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# Spatial, temporal and latitudinal components of historical fire regimes in mixed conifer forests, California

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## ABSTRACT

**Aim** This study seeks to document and compare historical temporal and spatial components of fire regimes in two watersheds in mixed conifer forests of the western slope of the Sierra Nevada, California, USA.

**Location** Watersheds in the southern Sierra Nevada (Sugar Pine, 2358 ha) and north-central Sierra Nevada (Last Chance, 3021 ha), California, USA are compared.

**Methods** Temporal (frequency, return interval, season) and spatial (extent, fire rotation, spatial mean fire interval) fire regime metrics were reconstructed from fire scar samples. Superposed epoch analysis (SEA) was used to examine relationships between fire occurrence and the Palmer drought severity index (PDSI) at each site. Thin plate splines were introduced as a tool for interpolating historical fire extent from dendroecological data. Point fire return intervals were compared between sites to better understand possible influences of historical Native American burning practices.

**Results** Differences emerged between sites in temporal and spatial fire regime metrics. The northern site had longer fire return intervals, more synchronized fire years, fewer point intervals < 4 years, longer fire rotation period and longer spatial mean fire interval. The northern site showed a significant reduction in PDSI values during fire years, whereas this climate–fire relationship in the southern site was likely decoupled by frequent Native American burning. Thin plate spline interpolation effectively reduced discontinuities at sample points compared to inverse distance weighting methods.

**Main conclusions** Differences in both temporal and spatial fire regime metrics between sites were likely due to interplay in latitudinal influence on climate as well as differential Native American burning practices. Reconstruction of historical fire areas via geographical interpolation of fire scar data holds great promise for spatially explicit fire frequency reconstruction. The use of thin plate spline interpolation methods has the potential to reduce the impact of 'false negatives' in dendroecological data from frequent-fire forests.

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**Keywords**

**dendrochronology, fire ecology, fire history, interpolation, inverse distance weighting, Native American, ponderosa pine, Sierra Nevada, thin plate spline**

## INTRODUCTION

Fire is a key ecological process in US western forests that impacts nutrient cycling, vegetative regeneration, species composition, stand structure and ecosystem resilience (Holling, 1973; Agee, 1993). A century of fire suppression and logging practices of the early 20th century have greatly altered many American forests that once burned frequently, creating more dense (Parsons & DeBenedetti, 1979) homogenous forests that are less resilient to drought, insect attack and are more likely to burn at high severity (Mallek *et al.*, 2013). Understanding how to manage these forests to retain



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their ecosystem services (Hassan *et al.*, 2005) and maintain resilience to climate change (Bonan, 2008) and uncharacteristically large and severe fire will be one of the most important challenges in this century.

Although the future promises to be different from the past and historical conditions may not be appropriate targets for future management (Millar *et al.*, 2007), understanding historical disturbance regimes, with which native plants and animals have evolved over thousands of years, is vital for building resilient ecosystems that can accommodate the uncertain future that lies ahead (Landres *et al.*, 1999). There is growing evidence that the heterogeneity created by historical fires is vital for the maintenance of species diversity and ecosystem resilience (North, 2012). Understanding spatial and temporal components of historical fire regimes can help us incorporate natural or planned disturbance into management plans aimed to promote ecosystem resilience.

Temporal components of historical fire regimes in the mixed conifer forests of the Sierra Nevada have been well studied (Kilgore & Taylor, 1979; Swetnam, 1993; Stephens & Collins, 2004; Scholl & Taylor, 2010), but there is still high uncertainty regarding spatial components of fire regimes in forests that historically experienced frequent, low- to moderate-severity fire (Taylor & Skinner, 2003). There has been greater success reconstructing spatial patterns in forests that historically experienced stand-replacing fires because ample evidence of these fires still exists. Estimations of spatial components of high severity, stand-replacing fires, have been conducted using tree stand age, tree height, density and composition (Heinselman, 1973; Agee *et al.*, 1990; Sibold *et al.*, 2006) yet this evidence depends on high tree mortality rates, which rarely occupy more than small patches in areas that historically burned frequently (Collins & Stephens, 2010; Stephens *et al*. 2015).

The most reliable evidence remaining in frequent, low-severity fire regimes is the presence of fire-scarred trees and a mosaic of multiaged stands (Swetnam, 1993). Unfortunately, these data types present challenges for reconstruction of the spatial patterns of fire. Since trees often survive low-severity fires and recruitment is typically chronic, tree ages tell us little about the spatial patterns of frequent low- to moderate-severity fires. Fire scars are evidence of the presence of fire, but trees that experience fire often do not scar. In fact, Stephens *et al.* (2010) have shown that when the fire interval is < 10 years, the probability of a previously scarred tree to scar again is only 5% in the mixed conifer forests of the Sierra Nevada and Baja California, Mexico. These ‘false negatives’ create spatially noisy datasets that make reconstructing spatial patterns of fire in these forest types difficult.

These problems have been partially overcome by using area-based rules to infer approximate fire sizes from the proportion of samples or geographical plots that record scars each year (Taylor & Beaty, 2005) or by using expert opinion to construct fire polygons (Heyerdahl *et al.*, 2001). These methods have been effective, but are difficult to reproduce, and require subjective decision-making. More recently, researchers have used automated methods in a GIS to produce objective fire areas across space and time. Hessl *et al.* (2007) evaluated Thiessen polygons, kriging and inverse distance weighted interpolation methods to reconstruct burned areas from fire scar data. Similarly, Collins & Stephens (2007) and Farris *et al.* (2010) used Thiessen polygons to reconstruct known fire areas from fire scar samples. Kernan & Hessl (2010) used an automated, spatially explicit inverse distance weighted interpolation method to create spatially explicit fire interval maps. This method has tremendous promise for understanding historical spatial fire dynamics via fire scar data, but the inverse distance weighting interpolation method can be problematic for data that contains many false negatives, such as fire scar data from frequent-fire forests. As a result, the maps produced from this method can display inaccuracies around sample points due to the exact nature of the interpolation.

In this manuscript, we reconstruct and compare both spatial and temporal fire regime metrics for two watersheds in the mixed conifer forest of the Sierra Nevada, California, USA. For each site, we explore the application of thin plate splines (TPS) as a spatially explicit fire-mapping interpolation method with the ability to overcome problems introduced by false negatives often present in fire scar data from frequent-fire forests. We also examine and compare the influence of climate and possible influence of Native American burning on fire occurrence.

## Study sites

Two mixed conifer forest watersheds were studied in the Tahoe and Sierra National Forests on the western slope of the Sierra Nevada of California (Fig. 1). The northern watershed, Last Chance (LC) is approximately 2358 ha, with elevation ranging from 800 to 1850 m above sea. Sugar Pine (SP), the southern watershed, encompasses 3021 ha with elevations ranging from 1200 to 2200 m. Annual mean precipitation, most of which falls as snow between November and April, is 118.2 cm at LC (1990–2008; Hell Hole RAWS) and 109.1 cm at SP (1941–2002, Yosemite National Park RAWS). Mean monthly temperatures are 3 °C and 2 °C in January and 21 °C and 18 °C in July for LC and SP, respectively. Soils are shallow, well-drained and developed from Mesozoic aged granite.

Vegetation on these landscapes is typical of the west slope of Sierra Nevada: a mixed conifer forest dominated by white fir (*Abies concolor* Gordon & Glend.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and incense-cedar (*Calocedrus decurrens* Torr. Florin), with sugar pine (*Pinus lambertiana* Dougl.), ponderosa pine (*Pinus ponderosa* Dougl.) and California black oak (*Quercus kelloggii* Newb.) appearing as a codominant at variable densities throughout. Mixed conifer forests differ between sites in that there is no Douglas-fir in the SP site.

