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Fire-regime complacency and sensitivity to centennial- through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA

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Summary

1. Key uncertainties in anticipating future fire regimes are their sensitivity to climate change, and the degree to which climate will impact fire regimes directly, through increasing the probability of fire, versus indirectly, through changes in vegetation and landscape flammability.
2. We studied the sensitivity of subalpine forest fire regimes (i.e. fire frequency, fire severity) to previously documented climate variability over the past 6000 years, utilizing pollen and macroscopic charcoal from high-resolution lake-sediment records in Rocky Mountain National Park, Colorado. We combined data from the four lakes to provide composite records of vegetation and fire history within a 200 km^2 study area.
3. Rates of forest burning were relatively complacent to millennial-scale summer cooling and decreased effective moisture. Mean return intervals between fire episodes, defined over 500-year periods, generally varied between 150 and 250 years, consistent with tree-ring-based estimates spanning recent centuries. Variability around these long-term means, however, was significantly correlated with variability in summer moisture (i.e. more burning with drier summers), inferred from existing lake-level and supporting palaeoenvironmental records.
4. The most pronounced change in fire regimes was in response to decreased subalpine forest density ca. 2400 cal. year BP, itself a response to regional cooling. This indirect impact of climate was followed by a decrease in charcoal production per fire, a proxy for crown-fire severity, while the long-term rate of burning remained unchanged. Over the last 1500 years, increased summer evaporation and drought frequency were associated with increased fire severity, highlighting a direct link between fire and climate.
5. *Synthesis*. Subalpine forest fire history reveals complacency and sensitivity of fire regimes to changing vegetation and hydroclimate over the past 6000 years. Complacency is highlighted by non-varying fire frequency over millennia. Sensitivity is evident through changes in biomass burned per fire (and inferred fire severity), in response to climate-induced changes in forest density and, more recently, increased summer drought. Overall, the palaeo record suggests that (i) fire severity may be more responsive to climate change than fire frequency in Rocky Mountain subalpine forests and (ii) the indirect impacts of climate on vegetation and fuels are important mechanisms determining fire-regime response to climate change.

Key-words: biomass burning, charcoal, climate change, fire history, fire severity, fuels, palaeoecology and land-use history, pollen, Rocky Mountain National Park

Introduction

Increased fire activity across the western United States is part of a suite of recent trends that highlight interactions among climate change, disturbance regimes and vegetation change (e.g. Westerling *et al.* 2006; van Mantgem *et al.* 2009, 2013). Large-scale disturbances have the potential to shape vegetation structure and composition, modify nutrient cycling (e.g. Smithwick *et al.* 2009; Turner 2010) and influence future disturbances for decades to centuries (e.g. Kulakowski & Veblen

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2007; Buma & Wessman 2011; Schoennagel *et al.* 2012; Kulakowski *et al.* 2013). In addition, large fire events increasingly impact human well-being at the wildland–urban interface, with firefighting costs representing a significant technical and budgetary challenge for land-management agencies. With projections for a more fire-conducive climate in future (e.g. Westerling *et al.* 2011), scientists and managers alike are questioning how fire regimes may respond.

Retrospective studies offer one of the best ways to understand fire-regime response to climate change (e.g. fire frequency, fire severity and biomass burned), and they provide a critical context for evaluating the precedence of ongoing and future conditions (e.g. Gavin *et al.* 2007; Pausas & Keeley 2009; Whitlock *et al.* 2010; Falk *et al.* 2011). Across multiple time scales, fire history reconstructions highlight two dominant pathways through which climate variability impacts fire occurrence. In ecosystems with abundant biomass, fire occurrence is directly driven by the frequency and magnitude of summer drought, necessary to dry out fuels that are typically too moist to sustain fire ignition and spread (termed 'climate-limited' fire regimes). Climate also influences fire regimes indirectly, by shaping fuel composition and structure on interannual through millennial time-scales. In ecosystems where fire occurrence is fuel limited, this indirect pathway can mediate the direct link between climate and fire. For example, in low-elevation montane forests in the southern Rocky Mountains, years with widespread burning are preceded by unusually moist years, required to stimulate fine-fuel production necessary to sustain fire spread (Baisan & Swetnam 1990; Veblen, Kitzberger & Donnegan 2000; Schoennagel, Veblen & Romme 2004). At significantly longer temporal scales, the palaeoecological record offers evidence that increased biomass burning was facilitated by increased biomass availability and landscape flammability associated with post-glacial vegetation change, itself driven by large-scale climate change (e.g. Marlon, Bartlein & Whitlock 2006; Power *et al.* 2008; Higuera *et al.* 2009).

Evaluating the relative role of the direct and indirect impacts of climate change on fire regimes is a key uncertainty in anticipating future fire regimes (Flannigan *et al.* 2009; Turner 2010; Westerling *et al.* 2011; Moritz *et al.* 2012). Here, we used high-resolution palaeoecological records to study the impacts of centennial- to millennial-scale climate and vegetation change on fire regimes over the past 6000 years in Rocky Mountain National Park, Colorado. We reconstructed fire and vegetation history using sediments from four small (< 12 ha), deep (> 7 m) subalpine lakes (3051–3231 m asl) within an ca. 200 km^2 region of Rocky Mountain National Park (Table 1 and Fig. 1). By combining the four records, each with an average resolution of ca. 15 years per sample, we developed subregional-scale composite records of fire occurrence and biomass burned. Comparisons with regional palaeoenvironmental records allowed us to infer the direct and indirect impacts of climate variability on fire regimes across multiple temporal scales. Our goal was to address two questions: (i) what are the long-term trends in vegetation and fire activity in subalpine forests; and (ii) how did changes in fire activity relate to variations in climate and vegetation on time-scales from centuries to millennia? Our results provide a long-term context for understanding the precedence of recent fire activity in similar forest types across western North America (e.g. Westerling *et al.* 2006; Littell *et al.* 2009), and they help highlight when and why fire regimes are sensitive to climate change, across time spans longer than the brief observational record. By highlighting the direct and indirect impacts of climate change on fire regimes over the past 6000 years, our results also help anticipate how subalpine forest fires regimes may respond to ongoing and future change in the region.

Materials and methods

STUDY AREA

Present-day climate in the study region is continental, with similar climatology east and west of the Continental Divide. In Allenspark, east of the Continental Divide at 2504 m asl, average maximum July and December temperatures are 23.2 and 0.9 °C, with total annual

Table 1. Site and record characteristics for four lakes in Rocky Mountain National Park, Colorado, USA, spanning the past 6000 years. 'SD' indicates standard deviation, and 'SNI' indicates signal-to-noise index, as defined in Kelly *et al.* (2011)

Characteristics	Lake name Odessa	Sand Beach	Thunder	Lone Pine
Site				
Latitude (N)	40° 19.822′	40° 13.126′	40° 13.314′	40° 13.964′
Longitude (W)	105° 41.124′	105° 36.108′	105° 38.837′	105° 43.899′
Elevation (m asl)	3051	3140	3231	3016
Surface area (ha)	3.3	4.9	6.0	4.8
Maximum water depth (m)	6.9	9.3	12.0	10.0
Record				
Record age (cal. year BP)	5872	6129	6150	4706
Mean sedimentation rate ± SD (cm per year)	0.0822 ± 0.0502	0.0326 ± 0.0184	0.0444 ± 0.0448	0.0563 ± 0.0317
Mean sample resolution ± SD (year per sample)	8 ± 4	17 ± 4	13 ± 3	11 ± 4
Median sample resolution (year per sample)	8	18	13	11
Median SNI (Kelly *et al.* 2011)	5.36	5.75	5.50	4.69

