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Palaeodata-informed modelling of large carbon losses from recent burning of boreal forests

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Wildfires play a key role in the boreal forest carbon cycle[1,2], and models suggest that accelerated burning will increase boreal C emissions in the coming century[3]. However, these predictions may be compromised because brief observational records provide limited constraints to model initial conditions[4]. We confronted this limitation by using palaeoenvironmental data to drive simulations of long-term C dynamics in the Alaskan boreal forest. Results show that fire was the dominant control on C cycling over the past millennium, with changes in fire frequency accounting for 84% of C stock variability. A recent rise in fire frequency inferred from the palaeorecord[5] led to simulated C losses of 1.4 kg C m^{-2} (12% of ecosystem C stocks) from 1950 to 2006. In stark contrast, a small net C sink of 0.3 kg C m^{-2} occurred if the past fire regime was assumed to be similar to the modern regime, as is common in models of C dynamics. Although boreal fire regimes are heterogeneous, recent trends[6] and future projections[7] point to increasing fire activity in response to climate warming throughout the biome. Thus, predictions[8] that terrestrial C sinks of northern high latitudes will mitigate rising atmospheric CO_2 may be over-optimistic.

The Arctic has experienced rapid climate change in recent decades and is projected to warm 4–5 °C—more than twice the global average—during the twenty-first century under moderate anthropogenic emissions scenarios[9]. High-latitude ecosystems impose critical feedbacks to global climate change by modulating the rise in atmospheric concentration of greenhouse gases. In particular, the vast boreal forest biome is estimated to serve as a net C sink of ~0.5 Pg C yr^{-1} (ref. 10), contributing substantially to a global terrestrial sink of 1–1.5 Pg C yr^{-1} in recent decades[9]. Longer growing seasons and rising atmospheric CO_2 concentration (p_{CO_2}) could enhance boreal forest productivity in the twenty-first century, and Earth system models (ESMs) indicate that these effects will strengthen the boreal C sink[8]. However, observed recent trends have been heterogeneous[11], and the sustainability of continued C uptake by the biome depends on many interacting factors that remain poorly understood, including changing disturbance regimes, thawing permafrost, and nutrient limitation. To constrain models of the global C cycle, it is critical to understand how these processes operate within boreal ecosystems and to scale their behaviour to the entire biome.

Wildfire plays a dominant role in the C dynamics of boreal forests[2,3]. In recent decades, climate warming has been linked to increased boreal forest burning, including record-breaking fire years and unprecedented regional fire regimes[5–7], and future climate change is expected to increase fire activity throughout the biome[7]. The potential for these changes to feed back to the climate system has not been formally evaluated using ESMs, because the inclusion of fire in such models is a relatively new development[8,12]. However, ecosystem models suggest that C emissions resulting from even moderate increases in burning could offset enhanced productivity caused by CO_2 fertilization and climate change[13], potentially converting the boreal biome from a sink to a source of C within the next century[3,14].

Efforts to model fire effects on boreal C cycling may be compromised by the brevity of observational fire records, which span only the past several decades in most boreal regions. The 'spin-up' procedure commonly used to initialize ecosystem models often requires hundreds to thousands of model years to reach an approximately steady state, and, for lack of empirical data, prehistoric fire regimes are typically assumed to be stationary and similar to modern for the purpose of the spin-up. Model results depend strongly on this assumption[3,4,15], and recent palaeoecological studies have challenged it by revealing striking variability in past boreal forest fire activity[16,17]. In particular, a fire history reconstruction from the Yukon Flats ecoregion of Alaska indicates transition to a new fire regime within the past several decades, providing unambiguous evidence that the modern fire regime is unrepresentative of prehistoric variability[5]. The Yukon Flats region has experienced among the most extensive burning of any North American boreal forest in recent years[18], and may therefore be indicative of widespread future change if predictions of increased burning are realized. Here we use palaeoecological data from this region as a basis for ecosystem modelling experiments to elucidate the implications of past fire-regime change to present and future C balance.