Native American activity in the SP study area was likely quite high before European settlement (Freedman, 2013). Up until 1901, Bass Lake (6 km from the study site) was a large,

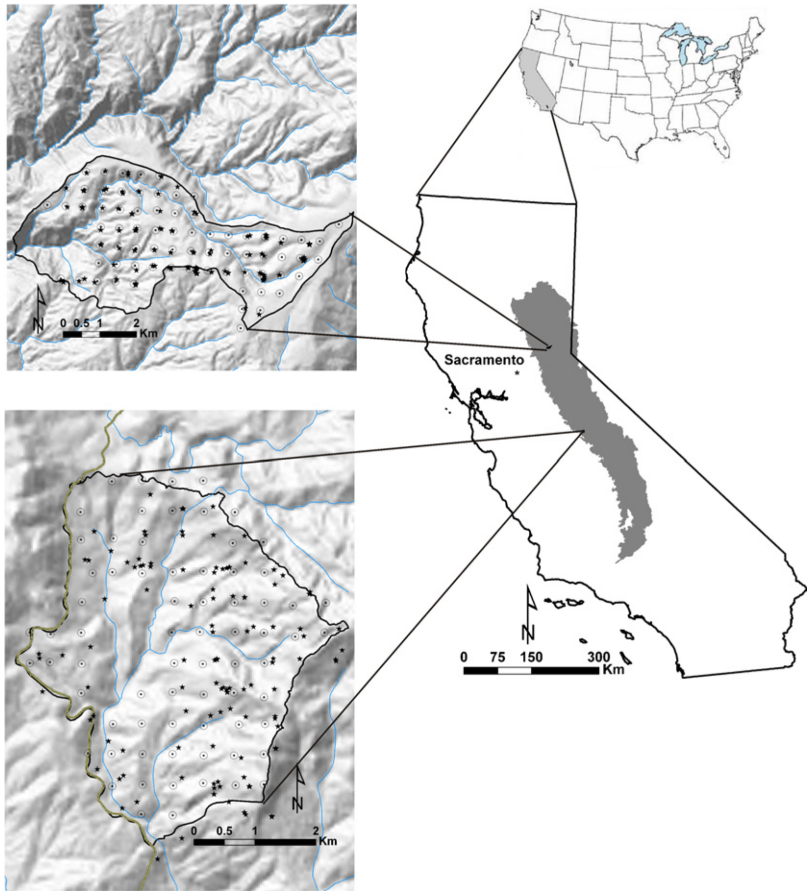


**Figure 1** Location of the northern (Last Chance) and southern (Sugar Pine) fire history study sites in the Sierra Nevada ecoregion (grey), California. Fire scars (stars) were sampled from trees within the forest inventory plot grid (circles) and opportunistically when moving from one plot to another.

lush meadow which was a convergence spot for Sierra Miwok, Chuckchansi Yokut and Western Mono tribes, who used fire extensively to keep the adjacent forest open, encourage herbaceous growth for game animals and to produce vegetative growth conducive to basket weaving and arrow construction (Anderson, 2005; Freedman, 2013). In 1901, Willow creek was dammed for the production of hydroelectric power, thus producing Bass Lake. From 1901 to 1931, the Sugar Pine Lumber Company operated kilometres of narrow gauge railroad in and around the SP study site (Johnston, 1984).

Little detailed information exists about Native American populations and activity in the LC site, although the Nisenan people once inhabited the forests of north-central Sierra Nevada and actively used fire in these forests to manage for diverse resources for at least 2000 years (Cook, 1976). An epidemic of malaria was introduced to northwest California in 1833 which decimated their population and the discovery of gold in California in 1849 resulted in widespread persecution, killing and destruction of villages that destroyed them as a viable culture by 1851 (Wilson & Towne, 1978).

## MATERIALS AND METHODS

### Sample collection and processing

In order to attain a geographically distributed collection of fire scars across the study areas, we sampled the gridded network of forest inventory plots (500 m intervals, $n = 75$ for SP and 71 for LC) within treatment watersheds used in the Sierra Nevada Adaptive Management Project (Fig. 1). Each grid point was visited and 0–5 pieces or fire-scarred wood were sampled with a chainsaw within a 100-m radius of each point. Samples were also opportunistically collected when travelling from one grid point to the next. A total of 148 samples were collected at SP and 134 samples were collected at LC (Table 1). Resulting fire scar density was 0.04 samples per hectare at both sites, which is comparable to sample densities in the fire history literature (Hessl *et al.*, 2007).

Fire dates were determined by sanding and crossdating each sample (Stokes & Smiley, 1968) against independent master tree-ring chronologies developed from increment cores from 30–50 trees without fires scars within the study area and/or nearby chronologies from Blodgett Research Forest (Stephens & Collins, 2004) and the international tree-ring database (https://data.noaa.gov/dataset/international-tree-ring-data-bank-itrdb, Snow White Ridge, Lemmon Canyon, Merced Grove and Oak Flat). If possible, scar position within the annual ring was used to assign seasonality to the fire event (Dieterich & Swetnam, 1984). Fire dates were checked by at least two researchers before being entered and summarized in FHX2 (Grissino-Mayer, 2001). If samples contained too few rings to cross-date, were not able to be cross-dated, or were too decayed to

**Table 1** Summary of fire scar samples, scar position and point fire intervals from both Sugar Pine and Last Chance study areas in the North American Sierra Nevada.

| | Sugar Pine | Last Chance |
|---|---|---|
| Size (ha) | 3021 | 2358 |
| Total samples collected | 148 | 134 |
| Total samples cross-dated | 118 (80%) | 102 (76%) |
| Live trees cross-dated | 61 (52%) | 42 (41%) |
| Dead trees cross-dated | 57 (48%) | 60 (59%) |
| Incense-cedar samples | 101 (86%) | 51 (50%) |
| Ponderosa pine samples | 17 (14%) | 37 (36%) |
| Sugar pine samples | 0 (0%) | 12 (12%) |
| Douglas-fir samples | 0 (0%) | 1 (1%) |
| Number of dated scars | 802 | 659 |
| Earliest dated fire scar | 1607 | 1577 |
| Most recent dated fire scar | 1947 | 1943 |
| Scars with inferred seasonality | 688 (86%) | 621 (94%) |
| Middle earlywood scars | 10 (2%) | 7 (1%) |
| Late earlywood scars | 23 (3%) | 13 (2%) |
| Latewood scars | 316 (46%) | 73 (12%) |
| Dormant position scars | 339 (49%) | 527 (85%) |
| Samples containing at least one point fire interval of three or fewer years | 22 (19%) | 7 (7%) |
| Point fire intervals of three or fewer years | 29 (6%) | 7 (1%) |

sand or visualize, they were not included in the present analysis ($n$ = 30 in SP and 32 in LC).

## Temporal fire interval calculations

The time period from 1750 to 1900 was selected as a window in which to analyse historical fire regimes for both study areas. This time frame was chosen because the fire scar sample depth drops considerably prior to 1750 and fire suppression practices were initiated shortly after the formation of the US Forest Service in 1905 (Scholl & Taylor, 2010). There have been reports of the fire intervals increasing in the second half of the 1800s due to Euro-American settlement in the Klamath Mountains (Fry and Stephens, 2006) and North Coast Range (Skinner *et al.*, 2009), but Scholl & Taylor (2010) did not detect a significant difference in fire interval statistics before 1850 (pre-settlement) and 1850–1904 (settlement) in a similar forest type in Yosemite National Park; nor do we detect a difference in fire frequency during the second half of the 1800s. Thus, our window of time between 1750 and 1900 should adequately represent the fire regime in the study areas before modern day fire suppression.

Point fire intervals (PFI) and composite fire intervals (CFI) were calculated in FHX2 (Grissino-Mayer, 2001). PFI are calculated from the intervals in each sample tree separately, and represent the fire return interval to a single point and are a more conservative estimate of fire frequency. CFI are calculated using all the samples in the study and may be filtered including only years that scar a certain per cent of the available samples (typically 10–25%).

Stephens *et al.* (2010) have shown in similar mixed conifer forests that the probability of a previously scarred tree ('recording' sample) re-scarring from a wildfire is only 5% if the interval since the last fire is < 10 years. We hypothesize that PFI of three or fewer years may be indicative of human ignitions rather than lightning-ignited fires (Finney & Martin, 1992), as humans have the ability to ignite and re-ignite fires to facilitate fire spread even when fuel moistures or fuel continuity would not support unassisted fire spread. To investigate the possible influence of Native American burning practices in each site, we determined the number of samples in each site that showed PFI of three or fewer years as well as the proportion of all point intervals in each site that were of three or fewer years. Differences between sites were examined with a two-sample test for equality of proportions.

## Spatially explicit fire area reconstructions

Fire scar data from recording samples during this study period were used to construct spatial mean fire interval (SMFI) maps for each study area (Kernan & Hessl, 2010). For each fire scar sample, its fire years and geographical coordinates were input into a spatial points data frame in the R statistical package (R Development Core Team, 2010). Individual samples were treated as binary point data across the study area. Fire perimeter maps were constructed for each year in which four or more samples recorded a fire to eliminate small spot fires. To do this, new spatial point data frames were constructed from only the recording samples for each fire year. Samples were coded as one (recording a fire) or zero (not recording a fire). For each year, the binary point data was then interpolated to construct a grid with an estimated value between zero and one in every pixel. Two interpolation methods were used and will be compared in the following analysis:

**1.** Inverse distance weighting (IDW) – a deterministic, exact interpolation method that predicts a value for any unmeasured location by using the known values surrounding the prediction location. IDW is an exact interpolator, meaning the prediction surface passes exactly through the value of each sample, causing the maximum and minimum values of the interpolated surface to occur at sampled points (1 and 0 respectively). Measured values that are nearest to the prediction location will have greater influence on the predicted value at that unknown point than those farther away (Cressie, 1993). Users can specify a power for IDW interpolation, which controls how quickly local influence diminishes with distance – lower power values give more influence to distant points and create smoother surfaces (Hessl *et al.*, 2007). In addition to the power, users control the number of neighbours included in the local calculations. Hessl *et al.* (2007) and Kernan & Hessl (2010) both use IDW interpolation to create SMFI maps using a power of two and 12 nearest neighbours. These same parameters were employed in the current study using the gstat package (Pebesma, 2004).

