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RESEARCH ARTICLE

Forest succession and climate variability interacted to control fire activity over the last four centuries in an Alaskan boreal landscape

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Abstract

Context The boreal forest is globally important for its influence on Earth's energy balance, and its sensitivity to climate change. Ecosystem functioning in boreal forests is shaped by fire activity, so anticipating the impacts of climate change requires understanding the precedence for, and consequences of, climatically induced changes in fire regimes. Long-term records of climate, fire, and vegetation are critical for gaining this understanding.

Objectives We investigated the relative importance of climate and landscape flammability as drivers of fire activity in boreal forests by developing high-resolution records of fire history, and characterizing their centennial-scale relationships to temperature and vegetation dynamics.

Methods We reconstructed the timing of fire activity in interior Alaska, USA, using seven lake-sediment charcoal records spanning CE 1550–2015. We developed individual and composite records of fire activity, and used correlations and qualitative comparisons to assess relationships with existing records of vegetation and climate.

Results Our records document a dynamic relationship between climate and fire. Fire activity and temperature showed stronger coupling after ca. 1900 than in the preceding 350 yr. Biomass burning and temperatures increased concurrently during the second half of the twentieth century, to their highest point in the record. Fire activity followed pulses in black spruce establishment.

Conclusions Fire activity was facilitated by warm temperatures and landscape-scale dominance of highly flammable mature black spruce, with a notable increase in temperature and fire activity during the twenty-first century. The results suggest that widespread burning at landscape scales is controlled by a combination of climate and vegetation dynamics that together drive flammability.

Keywords Boreal forest · Fire · Paleoecology · Multi-proxy · Climate · Black spruce

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Introduction

Fire is a primary control of carbon (C) cycling and vegetation dynamics in North American boreal forests, driving important feedbacks to the climate system through changes in atmospheric greenhouse gas concentrations and radiative balance (Bonan et al. 1992; Payette 1992; Chapin et al. 2000; Randerson et al. 2006; Bond-Lamberty et al. 2007). Furthermore, by altering soil properties, nutrient cycling, and microclimate, and by initiating primary succession, high-severity fires regulate forest structural patterns and ecosystem function (Johnson 1992; Johnstone et al. 2010a). Although the Alaskan boreal forest has sustained a high-severity fire regime for millennia (Lynch et al. 2002, 2004b; Hu et al. 2006; Higuera et al. 2009), increasing wildfire activity in North American boreal forests motivates investigation into the relative importance of climate and local ecosystem properties in controlling fire activity across the biome (Duffy et al. 2005; Hu et al. 2006; Parisien et al. 2011; Mann et al. 2012). Novel fire regimes, enabled by climate warming (Mann et al. 2012), could catalyze abrupt ecosystem shifts (Barrett et al. 2011), which could in turn have significant consequences for the resilience of boreal forests to future climate change (Chapin et al. 2004; Johnstone and Chapin 2006; Johnstone et al. 2010b, 2016).

Understanding the causes and consequences of fire in the boreal forest requires an accurate characterization of the frequency, severity, and spatial patterning of fire activity over centuries to millennia (Whitlock et al. 2010). Fire activity in the observational record (CE 1950 to present) varies widely across Alaskan boreal forests, with fire rotation periods (FRP, the time to burn an area equal in size to a landscape of interest) ranging from 80 yr in the Yukon Flats region to more than 2000 yr in the Copper River Basin (Kasischke et al. 2002; Young et al. 2017). Despite wide spatial variability in fire activity, the extent, frequency, and severity of burning across the Alaskan boreal forest has generally increased over the past several decades (Kasischke and Turetsky 2006; Kasischke et al. 2010), with statistical models predicting the trend to continue over the coming century in response to projected warming (Balshi et al. 2009; Mann et al. 2012; Young et al. 2017). Annual area burned in the North American boreal forest is tightly linked to the frequency and duration of blocking high-pressure ridges during summer months, driven by atmospheric teleconnections that vary over multi-annual to decadal time scales (i.e., El Nino Southern Oscillation, Pacific Decadal Oscillation). These climate dynamics control seasonal fuel moisture and fire weather, and thus have strong statistical and mechanistic links to annual area burned (Duffy et al. 2005; Macias Fauria and Johnson 2008).

In addition to direct coupling of fire and climate through changes in fuel moisture and ignitions, multi-decadal climate variability impacts fire activity indirectly across a productivity gradient, by regulating the abundance of flammable biomass within and across regions (Krawchuk and Moritz 2011; Genet et al. 2013; Pausas and Ribeiro 2013). The indirect impact of climate variability on fire is also observed in landscape change through time. Paleoecological records document the importance of landscape flammability (i.e., the relative proportions of vegetation types on the landscape that vary in fuel loading and average moisture content) in determining fire activity. In Alaska, a distinct increase in fire activity occurred across the modern boreal forest ca. 4000–6000 yr before present when white spruce woodlands were replaced by more flammable black spruce forests (*Picea mariana*), despite a concurrent long-term trend of climatic cooling (Lynch et al. 2002, 2004b; Higuera et al. 2009). In the eastern Canadian boreal forest, regions with a high proportion of deciduous species burned with less frequency than regions with low proportions of deciduous species, even under the warm conditions that prevailed 3000–6000 yr before present (Girardin et al. 2013). Analyses of modern fire activity also show complex interactions and feedbacks between vegetation and fire, where high-severity fires limit subsequent fire activity for decades (Héon et al. 2014; Parks et al. 2015), and variation in the flammability of different vegetation types controls fire occurrence and spread (Dash et al. 2016).

Because both climate and vegetation change are processes that unfold over decades to centuries, quantifying and understanding fire-regime change requires datasets that encompass appropriately broad temporal scales (Whitlock et al. 2010). Macroscopic charcoal preserved in lake sediment can supplement observational records and tree-ring based methods of reconstructing fire history by extending fire reconstructions further into the past. Fire history reconstructions from lake-sediment charcoal ("paleofire records") are particularly well suited to study systems characterized by infrequent, stand-replacing fire-regimes, like boreal forests.

Here, we quantified fire activity in an approximately 900 km^2 landscape from CE 1550–2015, and compared fire, climate, and vegetation datasets to test two main hypotheses: (i) fire activity was positively correlated to summer temperatures over decadal time scales, because of direct climatic controls on fire activity, including fire-conducive weather and low fuel moisture; and (ii) periods of widespread burning at the landscape scale drive spatial patterns in vegetation, and are inherently followed by periods of reduced fire activity due to lower fuel connectivity and flammability, irrespective of climate. Our results provide new insights about the controls of fire occurrence, and reveal interacting drivers and negative vegetation feedbacks to fire activity at landscape-to-regional scales, with important implications for anticipating future fire activity under climate warming.

Methods

To test our hypotheses about the interactions among climate, fire, and vegetation, and characterize the frequency of extensive fire activity in the past, we developed seven new paleofire records and compared them to tree demography records from 58 forest plots (c. 0.1 ha, Duffy 2006), reconstructed growing season temperatures from the Gulf of Alaska (Wiles et al. 2014), and modeled summer temperatures co-located with our study sites (SNAP 2015). Our fire-history and tree-demography datasets span 465 and 365 yr, respectively, while tree-ring-reconstructed temperatures span 465 yr and modeled summer temperatures span 105 yr (1900–2005).

