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Fire Ecology

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Fire history in northern Sierra Nevada mixed conifer forests across a distinct gradient in productivity

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Abstract

Background Understanding the role of fire in forested landscapes is fundamental to fire reintroduction efforts, yet few studies have examined how fire dynamics vary in response to interactions between local conditions, such as soil productivity, and more broadscale changes in climate. In this study, we examined historical fire frequency, seasonality, and spatial patterning in mixed conifer forests across a distinct gradient of soil productivity in the northern Sierra Nevada. We cross-dated 46 different wood samples containing 377 fire scars from 6 paired sites, located on and off of ultramafic serpentine soils. Forests on serpentine-derived soils have slower growth rates, lower biomass accumulation, and patchier vegetation than adjacent, non-serpentine sites. Due to these differences, we hypothesized that historical fire frequency and spatial extent would be reduced in mixed conifer forests growing on serpentine soils.

Results Fire scars revealed a history of frequent fire at all of our sites (median composite interval: 6–22.5 years) despite clear differences in soil productivity. Fire frequency was slightly shorter in more productive non-serpentine sites, but this difference was not consistently significant within our sample pairs. While fires were frequent, both on and off of serpentine, they were also highly asynchronous, and this was largely driven by differing climate–fire relationships. Fires in more productive sites were strongly associated with drought conditions in the year of the fire, while fires in less productive serpentine sites appeared to be more dependent on a cycle of wet and dry conditions in the years preceding the fire. Widespread fires that crossed the boundary between serpentine and non-serpentine were associated with drier than normal years.

Conclusions In our study, fine-scale variation in historical fire regime attributes was linked to both bottom-up and top-down controls. Understanding how these factors interact to create variation in fire frequency, timing, and spatial extent can help managers more effectively define desired conditions, develop management objectives, and identify management strategies for fire reintroduction and forest restoration projects.

Keywords Dendrochronology, Fire–climate interactions, Fire ecology, Fire return intervals, Fire regime, Fire scars, Soil productivity, Serpentine, Ultramafic

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Resumen

Antecedentes El entender el rol del fuego en paisajes forestales es fundamental en los esfuerzos destinados a su reintroducción; sin embargo, pocos estudios han examinado cómo la dinámica del fuego varia en respuesta a las interacciones entre condiciones locales, como la productividad del suelo, y cambios a gran escala en el clima. En este estudio, examinamos la frecuencia histórica del fuego, su estacionalidad, y patrones espaciales, en bosques mixtos de coníferas a lo largo de un gradiente de distinta productividad del suelo en el norte de la Sierra Nevada. Para ello, cruzamos datos de 46 muestras de leños conteniendo 377 cicatrices de fuego en seis sitios apareados ubicados dentro y fuera de suelos serpentinos ultramórficos. Los bosques en los suelos derivados de serpentinas tuvieron una tasa de crecimiento menor, menos acumulación de biomasa y vegetación en parches, que los suelos de sitos adyacentes no serpentinos. Debido a esas diferencias, hipotetizamos que la frecuencia histórica y la extensión espacial de los incendios puede ser más reducida en bosques mixtos de coníferas que crecen en suelos serpentinos.

Resultados Las cicatrices revelaron una historia de fuegos frecuentes en todos los sitios (el intervalo de la mediana compuesta fue de entre 6 y 22,5 años), a pesar de las claras diferencias en la productividad de los suelos. La frecuencia de fuegos fue ligeramente más corta en sitios no serpentinos más productivos, aunque esta diferencia no fue consistentemente significativa dentro de los pares analizados. Cuando los fuegos fueron frecuentes, tanto en suelos serpentinos como en no serpentinos, se presentaron también como altamente asincrónicos, y esto fue motivado mayoritariamente por diferencias en la relación entre fuego y clima. Los fuegos en los sitios más productivos estuvieron fuertemente asociados con las condiciones de sequía en el año de ocurrencia del fuego, mientras que los fuegos en sitios serpentinos menos productivos parecen ser más dependientes de ciclos de condiciones de sequía y humedad en los años precedentes a los fuegos. Los fuegos que se expandieron y cruzaron los bordes entre suelos serpentinos y no serpentinos se asociaron con períodos más secos que en años normales.

Conclusiones En nuestro estudio, la variación a escala fina en los atributos de los regímenes históricos de fuego, estuvo ligada a las variaciones de control de los tipos *bottom-up*y *top-down*. El entender cómo esos factores interactúan para crear variaciones en la frecuencia del fuego, el tiempo de ocurrencia, y su extensión espacial, puede ayudar a los gestores a definir de una manera más efectiva las condiciones deseadas, desarrollar objetivos de manejo, e identificar estrategias para la reintroducción del fuego y en proyectos de restauración.

Introduction

Understanding the factors that influence and control fire regime attributes is fundamental to fire reintroduction efforts in montane forests in the western USA. Land managers and scientists often use fire regime classifications as a way to broadly characterize and communicate predominant patterns in fire frequency, seasonality, and extent within a specific vegetation type or area. Yet, these characteristics can vary widely within individual forest stands and across landscapes, influenced by local site conditions (e.g., topography, soils, fuel availability, ignitions) and broadscale changes in climate (Beaty and Taylor 2001, Swetnam and Baison 2003).

Bottom-up controls, like topography, vegetation type, and disturbance history exert a strong influence on fire regime characteristics by impacting the amount, continuity, and availability of fuels (Taylor 2000; Heyerdahl et al. 2001; Stephens 2001; Taylor and Skinner 2003; Beaty and Taylor 2008; Gill and Taylor 2009; Ireland et al. 2012). For example, variation in slope and aspect can influence fire patterns by affecting vegetation type and abundance, fuel moisture, and flammability and by creating barriers to fire spread (Agee 1993; Taylor and Skinner 2003; Beaty and Taylor 2008). Basic physiological differences among different compositions of tree species (e.g., needle type and litter production) can influence fuel flammability and fire spread, resulting in stark differences in fire frequence and severity among forest types (Taylor 2000; Gill and Taylor 2009). Mosaics of past fires and forest treatments can limit the extent and severity of subsequent fires by reducing the abundance and availability of fuels to burn (Collins et al. 2009; Ireland et al. 2012; Stephens et al. 2023). Bottom-up controls can also interact, with one another as well as with broader regional factors (i.e., climate, regional drought), resulting in variation in fire occurrence and spread at both local and landscape scales (Skinner et al. 2009).