**2.** Thin plate spline (TPS) – a deterministic, inexact interpolation method, which is a smoothed version of a spline (an exact interpolation method). We used the TPS algorithm from the 'Fields' package (Furrer *et al.*, 2009) in the R statistical package (R Development Core Team, 2010). This algorithm fits a TPS surface to irregularly spaced data with a smoothing parameter that is chosen by generalized cross-validation, which minimizes the sum of squared errors of the fitted surface. The resulting surface from this inexact interpolation does not necessarily pass through the values of the sample points and generally gives a smoother fit (Craven & Wahba, 1978) than exact interpolators.

### Threshold values to differentiate burned from unburned pixels

In order to classify pixels ranging in value from 0–1 as burned or unburned, a threshold must be chosen as a cut-off. We tested the difference between two thresholds. First, we used the proportion of scarred samples relative to the total number of recording samples (hereafter called 'proportion scarred'), which has been used as a threshold for fire perimeter mapping (Kernan & Hessl, 2010) as well as predictive vegetation mapping (Franklin, 1998). As a more conservative threshold for fire area estimations, we also used half of the maximum value ('half-max') of the interpolated surface for the TPS interpolation method (the half-max value was always higher than the proportion scarred value in our dataset).

Each interpolation method produced a surface of interpolated values ranging from 0–1 for each fire year between 1750 and 1900. In each of these surfaces, the pixels greater than or equal to the threshold for that method were inferred to burn in that fire year. Those below the threshold were inferred to have not burned. The fire size was calculated for each fire year for each interpolation method. A map representing the number of times each pixel burned was then created from the sum of these resulting fire area maps and used to create a map of the number of fire intervals for each pixel.

Additionally, a 'recording ring depth' map was made for each interpolation method. To do this, the number of recording rings between 1750 and 1900 were calculated for each tree sample and the resulting values were interpolated with the same IDW and TPS methods described above. Finally, to compute a Spatial Mean Fire Interval (SMFI) map, we divided the recorder ring depth map by the interval number map (Kernan & Hessl, 2010). Additionally, for each resulting SMFI map, the pixel values were averaged to estimate the SMFI for that site as a whole. These were computed for the three combinations of interpolation method and threshold values examined in this study: (1) IDW with a threshold of the proportion of samples that scarred, (2) TPS with a threshold of the proportion of samples that scarred, and (3) TPS with a threshold of half the maximum interpolation value.

### Annual area burned, average fire size, and fire rotation period

For each fire year, site and interpolation method, we calculated the fire size by summing the area of all pixels classified as burned in each fire year. These values were divided by the size of the study area to compute a proportion of the study area burned. For each site, these metrics were averaged across all analysis years to yield an average fire size and mean per cent of the study area burned.

Fire rotation periods (Heinselman, 1973) were calculated for each study area and interpolation method by summing the total area burned (including areas that burned more than once) during our 150-year analysis period and then using the following formula.

$$\text{Fire Rotation Period} = \text{Total years in analysis period} / \text{proportion of the study area that burned during this period}$$

### Spatial mean fire interval map analysis

To examine the relationship of slope aspect and SMFI, values from each of the SMFI maps were extracted to the sample grid points in each site in order to examine if significant differences existed in SMFI between slope aspect categories. Each point was classified with a predominant aspect of north (316°–45°), east (46°–135°), south (136°–225°) or west (226°–315°). Grid points in the various aspect categories were examined for variation in SMFI using a distribution-free Kruskal–Wallis $H$ test (Scholl & Taylor, 2010).

### Influence of climate on fire occurrence

To examine the influence of proxy climate on fire occurrence at interannual time-scales, we used superposed epoch analysis (SEA) (Grissino-Mayer, 2001). SEA determines relationships between events (i.e. fire years) and climate by testing for departures of mean climate values from the period mean during, before, and after fire event years using Monte Carlo simulation with 1000 interactions to derive bootstrapped confidence interval estimates (Swetnam, 1993). Palmer drought severity index (PDSI) was used as a climate proxy in this study (Cook *et al.*, 1999; gridpoint 47). PDSI is a composite climate index that integrates immediate and lagged precipitation and temperature values to estimate drought severity. Negative values of PDSI represents drought, while positive values represent more climatic moisture. SEA was run for all of the identified fire years in each site as well as for fire years in which 10, 15 and 20% of the recording samples were scarred in each site. Significant departures from expected climate values were identified for 5 years before each fire year and 2 years following each fire year (Taylor & Beaty, 2005).

### Edge effects of interpolation methods

Undesirable edge effects can be introduced by spatial interpolation of point data and often vary by interpolation method, the relative location of sample points in reference to the edge of the interpolated surface and the perimeter to area ratio of the interpolated surface (Helzer & Jelinski, 1999). To investigate the impact of edge effects in each interpolation method compared in this study, we calculated the annual and average fire area, fire rotation period and SMFI of various sized interpolation surfaces. We calculate these metrics for the full interpolation extent (defined by the maximum and minimum latitude and longitude of the full set of fire scar samples for each site) as well as extents that were iteratively croped equally on all sides by 10-m increments until 50% of the study area was removed. Although the interpolation extent was iteratively cropped smaller and smaller, the point data for each fire year remained the same, effectively reducing the prediction at the 'edge' of the data points with each iteration of a smaller extent (and leaving an increasing number of the sample points outside the extent of the interpolation). The resulting curves for each fire metric were plotted as a function of proportion of the study area cropped from the perimeter. If the areas closer to the edge of the interpolated surface consistently have a significantly different proportion of the area classified as burned across fire years (versus the areas in the interior of the interpolation), we would expect to see significant changes to fire metrics as the edge of each interpolation is successively cropped from the extent used to calculate the fire statistics. Each curve was examined visually for any abrupt discontinuities that would indicate severe edge effects and were also fit to a linear regression model to examine if the slope was significantly different from zero, indicating a trend in the metric with a change in the extent of the interpolation surface.

## RESULTS

### Temporal fire regime characterization

In total, 118/148 fire scars (80%) were successfully cross-dated at SP and 102 (76%) at LC (Table 1). The PFI for SP and LC were 14.3 years and 17.5 years, respectively, which represents the average time required for fire to re-scar the same sample within the study area (Table 2). Many individual fire scar samples contained PFI of three or fewer years, especially in the SP site, which showed significantly more samples with at least one point interval of three or fewer years ($P = 0.02$) as well as a higher proportion of all point intervals that were of three or fewer years ($P = 0.0006$, Table 1).

The CFI for all fires was 1.1 for SP and 1.2 years for LC, and increased to 5 and 6.1 years, respectively, when only fires that scarred 10% of the recording trees were considered. In the SP site, there were not enough fire events that scarred 20% or 25% of the recording samples to calculate a statistic for the 20 or 25% CFI. For LC, the composite 20% and 25% scarred mean fire return interval was 11.0 and 19.8 years, respectively (Table 2).