Study area

Our study area is a boreal forest landscape in interior Alaska, USA, within and around the Nowitna National Wildlife Refuge, in the Kuskokwim Mountains ecoregion (Nowacki et al. 2003). The region has a continental climate, characterized by long cold winters and short, relatively warm summers. Air temperatures average a maximum (minimum) of 19.9 °C (11.1 °C) in July, and − 18.8 °C (− 27.7 °C) in January (1942–1993, Galena Airport, 64.733°N, 156.928°W, WRCC). Vegetation in the region is comprised primarily of spruce- (*Picea mariana* and *Picea glauca*) and deciduous-dominated (*Populus tremuloides, Betula papyrifera*) forest stands. Tall willow (*Salix* spp.) and birch (*Betula* spp.) thrive in recently burned areas, while *Populus* are common in recent burns and on well-drained upland sites. The mean fire rotation period (time required to burn an area equal in size to the area of interest) from 1950 to 2009 in the Kuskokwim Mountains ecoregion was 191 yr, indicating less fire activity than in the highly flammable Yukon Flats ecoregion (FRP = 82 yr), but more than the Alaskan-wide boreal forest average (FRP = 276 yr; Young et al. 2017).

Lake-sediment charcoal sampling

We characterized the past 465 yr of fire activity using a network of seven high-resolution lake-sediment cores collected in June 2015 (Fig. 1). Candidate lakes were identified prior to the field campaign using satellite imagery based on surface area (1–10 ha), hydrology, and landscape position. Candidate lakes were further evaluated in the field for simple, consistent shorelines, no or minimal inlet or outlet streams, limited topographic relief, and for suitable water depths, measured with an acoustic bathometer (Table 1).

Surface cores were collected using a 7.6-cm diameter polycarbonate tube fitted with a piston, and the sediment–water interface was preserved by adding sodium polyacrylate prior to transport. Each sediment core was divided lengthwise and imaged at the University of Minnesota's National Lacustrine Core Facility (LacCore), where one third of each core remains archived. Collected sediments were characterized by alternating laminations of light grey, allochthonous, siliceous silt and dark, highly decomposed organic sapropel (gyttja). Laminations approximately 1–5 mm thick were visible in the upper 15–40 cm of sediment before transitioning to > 10 cm thick layers of undecomposed peat and woody organic material mixed with silt and sand. The cores were not interpreted down-core of the deepest laminations.

Working sections of each core were sliced into continuous 0.25-cm sections. Prior to slicing, magnetic susceptibility was measured at 0.25-cm

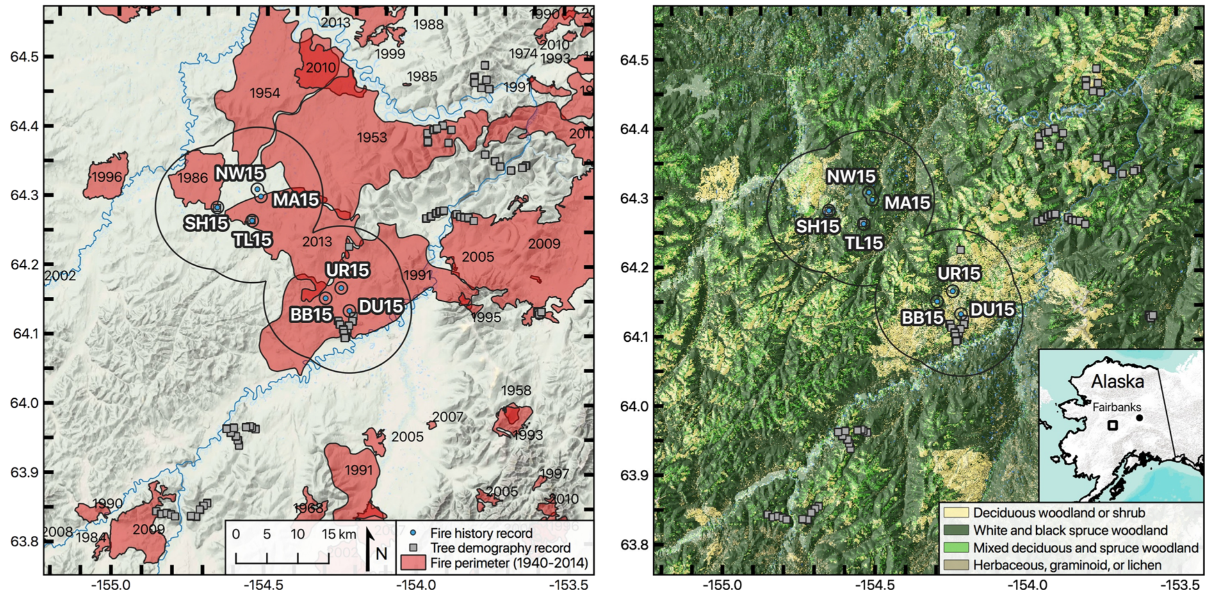


Fig. 1 Maps of study area. Both panels: lake-sediment cores (blue circles), and tree cores or cross-sections (gray squares). Blue points cover a ~ 500-m radius, and black circles show 1- and 10-km radii around each lake (approximating the spatial extent of the fire event and biomass burning reconstructions, respectively). *Note* Two tree demography records are immediately adjacent to SH15 and TL15 fire history records. Left panel: observed fire perimeters since 1940 (red polygons, Alaska Interagency Coordination Center, http://fire.ak.blm.gov/), and major rivers (blue lines). Right panel: vegetation classifications (simplified from Boggs et al. 2016) and topographic relief (USGS 3DEP). Vegetation classifications are based largely on Landsat imagery from 2001, highlighting deciduous vegetation in areas that burned in the prior 1–2 decades, but not after. (Color figure online)

Table 1 Sampled lakes and associated site-level information

Lake name	Site code	Latitude	Longitude	Depth (m)	Area (ha)	Record length (cm)	Fires < 1 km
Buster Brown	BB15	64.156	− 154.301	4.7	2	30	1991
Duffy	DU15	64.137	− 154.221	7.5	10	40	1991
Macchiato	MA15	64.302	− 154.518	17.3	4	16	2013
Nodwell	NW15	64.312	− 154.530	16.0	8	40	2013
Shapiro	SH15	64.286	− 154.663	7.1	3	18	1986
Three Lodge	TL15	64.267	− 154.545	10.0	5	39	2013
Ursa	UR15	64.170	− 154.249	5.7	1	15	1991

"Record length" indicates the length of the collected core used for the fire-history reconstruction. Years when a fire burned within 1 km of a lake, as documented by the Alaska Interagency Coordination Center (http://fire.ak.blm.gov/), are listed as "Fires < 1 km"

resolution, corresponding to the same intervals of sliced sections, with a Bartington MS3 Meter and MS2 Core Logging Sensor (Bartington Instruments Ltd., UK). To quantify macroscopic charcoal concentration, 1–3 cm^3 subsamples were taken from each 0.25-cm section and treated with a solution of equal parts 5% sodium metaphosphate and 5% sodium hypochlorite for 24 h to loosen the sediment and bleach non-charcoal organic material. Each subsample was sieved through a 150-μm sieve, and macroscopic charcoal was counted under a Nikon SMZ645 stereomicroscope at 10–40 × magnification (Nikon Instruments Inc. Melville, NY).

Chronological control

Sediment ages for the top 15 cm of each core were estimated from ^{210}Pb-activity using the constant-rate-of-supply model (Binford 1990). In some cores, estimates of background ^{210}Pb activity were corroborated with measurements of ^{226}Ra, a parent isotope to ^{210}Pb. Measurements of ^{210}Pb and ^{226}Ra activity were obtained from Flett Research Ltd. (Manitoba, Canada; *flettresearch.ca*). The age of material below 15 cm (approximately $>$ 150 yr old) was estimated from accelerated mass spectrometer (AMS) measurements of ^{14}C in terrestrial macrofossils, bulk sediments, or concentrated charcoal spanning 0.25–1.00 cm of core. Radiocarbon measurements were made at the Lawrence Livermore National Laboratory's Center for AMS (*cams.llnl.gov*).