Site productivity (defined as the capacity to accumulate biomass) plays an important role in determining the amount, continuity, and availability of fuel to burn. However, the influence of productivity on fire regime attributes is not well defined, particularly in montane forests. Theory predicts that more frequent or intense disturbances may be required in highly productive ecosystems to minimize competition and maximize species diversity, while less frequent or lower intensity disturbance may be sufficient in sites with lower productivity (Huston 1979; Kondoh 2001). A positive relationship between productivity and disturbance has been documented in Mediterranean shrublands, with less productive sites experiencing fewer and less severe fires than more productive sites (Safford and Harrison 2004; Pausas and Bradstock 2007). This link between fire and productivity has been attributed to fuel production and continuity, with faster accumulation of biomass on more productive sites supporting shorter intervals between fires (Safford and Harrison 2004).

Climate is one of the primary top-down drivers of fire occurrence and spatial patterns in western forests (Swetnam and Baisan 2003; Westerling et al. 2003; Collins et al. 2006). Climatic variability, which can often be driven by distant teleconnections such as El Nino-Southern Oscillation, influences regional moisture and temperature patterns and has been linked to widespread fire occurrence (Swetnam and Baisan 2003). Fire and climate reconstructions in dry pine forests of the southwestern USA have documented a canonical fire–climate relationship with wet years linked to subsequent dry years with more fire (Swetnam and Betancourt 1998; Brown et al. 2008; Roos et al. 2022). In these xeric forest types, antecedent wet conditions were considered necessary to produce sufficient fuels, while dry conditions in the year of the fire were critical for fire ignition and spread. This wet-then-dry pattern has also been associated with widespread fire years in the mixed conifer forests of the Sierra Nevada (Stephens and Collins 2004; Taylor and Beaty 2005; Taylor and Scholl 2012); however, it does not appear as consistent across individual study areas as it is in the southwestern USA. Several other historical fire reconstructions in the Sierra Nevada have only found strong linkages to dry conditions in the year of the fire (Swetnam and Baisan 2003; Moody et al. 2006; Gill and Taylor 2009). These inconsistent fire–climate relationships could be due to differing understory fuel types (grass/herbaceous vs. shrub/woody), for which lighter fuel types would be more responsive to the wet then dry cycles (Collins et al. 2006). Another factor contributing to these inconsistencies across regions/study areas is overall site productivity. Increased antecedent moisture may not be as important in more productive forest types because there is generally sufficient fuel to support fire spread (Heyerdahl et al. 2001).

Forests growing on distinctly different soils that also have old trees and remnant tree material provide a unique opportunity to examine the relative importance of top-down and bottom-up controls on historical fire regimes. In the Sierra Nevada of California, mixed conifer forests occur across a broad gradient of elevation, aspect, and soil types, including less productive serpentine soils. Serpentine soils are notable for their low levels of essential nutrients (calcium, potassium, nitrogen, phosphorous), high concentrations of heavy metals (magnesium and iron), and toxic trace elements (chromium, nickel, cobalt) (Kruckeburg 1984; Alexander 2007). Compared to more productive sites, mixed conifer forests growing on serpentine soils are generally characterized by slower growth rates, lower biomass accumulation, and more open and variable vegetation structure (Kruckeburg 1984; Safford and Harrison 2008; Safford and Mallek 2010; DeSiervo et al. 2015). Serpentine sites tend to favor certain tree and understory species over others (Kruckeburg 1984), which vary in litter compaction and drying rates (Banwell et al. 2013) as well as flammability (Fonda et al. 1998; Stevens et al. 2020). Nutrient-limited serpentine soils are also less likely to experience rapid shifts in plant composition in response to variation in climate (Briles et al. 2011). In California, serpentine outcrops range in size from a few square meters to hundreds of square kilometers (Grace et al. 2007), resulting in numerous places where serpentine soils contact more productive non-serpentine soils. Most of the research in these transitional zones has focused on quantifying changes in abiotic or biotic factors, while the influence that these abrupt changes in soil have on fuels and disturbance processes like fire has received very little scientific attention (Boyd et al. 2009).

In this study, we examine fire regime attributes in mixed conifer forests growing across a gradient of soil productivity. Our study area encompasses the contact zone between serpentine and non-serpentine soils, which can have considerable variation in soil chemistry and plant productivity (Boyd et al. 2009). To identify differences in soil productivity within our study area, we first measured soil nutrient composition within our sampling sites. We hypothesized that serpentine soils would have substantially lower concentrations of essential soil nutrients (i.e., calcium, potassium, nitrogen, phosphorous) and higher concentrations of heavy metals (magnesium) than adjacent non-serpentine sites, even when sites were situated in close proximity. We then used fire scar analysis to evaluate differences in fire regime attributes (frequency, seasonality, and spatial patterns) between sites with differing levels of soil fertility. We hypothesized that areas with lower soil fertility, which would historically have been characterized by lower biomass, slower forest growth rates, and more patchy vegetation (Kruckeburg 1984; Safford and Harrison 2008; Safford and Mallek 2010), would have experienced less frequent and more variable fires.

Methods

Study area

Our study sites are located near the community of Meadow Valley on the Plumas National Forest in the northern Sierra Nevada of California (Fig. 1). The climate is characterized as Mediterranean, with a warm and dry summer period that extends into the fall. Most of the precipitation in the study area falls during the winter months, with mean annual precipitation totaling approximately 1060 mm (Abatzoglou 2013). Mean monthly temperatures range from a minimum of 2.2 °C in December to a maximum of 20.3 °C in July (Abatzoglou et al. 2009).