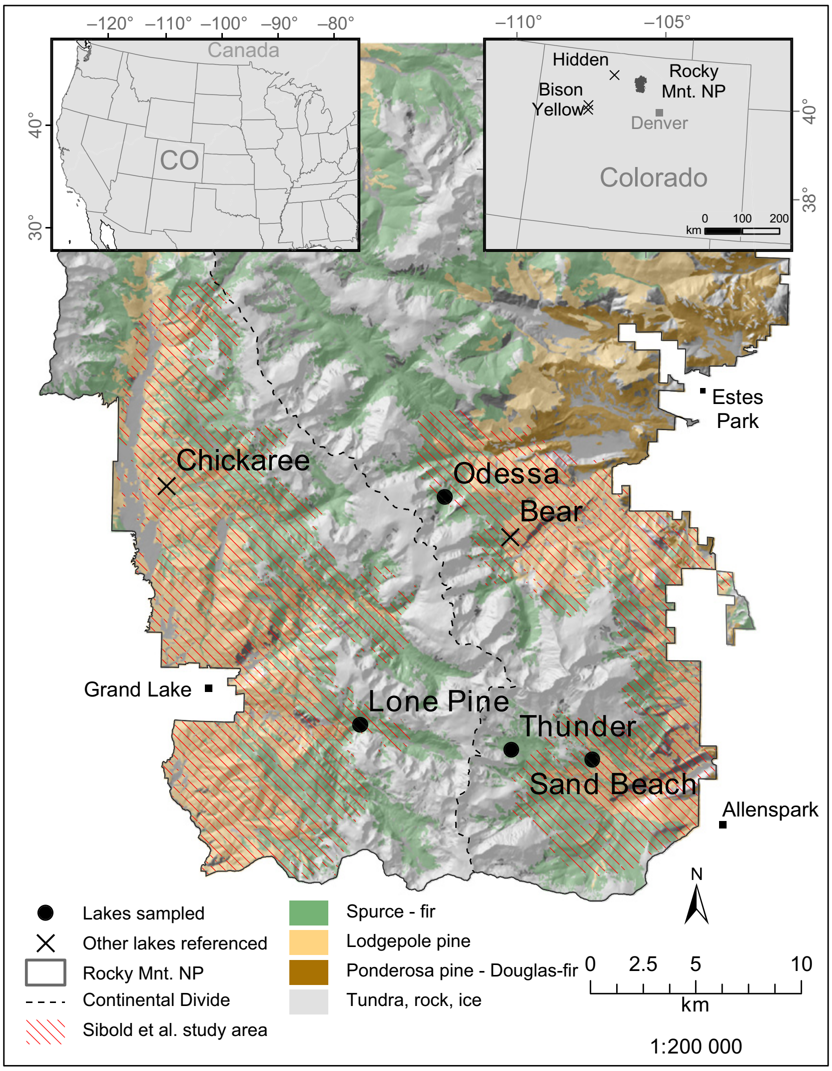

Fig. 1. Map of study area and sample lakes. Lakes sampled were located in upper-elevation subalpine forests, largely within the area of a tree-ring-based fire-history reconstruction by Sibold, Veblen & Gonzalez (2006). Palaeoclimate records from Hidden Lake (Shuman *et al.* 2009), Bison Lake (Anderson 2011) and Yellow Lake (Anderson 2012) are identified on the regional inset map, and the pollen and charcoal records from Bear Lake (Caffrey & Doerner 2012) and Chickaree Lake (Dunnette *et al.* 2014) are identified on the main map (X).

precipitation of 550 mm. West of the Continental Divide, average maximum July and December temperatures in Grand Lake (2658 m asl) are 24.9 and 0.1 °C, with total annual precipitation of 510 mm (Western Regional Climate Center, 1981–2010 observations, accessed September 2013; available online).[1] Subalpine forests occur between 2500 and 3500 m asl and are dominated by Rocky Mountain lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm) at lower elevations and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) at upper elevations. Limber pine (*Pinus flexilis* James), quaking aspen (*Populus tremuloides* Michx.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are minor components on rocky outcrops and/or south-facing slopes. East of the Continental Divide, lower subalpine forests transition to montane forests dominated by ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud.) and Douglas-fir, whereas west of the Continental Divide, elevations are above ca. 2600 m asl and do not support montane forests.

The fire history of the study area is well documented for the last 350 years, based on tree-ring reconstructions by Sibold *et al.* (2007), Sibold, Veblen & Gonzalez (2006) and Buechling & Baker (2004). High-severity, stand-replacing fires are the dominant fire type, occurring during years with significant moisture deficits, typically associated with strong La Niña conditions of the El Niño Southern Oscillation. Fire rotations in subalpine forests (the amount of time it takes to burn an area equal in size to a study area, also termed 'fire cycle', Baker 2009) range from 145 to 405 years across different watersheds, with longer rotations at higher elevations (mean = 244, n = 5).

[1]http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak5076

LAKE SEDIMENTS AND LABORATORY ANALYSIS

At each of the four lakes sampled, two overlapping sediment cores were collected from the deepest portion with a modified Livingstone-type piston corer (Wright, Mann & Glaser 1984). The sediment–water interface was collected with a polycarbonate tube (Klein core) and extruded vertically in the field at 0.5-cm intervals. Remaining sections of all cores were split lengthwise in the laboratory and visually correlated based on sediment stratigraphy. Correlated sections were sliced at 0.5-cm intervals, including 3–5 cm of overlap between drives to confirm visual correlation with stratigraphic, magnetic susceptibility (not presented) and charcoal data.

Chronologies were based on the ^{210}Pb activity in the uppermost sediments and AMS ^{14}C ages of terrestrial macrofossils and/or bulk gyttja from deeper sediments. Dating of bulk sediments was justified based on a lack of carbonates in the sediments and in the study area. Measurements of ^{210}Pb activity were obtained from Flett Research Ltd. (Manitoba, Canada; http://www.flettresearch.ca) on 14–18 samples from the top 20–33 cm of sediment. Sample age was estimated using a constant-rate-of-supply model adapted from Binford (1990). Terrestrial macrofossils and bulk gyttja were treated with an acid–base–acid procedure (Oswald *et al.* 2005) and submitted to the University of California, Irvine's KECK Carbon Cycle AMS Lab, or the Lawrence Livermore National Laboratory's CAMS for radiocarbon measurements. All ^{14}C ages were calibrated to years before present (BP, before CE 1950) using the IntCal 04 data set in CALIB v5.01 (Reimer *et al.* 2004). Age models were developed using the MCAge-Depth program in Matlab, which applies a weighted cubic smoothing spline function with confidence intervals estimated through Monte Carlo methods (following Higuera *et al.* 2009).

For charcoal analysis, subsamples of 2.5–5 cm^3 (median = 4 cm^3) were taken from continuous 0.5-cm slices and placed in a 16-mL solution of equal parts 6% bleach and 10% sodium metaphosphate to soak for ≈24 h. The treated sediment was gently washed with tap water through a 125-μm sieve, and charcoal was identified at 10–40× magnification. Charcoal concentrations (pieces cm^{-3}) were multiplied by the sediment accumulation rate (cm $year^{-1}$) to calculate charcoal accumulation rates (CHAR, pieces cm^{-2} $year^{-1}$).