The ^{210}Pb- and ^{14}C-estimated ages were used to develop a model of sediment accumulation rates over the length of the interpretable core. We developed age-depth models using the *Bacon* v2.2 program in R, which uses sample ages and their corresponding depths to model sediment accumulation as a semi-parametric autoregressive gamma process (Blaauw and Christen 2011; R Core Team 2016). All ^{14}C ages were converted to calibrated year before present ("cal yr BP", years before CE 1950) for modeling using the IntCal 13 dataset, but are presented here in Common Era units (yr CE; Online Appendix Fig. 1).

Site-level records of fire activity

We estimated the charcoal accumulation rate (CHAR, pieces cm^{-2} yr^{-1}) of each sample by taking the product of charcoal concentration (pieces cm^{-3}) and estimated sediment accumulation rate (cm yr $^{-1}$). CHARs represent variability in the influx of burned organic material to a lake through time. In small lakes with no or limited inlet streams, as sampled here, analysis and interpretation of CHAR time series is commonly based on the decomposition approach, which separates CHAR records into low-frequency ("background") and high-frequency ("peak") components (e.g., Clark and Royall 1996; Long et al. 1998; Higuera et al. 2010 and citations within). The background component is inferred to represent charcoal input that occurs in the absence of "local" fires: airborne charcoal input from "distant" fires, slope wash from terrain immediately surrounding a lake, and within-lake redeposition. The "peak" component is interpreted as representing the orders-of-magnitude greater input of airborne and slope-wash charcoal that occurs when a fire burns immediately around the lake, in addition to natural variability in charcoal deposition ("noise"). Based on theoretical and empirical studies in high-severity fire regimes (including Alaskan boreal forest), background CHAR (as well as total CHAR) represent(s) area burned within $\approx$ 10s of km of a lake, while statistically significant peaks in the peak component represent fire occurrence within a radius of approximately 500–1000 m of a lake (Gavin et al. 2003; Lynch et al. 2004a; Higuera et al. 2007, 2011; Kelly et al. 2013).

CHAR time series that met a minimum ratio of high-frequency "signal" to low-frequency "noise" (Kelly et al. 2011) were statistically decomposed using the *CharAnalysis* program (version 1.1, *github.com/phiguera/CharAnalysis*; Higuera et al. 2009, 2010). Each record was interpolated to a common resolution of 5 yr per sample. Background trends were estimated using a 200- or 250-yr LOWESS regression robust to outliers, and background CHAR was removed by subtraction to obtain the peak CHAR series. We modeled the noise component of the peak CHAR series using a globally fit Gaussian mixture model, and we used the 95th or 99th percentile of this distribution to identify statistically significant peaks in CHAR. Finally, to avoid identifying peaks based on insignificant changes in charcoal counts, we removed any peaks where charcoal counts had $>$ 5–25% probability of being drawn from the same Poisson distribution as the minimum count from samples in the preceding 150 yr (Higuera et al. 2010). Parameters for *CharAnalysis* (Table 2) were selected to maximize the correspondence between known fire events (within 1 km of each lake) and peaks identified in the sediment-charcoal record, and were generally consistent among sites.

Our procedures produced two forms of fire history information from individual charcoal records: time series of charcoal influx, reflecting trends in biomass burning within approximately 10 km of each lake, and a binary time series of charcoal peaks, used to estimate the timing of local fire events ("fires"; Fig. 1). For each individual record, we calculated fire return intervals ("FRI", the time between consecutive fires at a given lake), the mean FRI ("mFRI"), and fire frequency ("FF"), the total number of fires divided by the length of the record multiplied by 100 (fires per 100 yr).

Table 2 Parameters used in *Bacon* and *CharAnalysis* for age-depth modeling and charcoal peak analysis. Multiple values for parameter priors refer to values above and below a change-point in the age-depth model, respectively

	Parameter	BB15	DU15	MA15	NW15	SH15	TL15	UR15
Age-depth modeling (Bacon)	Acc. rate prior (yr cm^{-1})	10, 0.5	10, 10	20, 0.5	20, 0.5	20, 0.5	20, 0.5	50, 0.5
	Acc. rate shape prior	1, 1	1, 1	1, 1	1, 1	1, 1	1, 1	1
	AR memory prior	0.1	0.1	0.1	0.1	0.1	0.1	0.1
	Memory strength prior	10	10	10	10	10	10	10
Charcoal peak analysis (*CharAnalysis*)	Record end (yr BP)	− 65	− 65	− 65	− 65	− 65	− 65	− 65
	Record start (yr BP)	222	302	323	1046	228	469	610
	Interpolation (yr)	5	5	5	5	5	5	5
	Smoothing (yr)	200	250	200	250	250	250	250
	Threshold percentile	0.99	0.99	0.95	0.99	0.99	0.99	0.99
	Min. count p value	0.15	0.25	0.15	0.15	0.05	0.05	0.10
Native median resolution (yr $sample^{-1}$)		2	3	6	11	9	4	15
Signal-to-Noise Index (SNI)		9.9	3.3	8.7	6.0	11.1	14.2	10.5

Composite records of fire activity

To quantify the degree of synchrony in the timing of fires among records, we calculated the percentage of sites that recorded fire in continuous 50-yr windows as the sum of fires in the window, divided by the total number of sites recording in that window, following the methods of Calder et al. (2015). We calculated a study-wide mFRI as the mean of all FRI pooled from individual records.

We also developed a composite record of biomass burning and fire occurrence at the scale of our entire study area (ca. 900 km^2) by modeling CHAR at individual lakes as a zero-inflated log-normal process ("ZIL method"), following Kelly et al. (2013). To account for systematic differences in CHAR among individual sites, non-zero accumulation rates were log-transformed, rescaled within each site to a z-score (mean = 0, standard deviation = 1), and then returned to their original domain through exponentiation. We estimated the parameters of ZIL distributions centered on continuous windows using a Gaussian kernel-weighted smoothing function with 5-yr and 50-yr windows. The index of biomass burning at each time step was the mean of 1000 bootstrapped mean parameter estimates, and we derived 90% confidence intervals from the 5th and 95th percentiles of the simulations. The resultant values are a unitless index representing landscape-scale biomass burning. In the Yukon Flats boreal forest region (ca. 450 km NE of our study area) such a composite record based on 12 lake-sediment records was well correlated with modern observed area burned at distances within $\approx$ 10 km of sampled lakes, with maximum agreement within 5 km (Kelly et al. 2013).

Tree demography records

We compared composite records of fire history to stand-age reconstructions spanning the past 365 yr based on tree-ring records collected near our lake-sediment sites. We used pith dates from 1139 ground-level tree cross sections collected in 55 different plots in 2002 and 2003 (Duffy 2006), and 66 tree cores from three plots collected during the 2015 field campaign (Fig. 1). Tree-ring data from the cross sections were not cross dated, while those from the tree cores were cross-dated; nonetheless, we present tree ages from both datasets together, in 5-yr bins (from 1550 to 2015). In both datasets, tree cores or cross sections were collected from as close to the ground as possible, typically between 10 and 50 cm.