The study sites are situated on the western edge of some of the most extensive ultramafic terrain in the northern Sierra Nevada (Fig. 1). Soils derived from ultramafic rocks, broadly referred to as serpentine soils, are characterized by their unique chemistry—specifically high levels of iron and magnesium and relatively low levels of calcium (Alexander 2007). Within our study area, soils range from well-drained, productive Alfisols (suborder: Xeralfs) to less productive, strongly leached Ultisols (suborder: Xerults) (USDA Natural Resources Conservation Service 2023).

The vegetation in our study sites is predominantly conifer forest with varying mixtures of tree species. Stands growing on non-serpentine soils have a wider diversity

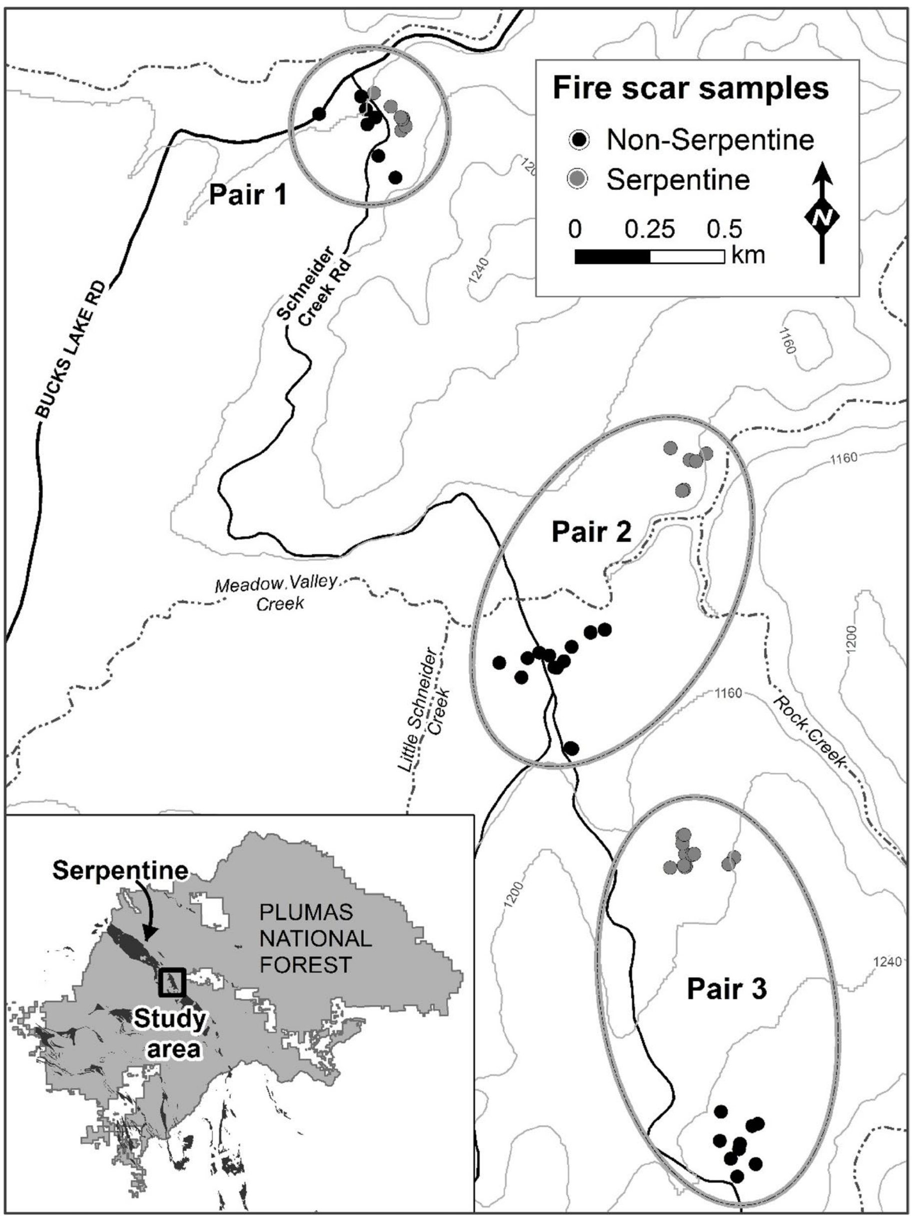

Fig. 1 Fire scar sample sites within three paired sites on the Plumas National Forest in northern California

of tree species, including a mixture of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), sugar pine (*Pinus lambertiana* Dougl.), white fir (*Abies concolor* [Gordon & Glend.] Lindl. ex Hildebr.), incense cedar (*Calocedrus decurrens* [Torr.] Florin), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), and California black oak (*Quercus kelloggii* Newb.). Many of these species are absent in adjacent forest stands growing on serpentine soils, which are primarily composed of Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), incense cedar, and Douglas fir. Although forest structure has changed dramatically over the past century due to a combination of fire exclusion and past harvest, compositional differences between forests on and off serpentine remain apparent (Fig. 2, Briles et al. 2011). Structural differences are also evident with mixed conifer forests on serpentine soils generally having fewer trees, lower biomass, and lower surface fuels than adjacent non-serpentine forests (DeSiervo et al. 2015).

The landscape within our study area has been managed in both the distant and recent past. The Mountain Maidu have lived in this area for thousands of years and used fire to enhance young shoot growth for basket weaving, to clear hunting grounds, enhance California black oak stands, and reduce fire risk (Dixon 1905; Young 2003; Stephens et al. 2023). More recently, forest thinning occurred in the area between 2003 and 2006, and small non-commercial trees and associated fuels were piled and burned (USDA Forest Service 2020). No wildfires have been recorded within the boundary of our study since 1900, when written records began.