We modelled C dynamics of the past millennium (850–2006) for ~2,000 km^2 of boreal forest in the Yukon Flats (Supplementary Fig. 1) using the dynamic organic soil version of the Terrestrial Ecosystem Model (DOS-TEM), a process-based model designed to simulate the cycling of carbon and nitrogen through the soil and vegetation of terrestrial ecosystems (Methods and Supplementary Fig. 2). We forced the model with fire frequency and severity proxies derived from sediment charcoal records[5], palaeoclimate simulations generated by the Max Planck Institute for Meteorology Earth System Model (MPI-ESM; ref. 19), and ice-core p_{CO_2} records[20]. Simulated total ecosystem carbon storage (C_{ECO}) was highly variable over centennial timescales (Figs 1 and 2a), ranging from 9.6 kg C m^{-2} in 1230 to a maximum of 12.5 kg C m^{-2} in 1870. Model experiments in which each forcing was allowed to vary or held stationary reveal that the majority (83.5%) of C_{ECO} variability was due to shifts in fire frequency, and most of the remainder (14.6% of total) was accounted for by fire severity. The direct effects of climate and p_{CO_2} were minor (1.6% and <0.1% of C_{ECO} variance, respectively). Thus, long-term C dynamics of the past millennium were almost entirely dictated by patterns of fire-regime variability.

Rather than downplaying the importance of climate change to the fate of high-latitude C stocks[10], our findings underscore

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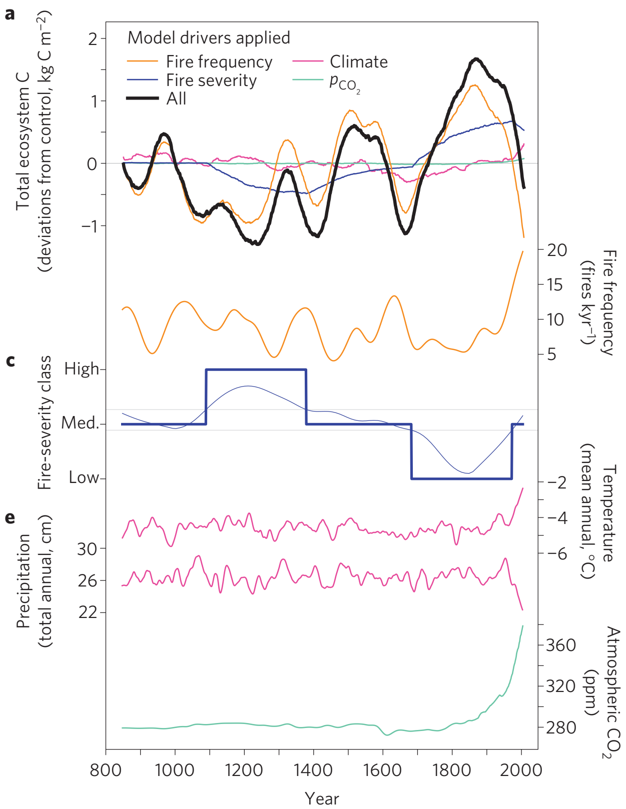

Figure 1 | Carbon dynamics of the past millennium. a, Simulated carbon stocks in response to model drivers (**b**–**f**) applied in combination (black) or individually (colours; see legend). Results are plotted as deviations from a control simulation with stationary inputs. **b**, Fire frequency estimated from palaeorecords. **c**, Fire-severity class (thick line) derived by stratifying a proxy variable (thin line) at its upper and lower quartiles (grey lines). **d**,**e**, Simulated palaeoclimate, summarized as trends in annual temperature and precipitation (actual inputs were monthly and included additional variables). **f**, Atmospheric CO_2 concentration from ice-core records. All lines are means over the study area.

