Fire-climate-vegetation linkages in quaking aspen forests during the late Holocene

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Abstract

Background

- Fire plays an important role in shaping forested systems around the globe. In the western US, fires are a ubiquitous process that affects virtually all forest types. Fires exhibit a wide range of frequencies and severity, which are often associated with forest type. Despite displaying a wide range of traits that would suggest they have evolved with fire, quaking aspen (*Populus tremuloides* Michx.) has been paradoxically considered resistant to fire (asbestos forests). Unlike many other fire-driven forest types, our understanding of pre-settlement fire behavior in quaking aspen systems is limited. To better understand the frequency and severity of fires in a putatively stable quaking aspen forest, we carefully selected a small, key watershed for sediment coring to reconstruct fire history.

Results

- For the past ~ 4,000 years this basin has been dominated by quaking aspen but also subalpine fir (*Abies lasiocarpa* (Hook.) Nutt), and their relative composition has shifted inversely over this time period. Large, stand-replacing fires occurred, on average, every 170 years, with individual fire-free intervals ranging from 132–323 years. With such a long fire return interval it is tempting to suggest that the fire regime was controlled from the top down, limited by climate. However, we found that the occurrence of fire was not predictably related to climatic conditions as characterized by cool-season, or warm-season, moisture availability (drought proxies). Rather, fire occurrence was most strongly related to fuel accumulation associated with the predictable successional shift in species dominance from quaking aspen to subalpine fir.

Conclusions

- The characterization of this aspen system as fuel-limited removes some barriers to contemporary fuels management. Unlike in climate-limited systems where managers have little control over fire occurrence due to climatic conditions (e.g., drought), fuel-limited systems are controlled from the bottom up, where the explicit reduction or redistribution of long-term fuel buildup is an effective approach to reducing the likelihood and/or effects of fire in the short-term. In the long-term, managers can expect stand-replacing fires in aspen forests, regardless of their characterization as asbestos forests.

Background

Management of quaking aspen (*Populus tremuloides* Michx.) forests has come under increased scrutiny due to their important contributions to regional biodiversity (Kuhn et al., 2011), landscape aesthetics (McCool, 2001), wildlife habitat (Madritch et al., 2009, LaRade & Bork, 2011), and their potential role in fire control (DeByle et al., 1987, Nesbit et al., 2023). In dry montane forest ecosystems of western North

America, quaking aspen is one of few hardwood species to form closed-canopy stands. Closed forest structure plays a crucial role in water retention (LaMalfa & Ryle, 2008) and supports ungulate browsing habitat (Lindroth & St. Clair, 2013), yet this canopy structure also promotes understory growth of shade-tolerant conifers during classical succession (Clements, 1910) that increase both ladder and surface fuel loads (DeRose & Leffler, 2014). As western North America continues to experience protracted drought (Anderegg et al., 2015) and amplified forest disturbance regimes (Raffa et al., 2008), quaking aspen's putative role as both a fire resistant and a fire-prone forest type (Morris et al., 2019) calls into question whether the principle drivers of wildfire are aligned with fuel-limitations, climate-limitations (Turner & Gardner, 2015), or both, especially over long time scales (Whitlock et al., 2010). The natural range of variability of fire in quaking aspen forests prior to the settlement era is of considerable interest for better understanding and management of the fire-climate-vegetation interactions in these important forests.

A probable outcome of advanced stand development in any forest ecosystem is increased biomass and concordant enhanced risk (probability) of a fire being severe or stand-replacing (Martin & Sapsis, 1991), especially over very long time-scales (Whitlock et al., 2010). This outcome is ideal for a fire-adapted species like quaking aspen; however, in western North America large fires tend to be suppressed in accordance with prevailing land management policies (Shinneman et al., 2013). In fact, over a century of fire suppression efforts in the US have likely contributed to declines in quaking aspen health, generally, across large areas of the landscape (DeByle & Winokur, 1985, Mueggler, 1989). Establishment and growth of conifers and other understory plants, regardless of their composition (Rogers et al., 2014), are associated with increases in surface fuel loading and ladder fuels, and an increasing probability that a surface fire can readily transition to the canopy (DeRose & Leffler, 2014), or that surface fuel loading is sufficient to create heat necessary to kill thin-barked aspen – in either case the result can be a stand-replacing fire (Fig. 1).

Contemporary fire planning and management is often guided by the best available reconstructions of pre-settlement-era fire behavior, e.g., return interval and fire severity (Kaufmann et al., 2006). Reconstructions of fire return intervals in fuel-limited systems, where wildfires were primarily of low-severity have been widely applied and are crucial for improved management, e.g., in Giant Sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz, Stephenson, 1999, Swetnam et al., 2009), and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson, (Stoddard et al., 2021). Reconstructing fire regimes in climate-limited systems, where fires were conventionally much larger and infrequent is rare, and therefore fire management in these systems has less guidance. While it has been suggested that management of fuels in climate-limited systems has little effect on fire hazard, and that management in fuel-limited systems can reduce fire hazard (Sharik et al., 2010, Stevens-Rumann et al., 2013), a longer-term perspective posits that it is possible that both fuel- and climate-limitations may drive fire regimes (Whitlock et al., 2010). Unfortunately, due to the short life span and relatively rapid decay of quaking aspen, virtually no reconstructions of pre-settlement fire regimes exist. Accordingly, whether quaking aspen-dominated systems exhibit climate-limited versus fuel-limited fire regimes has been largely unquestioned.

Fire’s role in promoting quaking aspen suckering is paramount; aspen’s ability to sucker vegetatively virtually guarantees a response to fire, or a fire surrogate (e.g., coppice silvicultural system, Frey et al., 2003). While recent work has indicated that quaking aspen appeared to be maintained in the absence of fire (Morris et al., 2019), more study is needed to detail and validate this functional relationship. It may be the case that quaking aspen stands are resistant to fire, but their ‘fireproof’ reputation is unhelpful for management, and complicates the science of better understanding aspen systems (Nesbit et al., 2023). Given the incomplete knowledge of the climate conditions that govern quaking aspen dominance over centennial to millennial timescales, coupled with a lack of understanding of the potential controls on disturbances, one could posit that the fire regime for quaking aspen-dominated systems is climate-limited, like has been found for other mid- to high-elevation forested systems (Margolis & Swetnam, 2013, Rocca et al., 2014). That is, the buildup of fuel is necessary, but not sufficient, for the occurrence of a high-severity (stand-replacing) fire. What is also necessary is an ignition during a suitable climatic period such as drought when fuel is drying (Hessilt et al., 2022).

Beyond the historical record, the potential linkages among climate, fire, and vegetation in quaking aspen-dominated landscapes are largely unknown. Only recently have retrospective studies examined the longer-term interactions of quaking aspen and its environmental determinants, and primarily using ecological proxy records from lake sediments (Morris et al., 2013b; 2019, Carter et al., 2017). The relatively limited number of paleoecological studies that address aspen ecology is due to the relative scarcity of perennial wetlands that favor preservation of terrestrial biological materials, like pollen, plant remnants, and charcoal. While these studies offer new insight into longer-term dynamics of fire, climate, and vegetation in quaking aspen-dominated forests, they specifically raise questions regarding how fire may have initiated and maintained quaking aspen dominance in montane settings. For example, quaking aspen-dominated the landscape during a period of frequent fires (~ 109-year fire return interval), above-average precipitation, and average temperature (Carter et al., 2017). By contrast, aspen pollen increased over a multi-millennial period where wet conditions limited fire occurrence (Morris et al., 2013).

Paleoecological data are poised to fill key knowledge gaps about longer-term dynamics of quaking aspen systems. Here we examine quaking aspen fire-climate-vegetation linkages using a 4,000-year, high-resolution pollen and charcoal record collected from a small lake situated in a large stable aspen forest in southwestern Utah (Fig. 1b). This record enables us to advance our understanding of how climate and fire interact with quaking aspen. We assess the possible linkages between fire, climate, and vegetation. If quaking aspen fire regimes are climate-driven, we would expect fire occurrence to be more likely during periods of suitable climate, i.e., cool-season moisture deficit, or warm-season moisture deficit, e.g., drought. Conversely, if the fire regime is fuel-limited then we would expect fires to occur predictably during times of fuel buildup or high biomass. We asked the following questions: 1) What is the long-term variability in fire return interval, vegetation composition, and climate for these quaking aspen-dominated forests? 2) Were fire events predictably fuel-limited or climate-limited? Specifically, we hypothesized: 1) Quaking aspen has not been dominant (i.e., stable) in this watershed for the last 4,000 years, and that fire events drove that instability, and; 2a) Fire occurrence will be predictably related to variability in seasonal moisture deficit, or; 2b) Alternatively, fire occurrence could be predictably related to fuel availability.

