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Linking sediment-charcoal records and ecological modeling to understand causes of fire-regime change in boreal forests

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Abstract. Interactions between vegetation and fire have the potential to overshadow direct effects of climate change on fire regimes in boreal forests of North America. We develop methods to compare sediment-charcoal records with fire regimes simulated by an ecological model, ALFRESCO (Alaskan Frame-based Ecosystem Code) and apply these methods to evaluate potential causes of a mid-Holocene fire-regime shift in boreal forests of the south-central Brooks Range, Alaska, USA. Fire-return intervals (FRIs, number of years between fires) are estimated over the past 7000 calibrated ^{14}C years (7–0 kyr BP [before present]) from short-term variations in charcoal accumulation rates (CHARs) at three lakes, and an index of area burned is inferred from long-term CHARs at these sites. ALFRESCO simulations of FRIs and annual area burned are based on prescribed vegetation and climate for 7–5 kyr BP and 5–0 kyr BP, inferred from pollen and stomata records and qualitative paleoclimate proxies. Two sets of experiments examine potential causes of increased burning between 7–5 and 5–0 kyr BP. (1) Static-vegetation scenarios: white spruce dominates with static mean temperature and total precipitation of the growing season for 7–0 kyr BP or with decreased temperature and/or increased precipitation for 5–0 kyr BP. (2) Changed-vegetation scenarios: black spruce dominates 5–0 kyr BP, with static temperature and precipitation or decreased temperature and/or increased precipitation. Median FRIs decreased between 7–5 and 5–0 kyr BP in empirical data and changed-vegetation scenarios but remained relatively constant in static-vegetation scenarios. Median empirical and simulated FRIs are not statistically different for 7–5 kyr BP and for two changed-vegetation scenarios (temperature decrease, precipitation increase) for 5–0 kyr BP. In these scenarios, cooler temperatures or increased precipitation dampened the effect of increased landscape flammability resulting from the increase in black spruce. CHAR records and all changed-vegetation scenarios indicate long-term increases in area burned between 7–5 and 5–0 kyr BP. The similarity of CHAR and ALFRESCO results demonstrates the compatibility of these independent data sets for investigating ecological mechanisms causing past fire-regime changes. The finding that vegetation flammability was a major driver of Holocene fire regimes is consistent with other investigations that suggest that landscape fuel characteristics will mediate the direct effects of future climate change on boreal fire regimes.

Key words: Alaska, USA; Alaska Frame-based Ecosystem Code; ALFRESCO; black spruce; boreal forest; Brooks Range; charcoal records; data-model comparison; fire regime; Picea; *white spruce.*

Introduction

Several recent investigations suggest that the effects of climate warming on Alaskan boreal fire regimes will be partially indirect due to strong interactions between climate, vegetation, and fire (Rupp et al. 2002, Duffy et al. 2007, Higuera et al. 2009). For example, analyses of fire events since CE (Common Era) 1950 show that forest type interacts with climate to modify the direct effects of climate on fire occurrence and spread (e.g., Kasischke et al. 2002, Duffy et al. 2007). This occurs because differences in the foliage and branching patterns of dominant tree species cause marked differences in vegetation flammability (Rupp et al. 2006), leading to unexpected relationships between local climate and fire. In particular, within Alaskan boreal forests, highly flammable black spruce stands occupy wet soils on north-facing slopes (Viereck et al. 1986), causing the shortest fire rotations to occur on cold, wet sites (Drury

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and Grissom 2008). Conversely, white spruce stands occupy warmer sites on well-drained soil (Viereck et al. 1986), but the low flammability of this species results in long fire-return intervals (Drury and Grissom 2008). Given such interactions, vegetation responses to future climate warming may cause complex and unexpected changes in fire regimes of Alaska and other boreal regions (Balshi et al. 2007, Soja et al. 2007, Ruckstuhl et al. 2008).

Ecological modeling and paleorecords provide insights about the potential effects of climate change on Alaskan fire regimes (e.g., Lynch et al. 2002, Rupp et al. 2002, Hu et al. 2006, Tinner et al. 2008, Higuera et al. 2009). Model simulations using ALFRESCO (Alaskan Frame-based Ecosystem Code), a spatially explicit model which depicts fire and vegetation-recruitment dynamics across Alaskan landscapes (Rupp et al. 2000 *a*, *b*), highlight the importance of vegetation flammability to boreal fire regimes (Rupp et al. 2002). These simulations emphasize that climate-induced changes in species composition can alter fire frequency and fire size, changing landscape-level vegetation patterns and feedbacks to fire regimes (Rupp et al. 2002, Chapin et al. 2003). Sediment-charcoal records document that major shifts in fire regimes during the Holocene corresponded more closely to vegetation characteristics than to inferred climate (Lynch et al. 2002, Higuera et al. 2009). Thus both model simulations and empirical data suggest that vegetation can modify the direct impacts of climate change on fire regimes by altering landscape flammability.

Although both ecological modeling and paleorecords can reveal fire-regime shifts associated with changes in climate and vegetation, neither approach provides a rigorous assessment of the relative effects of climate and vegetation on landscape burning. Paleorecords preserve long-term fire histories across a variety of climate and vegetation types, but do not provide direct evidence of the inferred roles of climate or vegetation. Ecological modeling predicts the consequences of vegetation–fire interactions under different climate conditions, but typically cannot check the realism of simulated climate and/or vegetation effects on fire occurrence and spread. Comparisons of paleorecords and model simulations offer a powerful means to evaluate alternative mechanisms of past ecosystem change (Anderson et al. 2006), and comparisons between pollen data and forest simulations have been used to examine climate, disturbance, and human impacts on forest ecosystems worldwide (e.g., Cowling et al. 2001, Hall and McGlone 2001, Keller et al. 2002). However, no study has used a data–model approach to evaluate the extent to which vegetation has modified the direct effect of climate on past fire regimes.

Here we link high-resolution lake-sediment-charcoal records (Higuera et al. 2009) to fire-history simulations from the landscape model ALFRESCO. Our main goal is to develop analytical methods for comparing ALFRESCO simulations with charcoal records as a proof of concept that such comparisons can reveal ecological processes underlying shifts in past fire regimes. The empirical and simulated data sets are then used to examine several potential causes of a fire-regime shift associated with the mid-Holocene (~5 kyr BP; calibrated ^{14}C ages are used throughout the paper) expansion of black spruce (*Picea mariana*) into areas dominated by white spruce (*P. glauca*) and shrub birch (*Betula glandulosa*) in the south-central Brooks Range of Alaska, USA. Previous paleoclimate studies suggest climate cooling and/or moistening during the mid-Holocene (see Anderson et al. 2003), and sediment records show increased charcoal content and inferred fire frequencies (Lynch et al. 2002, Higuera et al. 2009). Since the fire-regime shift was in an opposite direction than would be expected by climate cooling and/or moistening, investigators have proposed that the extreme flammability of black spruce drove the change in mid-Holocene fire regimes (Lynch et al. 2002, Hu et al. 2006, Higuera et al. 2009).

Methods and Rationale

Study sites and paleorecords

Vegetation and fire histories are reconstructed from pollen, stomata, and charcoal records at three sites (Ruppert, Wild Tussock, and Code Lakes) along the southern flanks of the central Brooks Range, Alaska, USA (Fig. 1). See Higuera et al. (2009) for a detailed description of the sediment records and analytical methods. The present vegetation near each site is a mosaic of black spruce (*Picea mariana*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), and aspen (*Populus tremuloides*), with shrub birch (*Betula glandulosa*) tundra in non-forested areas. Fire is the primary disturbance, with an estimated fire rotation period for the study area of 175 yr, based on data for CE (Common Era) 1950–2001 (Kasischke et al. 2002).

