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Proximity to grasslands influences fire frequency and sensitivity to climate variability in ponderosa pine forests of the Colorado Front Range

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Abstract. This study examines the influence of grasslands on fire frequency and occurrence in the ponderosa pine (*Pinus ponderosa*)-dominated forests of the central and northern Colorado Front Range. Fire frequency based on tree-ring fire-scar data was compared between 34 fire history sites adjacent to grasslands and 34 fire history sites not adjacent to grasslands for the time period 1675–1920. Relationships were examined between fire occurrence and values of the Palmer Drought Severity Index and sea-surface temperatures from the NINO3 region of the tropical Pacific Ocean (positive values indicating El Niño-like conditions and negative values La Niña-like conditions). Ponderosa pine stands adjacent to grasslands experienced more frequent fire than stands not adjacent to grasslands ($P < 0.05$) owing to proximity to prevalent fine fuels able to support relatively frequent surface fires. Fire activity adjacent to grasslands showed a lagged positive relationship with moist years (positive Palmer Drought Severity Index and positive NINO3) antecedent to fire events whereas fire occurrence at sites not adjacent to grasslands showed no relationship to antecedent moist years. This study illustrates how the presence of grasslands in a ponderosa pine landscape results in increased fire frequency (a bottom–up influence) and also increases the sensitivity of fire activity to interannual climate variability (a top–down influence).

Additional keywords: bivariate event analysis, El Niño–Southern Oscillation, fire history, grasslands, Palmer Drought Severity Index, *Pinus ponderosa*.

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Introduction

At a global scale, differences in wildfire activity across biomes are controlled by availability of biomass to burn, ignition sources and weather conditions suitable for fire initiation and spread (Chuvieco *et al.* 2008; Krawchuk *et al.* 2009). Macroscale examinations of broad-scale constraints on fire activity have documented that in biomass-rich biomes, such as wet forests, the dominant limitation to fire activity is fuel moisture rather than fuel amount; conversely, in drier biomes, such as xeric shrublands and many grasslands, fire activity is constrained more by amount or connectivity of fuels (van der Werf *et al.* 2008; Krawchuk and Moritz 2011). At the scale of the western USA, differences in fuel amount versus weather constraints on fire activity are also key to understanding variations in fire regimes across ecosystem types. In the US West, weather conditions are more limiting to fire occurrence in cool, mesic subalpine forests, whereas fuel amount and continuity are more likely to be limiting to fire spread and extent in dry shrub- and grass-dominated ecosystems (Knapp 1998) and in low-elevation ponderosa pine (*Pinus ponderosa*) woodlands (Schoennagel *et al.* 2004). Thus, higher-elevation forest types exhibit strong year-of-fire relationships with low precipitation whereas grass- or shrub-dominated ecosystems have positive relationships with antecedent precipitation implying fuel limitations to fire activity (Littell *et al.* 2009). Fire histories in many ponderosa pine ecosystems of the US Southwest demonstrate a lagged relationship of increased fire activity with above-average antecedent moisture availability (Swetnam and Betancourt 1990, 1998; Grissino-Mayer and Swetnam 2000; Westerling *et al.* 2002). The mechanism hypothesised to explain this statistical relationship is higher grass fuel amount and continuity resulting in increased potential for fire spread during a following dry year (Littell *et al.* 2009). However, we know of no studies that have systematically quantified differences in historic fire regime or sensitivity of fire activity to climate variability in relation to proximity or adjacency of ponderosa pine stands to grasslands.

Climate-related variability in wildfire activity in ponderosa pine ecosystems of the Colorado Front Range is broadly similar to patterns that have long been documented for ponderosa pine ecosystems in the US Southwest (Swetnam and Betancourt 1990, 1998; Grissino-Mayer and Swetnam 2000; Veblen *et al.* 2000; Sherriff and Veblen 2008). Annual variability in precipitation and temperature influencing fire regimes in Colorado and the Southwest has been related to major climate drivers such as the El Niño–Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and Atlantic Multidecadal Oscillation (AMO). PDO and AMO are important drivers of climate–fire regime variability at decadal and multidecadal time scales in ponderosa pine ecosystems in Colorado and the Southwest (Kitzberger *et al.* 2007; Sherriff and Veblen 2008). At an interannual time scale of 1 to 5 years, climatic teleconnections associated with ENSO correlate with fire occurrence in these ecosystems (e.g. Swetnam and Betancourt 1990; Veblen *et al.* 2000; Kitzberger *et al.* 2001). Widespread fire years in ponderosa pine ecosystems in the Front Range occur during dry springs and summers associated with La Niña and often lag by 1 to several years after wet springs associated with El Niño (Veblen *et al.* 2000; Sherriff and Veblen 2008). The mechanism explaining these lagged fire–climate relationships in the Front Range and in the Southwest is believed to be high production of grass fuels resulting from years of above-average moisture availability associated with El Niño that burn during the dry La Niña conditions (e.g. Swetnam and Betancourt 1990, 1998; Veblen *et al.* 2000; Grissino-Mayer *et al.* 2004; Sherriff and Veblen 2008). In contrast, years of widespread fire in nearby mesic subalpine forest types are statistically associated with drought alone and do not depend on prior years of above-average moisture availability (Schoennagel *et al.* 2005; Sibold and Veblen 2006).