Methods

Study area and sampling approach

We located an unmodified, east-facing cirque lake situated in a stable aspen community in the Dixie National Forest of southwestern Utah. At the time of coring in September 2015, Sugarloaf Pond (37°40'20.47" N, 112°54'13.29" W, 2886 m asl) had a relatively small surface area (0.27 ha) and shallow water depth of ~ 8 m (Fig. 1). The western edge of the pond had evidence of a seasonal outflow channel. We retrieved a 2.75 m long sediment core using a modified Livingstone corer (Wright, 1967) deployed from a pontoon raft anchored at the lake center. Sugarloaf Pond is situated immediately west of the Markagunt Plateau between High and Sugarloaf Mountains. The watershed draining into Sugarloaf Pond is spatially small (< 1 km^2), and is a tributary to Lake Creek and Coal Creek, where the latter terminates into the Cedar Valley Aquifer in the eastern Great Basin (Eisinger, 1998). The modern vegetation community at Sugarloaf Pond is dominated by a nearly pure, mature aspen forest (Fig. 1) with canopy dominant stems that are approximately 170 years in age as indicated by increment cores that were collected in September 2015 (Morris et al., 2019).

The upland landforms in southwestern Utah receive significant warm-season precipitation derived from the North American Monsoon and during the cool-season from Pacific frontal storms (Mock, 1996, Adams & Comrie, 1997). Despite broad seasonal trends across the region, monthly precipitation maxima are heterogeneous due to complex topography and steep elevation gradients (Mock, 1996). Cool-season precipitation is modified by El Niño–Southern Oscillation (ENSO) modality (Ropelewski & Halpert, 1986, McCabe & Dettinger, 1999). ENSO modes are described as positive (or negative) indicating warm (or cool) sea surface temperatures in the southern Pacific Ocean. During an El Niño episode the southwestern US tends to receive greater-than-average winter precipitation, whereas arid, cool-season conditions prevail during La Niña, but long-term ENSO frequency and intensity is variable (Moy et al., 2002). Long-term ENSO variability generally increased over the course of the Holocene (i.e., last 11,200 years). In southern Utah, elevated risk and recurrence of wildfire aligns with La Niña modality (Schoennagel et al., 2005, Brown et al., 2008), and this sensitivity is reflected in vegetation and fire history reconstructions from sites located in the same region as Sugarloaf Pond (Feiler et al., 1997, Morris et al., 2013b; 2013a; 2015).

To reconstruct the fire and vegetation history at Sugarloaf Pond, sediment subsamples (5 cm^3) were collected contiguously at 1-cm intervals. These subsamples were analyzed for charcoal and macrofossils following standard protocols, processed with 125 um sieves, and then counted using light microscopy (Clark, 1988, Whitlock & Millspaugh, 1996, Gardner & Whitlock, 2001). During macrofossil analysis, conifer needles (i.e., subalpine fir, *Abies lasiocarpa* (Hook.) Nutt) were collected and identified, and nine were submitted for radiocarbon (^{14}C) analysis to establish age-depth control (see Morris et al., 2019), calibrated in Calib 7.1 (http://calib.org, accessed 2017-8-01, (Stuiver & Reimer, 1993), and modeled using the CLAM package (Blaauw, 2010).

To reconstruct fire events and recurrence intervals (i.e., the fire regime) we converted charcoal counts to concentration (particles/cm) and then charcoal accumulation rates (CHAR, particles cm^{-1} yr^{-1}). The charcoal concentrations were binned using the median sediment deposition time (10 years/cm) to minimize variations resulting from shifting sedimentation rates. Binned concentrations were then converted to CHAR and decomposed into the background (BCHAR) and peak components using CharAnalysis (Higuera et al., 2009). BCHAR is the slowly varying CHAR trend, and fire peaks are positive deviations from BCHAR, which we have interpreted as originating from a fire episode (i.e., a fire event). Peaks were determined using a Lowess smoother, robust to outliers, within a 500-year window (Higuera et al., 2010). BCHAR values for each time interval were subtracted from total CHAR. Peaks were defined as intervals with CHAR values above BCHAR, and were tested for significance using a Gaussian distribution, where peaks that exceeded the 95th percentile were considered significant. This procedure was applied for every 500-year overlapping portion of the record, resulting in a unique threshold for each sample. All peaks were screened to eliminate those that may have resulted from statistically insignificant CHAR variations (Gavin et al., 2006). If the maximum count in a CHAR peak had a greater than 5% chance of coming from the same Poisson-distributed population as the minimum of the preceding 75 years, the peak was rejected. We used a signal-to-noise index > 3 to indicate that CharAnalysis results were statistically robust (Kelly et al., 2011). To bolster confidence in our detection of peaks we repeated the CharAnalysis at the 90%, 95% and 99% level, all of which resulted in nearly identical timing of peak detection (results not shown). Charcoal peaks were interpreted as large-scale (either locally severe and/or spatially large) fire events in the Sugarloaf Pond watershed.

Pollen analysis

Sediment subsamples (1 cm^3) for pollen were processed, including the introduction of a known quantity of tracers (*Lycopodium*), and counted at 2-cm intervals (i.e., every other cm) using light microscopy (400x, Faegri et al., 1989). Pollen data for species was used to indicate the dominance of vegetation type (i.e., quaking aspen or conifer Morris et al., 2019). To determine the proportional change in vegetation and characterize the accumulation of fuel buildup over time, pollen count data were converted to percentage of the terrestrial sum in C2 version 1.7.7 (Juggins, 2007). The ratio of fir to aspen pollen (fir:aspen) was normalized using the formula (a-b)/(a + b) where a = fir and b = aspen (e.g., Simpson, 2018). To address fuel limitation, fuel buildup (e.g., productivity) was proxied by the fir:aspen ratio. Where we assumed the higher proportion of fir pollen indicated later forest successional stage and therefore higher fuel accumulation in the system such that fuel would not be a limiting factor after fire ignition. We also calculated the ratio of arboreal pollen to non-arboreal pollen (AP:NAP). We explored historical climate data from the region using the Parameter-elevation Regression on Independent Slopes Model at monthly resolution for the period 1901–2020 (PRISM 2018) extracted with ClimateWNA (Wang et al., 2016) in order to characterize the cool-season climate (non-growing season, ~October-May), and warm-season climate (June-September), which is the time period when the North American Monsoon materialized, historically.

Pollen data were also used as proxies for climate conditions. Cool-season climate was assumed to be predictable by the presence and quantity of Cyperaceae (e.g., sedges), which is often used as a proxy for cool and moist conditions (Lu et al., 2011, Chen et al., 2014). Cool-season precipitation influences lake-level and water tables, i.e., wetter soils and expanded marshes on the lake fringe support high Cyperaceae. We expected that when Cyperaceae was high it indicated moist conditions when fuel accumulation was high and drought-caused drying of fuel to be rare. When Cyperaceae was low, moisture was lacking and we would expect fires to be more likely if they were driven by dry climate conditions (e.g., drought). Summer moisture availability was assessed using the sagebrush (*Artemisia* spp.) to ragweed (*Ambrosia* spp.) ratio (sagebrush:ragweed) as a proxy (Morris et al., 2013a). Sagebrush prefers later seasonal arrival of precipitation while ragweed prefers moisture arriving earlier in the growing season (Maher, 1963, Cable, 1977). We assumed that the sagebrush:ragweed ratio is a useful qualitative proxy for the North American Monsoon because a greater amount of late season precipitation from an intensified monsoon would favor sagebrush over ragweed (higher ratio) and declining late season moisture would favor ragweed over sagebrush (lower ratio). A low ratio likely indicated increased drying during the warm-season, which in the Sugarloaf Pond area means lower monsoon-delivered moisture, and therefore higher chance for seasonally dry conditions and fire in the late-summer thru fall.

Fire event analysis

We tested whether fire events occurred more or less often than expected using a composite analysis. We tested for correspondence to cool-season climate, the primary driver of production on our site using Cyperaceae (see above). In this region, cool-season moisture arriving as snow is generally responsible for water table recharge (Bowen et al., 2011). We tested for correspondence to summer moisture using the sagebrush:ragweed. We also tested for correspondence to fuel buildup as stands shifted in composition from quaking aspen to subalpine fir (fir:aspen). Fire events indicated by CHAR Analysis (n = 20 events) were binned in their closest associated calendar year. Because time-series of climate and vegetation data were not stationary over the nearly 4,000 years of record, they were smoothed using a 5-year low pass filter with a 50% frequency cut-off, and standardized to their mean and standard deviation before performing the composite analysis. To composite, we tallied the observed shift in climate or vegetation data as counts of when the value changed sign and passed the mean observation (0 in z-score value). We then tallied the count of fire events that were observed in either the positive or negative direction associated with each time-series. Counts of expected and observed events were then analyzed using a boot-strapped (n = 2000) chi-squared analysis. Significance was assessed at the $P < 0.05$ level.