### Spatially explicit fire regime characterization

For each fire year, there was a mean of 89.4 recorder samples (trees that have been previously fire scarred) at SP and 80.1 at LC (Table 3). On average seven samples (8%) were scarred during each fire year at SP and 11.3 (14.5%) at LC. Interpolation methods and thresholds had similar trends in fire shapes for fire years, but varied in the resultant fire sizes and continuity (Fig. 2). For IDW, the predicted fire perimeters often had unburned pockets around samples that did not record a fire (Fig. 2). When the same threshold was

**Table 2** Point and composite fire-return interval (FRI) statistics for the Sugar Pine (SP) and Last Chance (LC) study areas for 1750-1900 in the Sierra Nevada. SD = standard deviation; NA = an insufficient number of samples to calculate a value.

| | Number of intervals | | Mean FRI (yr) | | Median FRI (yr) | | SD (yr) | | Min. (yr) | | Max (yr) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site | SP | LC | SP | LC | SP | LC | SP | LC | SP | LC | SP | LC |
| Point (PFI) | 500 | 475 | 14.3 | 17.5 | 11.0 | 15.0 | 11.3 | 12.8 | 2 | 2 | 76 | 91 |
| Composite all | 140 | 120 | 1.1 | 1.2 | 1.0 | 1.0 | 0.3 | 0.5 | 1 | 1 | 3 | 3 |
| Composite 10% | 27 | 24 | 5.0 | 6.1 | 3.0 | 4.5 | 4.5 | 4.7 | 1 | 1 | 18 | 19 |
| Composite 20% | NA | 9 | NA | 11.0 | NA | 9.0 | NA | 9.1 | NA | 2 | NA | 33 |
| Composite 25% | NA | 5 | NA | 19.8 | NA | 15.0 | NA | 14.3 | NA | 7 | NA | 35 |

**Table 3** Fire scar sample summary during fire years analysed in the 1750–1900 period ($n = 74$ years for SP and 39 years for LC when 4 or more samples scarred). SD = standard deviation.

| | Minimum | | Maximum | | Mean ± SD | |
|---|---|---|---|---|---|---|
| Site | SP | LC | SP | LC | SP | LC |
| Number recording | 26 | 33 | 116 | 102 | 89.4 ± 23.8 | 80.1 ± 21.6 |
| Number scarred in fire year | 4 | 4 | 23 | 32 | 7.0 ± 3.6 | 11.3 ± 8.2 |
| Per cent scarred in fire year | 3 | 4 | 25 | 45 | 8.0 ± 4.0 | 14.5 ± 9.8 |

used, IDW interpolation had a lower mean fire size than did the TPS interpolation method (Table 4). Within TPS, changing the threshold from proportion scarred to half-max resulted in smaller fire areas (Table 4). Per cent of the study area burned and fire rotation period are both a function of the area burned and followed similar trends (Table 4).

Spatial mean fire interval maps from the various interpolation methods showed similar general trends in the sections of the study area that had the highest and lowest fire intervals, but varied in the predicted values (Figs 3 & 4). In SP and LC the IDW interpolation had an intermediate SMFI of 5.81 and 12.12 years, respectively, and showed the greatest discontinuities in the predicted values for both sites. The TPS interpolation with a proportion scarred threshold showed the lowest SMFI of all the compared methods with an average of 3.12 years and 8 years for SP and LC, respectively. Using the half-max threshold, the TPS interpolation method resulted in the highest SMFI of 7.27 and 21.79 years for SP and LC, respectively (Fig. 3, Table 4).

### Influence of climate on fire occurrence

When all fire years were tested, the LC site showed a significant reduction in average PDSI values on fire years ($n$ = 39) versus non-fire years (Fig. 5), whereas the SP site showed no significant departure from average PDSI values on the fire year ($n$ = 74) versus non-fire years examined. When only fire years that scarred 10, 15 or 20% of the recorder samples were considered, the LC site showed significant reduction in PDSI values on the fire year for 10, 15 and 20% recorder samples scarred ($n$ = 25, 15 and 9 fire years respectively); whereas the SP site did not show significant reduction in PDSI values for 10% scarred ($n$ = 21), but did for 15% scarred years ($n$ = 9, Fig. 5; the SP site did not have enough fire years that scarred 20% of recording samples to successfully conduct SEA analysis).

### Edge effects by interpolation method and site

In general, no obvious discontinuities in fire rotation or SMFI existed in the edge effect curves generated in our analysis (Fig. 6) and consistent trends in edge effects for the compared interpolation methods were not obvious. For TPS half-max and IDW, there was a lack of consistent slope direction in edge effects for both fire rotation period and SMFI between the two sites. The only consistent result for interpolation methods between sites in edge effects is for the TPS proportion scarred, that shows a significant negative slope on both fire rotation period as well as SMFI for both the LC and SP sites.

There were more robust patterns of edge effect at the site level (across all interpolation methods). Namely, for the LC site, all interpolation methods showed significantly negative slopes for both fire rotation and SMFI (Fig. 6), whereas for the SP site, half of the six slopes tested were not significantly different from zero.

### Slope aspect and fire frequency

No significant differences were detected in SMFI between plots in the four classes of slope aspect in any of the three interpolation methods for either site. Figure 7 shows the TPS half-max burn interval map with the topography of the SP site.

## DISCUSSION

### Latitude and fire frequency

When only examining temporal dynamics, the two sites differed slightly in their fire regime statistics, showing less frequent fires and more synchrony in fire scar formation in the northerly LC site (Table 2). This is consistent with other studies in North America that have shown more frequent burning as latitude decreases (Heyerdahl *et al.*, 2001). These differences become more pronounced when spatial dynamics are considered and modelled (Table 4). For instance, the 10% composite mean fire return interval for LC (6.1 years) is 22% longer than that for SP (5.0 years, Table 2), although when spatial dynamics are explicitly modelled using the TPS half-max method, the fire rotation period for LC (9.3 years) is 69% greater than that for SP (5.5 years). Similarly, the spatial mean fire return interval for LC (8.0 years) was 156% larger than that for SP (3.12 years). The increased difference in fire regime statistics when spatial dynamics of fire are explicitly modelled indicates that intervals alone relate only a fraction of the information available from fire scar samples. Without the explicit incorporation of geography, fire regime characterization from fire scar samples results in homogenized statistics for the area of interest, which may mask important within-site heterogeneity in historical fire occurrence. The resulting burn interval maps from the methods employed in this study aim to characterize important spatial variation in historical fire occurrence (Figs 3 & 4) and will have great benefits for better understanding spatial heterogeneity, which is increasingly becoming a management objective for maintenance of species diversity and ecosystem resilience (North, 2012).

### Comparison of interpolation methods

An exact interpolation method will yield more accurate values at sample points, but given the nature of this dataset (with many ‘false negatives’), the IDW interpolation does not appear to be the best choice for reconstructing spatial fire dynamics due to the resulting discontinuities at sample locations (Fig. 3). There is similar evidence of these artefacts around sample points in the IDW fire area maps published by Hessl *et al.* (2007) and Kernan & Hessl (2010), but these maps do not show the extreme discontinuities that resulted in the current IDW fire interval map. This is likely due to the longer fire intervals in the higher latitude forests of Washington State in these studies. With longer fire intervals,