Although broad-scale patterns of wildfire activity related to climate variability and major climate drivers have been extensively documented in ponderosa pine ecosystems and contrasted with other ecosystem types, variations associated with the effects of grasslands within the ponderosa pine landscape mosaic have not been specifically examined. Previous research in ponderosa pine-dominated forests of the Colorado Front Range has documented more frequent historic fires at low elevations (below ~2100 m) compared with higher elevations (2100 to ~2800 m; Veblen *et al.* 2000; Sherriff and Veblen 2006, 2007). Years of widespread fire in the low-elevation forests lag moister conditions by 2 years whereas fire occurrence above ~2100 m is associated only with dry conditions during the fire year (Sherriff and Veblen 2008). Most of the ponderosa pine woodlands below ~2100 m are adjacent to extensive plains grasslands but grass-dominated patches occur throughout the montane forest zone (Peet 1981). Given the broad-scale understanding of the ponderosa pine fire regime, variability related to elevation and topography in the Front Range (Sherriff and Veblen 2007, 2008), the current study employs an analytical framework that focusses on the quantification of fire activity and its sensitivity to climate variability in relation to proximity and extent of grasslands in the landscape.

We investigate relationships between the spatial distribution of grasslands, fire frequency and interannual climatic variation in ponderosa pine ecosystems along the elevation gradient on the eastern slope of the Colorado Front Range. Specifically, we address the following questions: (1) is spatial variability of fire frequency within the ponderosa pine zone related to adjacency to grass-dominated vegetation? (2) Does proximity of a ponderosa pine-dominated site to grasslands affect the sensitivity of its fire regime to interannual climate variability?

Methods

Study area

Climate in the montane zone (1800–2800 m) of the central and northern Front Range in Colorado is relatively arid and greatly influenced by a high elevation and interior continental location (Veblen and Donnegan 2006). The eastern slope of the Front Range has warm summer conditions and relatively cold winter temperatures (Veblen and Donnegan 2006). In the lower montane zone, annual mean precipitation is 43.4 cm and the mean annual temperature is 6.7°C (Lakewood Station; 1664 m; 1971–2000). The upper montane zone has an annual mean precipitation of 47.8 cm and an annual mean temperature of 6.6°C (Evergreen Station; 2325 m; 1971–2000). Precipitation is highest during spring months (April and May); however, thunderstorms can occur in summer months. Owing to the cooler late-spring temperatures and high winter precipitation levels at higher elevations, there is greater moisture availability during the beginning of the growing season (Peet 1981).

Vegetation patterns on the eastern slope of the Front Range are mainly determined by moisture conditions influenced by elevation and aspect (Peet 1981; Veblen and Donnegan 2006). The montane zone is primarily composed of forests but some grasslands and shrublands occur as a result of edaphic conditions (Marr 1961). In the lower montane zone and on drier slopes at higher elevations, ponderosa pine is dominant and juniper (*Juniperus scopularum*) is present in xeric sites (Kaufmann *et al.* 2006). On north-facing slopes, ponderosa pine is commonly co-dominant with Douglas fir (*Pseudotsuga menziesii*). At upper elevations or on mesic hillslopes within the montane zone, Douglas fir often dominates and lodgepole pine (*Pinus contorta* var. *latifolia*), aspen (*Populus tremuloides*) and limber pine (*Pinus flexilis*) are present (Peet 1981; Kaufmann *et al.* 2006). Understorey species composition is spatially heterogeneous and highly influenced by moisture gradients. Areas with historically frequent, low-severity fire regimes have a modern understorey dominated by herbs and graminoids such as *Artemisia ludoviciana* and *Carex* spp., stands with historic moderate-severity fire regimes have abundant shrub understories including *Cercocarpus montanus* and *Purshia tridentata*, and areas with high-severity fire regimes have the highest overall shrub species composition, including *Purshia tridentata* and *Juniperus communis* (Keith *et al.* 2010).

Site selection and field sampling

We obtained tree-ring fire history data from a network of 88 fire-scar sites in the central and northern Front Range of Colorado. Fifty-eight of the sites were previously sampled from the early 1990s to 2003, whereas 30 sites were sampled in 2007 and 2008 for this study (Fig. 1; Veblen *et al.* 2000; Sherriff and Veblen 2008). Site selection in the northern half of the study area (mostly Boulder County) was based on systematically targeting potential sample sites of homogeneous habitat along elevation gradients from the lowest to highest elevations of ponderosa pine-dominated vegetation along the five major west-to-east-running watersheds (Veblen *et al.* 2000; Sherriff and Veblen 2008). In the southern half of the study area, potential sample sites were randomly selected from vegetation maps to proportionally represent ponderosa pine-dominated cover types. In both the northern and southern areas, within each potential site of homogeneous forest cover and topography, sites for sampling fire-scars were subjectively located to avoid stands with evidence of significant historic logging or fuel-mitigation treatments. To characterise fire history at each site, we systematically searched for fire-scars (search areas ranged from 14 to 200 ha) following previously established procedures (McBride and Lavin 1976; Veblen *et al.* 2000; Sherriff and Veblen 2007). In addition, forest composition, stand structure, dominant understorey, elevation, slope and aspect were recorded at each site. To determine the adjacency of each site to a grassland, the length of the site perimeter adjacent to grasslands and total perimeter length were measured using satellite imagery (Google Earth, 2009, see earth.google.com). Fire-scar sample sites with greater than 25% of their perimeters bordering grasslands were defined as adjacent to a grassland ($n = 34$), whereas sites with less than 25% of their perimeters bordering grasslands were defined as not adjacent to grasslands ($n = 54$). In preliminary assessments, smaller percentages of perimeters adjacent to grasslands were explored and did not result in a significant difference. Hereafter, sites adjacent and not adjacent to grassland are referred to as grassland and non-grassland sites respectively.