We repeated the test of fire events over an independent gridded climate reconstruction data set, the Palmer Drought Severity Index record for southwest Utah (grid point 087, Cook & Krusic, 2004) which allowed us to verify the latter half of the Sugarloaf Pond record (~ 2,000 years, n = 11 fire events). We smoothed the annual drought record using a 100-year cubic smoothing spline with a 50% frequency cut-off, standardized to its mean and standard deviation, and repeated the compositing and chi-squared analysis.

Results

Charcoal influx was a persistent and continuous feature of Sugarloaf Pond and decreased only toward the present (Fig. 2a). Robust, and repeated CharAnalysis indicated that there were 20 distinct 'peak' fire events, that were either local, and/or severe (e.g., stand-replacing), that occurred at Sugarloaf Pond (Fig. 2a). The fire return interval calculated from the peak events ranged from 132–323 years, with a mean of ~ 178 over the 4,000-year period (Fig. 2b). Background char values indicated that other fires occurred within this interval but were not likely to drastically change overstory species composition and structure (i.e., low-severity fires). The shifting fire regime mirrored fir:aspen in general, where more quaking aspen corresponded to shorter fire return intervals and more subalpine fir corresponded to longer fire intervals (Fig. 2b and 2d).

The major arboreal components of the Sugarloaf Pond record include quaking aspen and subalpine fir, which are both found in the watershed today (Figs. 1 and 3). The arboreal species occurring at relatively less abundances, such as Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco), pines (*Pinus* spp.), and spruce (*Picea* spp.), were also common throughout the contemporary environment. Like the arboreal community, the key shrub types identified in the pollen record could be found growing both in the watershed and surrounding landscape today. In the forest understory, common juniper (*Juniperus communis* L.) was conspicuous where juniper pollen became well-established in the record at 2600 cal yr BP (Fig. 3). The extra-local shrub community consisted of sagebrush, ragweed, and oak (*Quercus* spp.) also common throughout southwestern Utah, especially at lower elevations relative to Sugarloaf Pond. The herbaceous plants largely consisted of grasses (Poaceae), daisies (Asteraceae), and amaranth (Amaranthaceae).

The AP:NAP was relatively stable over the record, although there was a period of sustained greater shrub abundance between 2800–3500 cal yr BP (Fig. 2c). A conspicuous shift in the AP:NAP ratio towards great forest cover occurred towards modern, and was driven largely by increased fir pollen (Fig. 2c, 2d, and 3). The fir:aspen (Fig. 2d), exhibited a generally monotonic decline from 2500–4000 cal yr BP with a stepwise decrease towards relative more aspen after ~ 1700 cal yr BP. Quaking aspen pollen was generally more prevalent towards the present time (Fig. 3). Subalpine fir pollen over the entire record was negatively correlated to quaking aspen pollen ($r = 0.67$, $p < 0.05$). Increases in other later successional arboreal species mirrored those we found for subalpine fir (e.g., Douglas-fir), although their relative amount was lower (Fig. 3). The total pollen influx was variable over the record with conspicuously high values between 1600–1800 and 2200–2700 cal yr BP. After 1600 pollen influx declined and remained relatively low towards modern (Fig. 2e).

Cool-season moisture (Cyperaceae) was the primary source of annual moisture (Fig. 4c), having contributed 74% annually, on average, over the historical record, but that varied from very low (dry winters) to very high (wet winters). The warm-season moisture proxy (sagebrush:ambrosia), exhibited wide variability but generally decreased over time, with higher moisture early in the record and relatively lower moisture later (Fig. 4b). In the historical record, the four months of the warm-season (June-

September) only accounted for one quarter (~ 26%) of the annual moisture received, on average (Fig. 5). The strength of the NAM was roughly proportional to total annual precipitation, historically, which in turn was driven noticeably by ENSO (Fig. 4a and 4b).

Fire events at Sugarloaf Pond were not predictably related to cool-season moisture based on their occurrence with Cyperaceae pollen. Thirty-eight percent of the time fire occurred during high cool-season moisture, and 62% otherwise (Fig. 6a). Fire events were not related to warm-season moisture, rather they were equally likely to occur in seasons of high moisture (47%) versus seasons with lower moisture (53%, Fig. 6b). Fire events occurred much more commonly during periods of high subalpine fir dominance. Seventy-six percent of fires occurred during higher fir:aspen, whereas only 24% occurred during low fir:aspen ($p < 0.05$, Fig. 6c). The timing of fire events that did not occur during subalpine fir dominance ($n = 5$) were distributed uniformly across the last 3,000 years of the record (Fig. 6c). Eleven fire events were not predictably related to PDSI over the last 2,000 years. Fifty-five percent of these fires occurred during wet periods, while 45% of the events occurred during dry periods ($p > 0.05$). Although fire events were not related to cool-season moisture, the fire return interval was strongly and significantly related to cool-season moisture over the entire record ($r = 0.48$, $p < 0.05$), and when considering only years with fire events ($n = 20$) the relationship strengthened ($r = 0.6$, $p < 0.05$). The fire return interval was also positively correlated with fir:aspen ($r = 0.36$, $p < 0.05$)

Discussion

We hypothesized that the stable quaking aspen-dominated forest that surrounded Sugarloaf Pond has not always been dominated by aspen, and that stand-replacing fire was the mechanism that drove that change. We expected that those fire events would be predictably related to time periods characterized by moisture deficit (i.e., drought), either in the cool-season or the warm-season. Counterintuitively, we found no relationship between fire events and moisture deficit. We did, however, find a strong relationship that indicated that fire events were much more likely to occur when the composition of the forest was dominated by subalpine fir, presuming that total stand biomass was relatively high and fuel loading sufficient to support a fire large enough to be recorded as charcoal in Sugarloaf Pond. To complicate the story, the fire return interval was strongly positively correlated to cool-season moisture for the entire ~ 4,000 years of record, and this relationship strengthened when we consider only the years in which the fires occurred. In combination, these results suggest that in high-elevation quaking aspen forests fuel buildup was the driver of individual fire events, support for the fuel-limited hypothesis, but the longer-term fire return variability was likely driven by cool-season moisture, support for the climate-limited hypothesis, where wetter periods had longer intervals between fires and subsequently become increasingly dominated by subalpine fir.

The long-term record indicates that the drainage was likely in flux between quaking aspen and subalpine fir as biomass dominant trees for virtually the entire ~ 4,000-yr period of record. Fire was likely the process that drove relatively rapid shifts from high biomass overstory to aspen dominance on a scale of 1–2 centuries, on average. High biomass accumulation was both necessary and sufficient to create conditions for fire. There was no evidence that climate was a limiting factor (e.g., drought) for fire occurrence. Droughty regional conditions, either in the cool-season or warm-season did not coincide with subalpine fir overstory dominance during fire events. Fire events led to post-fire dominance by quaking aspen, but at the scale of centuries aspen always eventually succeeded to subalpine fir. Of the metrics tested, the occurrence of fire events was much more likely at high subalpine fir composition, and did not predictably occur during cool-season or warm-season moisture deficits (Figs. 6c and 7).

That our reconstructed fire return interval was as short as 132 years, or as long as 323 years was consistent with some previous research speculating on the range of probable fire frequencies in aspen-dominated forest types (Shinneman et al., 2013). Age structure analyses in Colorado aspen forests estimated that the fire return interval prior to human settlement was ~ 140 years and required over a century for an area the size of their study to burn (~ 76 km^2, understanding some would burn more than once, and some never (Romme et al., 2001). In contrast, the modeled fire regime condition class characterization of the aspen biophysical settings for the Southern Rocky Mountain quaking aspen communities suggested that fire return intervals were ~ 10–120 years, whereas those for the Northern Rocky Mountain quaking aspen communities ranged from 10–165 years (Hann et al., 2005). It is not possible to differentiate from within these two different biophysical settings where Sugarloaf Pond would be associated. What is obvious is that our average fire return interval over the last ~ 4,000 years is at the upper end of the model-based estimates (Hann et al., 2005). Carter et al., (2017) found that the fire return interval averaged ~ 109 years when the landscape around Long Lake in southeast Wyoming was dominated by quaking aspen, but averaged ~ 166 when dominated by lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. ex S. Watson). However, at 2700m in elevation and at higher latitude, it is likely the dynamics of climate-fire-vegetation at Long Lake differs from Sugarloaf Pond. Perhaps most important is that unlike at Sugarloaf Pond, when quaking aspen presence decreased at Long Lake, it gave way to lodgepole pine–another fire-driven species–instead of other shade-tolerant conifers. As a result, the interaction between overstory dominance and fire return interval would be somewhat less dichotomized than was observed at Sugarloaf Pond.

