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Fire Ecology

REVIEW

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Systematic review and meta-analysis of fire regime research in ponderosa pine (*Pinus ponderosa*) ecosystems, Colorado, USA

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Abstract

Background: Forest management, especially restoration, is informed by understanding the dominant natural disturbance regime. In many western North American forests, the keystone disturbance is fire, and a plethora of research exists characterizing various fire regime parameters, although often only one or two parameters are addressed in individual studies. I performed a systematic review of the literature and meta-analysis of the derived data from 26 publications to characterize five parameters of the historical fire regime of ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) ecosystems in Colorado, USA: fire frequency, severity, extent, seasonality, and climate.

Results: The collection of evidence indicates a fire regime predominantly characterized by moderate to high frequency, low- and mixed-severity fires that occurred in late summer to fall, with fires occurring in drier than average years that were often preceded by two to three years of wetter than average conditions. The overall average mean fire return interval (MFI) was 21 years (SD = 1.4 years, *n* = 78 sites) and increased with site elevation ($r = 0.33$, $P < 0.05$). Low- and mixed-severity fires accounted for 83% of all observations, and 69% of fires occurred in late summer to fall with no relationship found between latitude and seasonality. Geographic region (Front Range and southwestern Colorado) was associated with variability in fire regime parameter values, with southwestern Colorado sites having a stronger association with wetter than average conditions in the three years preceding fire years and a shorter mean MFI (18 years) relative to Front Range sites (23 years). Data were insufficient to evaluate changes in fire severity and extent due to a lack of historical information, as well as differences in sampling methods and reporting.

Conclusion: This meta-analytic approach identified variation within and among fire regime parameter values that occurred along elevational and geographic axes, and this information should be useful to managers engaging in forest restoration aimed at enhancing resilience of fire-adapted forests to disturbance and climate change.

Keywords: fire–climate relationships, fire extent, fire frequency, fire seasonality, fire severity

Resumen

Antecedentes: El Manejo forestal, especialmente la restauración, está basada fundamentalmente en el conocimiento del régimen natural de disturbios. En varios bosques de Norte América, el disturbio clave es el fuego, y existen una plétora de investigaciones que caracterizan varios parámetros del régimen de fuego, aunque solo uno o dos son abordados en estudios individuales. Realicé una revisión sistemática de la literatura y un meta-análisis de datos derivados de 26 publicaciones para caracterizar cinco parámetros del régimen de fuegos histórico en ecosistemas de pino ponderosa (*Pinus ponderosa* Lawson & C. Lawson) en Colorado, EEUU: frecuencia de fuego, severidad, extensión, estacionalidad, y clima.

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Resultados: La colección de evidencias indican un régimen de fuego caracterizado predominantemente por frecuencias moderadas a altas, severidades bajas y mixtas que acontecen en el verano tardío y el otoño, y fuegos ocurridos en años más secos que el promedio y que fueron precedidos frecuentemente por dos a tres años de condiciones más húmedas que el promedio. El promedio general del intervalo medio de retorno de fuegos (MFI) fue de 21 días (DS = 1,4 años, *n* = 78 sitios) y se incrementó con la elevación de los sitios (r = 0,33, *P* < 0,05). Fuegos de severidad baja y media contabilizaron el 83% de todas las observaciones, y el 69% de los fuegos ocurrieron en el verano tardío y el otoño y no se relacionaron con la latitud o la estacionalidad. La región geográfica conocida como el *Colorado Front Range* y el sud-oeste de Colorado fue asociada con la variabilidad en los valores de los parámetros de los regímenes de fuego, con los sitios ubicados en el sudoeste de Colorado teniendo una asociación más fuerte con años húmedos en relación al promedio en los tres años precedentes al fuego y un período más corto de intervalo medio de retorno de fuegos (18 años) en relación al Colorado Front Range (23 años). Los datos fueron insuficientes para evaluar cambios en la severidad del fuego y la extensión debido a la falta de información histórica, y también a diferencias en los métodos de muestreo y de reporte de esa información.

Conclusiones: Esta aproximación basada en meta-análisis identificó la variación dentro y entre valores de parámetros de regímenes de fuego a través de ejes geográficos y de elevación, y esta información podría ser útil para los administradores de recursos enfocados en la restauración forestal cuyo objetivo es aumentar la resiliencia de bosques adaptados al fuego a distintos disturbios y al cambio climático.

Abbreviations

MFI: Mean fire return interval. The average number of years between successive fires over a given time period

y−x: Denotes fire year when $x = 0$, and years preceding a fire year when $x \geq 1$

Introduction

The concept of the fire regime, that there exists a combination of factors in a given location and over a specific time period that describes the role fire plays in an ecosystem (Agee 1993; Krebs et al. 2010), is important to understand when applying ecologically based fire management. Fire regimes are multivariate in nature and can be characterized by multiple parameters including fire frequency, severity, extent, seasonality, and relationship with climate. Fire regime parameters act on a system concurrently, and how they vary across space and time and with environmental factors (*e.g.*, elevation, latitude, climate) can reveal the underlying dynamics that constitute the fire regime for a given ecosystem.

Much information on fire regimes has been acquired and reported following decades of research. Typically only one or two parameters are addressed within a given study; however, a full understanding of a fire regime cannot be gained through the perspective of one or two parameters. Furthermore, conceptual disagreement or numerical discordance is common among studies addressing the same parameter. Thus, it is important to understand both the contributing sources of variability in estimates of a given fire regime parameter, and how fire regime parameters relate to one another across space and time. This understanding is difficult to achieve at an individual study level, and a “vote-counting” approach—by which a tally is made of significant and non-significant findings among studies that either support or fail to support an interpretation—is insufficient for robust inference because it fails to provide quantitative parameter estimates. A detailed systematic literature review coupled with a quantitative assessment of the distribution of values reported in individual studies can help explain variability among studies, identify areas in which disagreement is largely due to human-induced sources of variation, and reveal fundamental patterns from natural relationships. Importantly, broad claims made in the literature about the magnitude and characteristics of fire regime parameters or contemporary changes in these values can be more thoroughly explored by weighing the evidence from a population of studies within the same ecosystem.

Study system

Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a broadly distributed North American conifer. It ranges across much of western North America, covering approximately 15 million hectares, from southern Canada to central Mexico, including 16 states in the western United States. Ponderosa pine ecosystems, where ponderosa pine is either a dominant or subdominant but significant component of the stand, occur on both sides of the Continental Divide in Colorado, USA (Fig. 1). On the eastern side, ponderosa pine occurs throughout much of the montane zone (elevation ~1800 to 2800 m) along the Front Range of the Rocky Mountains. Associated plant species and typical stand structures vary with elevation, slope, and aspect, and include more open stands with Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) on xeric sites, and denser

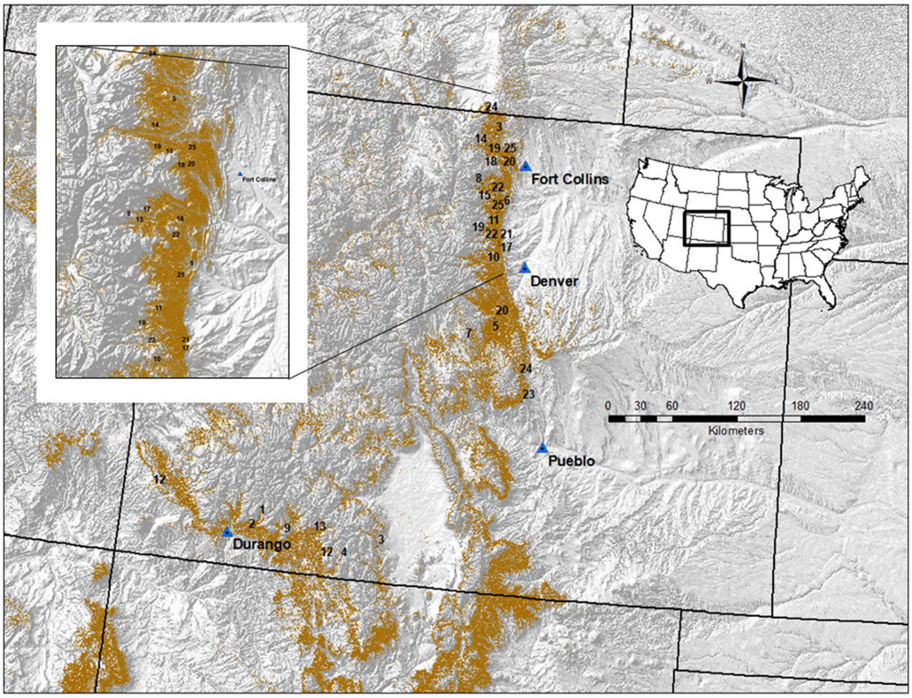

Fig. 1 Distribution of the ponderosa pine (*Pinus ponderosa*) ecosystems in Colorado, USA, that were used in the fire regime meta-analysis of 2017, based on LANDFIRE Biophysical Settings (LANDFIRE 2008). Numbers indicate approximate location of studies used in this meta-analysis and correspond to references presented in Table 1. For studies with more than one research site in close proximity, the approximate midpoint is shown. For studies with more than one site that spanned broad distances, the two distant endpoints are indicated with the same number. The map inset depicts a close-up of the northern area where some sites were too close to display separately on the larger map

stands with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on more mesic sites (Marr 1961). Tree species composition becomes more diverse and ponderosa pine becomes less of a canopy dominant with increasing elevation, but it can occur as high as 3077 m on warm south-facing slopes (Huckaby et al. 2003).

On the western side of the Continental Divide, ponderosa pine occurs primarily in the southwestern part of the state, largely in the San Juan Mountains and Uncompahgre Plateau, and occupies a narrower elevational range (~2100 to 2900 m) compared to the eastern side. On relatively xeric sites at lower elevations, ponderosa pine forms pure stands (Grissino-Mayer et al. 2004), while at mid-elevations, Douglas-fir typically codominates, and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) and aspen (*Populus tremuloides* Michx.) are common associates (Korb et al. 2013).

Fire regime parameters

The five fire regime parameters most frequently addressed by fire history studies in Colorado ponderosa pine ecosystems and evaluated in the current study are:

1. Fire frequency—the number of fires per unit time in a given area, reported as the average number of years between successive fires over a given time period (*i.e.*, mean fire return interval, hereafter MFI). Fire frequency is the most common parameter reported in fire history studies, and in ponderosa pine ecosystems it is derived from dendrochronological techniques that identify fire scars on annual rings of trees or remnant tree material (logs, snags).
2. Fire severity—generally indicates the degree of change caused by fire, such as the relative proportion of trees killed within a given area (*e.g.*, the fire perimeter or patches within). Typically classified as high, moderate, low, or mixed.
3. Fire extent—the size of the area burned by an individual fire, the distribution of individual fire sizes, or the total area burned by all fires within a specified time period.
4. Fire seasonality—the time of year a given fire occurred. In dendrochronological studies, the position of fire scars within annual growth rings indicates what time of year those fires occurred.
5. Fire–climate relationships—climate has a strong influence on fire regimes through its effects on fuel abundance, type, and moisture content. This relationship is examined using an analysis that integrates multiple lines of evidence to infer precipitation conditions during and prior to fire years.

An overview of fire regimes in Colorado ponderosa pine ecosystems

Several fire history studies in Colorado ponderosa pine ecosystems report a predominance of high-frequency, low-severity fire across multiple centuries (*e.g.*, Goldblum and Veblen 1992; Brown and Shepperd 2001; Donnegan et al. 2001; Gartner et al. 2012), similar to what has been reported for ponderosa pine ecosystems in the American Southwest (*e.g.*, Covington and Moore 1994; Fulé et al. 1997). A high-frequency, low-severity fire regime is generally considered to be one with a mean fire interval of 30 years or less in Colorado ponderosa pine ecosystems (Sherriff and Veblen 2006; Sherriff et al. 2014). However, Romme et al. (2003) describe a high degree of variability in fire regimes of ponderosa pine in the Colorado Front Range. Based on fire history data from 54 sites, they contend that most of the ponderosa pine ecosystems of the Front Range are characterized by a mixed-severity fire regime, a category that encompasses a broad range of conditions from high-frequency low-severity fires, to low-frequency high-severity fires (Agee 1993). In ponderosa pine forests, mixed-severity fires contain patches of high severity and low severity. Frequency, severity, extent, duration (and by extension, seasonality), and relationship with climate can all exhibit high variation within this regime (*e.g.*, Romme et al. 2003). Williams and Baker (2012a, 2012b) expanded on the idea that a mixed-severity fire regime dominated ponderosa pine ecosystems in the Front Range and proposed that the historical regime included a significant amount of high-severity, stand-replacing fires that were larger, on average, than those observed in contemporary times.