Sample processing

Partial cross-sections from all sites were sanded and prepared according to standard methods (Arno and Sneck 1977; McBride

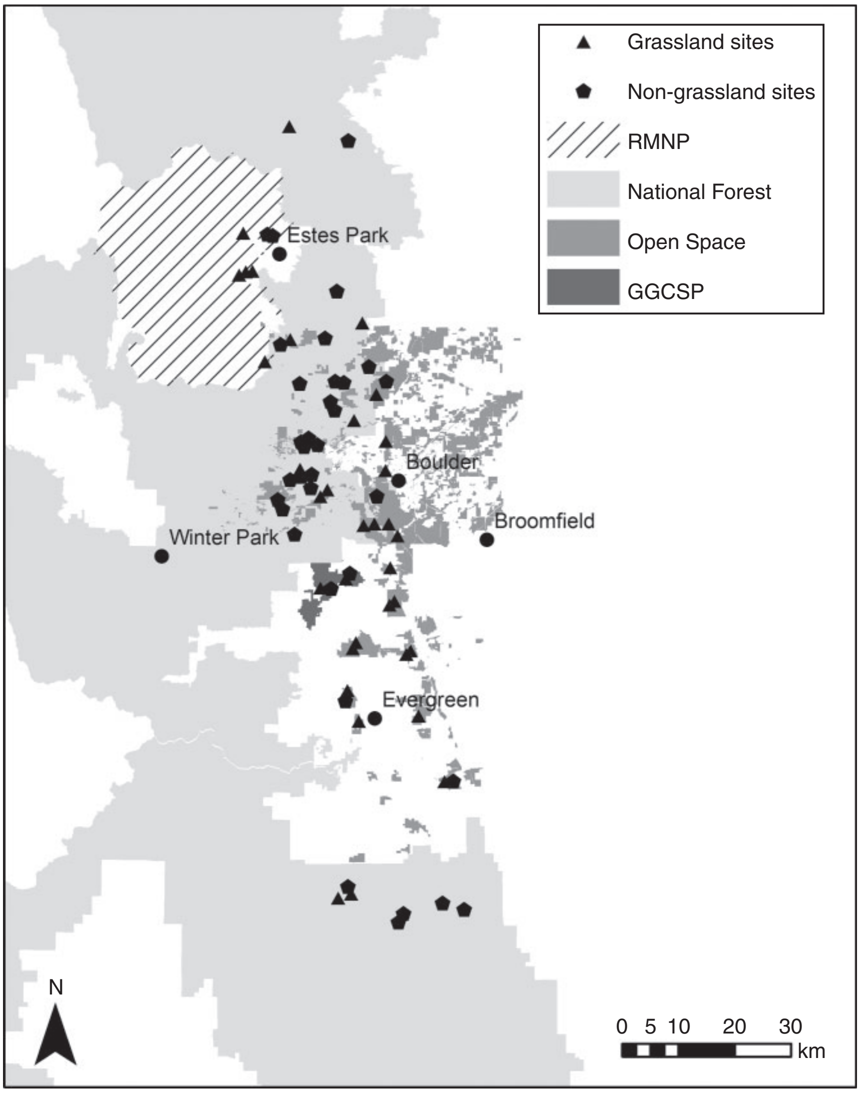

Fig. 1. The study area in the central and northern Front Range of Colorado. The sites span Jefferson County, Boulder County and City of Boulder Open Space, Rocky Mountain National Park (RMNP), Arapaho–Roosevelt and Pike National Forests and Golden Gate Canyon State Park (GGCSP). The study area is defined by elevations zones within the region of interest.

1983). Prepared cross-sections from live trees were visually crossdated using marker rings identified from a master chronology for the Front Range (Dieterich and Swetnam 1984; Veblen *et al.* 2000) to date the year the fire-scar was established. Fire dates were determined to annual precision or intra-annual (seasonal) precision when possible. Fire-scars with unclear tips or uncertain crossdating were excluded from the dataset. Annual precision is impossible to achieve for fires that occurred during the dormant season (between rings); however, fire records from Rocky Mountain National Park indicate that autumn fires are more common than spring fires (T. T. Veblen, unpubl. data). Consequently, dormant-season fires were assumed to be associated with the autumn following the main summer fire season rather than the spring of the next year. Cross-sections from dead trees and live trees that could not be confidently crossdated using only visual techniques were also measured and crossdated using *COFECHA* (Holmes 1993), a program that quantitatively compares the relative widths of annual rings of the sample with that of a master chronology for the region.

Fire chronologies and frequency comparisons

Fire events are defined as years in which two or more trees recorded a fire within a site. From the network of 88 fire-scar sample sites, fire-event chronologies were compiled for 34 grassland sites and 34 randomly selected sites from the 54 non-grassland sites; thus, fire frequencies were compared for similar total search areas of grassland and non-grassland sites. Fire-event chronologies were compiled for the grassland ($n = 34$) and the random selection of non-grassland sites ($n = 34$). For each group of sites, the number of fire intervals and composite mean fire interval (MFI; Dieterich 1980), which is the average time between consecutive fire years, were calculated for the time period 1675–1920. The time period for statistical analysis begins in 1675, when >12% of sites recorded fire events, and ends in 1920, the advent of effective fire suppression. An F test revealed unequal variances between the groups, and consequently we employed a Student's t test for unequal variances to compare the fire frequencies between grassland and non-grassland sites for 1675–1920.