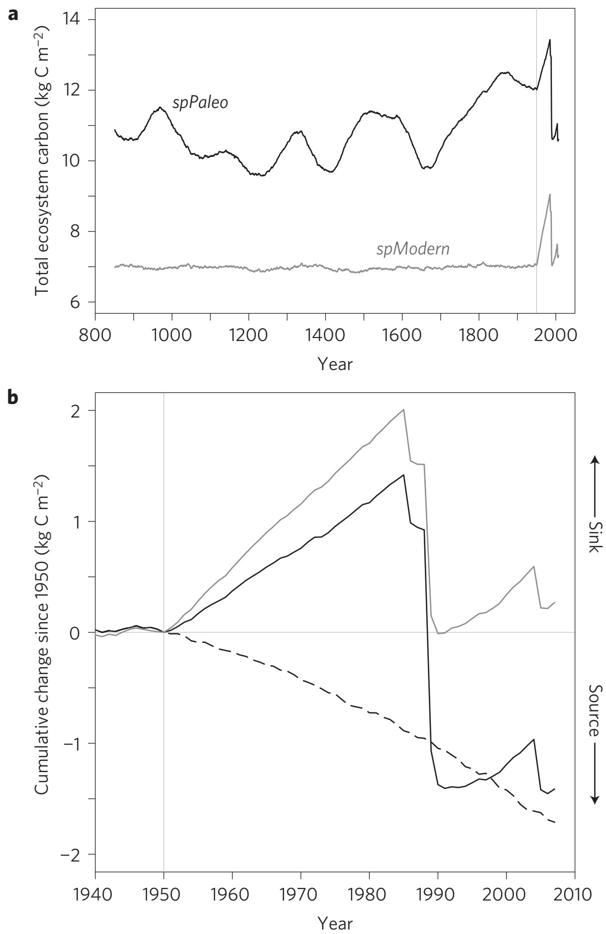

Figure 2 | Simulated recent carbon dynamics based on spin-up conditions prescribed from palaeodata (*spPaleo*; black) or the assumption that prehistoric conditions were stationary and identical to modern (*spModern*; grey). a,**b**, Both simulations experienced the same observation-based drivers beginning in 1950 (vertical line). Simulated ecosystem carbon storage is shown in terms of absolute quantity for the full experiment including spin-up (**a**), and the cumulative deviation from 1950 levels (**b**). Dashed line in **b** shows a simulation forced entirely with palaeodata (that is, experiment 'All' in Fig. 1) for reference. All lines are means over the study area.

that climate-driven impacts on fire activity can outweigh the direct effects of climate on C storage in the boreal forest biome. For example, sustained C losses from 970–1240 and gains from 1660–1870 correspond to periods of above- and below-average fire frequency, respectively. Notably, these shifts occurred during the Medieval Climate Anomaly (MCA) and Little Ice Age (LIA), periods known for relatively warm and cool temperatures (respectively) in Alaska[21]. The fire-regime changes that drove C_{ECO} variations during these periods were thus probably the result of climatic conditions, including associated changes in fuel load and vegetation composition. Similarly, the increase in fire frequency over the past half century is probably related to recent warming[5], and our simulations indicate that this has led to an approximate 12% reduction in regional C stocks. Despite these losses, our study area holds more C at present than during several periods in the past, which can be attributed to marked C accumulation during the LIA. Results from the MCA indicate that sustained periods of high fire activity can lead to even further C depletion. Given that the magnitude of twenty-first-century climate change will far exceed the range of past-millennium variability[9], and that current fire frequency is already well beyond MCA levels in some boreal regions[5], future climate-driven increases in fire activity could result in C losses throughout the biome.

Our results demonstrate the profound influence of fire-regime variability on the long-term C balance of boreal regions. Boreal forest fires initially represent sources of C to the atmosphere due to direct emissions and a transient decrease in net ecosystem productivity. Thereafter, recovering forests become a net C sink within several years, and C generally continues to accumulate as long as the stand persists fire-free[22]. Shifts in fire frequency dictate the balance between initial C losses and long-term C accumulation, and thus drive regional C_{ECO} variability over long timescales (or, analogously, broad spatial domains). DOS-TEM accurately represents these dynamics (Methods), and our palaeo-informed simulations illustrate that even relatively minor shifts in fire frequency can dominate long-term C dynamics. We acknowledge that past variability is an imperfect analogue for the future, and that future climate change and rising p_{CO_2} will probably increase the effects of these controls on boreal C cycling. Nevertheless, to the extent that future fire regimes are variable, as they have been in the past, we expect that changes in fire frequency will remain a key contributor to long-term C balance.