Climate records

To evaluate fire–climate relationships, we compared our fire-history records to empirical and modeled climate data. Our empirical dataset is a composite reconstruction of annual growing-season air temperature for the past 1200 yr, based on living and subfossil mountain hemlock tree-ring widths collected near the Gulf of Alaska (hereafter, "GOA") (Wiles et al. 2014). We selected this dataset because it is an annually resolved temperature record spanning the entirety of our fire-history records. We standardized the original dataset from Wiles et al. (2014) to anomalies relative to the GOA twentieth century values, to facilitate comparison with other proxies. Because of relatively frequent stand-replacing disturbances in interior Alaska, annually resolved tree-ring climate records are not available in closer proximity to our sites, and other proxies (e.g., midges or oxygen isotopes from lake sediments) do not provide appropriately fine temporal resolution for this analysis.

We used an additional modeled temperature dataset for the twentieth century from the Climate Research Unit (Harris et al. 2014), which was statistically downscaled to 2-km resolution and made publicly available by the Scenarios Network for Alaska and Arctic Planning (SNAP 2015). We relied on these data for the twentieth century because they are from downscaled units that encompass our study area, and are annually resolved. These data are rigorously validated for accuracy in interior Alaska, but are subject to the potential biases of their modeling and downscaling approaches. Here we present the 5-yr anomaly of mean April-September temperatures, averaged over all 4 km^2 pixels overlapping all of our sample lakes. This is a generous definition of months that could influence annual plant growth and fire activity; our interpretations were also robust to running this analysis using mean June–August temperature.

Evaluating fire–climate–vegetation relationships

To test our hypotheses about the relationships among fire, climate, and vegetation, we correlated fire history metrics with summer temperature metrics. All sources of temperature data were summarized into 5-yr mean values for continuous, non-overlapping time steps corresponding to interpolated fire history data. We calculated pairwise Pearson product-moment correlation coefficients for comparisons between biomass burning, percent of sites burned, and temperature anomalies from the GOA for the period 1550–1895, and among biomass burning, percent of sites burned, and modeled temperature and precipitation records between 1900 and 2005. We also relied on qualitative comparisons among proxies. Compositing individual proxies into broad-scale records and binning them into common temporal increments allowed for direct comparison among series.

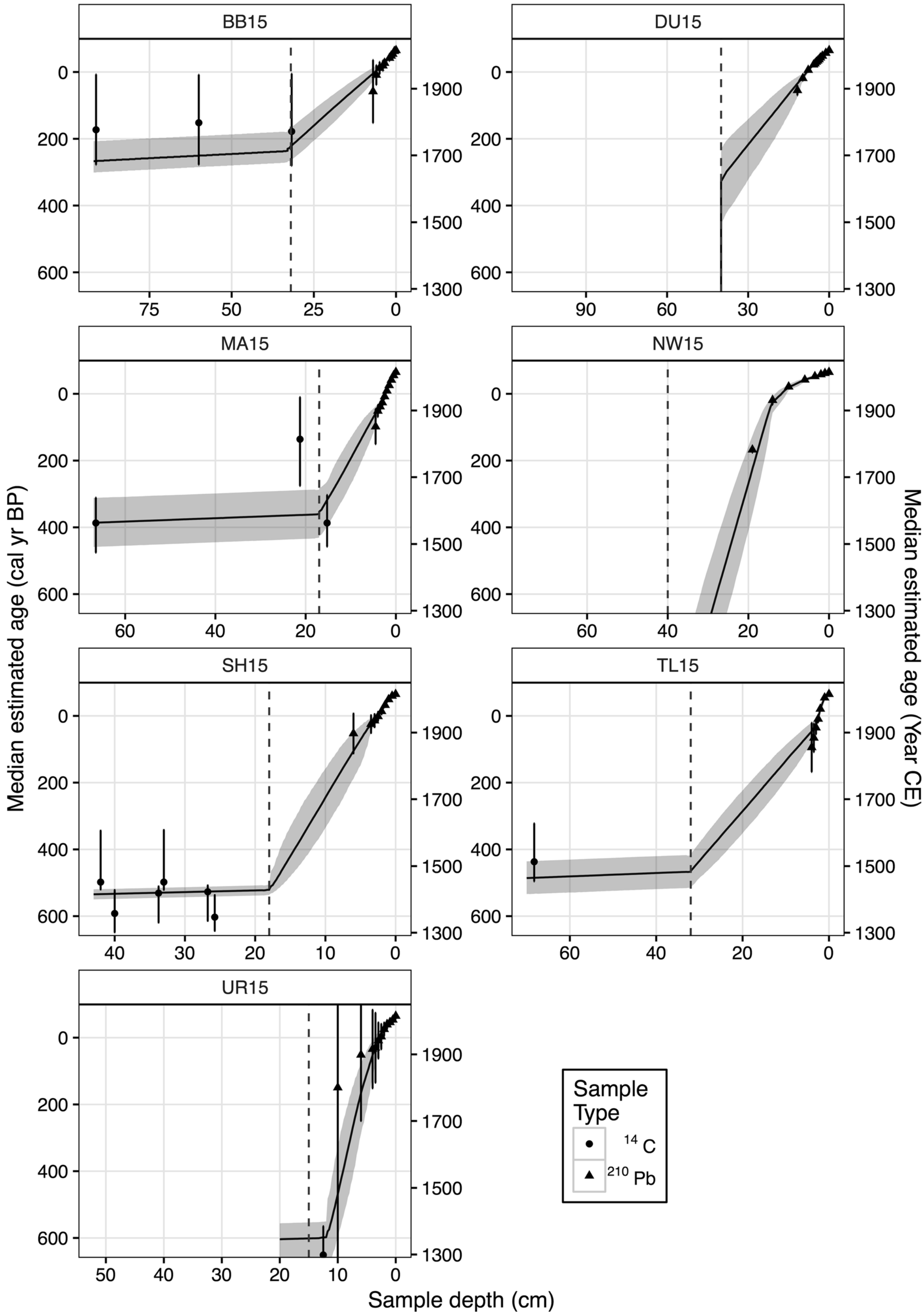
Results

Chronological control

Background ^{210}Pb activity was reached in the upper 3–10 cm of sediment in all cores, except for NW15 (where above-background decay was still sufficient to estimate sample ages). Radiocarbon ages of bulk sediments were generally thousands of years older than ages of terrestrial macrofossils or concentrated charcoal, suggesting the incorporation of "ancient" carbon into the lake sediments; thus, these samples were not used in our age-depth models (Fig. 2). Complex down-core sedimentation prevented us from developing robust chronologies for the entire length of sediment collected, but high-resolution records were obtained from the upper 15–40 cm of sediment. Multiple sources of evidence, including ^{14}C dates, changes in sedimentology and magnetic susceptibility (MS), and abrupt changes in charcoal concentration allowed us to identify rapid transitions in sedimentation rates, and model them with separate sediment accumulation parameters above and below the transition (Online Resource 1, Figs. 1–7). The median sample resolution of our records ranged from 2 to 15 yr $sample^{-1}$, yielding seven high-resolution records spanning the last 290–465 yr, after interpolation (Table 2). Uncertainty around age estimates (i.e., range of 90% confidence intervals) ranged from 4 yr in the upper portion of cores to 292 yr for some ages near 1550. The median age uncertainty among interpreted samples from all cores was 95 yr. We interpreted records from 1550 to 2015, the longest period covered by a majority of the records, and when chronological uncertainty was low (Fig. 3).