Fire–climate analysis

To characterise regional climate, we relied on an index of regional plant moisture availability based on a tree-ring reconstruction of the summer (June–August) Palmer Drought Severity Index (PDSI) for the northern Front Range (gridpoint 131; Cook *et al.* 1999), where negative values indicate drought conditions and positive values indicate moist conditions. To characterise ENSO, we relied on reconstructions of sea-surface temperatures from the NINO3 region of the equatorial Pacific Ocean (Cook 2000), which have been shown to have high correlations with climate patterns in the central and northern Colorado Front Range; the negative values of the index indicate the cool phase (La Niña-like) of sea-surface temperature anomalies and the positive values indicate the warm phase (El Niño-like) of sea-surface temperature anomalies.

We compared the relative frequency of fire events associated with positive (wet) and negative (dry) values of the PDSI index. Observed and expected numbers of fires during positive or negative PDSI years were compared when the climate coincided with the fire year (T), preceded it by 1 year (T − 1) and preceded it by 2 years (T − 2). Chi-square analyses compared the expected and observed number of fires for negative and positive PDSI years for the T, T − 1 and T − 2 years for grassland and non-grassland sites for the time period of analysis (1675–1920).

To examine relationships between fire events and antecedent climate events, we employed bivariate event analysis (BEA) using the *K1D* software (D. G. Gavin, unpubl. software). BEA is a temporal application of spatial point pattern analysis based on Ripley's K function (Ripley 1976; Gavin *et al.* 2006). BEA has been used to examine synchrony among fire events recorded by sedimentary records (Gavin *et al.* 2006), fire events in tree-ring records and climatic conditions (Schoennagel *et al.* 2007), and tree mortality episodes and droughts (Bigler *et al.* 2007). BEA allows statistical testing of both high-frequency (i.e. annual) and low-frequency (i.e. decadal) temporal relationships. The method avoids problems of serial autocorrelation by using specific dates of extreme climatic events, rather than a continuous time series of climate values. A forward selection in the BEA analysis was used to examine the synchrony or asynchrony of extreme climate events (PDSI, NINO3) and fire events for grassland and non-grassland sites. Extreme climate events were defined as the years with the 30 most extreme positive and 30 most extreme negative values for each index from 1675 to 1920. The bivariate Ripley's K function was transformed to an L function to stabilise the mean and variance and to facilitate graphical data interpretation (Gavin *et al.* 2006). One thousand Monte Carlo simulations with the randomisation of both the climate and fire events produce 95% confidence intervals for the L function. Values of the L function that fall above the upper confidence interval indicate fire synchrony (fires occur more often than expected) t years after the extreme climate events. Values of the L function that fall below the lower confidence interval indicate fire asynchrony (fires occur less often than expected) t years after the extreme climate events. L function values between the confidence intervals indicate fires

Table 1. Fire-scar summary information

Summary information for the fire-scar sampling for the time period 1675–1920 for grassland and non-grassland sites. Fire events are defined as two or more trees scarred within a site

	Elevation range (m)	Mean elevation (m)	Total search area (ha)	Number of fire-scars	Number of fire events	Unique number of fire events	Earliest fire event	Latest fire event
Grassland	1833–2747	2309	2018	255	121	72	1684	1916
Non-grassland	1980–2775	2472	1896	219	87	42	1684	1913

occur independently of climate events *t* years after the climate events. The relationship between PDO and AMO and fire events were also explored; however, owing to the small number of extreme PDO and AMO occurrences within the time period, statistical tests were invalid.

Results

Grassland adjacency and fire frequency

For the period of analysis (1675–1920), a total of 474 fire-scar dates and 87 unique fire-event years (minimum of two trees scarred) were derived from crossdated fire-scar samples for the fire history sites (34 grassland and 34 non-grassland sites) in the montane zone in the central and northern Front Range. In grassland sites, there were 255 fire-scars corresponding to 131 unique fire years based on a minimum of one tree scarred per site and 121 fire events based on a minimum two trees scarred per site (Table 1). In non-grassland sites, there were 219 fire-scars corresponding to 116 unique fire years based on a minimum of one tree scarred per site and 87 fire events based on a minimum of two trees scarred per site (Table 1).

A Student's *t* test for unequal variances determined the grassland sites had significantly shorter fire intervals than the non-grassland sites ($P < 0.05$; Table 2, Fig. 2). Grassland sites had 71 fire intervals and non-grassland sites had 41 intervals between unique fire events (minimum of two trees scarred in one or more sites) within the 1675–1920 time period (Table 2). The MFI for the grassland sites is 3.27 years (s.d. = 3.51) and 5.59 years for non-grassland sites (s.d. = 6.58; Table 2, Fig. 2).

Table 2. Fire interval statistics

Fire interval statistics for grasslands sites ($n = 34$) and non-grassland sites ($n = 34$) for the time period 1675–1920. Mean fire interval (MFI) and the standard deviation (s.d.) are presented for grassland and non-grassland sites. Fire intervals were compared using a Student's *t* test for unequal variances between the two categories (*t* test, $P < 0.05$; *F* test, $P < 0.05$)

	Number of fire intervals	MFI	s.d.	Minimum fire interval	Maximum fire interval
Grassland	71	3.27	3.51	1	19
Non-grassland	41	5.59	6.58	1	28