Pollen identification was performed on 1-cm^3 subsamples at varying intervals from Odessa, Thunder, and Lone Pine lakes. Sample preparation followed standard digestion methods (Faegri & Iversen 1975), and pollen grains were counted at 40–100 × magnification. Pollen data were expressed as a percentage of total terrestrial pollen grains.

STATISTICAL TREATMENT OF POLLEN AND CHARCOAL DATA

Pollen percentages from the eight dominant taxa were visually assessed for the past 6000 years in pollen diagrams. As an index of forest-cover change, we statistically analysed the ratio of *Picea* pollen grains, *a*, to *Pinus* pollen grains, *b*, in each sample (*Picea*:*Pinus* ratio), calculated as $[a - b]/[a + b]$, as used with pollen data to normalize values (e.g. Jimenez-Moreno *et al.* 2010). We created a composite record by averaging the *Z*-score of values from all three sites. In subalpine settings, the composite ratio can be interpreted as an index of forest density and/or proximity to treeline (Maher 1963; Fall 1997). Specifically, we interpret this ratio as an index of Engelmann spruce abundance (e.g. basal area, stem density or crown bulk density), based on the following rationale: (i) lakes today are surrounded by subalpine forests of spruce and fir, with lodgepole pine dominating at elevations immediately below the spruce–fir zone (Fig. 1); (ii) given prolific pollen production and dispersal of pine (e.g. Fall 1992), much of the pine pollen reaching our lakes likely originated from lower elevations (i.e. 'regional pollen rain'); even the uppermost samples in each lake averaged 62% pine pollen ($n = 3$, CE 1999–2007; Fig. S2), consistent with lakes in spruce–fir forests across western North America (Minckley *et al.* 2008); (iii) thus, if local pollen productivity was reduced, the relative proportion of regional pollen would increase. Based on this rationale, we would expect decreased forest density to be reflected by a lower *Picea/Pinus* ratio, consistent with modern samples from subalpine forests with dead vs. live canopy trees (Maher 1963). To identify the timing and magnitude of significant changes in the *Picea*:*Pinus* ratio, a regime-shift algorithm was applied to the composite record (with an alpha of 0.05 and a span of 2000 years; Rodionov 2004). Finally, to visually display millennial-scale trends, the composite record was smoothed to 1000 years using locally weighted regression (Cleveland 1979), and a 95% confidence envelope was generated via 1000 bootstrapped samples of all values in each 1000-year window.

Prior to statistical analyses, charcoal samples were interpolated to 15 years, approximately equal to the median sample resolution of each record (Table 1). To estimate the timing of local fires at each site, we decomposed charcoal records to identify distinct peaks by applying a uniform set of threshold criteria to interpolated CHAR series, C_{int}, using the *CharAnalysis* program (Version 1.1, available online; as in Higuera *et al.* 2009).[2] Although the term 'local' typically refers to distances within 500–1000 m of each lake, representing an area of 100–300 ha (1–3 km^2; Gavin, Brubaker & Lertzman 2003; Higuera *et al.* 2007, 2010; Lynch, Clark & Stocks 2004), it is possible that charcoal from more distant, lower elevation sources also contribute to the charcoal record of these mountain lakes. Low-frequency trends in CHAR ('background', C_{back}) were estimated using a 1000-year, locally weighted regression robust to outliers (Cleveland 1979), a time span that generally maximized the signal-to-noise index, and C_{back} was removed by subtraction to create a detrended 'peak' series, C_{peak} (i.e. $C_{peak} = C_{int} - C_{back}$). We used the 99th percentile of a locally fit Gaussian mixture model as the threshold value to identify charcoal peaks, assumed to represent local fires within the 15-year sample. Using the minimum-count test described in Higuera *et al.* (2010), peaks were screened to test whether variations between a 'peak' and the smallest 'non-peak' sample within the previous 10 samples (i.e. 150 years) differed statistically based on the charcoal counts and sample volume. Samples were considered different if the minimum-count test yielded a P-value < 0.05. Fire history at each site was quantified by plotting individual fire-event return intervals (FRI), and the mean FRI calculated over 1000-year periods; this long-term mean FRI was then smoothed using a locally weighted regression to highlight 1000-year trends. The 2.5th and 97.5th percentiles from 1000 bootstrapped mean FRIs were used to approximate 95% confidence intervals for each overlapping period.

To summarize fire history across the study area at decadal to millennial time-scales, we created composite records of FRIs and CHAR. The composite FRI record was created by pooling all site-specific FRIs and calculating the mean FRI within 500-year windows (with 95% confidence intervals estimates as for each individual site). We summarized charcoal accumulation rates across all sites with a CHAR index, created by transforming and standardizing interpolated CHAR series, C_{int}, from each site, and then averaging these series to create a single composite record (similar to Marlon *et al.* 2008, 2009, 2012). Specifically, we used a Box–Cox transformation to normalize C_{int} and then standardized this record by subtracting the mean value and dividing by the standard deviation (i.e. '*Z*-score'). For the nine samples (0.6%) with an interpolated CHAR value of 0, we added 0.01 before transformation. Results were virtually identical when transformed using a natural logarithm. The 2.5th and 97.5th percentiles from the 1000 bootstrapped samples were used to approximate 95% confidence intervals for each 15-year sample in the composite CHAR record. Specifically, for each bootstrapped sample, a composite was developed based on the average of *n* randomly selected sites, with replacement, where *n* is the total number of sites recording (three from 6000 to 4400 cal. year BP, and four from 4400 cal. year BP to present). This composite CHAR series has a 15-year resolution and was smoothed to highlight 100- and 500-year trends with a locally weighted regression.

[2] https://sites.google.com/site/charanalysis/

Results

CHRONOLOGIES AND SAMPLE RESOLUTION

In total, 32 ^{14}C dates and 45 ^{210}Pb samples were used to develop age-depth models for the records (See Table S1 and Fig. S1 in Supporting Information). Two ^{14}C dates at Thunder Lake, from concentrated charcoal at 21.0–21.5 cm depth and a wood macrofossil at 52.0–53.0 cm depth, were not used in the chronology because they were older than stratigraphically adjacent dates from bulk gyttja (within 8 cm) and inconsistent with two other dates constraining the chronology within ca. 30 cm depth. Rejected dates likely represent material with a long terrestrial residence time before burial in the lake sediments (Oswald *et al.* 2005).

The median time between discontinuous pollen samples was 231 years (mean = 216, standard deviation = 80, range = 52–437; Fig. S2). Median sample resolution for charcoal analysis ranged from 8 to 18 years per sample across sites (means = 8–17, standard deviations = 3–4), with 77% of all samples representing sediment deposition of ≤ 15 years (i.e. the interpolation interval for charcoal analysis; Table 1, Fig. S3). A 15-year resolution implies a minimum detectable fire return interval of 30 years and minimum mean fire return interval of ca. 75–125 years (i.e. ≈3.3–5.0 × sample interval; Clark 1988; Higuera *et al.* 2007), well below the minimum tree-ring-based fire rotation (FR) reconstructed in the study area over the past ca. 300 years (i.e. 145 years; Sibold, Veblen & Gonzalez 2006). The probability of repeated burning within 30-year intervals, assuming the minimum 145 year FR, is < 20%; we nonetheless use the term 'fire episode' to acknowledge that some peaks may include more than one fire.