To quantify the impact of palaeofire information on simulations of the modern C budget, we used our palaeodata-driven model run as the spin-up for a simulation of recent dynamics (hereafter, *spPaleo*). For comparison, we initialized a second simulation (*spModern*) following the typical spin-up assumption that past conditions were stationary, with fire frequency set to a constant estimate derived from modern observations (1950–2006; ref. 18). We ran the spin-up simulations to 1950, and then forced both model experiments with identical drivers based on fire observations, climate and p_{CO_2} from 1950–2006. In both experiments, C dynamics were dominated by pronounced C losses from large fires in 1985, 1988 and 2004 (15.3, 52.8 and 22.5% of total study area burned, respectively), with steady C accumulation in intervening years (Fig. 2). For *spPaleo*, the net result was a substantial regional C source of 1.4 kg C m^{-2} (25.1 g C m^{-2} yr^{-1}) from 1950 to 2006 (Fig. 2b). The result was comparable when we used palaeo-fire forcing data instead of fire observations for 1950–2006, attesting to the ability of the sediment record to capture decadal fire-regime changes[5], and verifying that our conclusions are not an artefact of smooth fire-frequency trends in the spin-up simulation versus highly episodic observed burning. In stark contrast to these palaeo-informed simulations, the *spModern* experiment led to the fundamentally different conclusion that the study area was a small net C sink of 0.2 kg C m^{-2} (4.0 g C m^{-2} yr^{-1}) from 1950–2006 (Fig. 2b).

By definition, in the *spModern* experiment the modern fire regime represented no change in mean fire frequency relative to spin-up, and therefore the net effect of fire on C_{ECO} from 1950 to 2006 was minimal. Rising temperature and p_{CO_2} over the past several decades caused a slight modelled C gain in *spModern* (Fig. 2b), similar to findings from other modelling studies[15]. By contrast, the rapid increase in fire frequency prescribed in *spPaleo* drove C losses that greatly outweighed the effects of climate and p_{CO_2}, producing a net C source. This contrast is related to the control of fire frequency on the forest age distribution across the landscape. Higher spin-up fire frequency resulted in an overall younger initial forest composition in *spModern* (mean age 31.1 yr) than in *spPaleo* (63.9 yr; Supplementary Fig. 3). This led to an initial C_{ECO} for *spPaleo* that was almost twice that of *spModern* (12.0 versus 7.1 kg C m^{-2}; Fig. 2a), and more consistent with C stock estimates from similar forests in Interior Alaska (Supplementary Discussion). The larger initial C_{ECO} resulted in greater fire emissions for *spPaleo*, whereas *spModern* exhibited the greater rate of C gain in non-fire years because its younger simulated landscape was nearer to the mid-successional peak in ecosystem productivity (Fig. 2b and Methods). These differences compounded over decades to produce very different regional C balances for the two model experiments, despite that they were driven by identical 1950–2006 forcing data.

Our results suggest that the assumption that the past fire regime was similar to modern leads to an overestimate of C sink strength in any region where fire frequency has recently increased from prehistoric levels. If the bias demonstrated for our study area was representative of the 1,250 Mha boreal forest biome (ref. 1), it would imply an overestimate of the mean annual boreal C sink of 364 Tg C yr^{-1} from 1950 to 2006—a sizeable error in comparison to the estimated global land sink of ~1 Pg C yr^{-1} (IPCC 2013). In reality, the biome-wide bias is probably smaller given that the exceptional recent increase in Yukon Flats fire activity is matched by few other regions. Nonetheless, climate warming has increased boreal forest burning in North America over the past several decades[6], and similar changes probably occurred in Eurasia, although this is difficult to evaluate owing to poor Siberian fire records[7]. To the extent that fire frequency has recently risen in the biome overall, models[8,14,23] have probably overestimated boreal C sink strength. Moreover, predictions that boreal fire activity will continue to increase under scenarios of future climate change[7] imply a growing tendency to overestimate boreal C balance in the future. These conclusions are not necessarily inconsistent with previous estimates of the boreal C sink, which are both variable and uncertain[10], but rather attribute some of the uncertainty to bias that could be reduced through improved constraints on model initial conditions.