Fire–climate relationships

Fires occurred more often than expected during negative PDSI years in both grassland and non-grassland sites ($P < 0.05$; Fig. 3*a*). However, grassland sites experienced more fires than expected 2 years after positive (wet) PDSI years ($P < 0.05$; Fig. 3*c*), whereas fires in non-grassland sites did not show a lagged relationship to wet years ($P > 0.05$, Fig. 3*c*). BEAs of extreme climate years and fire events indicated different antecedent climate conditions were favourable for fire in grassland versus non-grassland sites (Fig. 4). Grassland sites experienced fire events more often than expected 1–10 years after extreme negative PDSI (dry) years ($P < 0.05$, Fig. 4*a*), and also 2–3 years after extreme positive (wet) PDSI years ($P < 0.05$, Fig. 4*b*). Thus, fires at grassland sites occurred synchronously with annual- to decadal-scale drought but at a time scale of 2–3 years also tended to follow above-average moisture availability. Non-grassland sites experienced fire events more often than expected 1–6 and 8–10 years after extreme negative PDSI years ($P < 0.05$, Fig. 4*c*), thus showing a synchrony of fire and drought at annual to decadal time scales. The non-grassland sites did not show synchrony of fire with positive PDSI before the fire event (Fig. 4*d*).

BEA analyses of NINO3 and fire events indicate that grassland sites experienced fires more often than expected 1, 2 and 4 years after extreme negative NINO3 (dry La Niña-like) years ($P < 0.05$, Fig. 5*a*) and 5 years after positive NINO3 (wet El Niño-like) years ($P < 0.05$, Fig. 5*b*). Thus, fires at sites adjacent to grasslands show synchrony with dry La Niña-like conditions at a scale of 1 to a few years and also with wet El Niño-like conditions with a lag of 5 years. In contrast, fires at non-grassland sites show neither synchrony nor asynchrony with positive NINO3 years (i.e. wet El Niño-like conditions; Fig. 5*d*).

Discussion

Our results show that adjacency of forested stands to grasslands affects both the bottom–up (fine fuel abundance) and top–down (climate drivers) controls of wildfires in ponderosa pine-dominated forests in the Colorado Front Range. Stands with adjacent grasslands experienced more frequent fires than stands without adjacent grasslands. Fire events at grassland sites are not only synchronous with dry conditions but also lagged moist conditions by 2 years. In contrast, fire events at non-grassland sites were not associated with antecedent moist years. Grasslands play an important role in determining fire frequency in

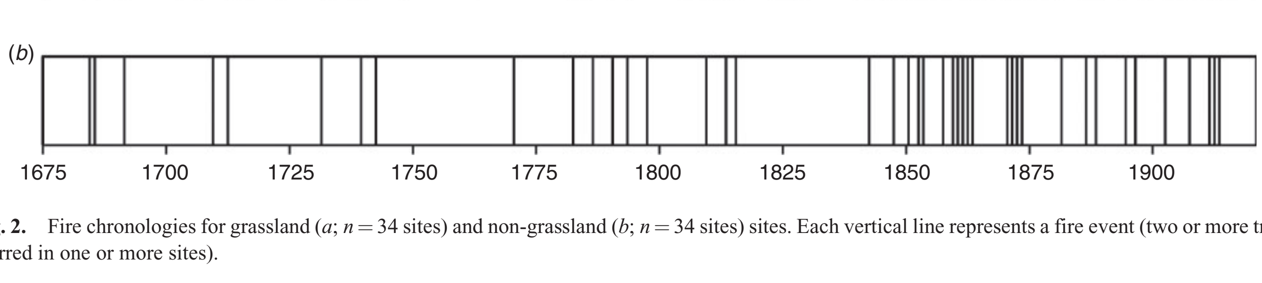

Fig. 2. Fire chronologies for grassland (*a*; $n = 34$ sites) and non-grassland (*b*; $n = 34$ sites) sites. Each vertical line represents a fire event (two or more trees scarred in one or more sites).

ponderosa pine-dominated forests by providing an abundant, continuous source of fine surface fuels that can support a surface fire during drought years, and which may be carried into neighbouring forested stands. In areas where grasslands are not present, however, low continuity of fine fuels likely limits surface fire spread, resulting in a lower overall fire frequency in adjacent forests.