SITE-SPECIFIC AND COMPOSITE POLLEN RECORDS

Seventy-eight pollen samples were counted across the three sites, with an average of 533 terrestrial grains per sample (standard deviation = 127, maximum = 826, minimum = 263). Pollen spectra were dominated by *Pinus*, *Picea*, *Abies* and *Artemisia*, which made up >65% of terrestrial pollen grains in all but one sample from all records (median = 83%). With Poaceae, Rosaceae, other Tubuliflorae and Chenopodiaceae, these eight pollen types accounted for 71–98% of the terrestrial pollen grains in all samples (median = 91%). Fifty-three per cent of the *Pinus* grains were preserved well enough to identify the subgenera, and of these, 98% were assigned to subgenus *Pinus* and 2% to subgenus *Strobus*. We therefore assume that *Pinus* pollen primarily represents lodgepole pine (*Pinus contorta*, subgenus *Pinus*) rather than limber pine (*Pinus flexilis,* subgenus *Strobus*).

Pollen spectra displayed subtle changes over the last 4000–6000 years, with the greatest variation in *Pinus*, *Picea* and *Artemisia* (Fig. S2). Changes in *Picea* and *Pinus* were highlighted in the composite *Picea/Pinus* ratio time series (Fig. 2a), which features two significant decreases at 5540 and 2440 cal. year BP. The latter shift (at 2440 cal. year BP) is the most robust because it is based on data from all three records, and it is the only shift consistent with the bootstrapped confidence intervals on the 1000-year smoothed record (Fig. 2b).

SITE-SPECIFIC CHARCOAL RECORDS AND INFERRED FIRE HISTORIES

Charcoal was abundant at all sites, with mean (median) charcoal counts in each sample at Sand Beach, Thunder, Odessa and Lone Pine lakes of 28 (17), 30 (24), 23 (18) and 42 (31) pieces, respectively; corresponding mean (median) charcoal accumulation rates were 0.26 (0.17), 0.32 (0.25), 0.42 (0.31) and 0.73 (0.50) pieces cm^{-2} $year^{-1}$ (Fig. S3). All records displayed high-frequency variability, with median signal-to-noise index values >3, the theoretical minimum value for justifying peak analysis (Kelly *et al.* 2011; Table 1).

Peak analysis was generally robust to the alternative threshold values, with a total of 19, 20, 19 and 18 peaks identified at Sand Beach, Thunder, Odessa and Lone Pine lakes, respectively, over their period of record (Table 2, Fig. S3). Individual fire-episode return intervals (FRIs) varied widely at any lake, from the minimum detectable 30 years (Odessa and Lone Pine) to 1035 years (Lone Pine), but confidence intervals on the record-wide mean (median) FRI did not overlap, ranging from 237 (150) to 328 (308) years across all sites (Table 2). Peak magnitude varied from 0.001 to 163, but median values of 6.86, 4.04, 3.54 and 7.17 pieces cm^{-2} $peak^{-1}$ at Sand Beach, Thunder, Odessa and Lone Pine lakes, respectively, were not significantly different (nonparametric Kruskal–Wallis ANOVA, $P = 0.730$; Fig. S3). When all sites were pooled, however, the median peak magnitude was higher before (7.17 pieces cm^{-2} $peak^{-1}$) relative to after (2.73 pieces cm^{-2} $peak^{-1}$) the drop in the *Picea/Pinus* ratio at 2440 cal. year BP (Wilcoxon rank sum test, $P = 0.022$).

Weibull models fit to record-wide FRI distributions passed the goodness-of-fit test ($P > 0.10$) and yielded Weibull-estimated means statistically similar to the calculated mean FRIs (Table 2). The distribution of FRIs was similar among all sites (as indicated by a likelihood ratio test) when comparing the entire period of record ($0.21 \leq P \leq 0.92$), and periods before ($0.10 \leq P \leq 0.92$) and after ($0.49 \leq P \leq 0.98$) the drop in the *Picea*-to-*Pinus* pollen ratio at 2440 cal. year BP. These results are consistent with visual display of 1000-year smoothed mean FRIs, which illustrate variability through time but overlapping 95% confidence intervals within and between records (Fig. S3).

COMPOSITE FIRE HISTORY

The composite FRI record generally varied non-significantly over the past 6000 years, with 500-year mean values typically between 150 and 250 years. The exception was a period centred on 3690 cal. year BP (incorporating data from 3440 to 3940 cal. year BP) when the 500-year mean FRI was 77 years (95% CI = 54–100 years), significantly shorter than periods before and immediately after (Fig. 2b). The overall