Our study includes uncertainties inherent to both modelling and palaeoenvironmental reconstruction, and no empirical observations of C dynamics of the past millennium exist to directly verify our results. However, we chose DOS-TEM for this study because it has been thoroughly calibrated and validated for use in boreal ecosystems (Methods), lending credence to the simulated responses to climate, fire and p_{CO_2} variability that are the basis for our conclusions. Furthermore, sensitivity experiments indicate our findings are robust to uncertainties in the palaeodata used to force the model (Supplementary Discussion and Supplementary Table 1). Replacing the MPI-ESM palaeoclimate forcing with simulations from other climate models has little qualitative impact on our results (Supplementary Fig. 4). The relative importance of fire frequency versus severity is sensitive to bias in the range of past variability in these drivers, but the overall dominance of fire over climate and p_{CO_2} in dictating past C_{ECO} variability is not (Supplementary Fig. 5a,b). Furthermore, assumptions about changes in boreal forest flammability with stand age influence the magnitude of simulated C stocks, but have little impact on temporal patterns of past variability, and thus do not alter our conclusions (Supplementary Fig. 5c). Finally, the conclusion that our study area has been a source of C in recent decades is robust, even though uncertainty in past fire frequency leads to a considerable range for our estimate of the strength of the source (7.9–60.4 g C m^{-2} yr^{-1}; Supplementary Fig. 6).

Our results demonstrate that accurately modelling future C dynamics requires careful constraints on initial ecosystem C stocks. Although models differ in the details of how initial conditions are generated, the dependence on spin-up procedures informed by recent observations is fairly widespread[15,24]. Our palaeo-informed simulations demonstrate that this practice may lead to large model biases when disturbance rates have undergone rapid recent change. This finding represents a new challenge to understanding the future of the northern high-latitude C sink, but there are many promising avenues to address this challenge. Although palaeodata are expensive and time consuming to collect, for example, an ongoing synthesis of palaeofire data[25] has the potential to facilitate palaeo-informed model spin-up at global scales. Concurrently, data resources for directly prescribing initial conditions are improving. The proportion of boreal stands with known age naturally rises as observational and satellite fire records continue to accumulate, and empirical stand-age distributions are a good indicator of C_{ECO} variability even though legacies of past burning can persist through multiple fire cycles. Coordinated research networks (for example, ref. 26) are also rapidly increasing the availability of empirical data for directly quantifying current high-latitude C stocks. Finally, modern data-model fusion methods[27] offer the promise of synthesizing multiple data streams into model initial conditions that reflect both modern observations and reconstructed past change.

Our study reveals that increased burning of boreal forests will probably cause massive losses of stored C, with the potential to amplify climate warming. This conclusion has sobering implications for the reliability of ESM predictions, because representation of fire in these models remains limited despite promising recent progress[12]. Fortunately, some boreal-specific models are capable of reproducing patterns of fire occurrence[3], suggesting that the problem of modelling boreal fire regimes is tractable, and perhaps offering insights that could improve ESM fire modules. However, our results also show that, in the absence of strong constraints on initial model conditions, calculations of long-term C balance are probably biased. Thus, accurate simulation of the boreal C cycle requires improved estimation of both the present ecosystem state and future rates of burning.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

R.K. conducted the analysis with assistance from H.G. All authors contributed in designing the study, interpreting results, and preparing the manuscript.

Additional information

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Competing financial interests

The authors declare no competing financial interests.

Methods

Overview. We used the dynamic organic soil version of the Terrestrial Ecosystem Model (DOS-TEM) to simulate C dynamics of the past millennium (the actual range of 850–2006 was chosen based on data availability), driven by forcings that included palaeofire reconstructions[5], palaeoclimate simulations[19] spliced with observational climate data[28], and p_{CO_2} values from modern observations combined with ice-core data[20]. We also conducted model experiments in which each of these inputs was held stationary or allowed to vary, to determine the contribution of each to overall variability in past C storage.