Fire history

Charcoal concentrations and charcoal accumulation rates (CHAR) from 1550 to 2015 ranged (mean, standard deviation) from 0 to 41.67 pieces cm^{-3} (2.40,


BB15
DU15
MA15
NW15
SH15
TL15
UR15
Median estimated age (cal yr BP)
Median estimated age (Year CE)
Sample depth (cm)
Sample Type
14 C
210 Pb

◀**Fig. 2** Age-depth models with uncertainty for lake-sediment records (black line, grey band) based on: age and standard error estimates from ^{210}Pb-based models (triangles), and calibrated ^{14}C-dated terrestrial macrofossils and concentrated charcoal (circles). Vertical dashed lines indicate the transition to near-instantaneous sedimentation (from top to bottom), as described in the text. Note: BB15, DU15, and NW15 are constrained by dates outside the (universal) plotting window; see Online Appendix for complete models alongside core images

4.54), and 0 to 3.82 pieces cm^{-2} yr^{-1} (0.11, 0.27) among all lakes, respectively (Fig. 3). The mean (range) signal-to-noise index for the period of analysis in all seven records was 9.8 (3.3–14.2), all above the threshold of 3 that indicates suitability for peak analysis (Kelly et al. 2011). Peak analysis revealed 1–6 statistically significant CHAR peaks at each site since 1550, and the most recent peak in each record generally corresponded to the most recent fire recorded in the observational dataset within 1 km of the lake. The difference between charcoal-estimated and observed fire years was less than 10 yr in 5 of 6 lakes where fires occurred, and the median (range) difference was 7 (3–19) yr (Fig. 3, grey circles vs. red diamonds). The results of peak analysis were also generally robust to variations in the threshold for peak analysis, among values between the 95th to 99.9th percentile (Fig. 3, small grey dots vs. larger grey circles).

Individual FRI ranged from 25 to 195 yr among sites (Fig. 4b). Site-specific mean FRI (SD) ranged from 50 to 130 yr (25–85; Table 3), and the mean FRI when pooling from all sites was 90 yr (60). The percentage of sites burned in a 50-yr period varied considerably over the record, ranging from 0–100% with maxima centered ca. 1665, 1710, 1800, 1855, 1985 and 1990. Periods with a very low or very high percent sites burned were short-lived, rarely lasting more than one window-width (i.e., 50 yr). The highest percentage of sites burned since 1550, 100%, was in the most recent 50-yr period (i.e., 1965–2015).

Our composite biomass burning record displayed significant variability (exceeding 95% confidence envelope) since 1550, with broad maxima in the 100-yr mean ca. 1600–1650, 1750–1900 and 1990–2015, and discrete peaks in the 5-yr mean (> 90th percentile) centered ca. 1555, 1620, 1640, 1645, 1765, 1845, 1850, and 2000–2010. The mean

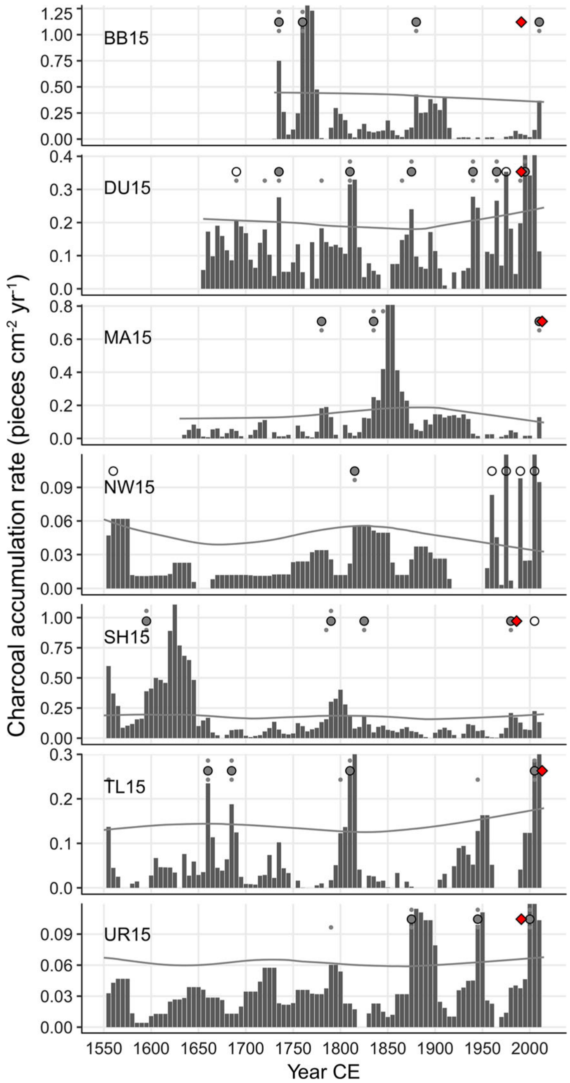


Fig. 3 Charcoal record and inferred fire history from each lake. Five-yr interpolated charcoal accumulation rates (CHAR, black bars), and thresholds (grey line) used to identify significant (filled circles) and insignificant (open circles) CHAR peaks, as well as peaks exceeding higher (99.9th percentile) and lower (95th percentile) noise distribution thresholds (small points), and fires from the observed record (1940–2014) that occurred within 1 km of a given lake (red diamonds). (Color figure online)

(standard deviation) time interval between these maxima in the 5-yr mean was 50 (55) yr.

Tree demography

Estimated pith ages from sampled trees ranged from 1650 to 1996, and included five species (number, %

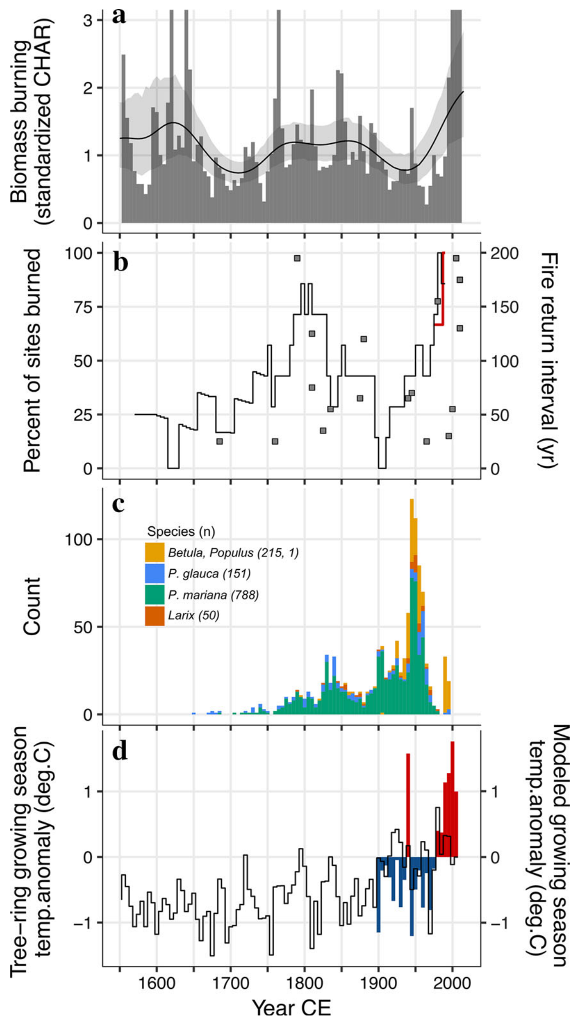


Fig. 4 Comparison of composite fire history, tree demography and climate reconstructions. **a** 5-yr mean of composite biomass burning (standardized CHAR, grey bars), 50-yr mean and bootstrapped 90% confidence interval (black curve and grey band); **b** fire return intervals (yr, squares) at the year they were observed, percent of sites burned in overlapping 50-yr windows (black stepped line); percent of sites burned in the past 50 yr based on the observed record from 1940 to present (red line); **c** count of trees per genus with estimated tree pith date (colored bars); and **d** tree-ring-based growing season temperature anomaly from the Gulf of Alaska (black stepped line, Wiles et al. 2014), and downscaled modeled April-September mean air temperature anomalies (red and blue bars, SNAP 2015). (Color figure online)

of total): *Picea mariana* (788, 65%), *Picea glauca* (151, 13%), *Larix laricina* (50, 4%), *Betula papyrifera* (215, 18%), and *Populus tremuloides* (1, 0.1%). Over 65% of the trees sampled had pith dates between 1900 and 1975. The combined age structure contains seven relatively distinct modes, which we interpret as pulses of tree establishment, ca. 1650, 1720, 1800, 1840, 1900, 1950, and 1990 (Fig. 4c). The average (standard deviation) interval between these modes was 55 yr (15 yr). We interpret pulses in establishment from this tree-demography record cautiously, assuming tree mortality limits our ability to directly compare the magnitude of distinct pulses deeper into the past, particularly prior to ca. 1800, due to a fading record.