Pollen percentages and stomata presence/absence were used to characterize past vegetation and to detect the development of black-spruce dominated forest. Analog analyses (Gavin et al. 2003) compare fossil and modern pollen assemblages and indicate the probability of a given past vegetation assemblage matching present boreal forests types of North America. The first presence of spruce stomata (Carlson 2003) confirmed analog interpretations of modern boreal forest development at the transition between the white and black spruce periods.

Past fire regimes are reconstructed from variations in charcoal accumulation rates (CHARs) in sediment cores. The temporal resolution of the analyzed sediments (~15 yr/sample; Higuera et al. 2009) is optimal for detecting CHAR peaks resulting from fires with return intervals >75 yr (Higuera et al. 2007). Peaks in CHARs were used to estimate fire-return intervals (FRIs) according to methods described by Higuera et al. (2009).

Knowledge of Holocene climate change in Alaska remains limited. Recent geochemical studies have revealed marked variations in temperature and moisture during the mid- and late-Holocene (Anderson et al. 2001, Hu et al. 2001, 2003). Recent summaries based on fossil, lake-level, and glacial records (Anderson et al. 2003, Kaufman et al. 2004) have suggested that central Alaska was generally warmer and/or drier than the present during the early Holocene (~10–5 kyr BP) and reached modern conditions by the late Holocene (~4–0 kyr BP). These two periods correspond roughly to the white spruce and black spruce zones of pollen records from the study area (Higuera et al. 2009). We examine the 7–0 kyr BP period because it spans the white and black spruce pollen zones and is documented by high-resolution charcoal records at all sites.

ALFRESCO model

ALFRESCO was originally developed to simulate the response of subarctic vegetation to a changing climate and disturbance regime (Rupp et al. 2000*a*, *b*). The boreal forest version of ALFRESCO was developed to explore the interactions and feedbacks among fire, climate, and vegetation in interior Alaska (Rupp et al. 2002). A detailed description of ALFRESCO can be obtained from the literature (Rupp et al. 2000*a*, *b*, 2002). For the purpose of our research, we focus our description on details relevant to this specific model application.

Rather than modeling fire behavior, ALFRESCO models the empirical relationship between growing-season climate (e.g., mean temperature and total precipitation for May–September) and total annual area burned (i.e., the footprint of fire on the landscape; Duffy et al. 2005, Rupp et al. 2007). It models changes in vegetation flammability during succession through a flammability coefficient that changes with vegetation type and stand age (i.e., fuel accumulation; Chapin et al. 2003). The fire regime is simulated stochastically as a function of climate (as defined here), vegetation type (i.e., fuel structure and loading), and time-since-last-fire. "Ignition" of a pixel is determined using a random number generator and a flammability value for each pixel, and an ignited pixel may spread to any of the eight surrounding pixels. Fire "spread" depends on the flammability of the receptor pixel and effects of natural firebreaks, including non-vegetated mountain slopes and large water bodies. ALFRESCO's coarse pixel resolution (1 km^2) precludes inclusion of fine-resolution factors such as wind and topography that are typically important components of fire behavior models.

Simulation landscape.—Because simulating the landscape of all sites was computationally too expensive, we chose a 100 × 100 km area centered on Ruppert Lake (Fig. 1). This area is large enough to capture parameters of Alaskan fire regimes, appropriate for comparison with sediment-charcoal records (Higuera et al. 2007), and representative of the other study sites. ALFRESCO models four vegetation types: upland tundra, black spruce forest, white spruce forest, and early successional deciduous vegetation (Rupp et al. 2000*a*, *b*, 2002). The current (~CE 1990) composition of the simulation landscape is black spruce (28%), white spruce (9%), and early successional deciduous vegetation (1%) in lowlands near Ruppert Lake, with tundra (62%) predominantly on mountain slopes to the north (Fig. 1).

Climate input.—ALFRESCO maintains mean temperature and total precipitation of the growing season (May–September) for each pixel because these climate variables are used to determine internal variables of vegetation types and to model fire (Rupp et al. 2000*a*, *b*). Geographically defined climate data for Alaska (CE 1960–1990; Fleming et al. 2000), which account for variability due to topography (e.g., aspect, elevation) and regional influences (e.g., synoptic weather patterns), were used to set up the spatial variability in climate across the simulated landscape. A temporal offset from the current climate was selected at each time step from a normal deviate for the entire simulation landscape (i.e., climate variability is assumed constant over the study region; Rupp et al. 2000*b*).

ALFRESCO requires quantitative climate estimates as inputs for both the white and black spruce periods, but only qualitative Holocene climate records are available from the study area. In our experiments, we prescribed a climate shift to cooler and/or moister conditions at the beginning of the black spruce period, which is qualitatively consistent with paleo evidence. However, two aspects of our choice may be unrealistic. First, we chose temperature and precipitation shifts that were large enough to affect ALFRESCO-simulated fire regimes but may have been larger than actual Holocene temperature and/or precipitation change (since the simulated 5–0 kyr BP climate is somewhat cooler and wetter than the closest climate station to the study area, Bettles, Alaska, USA). As a result, while the ALFRESCO experiments represent the qualitative effects of Holocene temperature decrease and/or precipitation increase, they may overestimate the magnitude of those effects. Second, centennial- to millennial-scale fluctuations in temperature and moisture occurred elsewhere in Alaska within the past 7 kyr BP (Anderson et al. 2001, Hu et al. 2001, 2003), and some of these fluctuations altered fire regimes (Tinner et al. 2008). Although these climate variations may have also affected the fire regimes of our study area, their effects are not addressed by our experiments. Given the exploratory stage of our research and the time and expense of running multiple ALFRESCO runs, we felt that our rather simple experiments were justified. We address the implication of these limitations to our results in the *Discussion*.

We generated climate input in three steps. First, climate for the white spruce period (7–5 kyr BP) was defined based on climate station data (growing season temperature, precipitation, and variability) in the southeastern Brooks Range (Arctic Village, Alaska, USA; *data available online*), where modern boreal forests