To evaluate the impact of typical spin-up assumptions on modelled C dynamics, we ran two DOS-TEM experiments spanning 1950–2006, the period for which reliable observational fire records exist[18]. Fire occurrence was prescribed directly from these observations, and climate and p_{CO_2} forcings were derived from the observation-based portions of the data sets described above. The *spModern* experiment followed a typical spin-up procedure in which the model was initially driven by modern forcings, repeated continuously until dynamic equilibrium was achieved, which typically requires ~1,000 model years for boreal forest ecosystems owing to large C stocks and slow turnover of deep soil C pools. The resulting modelled ecosystem state then served as the starting point for the *spModern* experiment. By contrast, the *spPaleo* experiment began from the 1950 model state of our past-millennium simulation. Thus, differences between the *spModern* and *spPaleo* simulations can be attributed to the replacement of spin-up assumptions with estimates of past environmental variability informed by palaeodata.

Study area. We ran DOS-TEM on a 1-km^2 grid delineated by the union of circular buffers of 10-km radius around each of the 14 sampling sites contributing to our palaeofire records[5] (Supplementary Fig. 1). This results in a contiguous area of 1,931 km^2, for which previous validation exercises confirmed that the charcoal data accurately capture observed patterns of recent burning. The area is near the southern boundary of the Yukon Flats ecoregion of interior Alaska. The region has a dry continental climate characterized by mean (1971–2000 climatology) January and July temperatures of −22.2 and 17.5 °C, respectively, and mean annual precipitation of 24.9 cm (ref. 28). Vegetation is primarily a matrix of black spruce (*Picea mariana*) and deciduous species (for example, *Populus tremuloides*) in various stages of postfire succession, as is typical of interior Alaska. Soils range from poorly to well drained, depending on landscape position[29].

Model description. DOS-TEM is a process-based model designed to simulate the cycling of carbon and nitrogen through the soil and vegetation of terrestrial ecosystems. The model is composed of four interacting modules (Supplementary Fig. 2): the environmental module uses climate information to calculate the dynamics of biophysical processes (for example, soil temperature and moisture); the ecological module uses information about vegetation composition, atmospheric and soil environment, and soil structure to calculate pools and fluxes of carbon and nitrogen; the dynamic organic soil module models loss and accumulation of soil organic matter due to fire and succession, and the thermal and hydrologic consequences of these changes; and the disturbance module calculates the fate of ecosystem carbon and nitrogen after fire, based on topography, climate conditions, soil characteristics, and fire severity.

DOS-TEM has been developed extensively for use in boreal forest ecosystems[23,30–32]. In particular, the model produces realistic temporal patterns of postfire ecosystem recovery, which dominate long-term C_{ECO} variability in our model experiments. Although numerous factors (for example, site drainage, fire severity, climate) influence successional dynamics in DOS-TEM, simulated burned areas generally lose C for one to two decades following fire before transitioning to a C sink, with peak C gains occurring 30–70 years after the burn[30,32]. These changes arise from mechanisms of vegetation recovery (via parametric formulations; DOS-TEM does not explicitly model vegetation community dynamics) and soil development that have been formally validated in the context of chronosequence and forest inventory data[30,31,33], and they are consistent with a number of other empirical studies[34,35]. The responses of the model to warming and rising p_{CO_2} have also been evaluated in the context of boreal forest C dynamics, and are generally consistent with available data[15]. Indeed, the moderate C sink of recent decades simulated by our *spModern* experiment is consistent with other model-based estimates in the absence of long-term fire history information[10].