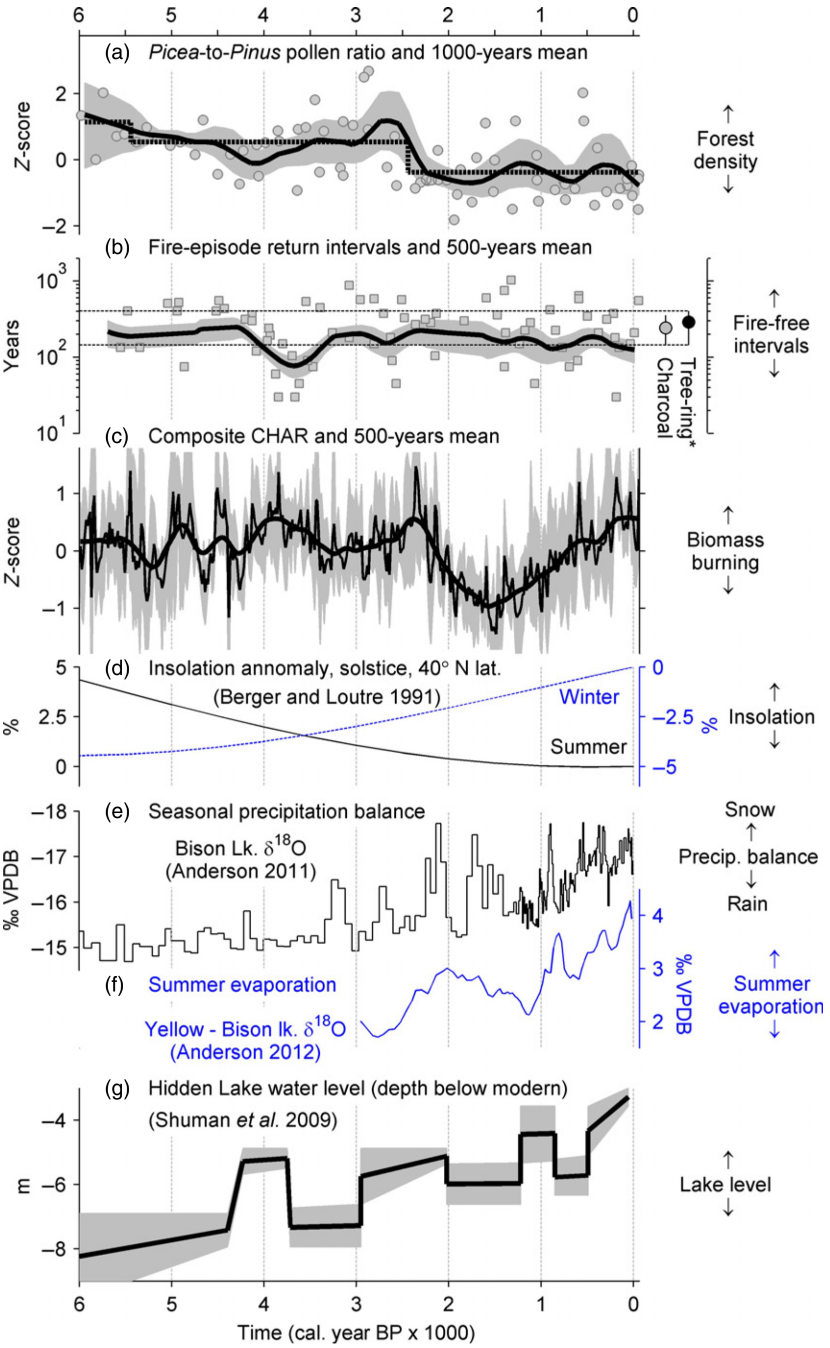

Fig. 2. Millennial-scale vegetation, fire and climate history. (a) The *Picea*-to-*Pinus* pollen ratio (points), a composite from three sites from 4400 cal. year BP to present and two sites from 6000 to 4400 cal. year BP (black curve and grey envelope representing 95% CI). The ratio shifts to lower values at 5400 and 2400 cal. year BP, as identified with a regime-shift algorithm (black dashed line; Rodionov 2004). (b) Individual fire-event return intervals (FRI) from each site (squares), and the composite mean FRI averaged and smoothed over 500-year periods (note log-scale *y*-axis). The mean FRI and bootstrapped 95% confidence intervals from the charcoal record for the period 300–0 cal. year BP (CE 1650–1950) are compared to estimated fire rotations from tree-ring records over the same period (*Buechling & Baker 2004; Sibold, Veblen & Gonzalez 2006) on the right side of the panel (grey and black circles). (c) Composite CHAR record at 15-year intervals (with bootstrapped 95% confidence intervals) and smoothed to 500 years. (d) Palaeo insolation for the summer (21 June) and winter (21 December) solstice at 40° N latitude (Berger & Loutre 1991). (e) Palaeoclimate record of seasonal precipitation balance, inferred from calcite oxygen isotopes preserved in Bison Lake (*y*-axis reversed; Anderson 2011), reflecting more snow- or rain-dominated precipitation regimes. (f) Palaeoclimate record of summer evaporation, inferred from the difference between calcite oxygen isotopes from Yellow Lake and Bison Lake (Anderson 2012), where greater differences suggest increased summer evaporation. (g) Lake-level history of Hidden Lake (with 95% confidence intervals; Shuman *et al.* 2009), where higher lake levels are interpreted to indicate more winter-dominated precipitation regimes.

range of mean FRIs (150–250 year) is generally consistent with tree-ring-estimated fire rotations (the area-based equivilant to a mean FRI; Johnson & Gutsell 1994) from within the study area since CE 1650, which ranged between 145 and 405 years (mean = 277, bootstrapped 95% CI = 222–353, $n = 5$ watersheds; Buechling & Baker 2004; Sibold, Veblen & Gonzalez 2006). When summarized over the same time period as this tree-ring data set, our composite FRI record is consistent, yielding an estimated mean FRI of 244 years (95% CI = 144–356, $n = 8$ FRIs; Fig. 2b).

In contrast to the FRI record, the composite CHAR record displayed significant high-frequency variability, indicated by non-overlapping 95% confidence intervals between multiple periods (Fig. 2c). The most striking trend in the composite CHAR record was a decrease in CHAR, initiated ca. 2350 cal. year BP, immediately after the significant decrease in the *Picea/Pinus* pollen ratio ca. 2440 cal. year BP (Fig. 2c). Low CHAR lasted until ca. 1500 cal. year BP, after which values increased towards present, returning to pre-2400 cal. year BP levels by ca. 500 cal. year BP (Figs 2c and 3a).

Discussion

VEGETATION AND FIRE HISTORY OF SUBALPINE FORESTS

The vegetation history of subalpine forests in Rocky Mountain National Park provides context for interpreting Holocene

Table 2. Fire-history statistics at the site and composite levels, from four lakes in Rocky Mountain National Park, Colorado, USA, spanning the past 6000 years

		Fire-history parameter (95% CI)						
Site(s)	n_{fri}	Range of fire return intervals (year)	Mean fire return interval (year)	Median fire return interval (year)	Weibull goodness-of-fit: KS stat. (P)[†]	Weibull *b* parameter (year)	Weibull *c* parameter (unitless)	Weibull-estimated firecycle[‡]
Sand Beach Lake	18	75–885	328 (244–425)	300 (195–405)	0.10 (0.99)	369 (268–484)	1.74 (1.36–2.75)	329 (239–430)
Thunder Lake	19	45–750	290 (201–383)	285 (120–375)	0.11 (0.95)	321 (225–430)	1.50 (1.15–2.29)	290 (206–383)
Odessa Lake	18	< 30–645*	314 (223–403)	308 (150–480)	0.11 (0.97)	346 (237–457)	1.49 (1.09–2.49)	312 (225–405)
Lone Pine Lake	17	< 30–1035*	237 (141–358)	150 (90–270)	0.16 (0.71)	250 (158–390)	1.14 (0.94–1.97)	239 (144–366)
Composite	72	< 30–1035*	293 (249–341)	233 (180–315)	0.06 (0.94)	323 (269–383)	1.42 (1.23–1.72)	294 (249–348)

*Given the 15-year resolution of the (interpolated) charcoal records, 30 years is the minimum possible FRI. Any return intervals < 30 years would not be resolved by these records.

†Results from a one-sample Kolmogorov-Smirnov (KS) test for the null hypothesis that the observed distribution of FRIs came from a Weibull distribution with the estimated parameters from the following columns. The KS statistic and the associated probability of Type I error, *P*, is provided. None of the *P* values suggests the Weibull models are poor fits to the empirical data.

‡The fire cycle, *FC*, is equivalent to the point-specific mean fire return interval (Johnson and Gutsell 1994), and it can be calculated from the Weibull model as: $FC = b\,\Gamma(1/c + 1)$, where Γ is a gamma function. To the extent that the Weibull model fits the observed data well, then *FC* will be equivalent to the calculated mean fire return interval.