Our study included three pairs of sites, each containing one sampling site established on serpentine soils and one adjacent sampling site on non-serpentine soils (Fig. 1). Sites were all located within an area of approximately 2 km^2, ranging in elevation from 1090 to 1220 m. The distance between sampling sites within a pair ranged from 22 m to over 800 m and the area sampled within each site ranged from 0.6 to 7.8 ha (Table 1). Paired sites were selected to represent similar aspects, topographic positions, and elevations.

Field sampling

In June 2020, we surveyed each of the six sites for fire-scarred trees, stumps, and logs. Samples were collected opportunistically to maximize the completeness of fire dates and were based on the presence of multiple well-preserved fire scars (Van Horne and Fulé 2006). During sample collection, Global Positioning System (GPS) coordinates were recorded for each sample and subsequently used to define the boundary of each sampling site.

We used a chainsaw to cut wedges from 57 fire-scarred trees, stumps, and logs. We focused our sampling on

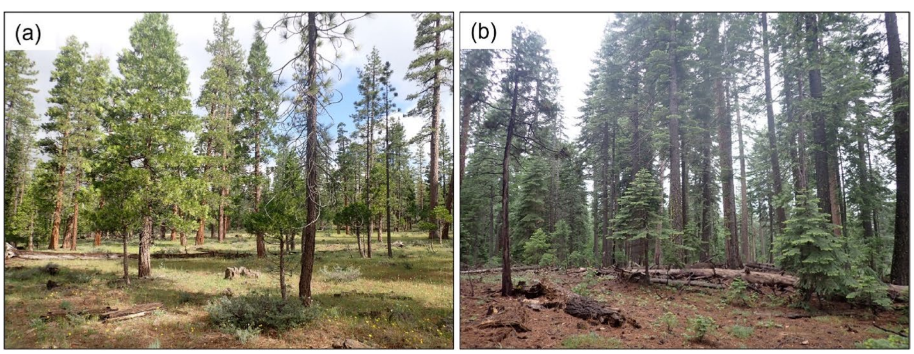

Fig. 2 Example of contemporary forest conditions in (**a**) serpentine and (**b**) non-serpentine sites within a pair

Table 1 Mean site characteristics of sampled areas. The area of each site was estimated within a perimeter defined by the sampled trees. Minimum distance represents the shortest distance between paired sites

Pair	Site	Area (ha)	Samples	Elevation (m)	Slope (%)	Aspect	Min distance (m)
1	Non-serpentine 1	3.3	7	1103	15	North	22.2
	Serpentine 1	0.6	6	1106	21	West	
2	Non-serpentine 2	7.8	7	1113	10	North	511.5
	Serpentine 2	1.3	7	1108	16	East	
3	Non-serpentine 3	2.5	8	1242	26	West	805.2
	Serpentine 3	1.9	11	1162	11	West	

ponderosa pine (37% of samples), Jeffery pine (22%), and incense cedar (41%). Samples were sanded and polished to a high sheen and cross-dated using standard dendrochronological techniques (Stokes and Smiley 1977).

To evaluate differences in productivity between study sites, we collected soil samples from five plots (0.04 ha) that were randomly placed within each of our six sampling sites (30 plots total). At each plot, we collected approximately 150 g of soil at 5–15 cm depth, from four locations 12 m from plot center and combined them to create one sample per plot. Soil samples were air dried, sieved, and analyzed for organic matter (OM), cation exchange capacity (CEC), pH, nitrate (NO3-N), phosphorous (Olsen-P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) by the UC Davis Analytical Laboratory. At the same four sampling locations, the depth of the litter and duff was measured and combined to obtain an average for each plot.

Analysis

Soil productivity

To examine variation in soil nutrients across our study area we used non-metric multidimensional scaling (NMDS) ordination utilizing a Bray–Curtis dissimilarity index with the metaMDS function in the vegan package in R (Oksanen et al. 2022). Correlation coefficients of soil nutrients with both axis 1 and axis 2 scores were used to identify which nutrients were most responsible for the variation described in the ordination. We used a multivariate analysis of variance (ANOVA) procedure for distance matrices (ADONIS) based on 9999 restricted permutations of the data to compare soil characteristics among serpentine and non-serpentine sites. We also used ANOVA to test for differences in soil nutrients and litter and duff depth between serpentine and non-serpentine sites. Two variables, soil Ca and the ratio of Ca to Mg, were log transformed to meet the assumptions of the model. All statistical analyses were conducted in R (R Core Team 2019).

Fire seasonality

The intra-ring position of each fire scar was used to assign a calendar year to each tree ring and fire event in our sample. Each scar was assigned to the early-earlywood, middle-earlywood, late-earlywood, latewood, or ring boundary (dormant season) position (Caprio and Swetnam 1995). In this region, earlywood scars are generally considered to be fires that burned in spring and early summer, while latewood scars are classified as mid- to late-summer fires, and dormant (ring-boundary) scars are characterized as fires occurring in late summer or fall, when tree growth has ceased for the season (Stephens et al. 2018). Scars that could not have their season identified were classified as unknown.

Fire frequency

After the initial processing of fire scar data using the FXH2 software package (Grissino-Mayer 2001), we used the R package *burnr* (Malevich et al. 2018) to read and process fire scar samples across all sites and to develop fire chronologies for each site. To account for variability in fire frequency at different scales, and to facilitate comparisons with other fire history studies, we estimated fire return interval (FRI) using three different methods.

We first calculated the mean number of years between successive fires for individual trees, not including the origin-to-first scar interval. We then averaged the individual tree FRIs, which were weighted by their corresponding number of intervals, to obtain a point estimate of FRI for each site (Baker and Ehle 2001). Tree-based point estimates often yield longer FRIs due to the fact that individual fires may be missed in the fire-scar record of an individual tree. While trees are often charred by low-intensity surface fires, they are not always scarred due to a wide range of factors, including low fuel loads at the base of the tree, wind shifts, high fuel moisture, as well as variations in species-specific vulnerability to scarring and the lack of previous scars or wounds (Baker and Ehle 2001; Stephens et al. 2010). Given that the absence of a scar on an individual tree does not definitively indicate the absence of fire in that location for a given year, this metric can be seen as a more conservative estimate of fire extent (Swetnam et al. 2011).