The fir:aspen ratio (Fig. 2d), while strongly influenced by the fire event at ~ 1600 cal yr BP, suggests influence by climate where the ratio exhibits a generally monotonic decline from 2500–4000 cal yr BP. The AP:NAP was relatively stable over the record, although there is a period of greater shrub abundance between 2800–3500 cal yr BP (Fig. 2c). A conspicuous shift in the AP:NAP ratio towards great forest cover occurs towards modern, driven largely by fir (Fig. 2c, 2d, and 3). Total pollen influx variability reflected high values between 1600–1800 and 2200–2700 cal yr BP. After 1600 pollen influx declines and remains relatively low towards modern (Fig. 2e), which mirrored the monotonic decrease in ENSO frequency and intensity (Fig. 4a). This trend suggests an association with higher snowpack (El Niño phase) and relatively high pollen production. This association could be explained by rising water tables driven by snow cover and/or depth (Bowen et al., 2011) that would benefit plant communities throughout the growing season. Indeed, episodes of high pollen influx within the context of Sugarloaf Pond record are more active ENSO (e.g., ~ 900, ~1.6K and ~ 2.7K). The converse is also true, where lower pollen influx is associated with La Nina phase (i.e., low snowpack conditions), such as modern, ~ 1.4 K, ~ 2 K, and ~ 3.5 K.

Large variability in cool-season moisture (Cyperaceae) can be seen across the past ~ 4,000 years and likely helped to drive the fir:aspen regionally. That the wettest winters in the entire 4,000-year record occurred over the last ~ 100 years, likely corresponded to the well-documented phenomenon of relatively high moisture during the 20th century. This high level of moisture might confound the interpretation that the fire suppression era is (solely) responsible for 20th century fuel build-up, and documented 21st century fire severity and extent increases (Holden et al., 2018, Parks & Abatzoglou, 2020). Rather, superimposed over a century of fire suppression is a period of relatively moist conditions that would have further exacerbated fire behavior, had they occurred. Indeed, Sugarloaf Pond is currently dominated by aging aspen, nearly 170 years old. In the absence of disturbance, it is only a matter of time before subalpine fir establishes in the understory of the quaking aspen, given the centennial-scale increase in moisture that is dominated by snowpack. Fire risk will continue to build as long as this happens. Regionally, other montane lakes have recorded a period of about the last ~ 2500 being wetter than previously in the Holocene, except during periods of exceptional drought, (e.g., Medieval Climate Anomaly, Morris et al., 2013b, Anderson et al., 2023), and this could be one reason we see decreasing charcoal influx to the present, increasing subalpine fir at the expense of quaking aspen, and an increasing AP:NAP at Sugarloaf Pond (Fig. 2d).

Although the four months of the warm-season (June-September) accounted for just 26% of the annual moisture historically (Fig. 5), this additional seasonal moisture is likely important for fuel build-up–especially in comparison to a strictly continental climate that has predictable seasonal droughts–and possibly ameliorated droughty conditions that are conducive to increased fire hazard. Furthermore, it has been speculated that the occurrence and intensity of the North American Monsoon has likely been highly variable, where periods of failed monsoon might be expected to increase drought and fire chances and vice-versa. However, it has been noted that North American Monsoon variability is coupled with cool-season moisture changes (Notaro & Zarrin, 2011), and therefore the effect of the monsoon drying could be buffered (when cool-season is inversely correlated with the NAM), or exacerbated (when cool-season is positively correlated with NAM). Studies focused on the potential relationship between NAM and antecedent snowpack (i.e., ENSO) suggest that there is a negative correlation between the strength and northward propagation of the NAM during years with above average snow cover and depth (i.e., El Nino, Gutzler & Preston, 1997, Gutzler, 2000, Zhu et al., 2005). Because 26% of the moisture in this region was from the NAM (June-Sept), the sagebrush:ragweed proxy likely reflects a weakening monsoon over the past ~ 4,000 years (Fig. 4b). For example, at ~ 1K BP there is a conspicuous peak in sagebrush:ragweed that coincided with a lull in ENSO activity. Furthermore, modeling studies have shown that there is a reciprocal relationship between the intensity of the NAM and antecedent snowpack. In the southwest, lower snow pack years corresponded to the La Niña phase, and El Niño brought greater snowpack. We speculate that the relationship between the NAM and cool-season moisture likely buffers or exacerbates the likelihood of fire depending on modality. That is, El Niño periods were wetter, having a suppressive effect on fire events, whereas La Nina's likely had drier springs that could result in drying of fuel that might result in a higher chance of a fire event.

Interestingly, if we look at the historical climate data (Fig. 5), the ratio of cool-season to warm-season moisture during El Niño versus La Niña years deviates only slightly from average 23% and 26%, respectively vs mean = 26%. This suggests that, at least over the last ~ 120 years of record, there was little trade-off between moisture delivered by the NAM and cool-season moisture, despite the modality of the ENSO, and despite the previously mentioned possible trade-offs. Perhaps more striking is that this ratio stays quite constant against the background of a nearly 30% difference in total annual precipitation between the most severe La Niña years (70.9 cm) compared to the most severe El Niño years (101.3 cm, Fig. 5). Total annual precipitation is probably a much stronger driver of long-term fuel buildup, and subsequently the fire return interval, as fire return interval was significantly related to cool-season moisture at Sugarloaf Pond.

Climate-driven fire events were not indicated in any of our analyses, suggesting that the fire events in this basin were less sensitive to climatic variability than to available fuel loading. It is possible, and likely, that many ignitions occur during periods of both favorable and unfavorable climate, especially considering the fact that Native Americans were responsible for ignitions during the entire time period of our record up until the late-1800s both regionally (Carter et al., 2021), and continent-wide (Stewart et al., 2002). It is hard not to imagine that Native Americans would be interested in promoting aspen-dominated forests. The typically luxuriant undergrowth harbors many more species of herbaceous and grass plants, ideal for promoting herbivores and edible plants. They probably didn't promote canopy removal for their foraging activities (Stewart et al., 2002). It is very likely the case that many fires started during dry climatic periods, but did not build into fires large enough to be detected by the CHAR analysis approach. Only when fuel loading was high were stand-replacing fires significantly recorded as peaks of CHAR in the sediment record. Conversely, the fire return interval was significantly related to cool-season moisture, and more strongly so when considering the relationship for the observed fire events, which suggested a protracted fire interval when moisture was high, and shortened interval between events when moisture was low. That there is variation in the relative role of top-down and bottom-up controls on fire activity has been found in previous work (e.g., Gill & Taylor, 2009), and as in our work, has been hypothesized to be associated with the temporal scale of observation (Whitlock et al., 2010).

That forest type, structure, and composition on the landscape are things that shift over long time periods and cause conclusive interpretation of multi-millennial records more tenuous than typical fire history reconstructions (i.e., centuries) where we can assume disturbance-driven forest types were constant. We don't know that for Sugarloaf Pond, although we could speculate this is the case given the pollen record given that both fir and aspen are prevalent on the modern landscape and that their relative pollen values in the context of the record are roughly similar. These considerations suggest that this Sugarloaf Pond landscape has been relatively consistent over the 4000-year record. Previously published records in the region include Morris Pond on the nearby Markagunt Plateau (Morris et al., 2013a), Purple Lake on the Aquarius Plateau (Morris et al., 2013b), and Blue Lake and Emerald Lake on the Wasatch Plateau (Morris et al., 2010; 2015) offer some insight into the vegetation community. While these sites occur at relatively higher elevations (> 3000 m), the increase of aspen in the subalpine zone in south-central Utah beginning ~ 3000 years ago suggests that aspen was well-established at mid-montane elevations in the region. Increasing evidence of aspen in the subalpine zone is accompanied by general declines in wildfire in recent millennia, similar to Sugarloaf Pond (e.g., Morris et al., 2013b).