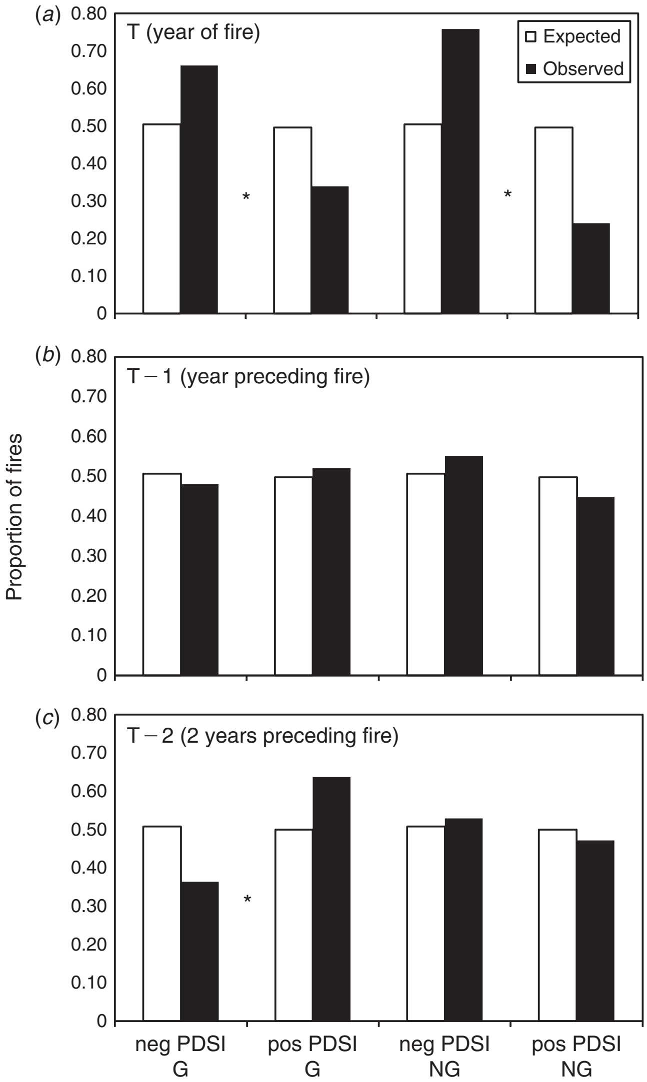

Fig. 3. Relative frequencies of fire and extreme Palmer Drought Severity Index (PDSI) events for grassland (G) and non-grassland (NG) sites during years of the fire (T) (*a*), 1 year before the fire (T − 1) (*b*), and 2 years before the fire (T − 2) (*c*). There are 122 positive (wet) and 124 negative (dry) PDSI years. For grassland sites, there are 80, 58 and 44 fire events for negative PDSI years during T, T − 1, and T − 2 years respectively, and 41, 63 and 77 fire events for positive PDSI years during T, T − 1 and T − 2 years respectively. For non-grassland sites, there are 66, 48 and 46 fire events for negative PDSI years during T, T − 1 and T − 2 years respectively, and 21, 39 and 41 fire events for positive PDSI years during T, T − 1 and T − 2 years respectively. Chi-square analyses compare the number of expected and observed fires for PDSI positive years to the number of expected and observed fires for PDSI negative years for T, T − 1 and T − 2 for the time period of analysis (1675–1920). Significant differences are indicated with an asterisk (degrees of freedom = 1; $P < 0.05$).

Changes in amounts of grass and other fine surface fuels have often been identified as a determinant of surface fire frequency, which in turn is widely believed to be a major factor in tree encroachments into grassland ecosystems and transition to dense woodlands or forests in western North America (Bachelet *et al.* 2000; Bai *et al.* 2004; Heyerdahl *et al.* 2007). Encroachment of conifers such as ponderosa pine, Douglas-fir and lodgepole pine into grasslands and savannas during the 20th century has been reported for many ecosystem types of western North America, but causes are often complicated and controversial (Arno and Gruell 1986; Butler 1986; Hansen *et al.* 1995; Mast *et al.* 1997; Bai *et al.* 2004; Heyerdahl *et al.* 2006). The key contributing factors are believed to be some combination of cessation of formerly frequent surface fires, effects of livestock (including their indirect influences through fuel reduction) and climate variability (Barrett 1994; Bachelet *et al.* 2000; Bai *et al.* 2004; Heyerdahl *et al.* 2006). For example, it has been suggested that in south-western Montana, 19th-century drought favoured Douglas-fir invasion of sagebrush and grassland as surface fires became less frequent owing to the advent of livestock grazing (Heyerdahl *et al.* 2006). Given the spatial variability of past fire frequency associated with grass versus woody fuels in mosaics of forests and grasslands (Bai *et al.* 2004; Heyerdahl *et al.* 2006), it follows that departures of modern fire regimes from historic fire regimes are also spatially variable. By adopting an analytical framework permitting the quantification of the effects of proximity of grasslands on fire activity and fire–climate relationships, the current study strengthens the inference that spatial variability in grasslands is a key source of variability in fire regime within a mosaic of conifer forest with grasslands.

In the Front Range ponderosa pine landscape, interannual climate variability affected fire occurrence at both grassland and non-grassland sites; fires occurred more often during years of extreme negative PDSI in both grassland and non-grassland sites. Although fires occurred during dry years regardless of fuel type, the fire-promoting effect of antecedent moist years is unique to the grassland sites. The relationship of widespread fire following above-average moisture availability in some stands has previously been assumed to involve enhanced production of fine (grass) fuels to facilitate fire spread in an otherwise fuel-limited ecosystem. Previous research has identified similar patterns of antecedent moist years for fires in ponderosa pine forests in southern Colorado where grasslands are common in the landscape (Brown and Shepperd 2001; Donnegan *et al.* 2001; Grissino-Mayer *et al.* 2004), at low elevations in the northern Colorado Front Range (Sherriff and Veblen 2008), and in other ponderosa pine-dominated ecosystems across the western USA (Swetnam and Betancourt 1990; Norman and Taylor 2003; Brown and Wu 2005; Brown *et al.* 2008) where fuel continuity, not drought, is often considered the limiting factor for fire.

Biome-scale studies have documented the positive influence of moister periods in advance of fire activity on fire extent in many tropical and temperate grassland and shrubland ecosystems where fuel quantity is often limiting to fire spread (van der Werf *et al.* 2008; Krawchuk *et al.* 2009). Studies conducted at a