To obtain a more comprehensive record of past fires, we also calculated composite fire histories for each site using (1) all fire-scarred trees (C00) and (2) a filter (C25) that required a minimum of (a) 25% recording trees scarred or (b) at least two fire-scarred trees for each fire year (whichever was smaller) (Dieterich 1980). The use of these filters reduces the likelihood of registering a tree scarred by means other than fire but may cause small fires with scars registered by a single tree to be missed. With each filtering method, we calculated the mean, median, minimum, and maximum fire return interval for each sampled site. We also calculated the Weibull median probability interval (WMPI), which represents the median value of a Weibull distribution. This flexible distribution is frequently used to represent the skewed distribution of fire return interval data (Grissino-Mayer 1999). We performed one-sample Kolmogorov–Smirnov (K-S) tests to evaluate goodness-of-fit between fire return interval data and the Weibull distribution at each site.

Our fire interval data were not normally distributed. To account for this, we used the non-parametric Kruskal–Wallis test to determine if FRI was different between the paired serpentine and non-serpentine types and among the six different sites in our study area. When significant differences were found, we used a pairwise Wilcoxon rank sum test to identify which group or groups varied from the others. We used a two-sample K–S test to compare the distribution of composite FRIs between serpentine and non-serpentine types.

Synchrony and patchiness

To evaluate the relative spatial extent of past fires, we compared the synchrony of fires between sites. To test this, we calculated Jaccard similarity (JS) as

$$JS = \frac{F_{11}}{F_{11} + F_{10} + F_{01}}$$

where F_{11} is the number of years in which two sites recorded a fire and F_{10} and F_{01} is the number of years when only one of the two sites recorded a fire. We used linear regression to evaluate the relationship between Jaccard similarity in the fire year and the geographic distance between each of the sites. Analysis of variance was used to investigate the amount of similarity in fire years between sites that occurred within and outside of study pairs. Jaccard similarity values were arcsine transformed to meet model assumptions. We limited individual analyses to the time period when sites had at least one recording tree and a minimum of one fire-scarred tree.

We estimated the degree of potential fire patchiness within a site by calculating the proportion of trees scarred (out of the total number of trees recording) in each fire year, recognizing that trees can also experience fire without scar formation. This is therefore a better indicator of relative fire patchiness, rather than actual fire patchiness, between sites. We tested for differences in percent scarred between non-serpentine and serpentine types, and among sites and pairs, using the non-parametric Kruskal–Wallis test.

Fire–climate relationships

In order to examine the relationship between fire occurrence and historical climate patterns, we applied a superposed epoch analysis (SEA) of the composite fire history dataset (Swetnam and Baisan 1996; Grissino-Mayer and Swetnam 2000) using the *burnr* package in R (Malevich et al. 2018). Climate data consisted of a reconstructed Palmer Drought Severity Index (PDSI) for our sampling area from 1632 to 1885 (the time period where trees were recording in at least two of the three pairs) and was extracted using the North American Drought Atlas web application (Cook et al. 2010). PDSI is a widely used index that integrates temperature, precipitation, and soil moisture to estimate drought severity (Palmer 1965). SEA isolates reconstructed PDSI values for each fire event year (year = 0), as well as the years prior to (lag years − 1 to − 6) and following (lags 1 to 4) the fire event. It calculates mean PDSI values for each time step and then assesses their statistical significance by comparing them to bootstrapped values from a random set of fire years (Grissino-Mayer and Swetnam 2000). To investigate the influence of climate on fire extent, we applied the SEA using fires that were limited to a single site and fires that burned more than one site. We also conducted separate SEA for serpentine and non-serpentine sites.

Results

Soil productivity

The NMDS ordination of soil nutrients resulted in a two-dimensional solution with a final stress of 0.017 and revealed a distinct clustering of serpentine and non-serpentine plots, driven almost entirely by the first axis (Fig. 3). Multivariate ANOVA on the underlying distance matrix indicated that this clustering was significant (pseudo-$F_{1,28} = 97.2$, $p = 0.001$). The variables with the strongest correlation with NMDS axis 1 were concentrations of K ($R^2 = 0.95$), Ca ($R^2 = 0.80$) and the ratio of Ca:Mg ($R^2 = 0.81$).

Serpentine sites had significantly higher concentrations of NO_3, Mg, and pH, and lower concentrations of K and Ca than non-serpentine sites in all pairs ($p \leq 0.001$). The ratio of Ca:Mg, a strong proxy for productivity (DeSiervo et al. 2015), was eight times greater on non-serpentine (5.1 ± 1.9) than serpentine sites (0.6 ± 0.6). Non-serpentine sites also had deeper litter and duff than serpentine sites ($F_{1,24} = 27.5$, $p < 0.001$).

Fire seasonality

We were able to estimate fire seasonality on 229 (61%) of the fire scars in our samples. Excluding unknown fire seasons, the highest proportion of scars were found in the latewood (37%) and dormant (39%) positions, indicating that most fires occurred after trees stopped growing. The remaining fire scars were found in the early-earlywood (2%), middle-earlywood (9%), and late-earlywood (13%) positions. The seasonality of fires in non-serpentine samples was very similar to serpentine samples, with almost equivalent proportions of earlywood fires (25% vs. 24%) and only slight differences in the proportion of fires documented in the latewood and dormant positions (Fig. 4).

