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Arctic and boreal paleofire records reveal drivers of fire activity and departures from Holocene variability

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Abstract. Boreal forest and tundra biomes are key components of the Earth system because the mobilization of large carbon stocks and changes in energy balance could act as positive feedbacks to ongoing climate change. In Alaska, wildfire is a primary driver of ecosystem structure and function, and a key mechanism coupling high-latitude ecosystems to global climate. Paleoecological records reveal sensitivity of fire regimes to climatic and vegetation change over centennial–millennial time scales, highlighting increased burning concurrent with warming or elevated landscape flammability. To quantify spatiotemporal patterns in fire-regime variability, we synthesized 27 published sediment-charcoal records from four Alaskan ecoregions, and compared patterns to paleoclimate and paleovegetation records. Biomass burning and fire frequency increased significantly in boreal forest ecoregions with the expansion of black spruce, ca. 6,000–4,000 years before present (yr BP). Biomass burning also increased during warm periods, particularly in the Yukon Flats ecoregion from ca. 1,000 to 500 yr BP. Increases in biomass burning concurrent with constant fire return intervals suggest increases in average fire severity (i.e., more biomass burning per fire) during warm periods. Results also indicate increases in biomass burning over the last century across much of Alaska that exceed Holocene maxima, providing important context for ongoing change. Our analysis documents the sensitivity of fire activity to broad-scale environmental change, including climate warming and biome-scale shifts in vegetation. The lack of widespread, prolonged fire synchrony suggests regional heterogeneity limited simultaneous fire-regime change across our study areas during the Holocene. This finding implies broad-scale resilience of the boreal forest to extensive fire activity, but does not preclude novel responses to 21st-century changes. If projected increases in fire activity over the 21st century are realized, they would be unprecedented in the context of the last 8,000 yr or more.

Key words: boreal forest; climate change; fire; Holocene; lake-sediment charcoal; paleoecology; paleofire.

Introduction

Boreal forest and tundra regions are experiencing rapid environmental change, driven by the amplified effects of increasing atmospheric CO_2 concentrations on high-latitude ecosystems (Chapin et al. 2000, Hinzman et al. 2005, Miller et al. 2010). Disturbance by fire couples terrestrial and climate systems, and can serve as a positive feedback to climate warming by accelerating the movement of carbon stocks into the atmosphere and altering radiative balance through changes in albedo and energy partitioning (Randerson et al. 2006, Bond-Lamberty et al. 2007, Bonan 2008, Bowman et al. 2009). In addition to the significant feedbacks between fire and the climate system, fire has the potential to catalyze abrupt change in the material and informational legacies that have promoted the landscape-scale resilience of boreal ecosystems to repeated disturbance and climate variability for at least six millennia (Lynch et al. 2004, Hu et al. 2006, Higuera et al. 2009, Johnstone et al. 2016). Increases in the annual extent and severity of fire in the boreal forest (Kasischke and Turetsky 2006, Kasischke et al. 2010) and the recent occurrence of large, rare fire events in the Alaskan tundra (Hu et al. 2010, Chipman et al. 2015) have raised questions about the capacity for fire to initiate widespread ecosystem state change and impact the trajectory of

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[Correction added on June 11, 2020, after first online publication: An earlier version of Fig. 2 was incorrectly posted in the published article and has since been fixed. We apologize to the authors for this error.]

ecosystem properties (Johnstone et al. 2010*a*, *b*, Barrett et al. 2011, Grosse et al. 2011, Mack et al. 2011, Turetsky et al. 2011, Brown and Johnstone 2012, Genet et al. 2013). For example, increased fire frequency and severity, and subsequently reduced organic-layer thickness, may initiate postfire shifts in species composition and promote permafrost thaw with important consequences for radiative balance and the potential mobilization of large soil-carbon stocks (Barrett et al. 2011, O'Donnell et al. 2011, Shenoy et al. 2011, Pastick et al. 2014, Hoy et al. 2016). The potential for fire to catalyze abrupt environmental change in boreal forest and tundra systems, with cascading feedbacks to global climate, motivates the need to quantify the sensitivity of fire regimes to climate forcing of the past, and the precedence of synchronous fire-regime change across ecoregions.

Because of the temporally infrequent and spatially complex nature of fire and its effects, inferences about the causes and consequences of disturbance are scale-dependent (Johnstone et al. 2010*a*, Turner 2010). Reducing uncertainty around the sensitivity of fire activity to climate change, its future trajectory, and the impact of changing disturbance regimes on the properties and function of high-latitude ecosystems requires approaches that are appropriately broad in their spatial and temporal scope (Kasischke et al. 2002, 2010, Hu et al. 2015, Kelly et al. 2016). Paleoecological records are one way to provide broad-scale perspective, and a body of published records documents the relationships among climate, fire, and vegetation dynamics in boreal forest and tundra ecosystems over the Holocene (Hu et al. 2006, Whitlock et al. 2010, Marlon et al. 2013, 2015). These records point to the sensitivity of boreal forest and tundra fire regimes to climate variability, and the important role that vegetation plays in mediating the direct link between climate and fire (Lynch et al. 2002, 2004, Brubaker et al. 2009, Higuera et al., 2009, 2011*a*, *b*, Barrett et al. 2013, Kelly et al. 2013). For example, fire activity in Alaska increased markedly with the expansion of black spruce ca. 6,000–4,000 calibrated years before present (yr BP; Lynch et al. 2002, Higuera et al. 2009, Kelly et al. 2013). In the boreal forest of the Copper River Basin, biomass burning and summer temperature varied independently before ca. 3,000 yr BP, but were positively correlated over the past three millennia (Barrett et al. 2013). Recent work from the Yukon Flats region documents strong links between centennial-scale climate warming during the Medieval Climate Anomaly (MCA, ca. 1,000–500 yr BP) and subsequent cooling during the Little Ice Age (LIA, ca. 600–300 yr BP), and changes in biomass burning (Kelly et al. 2013). This work also identified potential negative feedbacks to burning after prolonged periods of elevated fire severity, whereby successional-scale vegetation changes eventually reduce landscape flammability, and subsequent fire frequency. Despite the importance of these findings for revealing region-specific fire–climate–vegetation dynamics, variability in fire-regime sensitivity to climate and the extent to which fire-regime change occurs synchronously among regions remains unclear.

Understanding variability in fire activity over space and time is critical for assessing modern ecosystem states and anticipating fire-regime response to 21st-century warming. For example, incorporating paleoecological data into modeling frameworks can change predictions of the boreal forest as a net sink for atmospheric carbon to a net source (Kelly et al. 2016). Furthermore, predictions of future fire activity based on changes in fire-conducive weather and reduced fuel moisture with climate warming indicate widespread increases in fire activity in the boreal forest and tundra (Balshi et al. 2009, Flannigan et al. 2009, 2017). Fire–climate modeling shows nearly universal increases in fire frequency under median climate change scenarios, but highlights spatial variability in fire-regime changes across Alaska, particularly in areas near climatic thresholds to burning (Young et al. 2017). Although the implications of widespread increases in fire activity for global climate and local ecosystems are significant, the magnitude of fire-regime sensitivity to climate warming during the Holocene remains uncertain, and the degree to which it occurred simultaneously across diverse Alaskan ecosystems is untested.

To identify the mechanisms that drive fire regimes at multiple scales, and quantify the degree of spatiotemporal synchrony in fire activity (i.e., fire synchrony), we characterized Holocene fire activity in a broad portion of flammable regions of Alaska by synthesizing previously published paleofire records from four ecoregions (Fig. 1). We define fire synchrony as fire activity occurring in the same time period (e.g., a century), and among sites within a single ecoregion, or among sites across multiple ecoregions. Using metrics of biomass burning and estimates of the timing of fire events, we investigated whether spatially broad forcing (e.g., climate change or biome shifts) promoted fire synchrony across ecoregions at centennial to millennial timescales, or if variations in vegetation, regional climate, or other local factors limited widespread, concurrent changes in fire activity. We applied a robust method for estimating rates of biomass burning at regional (10^{1-3} km^2) and multiregional (10^{4-6} km^2) scales using 27 existing lake-sediment charcoal records. To quantify fire synchrony among sites and regions, we estimate the proportion of four regions, individually and collectively, that were affected by fire each century, and quantify the uncertainty around this metric by incorporating the uncertainty inherent to radiometric dating of lake sediments. Synchronous changes in biomass burning and fire occurrence among regions would provide evidence that broad-scale climatic variability or biome-scale changes in vegetation can act as dominant mechanisms driving fire-regime shifts, and homogenize fire activity across Alaska. Conversely, independent variability in biomass burning and fire timing across regions would indicate the importance of landscape-scale variation in ecosystem properties, or spatial variability in climate, in controlling fire activity. Finally, limits to high