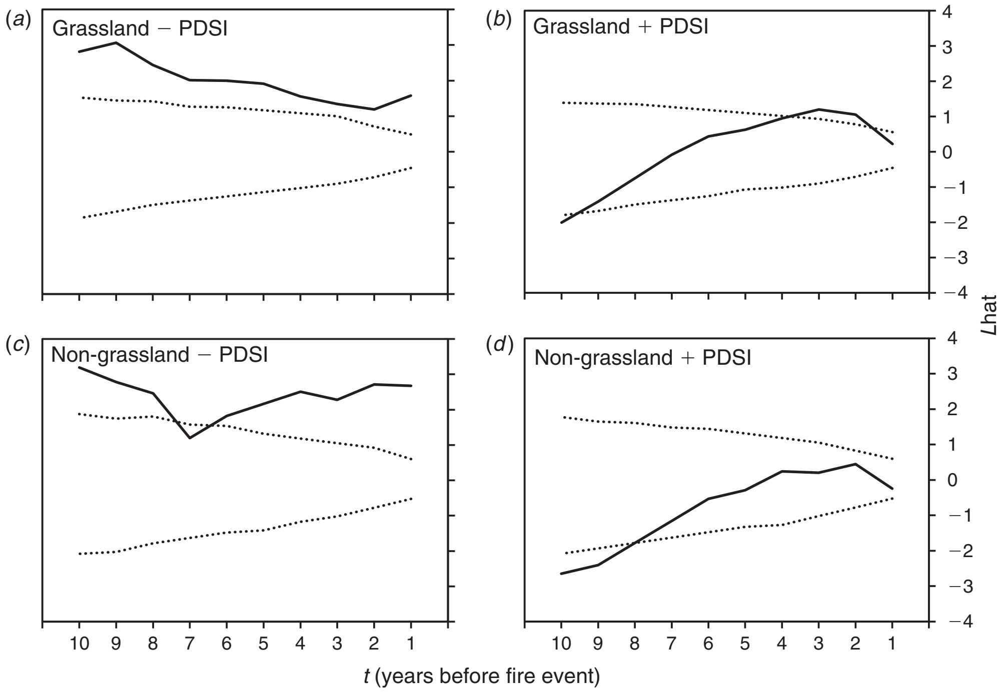

Fig. 4. Bivariate event analysis (BEA) of the temporal association of extreme Palmer Drought Severity Index (PDSI) years and fire events for grassland ((*a*) and (*b*); $n = 121$ fires) and non-grassland ((*c*) and (*d*); $n = 87$ fires) sites. Black lines indicate *L*hat values (*L* function values with stabilised mean and variance) for *t* years before the fire events ($t = 0$). Dotted lines indicate the upper and lower confidence intervals (95%). *L*hat values above the upper confidence interval indicate synchrony with fire, *L*hat values below the lower confidence interval indicate asynchrony with fire, and values between the confidence intervals indicate a random relationship of fire and climate events.

relatively fine spatial scale also document the importance of antecedent productivity of grass fuels in promoting fire activity in many semiarid temperate and tropical savanna and grassland environments on several continents (Swetnam and Betancourt 1990; Kitzberger *et al.* 1997; Veblen *et al.* 1999; Grau and Veblen 2000; Hély *et al.* 2003; Harris *et al.* 2008; Bravo *et al.* 2010). Analogously to the current study, in many of these other ecosystems fire activity is strongly linked to increased moisture availability associated with ENSO variability (e.g. Kitzberger *et al.* 2001; Harris *et al.* 2008). Drought is the key climatic driver of fire globally in biomass-rich biomes, but antecedent moist conditions promote fire activity in many ecosystems where fuel quantity limits fire (Krawchuk and Moritz 2011). Our results indicate that even within a landscape dominated by the same forest cover type, spatial variability of grass fuels has important influences on local fire history and sensitivity of the fire regime to climate variability.

The association of fire occurrence at grassland sites with antecedent moist conditions (positive PDSI) in the current study is also reflected by fire relationships with ENSO variability, which is the major driver of climate variability in the Colorado Front Range at an interannual time scale of 1 to 5 years. Moist spring conditions in the Front Range montane zone are associated with El Niño events (Veblen *et al.* 2000), and spring moisture conditions are visually associated with greater abundance of grass fuels in the ponderosa pine zone. When fine-fuel accumulation associated with El Niño-related moist springs is followed by La Nina-related drought 1 to several years later, large amounts of dry fine fuel become available. The association of greater than expected fire occurrence at grassland sites with positive NINO3 (wet El Niño-like conditions) in the current study is consistent with previous research showing a peak in fire activity in areas of the ponderosa pine landscape of the Front Range 3 to 4 years following historically documented El Niño events (Veblen *et al.* 2000; Sherriff and Veblen 2008). In contrast, in non-grassland sites in the current study, there is no association of fire activity with antecedent positive NINO3 (wet El Niño-like conditions) years. Furthermore, the lack of any association of fire activity at the non-grassland sites with negative NINO3 (dry La Niña-like conditions) implies that the mechanism by which ENSO variability affects fire activity in the ponderosa pine zone largely depends on climatic influences on grass fuels. This is consistent with previous research showing that fire activity is less sensitive to ENSO variability in higher-elevation (less grassland) than in lower-elevation (more grassland) ponderosa pine forests in the Colorado Front Range (Sherriff and Veblen 2008). Fire activity in upper montane ponderosa pine and adjacent subalpine forests in the Front Range shows a strong dependence on negative PDO and positive AMO, which drive climate and fire variability at multidecadal time scales (Sibold and Veblen 2006; Schoennagel *et al.* 2007; Sherriff and Veblen 2008) whereas ENSO variability alone is a key driver of fire activity in ponderosa pine stands adjacent to grasslands.