Previous work on Sugarloaf Pond indicated that the successional dynamics are such that quaking aspen succeeded to subalpine fir over centennial time-periods (Morris et al., 2019), where the current study builds on this story, by adding the caveat that in the absence of fire fuel accumulates. In other words, successional dynamics are not mutually exclusive from fuel buildup, such that the longer succession proceeds between disturbance events, the higher the risk of a stand-replacing fire. Previously, we suggested this dynamic indicated quaking aspen resilience at Sugarloaf Pond, until only recently, and this study indicates that the process that likely drove the maintenance of resilience was the occurrence of stand-replacing fire–corroborating the previous speculation that the cessation of fire (probably superimposed over regional increases in moisture) are responsible for the change in resilience that could shift the forests surrounding Sugarloaf Pond to subalpine fir dominance in the further absence of fire. Indeed, our composite analysis revealed predictable patterns of fire events related to fuel buildup (i.e., high subalpine fir composition), where subalpine fir dominance leads fire events, and that it takes more than a century on this site for sufficient fuel buildup before a large fire could occur.

However, it seems likely that at the earliest part of the record, where there are fewer fire events, but a high fir:aspen, that climate (at least the North American Monsoon) may have controlled the possibility of burning. The first two fire events are separated by ~ 500, and ~ 400 years, and there are no other events as infrequent anywhere in the record. Interestingly, these two fires occurred likely during very moist warm-season conditions and high fir:aspen (Fig. 2d, 4a, and 4b). It appears as though fire frequency may be increasing recently, and the time between fire events is nearly as infrequent as it was in the early part of the record. The past ~ 500 years has seen longer fire return intervals not seen since almost 4,000 years ago.

Management Implications

With just under 4,000 years of fire history reconstruction for a currently aspen-dominated landscape, there is ample information to guide how contemporary management might view fighting fire, setting fire, or the fire risk in quaking aspen-dominated stands. Previously, we argued the data from this site indicated that–at this long time-scale–whether the aspen was stable or seral misses the point that longer-term fire regime dynamics may be at play (Whitlock et al., 2010). Here we further point out that fuel accumulation is what drives the increased risk of fire, and this was predictable as succession proceeds. Previously, we showed that the alternation between quaking aspen and subalpine fir dominance was predictable and cyclical (Morris et al., 2019). Here, we quantitatively showed that the fuel accumulation associated with that shift between quaking aspen to subalpine fir resulted in a higher likelihood of stand-replacing fire, and therefore a shift back to quaking aspen dominance, but this shift occurred over much longer time periods than typically considered in land management. Moreover, the amount of charcoal in the record was strongly related to overall biomass production, further suggesting that fire events were driven by fuel buildup. Therefore, the observation that stable aspen communities are self-replacing (Rogers et al., 2014), and that fire is less common in the short-term (i.e., decades to centuries), does not preclude the longer-term (i.e., centuries to millennia) possibility that fire becomes more likely with fuel accumulation, regardless of species composition.

The range of fire return intervals for this quaking aspen-dominated forest was not unexpected (132–323 years), but does span the higher end of that expected for aspen (i.e., ~ 10–165 years). Such high variation for a single point in space is suspect. While the lower end of this range is a good approximation of the age of maturing aspen stands, the higher end is a period of time that is exceedingly rare for individual quaking aspen stems to achieve, i.e., ~ 300 years. At nearly three centuries between fires, it is not hard to imagine a senescent quaking aspen forest succeeding to subalpine fir along with the associated increase in ladder fuels, canopy fuels, etc. A time when we would expect large woody fuel accumulation to be increasing due to a combination of large canopy gaps from dying aspen, increased light penetration to the understory increasing grass and herbaceous components, and perhaps most importantly subalpine fir. At this advanced age, and in the continued absence of fire, the aspen will start to succeed to conifer, which will come to dominate the site. Even at the longest fire regime interval we measured, i.e., ~ 500 years, early in the record, fire is still likely to drive the turnover of forest vegetation.

The general positive relationship between fire return interval and fir:aspen is secondary evidence that when there was a high preponderance of subalpine fir the fire interval is longer, and when there was a high preponderance of quaking aspen the likelihood of fire events was lower, putatively because of the nature of aspen forests being more moist, which is likely true, at least earlier in stand development (Nesbit et al., 2023). Eventually, however, continued fuel accumulation is guaranteed in the absence of disturbance and results in higher flammability. Fire that was not stand-replacing immediately around Sugarloaf Pond no doubt occurred in this landscape, evident by the background charcoal. However, these fires likely encountered either low fuel accumulation, or moist conditions, or both, and were not likely to build to events that were recorded as CHAR peaks in the lake sediment. The occurrence of the biggest fires likely acted to shift composition from subalpine fir back to quaking aspen. The fires themselves likely acted on mostly non-aspen biomass (Fig. 1b), but the presence of quaking aspen root stock on or near the site guaranteed that it will predictably respond to the opening of growing space as would be expected of a pioneering species that suckers.

The absence of fire events during periods of quaking aspen dominance in the Sugarloaf Pond record suggests the possibility that fuel reduction approaches could effectively limit high-severity fire behavior in the short-term. Maintaining aspen in the overstory is a possible goal, but with time they will succeed, as they are not long-lived species. Silvicultural reproduction of aspen can be highly efficient and successful, and is an appropriate approach to retaining aspen on a given site. Fire is an efficient tool to regenerate aspen, but the coppice silvicultural system can achieve the same result (Frey et al., 2003). Setting back stand development via a coppice silvicultural system will ensure the stand is dominated by aspen for at least the next century. However, like all fuel treatments, re-treatment would be necessary to forestall the predictable increase of fuels (arboreal and non-arboreal) as stands succeed.

Conclusions

Directly testing proxies for cool- and warm-season climate and fuel accumulation against reconstructed fire events presented the possibility to better understand natural dynamics of quaking aspen fire regimes, and specifically the putative climate- versus fuel-limited drivers. Long-term records of quaking aspen fire regimes are sorely lacking, and studies like this greatly improve our understanding of the ecology of fuel-limited vegetation systems, and can influence our approach to quaking aspen fire management. Counterintuitive to expectations that the fire regime would be limited by climate, we found strong evidence that the occurrence of stand-replacing fires in this ecosystem were fuel-limited, i.e., predictably related to the accumulation of fuel necessary to support a large fire. However, cool-season moisture was positively related to fire return interval, especially during fire events, which suggested that climate is playing a long-term, top-down role–through its effect on fuel accumulation. While our sediment core-based reconstruction exceeds the estimated fire return interval by millennia, important for accurately characterizing fire regimes, its inherent point-based nature does not likely characterize the full extent of individual large fires, except to the extent that the Sugarloaf Pond watershed, which is relatively small, captures charcoal from primarily local fires.

Declarations

Availability of data and materials

Data used in this study is available upon request from the corresponding author on reasonable request.

Competing interests

The authors declare they have no competing interests.

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Authors' contributions

JLM and RJD designed the study, obtained the funding, oversaw and contributed to data collection and development, analysis writing and approve of the final manuscript.