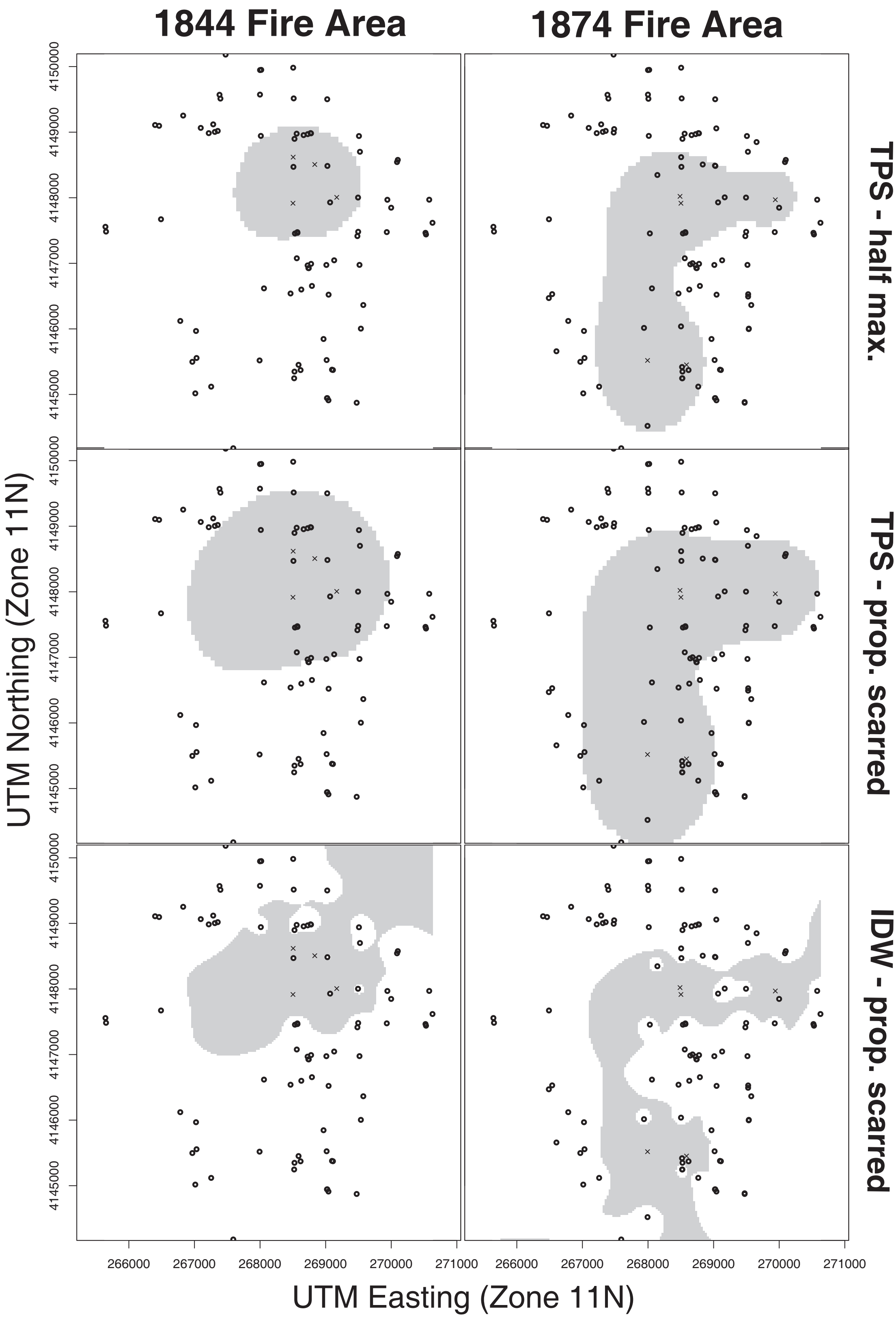


**Figure 2** Interpolated fire area (grey) for 1844 and 1874 in SP site, comparing thin plate spline (TPS) with a threshold of the half the maximum interpolation value (top), TPS with the proportion of recording samples scarred threshold value (middle), and inverse distance weighting (IDW) with a proportion of recording samples scarred threshold (bottom). Symbols are locations of recording trees scarred (x) and not scarred (o) in the given year.

**Table 4** Comparison of mean area burned, per cent of the study area burned, fire rotation period and spatial mean fire interval (SMFI) for inverse distance weighting (IDW) and thin plate spline (TPS) interpolation (Interp.) methods with thresholds of the proportion of samples with a fire scar relative to the total number of recording samples in a particular year (Prop. scarred) and half of the maximum value in the interpolated grid for a particular year (Half-max.).

| Interp. method | Threshold for area burned | Mean area burned (ha) in years with 4 or more trees recording fire | | Mean per cent of study area burned in years with 4 or more fires recorded | | Fire rotation period (yr) | | SMFI (yr) | |
|---|---|---|---|---|---|---|---|---|---|
| | | SP | LC | SP | LC | SP | LC | SP | LC |
| IDW | Prop. scarred | 884 | 782 | 29% | 32% | 6.8 | 11.6 | 5.81 | 12.12 |
| TPS | Prop. scarred | 1105 | 980 | 37% | 42% | 5.5 | 9.3 | 3.12 | 8.00 |
| TPS | Half max. | 565 | 514 | 19% | 22% | 10.7 | 17.6 | 7.27 | 21.79 |

the scarring probability for recording trees is increased (Stephens *et al.*, 2010), thus reducing the likelihood of false negatives which are the source of these discontinuities.

Thin plate spline is a good tool for smoothing noisy data (Craven & Wahba, 1978), and effectively eliminated the interpolation artefacts around sample points for our dataset. However, accuracy at sample points is sacrificed for this smoothness. For datasets with many false negatives, such as the fire scar data presented in this study, a smoothing interpolation method likely gives a more realistic surface than exact interpolators such as IDW. With any interpolation method, the cut-off value for classifying pixels as burned or not has important consequences for the predicted fire sizes and fire regime descriptors, and deserves further study.

Without a known history of spatial fire dynamics in these areas during the study period, it is hard to quantitatively evaluate the accuracy of the interpolation results from this study. But we can compare the predicted fire sizes to other studies in nearby areas and with the well-accepted non-spatially explicit fire statistics calculated with fire scar samples. In a recent study in a nearby forest in Yosemite National Park, Scholl & Taylor (2010) not only estimated the mean fire size for a comparable study period to be between 203–266 ha but also made the qualification that many of these fires burned up to the edge of their study area, so were likely larger. In this study, the TPS interpolation method using the half-max threshold predicted the smallest mean fire size and the closest to Scholl and Taylor's estimate with a mean fire size of 565 ha (Table 4).

Thin plate splines have promise for estimating spatial patterns of fire for areas that historically burned frequently and will likely have the presence of a large number of false negatives in the fire scar record. These false negatives create undesirable artefacts around most of the sample points with the IDW interpolation method. Likewise, the TPS method with the proportion scarred threshold predicted fire sizes that were too large in relation with Scholl & Taylor's (2010) estimates, and we believe consistently overestimates fire size.

We found, as did Kernan & Hessl (2010), that the SMFI was an intermediate value between the PFI, which is a conservative estimate of fire frequency, and the all sample CFI, which tends to estimate artificially low fire intervals (especially for large sample sizes). Other advantages of the SMFI are that it will explicitly model within site heterogeneity in fire occurrence, and with adequate sampling density, it should be scale independent, which CFI are not (Kou & Baker, 2006).

### High fire frequency, lack of fire scar synchrony and decoupling of climate–fire relationship in SP site

Curiously, in the SP site, there were not enough years in which 20% of the samples were scarred to calculate this composite statistic. One potential explanation of the lower level of synchrony of fire scars include the occurrence of many small fires due to high Native American use and burning in this area (Finney & Martin, 1992; Swetnam *et al.*, 2016). Bass Lake is in close proximity to the SP study area and was a vitally important confluence of at least three Native American Tribes: Sierra Miwok, Chuckchansi Yokut and Western Mono. These native people used this area extensively and burned the adjacent forest to keep it open, encourage herbaceous growth for game animals and produce vegetative growth conducive to basket weaving and arrow construction (Anderson, 2005; Freedman, 2013). This frequent use would likely have impeded fuel accumulation and fostered low-intensity fires and a landscape of fire-scarred trees that contain short fire intervals and non-synchrony in scar formation, which has also been found in similar forests in the Sierra San Pedro Martir, Mexico (Evett *et al.*, 2007).

Native American fire management is likely also responsible for the decoupling of fire–climate relationships often observed in fire history studies (Taylor & Beaty, 2005; Swetnam *et al.*, 2016; Fig. 5). In prescribed fires today, it is not uncommon for fire spread to falter in areas of fuel discontinuity or high fuel moisture, necessitating strategically placed ignitions and re-ignition. Native American burning was likely similar and facilitated burning even when climate and fuel conditions would likely not support natural fire spread, which could effectively decouple the fire–climate relationship that makes successful fire spread much more likely during drought years. In the SP site, 19% of the fire scar samples