Fire frequency

We cross-dated samples from a total of 46 trees from old stumps, logs, and standing snags within our six sampling sites. A total of 377 fire scars were identified, registering 94 different fire years in which at least one tree was scarred (Fig. 5). Fires spanned a period of over 500 years, with the earliest recorded fire occurring in 1402 and the

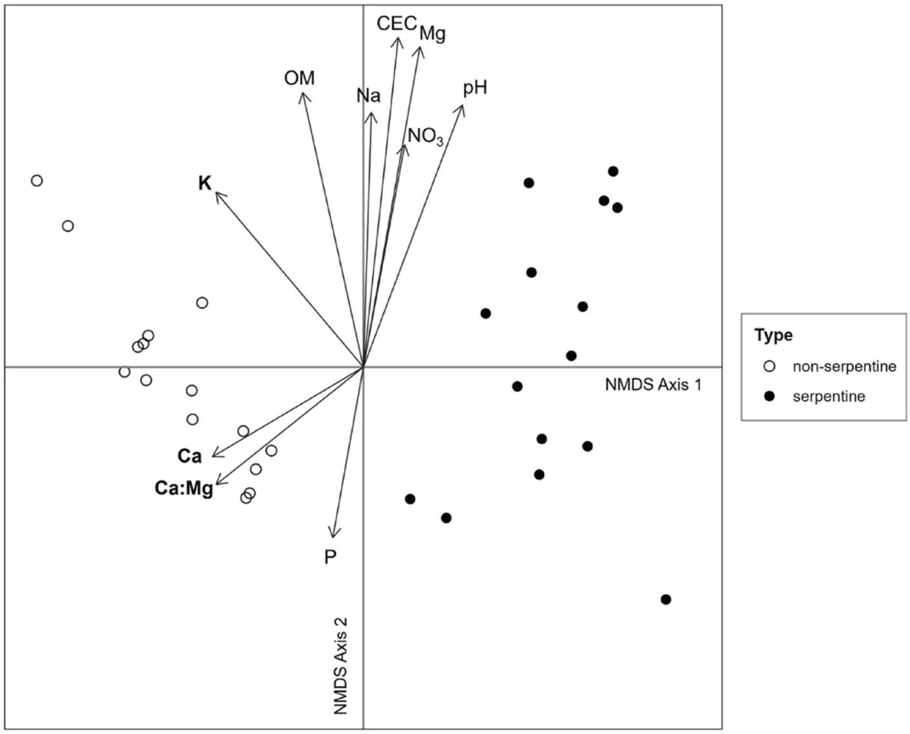

Fig. 3 Nonmetric multidimensional scaling (NMDS) ordination of soil nutrients from 30 plots on serpentine and non-serpentine sites. Arrows represent soil variables that were significantly correlated with NMDS axis 1 or 2. The length and direction of the arrows correspond to the magnitude and direction of correlation with the NMDS axes. Bold values had the highest correlation with NMDS axis 1

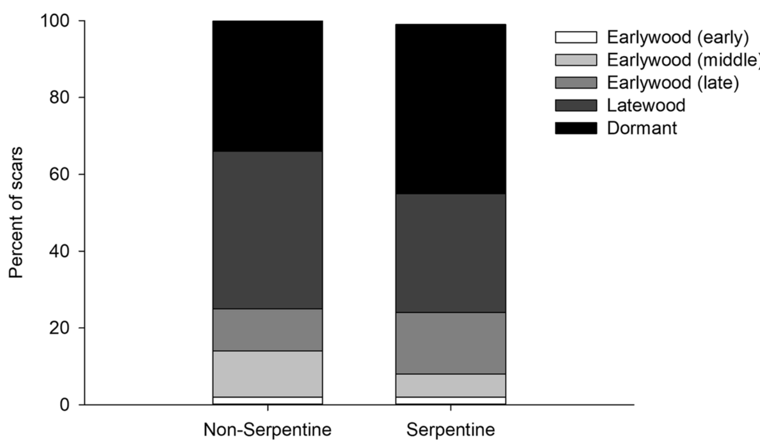

Fig. 4 Proportion of scars in the earlywood, latewood, and dormant (ring-boundary) position in non-serpentine ($n = 130$ scars) and serpentine ($n = 99$ scars) sites

latest in 1918. Most samples had a limited number of scars prior to the 1700s, and only one fire was recorded by one sample after 1893. The mean minimum age of sampled trees was estimated to be 258 years (range: 80–641; SD: 111 years); however, actual tree ages were underestimated because many samples did not reach pith due to wood decay.

We defined our period of analysis as 1632 to 1885, based on the criteria of having at least one tree recording at each site in two of our three pairs. These dates were selected to allow for statistical comparisons of fire intervals between paired serpentine and non-serpentine sites as well as among pairs. Within this time