Fire regimes in southwestern Colorado ponderosa pine ecosystems have been similarly described as highly variable, indicative of a mixed-severity fire regime across space and time. An influence of elevation on fire frequency is evident in some studies in which stands at higher elevations generally had longer fire return intervals than stands at lower elevations (*e.g.*, Grissino-Mayer et al. 2004). Fire frequency also varied temporally, as evidenced by multi-century chronologies in which individual forest stands were marked by periods with frequent fire (*e.g.*, 5-year MFI) and periods with less frequent fire (*e.g.*, 30-year MFI) (Grissino-Mayer et al. 2004). Bigio et al. (2010) coupled fire history data with alluvial sediment records and concluded that a low- to moderate- and mixed-severity fire regime likely dominated their study area northeast of Durango, Colorado, for about 2600 years. Other researchers are less convinced about the significance of high-severity fires in southwestern Colorado ponderosa pine fire regimes. Brown and Wu (2005) found substantial evidence for frequent surface fires, and pointed out that the existence of even-aged stands within a broader landscape composed of variable-aged stands does not necessarily indicate mixed-severity fire (*i.e.*, high-severity, stand-replacing fire within patches). Variation in stand age at the landscape scale could also arise from multiple mechanisms including drought stress, insects, pathogens, and wind-throw. Their broader point, however, is that climate is the overarching influence on finer-scale processes such as tree species population dynamics, such that cohort structure results more from climatic patterns than from specific and episodic mortality events.

There is similar uncertainty in reconstructing historical fire extent, making it difficult to determine if contemporary fires are larger than historical fires. Even when the size of a contemporary fire is known, determining whether that fire was larger in area than historical fires requires an understanding of the population distribution of fire sizes over a specified time period. Given the challenges of reconstructing both severity and extent, it becomes even more difficult to address these two parameters collectively. For example, a key question in fire science and management is whether contemporary fires are larger and more severe than historical fires. Our lack of this knowledge regarding historical fire size and severity is one reason why fire scientists can come to opposite conclusions. For example, the 550 km^2 Hayman Fire in 2002 in Colorado did (Fornwalt et al. 2016) or did not (Romme et al. 2003) have larger high-severity patches than historical fires.

Fire regimes can be influenced by regional climate at broad spatial scales, and by local landscape characteristics, such as slope and aspect, at finer spatial scales (Bigio et al. 2016). Local topography can mediate the influence of climate on fire regime parameters. Fire seasonality is one component of a fire regime that is likely to be driven more by the broad-scale influence of climate than by local topographic factors. Brown and Shepperd (2001) offered a latitude–seasonality hypothesis, whereby fires in southwestern Colorado should primarily occur during the dry period of May and June and before the onset of summer monsoon moisture during July and August. Conversely, fires in northern Colorado should primarily occur in late July, August, and September, after grasses and herbaceous fuels cure.

Whether fire occurrence is more strongly linked to broad-scale climate variability, landscape level topography, or local site characteristics such as fuel structure, can be addressed by evaluating the relationship between variability in climate indices and spatiotemporal occurrence of fire. Sherriff and Veblen (2008) found that the relationship between fire years and climatic variability varied as a function of elevation in Front Range ponderosa pine forests. They proposed that differences in fire frequency and severity between lower- and higher-elevation sites were due to differences in fuel structures that are linked to differences in patterns of climate variability (Sherriff and Veblen 2008). In southwestern Colorado ponderosa pine forests, Bigio et al. (2016) also found differences in fire–climate relationships, except the differences were across spatial extents and not elevational gradients.

Colorado ponderosa pine forests have experienced several large, high-severity fires over the past three decades, leading to intense interest and resource investment in restoration, via forest management, intended to reduce future risk (see Addington et al. 2018 for a thorough discussion of the topic). Understanding the dynamics of historical fire regimes, and in particular how the dominant tree species are affected, is important for planning restoration treatments because a primary goal of restoration forestry is to mimic historical tree mortality patterns and, therefore, forest structure at multiple spatial scales (Arno and Fiedler 2005). Patch mortality is known to be an important phenomenon in Colorado ponderosa pine forests (Addington et al. 2018) and, therefore, how fire effects vary in relative proportion across a landscape will provide a better blueprint by which to guide restoration planning.

A wealth of research on the fire ecology of ponderosa pine ecosystems in Colorado has been conducted over the past four decades, leading to multiple interpretations of the characteristics and driving mechanisms of the distribution of parameters that constitute a fire regime. To my knowledge, this paper is the first to synthesize and quantify this information using a meta-analytic approach to gauge the weight of evidence for and against specific interpretations. The overarching objective was to describe what the collective research indicates about the distribution of values within and among the fire regime parameters considered, and hence to address whether and how the fire regime varies with environmental characteristics. Below I outline the specific questions asked for each of five fire regime parameters based on concepts and hypotheses introduced in the literature.

1. *Frequency*. What is the distribution of historical MFI values, and does it suggest a high-frequency, low-severity fire regime, or a more variable frequency, mixed-severity regime? Is there support for the hypothesis that elevation has a strong effect on the predominant fire regime, whereby a high-frequency, low-severity fire regime occurs below an elevational level, and a variable-frequency, mixed-severity regime occurs above that level? Does geographic location affect variability in fire frequency?
2. *Severity.* What is the distribution of fire severity classes in historical fires; to what degree were high-severity fires a component of the historical fire regime; and are contemporary fires more severe than historical fires?
3. *Extent.* What is the historical distribution of fire size classes, and are fires larger today than in the past? For example, has mean fire size increased, and is the larger fire size class a higher proportion of all fires?
4. *Seasonality.* Was there a dominant fire season historically? Is there support for the seasonal–latitude hypothesis such that the relative proportion of fire scars in each season varies as a function of latitude?
5. *Climate relationships.* What is the relationship between fire occurrence and precipitation indices, and does it vary with elevation or geographic location?

Methods

Literature search

I searched the databases of the Citation Retrieval System of the US Forest Service Fire Effects Information System (https://www.feis-crs.org/feis/), Google Scholar (https://scholar.google.com/), and Web of Science (http://apps.webofknowledge.com) for published and unpublished studies using the following keywords: Colorado, fire regime, fire, ponderosa pine. I then searched the literature cited of relevant studies to find additional related papers. The search process concluded on 13 July 2017, and 95 papers were identified for possible inclusion. Papers were reviewed and included if they met the following criteria: research occurred in Colorado, in ponderosa pine ecosystems, addressed at least one of the five aspects of a fire regime (frequency, severity, extent, seasonality, or climate relationships), and were empirically based. Of the 95 papers identified, 43 met the inclusion criteria.

Data extraction and analysis

Twenty-six of the 43 studies that met the inclusion criteria reported results in a manner that allowed comparison to other studies and contained results that were not previously reported. I created a database and performed graphical and statistical analyses in R version 3.3.3 (R Core Team 2017).

Meta-analysis often employs approaches to calculate effect sizes as the mean difference between control and treatment groups, the correlation between two continuous variables, or the risk or odds ratio when the response variable is dichotomous. Statistics associated with these effect sizes are usually corrected for sample size and weighted by study-level variance. The type of results reported in fire history studies preclude this approach. Before- and after-control designs do not conform to the retrospective nature of fire history studies, and analyses are often descriptive, reporting the proportion of observations by categorical groupings (*e.g.*, severity classification, seasonality, climate). Because of these differences, I took a different analytical approach in this meta-analysis, and systematically extracted, combined, summarized, and compared results from the sample of studies that addressed a given parameter (Table 1). I did this because typical meta-analysis weighting and standardization of study-level results (*e.g.*, Hedge's g; Hedges and Olkin 1985), require knowledge of both the sample size and standard deviation (or variance), and many studies failed to report one or both of these statistics.

Fire frequency

I extracted site-level mean, minimum, and maximum fire return interval values (years), associated time period, elevation (m), and latitude and longitude (decimal degrees) from 17 studies comprising 78 independent sites (Table 1). Elevation, latitude, and longitude were derived using mapping software and were based on site descriptions or maps from publications when values were not explicitly provided. In cases for which there was not enough information to derive site-specific values, I used study-level values provided in the publications. When only minimum and maximum elevation values were given, I calculated the mid-point value and entered it as the site elevation.

MFI can be reported in multiple ways using different combinations of the same raw data (*e.g.*, by time period, elevation band, number or percentage of trees affected, etc.). I did not double count results from studies that reported multiple MFI values derived from the same raw data. Likewise, when a study reported MFI values using subsets of fire dates based on different filtering criteria

Table 1 Studies and their associated fire regime parameters included in the Colorado, USA, ponderosa pine fire regime meta-analysis of 2017

Map number (Fig. 1)	Reference	Fire regime parameter				
		Frequency	Severity	Extent	Seasonality	Climate
1	Bigio et al. 2010	x			x	
2	Bigio et al. 2016	x	x			x
3	Brown and Shepperd 2001	x			x	x
4	Brown and Wu 2005	x				x
5	Brown et al. 1999	x			x	
6	Brown et al. 2015	x				
7	Donnegan et al. 2001	x			x	x
8	Ehle and Baker 2003		x	x		
9	Fulé et al. 2009	x				x
10	Gartner et al. 2012	x				x
11	Goldblum and Veblen 1992	x				
12	Grissino-Mayer et al. 2004	x			x	x
13	Korb et al. 2013	x			x	x
14	Laven et al. 1980	x		x		
NA*	Litschert et al. 2012			x		
15	Rowdabaugh 1978	x				
16	Schoennagel et al. 2011		x			x
17	Sherriff 2004	x	x			x
18	Sherriff and Veblen 2006			x		
19	Sherriff and Veblen 2008					x
20	Sherriff et al. 2014		x			
21	Veblen et al. 1996				x	
22	Veblen et al. 2000	x				
23	Wieder and Bower 2004	x				x
24	Williams and Baker 2012a		x			
25	Williams and Baker 2012b		x			

*Study included all fires throughout the state from 1970 to 2006; locations cannot be mapped (*e.g.*, a minimum number or percentage of trees scarred), I only included results from the most inclusive level. I did include multiple MFI values from a given study if they were from independent sites and or independent time periods (*i.e.*, different raw data).

All studies calculated composite MFI (*i.e.*, dates of fire scars from all samples were combined into one time series). Most studies (71%), representing 64% of site-level values, reported composite MFI values without a filter ("all trees," hereafter). In instances where a study failed to report values for the all trees category but reported values derived using multiple filter levels, I chose the most inclusive level (least restrictive filter).

I performed graphical analyses of the MFI data and calculated Pearson's correlation coefficient (Sokal and Rohlf 1995) between MFI and elevation. I grouped sites into two elevation groups (greater than and less than 2400 m), plotted them with a histogram, and performed an independent samples, 2-tailed *t*-test (Sokal and Rohlf 1995) to determine if mean MFI differed between elevation groups. I constructed box plots of the distribution of MFI values by elevation group to compare median values and data spread. Finally, I grouped sites into either Front Range or southwestern Colorado, created box plots to explore whether geographic region explained variation in MFI values, and tested for differences in regional mean MFI values with a *t*-test.

Fire severity

Seven studies provided quantitative results of the percentage of fire severity observations in low, mixed or moderate, and high groups (Table 1). I calculated means for the three severity classes for studies in which only the number of observations by severity class were given so that the percentage of observations in each severity class could be compared among studies. I constructed a table summarizing study-level observations of percentage fire severity by each class, overall fire severity class means and associated standard errors, and detailed descriptions of sampling methods to highlight differences.

Fire extent

Only four studies provided quantitative results of historical fire extent from multiple sites over time (Table 1). I described and compared the distribution of fires by fire extent classes for these four studies.

