 = 0.8$); well to moderately well drained ($\alpha_0 = 0.0$, $\alpha_1 = 1.0$, $\alpha_2 = 0.5$); poorly drained ($\alpha_0 = 0.5$, $\alpha_1 = 0.1$, $\alpha_2 = 0.01$); very poorly drained ($\alpha_0 = 1.0$, $\alpha_1 = 0.01$, $\alpha_2 = 0.0$).

Meteorological data were downloaded directly from the Climate Analysis Branch at NOAA (<http://www.cdc.noaa.gov/cdc/reanalysis/reanalysis.shtml>) for the years 1948–2005. These global data included maximum daily temperature, minimum daily temperature, specific humidity, shortwave radiation, surface pressure and precipitation rate, and were on the T1 gaussian grid. A subset of

the global grid was chosen to adequately cover the study area, and the data resampled to the simulation grid, with 20 km resolution using weighted distance interpolation with the six nearest latitude/longitude points. Vapour pressure deficit was calculated from surface pressure and specific humidity. In order to make a simple link to cells on the BOREAS grid, a 'met key' grid was created, in which each 1 km² cell contained the values of its corresponding meteorology cell. Spatially and temporally explicit data from the Canadian Forest Service's Large Fire Database (LFDB) were used to drive the model; these data include 97% of the area burned in Canada³. The LFDB covers 1959–2005; data for 1948–58 were derived on the basis of provincial records of total area burned and the known fire size distributions data of the LFDB. Plant physiological parameters were standardized across the entire simulation grid and published previously¹⁵.

Simulation and statistical procedures. The simulation grid was 10⁶ km²; simulation cell size was 1 km². Each grid cell was independently self-initialized under historical conditions, with a fire return interval of 175 yr, from an initial empty state until just before its deep soil carbon stabilized (that is, leaving a small ongoing carbon sink). From this point eight 58-yr simulations, each a combination of the three main effects (meteorology, disturbance and CO₂) being tested, were run. Each effect could be set to either 'mid-century' or 'changed' states. Mid-century meteorological and fire data consisted of the 1948–67 time period, cycled as necessary to fill out a 58-yr simulation; changed conditions consisted of the actual 1948–2005 record. Mid-century CO₂ was 310 p.p.m., while in changed conditions it rose from 310 to 380 p.p.m. All simulations were performed on a distributed computing grid using Apple Computer's Xgrid software to handle job distribution and processing.

Steady-state carbon balance in models such as Biome-BGC tends to oscillate around a mean; this was modelled with a nonlinear model:

$$y = \beta_0 + \beta_1 t + (\beta_2 + \beta_3 t) \sin \left[\frac{(t - \phi)}{\beta_4 + \beta_5 t} \right] \quad (1)$$

where y is carbon balance; t the year, normalized with 1948 as year 0; ϕ the initial wave phase; and β_0 , β_2 and β_4 the wave offset, amplitude and period, respectively. The three main effects were tested for their separate effects on the linear trends of offset, amplitude and period relative to the detrended base case data. Thus β_1 , β_3 and β_5 were each the sum of a base value plus main effects and their interactions (that is, $\beta_i + \beta_{iC} + \beta_{iD} + \beta_{iM} + \beta_{iCD} + \beta_{iCM} + \beta_{iDM} + \beta_{iCDM}$; for clarity these are not expanded in equation (1)). This final model had 28 parameters, 464 observations (= 8 scenarios $\times$ 58 years) and was simplified, after initial fitting, by stepwise removal of non-significant terms. Statistical analyses were conducted in R version 2.4.0 (ref. 30), used annual flux or pool as the experimental unit, and a significance level of $\alpha = 0.05$.