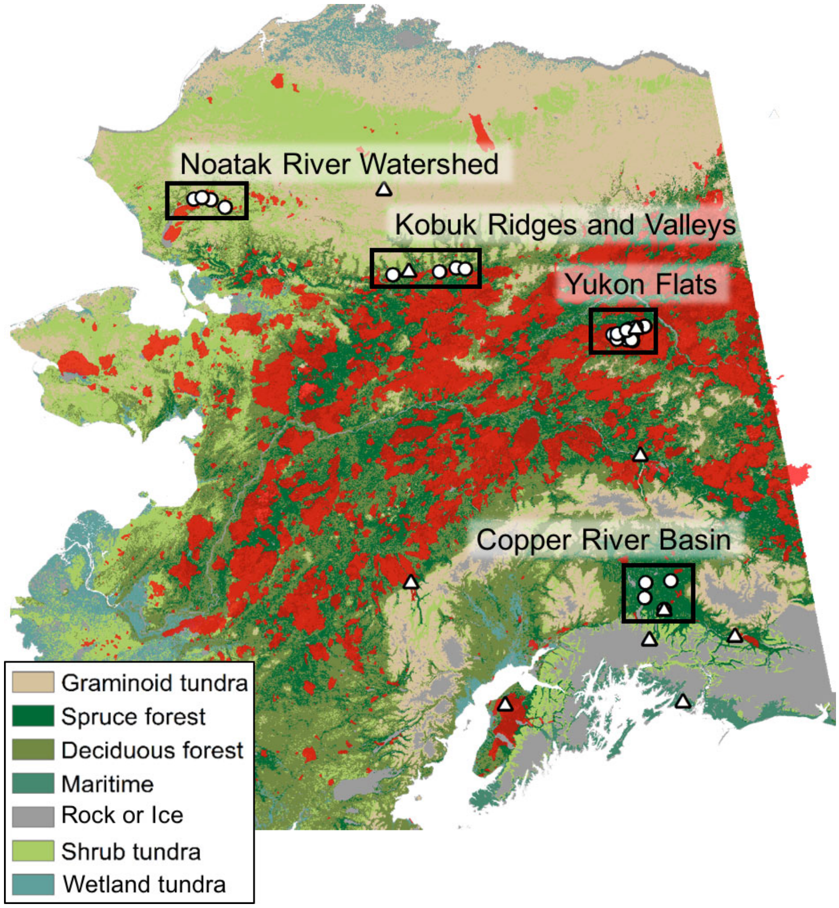


FIG. 1. Locations of paleofire and paleoclimate records used in this study. White circles are paleofire records, white triangles are paleoclimate records, and red areas are observed fire perimeters from 1950 to 2014. Labels identify four regions of study, and colors represent dominant vegetation type as described in the legend (simplified from 2012).

fire activity at multiregion scales could indicate that fire–vegetation interactions served as negative feedbacks to widespread, synchronous increases in fire activity during the Holocene.

DATA AND METHODS

Study area

We analyzed records from three boreal forest and one tundra ecoregion (Table 2, n = 27 for biomass burning metric, and n = 25 for fire events) that are all fire-prone systems, and represent a range of variation in climate, geomorphology, and vegetation (Nowacki et al. 2003, Gavin and Hu 2013). To quantify how landscape-scale variation in ecosystem properties mediates the impacts of broad-scale forcing on fire activity, our records span an order-of-magnitude range in modern fire rotation periods (60–1,100 yr; Table 1). We used records from the south-central Brooks Range in the Kobuk Ridges and Valleys ecoregion (Kobuk), the Copper River Basin ecoregion (Copper River), and the Yukon Flats area in the Yukon–Old Crow ecoregion (Yukon Flats), all considered part of the boreal forest biome. We also used records from the Noatak River Watershed (Noatak), located within the boundaries of the Kobuk Ridges and Valleys ecoregion. These study areas span a climatic and environmental gradient representing much of Alaska's fire-prone area (Table 1), from the tundra systems of the Noatak, which experience frequent fire relative to graminoid-tundra systems further north and east (Rocha et al. 2012), to boreal forest ecosystems that vary widely in contemporary flammability.

Paleoclimate

To evaluate potential relationships between fire activity and millennial-scale climatic change, we rely on a recent summary of paleoclimate in northwestern North America (Kaufman et al. 2016) spanning the entire Holocene, and a tree-ring–based air temperature reconstruction from 1,200 yr BP to present (Wiles et al. 2014). The composite temperature reconstructions from Kaufman et al. (2016) include midge-inferred July air

TABLE 1. Modern climate and fire regimes in each study region.

Region	January minimum (°C)	January maximum (°C)	July min. (°C)	July max. (°C)	Annual precipitation (mm)	Fire rotation period (yr)
Noatak	−26.9	−17.2	7.3	19.4	391	425†
Kobuk	−29.2	−20.3	9.4	20.7	361	163‡
Yukon Flats	−33.2	−23.8	10.7	22.9	167	82‡
Copper River	−25.7	−16.4	7.9	20.2	280	2,178‡

Notes: Temperatures are average January and July minimum and maximum values from the nearest meteorological station. Precipitation is the mean annual total. Fire rotation periods statistics are based on observed fire perimeter data from the Alaskan Interagency Coordination Center published by Young et al. (2017) and Rocha et al. (2012).
†Rocha et al. (2012).
‡Young et al. (2017).

temperature (Clegg et al. 2011, Irvine et al. 2012), pollen-inferred air temperature (Szeicz et al. 1995, Bunbury and Gajewski 2009, Viau and Gajewski 2009), and temperature anomalies from other proxies (McKay et al. 2008; Fig. 1). Together these reconstructions document significant spatiotemporal variability in climate throughout the Holocene, with most records documenting temperature variability of 1–2°C. Records showed general agreement in a mid-Holocene thermal maximum centered around 6,000 yr BP, with annual mean temperatures 0.2–0.5°C warmer than the most recent millennium. Temperature reconstructions had the greatest variability in the early Holocene, but generally document a warming trend through the mid-Holocene and a cooling trend after ca. 6,000 yr BP, in agreement with results from a global Holocene temperature reconstruction for 30–90° N latitude (Marcott et al. 2013). Because the 500-yr subcontinental resolution of this composite paleoclimate record is lower than that of our paleofire records, we interpret it cautiously and present it as the best available proxy for the average climatic conditions at any given time and location in our study. The composite effective moisture reconstruction published by Kaufman et al. (2016) includes a high diversity of proxy types that results in high uncertainty and limited temporal variability. Thus, although we compared the composite effective-moisture reconstruction to our fire proxies, we do not present these results in the main text. As a record of decadal- to centennial-scale climatic variability over the last 1,200 yr, we also call on a composite reconstruction of annual growing-season air temperatures based on living and subfossil tree-ring widths from the Gulf of Alaska (GOA; Wiles et al. 2014). The GOA record provides a climate proxy with substantially higher temporal resolution for the most recent millennium (i.e., annual vs. 500-yr resolution). In this late-Holocene period, paleoclimate reconstructions from tree-ring widths show strong spatiotemporal agreement in the magnitude of the Medieval Climate Anomaly and Little Ice Age, relatively warm and cool periods (+/−0.5°C) that occurred from ca. 1,000 to 500 yr BP and 600 to 300 yr BP, respectively (Wilson et al. 2016, Anchukaitis et al. 2017).

In the case of the composite temperature record from Kaufman et al. (2016), attributing changes in fire activity to climate variability is limited by the record's coarse spatiotemporal resolution. Although the GOA record improves resolution, it likely represents the climate at some of the paleofire record locations more accurately than others (e.g., in the Copper River Basin compared to the Noatak). However, understanding the degree of synchrony in fire activity among regions has significant implications even in the absence of clear attribution to a specific broad-scale forcing. We take advantage of the variability in climate, vegetation, and biophysical properties among our study regions in the modern record to infer the relative importance of broad-scale forcing vs. local heterogeneity as mechanisms controlling spatiotemporal patterns in fire activity.

Paleovegetation

To interpret changes in Holocene fire activity in the context of millennial-scale vegetation change, we rely on four previously published pollen records from each ecoregion (Fig. 2; Tinner et al. 2006, Higuera et al. 2009, 2011*a*, Kelly et al. 2013). We present these records smoothed to millennial time scales, rather than at their native resolution, to emphasize broad-scale trends in vegetation assemblages that are consistent with other records across each region (Anderson 1988, Anderson and Brubaker 1993, Anderson et al. 2003). For example, these records illustrate well the expansion of *P. mariana* (black spruce) in interior Alaska ca. 4,000–6,000 yr BP, the longer presence of black spruce in the Copper River Basin, and the absence of black spruce in the Noatak River watershed. The expansion of *Alnus* (alder) in the early Holocene, ca. 7,000–8,000 yr BP, is also well illustrated.

Records of biomass burning and fire occurrence

We utilize two metrics of fire activity commonly derived from sediment-charcoal records: estimates of biomass burning based on a metric of standardized