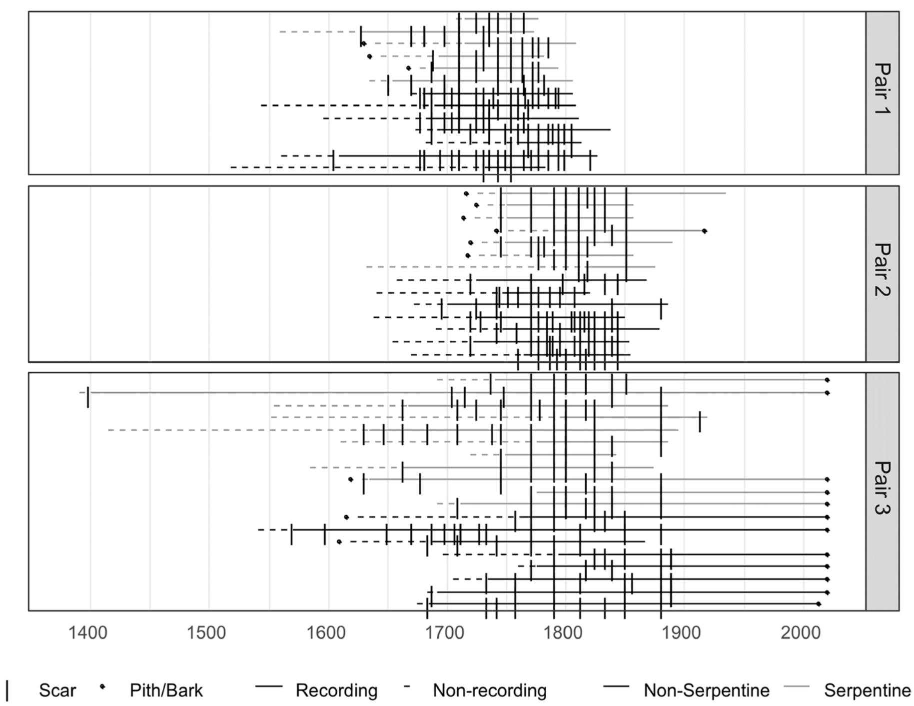

Fig. 5 Fire chronology for the three paired sites in our study area. Horizonal lines represent individual trees in serpentine (gray) and adjacent non-serpentine (black) sites. Solid lines indicate the period of time when a tree was recording (i.e., after it had been scarred at least once). Each vertical tick is a dated fire scar

period, we documented 88 different fire years in which at least one tree was scarred.

Fire was a frequent occurrence at all of our sites prior to the 1900s. Within our analysis period (1632–1885), estimates of mean and median FRI varied slightly depending on the composite criteria used. When all fire-scarred trees were used (i.e., no filter—C00), mean FRI ranged from 4.8 to 12 years, median FRI ranged from 4.5 to 12 years, and the Weibull median probability interval (WMPI) ranged from 4.4 to 11 years (Table 2). Composite FRIs lengthened when a 25% filter (C25) was applied, which is to be expected with the exclusion of isolated fire events that only scar a single tree. Mean FRI ranged from 7.1 to 25.1 years, median FRI ranged from 6 to 22.5 years, and WMPI ranged from 6.8 to 23.7 years (Table 2). Approximately 63% ($n=46$) of intervals were 10 years or less and 25% ($n=18$) were 5 years or less. Approximately 86% of the intervals ($n=63$) in our composite fire history were 20 years or less. The intervals had a similar

Table 2 Composite fire return interval (FRI) estimates from paired serpentine and non-serpentine sites. The analysis period for both estimate methods was 1632–1885. Superscript letters indicate significant differences between sites (i.e., a is significantly different than b, c). *WMPI* Weibull median probability interval

		Composite FRI (no filter)				Composite FRI (25% filter)[a]			
Pair	Site	Mean	Median	WMPI	Range	Mean	Median	WMPI	Range
1	Non-serpentine 1	4.8 [a]	4.5	4.4	1–15	7.1[a]	6	6.8	4–17
	Serpentine 1	7.5 [ab]	6	6.1	1–23	7.4[ab]	8	7	1–14
2	Non-serpentine 2	6.4 [a]	5	4.9	1–37	7.8[ab]	6	6.9	2–22
	Serpentine 2	9.6 [bc]	8	9	4–26	11.8[bd]	9	11.2	6–26
3	Non-serpentine 3	11 [bc]	9	10	2–25	17.9 [cd]	16	16.1	3–47
	Serpentine 3	12 [c]	12	11	2–29	25.1[c]	22.5	23.7	7–47

[a] Composite criteria: fires burned two or more trees or > 25% of recording trees

distribution on serpentine and non-serpentine sites (Kolmogorov–Smirnov, $D = 0.28$, $p = 0.07$), with more than half of the intervals recorded as 10 years or less (Fig. 6).

As expected, tree-based point FRIs were slightly longer than our composite FRIs. Mean FRI averaged 9.3 to 26.1 years across sites and median FRI ranged from 9.5 to 24.6 years (Table 3). We documented an average of eight scars per tree (range: 3–19). Approximately 41% ($n = 134$) of the intervals recorded on individual trees were 10 years or less and 10% ($n = 33$) were 5 years or less. Four of the samples recorded intervals of 2 years (2 intervals) and 3 years (4 intervals); all of these trees were on non-serpentine soils and three of the trees occurred in pair 2. An estimated 73% of the fire return intervals ($n = 238$) recorded on individual trees were 20 years or less.

Mean FRI trended slightly longer in serpentine sites compared to non-serpentine sites, but this difference was not consistently significant within our paired sites (Table 2, Fig. 7). When all fire-scarred trees were used to calculate the composite (C00), mean FRI in serpentine was significantly longer than non-serpentine, but only for the sites in pair 2 (Table 2). We found no significant difference in mean FRI between any of the paired serpentine and non-serpentine sites using the other methods of calculation (PFRI or C25). We did find differences among the three paired sites. Point and composite mean FRI (C00 and C25) was significantly longer in pair 3 compared to the other two pairs (Kruskal–Wallis, C00: $\chi^2 = 26.0$, $P < 0.001$; C25: $\chi^2 = 22.6$, $P < 0.001$).

Table 3 Individual tree fire return interval (Point FRI) estimates from paired serpentine and non-serpentine sites. The analysis period was 1632–1885. Superscript letters indicate significant differences between sites (i.e., a is significantly different than b, c)

		Point FRI (years)[a]		
Pair	Site	Mean	Median	Range
1	Non-serpentine 1	9.3 [a]	10.1	7.3–13
	Serpentine 1	14.0 [ab]	12.8	10.7–18.7
2	Non-serpentine 2	12.6 [abc]	9.5	8.2–37
	Serpentine 2	15.0 [b]	15.1	12.2–20.5
3	Non-serpentine 3	25.3 [c]	24.6	18.4–48.5
	Serpentine 3	26.1 [c]	22.8	19.2–62.8

[a] Average of individual tree Point FRIs, weighted by their corresponding number of intervals

Synchrony and patchiness

Of the 88 discrete fire years recorded by fire scars within our six sites between 1632 and 1885, 53 (60%) were recorded on only a single site, and 29 (33%) were recorded by only a single tree at a single site (Fig. 8.). Approximately two-thirds of these (35 fires) were recorded in a single non-serpentine site, while the remaining one-third (18 fires) were recorded in a single serpentine site. Our chronology identified 35 years that fire was recorded in more than one site. There were 4 years (1729, 1782, 1829, 1843) when fires were recorded in four of the six sites, and a single year (1776) when five of the six sites recorded a fire.