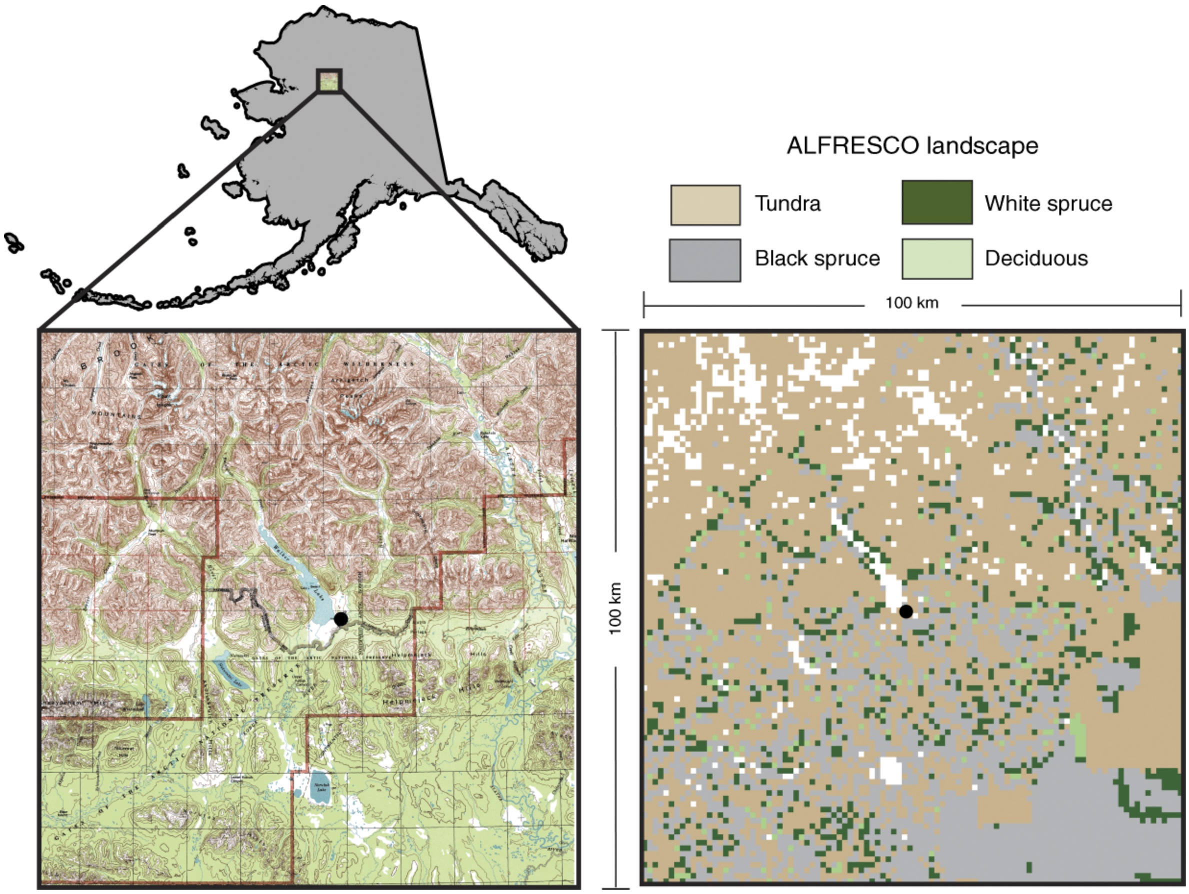

FIG. 1. Ruppert Lake, Alaska, USA, study area. The dark circle near the center of both panels shows Ruppert Lake. The left panel shows site location and real topography. The right panel shows simulation landscape with simulated vegetation types in 1-km^2 pixels. White indicates no vegetation cover. This simulated landscape was modified in ALFRESCO (Alaskan Frame-based Ecosystem Code) experiments.

are dominated by white spruce.[8] These climate data were also used in simulations of the black spruce period under conditions of static temperature and/or precipitation. Second, we generated temperature and precipitation values for each time step of the simulation, accounting for observed interannual variability, by developing temporal offset vectors for each climate variable for the length of the simulation period. This was done by sampling with replacement from the station data and then summarizing by decade. Third, climate for the black spruce period was generated by applying a linear-ramping algorithm to the simulated climate data for 5–4 kyr BP, representing a 2°C decrease in temperature and an 86 mm (50%) increase in precipitation.

Model simulations

ALFRESCO scenarios reveal the separate and interactive effects of climate (shifts in growing-season mean temperature and/or total precipitation) and vegetation (presence/absence of black spruce) on the fire regimes of non-tundra vegetation types in the study area. Prior to simulations, we conducted model calibrations and followed a standard "spin-up" methodology (Rupp et al. 2007) to generate realistic modern vegetation patterns (i.e., vegetation type, age, and patch dynamics), which were modified in the simulation experiments. Model calibration (Rupp et al. 2006) focused on calibrating the fire routine to generate fire numbers and area burned similar to modern observations (~6 ignitions and 19 200 ha burned per decade, CE 1950–2000). Single-replicate simulations were conducted at a 1 × 1 km pixel resolution on the Ruppert Lake landscape, run at decadal time steps for 7–0 kyr BP. Fire occurrence (or absence) for each pixel and each time step was archived to calculate FRIs.

Fire history from each ALFRESCO simulation was summarized using FRIs and mean annual area burned. Each simulation produced a series of FRIs for each non-tundra pixel, yielding many thousands of FRIs. FRIs were calculated for non-tundra pixels at the spatial scale of each ALFRESCO pixel. When a non-tundra pixel

[8] ⟨http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?akarct⟩

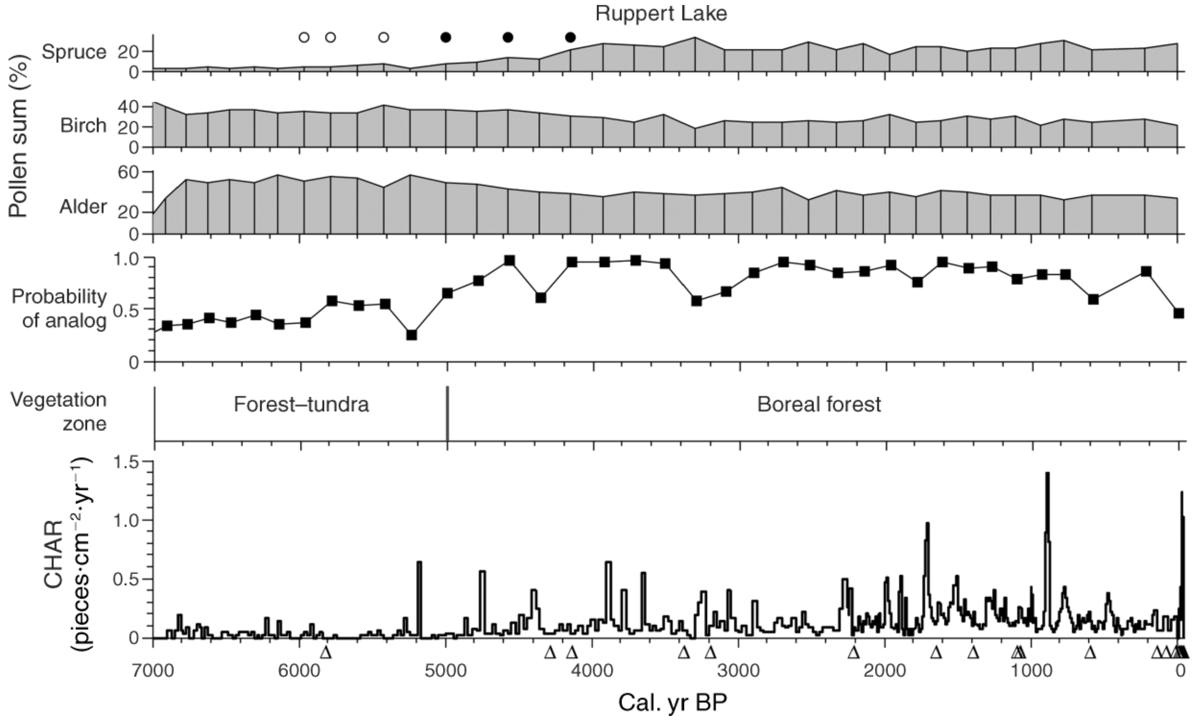

FIG. 2. Pollen percentages of spruce, birch, and alder; probability of analog values for comparisons between fossil samples and modern boreal forest, forest–tundra, and arctic tundra vegetation zones; and charcoal accumulation rate (CHAR) for Ruppert Lake over time (calibrated years before present). Solid and open circles on the top panel represent presence or absence of spruce stomata. Triangles along the *x*-axis indicate locations of radiocarbon dates.

burned in a simulation, the time (in years) since the last fire occurred was recorded. Annual area burned represents the total number of pixels (1 km^2) burned in each simulated decade, divided by 10 yr.

Vegetation and climate periods.—The white spruce and black spruce periods are defined as 7–5 and 5–0 kyr BP, respectively. Climate and vegetation changes are depicted as ramped transitions between 5–4 kyr BP, generally similar to the time of black spruce pollen increase in sediment records (Fig. 2). Our results did not differ when we examined the impact of using other transition periods. Because our goal was to examine the responses of fire regimes to alternative vegetation and climate scenarios, rather than to simulate transient responses to a specific paleoenvironmental proxy, the time of the transitions in paleodata and model simulations did not need to match.

To create input for the white spruce period (7–5 kyr BP), we generated a spin-up landscape by converting all modern black spruce pixels to tundra, resulting in roughly 90% tundra and 10% white spruce. This simulated landscape is consistent with the finding (see *Results*) that the closest modern analogs to fossil pollen assemblages during the white spruce period are in forest–tundra ecotones (Higuera et al. 2009), where black spruce is absent and white spruce is a minor component of the vegetation. For the 5–4 kyr BP transition period, when modern pollen analogs are located in black spruce-dominated forests, we forced the converted tundra cells back to black spruce using a linear-ramping algorithm that re-established black spruce to be consistent with the modern landscape (Fig. 1). For the remainder of this period, the vegetation cover of all cells was allowed to change in response to burning. While these vegetation changes are not the focus of the present study, they are mentioned as context for discussing past vegetation–fire interactions.