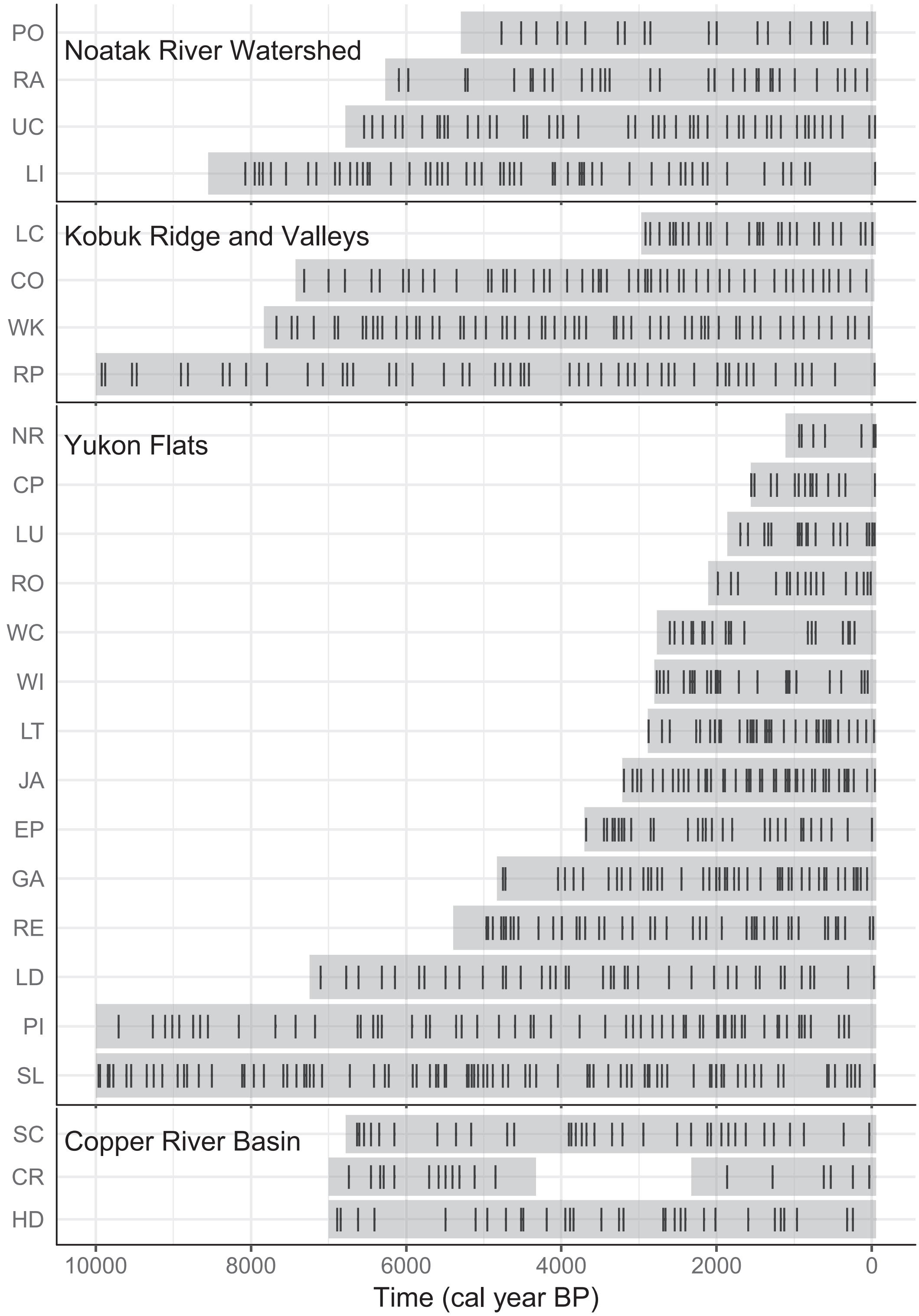


FIG. 2. Paleofire records used in this study. Each horizontal line represents an individual paleofire record, grouped by region. Gray bars indicate the temporal range of each record where signal-to-noise ratios were >3, and black vertical ticks indicate the timing of peaks in charcoal accumulation rates, inferred as local fire events. For lake names associated with two-letter code, see Table 2.

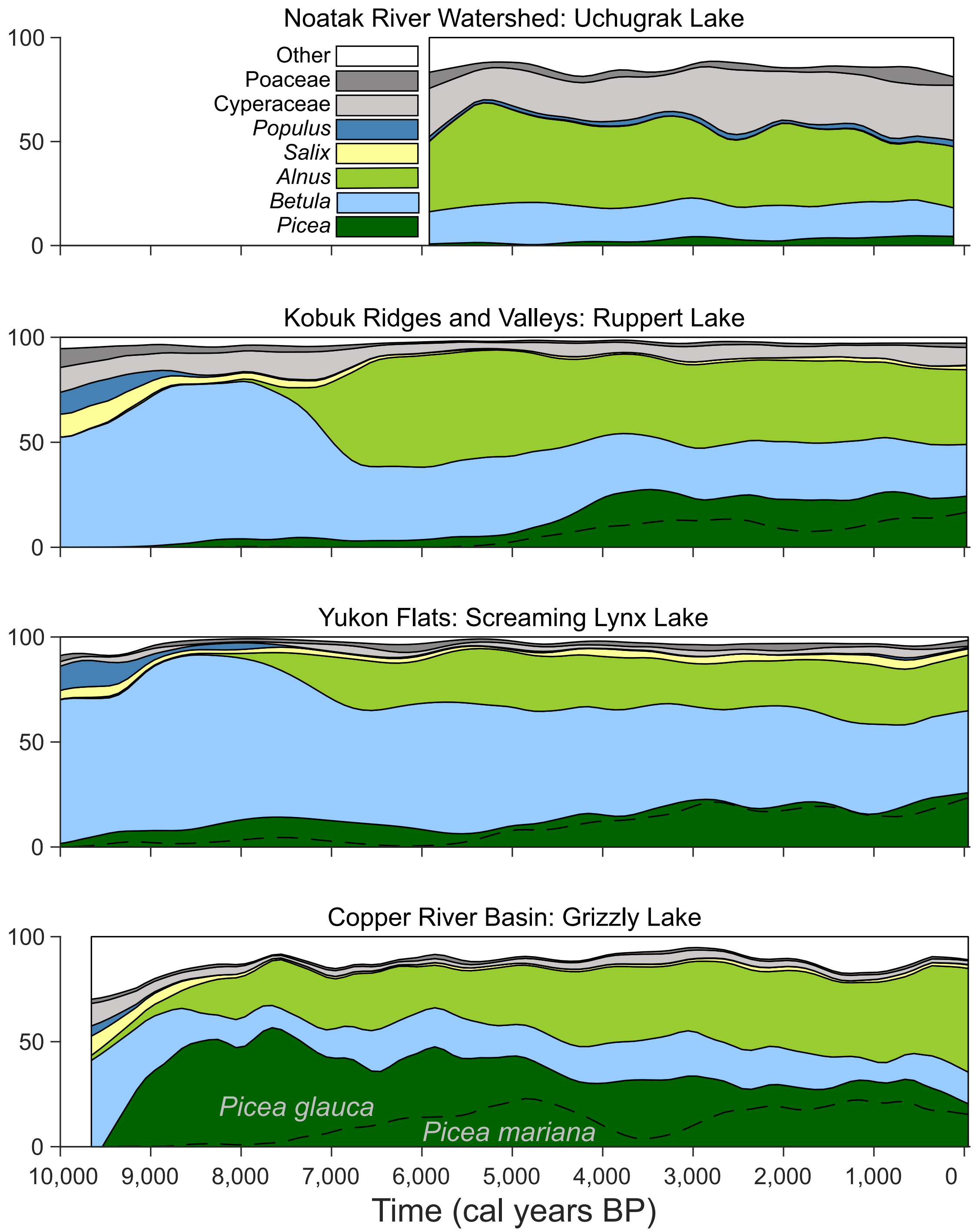


FIG. 3. Representative pollen diagrams from each focal region in this study. Pollen percentage data are smoothed to 1,000-yr trends to emphasize millennial-scale patterns present in other regional records. Records are organized from northwestern to south-central Alaska, from top to bottom: Uchugrak Lake (Higuera et al. 2011*a*), Ruppert Lake (Higuera et al. 2009), Screaming Lynxch Lake (Kelly et al. 2013), and Grizzly Lake (Tinner et al. 2006). The black dashed lines indicate the proportion of spruce (Picea) pollen grains attributed to black spruce (P. mariana) vs. white spruce (P. glauca). Black spruce is not present in the Noatak River watershed currently. Pollen abundance does not scale directly to plant abundance.

Table 2. Summary of paleofire records used in this synthesis.

Site	Code	Ecoregion	Median resolution (yr)	Latitude	Longitude	Publication	Peak analysis
Code	CO	Kobuk Ridges and Valleys	16	67.16	−151.86	Higuera et al. (2009)	Yes
Last Chance	LC	Kobuk Ridges and Valleys	7	67.13	−150.75	Higuera et al. (2007)	Yes
Rupert	RU	Kobuk Ridges and Valleys	11	67.07	−154.25	Higuera et al. (2009)	Yes
Wild Tussock	WK	Kobuk Ridges and Valleys	13	67.14	−151.51	Higuera et al. (2009)	Yes
Xindi	XI	Kobuk Ridges and Valleys	21	67.11	−152.49	Higuera et al. (2009)	No
Crater	CR	Copper River Basin	13	62.10	−146.24	Barrett et al. (2013)	Partial
Hudson	HD	Copper River Basin	9	61.90	−145.67	Barrett et al. (2013)	Yes
Minnesota Plateau	MP	Copper River Basin	17	62.32	−146.15	Barrett et al. (2013)	No
Super Cub	SC	Copper River Basin	12	62.30	−145.35	Barrett et al. (2013)	Yes
Little Issac	LI	Kobuk Ridges and Valleys	13	67.94	−160.80	Higuera et al. (2011*a*, *b*)	Yes
Poktovik	PO	Kobuk Ridges and Valleys	9	68.03	−161.38	Higuera et al. (2011*a*, *b*)	Yes
Raven	RA	Kobuk Ridges and Valleys	8	68.01	−162.04	Higuera et al. (2011*a*, *b*)	Yes
Uchugrak	UC	Kobuk Ridges and Valleys	8	68.05	−161.73	Higuera et al. (2011*a*, *b*)	Yes
Chopper	CP	Yukon–Old Crow	4	66.00	−146.28	Kelly et al. (2013)	Yes
Epilobium	EP	Yukon–Old Crow	9	65.97	−145.57	Kelly et al. (2013)	Yes
Granger	GA	Yukon–Old Crow	9	66.06	−145.65	Kelly et al. (2013)	Yes
Jonah	JA	Yukon–Old Crow	5	66.07	−145.08	Kelly et al. (2013)	Yes
Landing	LD	Yukon–Old Crow	20	65.90	−145.78	Kelly et al. (2013)	Yes
Latitude	LT	Yukon–Old Crow	6	65.93	−146.14	Kelly et al. (2013)	Yes
Lucky	LU	Yukon–Old Crow	5	66.02	−145.53	Kelly et al. (2013)	Yes
Noir	NR	Yukon–Old Crow	2	66.00	−145.93	Kelly et al. (2013)	Yes
Picea	PI	Yukon–Old Crow	16	65.88	−145.59	Kelly et al. (2013)	Yes
Reunion	RE	Yukon–Old Crow	8	66.01	−146.11	Kelly et al. (2013)	Yes
Robinson	RO	Yukon–Old Crow	6	65.97	−145.70	Kelly et al. (2013)	Yes
Screaming Lynx	SL	Yukon–Old Crow	7	66.07	−145.40	Kelly et al. (2013)	Yes
West Crazy	WC	Yukon–Old Crow	2	65.89	−145.62	Kelly et al. (2013)	Yes
Windy	WI	Yukon–Old Crow	7	66.04	−145.75	Kelly et al. (2013)	Yes