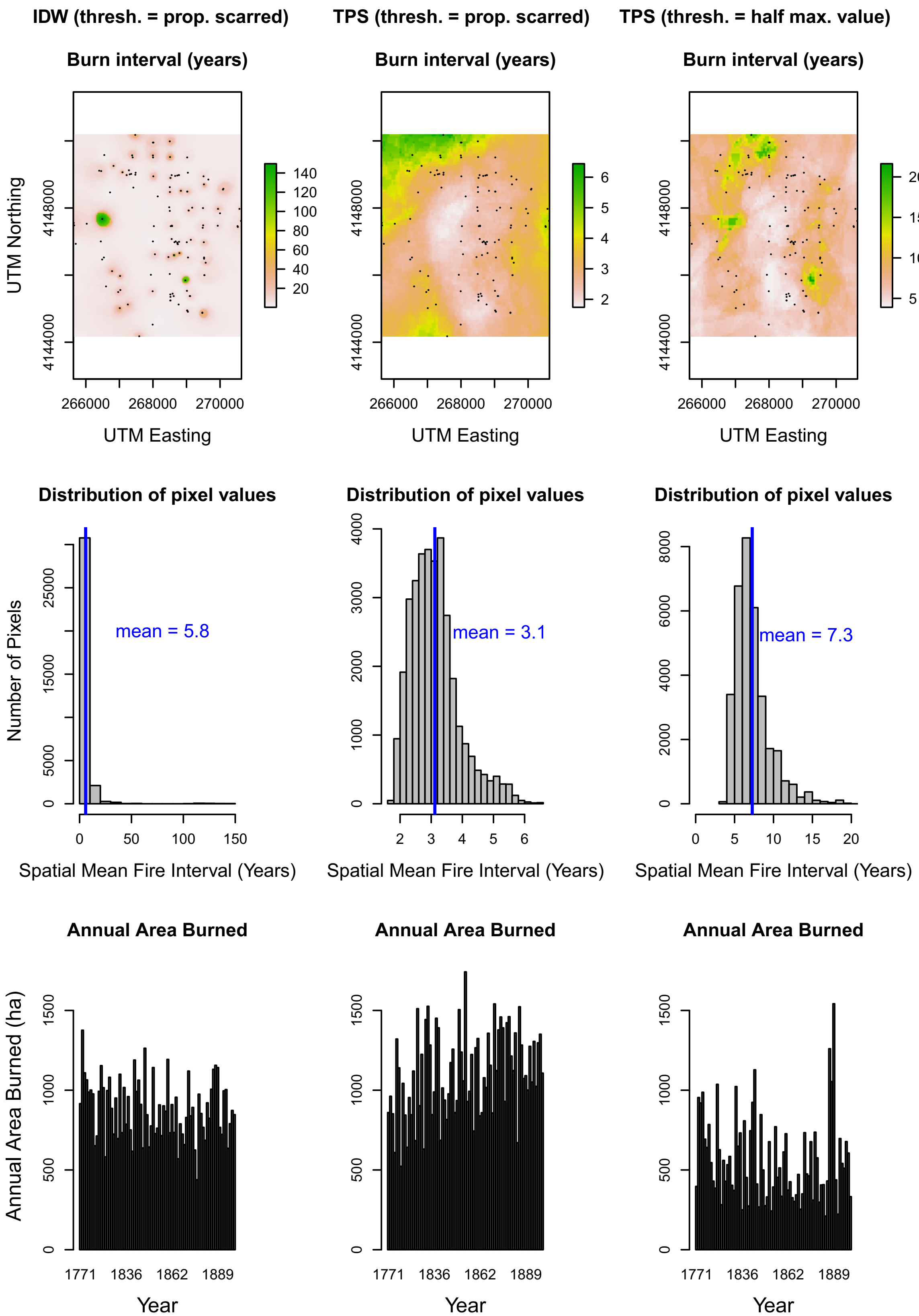


**Figure 3** Comparison of fire scar-interpolated burn interval maps (top row) for Sugar Pine site, Sierra Nevada, California, pixel value distribution for each map and mean pixel value (middle row), and annual area burned (bottom row) for IDW with the proportion of recording samples scarred threshold (left column), Thin Plate Spline (TPS) with the proportion of recording samples scarred threshold (middle column), and TPS with a threshold of half the maximum interpolation value (right column).

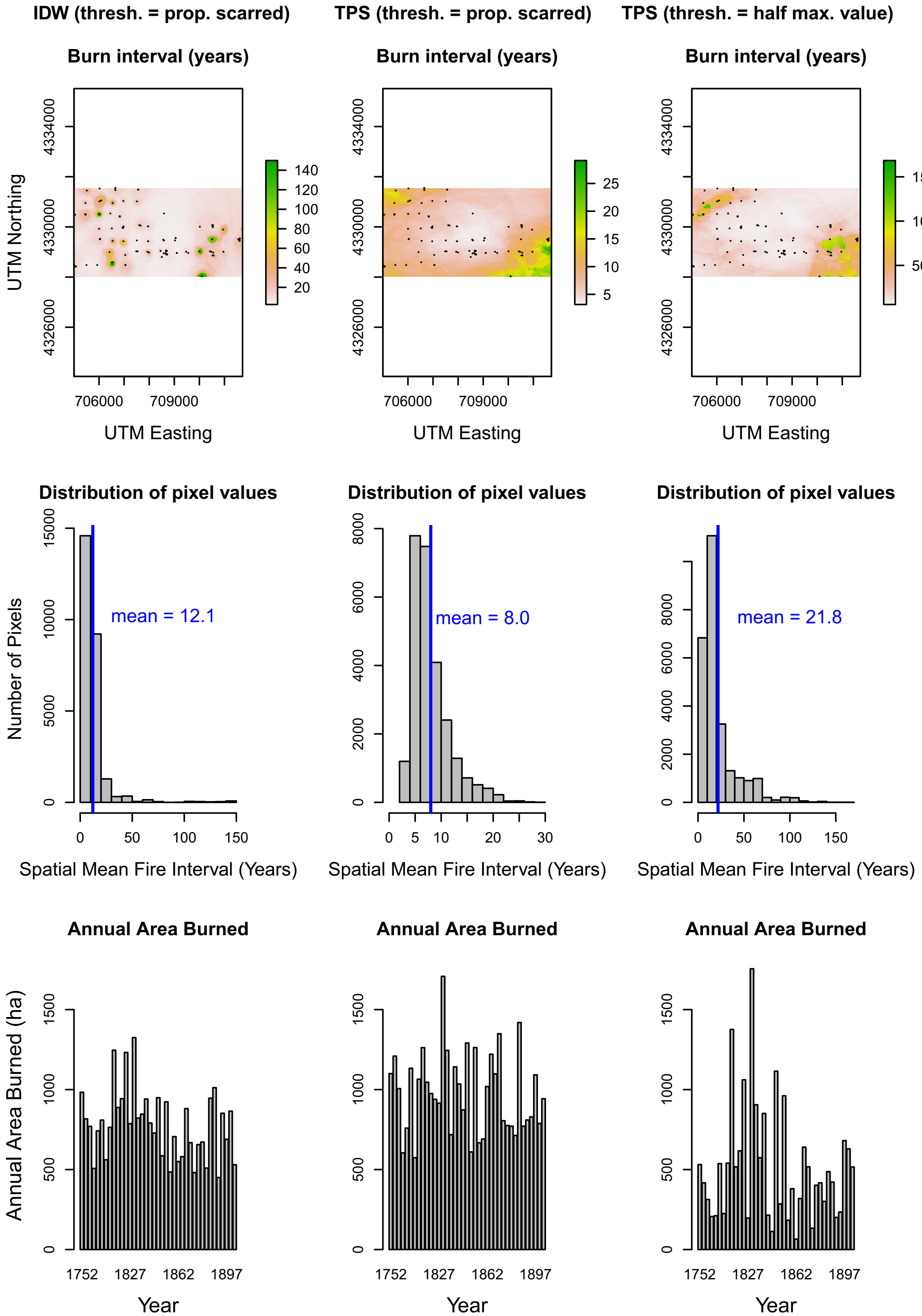


**Figure 4** Comparison of fire scar-interpolated burn interval maps (top row) for Last Chance site, Sierra Nevada, California, pixel value distribution for each map and mean pixel value (middle row), and annual area burned (bottom row) for IDW with the proportion of recording samples scarred threshold (left column), thin plate spline (TPS) with the proportion of recording samples scarred threshold (middle column), and TPS with a threshold of half the maximum interpolation value (right column).