Experiments.—The 7–5 kyr BP baseline vegetation and climate are modeled as just described. Two sets of experiments (Table 1) were designed to address hypotheses about the independent and interactive effects of vegetation and climate on the shift in fire regimes between the white and black spruce periods (e.g., Fig. 3).

Comparison of charcoal-based and ALFRESCO fire history records

We compared FRIs from charcoal and ALFRESCO records based on two well-founded assumptions: (1) the spatial scale represented by peaks identified in the sediment-charcoal records is approximated by the 1-km^2 cell size of ALFRESCO, based on empirical (Gavin et al. 2003, Lynch et al. 2004) and theoretical considerations (Higuera et al. 2007) of how charcoal data record fire occurrence and (2) at least part of the landscape was covered by trees for the past 7 kyr BP (Fig. 2; Higuera et al. 2009).

TABLE 1. Alaskan Frame-based Ecosystem Code (ALFRESCO) scenarios and rationales.

ALFRESCO scenario	Factors†	Rationale
Static vegetation		
Static climate	sV, sT, sP	*Did fire regimes change in the absence of vegetation and climate change?* A control for identifying vegetation and/or climate effects. Vegetation and climate are modeled as for 7–5 kyr BP.
Changed climate	sV, sT, ΔP sV, ΔT, sP sV, ΔT, ΔP	*Did climatic cooling and/or moistening* ***alone*** *cause past fire-regime shifts?* The initial vegetation is set at 7–5 kyr BP and allowed to change in response to temperature decrease (2°C) and/or precipitation increase (86 mm) ramped over 5–4 kyr BP.
Changed vegetation		
Static climate	ΔV, sT, sP	*Did increased black spruce* ***alone*** *cause past fire-regime shifts?* Black spruce cover is increased from 0% to 28% to match the modern landscape near Ruppert Lake, Alaska, USA. Climate is modeled as for 7–5 kyr BP.
Changed climate	ΔV, ΔT, sP ΔV, sT, ΔP ΔV, ΔT, ΔP	*Did* ***both*** *increased black spruce and climate change influence past fire regimes?* Black spruce, precipitation, and/or temperature are ramped over 5–4 kyr BP.

Note: Each scenario represents an alternative hypothesis about the cause of mid-Holocene fire-regime shifts documented in charcoal accumulation rate (CHAR) records from the south-central Brooks Range, Alaska, USA.

† Abbreviations are: V, vegetation; T, temperature; P, precipitation; s, static; Δ, change.

Fire-return intervals.—For each vegetation period, we pooled FRIs inferred from CHAR records at individual sites to form a distribution representing FRIs across the study transect as a whole. Given the small number of inferred fires at each site, this step enhanced the rigor of comparisons between CHAR and ALFRESCO records and is justified because FRI distributions of individual sites did not differ statistically ($P > 0.05$) within vegetation periods, based on statistical comparisons used by Higuera et al. (2009). To compensate for inherent biases in the ALFRESCO data set, FRIs from ALFRESCO records were truncated to remove FRIs > 500 yr. This step is justified because ALFRESCO does not model age-dependent mortality within the late successional spruce forest trajectories, thus allowing a small number of pixels to record unrealistically long FRIs in ALFRESCO simulations that encompass multi-millennial time periods. We chose to truncate the ALFRESCO FRIs at 500 yr because this was the longest FRI in the CHAR data set. Additionally, we removed charcoal-based FRIs < 90 yr from the 7–5 kyr BP period because ALFRESCO rules that govern succession on white spruce sites do not allow the early-successional deciduous state to switch to white spruce until 90 yr after fire (Rupp et al. 2000*b*). While reasonable on the modern landscape, this may be a limitation of ALFRESCO when simulating paleofire regimes during the white spruce zone, as paleorecords show evidence of shorter FRIs during this period (Higuera et al. 2009). Nevertheless, this truncation step should have little impact on our interpretation of fire regimes within the white spruce period because FRI distributions including vs. excluding FRIs < 90 yr are not statistically different based on Kolmogorov-Smirnov or likelihood-ratio tests (Higuera et al. 2009; $\text{median}_{\text{allFRI}}$ FRIs = 135, range = 90–210 years between fires; $\text{median}_{\text{FRI}\geq 90}$ = 188, range = 142–263 years between fires; $P_{\text{K-S}} = 0.17$; $P_{\text{lk-rat}} = 0.26$).

We developed a three-step statistical test for comparing charcoal-based FRIs and ALFRESCO FRIs for each period: (1) calculate pixel-specific FRIs (i.e., fire-return intervals for each pixel) for all non-tundra pixels on the ALFRESCO landscape, (2) combine these into a single FRI distribution, and (3) compare the cumulative distribution function (CDF) of the ALFRESCO FRIs to the CDF of pooled FRIs from the charcoal data set. We compared CDFs using a two-sample Anderson-Darling (AD) test (Anderson and Darling 1954, Pettitt 1976) and evaluated the null hypothesis that both populations (charcoal and ALFRESCO FRIs) come from the same continuous distribution. To compare the CHAR and ALFRESCO data sets under conditions of similar spatial sample densities, we randomly sampled FRIs from non-tundra pixels in each ALFRESCO scenario with the number of sampled pixels equal to the number of sites recording charcoal accumulation (i.e., three). As with the charcoal data set, FRIs from the ALFRESCO pixels were combined to form a pooled FRI record. We used a Monte Carlo approach to compare FRIs from the pooled CHAR and ALFRESCO data sets to derive a "model score" that quantifies the similarity of these data sets. For each vegetation zone, the subsample of FRIs from the ALFRESCO landscape was compared to the charcoal-based FRI data set with the Anderson-Darling test. If the comparisons yielded a P value < 0.10, the null hypothesis of no difference between charcoal-based and ALFRESCO FRI distributions was rejected and 0 was recorded; if $P > 0.10$, the null hypothesis was not rejected and 1 was recorded (note that using a P value of 0.10 in this case is more conservative that using a P value of 0.05). The model score equals the proportion of 1s recorded when this procedure was repeated 10 000 times. Thus the model score ranges from 0 to 1, with 0 representing perfect dissimilarity (100% rejection of null hypothesis of no difference between FRI distributions estimated by CHAR and ALFRESCO data sets) and 1 representing perfect similarity (100% acceptance of null hypothesis) in CDFs.

Area burned.—We compared long-term variations in CHARs (generally termed "background CHAR"), as a proxy for area burned, to long-term variations in area burned calculated from ALFRESCO simulations. Although background CHAR has often been considered to be the "noise" component of charcoal records, recent theoretical work (Higuera et al. 2007) indicates that for a given vegetation type over long time periods, charcoal deposition to a lake should be related to area burned. Thus we explored whether these theoretical inferences are supported by comparisons between background charcoal in empirical data and ALFRESCO simulations of area burned. In our comparison, the CHAR and ALFRESCO series were treated identically to isolate long-term trends and standardized to facilitate visual comparisons. Each time series was smoothed with a locally weighted regression using a 500-yr window (Cleveland 1979), and the resulting time series were standardized to a mean of 0 and a standard deviation of 1. For the CHAR time series, each record was interpolated to uniform 15-yr intervals (Higuera et al. 2009) and a composite time series was developed by averaging the three standardized time series.