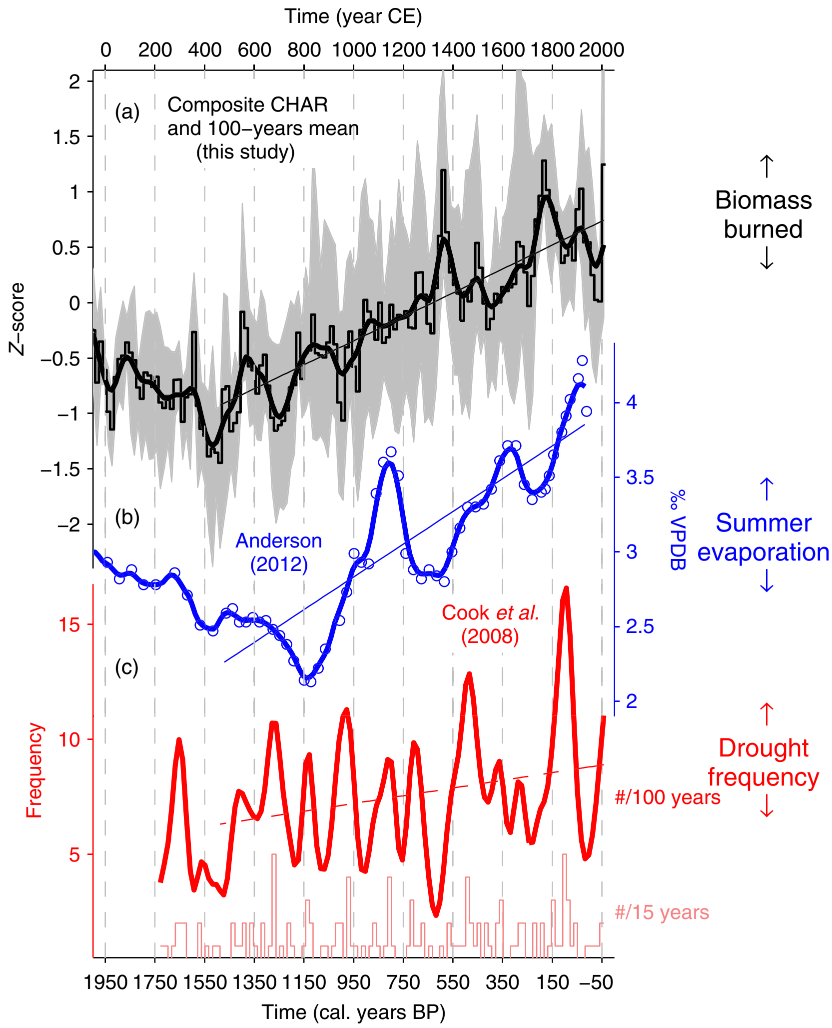

Fig. 3. Centennial-scale fire–climate relationships. (a) Composite CHAR at 15-year intervals (with bootstrapped 95% confidence intervals) and smoothed to 100 years. The linear trend since 1500 cal. year BP is significant (Pearson's $r = 0.832$, $P = 0.004$, accounting for autocorrelation). (b) Palaeoclimate record of summer evaporation, inferred from the difference between calcite oxygen isotopes from Yellow Lake and Bison Lake (Anderson 2012), where greater differences suggest increased summer evaporation. The linear trend since 1500 cal. year BP is significant (Pearson's $r = 0.867$, $P = 0.007$, accounting for autocorrelation). (c) Reconstructed drought frequency (Cook *et al.* 2007, grid point 131), calculated as the number of years within the same 15-year intervals represented by the charcoal record with reconstructed PDSI values < −4 and smoothed to 100 years. The linear trend since 1500 cal. year BP is moderately significant (Pearson's $r = 0.279$, $P = 0.099$, accounting for autocorrelation).

fire regimes by establishing the major fuel types available for burning and aspects of forest density and fuel structures relevant to fire behaviour. The pollen records from Odessa, Thunder and Lone Pine lakes highlight a dominance of subalpine forest taxa over the past 6000 years (i.e. Engelmann spruce, subalpine fir and lodgepole pine), with no major changes in species composition relative to modern forest composition (Fig. S2). This lack of change is consistent with pollen records from subalpine forests in Rocky Mountain National Park (Caffrey & Doerner 2012; Dunnette *et al.* 2014) and the region (e.g. Minckley, Shriver & Shuman 2012). A significant difference between past and modern subalpine vegetation was the likely higher forest density that persisted from 6000 to 2400 cal. year BP, indicated by higher *Picea/Pinus* pollen ratios at our sites (Fig. 2a) and consistent with inferred dense spruce–fir forests from 7000 to 3520 cal. year BP at Bear Lake (Fig. 1; Caffrey & Doerner 2012). Plant macrofossil and pollen evidence from other sites in southern, central and northern Colorado suggests that treeline was above its present elevation from ca. 9000 to 3500 cal. year BP (Carrara, Trimble & Rubin 1991; Fall 1997; Benedict *et al.* 2008; Jiménez-Moreno & Anderson 2013), which is also consistent with our interpretation of higher-than-present forest density in Rocky Mountain National Park.

Based on tree-ring and composite lake-sediment records, the fire history in subalpine forests of Rocky Mountain National Park is characterized by persistent low-frequency (i.e. mean return intervals >100 year), stand-replacing fires. From multicentennial through millennial scales, the rate of subalpine forest burning (i.e. the frequency component of the fire regime) did not change significantly over the past 6000 years, with mean fire-episode return intervals (FRIs) generally consistent with the variability evident in tree-ring records spanning the past several centuries (Buechling & Baker 2004; Sibold, Veblen & Gonzalez 2006; Table 2, Fig. 2b). At shorter time-scales and the site level, however, individual FRIs varied widely, from the minimum detectable value of 30 years up to 1035 years (Table 2). Several aspects of our records suggest that most fires were likely stand-replacing crown fires, although we cannot rule out the occurrence of low or mixed severity fires in the past because sediment charcoal records are best able to detect high-severity fires (Higuera *et al.* 2010). First, the high signal-to-noise index (SNI) in the charcoal records (Table 1) indicates good separation between peak and background values (Kelly *et al.* 2011), as typically seen in stand-replacing fire regimes (e.g. boreal and subalpine forests, Higuera *et al.* 2009; Courtney Mustaphi & Pisaric 2013). A surface-fire dominated fire regime would likely result in lower SNI values, as surface fires in this vegetation type create significantly less charcoal than stand-replacing fires (e.g. Dunnette *et al.* 2014). Secondly, long fire return intervals are likewise consistent with modern stand-replacing fire regimes (Baker 2009). And finally, the persistence of subalpine forest vegetation over millennia, dominated by thin-barked, fire-sensitive spruce, fir and pine species, would be difficult to maintain under a regime of frequent surface fires (Baker 2009).

In contrast to relatively stable mean FRIs, total biomass burning varied significantly from decadal through multicentennial time-scales (as inferred from the composite CHAR record, Fig. 2c). The most pronounced shift occurred ca. 2400 cal. year BP, when composite CHAR decreased from its 6000 to 2400 cal. year BP average of 0.166 (unitless; std. = 0.424) to the record low of −1.448 by 1500 cal. year BP (Fig. 2c). Because the rate of forest burning did not vary significantly over this transition, we interpret decreased CHAR as reflecting less biomass burned per fire episode, one aspect of fire severity. Specifically, we use the term 'fire severity' here to refer to the total biomass burned in a given number of fires (Kelly *et al.* 2013). An alternative interpretation that decreased charcoal production resulted from smaller fires (Ali *et al.* 2012) is unlikely, because of the mathematical equivalency between fire frequency and area burned per unit time at the landscape scale (Johnson & Gutsell 1994). That is, smaller fires at the landscape scale (i.e. as indicated by a composite CHAR record) would ultimately lead to less frequent burning at the point scale (i.e. as reflected in a composite FRI record).

Decreased biomass burning after ca. 2400 cal. year BP thus likely reflects a shift to lower severity crown fires relative to those of the middle Holocene. Significantly lower charcoal peak magnitudes (Fig. S3), an assumed proxy for fire severity (and/or proximity) at local scales (e.g. Whitlock *et al.* 2006), and a reduced frequency of high-severity fires at nearby Chickaree Lake (Dunnette *et al.* 2014) after ca. 2400 cal. year BP also support the interpretation of less charcoal production per fire episode and reduced fire severity. Since ca. 1500 cal. year BP, biomass burning increased steadily, suggesting an increase in the severity of stand-replacing fires, burning more biomass per fire episode relative to fire activity from 1500 to 2000 cal. year BP. Specifically, while the composite CHAR record increased from 1500 cal. year BP to present, fire frequency (Fig. S4), mean FRIs and forest density (indicated by the *Picea*:*Pinus* ratio) remained largely unchanged (Fig. 2a,b).