Fire–climate–vegetation relationships

Relationships among fire, climate, and vegetation proxies varied through time, with a clear distinction in the strength and direction of the fire–climate relationship before and after 1900. Fire activity and temperature were uncorrelated before 1900 (Table 4, Fig. 5a). Strong positive relationships after 1900 were detected between modeled ("CRU") growing season (AMJJAS) temperature and 50-yr mean composite biomass burning ($r = 0.71$, $p = 0.05$; Table 4 and Fig. 5).

In addition to significant correlations between measures of fire activity and summer temperature during the twentieth century, there were clear qualitative relationships among fire, climate, and vegetation proxies throughout the record. Periods of high fire activity, reflected in 50-yr mean composite biomass burning and high percent sites burned, generally preceded pulses in tree establishment (Fig. 4a, c): for example, all of the trees in our record established after the earliest detected peak in biomass burning ca. 1650, and subsequent pulses in tree establishment occurred after the periods of elevated fire activity ca. 1800 and 1850. Conversely, periods of lower fire activity ca. 1675–1725 and 1900–1950 correspond with pulses in tree establishment.

Discussion

Our 465-yr landscape-scale records of fire activity, tree establishment, and temperature document high variability in the relationship between climate and fire over time. The dynamic nature of fire–climate relationships suggests that fire activity was likely mediated by landscape-scale changes in flammability resulting from forest succession and the dominance of black spruce. Our records showed stronger coupling

Table 3 Summary of peak analysis results

Site	Record length (yr)	Total fires recorded	Mean fire return interval (SD) (yr)	Fire frequency (# 100-yr^{-1})
BB15	285	4	90 (60)	1.4
DU15	360	6	50 (25)	1.67
MA15	385	3	115 (85)	0.78
NW15	465	1	–	0.22
SH15	465	4	130 (85)	0.87
TL15	465	4	115 (85)	0.87
UR15	465	3	65 (10)	0.65

Table 4 Pearson product-moment correlation coefficients (r) among proxies, and their significance

Period	50-yr mean CHAR	5-yr mean CHAR	Percent of sites burned
1550–1895			
GOA temp.	0.09	0.06	0.15
1900–2010			
CRU temp.	***0.71***	**0.52**	0.33
GOA temp.	0.14	− 0.02	0.19

Bold-italicized values are significant at α = 0.01, bold values are significant at α = 0.10

CRU temp. downscaled, modeled growing season temperature (°C), *GOA temp.* tree-ring based growing season temperature (°C)

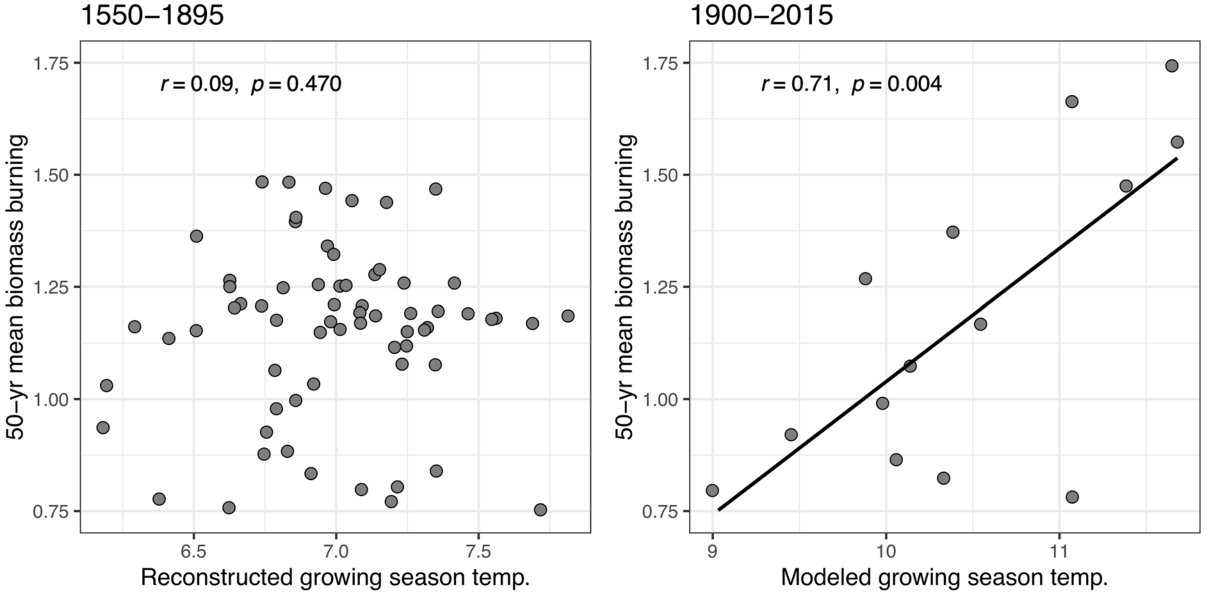


Fig. 5 Relationships between biomass burning and 5-yr mean growing season and modeled summer temperature from 1550 to 1895 (left) and from 1900 to 2015 (right), respectively. Linear fit (black line) indicates significant relationship for linear model from 1900 to 2015

between fire activity and temperature after ca. 1900 than in the preceding 350 yr, with tightly linked increases in biomass burning and temperatures during the second half of the twentieth century, and elevated fire activity following pulses of black spruce establishment.

Variable fire–climate relationships were mediated by black spruce succession

Our records show high variability in direct coupling between climate and fire activity throughout the study period, with the relationship between high rates of burning and warm temperatures strongest after 1900. The period of elevated fire frequency ca. 1800 coincided with a positive temperature anomaly, consistent with the expectation that warm temperatures facilitate burning through low fuel moisture (Duffy et al. 2005; Flannigan et al. 2009; Parisien et al. 2011), but the link between climate and fire activity was variable (e.g., temperatures were cooler than average during a peak in biomass burning ca. 1760) and statistically insignificant. The lack of correlation between the paleoclimate record and our composite record of biomass burning does not necessarily imply that individual years with high fire activity were not facilitated by warm, dry conditions at inter-annual or biome-wide scales (Duffy et al. 2005; Hu et al. 2006; Mann et al. 2012). By averaging the paleoclimate record over 5-yr periods to align with interpolated lake-sediment fire history records, we inherently smooth over inter-annual variability, thus reducing the ability to detect annual-scale relationships. Additionally, a lack of correlation between climate and fire proxies prior to the twentieth century may reflect limited chronological control in our fire-history records, and/or limitations of using the GOA temperature reconstruction as a proxy for fire-conducive conditions. While ^{210}Pb chronologies constrain our records over the twentieth century, and back to c. 1850 CE, ^{14}C dating prior c. 1850 is more limited. Perhaps equally plausible, the GOA tree-ring reconstruction may reflect climate conditions outside of the summer fire season, or it may not accurately reflect growing-season climate variability in the Nowitna study area. The latter possibility is supported by the poor correlation between the GOA temperature proxy and the CRU data over the twentieth century. Finally, the significant correlation between biomass burning and CRU-inferred temperature over the twentieth century is strongly driven by the 5–7 warmest values in the CRU dataset, most occurring in the last two decades, when CHAR-inferred biomass burning is also consistently high. While the GOA temperature record also registers the warmest values in the twentieth century, the temporal variability differs from the GOA record, and the range of variability is smaller than in the CRU dataset.