charcoal accumulation rates (CHAR), and estimates of the timing of past fire occurrence inferred from significant peaks in CHAR. All 27 records used in this study were developed with virtually identical methods (Table 1), briefly summarized here. Sediment cores were collected from small (<10 ha), deep (>5 m) lakes with simple basin shapes and minimal inlets or outlets, using a polycarbonate tube fitted with a piston and/or a modified Livingstone coring device. Core tops were sampled in the field at continuous 0.5–1.0-cm intervals, and in the laboratory cores were sampled in contiguous 0.25–0.5-cm intervals, with 0.5–3.0-cm^3 samples taken for charcoal analysis. Samples were treated with sodium metaphosphate, oxidized with sodium hypochlorite or hydrogen peroxide, and sieved to isolate macroscopic charcoal (>150–180 μm). Charcoal particles were counted at 10–40× with a stereomicroscope, and CHAR (pieces·cm^{-2}·yr^{-1}) was derived as the product of charcoal concentrations (pieces/cm^3) and sediment accumulation rates (cm/year). Sediment accumulation rates were based on age-depth models, developed from ^{210}Pb (in 26 of 27 records) and accelerator mass spectrometry ^{14}C (in all records) dating of terrestrial macrofossils or concentrated charcoal particles. All records underwent a decomposition and peak analysis procedure by their original authors using the CharAnalysis software (github.com/phiguera/CharAnalysis), which separates background (noise) from foreground (signal) patterns in CHAR to identify statistically significant peaks. The estimated age of CHAR peaks is used to infer the timing of local fire events, interpreted as occurring within ca. 500–1,000 m of a lake, based on simulation modeling and comparisons to modern fire activity (Higuera et al. 2007, Kelly et al. 2013). We made no changes to the chronologies or peak identification analyses from the original publications, which were developed using equivalent methods, but only used portions of the records from the past 10,000 yr. As in the original publications, we also exclude (portions of) records with a signal-to-noise index <3 from metrics that rely on peak identification (Kelly et al. 2011), reducing the number of records uses for fire-event analyses from 27 to 25 (Fig. 3).

Composite records of biomass burning

We used CHAR data from multiple sites to develop indices of biomass burning at the landscape and biome scales. We produced composite records of biomass burning from networks of individual records using the method introduced by Kelly et al. (2013), which models CHAR as a zero-inflated log-normal process (ZIL method). The ZIL method avoids the Box–Cox transformation of CHAR, and the associated addition of an arbitrary constant to zero values, used in other approaches. The ZIL method thereby reduces the introduction of bias that can accompany transformation, and preserves the natural distribution of CHAR data (log-normal with a high proportion of zero values; Appendix S1: Fig. S1). To account for systematic differences in CHAR among individual sites, nonzero accumulation rates were temporarily log-transformed, rescaled within each site to a *z*-score (mean = 0, standard deviation = 1), and then returned to their original scale through exponentiation. We estimated the parameters of ZIL distributions centered at continuous 10-yr time steps using a Gaussian kernel-weighted smoothing function with a 100-yr window (overall median sample resolution = 9 yr). The index of biomass burning at each time step was the mean of 1,000 bootstrapped mean parameter estimates, and 90% confidence intervals were derived from the 5th and 95th percentiles. We derived a ~1,000-yr mean biomass burning estimate by applying a LOESS regression to the 100-yr mean and confidence-interval values. We interpreted changes in the 1,000-yr mean estimate of biomass burning that exceeded these confidence intervals to be statistically significant.

To quantify variability in biomass burning at the ecoregional scale, we applied the ZIL method to networks of records within ecoregions (Kobuk, n = 5; Copper River, n = 4; Yukon Flats, n = 14; and Noatak, n = 4), and developed a multiregion composite record representative of fire-prone ecoregions in Alaska (Alaska-wide) by applying the ZIL method to all sites together (n = 27). Because the records contributing to our Alaska-wide composite were drawn from multiple ecoregions containing different numbers of sites, we weighted every measure of charcoal accumulation such that each region contributed equally to the composite before estimating the mean of standardized CHAR using the ZIL method (Appendix S1: Fig. S1).

Fire-event frequency

To quantify the frequency and synchrony of fire events within and among regions, we calculated the proportion of sites that recorded fire each century (Calder et al. 2015). Within each region, we summed the number of fire events recorded in a 100-yr window, at continuous 10-yr time steps, and divided that sum by the average number of sites recording within the window. This was done over all periods with at least two sites recording. There are a finite number of possible unique percentages with this metric, which is equivalent to n sites + 1 if all records were of equal length; and, because a site can record more than one fire per century, the percentage of sites burned can exceed 100.

To account for uncertainty in estimating the timing of fire events from CHAR, we resampled fire ages from a distribution of possible ages, based on uncertainty associated with ^{210}Pb and ^{14}C dating. To quantify age uncertainty, but preserve the chronologies originally published with our records, we evaluated age uncertainties in the published records and identified a conservative standard deviation around resampled fire ages of 50 yr (Appendix S1: Fig. S2).

We derived the median percentage of sites burned per century from the 50th percentile of 1,000 simulated combinations of fire ages, and used the 5th and 95th percentile of these simulations to estimate 90% confidence intervals. We calculated an Alaska-wide version of this metric that reflects each region equally, regardless of the number of sites it included, by taking the mean of the 5th, 50th, and 95th percentiles of the regional values at each time step (i.e., the mean of ~4000 values [4 regions × 1,000 simulations] per time step). Results are

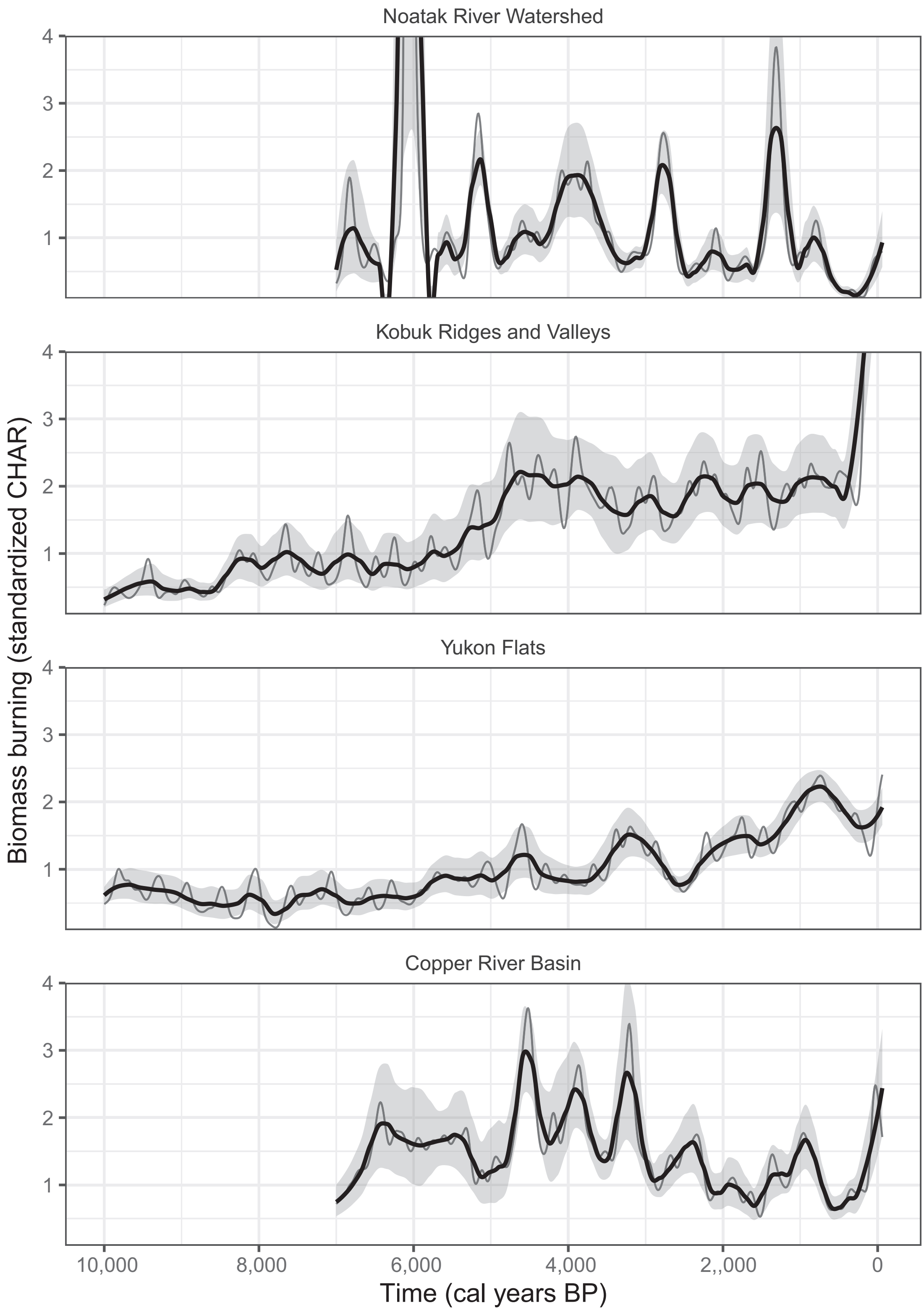


FIG. 4. Composite records of biomass burning (standardized charcoal accumulation rates [CHAR]) within each study region. The black curves indicate biomass burning at 500-yr timescales, the thin gray lines show 100-yr mean biomass burning, and the gray band is a bootstrapped 90% confidence interval. The axes of all panels are scaled to 4, for clarity, but values >4 observed in Noatak and Kobuk lie outside the axis limits and are not visible.