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Figures

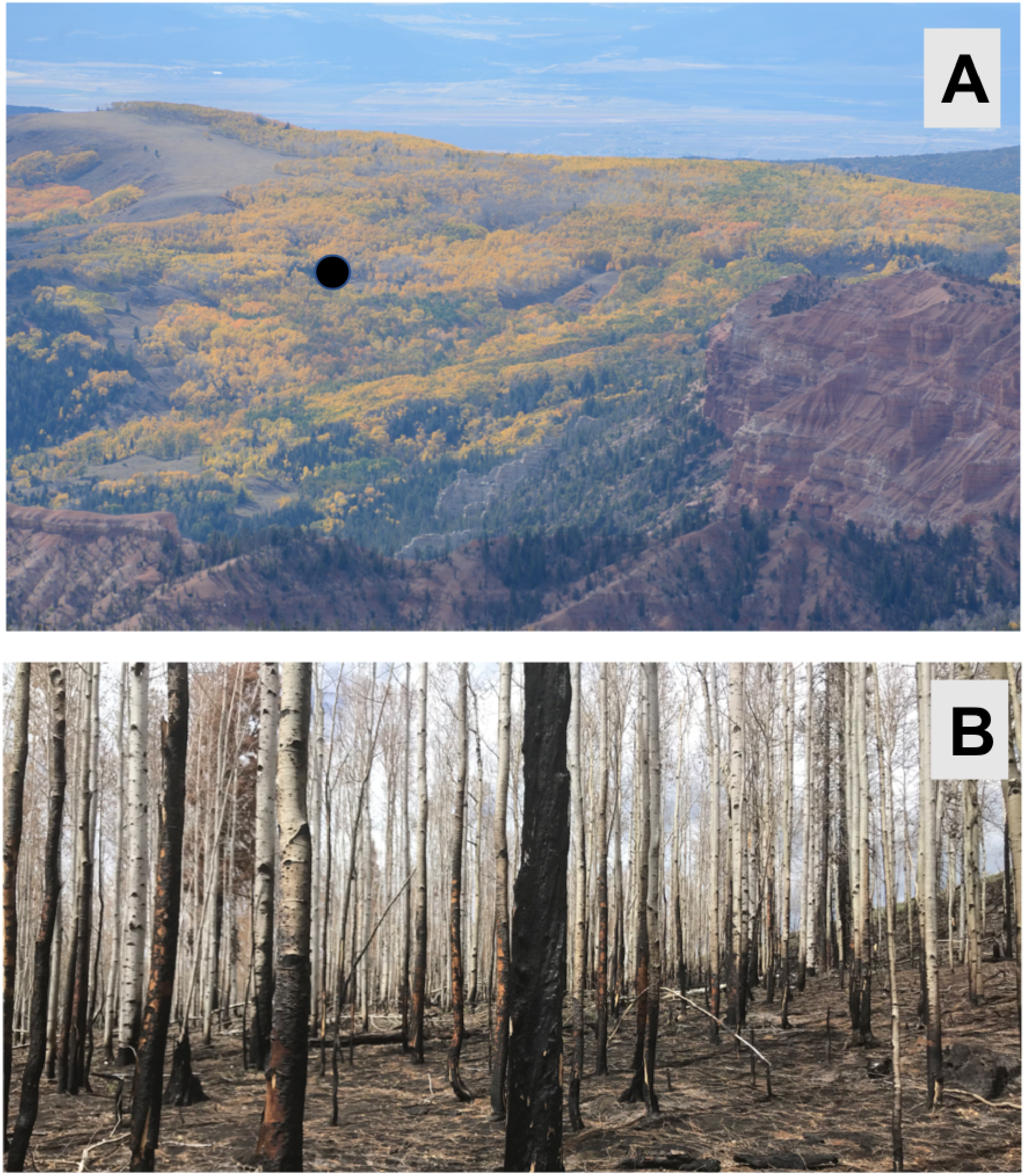

Figure 1

Sugarloaf Pond (a) situated in a landscape of quaking aspen (black dot), and (b) stand-replacing fire in mature quaking aspen in the Central Rocky Mountains where mortality was 100% but fire never reached the canopy (photo credit – the authors).

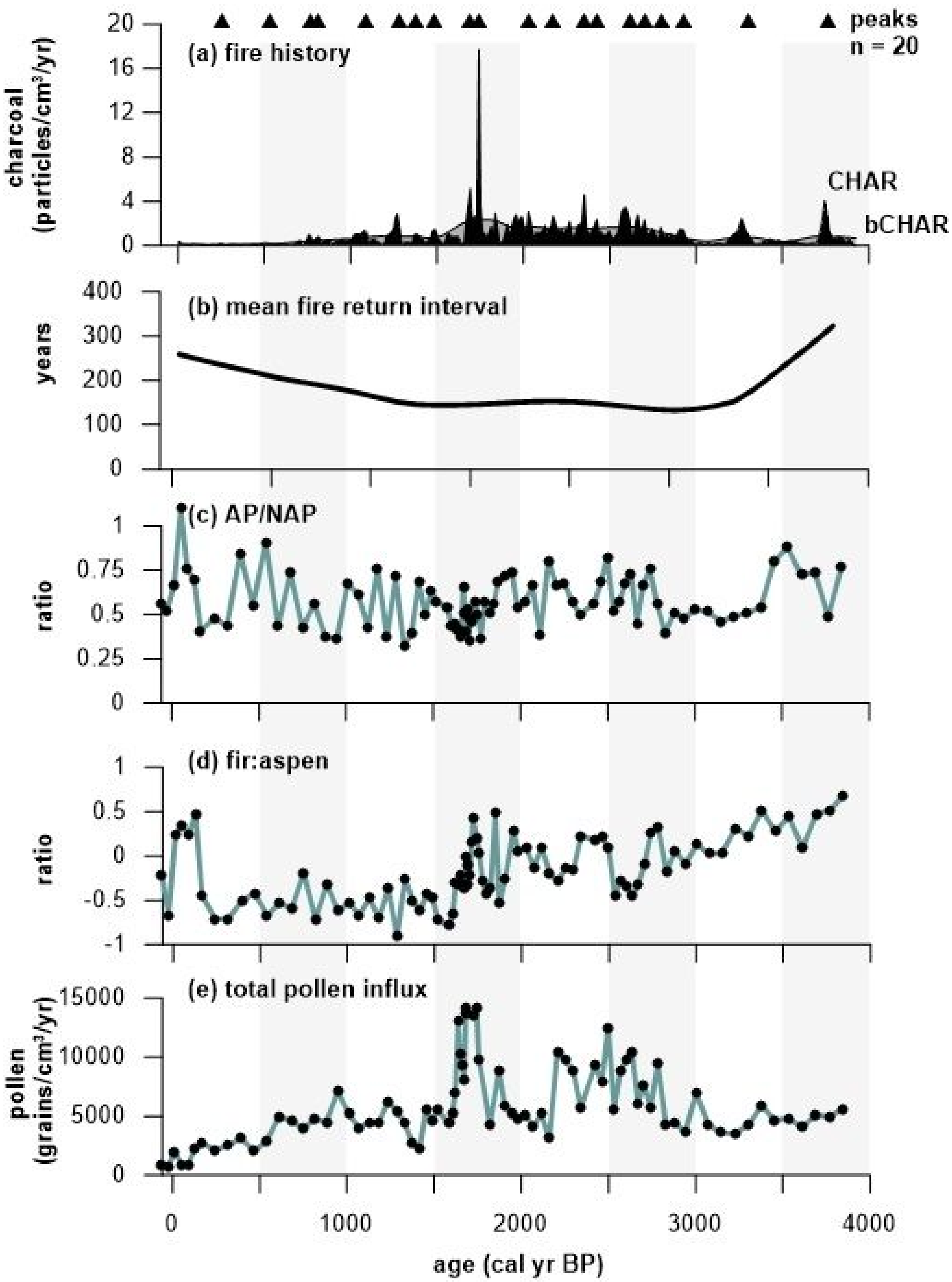

Figure 2

Fire history (a), mean fire return interval (b), ratio of arboreal to non-arboreal pollen (c), ratio of fir (*Abies*) to aspen (*Populus*) pollen, and total pollen influx (e) at Sugarloaf Pond over the last ~4,000 years. The fire history panel (a) is composed of charcoal influx (CHAR), background charcoal influx (bCHAR), and peaks (▲) are identified as statistically significant deviations of CHAR above bCHAR. Mean fire return interval (b), or fire frequency, is the number of peak fire events (a) per century. In panel (c) the ratio of arboreal (i.e., trees) to non-arboreal (i.e., shrubs, herbs) reflects changes to ecosystem structure where the forest canopy is more closed (high ratio) or open (low ratio). Panel (d) shows the ratio of the two dominant tree types (d) in the Sugarloaf Pond watershed where high ratios indicate dominance of fir while low ratios reflect the dominance of aspen.