The strongest evidence for direct coupling between climate and fire activity comes after 1900, when both fire activity and summer temperatures increased distinctly, and were significantly positively correlated. The significant increases in biomass burning and percent of sites burned that began ca. 1900 coincides with an increase in local modeled temperatures, which were above average for much of the late twentieth century, particularly after 1975. Biomass burning and percent sites burned both reached their highest points in our 465-yr record in the decades since 1980, consistent with other evidence of recent increases in fire activity from modern observational records (Kasischke and Turetsky 2006; Kasischke et al. 2010).

The widespread burning we observed under average and above-average temperatures was likely mediated by the landscape-scale dominance of mature black spruce during the twentieth century. Even after 1900, when the fire–climate relationship in our study area was strongest, alternating periods of fire activity and tree establishment suggest that variability in landscape-scale fire activity was driven by complex interactions with climate and vegetation, rather than unidirectional forcing by either independently. Periods of elevated biomass burning and a high percentage of sites burned were preceded by several decades of tree establishment, and establishment was conversely highest during periods of low fire activity (Fig. 4). At this multi-decadal, landscape scale, our results are consistent with findings from the eastern Canadian boreal forest, where mid- to late-Holocene fire activity was facilitated and attenuated by variability in fire-conducive climatic conditions as well as the landscape-scale continuity of flammable vegetation (Girardin et al. 2013; Héon et al. 2014). The substantial increase in fire activity since 1950 documented in our records was likely facilitated by the preceding decades of black spruce establishment ca. 1900–1960. Concurrent with a warming trend, by the late twentieth century, this would have resulted in warmer-than-average conditions on a landscape dominated by 30–90 yr old black spruce, creating highly flammable fuels suitable for widespread burning. Similarly, the period of high fire activity ca. 1800 may have initiated the pulse of recruitment that began later in the century and continued into the twentieth century. The late twentieth and early twenty-first century increase in fire activity in this study area was, therefore, probably a result of vegetation dynamics and warming summer temperatures operating synergistically to create a landscape of continuous, flammable fuels under suitable climatic conditions.

The changes in fire activity we observed after 1900 may point toward the nature of future fire regimes in Alaskan boreal forests. The peak in fire activity ca. 1800 was characterized by a percentage of sites burned similar to the peak in fire activity after 1980 (i.e., 80% ca. 1800 vs. 100% after 1980), but with significantly lower biomass burned in 1800 than in 1980. Greater biomass burning per fire event after 1980 could indicate an increase in fire severity under warmer twentieth- and early twenty-first-century conditions, a pattern documented elsewhere in the boreal forest in recent decades (Shenoy et al. 2011; Mann et al. 2012) and during the warm Medieval Climate Anomaly ca. 1000–1500 (Kelly et al. 2013). This empirical and model-based evidence from across the boreal forest documents similar patterns: the combination of widespread late-successional black spruce dominance and consistently warm temperatures in recent decades have resulted in unusually high fire frequency and severity (Mann et al. 2012), with subsequent feedbacks to successional trajectories and species composition (Johnstone and Chapin 2006; Johnstone et al. 2010b; Shenoy et al. 2011; Brown and Johnstone 2012).

Negative vegetation feedbacks could limit widespread increases in fire activity

If coincident warming and increases in fire activity like those observed in our study landscape and elsewhere in the Alaskan boreal forest in recent decades continue into the twenty-first century, such changes could initiate an ecosystem-wide transition from black-spruce-dominated to deciduous-dominated forests (Johnstone et al. 2010b; Mann et al. 2012; Kelly et al. 2013). Alternatively, the connections we observed between the timing of widespread fire activity and landscape-scale spruce establishment are also consistent with modern and paleoecological observations of negative feedbacks between fire activity and post-fire vegetation change. Periods of elevated landscape-scale fire activity reset successional trajectories, initiating a temporary shift in the dominant vegetation type at the landscape scale from coniferous to deciduous species. Because boreal forest species vary widely in their flammability, their relative proportions and arrangement on the landscape modify the subsequent influence of weather on fire occurrence and spread (Dash et al. 2016). Recently burned landscapes may thus be less supportive of fire activity (Parks et al. 2015, 2016), limiting the extent and magnitude of fire activity for decades to centuries (Ali et al. 2009; Girardin et al. 2013; Héon et al. 2014). The wide range and rapid swings in the percent of sites burned documented by our record support the idea that prolonged increases in fire activity at the landscape scale cannot be supported by vegetation for prolonged periods (Fig. 4b).

Although a broad shift in the dominant forest type in Alaska from black spruce to deciduous species would reduce fire activity in the near term (decades to centuries), it could promote synchronous fire activity in the future, if large areas of deciduous-dominated stands follow similar successional trajectories and return to black spruce dominance simultaneously. These diverging potential trajectories reveal the complex interaction among mechanisms that drive fire activity, and their varying importance across scales (Turner et al. 1989). Our findings indicate that landscape-scale fire–climate relationships are strongly mediated by forest succession and vegetation patterns. Our study does not predict how fire-vegetation feedbacks scale to the larger boreal forest, which has yet to exhibit a biome-scale fuel limitation. However, it supports the notion that forested landscapes are a dynamic mosaic of vegetation states, with components that do not respond uniformly to climatic forcing, and underscores the importance of understanding variation in landscape flammability and connectivity of fire-prone vegetation for anticipating the trajectory of landscape-scale fire activity. As fire-conducive climatic conditions become more common in Alaska (Young et al. 2017), it will be increasingly important to monitor vegetation change across the boreal forest biome and continue to evaluate subsequent feedbacks on fire activity.

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References

Ali AA, Carcaillet C, Bergeron Y (2009) Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. Glob Change Biol 15:1230–1241

Balshi MS, McGuire AD, Duffy P, Flannigan M, Walsh J, Melillo J (2009) Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. Glob Change Biol 15:578–600

Barrett K, McGuire AD, Hoy EE, Kasischke ES (2011) Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. Ecol Appl 21:2380–2396

Binford MW (1990) Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores. J Paleolimnol 3:253–267

Blaauw M, Christen JA (2011) Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal 6:457–474

Boggs K, Flagstad T, Boucher T, Kuo T, Fehringer D, Guyer S, Aisu M (2016) Vegetation map and classification: Northern, western and interior Alaska, 2nd edn. Anchorage, AK

Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. Nature 359:716–718

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89

Brown CD, Johnstone JF (2012) Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. For Ecol Manage 266:34–41

Calder WJ, Parker D, Stopka CJ, Jiménez-Moreno G, Shuman BN (2015) Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. Proc Natl Acad Sci USA 112:13261–13266

Chapin FS, Callaghan TV, Bergeron Y, Fukuda M, Johnstone JF, Juday G, Zimov SA (2004) Global change and the boreal forest: thresholds, shifting states or gradual change? Ambio 33:361–365

Chapin FS, McGuire AD, Randerson J, Pielke R, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kasischke E, Rastetter EB, Zimov SA, Running SW (2000) Arctic and boreal ecosystems of western North America as components of the climate system. Glob Change Biol 6:211–223