The important influence of proximity to grasslands on fire frequency and sensitivity to climate variability found in the

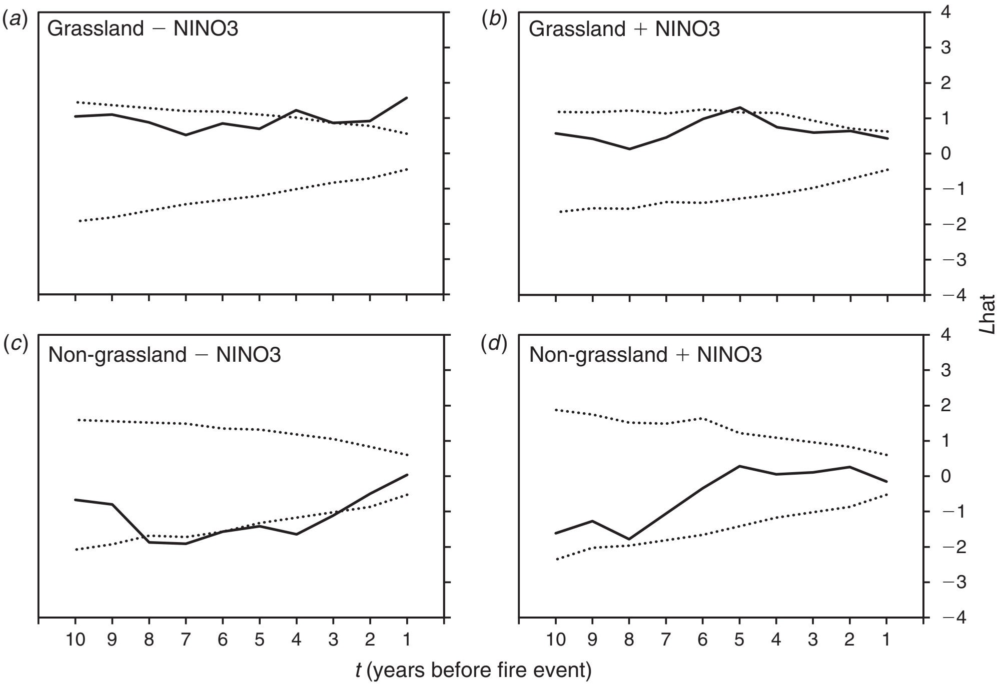

Fig. 5. Bivariate event analysis (BEA) of the temporal association of extreme NINO3 years and fire events for grassland ((*a*) and (*b*); $n = 121$ fires) and non-grassland ((*c*) and (*d*); $n = 87$ fires) sites. Extreme negative (positive) NINO3 years are teleconnected to higher (lower) moisture availability in Colorado. Black lines indicate *L*hat values for *t* years before the fire events ($t = 0$). Dotted lines indicate the upper and lower confidence intervals (95%). *L*hat values above the upper confidence interval indicate synchrony with fire, *L*hat values below the lower confidence interval indicate asynchrony with fire, and values between the confidence intervals indicate a random relationship of fire and climate events.

current study is consistent with recent research in the Front Range showing that the modern understorey vegetation can be used as an indicator of historic fire regime. In the ponderosa pine zone of the Front Range, the species composition of the modern understorey vegetation can be used to discriminate between sites that experienced higher versus lower fire frequency during the 18th and 19th centuries (Keith *et al.* 2010). Grass genera such as *Stipa*, *Andropogon*, *Poa* and *Bromus* are important indicator species of sites where historic fire regimes reconstructed from tree rings were characterised by frequent, low-severity fires whereas indicator grass species are absent from sites with historic fire regimes of infrequent, high-severity fires. The same biotic site factors that determine understorey composition when a quasi-equilibrium has been reached many decades after the most recent fire (Keith *et al.* 2010) also appear to affect fuel-defined fire potential and sensitivity of the fire regime to climate variation. Although fire regimes are often generalised by cover types defined by the arboreal dominants, it is important to recognise that within ponderosa pine-dominated ecosystems, there is ecologically important variation both in understorey vegetation and fire regime as well as the sensitivity of the historic fire regime to climatic and human-related influences.

In ponderosa pine ecosystems adjacent to grasslands or with important grass components in the understorey, grazing by livestock can easily alter fine-fuel quantities and therefore modify fire potential. For example, in many areas of ponderosa pine woodlands in Arizona and New Mexico, declines in fire frequency have been associated with fuel reductions due to grazing by livestock (Savage and Swetnam 1990; Covington and Moore 1994; Borman 2005). However, in the Colorado Front Range, this mechanism of reduced fire frequency due to fine-fuel removal by livestock would only apply to areas where grasslands were important in the ponderosa pine zone, mostly at lower elevations. Extensive areas of ponderosa pine forests in the upper montane zone in the Front Range occur on steep rocky slopes, currently lack grasses in the sparse understorey (Keith *et al.* 2010) and would not have been accessible to grazing by livestock. Understanding the role of grasslands in affecting historic fire regimes is essential to modelling future effects of both grazing and climate change on ponderosa pine ecosystems (Bachelet *et al.* 2000). The findings of our study support the connection between past widespread grazing, surface-fuel reduction and a coinciding decrease in fire frequency in ponderosa pine ecosystems that had an abundance of grass fuels, either in the understorey or as interspersed grasslands in a mosaic with forest patches.

The historical range of variability of fire within the ponderosa pine forests of the Colorado Front Range is complex, with variable determinants of fire frequency and fire timing. This study improves the understanding of the role of grasslands interspersed in the ponderosa pine landscape in increasing fire frequency and enhancing fire potential under increased wet–dry interannual climate variability. The important role of proximity to grassland in determining future fire potential and sensitivity to climate variability in ponderosa pine ecosystems may be a helpful consideration in both restoration and fuel-mitigation efforts.

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