presented as a LOESS regression with a 1,000-yr window. For comparison to other fire-regime metrics, a value of 50% of sites burned per century is analogous to a 200-yr fire rotation period (FRP) and a 200-yr point-based mean fire return interval (mFRI; Johnson and Gutsell 1994, Calder et al. 2015).

In addition to the percent of sites burned per century, we also quantified fire-event frequency by calculating an Alaska-wide mFRI. FRI were measured as the years between the estimated ages of consecutive fire events in a record, and the Alaska-wide mFRI is presented as a 1,000-yr LOESS regression calculated form all FRIs in a given 1,000-yr period. Finally, we also present the ratio of composite biomass burning to the composite mFRI, interpreted as a metric of total biomass burned per fire event, or fire severity (Kelly et al. 2013).

Correlation analysis

To quantify the relationships among our fire and climate proxies, we conducted a pairwise correlation analysis between measures of fire activity and temperature proxies. We calculated a Pearson product-moment correlation coefficient between the Kaufman et al. (2016) composite temperature record and binned 500-yr mean composite biomass burning, binned 500-yr mFRI, and the percent of sites burned per century from 8,000 to 0 yr BP. From 1,200 to 0 yr BP we calculated correlation coefficients between decadal mean temperature from the GOA record and all three measures of fire activity.

Results

Composite records of biomass burning

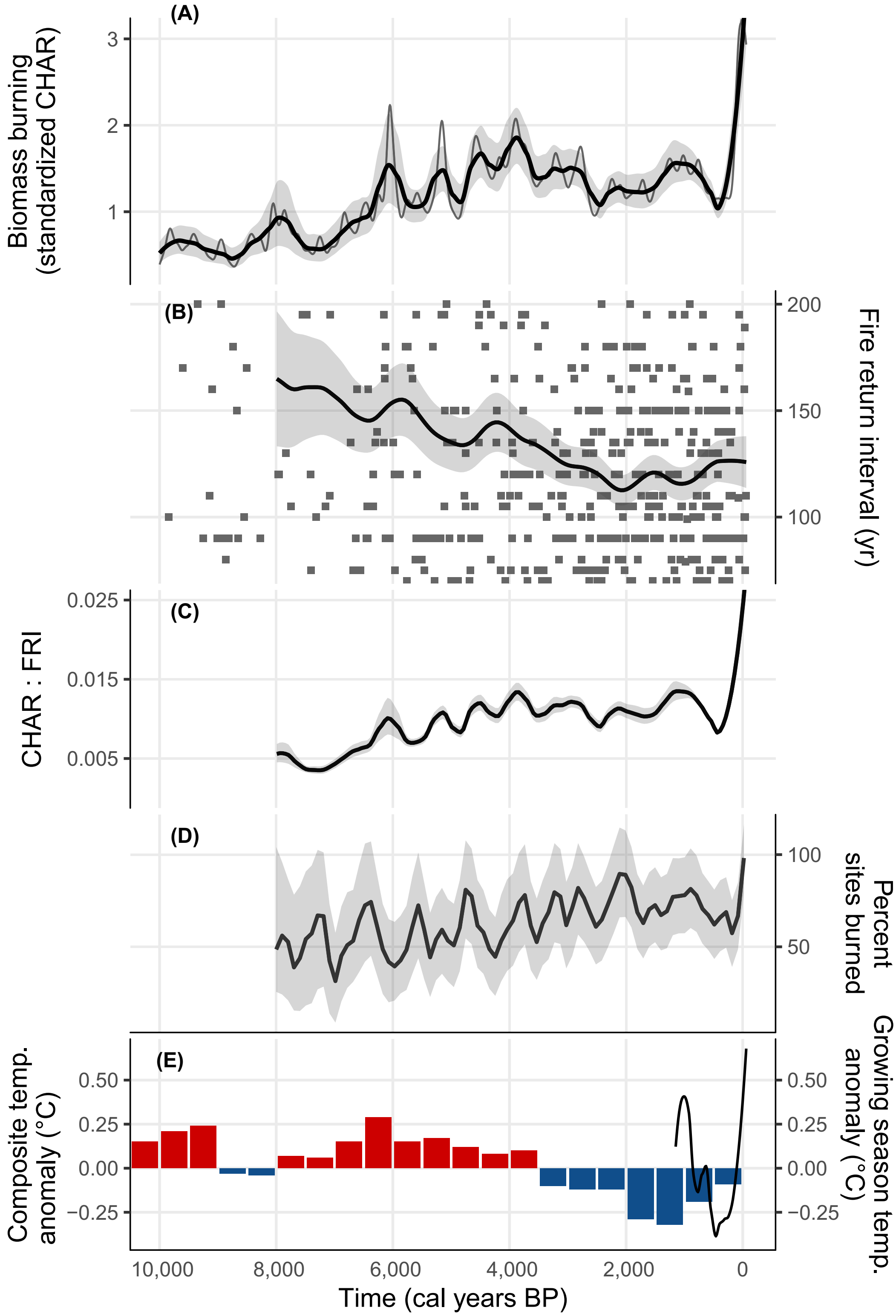
Our Alaska-wide composite record of biomass burning showed significant high- and low-frequency variability during the Holocene. Biomass burning generally increased over the Holocene, with elevated periods centered at ca. 8,000, 6,000, 4,000, and 1,000 yr BP. Biomass burning increased steadily from ca. 8,000 to 4,000 yr BP, with the 1,000-yr mean reaching its maximum value ca. 4,000 yr BP. Biomass burning was elevated for a ca. 500-yr period centered at 1,000 yr BP, declined temporarily thereafter, and then increased from 400 yr BP through present. The 100-yr mean biomass burning record also showed high variability, with several distinct peaks between ca. 6,000 and 3,000 yr BP, and again at 1,000 yr BP. Biomass burning at both timescales was substantially higher in the most recent century than at any other time in the Holocene.

Region-specific records of biomass burning likewise showed significant high- and low-frequency variability, both within and among regions (Fig. 4). The Noatak exhibited the greatest variability in biomass burning, with alternating high and low periods approximately every 1,000 yr. Within this range of variability, biomass burning in the Noatak lacked a significant directional trend over the Holocene. Biomass burning in the Kobuk region increased over the Holocene, with abrupt increases ca. 8,000 and 5,000 yr BP. After decreasing slightly at ca. 4,000 yr BP, biomass burning in the Kobuk region began to increase again ca. 300 yr BP, which continued through the present. Biomass burning in the Kobuk was substantially higher over the last several centuries than at any other point in the 10,000-yr record. The Yukon Flats composite also showed an increasing directional trend over the Holocene, with notable peaks at ca. 5,000 and 3,000 yr BP. The record reaches its maximum at ca. 1,000 yr BP, before decreasing for several centuries until an abrupt increase in the 100-yr mean that began ca. 100 yr BP. Biomass burning in the Copper River increased significantly from ca. 7,000 to 5,000 yr BP, but then declined through ca. 1,500 yr BP when it rose for several centuries, decreased, and then returned to an increasing trend ca. 300 yr BP that continues through present. Current rates of biomass burning in the Copper River are similar to a maxima ca. 1,000 yr BP, higher than any point since ca. 3,000 yr BP.