Results

Vegetation and fire history

Vegetation and fire histories are summarized here and described in full by Higuera et al. (2009). Between 7 and 5 kyr BP, forest–tundra dominated the landscape near Ruppert Lake. The strongest modern analogs to fossil pollen assemblages are in North American forest–tundra vegetation; further, the absence of stomata indicates a sparse tree cover during this period (Fig. 2). Spruce pollen during 7–5 kyr BP (Brubaker et al. 1983, Higuera et al. 2009) is almost exclusively white spruce. Charcoal accumulation rates (CHARs) for the white spruce period are low (Fig. 4), with means at Ruppert, Wild Tussock, and Code Lakes of 0.031–0.044 pieces$\cdot$cm$^{-2}\cdot$yr^{-1}. The median fire-return interval (medFRI) of the charcoal data set is 135 years (95% CI = 90–210); the medFRI of the truncated data set is 188 years (95% CI = 142–263; Table 2). The establishment of black spruce forests ~5 kyr BP is evidenced by the high probability of analog (>75%) to pollen assemblages in modern black spruce forests of North American and by the consistent presence of spruce stomata (Fig. 2), which implies continuous forest cover (Carlson 2003). Charcoal is most abundant 5–0 kyr BP (Fig. 4): mean CHAR increases to 0.09–0.19 pieces$\cdot$cm$^{-2}\cdot$yr^{-1}, and medFRI decreases to 120 years (95% CI = 120–150; Table 2).

ALFRESCO simulations

7–5 kyr BP period.—As just described, vegetation consisted of ~10% white spruce, with tundra dominating the remaining landscape, particularly north of Ruppert Lake (Fig. 3). Mean annual area burned was 28 km^2 (Figs. 5 and 6, Table 2); medFRI was 180 years (Table 2). Descriptions of simulations will use abbreviations: vegetation as V, temperature as T, precipitation as P, static as s, and change as Δ.

5–0 kyr BP period: Static vegetation.—

1. *Static climates* (V, sT, sP).—Vegetation cover did not change, and fire regimes differed slightly from 7–5 kyr BP (mean annual area burned = 29 km^2, medFRI = 150 years; Table 2; Figs. 5 and 6) due to stochastic processes in ALFRESCO.

2. *Changed climates* (V, ΔT, sP; sV, sT, ΔP; sV, ΔT, ΔP).—Mean annual area burned remained constant or decreased slightly (16–29 km^2; Table 2, Fig. 6), and medFRIs increased somewhat (190–200 years; Table 2, Fig. 5). In each case, the changes were greatest with shifts in both temperature and precipitation (sV, ΔT, ΔP). Deciduous cover declined and white spruce cover increased slightly with a change in both climate variables, but neither responded to an individual shift in temperature or precipitation.

5–0 kyr BP period: Changed vegetation.—

1. *Static climate* (ΔV, sT, sP).—Median FRIs decreased markedly to 110 years and mean annual area burned increased to 181 km^2 (Table 2, Figs. 5 and 6). Deciduous cover increased and white spruce cover declined markedly.

2. *Changed climate* (ΔV, sT, ΔP; ΔV, ΔT, sP [see Fig. 3]; ΔV, ΔT, ΔP).—Median FRIs and mean annual area burned changed less dramatically in these scenarios (medFRIs, 120–150 yr; mean area burned, 79–129 km^2), with the ΔV, ΔT, ΔP scenario showing the smallest changes (Table 2, Figs. 5 and 6). Deciduous cover increased in all scenarios. White spruce cover declined somewhat in ΔV, sT, ΔP and ΔV, ΔT, sP, but remained relatively stable in ΔV, ΔT, ΔP.

Comparison of ALFRESCO simulations and charcoal records

FRIs.—For 7–5 kyr BP, high model scores (0.967) indicate strong similarity in CDFs of empirical and simulated FRIs, and low Anderson-Darling (AD) statistics (0.65, $P > 0.10$; Table 2) indicate no statistical differences in these records. For 5–0 kyr BP, empirical FRIs are lower than simulated FRIs in all static-vegetation scenarios (medFRI = 120, medFRIs = 150–200, respectively). Low model scores (0.014–0.065) and high AD statistics (17.21–34.16) confirm significant differences in these data sets (Table 2). Empirical and simulated FRIs are more similar for changed-vegetation scenarios (model scores = 0.328–0.460; Table 2), with no statistical difference for the ΔV, sT, ΔP and ΔV, ΔT, sP scenarios (AD = 1.32, 1.37, respectively; $P > 0.10$; Table 2).

Area burned.—Both the individual and composite CHAR records and all ALFRESCO changed-vegetation scenarios show long-term increases between 7–5 and 5–0 kyr BP (Fig. 6). However, the CHAR series increase more gradually and lack a peak that is evident in

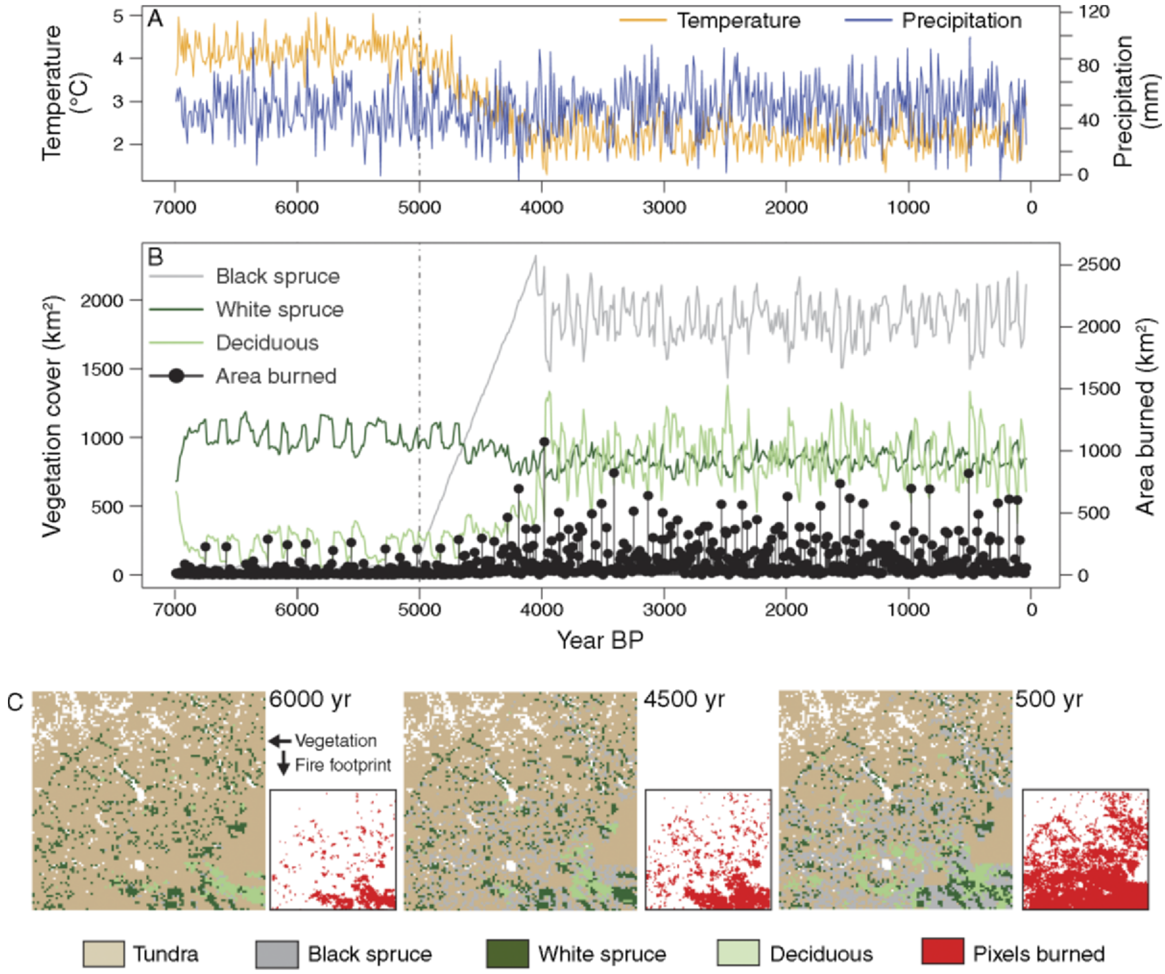

FIG. 3. Example ALFRESCO output for the ΔV, ΔT, sP scenario. (Abbreviations are: V, vegetation; T, temperature; P, precipitation; s, static; Δ, change.) Time series A shows temperature and precipitation over the simulation period (simulated years BP). Time series B shows cover (km^2) of simulated vegetation types and annual area burned (km^2) on the Ruppert Lake landscape, with the panels of C illustrating the pattern of vegetation types on simulated landscape. The dashed line in panels A and B separates the white spruce period (7000–5000 yr BP) from the black spruce period (5000–0 yr BP) within the simulation.