Fire seasonality

Seven studies (n = 39 sites) reported either the percentage or number of fire scars by seasonal position within annual growth rings (Table 1). If the number of fire scars by season was reported, I calculated the percentage of these scars among seasons. Studies varied as to which months were included in a given seasonal category and in the number of seasonal categories a study included, ranging from a maximum of five to a minimum of two. How dormant season scars were reported varied among the studies and in three papers it could not be determined how many scars were specifically dormant. Because of this, I collapsed studies with more than two seasonal categories into two categories: earlywood and latewood. In general, the latewood category represented fire scars that occurred from July until the initiation of the following year's growing season (*i.e.*, mid-summer through fall and winter, and into early spring). The earlywood category represented fire scars from as early as April until mid-July.

I calculated the ratio of earlywood to latewood fire scars for each site and plotted these values with a histogram. Values between 0.0 and 0.961 indicated a higher proportion of latewood scars, and hence late summer and fall fires. Values between 1.041 and 100 indicated a higher proportion of earlywood scars, and hence spring and early summer fires. A ratio of 1.0 (50%:50%) indicated no seasonal dominance of fire scars. I calculated Pearson's correlation coefficient between latitude and earlywood:latewood. I created three latitude groups (low, mid, and high) defined by equal breaks (1.2° per group) in the range of latitude values for all 39 sites (range = 3.6°, minimum = 37.13°, maximum = 40.73°). I plotted latitude group data with a box plot, and calculated the mean earlywood:latewood and its standard deviation for each latitude group and for the overall data set. I also calculated the correlation between latitude and fire seasonality for each of the four studies that reported multiple sites to control for study variability in sampling methods and to determine if a relationship existed within studies. Finally, I calculated the correlation between site elevation and earlywood:latewood.

Fire–climate relationships

Superposed epoch analysis (SEA; Grissino-Mayer 2001) is a statistical method used to measure responses to an event and how a given variable relates prior to and during the event. The purpose is to determine whether patterns can be discerned in a time-series consisting of an event (*i.e.*, fire year) and putative explanatory variables (*i.e.*, reconstructed climatic indices) (Grissino-Mayer 2001).

Twelve studies provided results from a SEA of fire year and climate indices (Table 1). Five precipitation-related indices were used among the 12 studies (n = 39 analyses), and 11 of the 12 studies performed analyses on more than one index. Indices were derived from tree-ring chronologies and were reconstructions of conditions extending back centuries prior to the advent of instrumental measurements. The five indices used were:

1. Palmer Drought Severity Index (PDSI), which incorporates contemporary temperature and precipitation data to determine whether there was an excess or deficit of water. In fire history studies (n = 14 analyses), PDSI is inferred from reconstructions of summer (June to August) conditions (Sherriff and Veblen 2008).
2. Tree-Ring Indices (TRI, n = 13 analyses) are used to infer moisture availability by calculating the departure from mean tree-ring growth in a ponderosa pine tree-ring index (Sherriff 2004).
3. NINO3 is an index of sea surface temperature from the NINO3 region of the Pacific Ocean (5°N to 5°S, 90°W to 50°W) and is used as a proxy record of the El Niño-southern oscillation (ENSO). In fire history studies (n = 7 analyses), NINO3 reconstructions for December to February are used and date back to AD 1408 (D'Arrigo et al. 2005).
4. Southern Oscillation Index (SOI; n = 3 analyses) is another proxy record for ENSO, and is a measure of the difference in surface air pressure between Darwin, Australia, and Tahiti (Stahle et al. 1998).
5. Pacific Decadal Oscillation index (PDO) is a measure of sea surface temperature anomalies over the North Pacific Ocean. PDO reconstructions (n = 2 analyses) date back to AD 1700 (D'Arrigo et al. 2001).

I extracted results from each SEA on the departure of a given climate index from the average climate conditions in years prior to and during fire years (Grissino-Mayer 2001), and recorded dry, wet, or average for each of the five years analyzed within each SEA based on whether a given year was drier, wetter, or had no change from the mean. I created stacked bar graphs of the percentage of observations in each of the three precipitation conditions (wet, dry, average) for the three most commonly used indices (PDSI, TRI, NINO3) and for all indices combined. I then evaluated whether there was a distinction in the temporal pattern of precipitation conditions between sites above and below 2400 m elevation, and between Front Range and southwestern Colorado sites by constructing bar graphs of the percentage of observations in each precipitation condition for each of the five years and for each group.

Results

Clear patterns and relationships existed in some fire regime parameters, while extreme methodological variation obscured underlying phenomena in others. The number of studies reporting values for each parameter varied, ranging from 17 for fire frequency to 4 for fire extent (Table 1). Study sites were well distributed throughout the range of Colorado ponderosa pine ecosystems (Fig. 1).

Fire frequency

Evidence of low-severity fire ended abruptly prior to or by the early twentieth century (1920) in the fire-scar record from 73 of the 78 sites. Only five sites had fire-scar records that included fires after 1920. Four of these records included fires up to the 1930s and 1960s, and the last fire was recorded in 1989. Data were insufficient to perform a time period analysis on MFI. However, as a rough comparison, the mean MFI of the five sites where the fire record ended after 1920 was 2.6 years longer than the mean MFI derived from sites with a pre-1920 record (n = 73 sites).

Site-level MFI varied with a 63-year difference between the shortest and longest MFI (Table 2). Despite the broad spread of MFI values, 85% of sites fell within the shorter half of the interval range, with MFI values ≤31 years (*i.e.*, one half of the interval range; Fig. 2), and an overall low relative standard error of 6.6%. The distribution of values was right-skewed by four site-level means that were longer than 46 years (Additional file 1: Appendix, Fig. 2). The two longest intervals (64 and 66 years) represented outliers of the overall frequency distribution. Both sites were located in the Front Range, included samples from partially overlapping time periods, and occurred at the upper end (2650 m) of the elevation range of all sites (minimum = 1910 m, maximum = 3078 m); only 11 of all 78 sites, and 8 of 56 Front Range sites were higher in elevation. The 66-year estimate may also be an artifact of small sample size as only six trees were used to generate this estimate.

Fire return interval increased with site elevation. Elevation and MFI were moderately correlated at the site-level and the relationship was significantly positive (r = 0.33, df = 76, $P < 0.05$; Fig. 3). Classifying sites into two broad elevation groups (low elevation: <2400 m, range from 1910 m to 2385 m, mean = 2202 m; and high elevation: >2400 m, range from 2400 m to 3078 m, mean = 2602 m) revealed a clear distinction in the distribution of MFI values. The low-elevation (<2400 m) group had significantly shorter MFI values and less variability than the high-elevation (>2400 m) group (t-test: df = 65, t = −3.904, $P < 0.05$; Table 2, Fig. 4). Hence, elevation acts to separate Colorado ponderosa pine into distinct

Table 2 Summary statistics of site-level mean fire return interval results from 17 fire history studies by elevation group in ponderosa pine ecosystems in Colorado, USA, used in the fire regime meta-analysis of 2017. SE = standard error

		Fire return interval (yr)				
Group	*n*	Minimum	Maximum	Mean	Median	SE
All sites	78	3	66	21	19	1.4
<2400 m	24	3	40	15	14	1.6
>2400 m	54	6	66	24	22	1.8

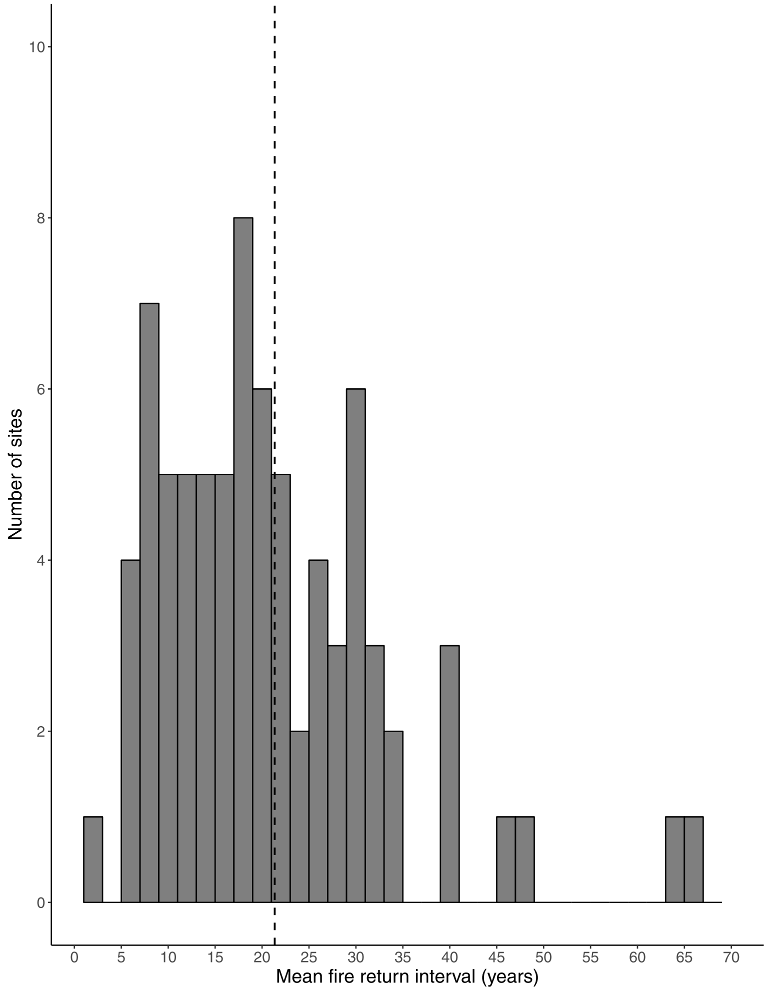

Fig. 2 Frequency distribution of site-level mean fire return intervals (n = 78) from 17 studies in ponderosa pine (*Pinus ponderosa*) ecosystems in Colorado, USA, used in the fire regime meta-analysis of 2017. Vertical dashed line indicates overall mean

statistical populations with respect to MFI when the elevation cutoff is set at 2400 m.

The two sites with the longest MFI (64 and 66 years) were also outliers of the high elevation group, while a site with an MFI of 40 years was an outlier of the low elevation group (Fig. 4). This latter site occurred at an elevation (2165 m) that was in the middle of the lower elevation group range (14 of 24 sites were of higher elevation), and was located at a mid-latitude position (39.19° N) relative to the latitude range of the studies (latitude ranged from 37.13° to 40.73°; Fig. 1). Thus, neither an elevation nor a latitude effect on MFI explains the large outlier value, and it may be due to local site conditions (*e.g.*, aspect and slope) or human history, but can't be determined from the information given in the paper.

The geographic distribution of fire frequency study sites fell into two general regions within Colorado—Front Range and southwestern—reflecting the distribution of ponderosa pine ecosystems (Fig. 1). Front Range and southwestern sites were broad distances apart (mean latitude difference = 2.51°, mean longitude difference = 2.05°; Table 3), and mean MFI values differed by 5 years, with southwestern sites experiencing more frequent fire (*t*-test: df = 51, t = 1.932, P = 0.059; Table 3). The moderate difference in MFI values between the two regions corresponds with a similarly moderate difference in mean elevation: southwestern sites were 81 m higher, on average, than Front Range sites (*t*-test: df = 76, t = −1.988, P = 0.050; Table 3). Based on the positive correlation between MFI and elevation, the mean MFI for southwestern sites was shorter than expected, given their higher average elevation, indicating different historical fire frequencies between the two regions. Although the relationship between geographic region and MFI was not as strong as that between elevation group and MFI, geography did account for variability in the distribution of MFI values (Fig. 5). The two sites with the longest MFI were outliers again in

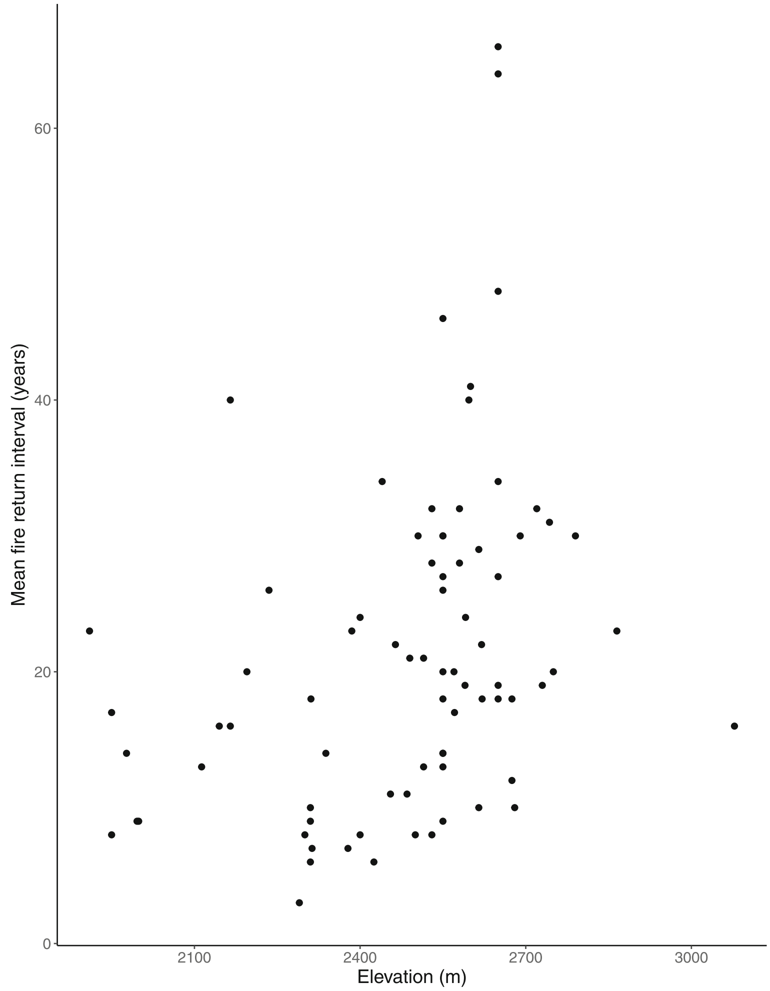

Fig. 3 Relationship between site-level mean fire return interval and elevation for 78 ponderosa pine (*Pinus ponderosa*) sites in Colorado, USA, used in the fire regime meta-analysis of 2017

the Front Range group distribution. Southwestern sites had a single outlier with a MFI of 46 years that occurred at 2550 m, and only 5 of 22 southwestern sites were higher in elevation than this site.