Fire-frequency forcing data. To prescribe fire occurrence in our past-millennium experiments, we used a palaeorecord of reconstructed fire frequency from the Yukon Flats ecoregion of Alaska (Fig. 1b). The record is a composite of individual fire events identified by analysing charcoal deposits in sediment cores from 14 lakes, and was previously shown to accurately represent the regional fire regime within an ~2,000-km^2 area surrounding the lakes[5]. DOS-TEM requires fires to be prescribed annually for each simulated cell on the landscape, whereas the Yukon Flats palaeorecord represents regional variability on decadal–centennial timescales. To convert charcoal-inferred fire frequency to a DOS-TEM driver, in each simulated year we multiplied regional fire frequency by the number of simulated cells to determine the total number of burned cells to prescribe. The spatial arrangement of burned area is unimportant in DOS-TEM because grid cells do not interact, so we did not attempt to mimic real fire size distributions or connectivity of burned areas. Instead, we prescribed burned grid cell locations initially at random and, after all cells had burned at least once, we chose the specific cells to burn in each model year as those that had been longest without fire. This strategy reflects the observation that the flammability of boreal forest stands increases as fire-prone spruce species replace early successional deciduous species[36]. For past-millennium experiments requiring stationary fire frequency (that is, those designed to isolate the influence of one of the other forcing variables), we followed the procedure outlined above, but prescribed constant frequency equal to the past-millennium mean. For the *spPaleo* and *spModern* experiments, individual fires from 1950 to 2006 were prescribed from the database of observed fire perimeters in Alaska[18]. These observed fires were also used to derive a single estimate of modern fire frequency to specify spin-up fire occurrence for the *spModern* experiment, following the typical assumption when historic fire data are unavailable[15].

Fire-severity forcing data. DOS-TEM simulates fire severity as a categorical variable with three classes. For the past-millennium simulation we assigned fires to these classes based on a record of charcoal production per fire derived from the Yukon Flats palaeodata (Fig. 1c). Previous analysis identified this metric as a qualitative proxy for past fire severity in the region, although we acknowledge there is considerable uncertainty associated with this interpretation[5]. We separated the record into three levels using its lower and upper quartiles of the past millennium, and mapped these to the DOS-TEM severity classes (Fig. 1c). For each simulation year, we assigned the severity class thus determined to all fires in that year. In past-millennium experiments lacking fire-severity variability, we defined all fires as moderate severity. For the *spModern* and *spPaleo* experiments we prescribed fire severity for the period 1950–2006 following the default procedure in DOS-TEM, which is based on empirical relationships involving burn season, vegetation type, and site drainage[32].

Climate forcing data. DOS-TEM requires monthly inputs of mean temperature, total precipitation, vapour pressure, and incoming radiation (Fig. 1d,e). We obtained these data from a palaeoclimate simulation spanning 850–1950 using the Max Plank Institute Earth System Model (MPI-ESM; ref. 19). We merged the simulated palaeoclimate to observation-based climate data for 1900–2006 derived from observations[28]. We bias-corrected the former using either differencing (temperature) or ratios (precipitation, vapour pressure, radiation) to ensure matching mean climatology between the two data sets for the 1900–1950 overlap period. We then spliced the two at 1950 and downscaled the resulting product to 1-km^2 resolution. For past-millennium experiments requiring stationary climate inputs, we calculated centennial-scale trends using a lowess smoother, and then removed these trends by differencing (temperature) or dividing (all others). This approach retains interannual variability while ensuring approximate stationarity over centennial timescales.

Atmospheric CO_2 forcing data. We prescribed uniform p_{CO_2} across the simulation landscape based on modern instrumental measurements spliced to ice-core records[20] (Fig. 1f). Control p_{CO_2} was defined as the past-millennium mean (285 ppm) as needed for model experiments.

Attribution of variability. We analysed C_{ECO} variability among the past-millennium experiments by first calculating C_{ECO} deviations from the control run (that is, the experiment with all inputs held stationary) to remove patterns of interannual variability and emphasize the response to long-term changes in model forcings. We then used multiple regression to model the annual C_{ECO} deviations of the full-forcing experiment (that is, the simulation informed by all available palaeodata) as a linear combination of experiments in which only one forcing was allowed to vary. We then conducted analysis of variance on the resulting regression. We report the sum-of-squares variability accounted for by each single-factor experiment as a means to quantify the influence of individual forcing variables on overall C_{ECO} variability of the past millennium.