ALFRESCO data sets between 4.5–4.0 kyr BP. In contrast, all static-vegetation scenarios differ from CHAR series by showing no long-term trends in area burned between 7–5 and 5–0 kyr BP.

Discussion

Using data-model comparisons to investigate past fire regimes

The comparison of empirical and simulated records is a critical step in investigations linking paleodata and ecosystem models because the degree of similarity between data sets can help distinguish between alternative hypotheses to explain past change. However, given the disparate metrics and spatial/temporal scales of many empirical and simulated records, this step is not straightforward. Even the most recent comparisons between pollen records and forest models (Cowling et al. 2001, Keller et al. 2002, Heiri et al. 2006) mention the challenges of meshing pollen and simulated data sets. As discussed next, we paid particular attention to the metrics of charcoal and ALFRESCO data sets when selecting methods for data-model comparisons.

Qualitative (visual) comparisons were used to evaluate the similarity of the unlike metrics of long-term charcoal accumulation rates (CHARs) and area burned by ALFRESCO. At the most general level, the similarity of multi-centennial variations in CHARs and mean annual area burned supports the hypothesis that changes in sediment-charcoal content reflect changes in area burned. This inference is supported by three recent investigations that indicate variations in background charcoal reflect aspects of landscape burning. The Higuera et al. (2007) model of charcoal dispersal and incorporation into lake sediments predicts that at multi-centennial to millennial time scales the amount of charcoal deposited in lake sediments is a function of

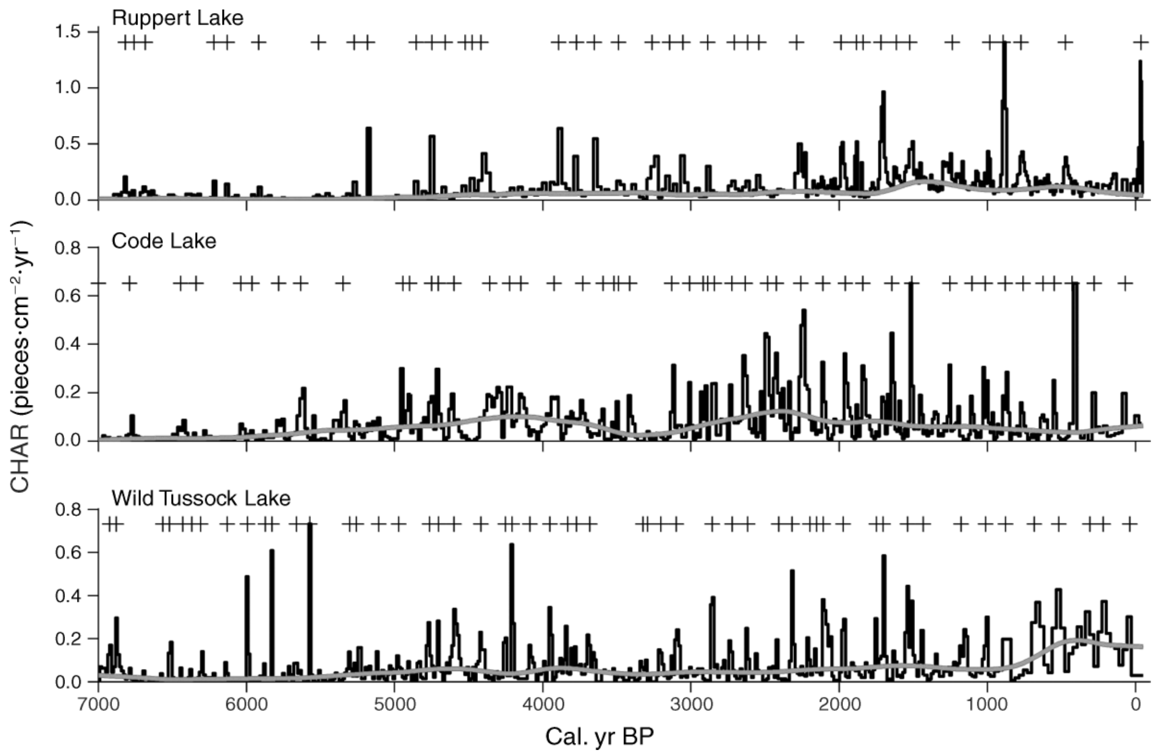

FIG. 4. CHAR records for Ruppert, Code, and Wild Tussock lakes over time (calibrated years before present). Plus signs (+) indicate inferred fire events at each site.

the area burned within ~10–20 km of the lake. Empirical studies at regional and global scales suggest a correspondence between long-term CHARs and the amount of woody fuels on the landscape (Marlon et al. 2006) or the influence of climate and human drivers (Marlon et al. 2008). Thus our qualitative comparisons agree with recent findings that CHAR records have potential to expand the understanding of past fire regimes beyond the conventional inference of fire frequencies.

TABLE 2. Mean annual area burned for ALFRESCO scenarios and results of Anderson-Darling (AD) test for no difference between fire-return interval (FRI) distributions for truncated CHAR and ALFRESCO data sets.

Period (kyr BP)	Scenario	Mean annual area burned		Median FRI (yr)†	Model score‡	AD§	*P*¶
		7–5 kyr BP	5–0 kyr BP				
Paleo							
7–5	na	na	na	188 (142, 263)	na	na	na
5–0	na	na	na	120 (120, 150)	na	na	na
ALFRESCO							
7–5	baseline	28	na	180	0.967	0.65	>0.10
5–0	sV, sT, sP	na	29	150	0.065	17.21	<0.01
	sV, sT, ΔP	na	29	200	0.014	34.16	<0.01
	sV, ΔT, sP	na	23	190	0.023	27.85	<0.01
	sV, ΔT, ΔP	na	16	200	0.036	32.99	<0.01
5–0	ΔV, sT, sP	na	181	110	0.328	4.14	<0.01
	ΔV, sT, ΔP	na	127	120	0.457	1.32	>0.10
	ΔV, ΔT, sP	na	129	120	0.460	1.37	>0.10
	ΔV, ΔT, ΔP	na	79	150	0.421	4.39	<0.01

Note: Scenario abbreviations are: V, vegetation; T, temperature; P, precipitation; s, static; Δ, change; na, not applicable.

† Fire-return intervals (FRIs), with 95% confidence intervals for the paleodata in parentheses. Confidence intervals are not given for the ALFRESCO median FRI because the populations of FRIs are completely sampled, making the median FRI a known rather than estimated statistic.

‡ Proportion of comparisons between paleo and ALFRESCO FRIs resulting in nonsignificant differences at alpha = 0.10, from 10 000 bootstrapped samples of the ALFRESCO data set. Model score ranges from 0 (imperfect) to 1 (perfect).

§ Anderson-Darling statistic for comparisons between ALFRESCO scenario and the appropriate paleo time period.

¶ *P* values >0.10 are significant.