Fire severity

The goal of the fire severity meta-analysis was to extract and analyze study results that describe the relative proportion of observations in low-, mixed-, and high-severity classes. The high degree of variation among studies in sampling design and methods, and in how severity classes were defined, precluded a detailed quantitative evaluation of fire severity class distribution and its relationship with environmental factors (*e.g.*, elevation and geography).

Seven studies provided numerical results on fire severity class distribution (Table 4). The mixed-severity class had the highest overall mean percentage of observations (observations are sample units, which differ among studies) followed by the low-severity class, with considerable variation within each fire severity class. Low- and mixed-severity class means combined for 83% of all observations. The high-severity class accounted for more than an insignificant component of the fire regime (class mean = 17%), pointing to the periodic occurrence of stand-replacing fire in Colorado ponderosa pine ecosystems. The low-severity class had the greatest range of study-level mean values (range from 0% to 90%; Table 4), while the high-severity class had the greatest relative variation (least precise estimate) among study-level means (RSE low = 36%, mixed = 28%, high = 49%).

Vastly different study methods precluded further comparisons and evaluation of fire severity among studies. Sampling methods ranged from the reconstruction of historical forest conditions based on General Land Office (GLO) surveys in the late nineteenth and early twentieth centuries that were then used to estimate fire histories and assign fire severity classes to large areas (Williams and

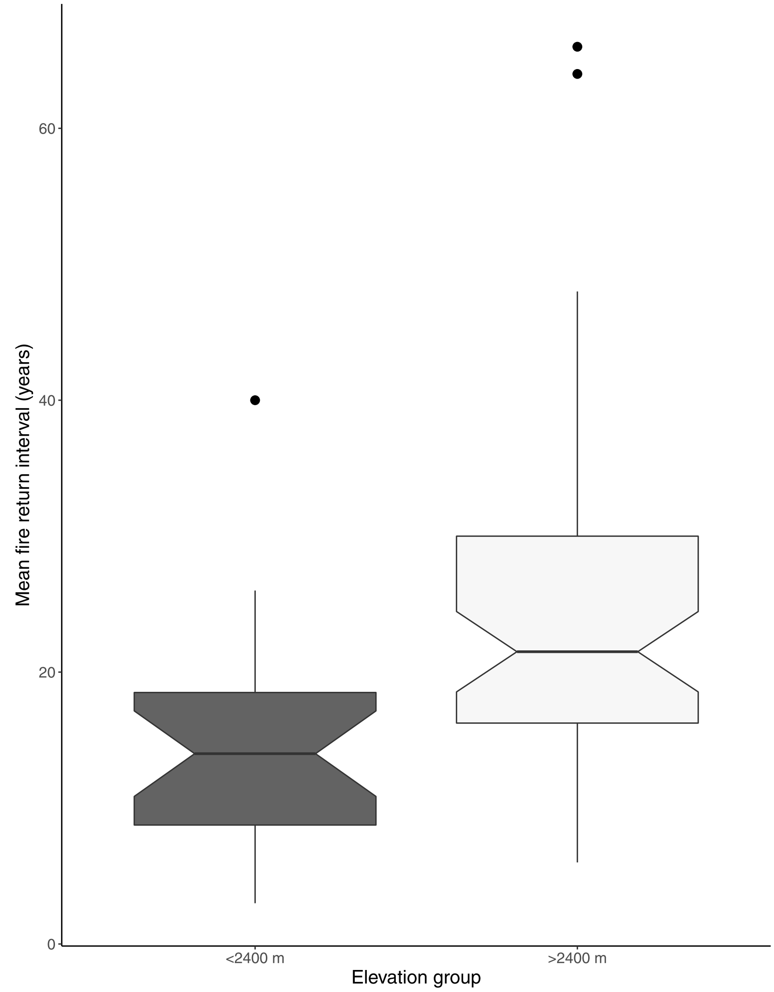

Fig. 4 Variability of site-level mean fire return interval by two elevation groups (<2400 m, n = 24; and >2400 m, n = 54) from 17 fire history studies on ponderosa pine (*Pinus ponderosa*) in Colorado, USA, used in the fire regime meta-analysis of 2017. The horizontal line in the middle of each box represents the median value (50th percentile), the ends of the boxes are the first (Q1) and third (Q3) quartiles, which cover the central 50% of the data, and the difference between Q3 and Q1 is the interquartile range (IQR). The notches are an approximation of the 95% confidence interval for the median values. Vertical lines extend to the most extreme data points that are no more than ±1.5 × IQR, and outliers beyond the lines are individually displayed as dots

Baker 2012a, 2012b), to a structural-based approach that assigns severity classes based on the proportion of remnant (*i.e.*, surviving) and recruitment (*i.e.*, establishment) trees in existing stands (Sherriff 2004; Schoennagel et al. 2011; Sherriff et al. 2014; Table 4). Furthermore, the validity of the GLO approach to estimating historical fire severity has been challenged for its assumptions, reproducibility, precision, accuracy, and appropriate level of inference, further complicating meta-analysis of fire severity data. The interested reader is directed to the following literature to gauge the merits of this debate, which are beyond the scope of the current paper (Fulé et al. 2014; Levine et al. 2017; Baker and Hanson 2017; Baker et al. 2018; Cogbill et al. 2018; Hagmann et al. 2018).

Table 3 Geographic and mean fire return interval (MFI) summary statistics from 17 fire history studies in two regions of ponderosa pine distribution in Colorado, USA, used in the fire regime meta-analysis of 2017. SD = standard deviation

	Longitude (decimal degrees)		Latitude (decimal degrees)		Elevation (m)		MFI (yr)	
Region	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Front Range	105.43	0.23	39.83	0.63	2456	221	23	13
Southwestern	107.48	0.60	37.32	0.10	2537	112	18	10

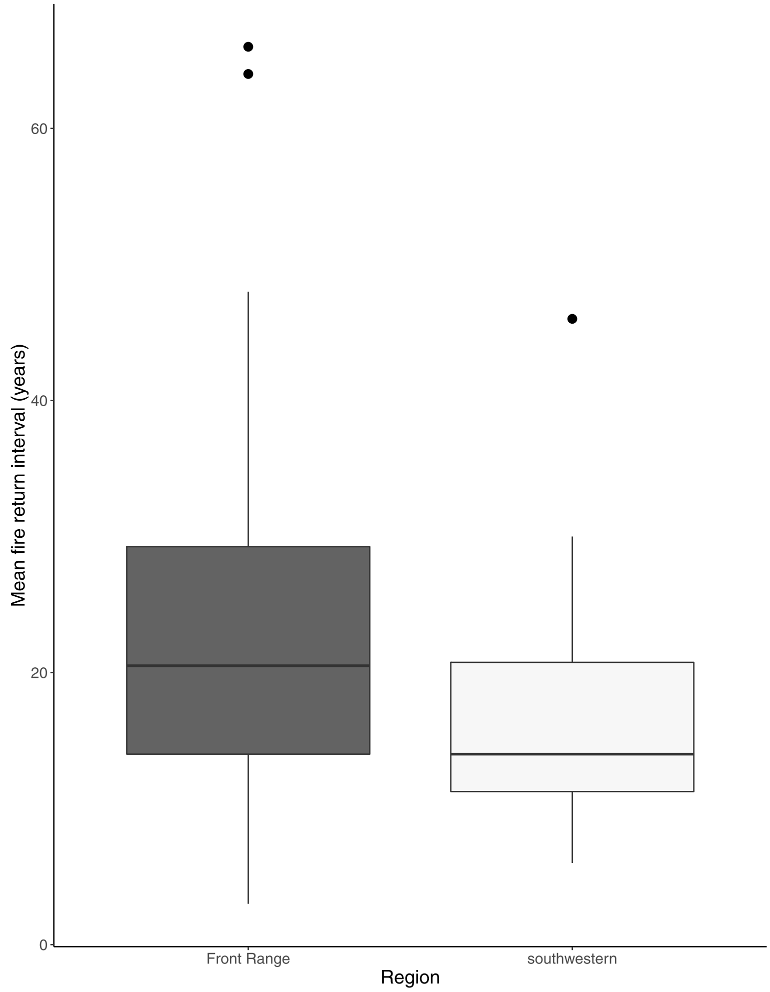

Fig. 5 Variability of site-level mean fire return interval by two geographic regions (Front Range, n = 56; and southwestern, n = 22) from 17 fire history studies on ponderosa pine (*Pinus ponderosa*) in Colorado, USA, used in the fire regime meta-analysis of 2017. The horizontal line in the middle of each box represents the median value (50th percentile), the ends of the boxes are the first (Q1) and third (Q3) quartiles, which cover the central 50% of the data, and the difference between Q3 and Q1 is the interquartile range (IQR). Vertical lines extend to the most extreme data points that are no more than ±1.5 × IQR, and outliers beyond the lines are individually displayed as dots

Even among studies using the structural-based approach, severity classification criteria differed (Table 4), obfuscating comparative estimates. Fire severity studies also differed as to whether the study emphasis was on space or time. Severity of specific events within a site was estimated in some studies such that a given location could be assigned more than one severity class (Schoennagel et al. 2011; Sherriff et al. 2014; Bigio et al. 2016; Table 4), while other studies estimated the overall severity of a site considering all events that occurred within a given time frame to assign that location a single severity class (Ehle and Baker 2003; Sherriff 2004; Table 4).

Fire extent

Only four studies provided estimates of historical fire extent, making it difficult to compare with contemporary fire extent, and the variation in sampling methods and reporting of results made inter-study numerical comparisons difficult (Table 1). A single study addressed changes in fire size and area burned in the postsettlement period (1930 to 2006) in the Southern Rockies Ecoregion (US Environmental Protection Agency 2013) and included multiple forest types, not just ponderosa pine. It concluded that average fire size and annual area burned have increased over this period.