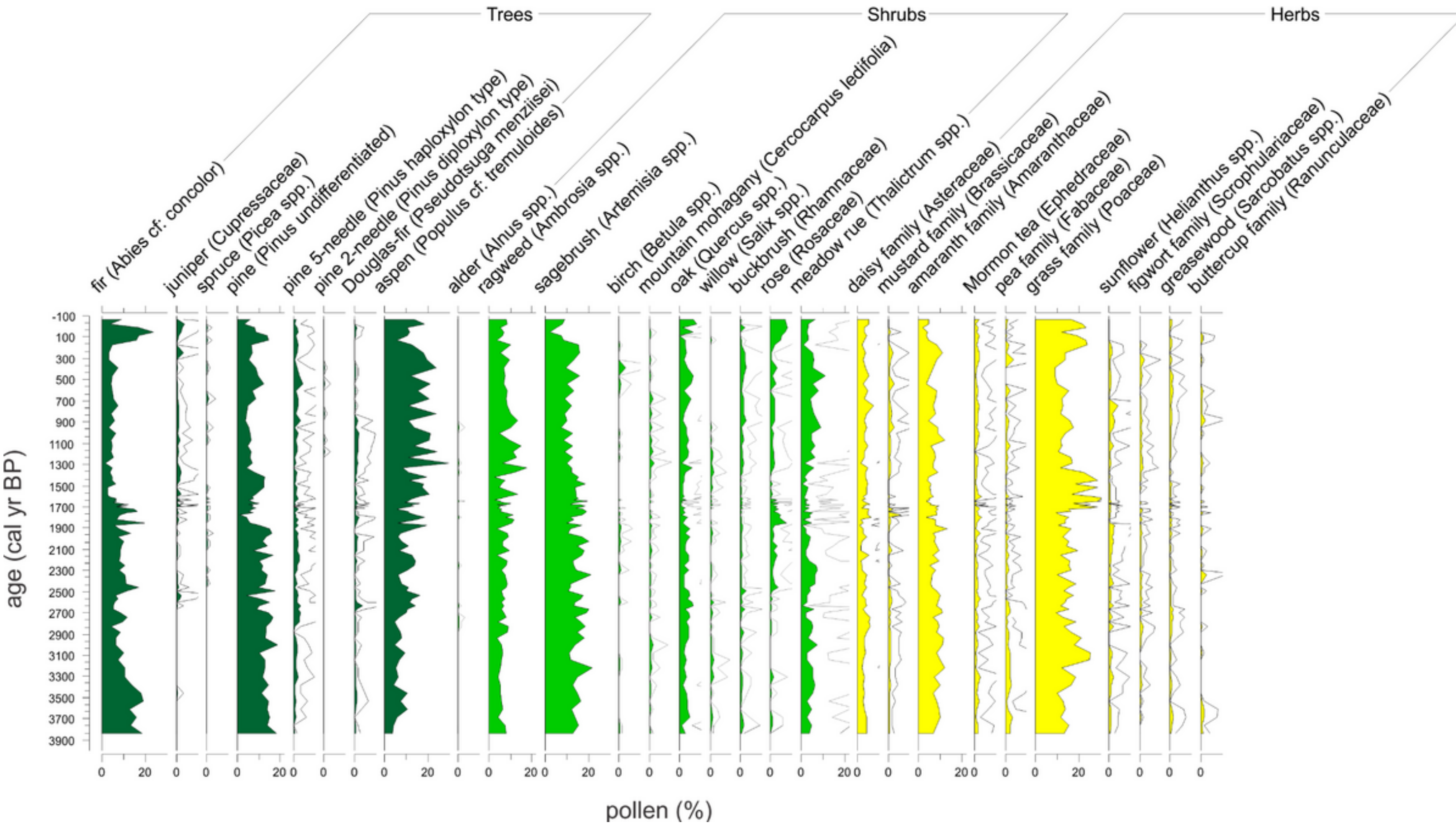

Figure 3

Pollen diagram for Sugarloaf Pond over the last ~4,000 years with dark green plots for trees, light green plots for shrubs, and yellow plots for herbs. Fir (*Abies* spp.) and aspen (*Populus* spp.) are the two locally dominant forest species while pines (*Pinus* spp.), spruce (*Picea* spp.), and Douglas-fir (*Pseudotsuga menziesii*) are found in abundance near Sugarloaf Pond. The shrub pollen assemblage is dominated by sagebrush, ragweed, and oaks which are common throughout the area, especially at lower elevations relative to Sugarloaf Pond. The herbaceous plant spectrum largely consists of grasses (Poaceae), daisies (Asteraceae), and amaranth (Amaranthaceae) which occur frequently in the Sugarloaf Pond watershed and surrounding landscape.

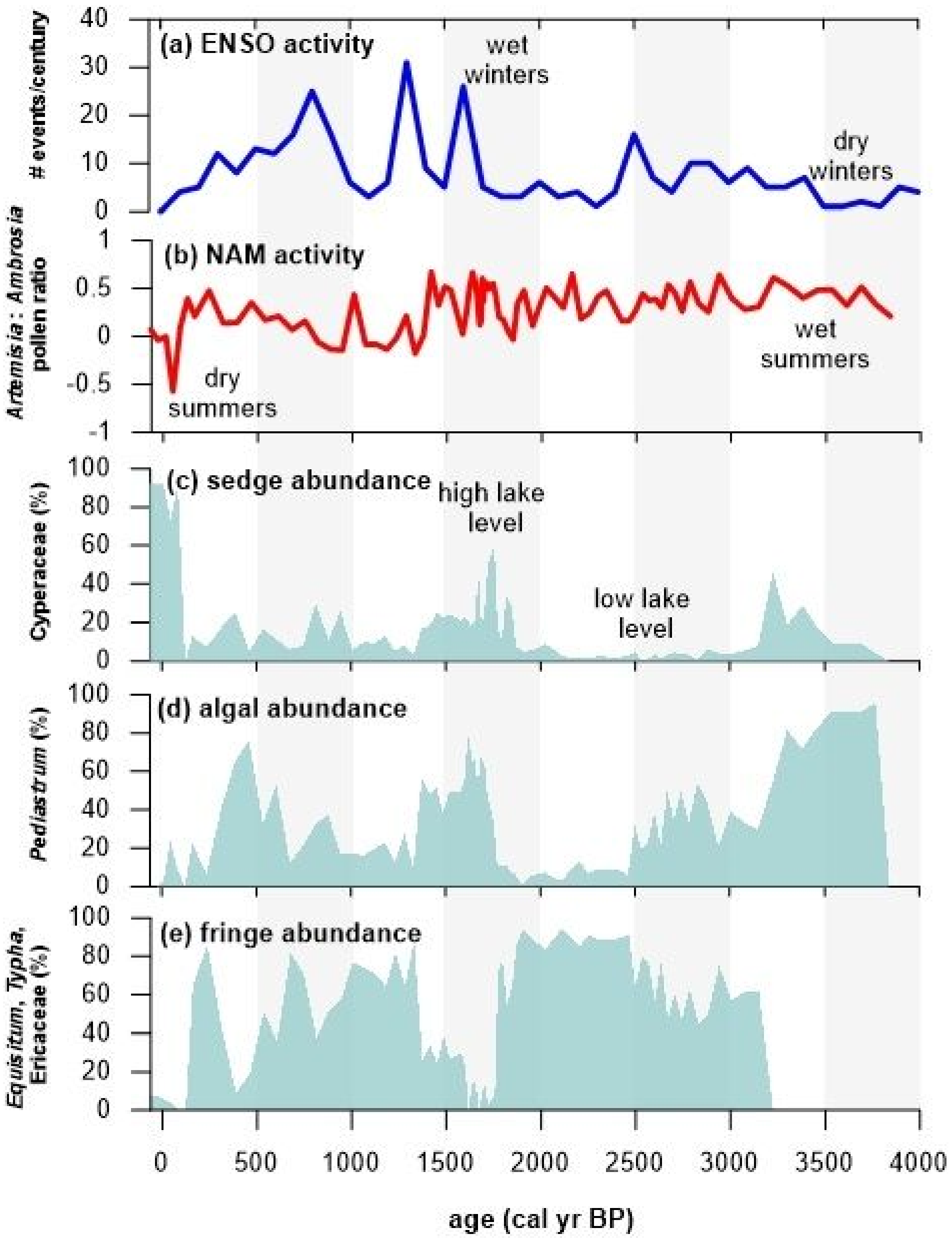

Figure 4

Vegetation, hydrologic, and climate proxies at Sugarloaf Pond (2886 m asl) over that last ~4,000 years. Panel (a) shows El Nino - Southern Oscillation (ENSO) activity reconstructed from Laguna Pallcacocha as a proxy from winter precipitation (Moy et al. 2002). Summer precipitation is delivered by the North American monsoon and is reconstructed using the ratio of sagebrush (*Artemisia*) to ragweed (*Ambrosia*) pollen from Sugarloaf Pond in panel (b). In panels (c) and (d) sedge (Cyperaceae) and pediastrum abundances are shown to correspond to wet winters and high lake levels. Panel (e) shows that fringe aquatic species, such as horsetail (*Equitum*) and cattail (*Typha*), are abundant during dry winters and wet summers.