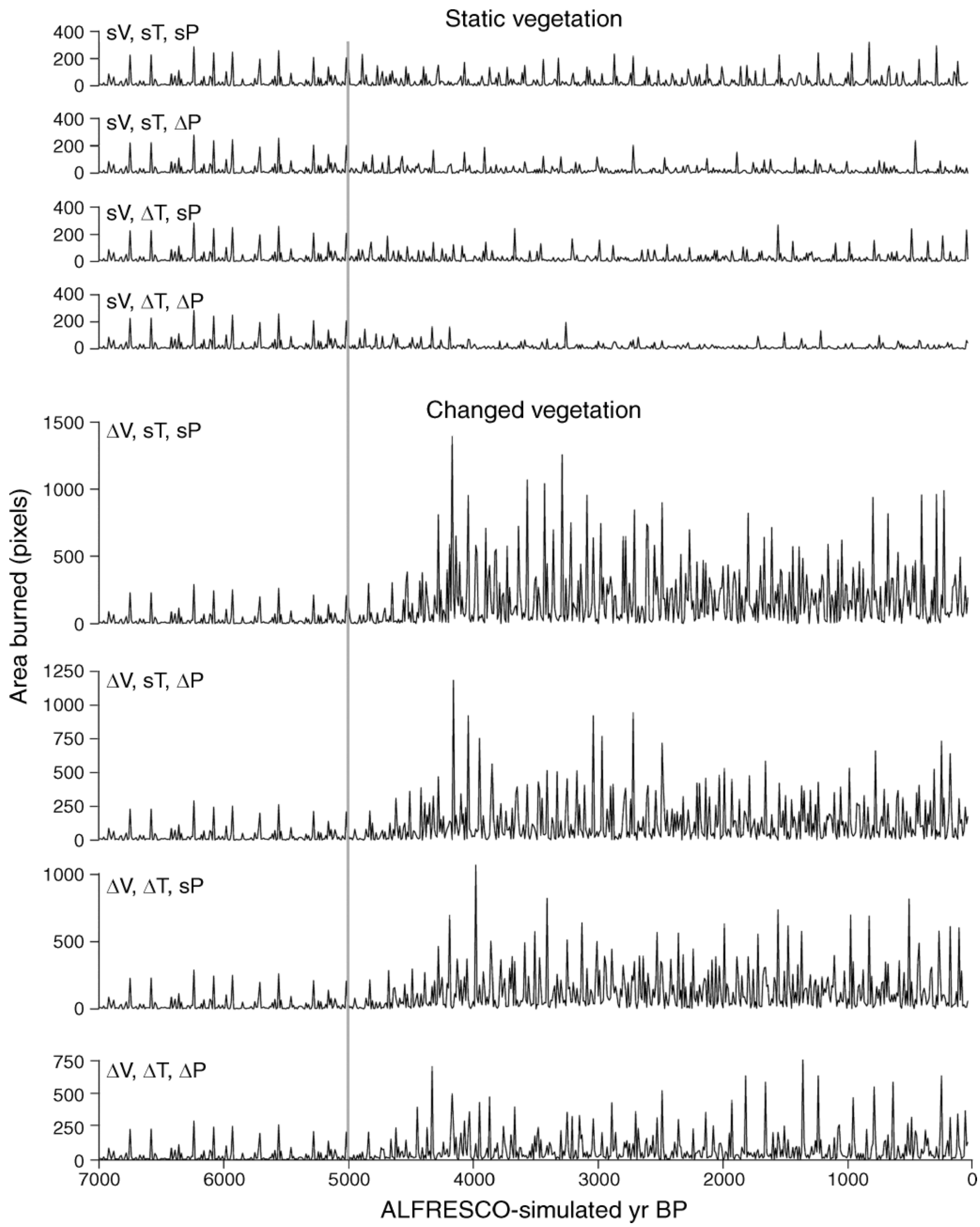

FIG. 5. Time series of area burned for ALFRESCO simulations. The gray line separates the two simulation periods.

We developed a quantitative measure (model scores) to compare FRIs, which could be calculated from both CHAR records and ALFRESCO simulations. The model score is a versatile similarity index that accounts for differences in sample sizes and spatial variability in the simulated landscape. Model scores are particularly useful when comparing multiple simulations (i.e., different hypotheses) to one set of empirical data. For example, model scores show that charcoal-based FRIs are more similar to the FRIs of the ΔV, ΔT, ΔP (0.421) than the sV, sT, sP (0.065) scenario (Table 2), even though medFRIs in both scenarios are identical (150 yr). This example also illustrates that comparisons of FRI *distributions* can lead to different conclusions than comparisons of simple metrics such as the median FRI, providing a potentially more rigorous test of the similarity between empirical and simulated data sets.

Our second quantitative comparison applied the Anderson-Darling statistic to test the similarity of empirical and simulated FRI series. To our knowledge, this is the first time a statistical test has been used to evaluate the adequacy of alternative causal hypotheses to account for variations in paleodata (in our study, the adequacy of ALFRESCO scenarios to describe shifts in

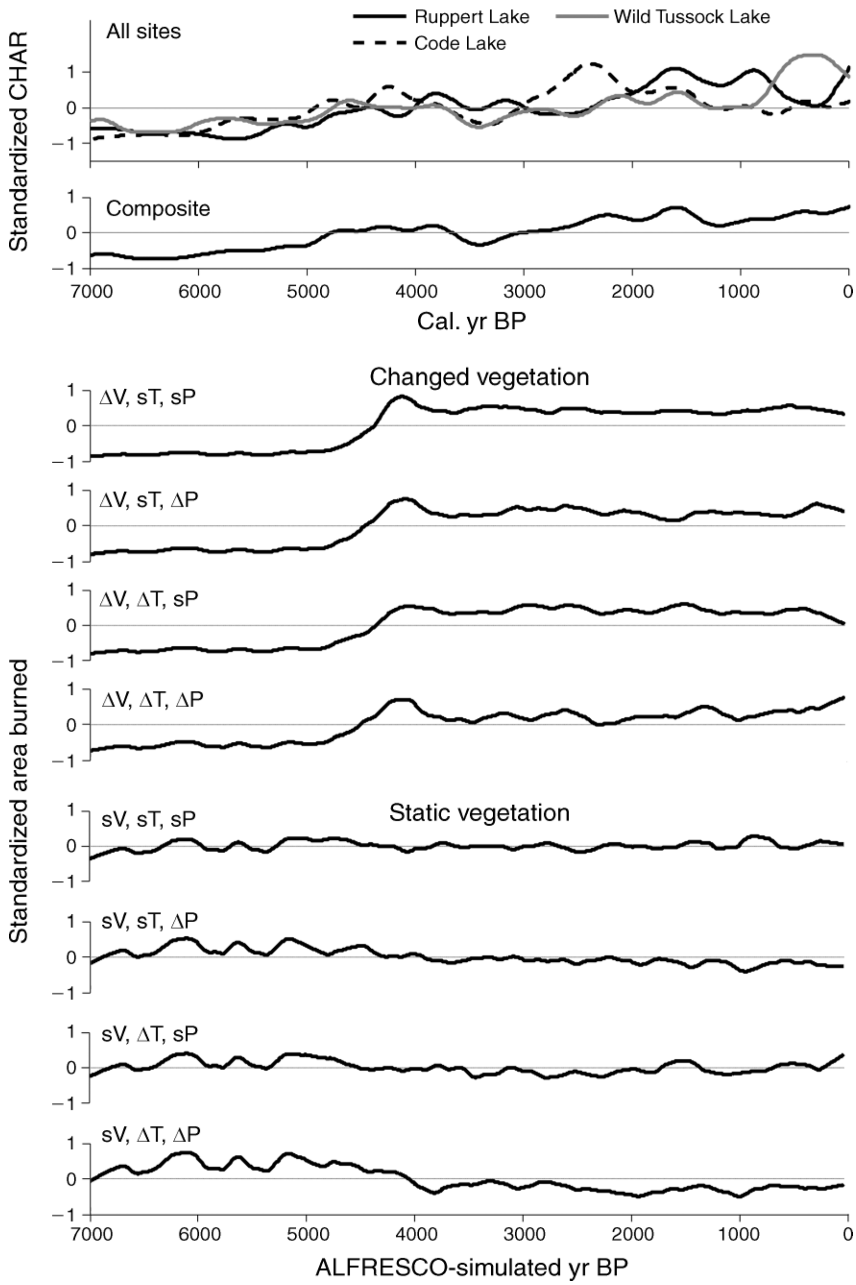

FIG. 6. Time series of standardized CHAR for Ruppert, Code, and Wild Tussock Lakes; composite standardized CHAR (originally measured as pieces of charcoal per cm^2 per year) for all lakes; and standardized annual area burned (originally measured at km^2/yr) simulated by ALFRESCO. All series have been smoothed with a locally weighted regression using a 500-yr window.