Laven et al. (1980) examined historical fires occurring between 1708 and 1973 in a 50 ha study area and assigned them to two size categories. For the total period, the mean frequency of occurrence was 21 years for small fires (~1 ha) and 42 years for large fires (~25 ha). During the settlement era (1840 to 1905), large fires occurred more frequently (16 years), suggesting a positive

Table 4 Fire severity classification results from studies in ponderosa pine ecosystems in Colorado, USA, used in the fire regime meta-analysis of 2017. *n* = number of sample units

	Fire severity (%)					
Reference	Low	Mixed	High	*n*	Time period	Region
Bigio et al. 2016 [a]	31	69	0	13	Before 1880	Southwestern
Ehle and Baker 2003 [b]	90	3	7	80	1540 to 2000	Front Range
Schoennagel et al. 2011 [c]	0	79	21	20	1601 to 1953	Front Range
Sherriff 2004 [d]	72	20	8	86	1700 to 1920	Front Range
Sherriff et al. 2014 [e]	12	88	0	150	1597 to 1995	Front Range
Williams and Baker 2012a [f]	55	24	21	13	1984 to 2009	Front Range
Williams and Baker 2012b [g]	3	33	64	145	Before 1880	Front Range
Mean severity (%SE)	38 (36)	45 (28)	17 (49)			

[a] Fire severity estimated within plots through time:
- low: ≥1 fire-scarred tree was present within 2 ha of the plot and no distinct cohorts were evident.
- mixed:
  - ≥1 fire-scarred tree present and ≥1 distinct cohort evident, or
  - no fire-scarred trees present, but ≥1 distinct cohort evident and one surviving tree established prior to the cohort.
- high: no fire-scarred trees, ≥1 distinct cohort, and no surviving trees established prior to the cohort.

[b] Fire severity estimated within plots based on tree mortality and regeneration patterns:
- low: no or low mortality and little or no regeneration.
- mixed: mortality of at least one small group of trees within 10 m of each other.
- high: high overstory mortality and a subsequent large regeneration pulse.

[c] Fire severity estimated within plots through time, based on relative proportions of trees that survived fires (remnant) and trees that established ≤40 years after fire (establishment):
- low: ≥80% remnant, ≤20% establishment.
- moderate: 21 to 79% remnant, 79 to 21% establishment.
- high: ≤20% remnant, ≥80% establishment.

[d] Fire severity estimated for fires within sites based on relative proportions of live trees that survived fire (remnant) and trees that established ≤40 years after fire (establishment), in addition to tree spatial pattern and ring-width changes:
- low: ≥40% remnant, <20% establishment.
- moderate: <70% remnant, 20 to 70% establishment.
- high: <20% remnant, >70% establishment.

[e] Fire severity estimated at each site using the same criteria as Schoennagel et al. 2011, then assigned site-level severity classification of cumulative effects over time.

[f] Fire severity estimated with Monitoring Trends in Burn Severity (MTBS) data of 13 fires >400 ha. MTBS assigns four severity classes (unburned to low, low, moderate, high) to the area of each fire. Results are percent severity class for combined 13 fires. MTBS severity classes "unburned to low" and "low" were combined as Low here for consistency and comparison with the other studies.

[g] Fire severity estimated using General Land Office survey data to reconstruct historical stand structures, which were used to derive percent severity for 260 ha polygons in a 65 525-hectare area, based on the assumptions that tree size is related to tree age and that stand structure and disturbance severity are linked. Polygon severity classified as:
- low:
  - mean tree density was <178 trees ha^{-1}
  - the percentage of large trees was >29.2%, and
  - the percentage of small trees was <46.9%.
- mixed: remaining areas (*i.e.*, influenced by fires of moderate severity or a mosaic of different severities).
- high: percentage of small trees was >50% and percentage of large trees <20%.

relationship between human settlement and the incidence of large fires. Mean frequencies were not provided for the presettlement (before 1840) or postsettlement (after 1905) periods, preventing further comparisons.

Ehle and Baker (2003) estimated mean minimum low-severity fire size within plots and showed a decline from 0.24 ha during the presettlement period (before 1860) to 0.03 ha during the fire suppression period (1915 to 1999). There was no difference in mean minimum fire size between presettlement and settlement (1860 to 1914) periods, but the mean minimum fire size during the suppression period was smaller than that of the two earlier time periods.

Sherriff and Veblen (2006) estimated minimum fire size of the most recent moderate- to high-severity fires that occurred at each of 22 study sites between 1782 and 1913. Twenty sites had evidence of moderate- or high-severity fires during this 130-year period, and 16 of these fires (80%) occurred during a 21-year period between 1859 and 1880. The overall mean minimum fire size was 70 ha with considerable variation around the mean (SD = 54 ha) and a range of 129 ha (minimum = 6 ha, maximum = 135 ha).

The studies by Sherriff and Veblen (2006) and Ehle and Baker (2003) sampled overlapping time periods from 1782 to 1913 and used similar methods to estimate minimum fire extent, allowing comparisons of mean minimum fire size. Ehle and Baker (2003) provided only the mean values for the earliest (1760 to 1860) and latest (1915 to 1999) time periods, and thus only the earliest time period could be compared with Sherriff and Veblen (2006). Mean minimum fire extent for 1782 to 1859 calculated from results in Sherriff and Veblen (2006) was 68 ha (n = 11), and is two orders of magnitude larger than the estimated mean minimum fire size (0.24 ha) for the corresponding period (1760 to 1860) in Ehle and Baker (2003), and more closely aligns with the "large" fire size category of 25 ha broadly defined by Laven et al. (1980).

Litschert et al. (2012) used spatial data of wildfires from eight national forests in the Southern Rockies Ecoregion that occurred between 1930 and 2006 to classify fire extent into seven fire-area classes by 20-year intervals. Their results included data from southern Wyoming and northern New Mexico, USA, and from multiple vegetation types. Colorado fires formed the overwhelming majority of fires in the data set (see Figure 1 in Litschert et al. 2012), and I estimated from their Table 2 that approximately 66% of the fires in the data set involved ponderosa pine forests. Hence, despite some limitations, the data are useful if only for a general assessment of fire size class distribution over time, a conclusion made more salient given the general dearth of fire extent data.

A summary of their findings follows (note that I calculated the results for findings 2 to 6, below, from results in their Table 1).

1. The total number of fires in the two largest fire size classes (class means = 11 km^2 and 97 km^2) increased from two fires in the earliest period (1930 to 1950) to 32 fires in the most recent period (1991 to 2006).
2. The percentage of fires in the two largest size classes relative to the total number of fires increased slightly from the earliest (0.20%) to most recent (0.48%) time periods. The number of large fires increased, but so did the number of all fires.
3. The total area burned by large fires increased from 22 km^2 in the earliest period to 1986 km^2 in the most recent period.
4. The percentage of total area burned by fires in the two largest fire size classes relative to total area burned increased from 52% in the earliest period to 93% in the most recent period.
5. Mean fire size increased from 0.043 km^2 in the earliest period to 0.320 km^2 in the most recent period.
6. The area burned per fire per year increased nearly 6-fold from the earliest period (0.86 km^2 $fire^{-1}$ $year^{-1}$) to the most recent period (5.12 km^2 $fire^{-1}$ $year^{-1}$).

When evaluating the relative change in the number of large fires, there was little increase observed because, although the number of large fires was increasing, so was the total number of all fires. Yet, this small relative change still translated to a large increase in burned area (absolute and relative) because of the skewed nature of the fire size classes; a small increase in the number of fires in the largest size class has a large effect on total area burned. For example, it would take 97 000 fires of the smallest size class (0.001 km^2) to equal the size of one average fire in the largest class. The clearest indication of an increase in fire extent over the 77 years of the data set is the change in rate of burned area (finding 6, above). This metric integrates information from the number of fires per size class, the mean area of the size classes, and the mean number of fires per year in each time period, and standardizes it for direct comparison and easy interpretation. For example, it would take about six average fires from the 1930 to 1950 time period to equal the size of one average fire from the 1991 to 2006 time period.

Fire seasonality

Latewood fire scars dominated the seasonality record (69% of observations, n = 39). Ratios indicating latewood dominance (*i.e.*, <1.0) were found in 87% of all sites, while ratios indicating earlywood dominance (*i.e.*, >1.0) were found in 10% of sites (Fig. 6). One site (3%) had an equal proportion of earlywood and latewood fire scars. The mean ratio of all 39 sites was 0.72 (proportionally more fires in late summer and fall relative to spring and early summer). Thus, the overall evidence suggests that fires in Colorado ponderosa pine forests scar trees at a higher rate (approximately three to one) in late summer and fall relative to spring and early summer.

Three of the four sites with ratios >1.0 were identified as outliers and were all equal to 4.0 (80% earlywood to 20% latewood). Nothing obviously unique sets the three outlier sites apart from the other sites that might explain this pattern. All three sites were located at the upper middle portion of the elevation distribution (two sites at 2550 m, and the other at 2597 m), with 14 and 12 sites in the data set at higher elevation, respectively. Two sites were in the lower portion of the latitude distribution (37.30° and 37.34°), while the third site was from a higher latitude location (40.07°). The number of scars used to identify seasonality in the three sites (67, 61, and 44) differed little from the mean value of 66 scars for all 39 sites. The time period of analysis of the three studies (1600 to1900, 1680 to 1880, 1703 to1920) overlapped substantially with the rest of the data set. Finally, each of the three sites was from a different study, reducing the likelihood that methodological bias may have influenced the results.

There was no evidence for a latitude effect on fire seasonality at the site level. The hypothesis that latitude

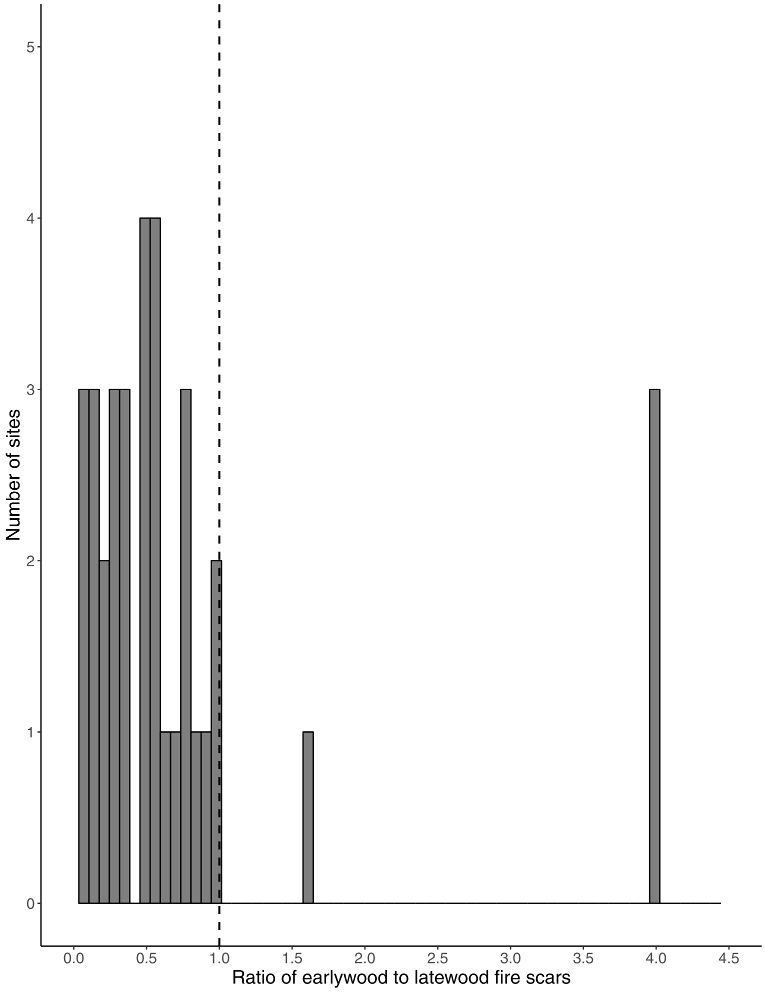

Fig. 6 Distribution of site-level values (n = 39) of the proportion of fire scars present in earlywood relative to latewood from seven studies on ponderosa pine (*Pinus ponderosa*) in Colorado, USA, used in the fire regime meta-analysis of 2017. The dashed black line at value 1.0 marks the point at which observations are equal between seasons; to the left of the line are observations with a majority of latewood fire scars, and to the right of the line are observations with a majority of earlywood fire scars

position influences fire seasonality (by way of differences in climatic patterns such as monsoonal moisture flow) predicts that there will be an inverse relationship between latitude and the ratio of earlywood to latewood fire scars. This hypothesis was not supported by results from the 39 sites, as the correlation between latitude and earlywood:latewood ratio was not different from zero (r = −0.04, P = 0.81). Two of the outliers with a ratio value of 4.0 discussed above lent general support to the latitude hypothesis as they were from low latitude sites; however, the other 37 sites exhibited no relationship between latitude and fire seasonality, swamping out any signal from the two sites.