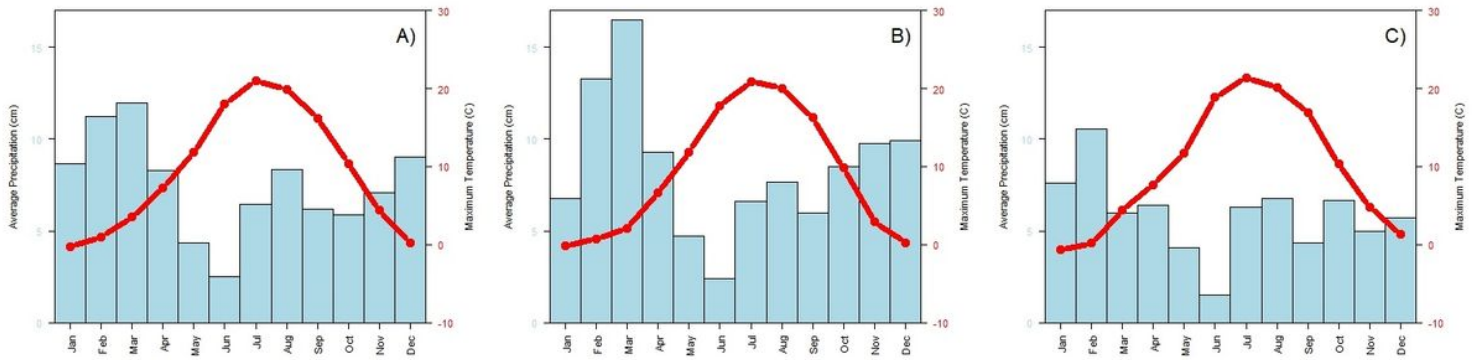

Figure 5

Average monthly precipitation and average monthly maximum temperatures over 1901-2020 for, A) All years at Sugarloaf Pond, B) 10 highest ranked El Nino years, and C) 10 highest ranked La Nina years. El Nino - Southern Oscillation January, February, and March data were used for B and C (https://psl.noaa.gov/enso/climaterisks/years/top24enso.html).

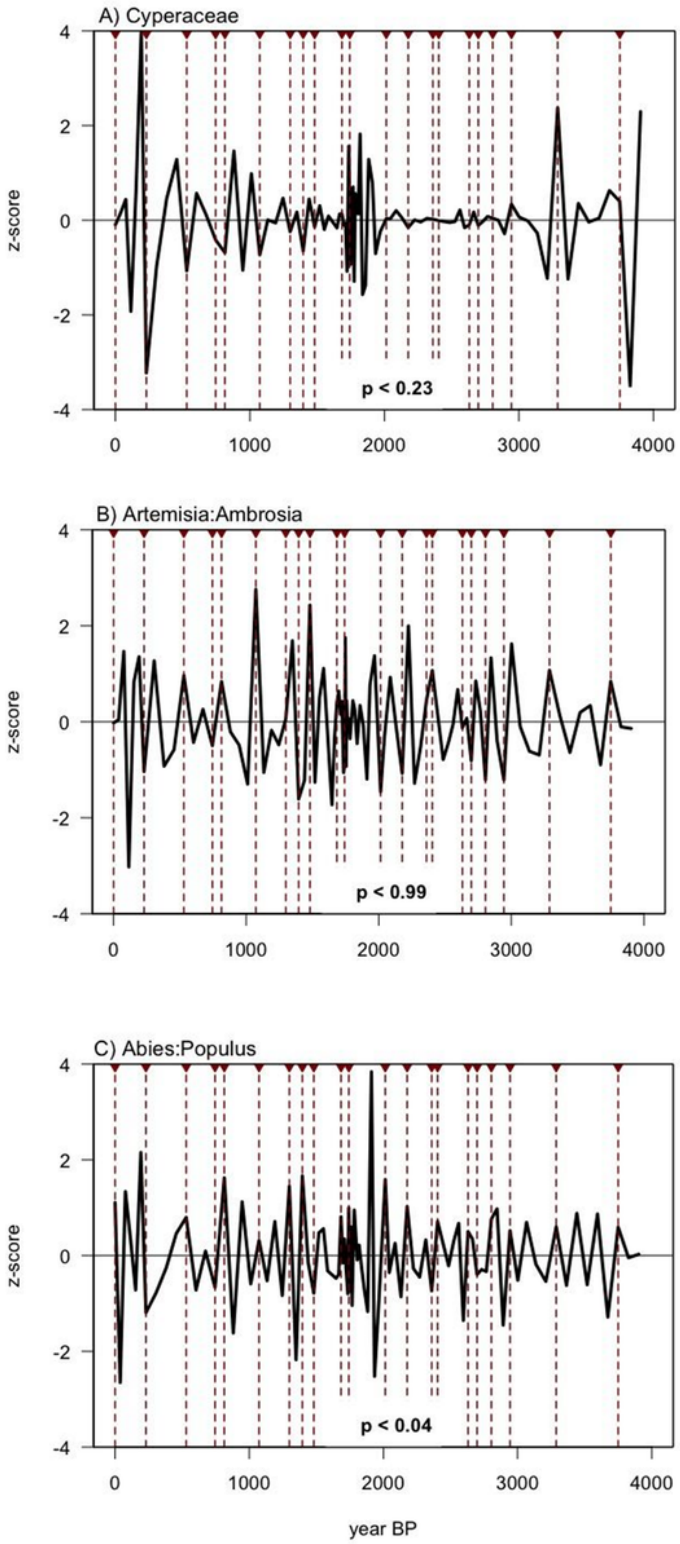

Figure 6

Standardized and smoothed proxy data for A) cool-season moisture availability (Cyperaceae), B) warm-season moisture availability (sagebrush:ragweed), and C) fuel buildup (fir:aspen), with fire events (n=20) from charAnalysis plotted as red triangles and vertical dashed lines. Significance from Chi-square test plotted on bottom of panel.

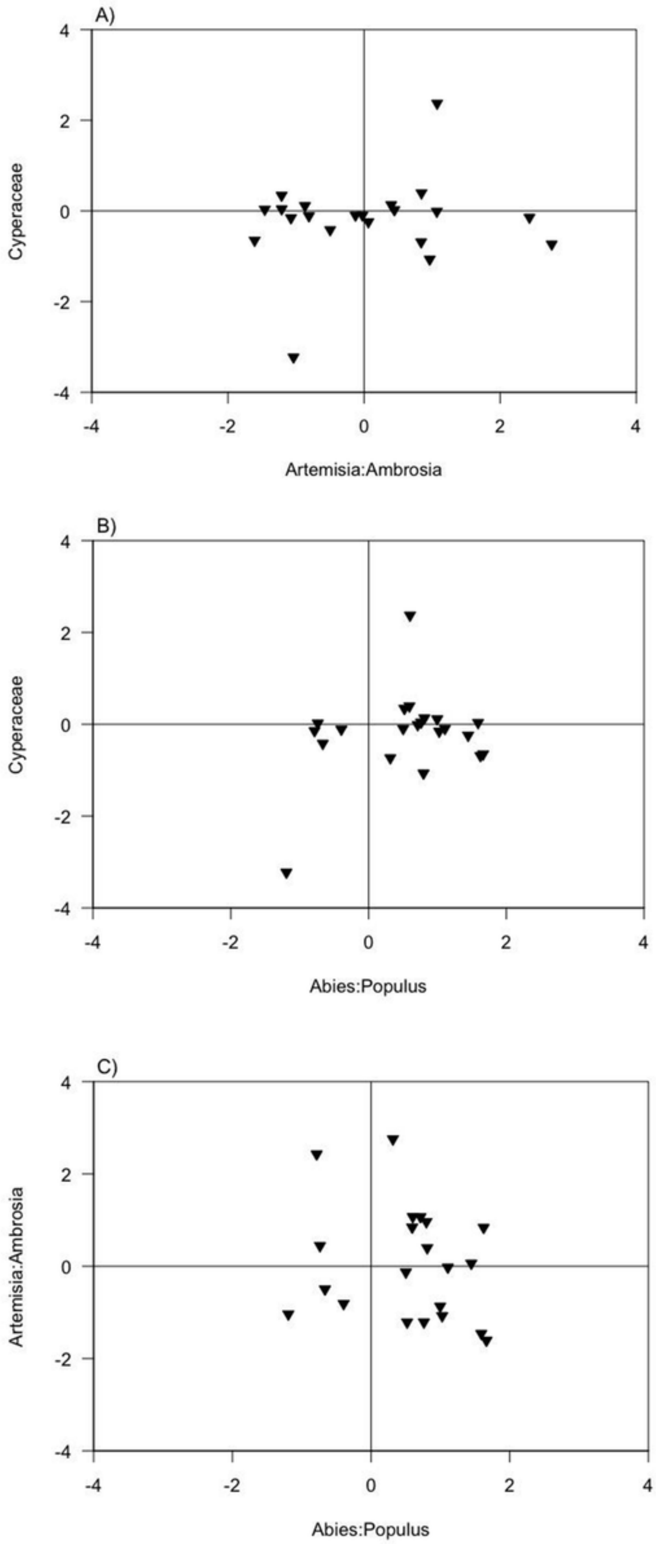

Figure 7

Biplots of the standardized and smoothed proxy climate and vegetation data associated with fire event dates (n=20). a) Cool-season moisture (Cyperaceae) over warm-season moisture (sagebrush:ragweed), b) Cool-season moisture (Cyperaceae) over fuel accumulation (fir:aspen), and c) Warm-season moisture (sagebrush:ragweed) over fuel accumulation (fir:aspen).