Fire synchrony

The Alaskan record of centennial-scale fire synchrony shows considerable high-frequency variability, but no significant long-term trend. Maxima above 75% occurred periodically throughout the Holocene, and minima were generally above 50% (Fig. 5D). Ecoregion-specific records of fire synchrony also show considerable high-frequency variability through time, but with long-term trends apparent only in the Kobuk and Yukon Flats regions (Appendix S1: Fig. S3). In the Kobuk region, fire synchrony increased through ca. 5,000 yr BP, and decreased after. Synchrony in the Yukon Flats was variable, showing no long-term trend until the mid-Holocene, when fire synchrony increased ca. 4,000 yr BP. Fire synchrony in the Noatak was highly variable, with no long-term trend throughout the Holocene. The Copper River showed the lowest degree of within-region

Fig. 5. Composite fire and climate proxies for Alaska during the Holocene. (A) Mean biomass burning (standardized charcoal accumulation rates [CHAR]) at 100-yr (thin line) and 1,000-yr (thick line) timescales, with gray band representing bootstrapped 90% confidence intervals. (B) Fire events (gray squares) and time since previous fire (FRI, yr), with 1,000-yr mean FRI (thick line) and 90% bootstrapped confidence interval. (C) Ratio of CHAR to FRI (interpreted as fire severity), with 90% bootstrapped confidence interval. (D) Median fire synchrony (percent sites burned per century) with 90% confidence intervals based on simulated age uncertainty. (E) Composite of temperature-sensitive paleoclimate proxies from Kaufman et al. (2016; bars) and tree-ring–derived growing-season temperature from Wiles et al. (2014; line).



synchrony, with a notable maximum ca. 4,000 yr BP, but no long-term trend. The Yukon Flats had the highest average rate of burning (5th, 95th percentiles) at 86% (0,152) of sites burned per century, and the Copper River had the lowest rate of burning at 42% (0, 100) of sites burned per century. This contrast is consistent with the relative differences between these regions in the observational record of the past 60 yr, where mean FRPs are 82 and 2,178 yr, respectively (Young et al. 2017). Clearly, however, the Copper River experienced significantly more fire activity earlier in the Holocene than during the modern observational period.

Correlation analyses

Relationships between fire and temperature records varied by proxy and time period. Over the last 8,000 yr, biomass burning was uncorrelated with temperature, and the percent of sites burned per century was negatively associated with temperature ($r = -0.77$, $P = <0.001$). The percent of sites burned per century was positively correlated with our measure of fire severity (the ratio of CHAR to mFRI; $r = 0.66$, $P = 0.01$). Over the past 1,200 yr, biomass burning (500-yr and 100-yr means), the percent of sites burned per century, and fire severity were all positively correlated with the decadal mean of growing-season temperature in the GOA ($r = 0.43$, $P < 0.001$; $r = 0.41$, $P < 0.001$; $r = 0.36$, $P < 0.001$; $r = 0.43$, $P < 0.001$, respectively), and mFRI was negatively correlated with growing-season temperature in the GOA ($r = -0.41$, $P = 0.05$).

Discussion

We hypothesized that changes in broad-scale drivers of fire activity, like climate warming, would facilitate synchronous change in biomass burning and fire activity among ecoregions. Or in contrast, spatiotemporal variability in climate change or heterogeneity in landscape-scale drivers of fire could result in variability in biomass burning among regions. Our results complement regionally specific findings and provide evidence that both climate and biome-scale vegetation change drove millennial-scale variability in biomass burning. However, at centennial time scales, we found that synchronous burning across regions was rare during the Holocene (never exceeding 100% of sites burned per century), likely because of the muting of broad-scale forcing by local variation in vegetation and ecosystem properties, or high local variability in the magnitude of broad-scale forcing trends.

Direct climatic controls of fire

Our record provides a single reference for the average trends in biomass burning across fire-prone ecosystems of Alaska, and highlights significant shifts in biomass burning during the Holocene that occurred in conjunction with millennial-scale changes in temperature and vegetation composition. Biomass burning increased during relatively warm periods ca. 10,000–9,000, and 8,000–4,000 yr BP, and decreased with climatic cooling from ca. 9,000 to 8,000 and 4,000 to 2,500 yr BP. At Holocene time scales, broad agreement between trends in biomass burning and temperature from ca. 10,000 to 2,500 yr BP, even during a period of substantial vegetation change in the boreal forest biome, suggests that climate exerted substantial controls on biomass burning (Fig. 5A, C), likely through mechanisms of fuel abundance and flammability, from local to landscape scales (Macias-Fauria et al. 2011). At ca. 2,500 yr BP the direct relationship between the Alaskan composite record of biomass burning and temperature estimates (Kaufman et al. 2016) degrades, as biomass burning increases but temperature estimates decrease. Rather than a change in the dominant fire–climate relationship, this divergence may reflect spatial heterogeneity in climate, or the coarse resolution of temperature proxies (Barrett et al. 2013). The 500-yr, subcontinental resolution of the Holocene climate record (Kaufman et al. 2016) may not be adequately resolved to capture the centennial-scale climate variability that characterized the late Holocene. Annual temperature anomalies from tree-ring records (Wiles et al. 2014), in contrast, are generally positively correlated with biomass burning over the past 1,200 yr, including maxima during the Medieval Climate Anomaly (MCA, ca. 1,000–600 yr BP), and subsequent declines in biomass burning with temperature during the Little Ice Age (LIA, ca. 600–300 yr BP), in the Noatak, Yukon Flats, and Copper River. Disagreement between the two paleoclimate records limits our ability to attribute increases in biomass burning from ca. 1,500 to 1,000 yr BP to directional climate forcing, but points toward spatial heterogeneity in climate in the study area and the possibility that centennial- to millennial-scale climate variability is less directly linked with fire activity than annual- to decadal-scale variability. No significant relationships between proxy records of effective moisture (Kaufman et al. 2016) and metrics of fire activity were detected in our analysis (Appendix S1: Fig. S4). This likely reflects the greater spatial complexity in paleo moisture trends across Alaska, relative to paleo temperature (Kaufman et al. 2016). Regional changes in effective moisture may have been more influential on fire activity through impacts on vegetation composition, for example, with the expansion of black spruce with cooler and wetter conditions leading to increased biomass burning through increased fuel abundance (Lynch et al. 2004, Higuera et al. 2009, Kelly et al. 2013; Fig. 2).

Regional trends in biomass burning were also qualitatively related to climate variability, but sensitivity to climate varied through time. Fire activity in the Copper River and in the Noatak regions showed significant millennial-scale sensitivity to climate, evidenced by elevated biomass burning under the relatively warm temperatures of the middle Holocene, centered at ca. 6,000 yr BP. The Yukon Flats, Copper River, and Noatak regions showed centennial-scale maxima during the MCA, suggesting sensitivity to MCA warming likely occurred outside of the previously documented response in the Yukon Flats (Kelly et al. 2013). Biomass burning peaked during the MCA a few centuries earlier in the Noatak and Copper

River regions, relative to the Yukon Flats, but changes in biomass burning in all three regions correspond strongly with positive temperature anomalies in the GOA during the MCA and negative anomalies during the LIA.

The Noatak showed the highest variability in biomass burning among regions, with abrupt increases/decreases every ca. 1,000 yr. This variability may be an artifact of the overall lower charcoal accumulation rates in these records relative to boreal forest records (Higuera et al. 2011*a*), but it suggests the possibility of high sensitivity in tundra biomass burning to climate variability. Fire–climate relationships estimated from modern observational records in both boreal forest and tundra ecosystems are strongly nonlinear, with distinct temperature thresholds to burning (Hu et al. 2015, Young et al. 2017). The high variability in biomass burning in the Noatak relative to the other regions may stem from the region's proximity to a temperature threshold to burning, such that small changes in temperature can result in large changes in the probability of burning (Young et al. 2017). Statistical modeling suggests that regions well above temperature thresholds to burning (+1–2°C) will have high probabilities of fire, regardless of decadal- to centennial-scale climate variability, and may therefore be limited more by landscape flammability or ignitions than by climatic conditions. Conversely, systems that are near temperature thresholds may show greater sensitivity to climatic variability (Young et al. 2019).

Our regional records of fire synchrony all document short periods of simultaneous fire activity among sites, but when composited display limited evidence of widespread synchrony in fire activity across Alaska. Furthermore, the coupling between climate and fire suggested by the trends in biomass burning described above do not emerge in the long-term pattern of fire synchrony across Alaska. Abrupt increases in biomass burning during the warm MCA were significant in the Copper River and Noatak regions, but changes in fire synchrony or mFRI were not statistically significant across Alaska. This pattern suggests that the inferred increases in fire severity (i.e., increases in biomass burning per fire event) under anomalously warm conditions in the Yukon Flats region of Alaska (e.g., Kelly et al. 2013) may have occurred in other boreal forest and tundra regions in Alaska as well. Paleofire records from the eastern North American boreal forest also display increased biomass burning with nonvarying fire frequency (the inverse of mFRI) over the past 2,000 yr (Ali et al. 2012). In this case, increases in the ratio of biomass burning to fire frequency were interpreted as reflecting mean fire size, but the authors note the covarying nature of fire frequency and mean fire size.

The low temporal resolution and proxy-related uncertainty of climate reconstructions for Alaska limit our ability to infer climatic forcing of fire activity throughout the Holocene. Modern observations indicate strong spatial autocorrelation in climate across Alaska, but heterogeneity in local climate could have also contributed to variability in biomass burning and synchrony in fire activity during the Holocene, without being reflected in multicentury, biome-wide anomalies. Such a pattern could potentially mask direct impacts of climate on fire activity. Alternatively, the absence of any prolonged periods of synchronous fire activity across Alaska could indicate that the magnitude of centennial-scale climate variability over the Holocene was never extreme enough to initiate synchronous increases in fire across multiple regions. Chronological uncertainty also hinders our ability to detect centennial-scale fire synchrony from paleofire data sets. Our uncertainty estimate is conservative, so a lack of statistically significant periods of fire synchrony across Alaska may indicate the lack of adequate temporal precision to detect synchrony at centennial scales accurately, rather than a true lack of synchrony in fire activity across landscapes or regions.