DRIVERS OF FIRE-REGIME VARIABILITY

Shifts in crown-fire severity and subtle variability in mean fire return intervals reflect the direct and indirect impacts of millennial-scale changes from warmer-than-present summers in the middle Holocene to cooler, likely drier summers and more snow-dominated precipitation balance in the late Holocene (Bartlein *et al.* 1998; Anderson 2011, 2012; Shuman 2011). These climate changes were ultimately governed by decreasing summer and increasing winter insolation, which at 40° north latitude were 4% higher and lower than present at 6000 cal. year BP, respectively (Fig. 2d; Berger & Loutre 1991). Although summers were warmer than present in the middle Holocene, the evidence of higher treeline, dominated by mesophilic Engelmann spruce and subalpine fir (Thompson, Anderson & Bartlein 1999), implies higher-than-present moisture availability during the growing season (e.g. Hessl & Baker 1997; Minckley *et al.* 2008). The moisture source was likely summer precipitation, as suggested by above-average oxygen isotope values (i.e. more enriched in ^{18}O) in carbonate-rich sediments from Bison Lake and Yellow Lake, located ca. 150 km south-west of the study area (Anderson 2011, 2012; Figs 1 and 2e,f), and by palaeoclimate simulations that suggest stronger-than-present summer monsoons in the middle Holocene (Bartlein *et al.* 1998). While seemingly contradictory, evidence of lower lake levels during the middle Holocene at Hidden Lake (ca. 80 km to the northwest of the study area; Shuman *et al.* 2009; Figs 1 and 2f) and elsewhere in the Rockies (Shuman *et al.* 2010) may have been a response to reduced winter precipitation as well as earlier timing of snowmelt. We suggest that the combination of warmer summers, greater summer precipitation and reduced snowfall in the middle Holocene may explain the near-modern rates of fire activity over this period as well as the expansion of subalpine forest and low lake-level records in the region. These changes could have favoured increased crown-fire occurrence or intensity during the middle Holocene through several mechanisms. Increased forest density suggested by the pollen record was likely associated with increased crown bulk density and/or lower canopy base heights, both of which would favour crown-fire occurrence and spread (van Wagner 1977). Lower fuel moistures during the summer, due to warmer temperatures and/or early snow melt, would have exacerbated the fuel-related changes and further increased fire intensities (van Wagner 1977).

CLIMATE INFLUENCED FIRE REGIMES INDIRECTLY AT MILLENNIAL TIME-SCALES

In the middle Holocene (ca. 6–2.4 ka BP), fires were more severe than in recent millennia, reflecting the impacts of warmer-than-present summers on fuels. Increased forest density (*Picea*:*Pinus* ratios, Fig. 2a) and extent (Carrara, Trimble & Rubin 1991; Fall 1997; Benedict *et al.* 2008; Jiménez-Moreno & Anderson 2013) would have elevated fire hazard by increasing crown bulk densities and fuel loading, relative to subalpine forests of the past two millennia. With the lowering of regional treeline after ca. 3500 cal. year BP and decreased forest density locally at ca. 2400 cal. year BP, fire regimes exhibited a pronounced decline in crown-fire severity, which lasted from ca. 2000–1000 cal. year BP.

The importance of climate's indirect impacts on fire regimes, namely through altering fuel composition or structure, is an emerging theme from studies of fire regimes at broad spatial and/or long temporal scales. For example, biomass burning increased globally with the transition from the late-glacial period to the early Holocene, coincident with post-glacial warming and increases in biomass availability (16 000–8000 cal. year BP, Daniau *et al.* 2012), with similar patterns documented across western North America (e.g. Marlon, Bartlein & Whitlock 2006; Marlon *et al.* 2009). In boreal Alaska, pronounced millennial-scale increases in fire activity have been consistently associated with the development of boreal forests, presumably because increased forest density and the flammable nature of black spruce (Viereck, Van Cleve & Dyrness 1986; Johnson 1992) increased landscape flammability (ca. 6000–4000 cal. year BP; e.g. Lynch *et al.* 2003; Brubaker *et al.* 2009; Higuera *et al.* 2009; Kelly *et al.* 2013). Moreover, analyses of modern fire data at regional and global scales also link the probability of burning over decadal time-scales to biomass availability (e.g. Krawchuk *et al.* 2009; Parisien & Moritz 2009; Krawchuk & Moritz 2011; Moritz *et al.* 2012; Pausas & Paula 2012; Pausas & Ribeiro 2013).

In comparison with these large shifts in fire activity across broad vegetation gradients, past variations in fire regimes in Rocky Mountain subalpine forests seem rather subtle. Their significance lies in illustrating how climate change can impact fire severity through fuel modifications alone, without necessarily altering fire frequency (or mean FRIs). This information adds complexity to our understanding of 'high-severity' fire regimes (e.g. Schoennagel, Veblen & Romme 2004) by suggesting that fire severity (and associated impacts on carbon and nutrient cycling) can be altered even when the frequency of burning remains constant. This finding points to the merits of a recent classification of modern global fire regimes, which emphasizes that even low-frequency, high-severity fire regimes are characterized by a range of fire intensities (Archibald *et al.* 2013).

CLIMATE IMPACTED FIRE REGIMES DIRECTLY FROM MULTIDECADAL THROUGH MILLENNIAL TIME-SCALES

In contrast to the decrease in fire severity ca. 2400 cal. year BP, which was associated with decreased forest density, the distinct increase in CHAR and inferred fire severity over the past 1500 years likely reflects the direct impacts of hydroclimatic change. Summer moisture deficits (precipitation minus evaporation) increased strongly from 1500 cal. year BP to present (Anderson 2011; Fig. 3b), as did drought frequency (PDSI < -4, Cook *et al.* 2007; Fig. 3c). Taken together, these changes suggest that multicentennial scale increases in summer drought resulted in more severe crown fires through greater drying of woody fuels over weeks to months.

Similar mechanisms linking summer moisture deficits to increased biomass burning likely explain more gradual shifts in fire activity over the past 6000 years as well. The Hidden Lake record indicates a late Holocene trend of increasing lake levels, associated with progressive summer cooling, more snow-dominated precipitation and, in the past 3000 years, increased summer evaporation (Fig. 2d–f). Superimposed on the trend of increasing lake level are short-term fluctuations, with below- (above-) average lake levels centred at ca. 5200 (4000), 3300 (2500), 1600 (1000) and 700 (300) cal. year BP (Fig. 4a). Millennial-scale mean FRIs were well correlated with these shorter-term fluctuations in lake level ($r = -0.78$, $P < 0.02$; Fig. 4b): when lake level was higher than average, likely reflecting a snow-dominated precipitation balance, mean FRIs were shorter, reflecting more frequent burning and likely drier summers. The only period when mean FRIs were significantly shorter than average, ca. 4000–3500 cal. year BP, likewise corresponded with the most prominent period of above-average lake levels of the past 6000 years. The significant correlation between records suggests that shifts in the hydroclimate (specifically, trade-offs between winter and summer precipitation) from multicentennial through millennial time-scales drove the variability around what were relatively stable long-term mean FRIs.