Validation data for alternative spin-up approaches. There are no empirical data from the Yukon Flats study area with which to directly assess the accuracy of initial conditions generated by our spin-up experiments, but comparison to summary data on soil and vegetation C stocks for similar forests in Interior Alaska allows a qualitative evaluation. We compared the soil C pools simulated by DOS-TEM to measured C stocks in the upper 1 m of soil from the National Cooperative Soil Survey at sites similar to our study area (classified as intermontane boreal, upland black spruce forests)[37]. Similarly, we evaluated simulated vegetation C against data from the Cooperative Alaska Forest Inventory[38] for upland black spruce plots. We converted the inventory measurements to C stock estimates using allometric relationships[39,40], assuming 50% carbon content of vegetation biomass and an aboveground:total biomass ratio of 0.8.

Sensitivity experiments. Our conclusions regarding the relative importance of drivers of past C balance depend on the data used to force our past-millennium simulations. We conducted a suite of sensitivity experiments using alternate past-millennium drivers to confirm that our results are robust to uncertainties in these data.

We first evaluated the sensitivity of our results to uncertainties in the palaeofire data used to drive DOS-TEM. As discussed in the main text, our results suggest that fire frequency outweighs fire severity as a driver of ecosystem C balance. Thus, we specifically considered the possibilities that our initial analysis had overestimated the role of the former, or underestimated the role of the latter. For fire frequency, we produced an alternate driver by transforming the original data set to have the same mean and temporal patterns, but only 25% of the original variance (that is, half the original standard deviation; Supplementary Fig. 5a). In the case of fire severity, we modified the DOS-TEM code to simulate a broader range of soil organic matter consumption in response to variability in fire severity. The current version of the model equates low, medium and high severity classes to 54%, 69% and 80% consumption (respectively; ref. 32). As a conservative alternative, we defined the severity classes to span the full range of empirical measurements from 178 burn sites in black-spruce-dominated stands in Alaska[41], by assigning their minimum (20%), median (70%) and maximum (100%) values of soil organic matter consumed to the low, medium and high severity classes (respectively) in DOS-TEM (Supplementary Fig. 5b).

The conclusion that recent burning has led to a large net loss of C from our study area depends mainly on the large recent increase in fire frequency, represented by the rate of observed modern burning compared to past fire activity inferred from the palaeorecord. Uncertainty in palaeofire frequency could cause the magnitude of this recent change to be poorly estimated, which would in turn influence our conclusions about modern C balance. To evaluate this possibility, we repeated the *spPaleo* experiment using the bounds of a 90% confidence interval around the palaeofire frequency record to prescribe spin-up fire occurrence. The confidence interval is calculated based on methods described previously[5].

We also considered an alternate methodology for converting fire-frequency data to spatially explicit fire occurrence in DOS-TEM, by repeating our simulations assuming that the burned area prescribed by fire-frequency inputs (either palaeo-derived or constant, depending on the experiment) was distributed randomly among simulated grid cells. This is unrealistic in that it implies no effect of stand age on flammability, but it provides a logical counterpart to the approach described previously—that is, assuming that area burned always occurs in areas that have been without fire the longest. The real palaeofire regime is almost certainly bounded by these extremes of purely stochastic and purely deterministic patterns of burning.

We next considered whether our findings depend on the particular climate driver used in our past-millennium experiments. We chose the MPI-ESM simulation for this study, on the basis of the outstanding performance of its predecessor MPI ECHAM5 in reproducing patterns of modern Arctic climate[42]. However, palaeoclimate simulations face uncertainties due to differences among the climate models used to produce them, and among the forcing data—especially time series of past insolation and volcanic aerosol production—used to drive the models[20]. We repeated our experiments using climate data sets generated by the GISS-E2-R version of the Goddard Institute for Space Studies General Circulation Model[43] and the Community Climate System Model version 4 (ref. 44; Supplementary Fig. 4). Together, the three palaeoclimate simulations considered encompass different combinations of the most widely used volcanic[45,46] and solar irradiance forcings[47,48] specified in the Palaeo Modelling Intercomparison Project phase 3 (PMIP3) design for past-millennium experiments[20].

Given that past p_{CO_2} is relatively well constrained by ice-core records, shows little variability during the past millennium, and had a minimal impact on our palaeo-ecosystem simulations, we did not conduct sensitivity analyses specific to this input.

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