Vegetation-mediated control of fire and limits to synchronous burning

Increased biomass burning in the boreal forest (Kobuk, Yukon Flats, and Copper River regions) during the period of black spruce expansion 7,000–4,000 yr BP supports previous evidence that biome-scale changes in vegetation can initiate widespread shifts in biomass burning (Lynch et al. 2004, Brubaker et al. 2009, Higuera et al. 2009, Kelly et al. 2013). The contrast in biomass burning trends between the Noatak and boreal forest regions (Kobuk, Yukon Flats, Copper River) suggests that vegetation change was a more important driver of fire-regime variability in boreal forest than in tundra systems. The Noatak was not characterized by gradual increases in biomass burning as in the boreal forest, but instead by punctuated periods of elevated burning lasting ca. 1,000 yr. *Picea glauca* and *Alnus* expanded into northwestern Alaska to form a mix of shrub and open woodland ecosystems during in the early Holocene (Anderson 1988, Anderson and Brubaker 1994), so all species present in modern tundra were present 8,000–7,000 yr BP (Higuera et al. 2011*b*; Fig. 2). This is in contrast with interior Alaska, where black spruce expanded 6,000–4,000 yr BP and eventually became a dominant tree species (Lynch et al. 2002, 2004, Anderson et al. 2003, Higuera et al. 2009, Kelly et al. 2013). The change in fire activity after the arrival of black spruce is also evidenced by the degree of fire synchrony in the Kobuk and Yukon Flats regions, which increases with the biome-scale change in landscape flammability that occurred with the establishment of the modern boreal forest ca. 6,000–4,000 yr BP (Fig. 2).

The high-frequency variability in biomass burning (Fig. 4) and absence of widespread fire synchrony among regions (Fig. 5D; Appendix S1: Fig. S3) underscores the significant heterogeneity in fire activity across ecosystems. Our results suggest that periods of high fire synchrony occurred within a single or a few regions in any given century, but rarely (or never) in all regions at once. The broad agreement in fire synchrony between the Kobuk and Yukon Flats regions highlights the impact of broad shifts in species composition on fire activity, but variations in regional weather, vegetation composition, soil moisture, permafrost, and topography likely moderated synchronous burning across Alaska. Although synchrony within any given region exceeded 100% for short periods of time, these periods did not occur at the same time across Alaska, resulting in a consistent upper limit to synchrony in fire events across Alaska near 100%. This limit points toward a potential negative feedback to high fire activity, where lower flammability in the decades following fire limits burning until ecosystems redevelop continuous, flammable fuels (Johnstone et al. 2010*b*, Mann et al. 2012, Kelly et al. 2013, Hoecker and Higuera 2019). Our findings are consistent with those from the eastern North American boreal forest, where drought-induced increases in fire activity over the past 200 yr were only sustained for short periods, and the abundance of young, low-flammability stands imposed a negative feedback to subsequent fire occurrence and spread for decades (Héon et al. 2014). Although the self-limiting nature of fire is particularly strong in stand-replacing fire regimes, where live crown fuels are significantly reduced after fire, it has also been documented in mixed-conifer forests of the Rocky Mountains (Parks et al. 2016) and in the Sierra Nevada of California (Collins et al. 2009).

This synthesis provides a novel comparison of Holocene fire activity among flammable regions of Alaska, revealing the varying controls of fire at multiple spatial and temporal scales. Over millennial timescales, biomass burning was affected by climate indirectly, through broad-scale vegetation shifts. At centennial timescales, however, fire regimes across Alaska were characterized by substantial heterogeneity. Increases in biomass burning were greater than declines in fire return intervals, particularly during warm periods (Fig. 5C). This dynamic could indicate that increases in biomass burning from direct climate forcing manifest as increases in fire severity rather than increased fire frequency. Ecosystem models indicate that, together with variability in fire frequency, fire severity accounted for as much as 84% of the variability in total carbon stocks in a boreal forest ecosystem over the past 1,200 yr, implicating fire, and fire severity, as a major driver of carbon dynamics in boreal forests ecosystems (Kelly et al. 2016). The apparent variability in fire severity over decadal–millennial timescales challenges the accuracy of steady-state initial conditions in fire activity typically used in ecosystem models, and indicates the potential for significantly different outcomes when empirically based fire data are used to drive the timing and characteristics disturbances in ecosystem models. The important role of fire in driving boreal forest carbon dynamics is also increasingly seen through contemporary increases in fire frequency and severity (Walker et al. 2019).

Projections of fire activity for the 21st century, based on modern fire–climate relationships and global circulation model ensembles, indicate that climate conditions will become increasingly conducive to burning across nearly all of Alaska (Young et al. 2017). The generally low synchrony of increased fire activity among regions documented here suggests that regional heterogeneity may limit synchronous increases in fire activity (Héon et al. 2014). However, the rates of ongoing and expected climate warming are increasingly exceeding those observed in the Holocene, implying that the past does not ensure ecosystem resilience to future fire activity. Based on our evidence from long-term records collected across Alaska, climate-driven changes in fire activity that are predicted for the 21st century would be unprecedented over the last 8,000 yr. Novel fire regimes and postfire environmental conditions could result in substantial changes to boreal forest and flammable tundra ecoregions. More work to define the "safe operating space" (Johnstone et al. 2016) for fire-regime variability in boreal forests and tundra ecosystems is required to anticipate whether high-latitude systems will retain their historical character and function into the future.

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Literature Cited

Ali, A. A., et al. 2012. Control of the multimillennial wildfire size in boreal North America by spring climatic conditions. Proceedings of the National Academy of Sciences of the United States of America 109:20966–20970.

AnchukaitisK. J., et al. 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163 1 – 22. https://doi.org/10.1016/j.quascirev.2017.02.020.

Anderson, P. M. 1988. Late quaternary pollen records from the Kobuk and Noatak river drainages, northwestern Alaska. Quaternary Research 29:263–276.

Anderson, P. M., and L. B. Brubaker. 1993. Holocene vegetation and climate histories of Alaska. H.E. WrightJr., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, A. F. Stree-Perrott and P. J. Bartlein, Pages 385–400 *in* Global climates since the last glacial maximum, Minneapolis: University of Minnesota Press.

Anderson, P. M., and L. B. Brubaker. 1994. Vegetation history of northcentral Alaska: A mapped summary of late-Quaternary pollen data. Quaternary Science Reviews 13:71–92.

Anderson, P. M., M. E. Edwards, and L. B. Brubaker. 2003. Results and paleoclimate implications of 35 years of paleoecological research in Alaska. Development in Quaternary Science 1:427–440.

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

Barrett, C. M., R. Kelly, P. E. Higuera, and F. S. Hu. 2013. Climatic and land cover influences on the spatiotemporal dynamics of Holocene boreal fire regimes. Ecology 94:389–402.

Barrett, K., A. D. McGuire, E. E. Hoy, and E. S. Kasischke. 2011. Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. Ecological Applications 21:2380–2396.

Bonan, G. B. 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449.

Bond-Lamberty, B., S. D. Peckham, D. E. Ahl, and S. T. Gower. 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89.

Bowman, D. M. J. S., et al. 2009. Fire in the earth system. Science 324:481–484.

Brown, C. D., and J. F. Johnstone. 2012. Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. Forest Ecology and Management 266:34–41.

Brubaker, L. B., P. E. Higuera, T. S. Rupp, M. A. Olson, P. M. Anderson, and F. S. Hu. 2009. Linking sediment-charcoal records and ecological modeling to understand causes of fire-regime change in boreal forests. Ecology 90:1788–1801.

Bunbury, J., and K. Gajewski. 2009. Postglacial climates inferred from a lake at treeline, southwest Yukon Territory, Canada. Quaternary Science Reviews 28:354–369.

Calder, W. J., D. Parker, C. J. Stopka, G. Jiménez-Moreno, and B. N. Shuman. 2015. Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains. Proceedings of the National Academy of Sciences of the United States of America 112:13261–13266.

Chapin, F. S., et al. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology 6:211–223.

Chipman, M. L., V. Hudspith, P. E. Higuera, P. A. Duffy, R. Kelly, W. W. Oswald, and F. S. Hu. 2015. Spatiotemporal patterns of tundra fires: Late-Quaternary charcoal records from Alaska. Biogeosciences 12:4017–4027.

Clegg, B. F., R. Kelly, G. H. Clarke, I. R. Walker, and F. S. Hu. 2011. Nonlinear response of summer temperature to Holocene insolation forcing in Alaska. Proceedings of the National Academy of Sciences of the United States of America 108:19299–19304.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. Ecosystems 12:114–128.

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

Gavin, D. G., and F. S. Hu. 2013. Northwestern North America. S. A. Elias and C. J. Mock, Pages 124–132 *in* Encyclopedia of Quaternary Science, Amsterdam: Elsevier.

Genet, H., et al. 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. Environmental Research Letters 8:045016.

Grosse, G., et al. 2011. Vulnerability of high-latitude soil organic carbon in North America to disturbance. Journal of Geophysical Research: Biogeosciences. https://doi.org/10.1029/2010JG001507

Héon, J., D. Arseneault, and M.-A. Parisien. 2014. Resistance of the boreal forest to high burn rates. Proceedings of the National Academy of Sciences of the United States of America 111:13888–13893.

Higuera, P. E., J. L. Barnes, M. L. Chipman, and F. S. Hu. 2011*a*. The burning tundra: A look back at the last 6,000 years of fire in the Noatak National Preserve, northwestern Alaska. Alaska Park Science 10:36–41.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. Ecological Monographs 79:201–219.

Higuera, P. E., M. L. Chipman, J. L. Barnes, M. A. Urban, and F. S. Hu. 2011*b*. Variability of tundra fire regimes in Arctic Alaska: Millennial-scale patterns and ecological implications. Ecological Applications 21:3211–3226.

Higuera, P. E., M. E. Peters, L. B. Brubaker, and D. G. Gavin. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. Quaternary Science Reviews 26:1790–1809.