charcoal-based FRIs between 7–5 and 5–0 kyr BP). The AD statistic was critical to interpreting the similarity of FRIs in charcoal records and changed-vegetation scenarios. AD tests identified only the ΔV, sT, ΔP and ΔV, ΔT, sP scenarios as being indistinct from empirical FRIs, leading to the inference that temperature or precipitation interacted with vegetation to cause the mid-Holocene shift in fire regimes (see *Discussion: Implications to fire ecology and vegetation responses to future climate change* for ecological implications).

Because statistical tests set a rigorous standard for recognizing the similarity of data sets derived from disparate approaches, the absence of statistical differences between empirical and simulated FRIs in two scenarios supports a central premise of our approach: that the similar spatial and temporal scales of CHAR records and ALFRESCO simulations allow a rigorous exploration of hypotheses about the causes of past fire-regime shifts. The compatibility of CHAR and ALFRESCO data sets is due to several factors. First, CHAR series are derived from contiguous, high-resolution samples of sediment cores. Since no sediment levels are skipped within a sediment record and sample resolution is at decadal time scales, these series continuously register charcoal deposition from the theoretical number of fires within the potential charcoal source area (Higuera et al. 2007, Peters and Higuera 2007). As a result, CHAR series can be used to calculate the same metrics of fire regimes as estimated by ALFRESCO (e.g., FRIs, potentially annual area burned), permitting direct comparisons between empirical and simulated data sets. Second, the temporal scales of CHAR records are suitable for investigating the dynamics of fire regimes with long fire-return intervals (such as boreal forests). The limiting constraints are slow sediment accumulation and sediment mixing, which prevent charcoal peaks from being isolated by laboratory sampling and/or dampen high-frequency variations in charcoal records (Higuera et al. 2007). Third, the spatial scales of sediment-charcoal records and ALFRESCO are similar. Theoretical considerations (Higuera et al. 2007) indicate that short-term variations in CHARs in boreal forests register fire occurrence within ~500 m of lakes (corresponding to the spatial scale of 1 km^2 pixels in ALFRESCO) and long-term trends in total CHARs ("background CHAR") register area burned within ~10–20 km.

Inferring causes of Holocene fire-regime shifts

By depicting ecological interactions in vegetation/climate scenarios, ALFRESCO simulations provide insights about the vegetation–fire feedbacks driving changes in past fire regimes. For example, in the static-vegetation scenarios, decreased temperature and increased precipitation (sV, ΔT, ΔP) resulted in fewer ignitions and lower rates of fire spread, leading to fewer fires and less area burned. The cover of deciduous vegetation decreased in response to the decline in area burned, which favored the development of late-successional white spruce forests. In contrast, when black spruce increased in the changed-vegetation scenarios, landscape burning increased dramatically in response to fuel buildup that occurred when flammable black spruce forests became extensive. Although the extent and continuity of vegetation types influence the fire regime (Rupp et al. 2000*b*), species-specific flammability (i.e., differences between white and black spruce forests) is the dominant factor driving increased burning in the simulated records (Rupp et al. 2002*a*). In these scenarios, decreases in temperature and/or increases in moisture dampened the effects of increasing black spruce, resulting in fewer fires and less area burned than when climate did not change. Overall, our results support evidence of several other paleoecological investigations (Clark et al. 1996, Lynch et al. 2002, Gavin et al. 2007), suggesting that in some instances the quality and quantity of fuels have overridden the direct effect of climate on Holocene fire regimes.

Comparisons of empirical and simulated data allowed us to identify which of the ALFRESCO scenarios best describe the climate–vegetation–fire interactions responsible for the fire-regime shift in paleorecords. For example, model scores indicate that all changed-vegetation scenarios are more similar than static-vegetation scenarios to the paleodata (Table 2), implying that vegetation change had a greater influence than climate on the mid-Holocene fire-regime shift. However, AD tests indicate that vegetation change was not the sole explanation of altered fire regimes, as empirical and simulated FRIs were statistically indistinct only when temperature or precipitation shifts accompanied vegetation change. The inference that cooler temperature or greater precipitation (but not both) dampened the effect of increased landscape flammability is a novel interpretation of the cause of mid-Holocene increased burning. This interpretation illustrates that data-model comparisons have potential to identify the relative importance and interactive effects of climate and vegetation on landscape burning, a difficult task using pollen and charcoal records alone.

We emphasize two cautionary notes to these results, however. First, although the response of fire regimes to prescribed temperature and precipitation changes are plausible, given the direct effects of decreased temperature and increased precipitation on landscape burning, the temperature and precipitation influences may be too large due to our choice of climate offsets in these simulations. We suspect that with smaller temperature and precipitation changes, the ΔV, ΔT, ΔP scenario (which represents modern) would be most similar to paleorecords for 5–0 kyr BP. Second, although the magnitude of black spruce increase in our simulations is reasonable (pollen assemblages became similar to modern black spruce forests 5–0 kyr BP; Higuera et al. 2009) and simulated vegetation matches current vegetation near Ruppert Lake, our results do not address the degree to which climate forced the mid-Holocene increase in landscape flammability because the increase in black spruce was not a function of climate in ALFRESCO simulations. To improve the realism of our simulations, we are developing independent quantitative climate proxies of mid-Holocene climate change and species-specific climate responses for black spruce in ALFRESCO.

Implications to fire ecology and vegetation responses to future climate change

Our comparisons between simulated and empirical records suggest that the mid-Holocene expansion of black spruce fundamentally altered landscape flammability and caused fire regimes to change in a direction opposite to that predicted by the direct effects of climate (see also Higuera et al. 2009). Our study, therefore, adds to growing evidence that changes in species- and community-level traits can alter ecosystem processes (e.g., Suding et al. 2008), which in turn may have consequences to the climate system (Chapin et al. 2008). Although the expansion of highly flammable species is known to increase fire occurrence in diverse ecosystems (e.g., Brooks et al. 2004), vegetation-mediated changes in fire regimes are not a universal finding of modern or paleologic studies (Brooks et al. 2004, Gavin et al. 2007). The extent to which species-level traits affect larger scales of ecological organization (including fire regimes) is poorly understood and difficult to predict in many regions (Suding et al. 2008). In black spruce ecosystems, the influence of vegetation on fire regimes results from a suite of species-level traits, including flammable foliage and tree architecture, semi-serotinous cones, and rapid recruitment following fire (Rupp et al. 2002).

The results of our study provide insights to potential ecosystem responses to climate change at high latitudes, where major changes in fuel types are predicted for the future (ACIA 2004). For example, flammable shrubs are currently increasing in Alaskan tundra, with potential to facilitate fire occurrence and spread (Tape et al. 2006, Higuera et al. 2008). In addition, some future scenarios for boreal forests (Calef et al. 2005, Flannigan et al. 2005, Johnstone and Chapin 2006) predict an increase in deciduous trees. With the high water content of deciduous compared to coniferous fuels, this vegetation change could lead to reduced fire occurrence. Our findings imply that such fuel changes are potentially important for future fire regimes and that ALFRESCO modeling can explore the range of conditions in which vegetation can substantially alter the direct effect of climate on fire regimes.

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