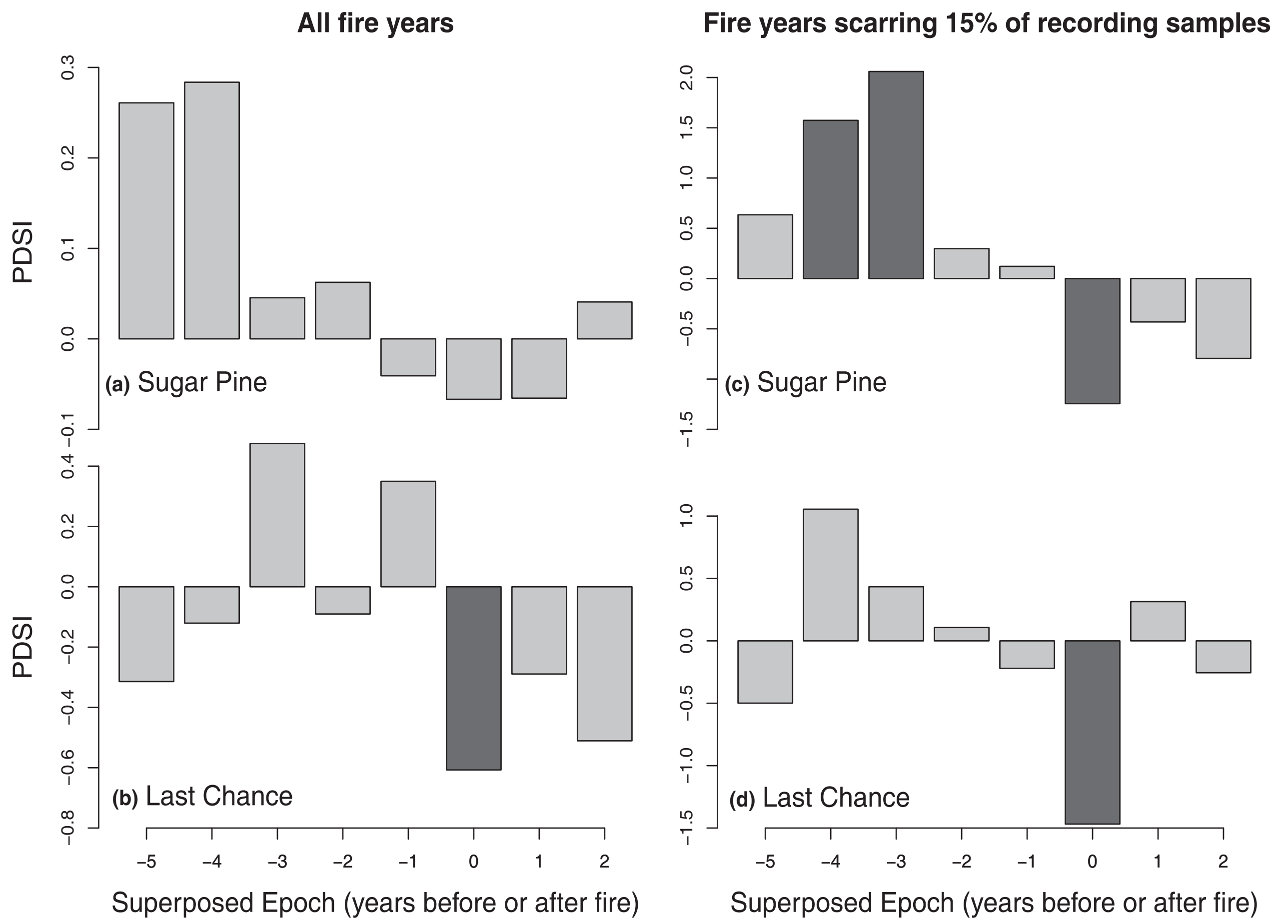


**Figure 5** Superposed Epoch Analysis (SEA) for reconstructed PDSI (Cook *et al.*, 1999) in LC and SP for 5 years before and 2 years after each fire year. Dark grey indicates a significant departure from mean PDSI values determined from bootstrapped confidence interval estimates (95%) based on 1000 Monte Carlo simulations. On the left, (a) and (b) show SEA for all fire years in each site (SP = 74 fire years, LC = 39 fire years). On the right, (c) and (d) show the SEA for only fire years where 15% or more of the recording samples were scarred (SP = 9 fire years, LC = 15 fire years).

contained point intervals of three or fewer years and 6% of all the fire intervals for the entire site were shorter than 4 years (Table 1). This is likely a conservative estimate of point fire frequency as many fires of such short intervals likely did not re-scar existing recorder trees (Stephens *et al.*, 2010). We believe these widespread and extremely short fire intervals represent a signal of Native American burning (Finney & Martin, 1992) and provide a likely explanation for the decoupling of fire–climate relationships in the SP site.

However, even in the presence of a high level of anthropogenic burning, a climate-fire relationship is still detectable in the SP site when only fire years that scarred at least 15% of the recording samples are used for SEA analysis ($n$ = 9 fire years, Fig. 5). During these years, there is a significant reduction in the PDSI, which likely resulted in more extensive fires and/or a higher likelihood for trees to form fire scars.

### Aspect and fire frequency

When there are discreet features that separate slope aspects (such as steep ridges or large rivers) that can effectively limit the spread of fire, then differences in fire frequency are more likely between varying aspects or topographic facets (Heyerdahl *et al.*, 2001; Taylor & Skinner, 2003). The current study sites did not have extreme terrain features that would likely limit fire spread, making it unsurprising that differences in fire frequency between slope aspects were not detected (Scholl & Taylor, 2010).

### Edge effects

There was no evidence of extreme edge effects for any of the interpolation methods examined in this study. Instead, trends were idiosyncratic and seemed to depend heavily on the perimeter to area ratio of the study areas. For instance, the LC site was a more elongated watershed and as a result had a 19% larger perimeter to area ratio than SP (0.00087 $m^{-1}$ vs. 0.00073 $m^{-1}$ respectively). As a result, in the LC site, all slopes for all interpolation methods were significantly different from zero for both SMFI and fire rotation period, whereas only half of the slopes were different from zero in the SP site (Fig. 6).

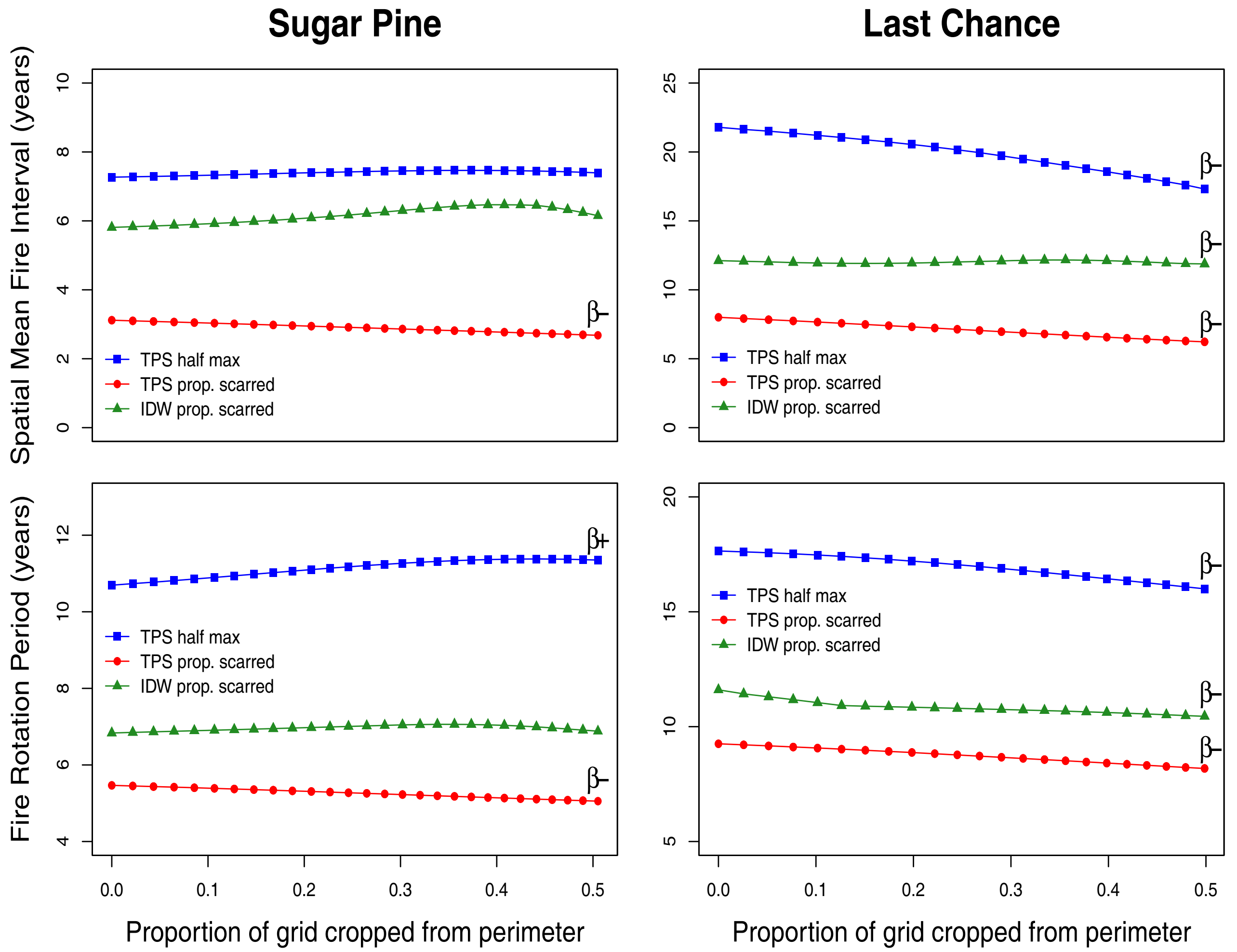


**Figure 6** Assessing the edge effects of the three interpolation methods on SMFI and fire rotation period in both SP and LC. 'β +' indicates a significantly positive slope when points are fit to a linear regression equation and 'β –' indicates a significantly negative slope when points are fit to a linear regression equation. The absence of notation on a line indicates that the regression equation slope is not significantly different from zero.

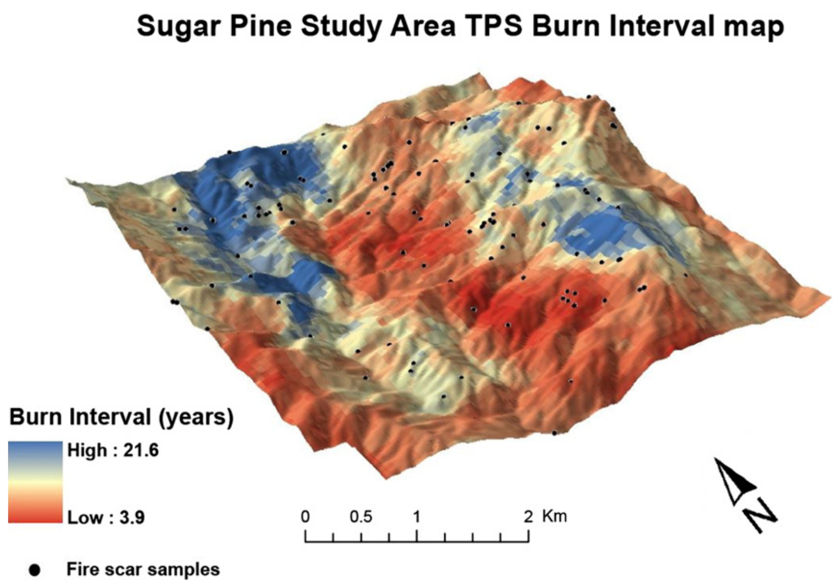


**Figure 7** Spatial mean fire interval map for the TPS half-maximum threshold interpolation method overlaid on topography for the Sugar Pine study site, Sierra Nevada, California. Fire scar sample locations are shown with black dots.