Latitude grouping also failed to show a clear relationship with fire seasonality. The distribution of seasonal fire scar observations differed little between latitude groups, and a subtle trend in median values suggested an opposite direction of latitude and fire seasonality than expected (*i.e.*, a greater proportion of latewood fire scars at lower latitudes; Fig. 7). Mean ratio values were also highest in the high latitude group, but lowest in the mid latitude group, indicating no relationship between latitude group and fire seasonality (Table 5).

Four studies reported results from multiple sites, allowing calculations of within-study correlations between latitude and fire seasonality. Brown and Shepperd (2001) had the greatest north-south spread of 14 sites spanning 3.44° latitude. Although there was some support for a latitude effect (*i.e.*, direction of the relationship was negative and the correlation was stronger than that of the overall data set), the correlation was not different from zero (r = −0.41, P = 0.146). Grissino-Mayer et al. (2004) reported on nine sites spanning 0.55° latitude and showed a negative but non-significant relationship

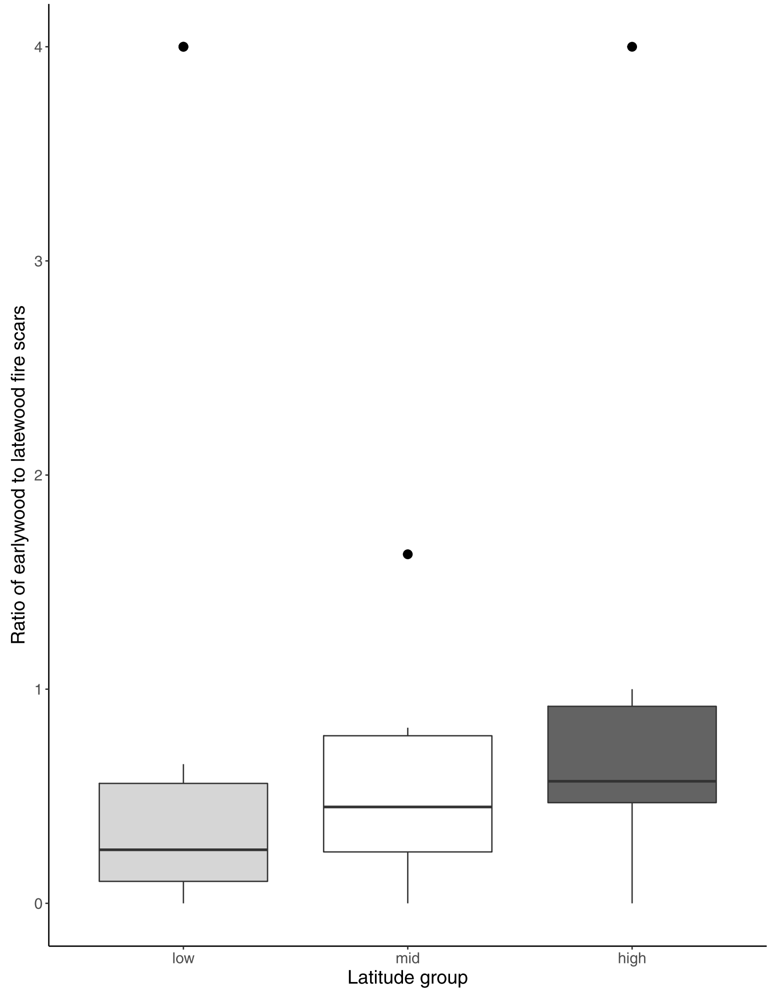

Fig. 7 Variability in the ratio of earlywood to latewood fire scars by three latitude groups (*n* = 12 for each group) from seven fire history studies on ponderosa pine (*Pinus ponderosa*) ecosystems in Colorado, USA, that were used in the fire regime meta-analysis of 2017. Latitude groups (low, mid, and high) are defined by equal breaks (1.2° per group) in the range of latitude values for all 39 sites (minimum = 37.13°, maximum = 40.73°). The horizontal line in the middle of each box represents the median value (50^{th} percentile), the ends of the boxes are the first (Q1) and third (Q3) quartiles, which cover the central 50% of the data, and the difference between Q3 and Q1 is the interquartile range (IQR). Vertical lines extend to the most extreme data points that are no more than ±1.5 × IQR, and outliers beyond the lines are individually displayed as dots

between latitude and fire seasonality (r = −0.30, P = 0.425). Data from Donnegan et al. (2001) from five sites spanning 0.40° latitude showed a positive and non-significant correlation between latitude and fire seasonality (r = 0.25, P = 0.683). Veblen et al. (1996) reported from eight sites that spanned 0.37° latitude with a weak negative association that was similar to that of the overall data set (r = −0.040, P = 0.924). Thus, site-level latitude, latitude groups, and within-study correlations all failed to support a latitude effect hypothesis for fire seasonality. Likewise, elevation had no association with fire seasonality (r = 0.089, P = 0.589).

Fire–climate relationship

The three most commonly used climate indices (NINO3, Palmer Drought Severity, and Tree Ring Growth) among the 12 studies that analyzed fire–climate relationships via superposed epoch analysis showed a similar pattern in precipitation conditions in each of the four years preceding fire years (Fig. 8). When results from analyses using these three indices were combined with results from the two less frequently used indices (Southern Oscillation and Pacific Decadal Oscillation) into an “All” group, a similar pattern was evident (Fig. 8). Subsequent analyses were thus based on the combined “All” group results.

Fire year (year y−0) exhibited the most consistent pattern with 100% of observations (n = 39) showing drier than average conditions during fire years (Fig. 9). The year preceding a fire year (y−1) showed equal observations of drier and wetter than average conditions (41% each), while wetter than average conditions were prevalent in y−2 (62%), and more so in y−3 (68%, Fig. 9).

Table 5 Summary statistics for the ratio of earlywood to latewood fire scars by three latitude groups from seven studies within the ponderosa pine zone in Colorado, USA, used in the fire regime meta-analysis of 2017. Groups determined by equal breaks (1.2° per group) in the overall latitude range of the studies included in this meta-analysis; *n* is the number of sites in each group, and SD is the standard deviation

Latitude group	Latitude range (decimal degrees)	Mean (early:late)	SD	*n*
Low	37.13 to 38.33	0.79	1.37	14
Mid	38.34 to 39.54	0.54	0.44	12
High	39.55 to 40.75	0.82	1.01	13
Overall	37.13 to 40.75	0.72	1.02	39

Most results (57%) showed drier than average conditions four years prior to a fire year (y–4, Fig. 9). These results support the hypothesis that climatic conditions act as an overriding control on the timing of fires in these ecosystems—specifically, that fire years are preceded by wetter than average years, potentially increasing rates of biomass production that is later desiccated and burned during drier than average fire years.

Site elevation had no effect on fire–climate relationships during fire years as all sites experienced drier than average conditions in y–0 (Fig. 10). Lower elevation sites (*i.e.*, <2400 m) saw wetter than average antecedent conditions during the three years preceding a fire year and drier than average conditions four years before a fire year (y–4), while higher elevation sites saw wetter than average conditions two and three years before a fire year (y–2 and y–3, respectively) and drier than average conditions during the year preceding a fire year and four years before a fire year (y–1 and y–4, respectively; Fig. 10). Except for the year preceding a fire year, both elevation groups exhibited the same pattern of wetter than average conditions in y–2 and y–3, and drier than average in y–4.

While the two elevation groups showed mostly similar antecedent fire year precipitation patterns, the lower elevation group had a relatively stronger association with wetter conditions and the higher elevation group with drier conditions. Higher elevation sites experienced drier than average conditions compared to lower elevation sites in 23% more of y–1 observations, and in 29% more of y–2 and y–4 observations. Conversely, lower elevation sites showed drier than average conditions compared to higher elevation sites in 12% more of y–3 observations (Fig. 10).

The pattern of precipitation conditions preceding a fire year differed between Front Range and southwestern sites in years y–1 and y–4, and were similar in years y–2 and y–3 (Fig. 11). Front Range sites exhibited the same pattern as higher elevation sites for the three years preceding a fire year, with drier than average conditions in year y–1 and wetter than average conditions in years y –2 and y–3 (Figs. 10 and 11). Southwestern sites exhibited the same pattern as lower elevation sites for the three years preceding a fire year, with wetter than average conditions in all three years (Figs. 10 and 11), despite southwestern sites occupying elevations 81 m higher, on average (Table 3), than Front Range sites. Thus, a confounding effect with elevation is likely not responsible for the similarity in patterns between the regions and elevation groups. Instead, the geographic relationship with fire–climate likely represents a true distinction between southwestern and Front Range ponderosa pine forests.

Discussion

Analyzing multiple parameters of an ecosystem's fire regime provides a more thorough understanding of the disturbance agent than analyzing a single parameter because the continuum of conditions that often exists can be revealed and the putative environmental variables on which the continuum operates, evaluated. This level of understanding is important to formulating ecologically based restoration plans, especially as they relate to treatments designed to enhance resilience of fire-adapted forests to disturbance and climate change (*e.g.*, Addington et al. 2018). The collection of evidence evaluated in this study points to a historical fire regime in Colorado ponderosa pine ecosystems that was predominantly characterized by high- to moderate-frequency, low- and mixed-severity fires that occurred in late summer to fall, with fires occurring in drier than average years that were often preceded by two to three years of wetter than average conditions.

Site-specific MFI values within Colorado ponderosa pine ecosystems were strongly related to elevation, with more frequent fires at lower elevations, where ponderosa pine ecosystems transition to grassland. Variation in the relationship between fire and precipitation conditions also was related to elevation. Drier than average conditions during fire years characterized all sites, regardless of elevation, but lower elevation sites showed a strong pattern of wetter than average conditions in each of the three years preceding a fire year, while higher elevation sites failed to exhibit this pattern. This finding supports the idea that fire occurrence in lower elevation sites is more strongly associated with growth of fine fuel biomass than by dry conditions needed to desiccate existing fuels (Sherriff and Veblen 2008; Gartner et al. 2012). A positive relationship between MFI and elevation is well documented by individual studies in both the Front Range (Veblen et al. 2000; Brown and Shepperd 2001; Schoennagel et al. 2011) and southwestern Colorado (Grissino-Mayer et al. 2004). The results of this meta-analysis confirm that this relationship holds across a large area of the distribution of ponderosa pine ecosystems in Colorado.