Hinzman, L., et al. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Climatic Change 72:251–298.

Hoecker, T. J., and P. E. Higuera. 2019. Forest succession and climate variability interacted to control fire activity over the last four centuries in an Alaskan boreal landscape. Landscape Ecology 34:227–241.

Homer, C. G., Fry, J. A., and Barnes, C. A. 2012. The National Land Cover Database . Report 2012-3020http://pubs.er.usgs.gov/publication/fs20123020.

Hoy, E. E., M. R. Turetsky, and E. S. Kasischke. 2016. More frequent burning increases vulnerability of Alaskan boreal black spruce forests. Environmental Research Letters 11:095001.

Hu, F. S., L. B. Brubaker, D. G. Gavin, P. E. Higuera, J. A. Lynch, T. S. Rupp, and W. Tinner. 2006. How climate and vegetation influence the fire regime of the Alaskan boreal biome: The Holocene perspective. Mitigation and Adaptation Strategies for Global Change 11:829–846.

Hu, F. S., P. E. Higuera, P. Duffy, M. L. Chipman, A. V. Rocha, A. M. Young, R. Kelly, and M. C. Dietze. 2015. Arctic tundra fires: Natural variability and responses to climate change. Frontiers in Ecology and the Environment 13:369–377.

Hu, F. S., P. E. Higuera, J. E. Walsh, W. L. Chapman, P. A. Duffy, L. B. Brubaker, and M. L. Chipman. 2010. Tundra burning in Alaska: Linkages to climatic change and sea ice retreat. Journal of Geophysical Research: Biogeosciences 115:1–8.

Irvine, F., L. C. Cwynar, J. C. Vermaire, and A. B. H. Rees. 2012. Midge-inferred temperature reconstructions and vegetation change over the last ~15,000 years from Trout Lake, northern Yukon Territory, eastern Beringia. Journal of Paleolimnology 48:133–146.

Johnson, E. A., and S. L. Gutsell. 1994. Fire frequency models, methods and interpretations. Pages 239–287*in*M. Begon and A. H. Fitter, editors. Advances in ecological research, San Diego, London: Academic Press.

Johnstone, J. F., F. S. Chapin, T. N. Hollingsworth, M. C. Mack, V. Romanovsky, and M. Turetsky. 2010*a*. Fire, climate change, and forest resilience in interior Alaska. Canadian Journal of Forest Research 40:1302–1312.

Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010*b*. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281–1295.

Kasischke, E. S., and M. R. Turetsky. 2006. Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. Geophysical Research Letters 33:L09703.

Kasischke, E. S., D. Williams, and D. Barry. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. International Journal of Wildland Fire 11:131–144.

Kasischke, E. S., et al. 2010. Alaska's changing fire regime—implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research 40:1313–1324.

Kaufman, D. S., et al. 2016. Holocene climate changes in eastern Beringia (NW North America): A systematic review of multi-proxy evidence. Quaternary Science Reviews 147:312–339.

Kelly, R., M. L. Chipman, P. E. Higuera, I. Stefanova, L. B. Brubaker, and F. S. Hu. 2013. Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. Proceedings of the National Academy of Sciences of the United States of America 110:13055–13060.

Kelly, R., H. Genet, A. D. McGuire, and F. S. Hu. 2016. Palaeodata-informed modelling of large carbon losses from recent burning of boreal forests. Nature Climate Change 6:4–9.

Kelly, R. F., P. E. Higuera, C. M. Barrett, and F. S. Hu. 2011. A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quaternary Research 75:11–17.

Lynch, J. A., J. S. Clark, N. H. Bigelow, M. E. Edwards, and B. P. Finney. 2002. Geographic and temporal variations in fire history in boreal ecosystems of Alaska. Journal of Geophysical Research 108:1–17.

Lynch, J. A., J. L. Hollis, and F. S. Hu. 2004. Climatic and landscape controls of the boreal forest fire regime: Holocene records from Alaska. Journal of Ecology 92:477–489.

Macias-Fauria, M., S. T. Michaletz, and E. A. Johnson. 2011. Predicting climate change effects on wildfires requires linking processes across scales. Wiley Interdisciplinary Reviews—Climate Change 2:99–112.

Mack, M. C., M. S. Bret-Harte, T. N. Hollingsworth, R. R. Jandt, E. A. G. Schuur, G. R. Shaver, and D. L. Verbyla. 2011. Carbon loss from an unprecedented Arctic tundra wildfire. Nature 475:489–492.

Mann, D. H., T. Scott Rupp, M. A. Olson, and P. A. Duffy. 2012. Is Alaska's boreal forest now crossing a major ecological threshold? Arctic, Antarctic, and Alpine Research 44:319–331.

Marcott, S. A., J. D. Shakun, P. U. Clark, and A. C. Mix. 2013. A reconstruction of regional and global temperature for the past 11,300 years. Science 339:1198–1201.

Marlon, J. R., P. J. Bartlein, A.-L. Daniau, S. P. Harrison, S. Y. Maezumi, M. J. Power, W. Tinner, and B. Vanniére. 2013. Global biomass burning: a synthesis and review of Holocene paleofire records and their controls. Quaternary Science Reviews 65:5–25.

Marlon, J. R., et al. 2015. Reconstructions of biomass burning from sediment charcoal records to improve data-model comparisons. Biogeosciences Discussions 12:18571–18623.

McKay, N. P., D. S. Kaufman, and N. Michelutti. 2008. Biogenic silica concentration as a high-resolution, quantitative temperature proxy at Hallet Lake, south-central Alaska. Geophysical Research Letters 35:4–9.

Miller, G. H., R. B. Alley, J. Brigham-Grette, J. J. Fitzpatrick, L. Polyak, M. C. Serreze, and J. W. C. White. 2010. Arctic amplification: can the past constrain the future? Quaternary Science Reviews 29:1779–1790.

Nowacki, G. J., P. Spencer, M. Fleming, T. Brock, T. Jorgenson, and S. Geological. 2003. Unified ecoregions of Alaska: 2001. Page Open-File Report. No. 2002-2.

O'Donnell, J. A., J. W. Harden, A. D. Mcguire, M. Z. Kanevskiy, M. T. Jorgenson, and X. Xu. 2011. The effect of fire and permafrost interactions on soil carbon accumulation in an upland black spruce ecosystem of interior Alaska: Implications for post-thaw carbon loss. Global Change Biology 17:1461–1474.

Parks, S. A., C. Miller, L. M. Holsinger, L. S. Baggett, and B. J. Bird. 2016. Wildland fire limits subsequent fire occurrence. International Journal of Wildland Fire 25:182–190.

Pastick, N. J., M. Rigge, B. K. Wylie, M. T. Jorgenson, J. R. Rose, K. D. Johnson, and L. Ji. 2014. Distribution and landscape controls of organic layer thickness and carbon within the Alaskan Yukon River Basin. Geoderma 230–231:79–94.

Randerson, J. T., et al. 2006. The impact of boreal forest fire on climate warming. Science 314:1130–1132.

Rocha, A. V., M. M. Loranty, P. E. Higuera, M. C. Mack, F. S. Hu, B. M. Jones, A. L. Breen, E. B. Rastetter, S. J. Goetz, and G. R. Shaver. 2012. The footprint of Alaskan tundra fires during the past half-century: Implications for surface properties and radiative forcing. Environmental Research Letters 7:044039.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management 261:381–390.

Szeicz, J. M., G. M. MacDonald, and A. Duk-Rodkin. 1995. Late Quaternary vegetation history of the central Mackenzie Mountains, Northwest Territories, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology 113:351–371.

Tinner, W., F. S. Hu, R. Beer, P. Kaltenrieder, B. Scheurer, and U. Krähenbühl. 2006. Postglacial vegetational and fire history: pollen, plant macrofossil and charcoal records from two Alaskan lakes. Vegetation History and Archaeobotany 15:279–293.

Turetsky, M. R., E. S. Kane, J. W. Harden, R. D. Ottmar, K. L. Manies, E. Hoy, and E. S. Kasischke. 2011. Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. Nature Geoscience 4:27–31.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Viau, A. E., and K. Gajewski. 2009. Reconstructing millennial-scale, regional paleoclimates of boreal Canada during the Holocene. Journal of Climate 22:316–330.

Walker, X. J., et al. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. Nature 572:520–523.

Whitlock, C., P. E. Higuera, D. B. McWethy, and C. E. Briles. 2010. Paleoecological perspectives on fire ecology: Revisiting the fire-regime concept. Open Ecology Journal 3:6–23.

Wiles, G. C., R. D. D'Arrigo, D. Barclay, R. S. Wilson, S. K. Jarvis, L. Vargo, and D. Frank. 2014. Surface air temperature variability reconstructed with tree rings for the Gulf of Alaska over the past 1200 years. Holocene 24:198–208.

Wilson, R., et al. 2016. Last millennium northern hemisphere summer temperatures from tree rings: Part I: The long term context. Quaternary Science Reviews 134:1–18.

Young, A. M., P. E. Higuera, J. T. Abatzoglou, P. A. Duffy, and F. S. Hu. 2019. Consequences of climatic thresholds for projecting fire activity and ecological change. Global Ecology and Biogeography 28:521–532.

Young, A. M., P. E. Higuera, P. A. Duffy, and F. S. Hu. 2017. Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. Ecography 40:606–617.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3096/suppinfo

Data Availability

The data used in the analysis are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.0gb5mkkxv, Code is stored in a GitHub repository archived by Zenodo: https://doi.org/10.5281/zenodo.3736520.