Edge effects were likely buffered by the analysis period of 150 years, in which final burn interval maps and spatial fire regime statistics were the combination of many fire years (74 fire years in the SP site and 39 in LC). Overall, edge effects did not seem to present major problems for any of the interpolation methods employed in this study, although this topic warrants further study, especially as it relates to the relative location of recording samples, the perimeter to area ratio of the study area, and the length of the analysis period and number of fire years.

Spatially explicit fire frequency reconstruction holds great promise for better understanding processes that build spatial heterogeneity, especially in forests that have been greatly homogenized from logging and fire suppression. The methods employed in this study can be applied to any fire scar collection that includes geographical locations and could prove valuable to inform resilience-based ecosystem management.

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## REFERENCES

Agee, J.K. (1993) *Fire ecology of Pacific Northwest forests*. Island Press, Washington, DC.

Agee, J.K., Finney, M. & De Gouvenain, R. (1990) Forest fire history of Desolation Peak, Washington. *Canadian Journal of Forest Research*, **20**, 350–356.

Anderson, M.K. (2005) *Tending the wild: native American knowledge and the management of California's natural resources*. University of California Press, Berkeley, CA.

Bonan, G. (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*, **320**, 1444.

Collins, B.M. & Stephens, S.L. (2007) Fire scarring patterns in Sierra Nevada wilderness areas burned by multiple wildland fire use fires. *Fire Ecology*, **3**, 53–67.

Collins, B.M. & Stephens, S.L. (2010) Stand-replacing patches within a 'mixed severity' fire regime: quantitative characterization using recent fires in a long-established natural fire area. *Landscape Ecology*, **25**, 927–939.

Cook, S.F. (1976) *The population of the California Indians, 1769–1970*. University of California Press, Berkeley, CA.

Cook, E.R., Meko, D.M., Stahle, D.W. & Cleaveland, M.K. (1999) Drought reconstructions for the continental United States. *Journal of Climate*, **12**, 1145–1162.

Craven, P. & Wahba, G. (1978) Smoothing noisy data with spline functions. *Numerische Mathematik*, **31**, 377–403.

Cressie, N. (1993) *Statistics for spatial data*. John Wiley and Sons. Inc., New York.

Dieterich, J.H. & Swetnam, T.W. (1984) Dendrochronology of a fire scarred ponderosa pine. *Forest Science*, **30**, 238–247.

Evett, R., Franco-Vizcaino, E. & Stephens, S.L. (2007) Comparing modern and past fire regimes to assess changes in prehistoric lightning and anthropogenic ignitions in a Jeffrey pine-mixed conifer forest in the Sierra San Pedro Martir, Mexico. *Canadian Journal of Forest Research*, **37**, 318–330.

Farris, C.A., Baisan, C.H., Falk, D.A., Yool, S.R. & Swetnam, T.W. (2010) Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecological Applications*, **20**, 1598–1614.

Finney, M.A. & Martin, R.E. (1992) Short fire intervals recorded by Redwoods at Annadel State Park, California. *Madroño*, **39**, 251–262.

Franklin, J. (1998) Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, **9**, 733–748.

Freedman, M.P. (2013) *Willow Creek History: Tales of Cow Camps, Shake Makers and Basket Weavers*. The History Press, Charleston, SC.

Fry, D.L. & Stephens, S.L. (2006) Influence of humans and climate on the fire history of a Ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. *Forest Ecology and Management*, **223**, 428–438.

Furrer, R., Nychka, D. & Sain, S. (2009) Fields: *Tools for spatial data*. Rpackage version 6.

Grissino-Mayer, H.D. (2001) FHX2–Software for analyzing temporal and spatial patterns in fire regimes from tree rings. *Tree-Ring Research*, **57**, 115–124.

Hassan, R., Scholes, R. & Ash, N. (2005) *Ecosystems and human well-being: current state and trends*, Vol. 1. Island Press, Washington, DC.

Heinselman, M.L. (1973) Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research*, **3**, 329–382.

Helzer, C.J. & Jelinski, D.E. (1999) The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications*, **9**, 1448–1458.

Hessl, A., Miller, J., Kernan, J., Keenum, D. & McKenzie, D. (2007) Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. *The Professional Geographer*, **59**, 87–104.

Heyerdahl, E.K., Brubaker, L.B. & Agee, J.K. (2001) Spatial controls of historical fire regimes: a multiscale example from the interior west, USA. *Ecology*, **82**, 660–678.

Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, **4**, 1–23.

Johnston, H. (1984) *The whistles blow no more: railroad logging in the Sierra Nevada 1874–1942*. Tans-Anglo Books, Glendale, California.

Kernan, J.T. & Hessl, A.E. (2010) Spatially heterogeneous estimates of fire frequency in ponderosa pine forests of Washington, USA. *Fire Ecology*, **6**, 117–135.

Kilgore, B.M. & Taylor, D. (1979) Fire history of a Sequoia mixed conifer forest. *Ecology*, **60**, 129–142.

Kou, X. & Baker, W.L. (2006) A landscape model quantifies error in reconstructing fire history from scars. *Landscape Ecology*, **21**, 735–745.

Landres, P.B., Morgan, P. & Swanson, F.J. (1999) Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications*, **9**, 1179–1188.

Mallek, C., Safford, H., Viers, J. & Miller, J. (2013) Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere*, **4**, article 153.

Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications*, **17**, 2145–2151.

North, M. (2012) *Managing Sierra Nevada forests*. USDA Forest Service General Technical Report PSW-GTR-237, Albany, CA.

Parsons, D.J. & DeBenedetti, S.H. (1979) Impact of fire suppression on a mixed-conifer forest. *Forest Ecology and Management*, **2**, 21–33.

Pebesma, E.J. (2004) Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, **30**, 683–691.

R Development Core Team (2010) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Scholl, A.E. & Taylor, A.H. (2010) Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications*, **20**, 362–380.

Sibold, J.S., Veblen, T.T. & Gonzalez, M.E. (2006) Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography*, **33**, 631–647.

Skinner, C.N., Abbott, C.S., Fry, D.L., Stephens, S.L., Taylor, A.H. & Trouet, V. (2009) Human and climatic influences on fire occurrence in California's North Coast Range, USA. *Fire Ecology*, **5**(3), 73–96.

Stephens, S.L. & Collins, B.M. (2004) Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northwest Science*, **78**, 12–23.

Stephens, S.L., Fry, D.L., Collins, B.M., Skinner, C.N., Franco-Vizcaíno, E. & Freed, T.J. (2010) Fire-scar formation in Jeffrey pine –mixed conifer forests in the Sierra San Pedro Mártir, Mexico. *Canadian Journal of Forest Research*, **40**, 1497–1505.

Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L. & Meyer, M.D. (2015) Historical and current landscape-scale ponderosa pine and mixed-conifer forest structure in the Southern Sierra Nevada. *Ecosphere*, **6**(5) art 79.

Stokes, M.A. & Smiley, T.L. (1968) *An introduction to tree-ring dating*. University of Chicago Press, Chicago, IL.

Swetnam, T.W. (1993) Fire history and climate change in giant sequoia groves. *Science*, **262**, 885–888.

Swetnam, T.W., Farella, J., Roos, C.I., Liebmann, M.J., Falk, D.A. & Allen, C.D. (2016) Multiscale perspectives of fire, climate and humans in western North America and the Jemez Mountains, USA. *Philosophical Transactions of the Royal Society of Biology*, **371**, 20150168.

Taylor, A.H. & Beaty, R.M. (2005) Climatic influences on fire regimes in the northern Sierra Nevada Mountains, Lake Tahoe Basin, Nevada, USA. *Journal of Biogeography*, **32**, 425–438.

Taylor, A.H. & Skinner, C.N. (2003) Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications*, **13**, 704–719.

Wilson, N.L. & Towne, A.R. (1978) Nisenan. *Handbook of North American Indians*, Vol. 8 (ed. by R.F. Heizer), pp. 387–397. Smithsonian Institution Press, Washington, DC.

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