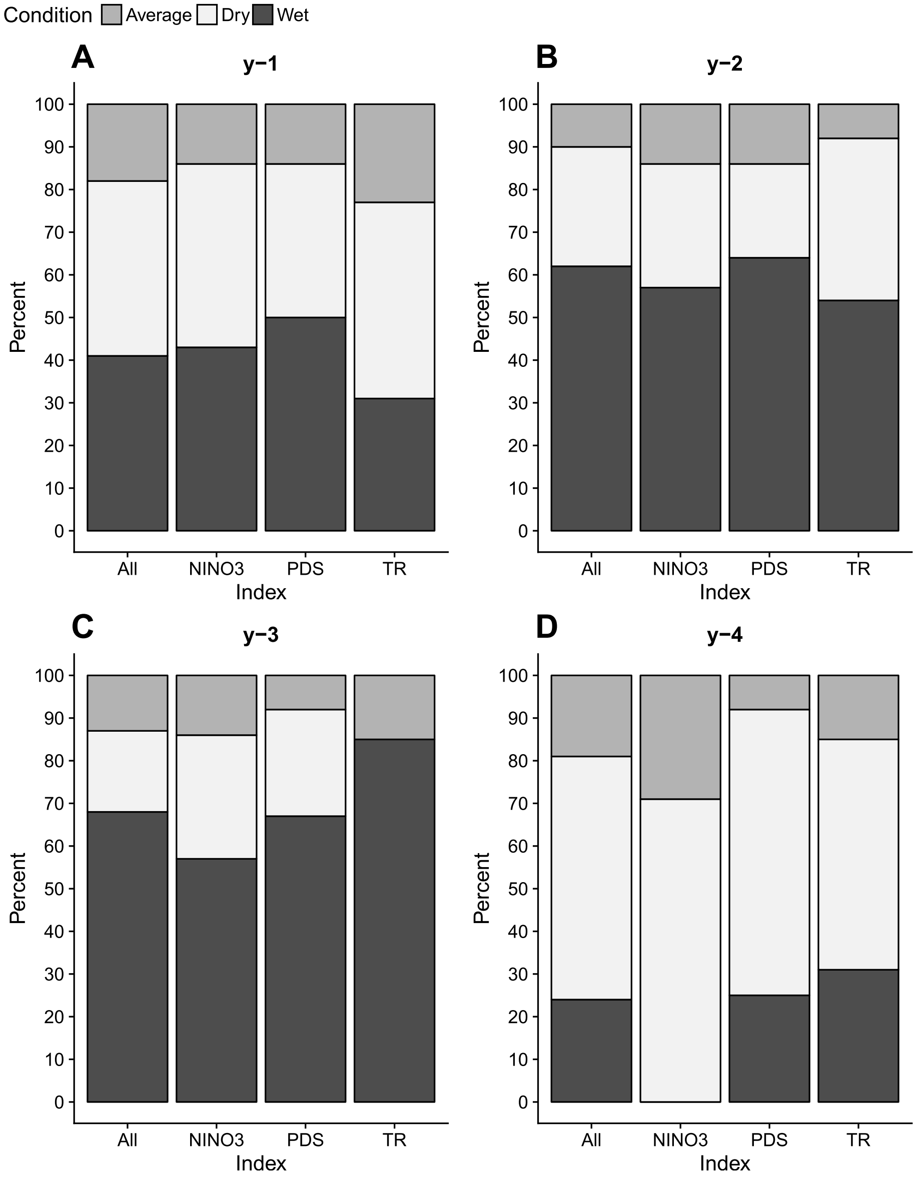

Fig. 8 Comparison of three climate indices used to evaluate the relationship between fire year and antecedent precipitation conditions from 12 fire history studies on ponderosa pine (*Pinus ponderosa*) in Colorado, USA, used in the fire regime meta-analysis of 2017. *Y*-axis is the percent of all observations in each of three precipitation conditions: average precipitation, dry (below average), and wet (above average). Index categories are All, the combination of precipitation indices (*n* = 39); NINO3, sea surface temperature index (*n* = 7); PDS, Palmer Drought Severity index (*n* = 14); and TR, tree-ring growth index (*n* = 13). The four panels represent the number of years preceding a fire year: (**A**) y−1, one year prior; (**B**) y−2, two years prior; (**C**) y−3, three years prior; and (**D**) y−4, four years prior

Although the relationship between elevation and fire frequency is well documented in the literature and supported by results of this meta-analysis, the relative distribution of sites with a history of high-frequency fire (MFI ≤ 30 years) versus less frequent, or variable frequency fire, differs among analyses. Sherriff and Veblen (2007) classified 15% of their sampled sites as high-frequency, low-severity fire regimes, and 85% as low-frequency, high-severity fire regimes. Their model classified 20% of the ponderosa pine zone in the Arapahoe-Roosevelt National Forest (northern Front Range) with a historical high-frequency, low-severity fire regime. Sherriff et al. (2014) classified 8% of their sampled sites (232) as a high-frequency, low-severity fire regime, and 92% as less-frequent, mixed-severity fire regime. Their model classified 28% of the montane zone of the northern Colorado Front Range as a high-frequency, low-severity fire regime, and 72% of the area as a variable-frequency, mixed-severity fire regime. In contrast, this meta-analysis found that 75% of Front Range sites would be

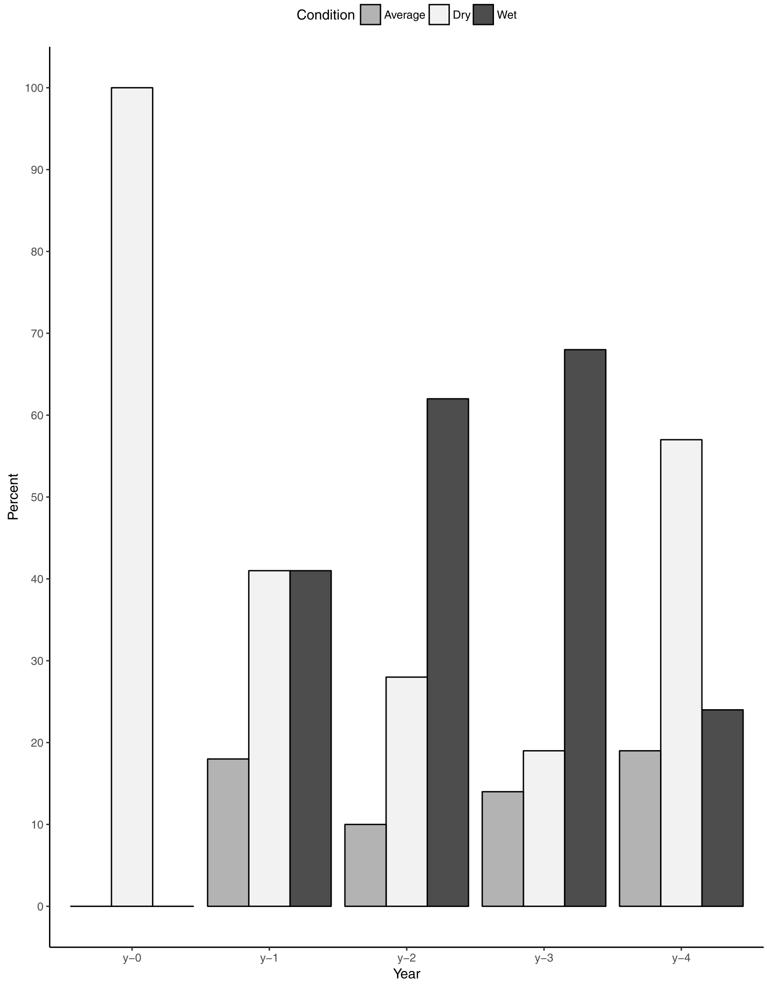

Fig. 9 Relationship between fire year and antecedent precipitation conditions from 12 fire history studies on ponderosa pine (*Pinus ponderosa*) ecosystems in Colorado, USA, used in the fire regime meta-analysis of 2017. *Y*-axis represents the percent of all observations in each of three precipitation conditions: average precipitation, dry (below average), and wet (above average). Precipitation condition is derived from a combination of climate indices including Palmer Drought Severity, tree-ring growth, NINO3 sea surface temperature, and others. *X*-axis represents the year relative to fire year (y–0 is fire year, y–1 is year before fire year, and so on)

classified in the low-severity fire regime, if based only on the criterion of MFI ≤ 30 years (Sherriff and Veblen 2007; Sherriff et al. 2014). I separated low-elevation from high-elevation sites at 2400 m (based on the distribution of MFI values in my data set), whereas Sherriff and Veblen (2007) delimited their sites at 2100 m. However, this does not explain the broad discrepancy in estimated fire regime class distribution (75% of meta-analysis sites, compared to 15% and 8% of sites from the two papers, were high-frequency) as meta-analysis sites above 2400 m had a mean MFI of 24 years, which would still be classified as high frequency.

Geographic location was also associated with variability in fire frequency and climate. Front Range sites had a longer mean MFI than southwestern sites, although the difference between geographic groups was smaller than the difference between elevation groups. The pattern of the relationship between fire year and climate differed between geographic regions, and the strength of the relationship between fire year and climate was more strongly associated with geography than with elevation. For the three years preceding a fire year, the mean difference in the proportion of sites with wetter than average conditions was 9% between elevation groups compared to a 32% difference between geographic groups. Southwestern Colorado sites experienced a stronger pattern of wetter than average conditions in the three years preceding a fire year than did Front Range sites, and this difference was greater than the difference between elevation groups.

An interesting pattern emerged from among and within elevation and geographic group comparisons of fire frequency and fire–climate relationships. Both southwestern and low-elevation sites had shorter MFIs

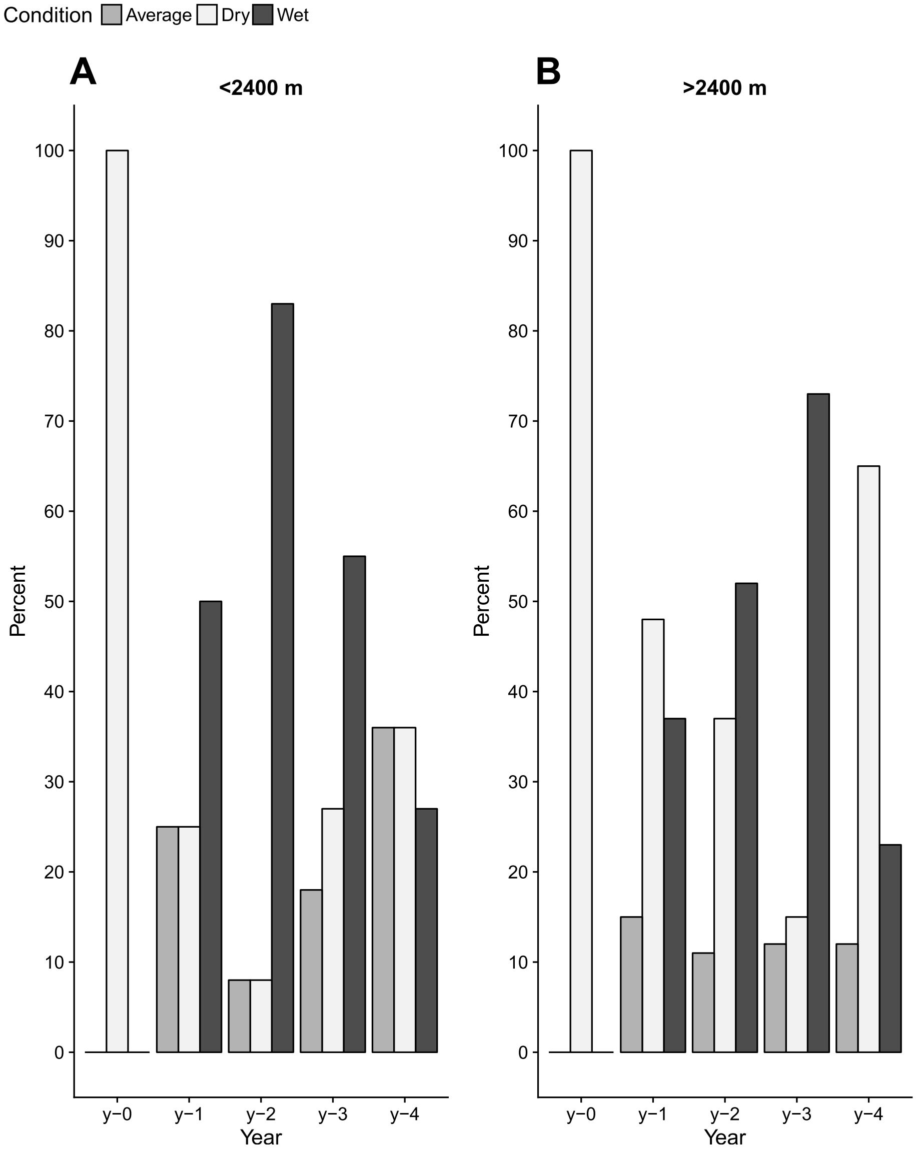

Fig. 10 Relationship between fire year and antecedent precipitation conditions for two elevation groups, (**A**) <2400 m (*n* = 12) and (**B**) >2400 m (*n* = 27), from 12 fire history studies on ponderosa pine (*Pinus ponderosa*) ecosystems in Colorado, USA, used in the fire regime meta-analysis of 2017. *Y*-axis represents the percent of all observations in each of three precipitation conditions: average precipitation, dry (below average), and wet (above average). Precipitation condition is derived from a combination of climate indices including Palmer Drought Severity, tree-ring growth, NINO3 sea surface temperature, and others. *X*-axis represents the year relative to fire year (y–0 is fire year, y–1 is year before fire year, and so on)

relative to their corresponding groups (Front Range and high elevation, respectively), and both exhibited the same pattern in fire–climate relationships with the three years preceding a fire year being wetter than average. Conversely, Front Range and high-elevation sites had longer MFIs than their corresponding group and the same fire–climate pattern of drier than average conditions one year before a fire year, and wetter than average conditions two and three years before a fire year. Hence, southwestern and lower-elevation sites resembled each other in fire frequency and fire–climate relationships, while Front Range and higher-elevation sites resembled each other in the same two parameters.