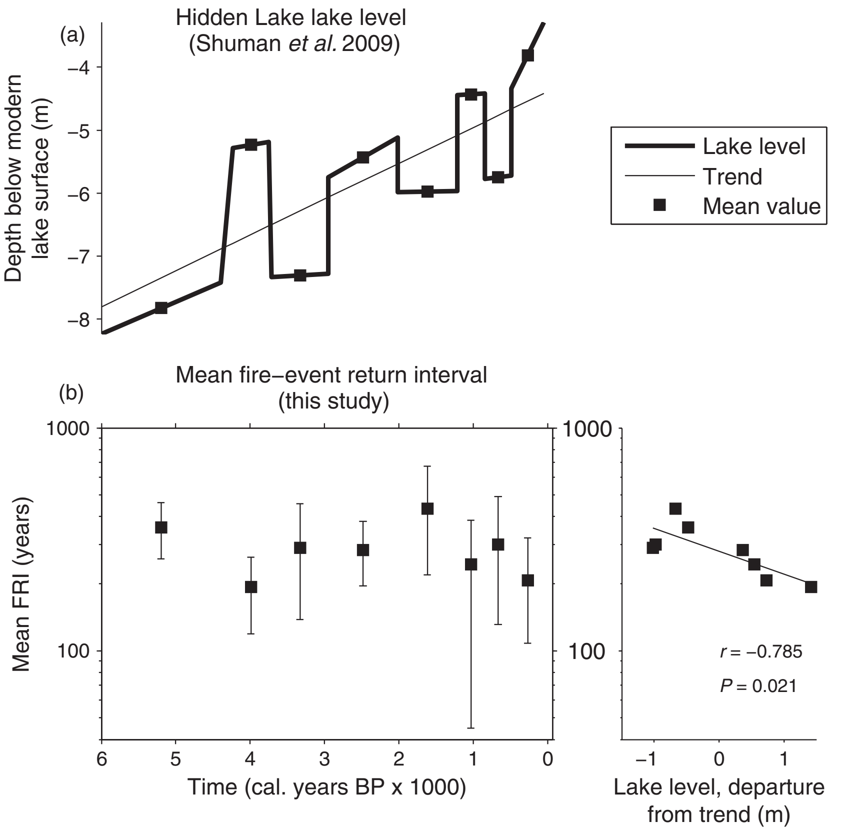

Fig. 4. Millennial-scale fire–climate relationships. (a) Lake-level data from Hidden Lake (Shuman *et al.* 2009) fit with a linear regression to represent the series-wide trend. (b) Mean fire-event return intervals for periods of above- and below-average lake level, with bootstrapped 95% confidence intervals. When lake-level anomalies were high ('departure from trend'), mean FRIs were low, suggesting more frequent fires during periods with winter-dominated moisture regimes (Pearson's $r = -0.785$, $P = 0.021$).

This interpretation of drier summers leading to lower mean FRIs over millennial time-scales is consistent with other studies in Rocky Mountain subalpine forests (e.g. Millspaugh, Whitlock & Bartlein 2000; Gavin *et al.* 2006; Anderson *et al.* 2008; Whitlock *et al.* 2011). Together, these studies highlight links between warm and/or dry summer climate and increased fire occurrence (i.e. suggesting 'climate-limited' fire regimes). The relationship between more frequent burning (lower mean FRIs) and elevated lake levels (Fig. 4b) is also evident at a subalpine forest site in Wyoming, dominated by lodgepole pine (Little Windy Pond, ca. 150 km north of Rocky Mountain National Park; Minckley, Shriver & Shuman 2012). Our interpretations of the cause of this relationship, however, differ from that offered for Little Windy Pond. We suggest that higher lake levels indicate snow-dominated winters and drier summers, on the grounds that higher lake levels occur with (i) lowering of regional treeline after ca. 3500 cal. year BP, as evidenced by macrofossil and pollen records; (ii) increasing summer evaporation and more snow-dominated precipitation regimes over the past 3000–6000 years inferred from oxygen isotope records; and (iii) increasing drought frequency over the past 1500 years inferred from tree-ring records. Minckley, Shriver & Shuman (2012), in contrast, interpreted high lake levels at Little Windy Pond as indicative of wetter summer conditions, with no analysis of winter conditions. They argued that during periods of low lake levels, lower effective moisture decreased fuel loading, prolonged post-fire regeneration and led to infrequent burning. Choosing between these two possibilities will require additional high-resolution fire-history records to resolve the spatial and temporal patterns of past fire regimes, as well as independent palaeoclimate proxies with clear sensitivities to summer moisture deficits.

Conclusions

The fire history of subalpine forests in Rocky Mountain National Park reveals complacency and sensitivity of fire regimes to changes in forest vegetation and hydroclimate over the past 6000 years. The rate of subalpine forest burning over the late Holocene was relatively constant, with variability largely consistent with that defined over the past several centuries from tree-ring data (Buechling & Baker 2004; Sibold, Veblen & Gonzalez 2006; Fig. 2b). This overall lack of distinct change indicates the persistence of a low-frequency, stand-replacing fire regime, despite significant changes in regional hydroclimate (Fig. 2e–g) and more subtle changes in forest density (Fig. 2a).

The relatively constant rates of forest burning contrast with the variability that occurred from multidecadal through multicentennial time-scales, reflecting the direct and indirect impacts of climate on fire regimes. Climate change impacted fire regimes directly by altering seasonal moisture balance and drought frequency. For example, over the last 1500 years, increased summer evaporation and drought frequency increased crown-fire severity. Indirectly, climate influenced fire regimes through changes in forest structure and ultimately fuels. For example, the shift to lower conifer density (i.e. lower stem density or crown bulk density) at ca. 2400 cal. year BP reduced fire severity, independently of any change in mean FRIs (Fig. 2).

Fire history of these subalpine forests provides an important context for considering the impacts of future climate change on fire regimes. Over the past several decades, mean annual temperature has increased by ca. 1 °C in Colorado, with more pronounced warming in subalpine environments; climate predictions suggest a continued shift towards higher summer temperatures (ca. 2.75 °C) and more winter-dominated precipitation by mid-century (Ray *et al.* 2008). A number of studies spanning recent centuries suggest that warmer, drier summers will increase the probability of subalpine forest fires (e.g. Schoennagel, Veblen & Romme 2004; Sibold & Veblen 2006; Westerling *et al.* 2011). The longer-term perspective offered here suggests a certain level of fire-regime resilience to late Holocene climate change. Over decadal to centennial time-scales, future climate warming may have more notable influences on fire severity, through direct impacts on fuel moisture and indirect impacts mediated by vegetation and fuels.

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Data accessibility

Data and code deposited in the Dryad repository (Higuera, Briles & Whitlock 2014). Charcoal data are also available via the International Multiproxy Paleofire Database (http://www.ncdc.noaa.gov/paleo/impd/) and the correspondence author's Web page or e-mail.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Radiometric dates for all sites.

Figure S1. Age-depth models for all sites.

Figure S2. Pollen records for Thunder, Odessa, and Lone Pine lakes.

Figure S3. Full charcoal records and inferred fire history for all sites.

Figure S4. Centennial-scale fire-climate relationships.