Clark JS, Royall PD (1996) Local and regional sediment charcoal evidence for fire regimes in presettlement northeastern North America. J Ecol 84:365

Dash CB, Fraterrigo JM, Hu FS (2016) Land cover influences boreal-forest fire responses to climate change: geospatial analysis of historical records from Alaska. Landscape Ecol 31:1781–1793

Duffy PA (2006) Interactions among climate, fire, and vegetation in the Alaskan boreal forest. PhD Dissertation, Department of Forest Sciences, University of Alaska, Fairbanks

Duffy PA, Walsh JE, Graham JM, Mann DH, Rupp TS (2005) Imapcts of large-scale atmospheric–ocean variability on Alaskan fire season severity. Ecol Appl 15:1317–1330

Flannigan M, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob Change Biol 15:549–560

Gavin DG, Brubaker LB, Lertzman KP (2003) An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. Can J For Res 33:573–586

Genet H, McGuire AD, Barrett K, Breen A, Euskirchen ES, Johnstone JF, Kasischke ES, Melvin AM, Bennett A, Mack MC, Rupp TS, Schuur AEG, Turetsky MR, Yuan F (2013) Modeling the effects of fire severity and climate warming on active layer thickness and soil carbon storage of black spruce forests across the landscape in interior Alaska. Environ Res Lett 8:045016

Girardin MP, Ali AA, Carcaillet C, Blarquez O, Hély C, Terrier A, Genries A, Bergeron Y (2013) Vegetation limits the impact of a warm climate on boreal wildfires. New Phytol 199:1001–1011

Harris I, Jones PD, Osborn TJ, Lister DH (2014) Updated high-resolution grids of monthly climatic observations—the CRU TS3.10 Dataset. Int J Climatol 34:623–642

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci USA 111:13888–13893

Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA (2009) Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecol Monogr 79:201–219

Higuera PE, Gavin DG, Bartlein PJ, Hallett DJ (2010) Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. Int J Wildland Fire 19:996–1014

Higuera PE, Peters ME, Brubaker LB, Gavin DG (2007) Understanding the origin and analysis of sediment-charcoal records with a simulation model. Quatern Sci Rev 26:1790–1809

Higuera PE, Whitlock C, Gage JA (2011) Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. Holocene 21:327–341

Hu FS, Brubaker LB, Gavin DG, Higuera PE, Lynch JA, Rupp TS, Tinner W (2006) How climate and vegetation influence the fire regime of the Alaskan boreal biome: the Holocene perspective. Mitig Adapt Strat Glob Change 11:829–846

Johnson EA (1992) Fire and vegetation dynamics: studies from the North American boreal forest. Cambridge University Press, Cambridge

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GLW, Schoennagel T, Turner MG (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14:369–378

Johnstone JF, Chapin FS (2006) Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems 9:268–277

Johnstone JF, Chapin FS, Hollingsworth TN, Mack MC, Romanovsky V, Turetsky MR (2010a) Fire, climate change, and forest resilience in interior Alaska. Can J For Res 40:1302–1312

Johnstone JF, Hollingsworth TN, Chapin FS, Mack MC (2010b) Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Glob Change Biol 16:1281–1295

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33:L09703

Kasischke ES, Verbyla DL, Rupp TS, McGuire AD, Murphy KA, Jandt R, Barnes JL, Hoy EE, Duffy PA, Calef M, Turetsky MR (2010) Alaska's changing fire regime—implications for the vulnerability of its boreal forests. Can J For Res 40:1313–1324

Kasischke ES, Williams D, Barry D (2002) Analysis of the patterns of large fires in the boreal forest region of Alaska. Int J Wildland Fire 11:131–144

Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proc Natl Acad Sci USA 110:13055–13060

Kelly RF, Higuera PE, Barrett CM, Hu FS (2011) A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quatern Res 75:11–17

Krawchuk MA, Moritz MA (2011) Constraints on global fire activity vary across a resource gradient. Ecology 92:121–132

Long CJ, Whitlock C, Bartlein PJ, Millspaugh SH (1998) A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. Can J For Res 28:774–787

Lynch JA, Clark JS, Bigelow NH, Edwards ME, Finney BP (2002) Geographic and temporal variations in fire history in boreal ecosystems of Alaska. J Geophys Res 108:1–17

Lynch JA, Clark JS, Stocks BJ (2004a) Charcoal production, dispersal, and deposition from the Fort Providence experimental fire: interpreting fire regimes from charcoal records in boreal forests. Can J For Res 34:1642–1656

Lynch JA, Hollis JL, Hu FS (2004b) Climatic and landscape controls of the boreal forest fire regime: Holocene records from Alaska. J Ecol 92:477–489

Macias Fauria M, Johnson EA (2008) Climate and wildfires in the North American boreal forest. Philos Trans R Soc B 363:2315–2327

Mann DH, Scott Rupp T, Olson MA, Duffy PA (2012) Is Alaska's boreal forest now crossing a major ecological threshold? Arct Antarct Alp Res 44:319–331

Nowacki GJ, Spencer P, Fleming M, Brock T, Jorgenson T (2003) Unified Ecoregions of Alaska, 2001. Unified ecoregions of Alaska and Neighboring Territories, U.S. Geological Survey Map

Parisien MA, Parks SA, Krawchuk MA, Flannigan MD, Bowman LM, Moritz MA (2011) Scale-dependent controls on the area burned in the boreal forest of Canada, 1980–2005. Ecol Appl 21:789–805

Parks SA, Holsinger LM, Miller C, Nelson CR (2015) Wildland fire as a self-regulating mechanism: the role of previous burns and weather in limiting fire progression. Ecol Appl 25:1478–1492

Parks SA, Miller C, Holsinger LM, Baggett LS, Bird BJ (2016) Wildland fire limits subsequent fire occurrence. Int J Wildland Fire 25:182–190

Pausas JG, Ribeiro E (2013) The global fire–productivity relationship. Glob Ecol Biogeogr 22:728–736

Payette S (1992) Fire as a controlling process in the North American boreal forest. In: Shugart HH, Leemans R, Bonan GB (eds) A systems analysis of the global boreal forest. Cambridge University Press, Cambridge, pp 144–169

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Randerson JT, Liu H, Flanner MG, Chambers SD, Jin Y, Hess PG, Pfister G, Mack MC, Treseder KK, Welp LR, Chapin FS, Harden JW, Goulden ML, Lyons E, Neff JC, Schuur EAG, Zender CS (2006) The impact of boreal forest fire on climate warming. Science 314:1130–1132

Shenoy A, Johnstone JF, Kasischke ES, Kielland K (2011) Persistent effects of fire severity on early successional forests in interior Alaska. For Ecol Manage 261:381–390

SNAP: Scenarios Network for Alaska and Arctic Planning, University of Alaska (2015) Historical Monthly and Derived Temperature Products Downscaled from CRU TS data via the delta method - 2 km. http://data.snap.uaf.edu/data/Base/AK_CAN_2km/historical/CRU_TS/Historical_Monthly_and_Derived_Temperature_Products_2km_CRU_TS/. Accessed Jan 2016

Turner MG, Dale VH, Gardner RH (1989) Predicting across scales: theory development and testing. Landscape Ecol 3:245–252

Whitlock C, Higuera PE, McWethy DB, Briles CE (2010) Paleoecological perspective on fire ecology: revisiting the fire regime concept. Open Ecol J 3:6–23

Wiles GC, D'Arrigo RD, Barclay D, Wilson RS, Jarvis SK, Vargo L, Frank D (2014) Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. Holocene 24:198–208

Young AM, Higuera PE, Duffy PA, Hu FS (2017) Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography 40:606–617