The most commonly offered hypothesis for low-elevation fire–climate relationships is a model of a fuel-limited system whereby moist antecedent conditions promote growth of fine fuels that dry and carry fire during drier than average fire years (*e.g.*, Sherriff and Veblen 2008; Gartner et al. 2012). It is possible that the similarity in fire–climate relationship between low-elevation and southwestern groups is because southwestern sites conform to a similar fuel-limited model, reflecting the

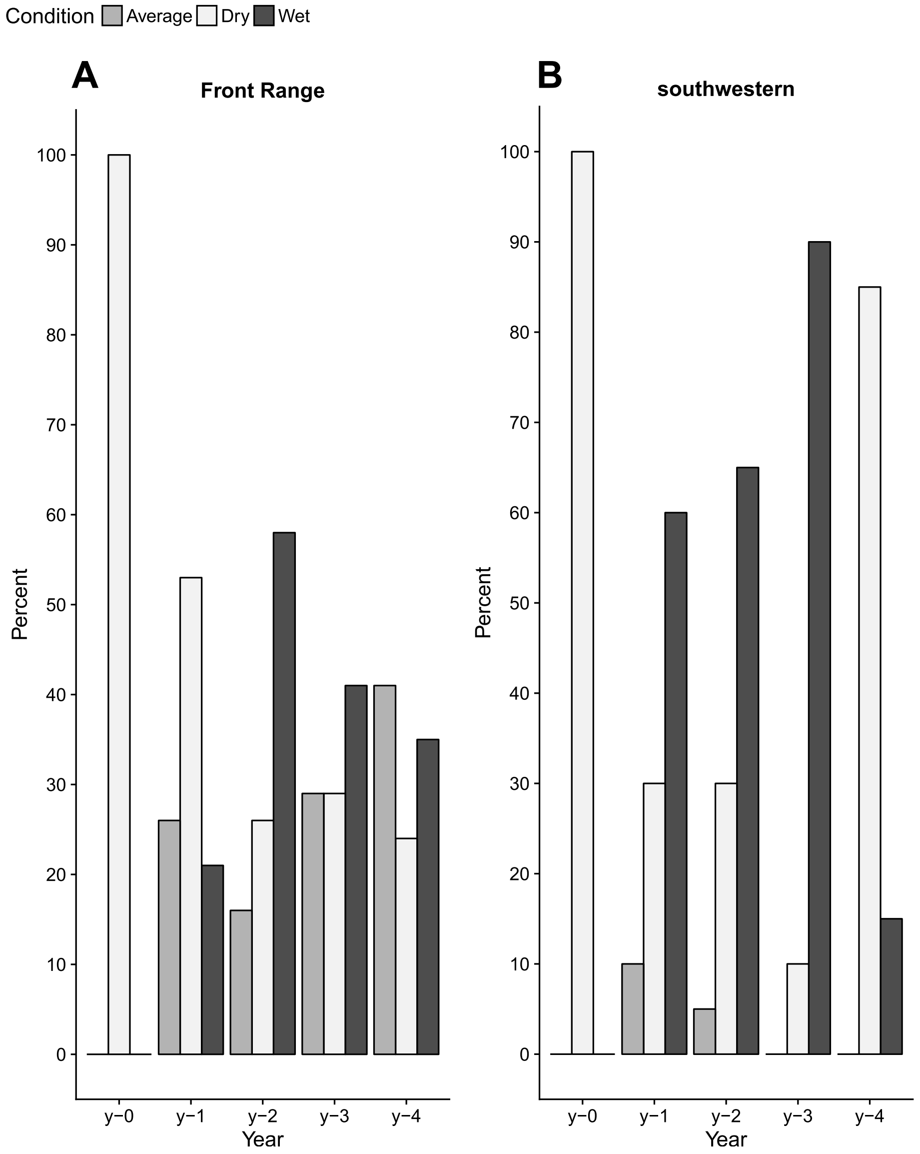

Fig. 11 Relationship between fire year and antecedent precipitation conditions from 12 fire history studies in ponderosa pine (*Pinus ponderosa*) ecosystems for two geographic regions, (**A**) Front Range (*n* = 19) and (**B**) southwestern (*n* = 20) in Colorado, USA, used in the fire regime meta-analysis of 2017. *Y*-axis represents the percent of all observations in each of three precipitation conditions: average precipitation, dry (below average), and wet (above average). Precipitation condition is derived from a combination of climate indices including, Palmer Drought Severity, tree-ring growth, NINO3 sea surface temperature, and others. *X*-axis represents the year relative to fire year (y−0 is fire year, y−1 is year before fire year, and so on)

fire–climate-vegetation dynamics of low-elevation sites. Swetnam and Betancourt (1998) found the same pattern in the fire–climate relationship in ponderosa pine ecosystems of Arizona and New Mexico, USA, and they attributed the production of fine fuels to antecedent wet conditions in the three years prior to a fire year. They did not find this same pattern in corresponding mixed-conifer forests that generally occupy higher elevations. In higher elevations, drying of fuels is the primary hypothesized mechanism leading to fire, and hence these areas are not fuel limited but rather "climate" limited (Littell et al. 2009). Interestingly, southwestern group sites were higher elevation (mean = 2510 m), than both the corresponding low-elevation group (mean = 2194 m) and Front Range group (mean = 2373 m). Thus, the similarity between southwestern and low-elevation fire–climate patterns is not due to similarity in elevation. Indeed, when low-elevation sites are removed from the southwestern group, the same pattern and relative percentages in fire–climate relationship hold, with three wetter than average years preceding a fire year.

It is possible that southwestern Colorado ponderosa pine forests are more influenced by the same regional climate that influences patterns in the American Southwest than by the elevation effect documented in the Front Range (Gartner et al. 2012). Littell et al. (2009) found similarly broad, regional relationships in fire–climate patterns in an analysis of area burned in the western US grouped by ecoprovince. They found that most ecoprovinces are more strongly limited either by fuels or by climate, but that there is a range of vegetation types and climates resulting in fire regimes that are limited by both fuels and climate. Colorado ponderosa pine ecosystems may occupy an intermediate space in the fire–climate relationship between fire regimes that are largely fuel limited and those that are primarily climate limited, with the relative contribution of each varying spatially. Under this scenario, regional climate would dampen the effect of elevation in the southwestern Colorado fire–climate relationship, leading to a more widely distributed fuel-limited system. Farther north in the Front Range, regional climate effects would be lessened, and elevation would play a larger role in driving variability in fire–climate patterns, with higher elevation sites reflecting a climate-limited system. Both of these predictions are generally supported by results of this meta-analysis. One possible explanation for this geographic variation in fire–climate patterns is the difference in precipitation patterns between the two regions, specifically the more pronounced influence of monsoonal moisture in southwestern Colorado relative to the Front Range (Brown and Shepperd 2001; Grissino-Mayer et al. 2004).

A geographic effect on fire seasonality was not detected in the meta-analysis. Late-summer to early-fall fire scars accounted for nearly 70% of the fire-scar record in ponderosa pine ecosystems statewide, and evidence for a dominance of fires in late summer to early fall did not diminish when assessed geographically. In the lowest latitude sites, 73% of fire scars indicated late-summer or early-fall fires. Thus, observed geographic differences in precipitation patterns, largely due to late-summer monsoonal rain in southwestern Colorado, did not translate to proportional differences in fire seasonality. Grissino-Mayer et al. (2004) found a slight majority (57%) of fire scars occurred early in the season (April to mid-June) in their southwestern Colorado sites (San Juan Mountains). However, they also found a high level of variability among study sites, and an appreciable proportion (31%) of latewood scars (mid-July and after). This suggests that if a difference exists between the two geographic regions, it is likely subtle, and could be obscured by among-study differences in sampling design and rules defining the classification of fire-scar seasonality.

I was unable to extract enough comparable study-level values on either fire severity or extent to adequately address whether contemporary fires are more severe and larger than historical fires. This finding is unfortunate because these are two issues important to forest managers and that often form the basis of forest restoration objectives (*i.e.*, reducing the extent and severity of future fires). In general, two issues contribute to the lack of comparable data in the literature: (1) evidential limitation for establishing initial time period conditions; and (2) discrepancy in researcher approach including terminology, classification definition criteria, and sampling methods.

Due to a lack of historical fire records, fire severity is inferred by existing evidence; fire scars at short intervals in extant trees strongly suggest a low-severity fire regime. Unbiased sampling across all severity classes is difficult because high-severity fires, by definition, kill most of the living trees. Over time, the evidence from dead trees will diminish more quickly than the evidence from living trees (*i.e.*, fire scars). However, within some reasonable postfire time period, the probability of detecting evidence from low-, moderate-, and high-severity fires should be comparable. It is within this postfire time period that the lack of comparable severity data in the literature is largely due to differences in researcher methods and severity classification criteria. For example, of the seven studies that provided usable values, no two had the same definition for all of the severity classes. The discrepancy in researcher approach to fire-severity classification is an important issue in fire ecology research that can be more readily addressed compared to more intractable problems of diminishing evidence with time.

The lack of clear evidence regarding a change in fire size over time is due, in part, to the difficulty in accurately estimating the size of historical fires with which to compare contemporary fire size. A loss of information (trees die and decay) over time, fires that fail to leave scars on extant trees, and incomplete surveys of fire areas can all lead to an underestimation of fire size (Kulakowski and Veblen 2006). One way to address this sampling bias is to report "minimum fire extent," and some researchers follow that approach (*e.g.*, Ehle and Baker 2003; Sherriff and Veblen 2008). Contemporary fire extent can be directly measured with a relatively high degree of accuracy since the 1980s, whereas historical fire extent estimates are likely biased towards underestimating fire size because of the issues discussed above. Thus, even when historical and contemporary values are derived, the comparison will often be between minimum size and maximum size.

The difficulty in estimating historical fire sizes leads to discrepancies in methodological approach and terminology. At a more fundamental level, these differences make it difficult to address the same specific research question under study. For example, to address the problem of whether contemporary fires are larger than historical fires we could compare: (1) mean area burned or mean fire size between time periods, or (2) the frequency of "large" fires between time periods. But these two questions require different types of data, and answering one or the other within studies does not allow for a meta-analytic comparison to gauge the strength of evidence for or against a specific claim.

Data collection and presentation should be sufficiently similar among studies that are used in a meta-analysis so that they can be grouped to investigate patterns and relationships. I attempted to account for differences in data presentation, and ambiguous or unspecified sampling details among the sampled studies, but a certain degree of uncontrolled variation still existed. This introduced variation should therefore be taken into account when interpreting the resolution and site-specific applicability of this study's findings; broad patterns of elevation and geographic effects are most appropriate. Despite these limitations, I believe that the patterns and relationships revealed by this meta-analysis are meaningful. Indeed, given sources of introduced error into the data set, patterns that emerged should represent a signal of natural effects.

Conclusion

Given the considerable level of variation in natural systems on which fire regimes operate, describing the characteristics of a fire regime by evaluating multiple parameters provides a more thorough understanding on which to base management decisions. This systematic review and meta-analysis identified key relationships between fire regime parameters and environmental variables, notably, that the dynamics of ponderosa pine fire regimes in Colorado vary along two dimensions: elevation and latitude. The historical fire regime was broadly characterized by high- to moderate-frequency, low- and mixed-severity fires that occurred in late summer to fall, during drier than average years that were often preceded by two to three years of wetter than average conditions. This range of conditions varied considerably, however, and much of that variation can be explained by site elevation and geographic location.

This analysis also revealed shortcomings in certain aspects of fire history research, including a lack of consistency in classification, definitions, sampling approach, and data presentation regarding fire severity, extent, and seasonality. Some issues are largely insurmountable (*e.g.*, the ability to accurately estimate historic baseline conditions), while others can be remedied by a focused effort on consistency in research approach. Considering the importance of fire ecology research to forest management, the ability to determine whether there is a clear signal from comparable research findings is a valuable goal. Applying restoration that promotes system resilience to fire and climate change requires a solid understanding of the complex drivers of vegetation structure and composition, including keystone disturbances such as fire. The meta-analytic approach to evaluating the plethora and diversity of fire research can be best leveraged to accomplish this goal when introduced variation is diminished so that the signal is stronger than the noise.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s42408-019-0056-6.

Additional file 1. Appendix. Studies used in the Colorado, USA, fire regime meta-analysis of 2017 and their associated site-level values for fire frequency, time period of analysis, and elevation. Map ID corresponds to locations in Fig. 1.

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Author's contributions

STM is the sole author. The author read and approved the final manuscript.

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Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The author declares that he has no competing interests.

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