Similarity in fire years was significantly and negatively correlated with the distance between sites ($R^2 = 0.52$, $p = 0.002$), with sites in close proximity sharing the highest percentage of fire years (Fig. 9). We

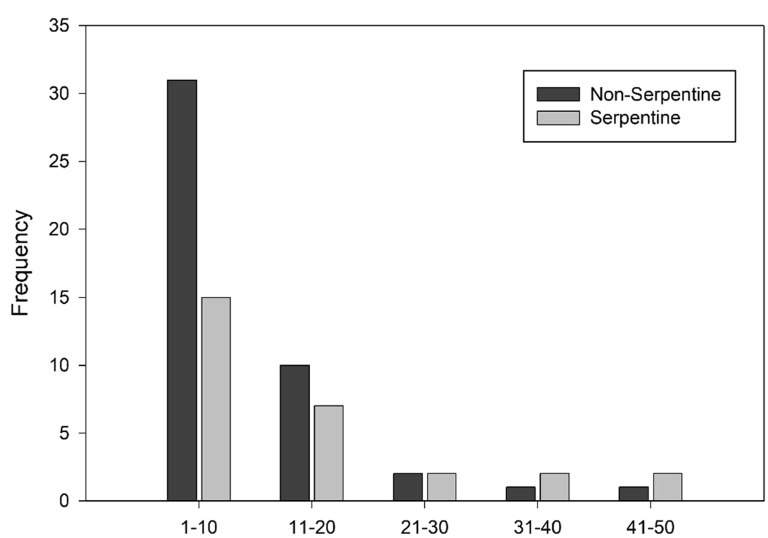

Fig. 6 The distribution of composite fire return intervals (C25) in serpentine and non-serpentine sites

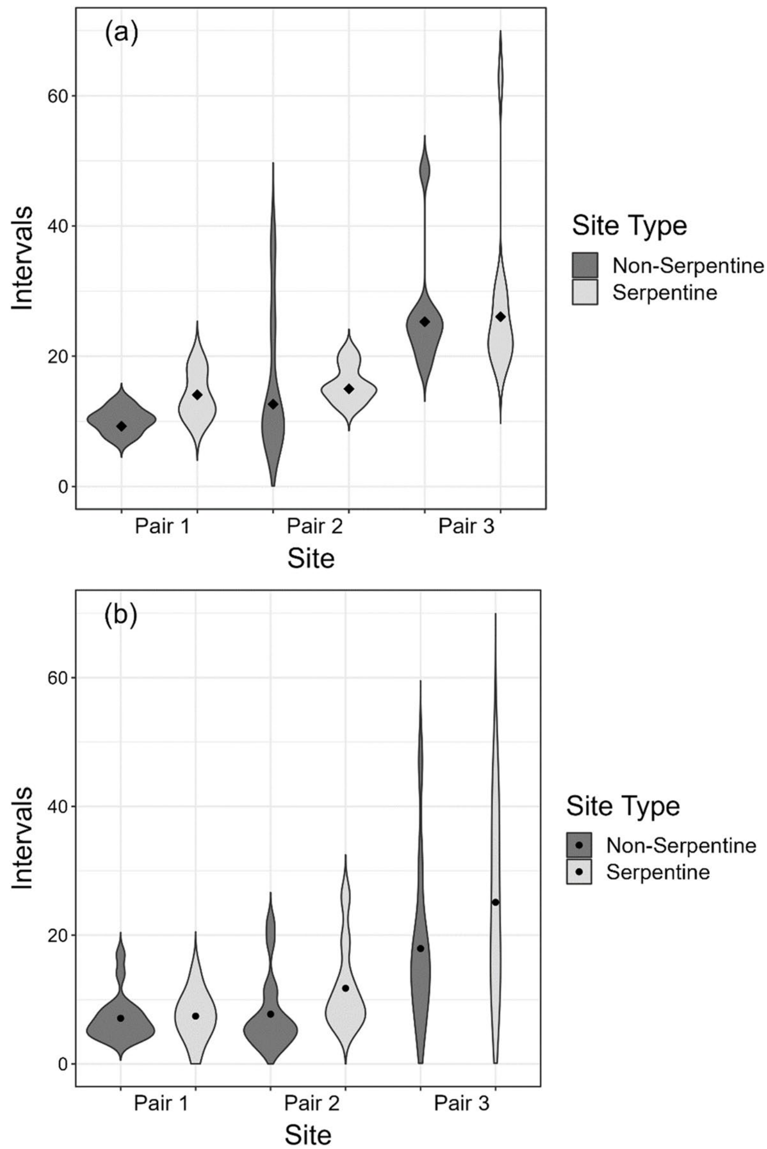

Fig. 7 Violin plots showing (**a**) point and (**b**) composite (25% filter) estimates of fire return interval in non-serpentine and serpentine sites within pairs. Points represent median values

found some evidence of synchrony in paired serpentine and non-serpentine sites, but this was likely due to the close proximity of these sites within study pairs (Fig. 9). The highest percentage of boundary-spanning fires (35%) was documented in pair 1, where sites were situated less than 25 m apart. The other two pairs shared 17% and 19% of fires, respectively. Fires crossed the boundary between serpentine and non-serpentine sites in 27 of the fire years; however, 10 of these boundary-spanning fires were part of larger fire events that were recorded in three or more sites. The proportion of trees scarred (out of total number recording) in each fire year was highly variable and did not differ significantly among sites, pairs, or between serpentine and non-serpentine forest types (Fig. 10).

Fire–climate relationships

Climatic conditions in our study area ranged from severe drought (PDSI: −5.8) to very wet (PDSI: 4.1) over the analysis period (1632–1885). In non-serpentine sites, fires were associated with drought conditions (negative PDSI) in the year of the fire (Fig. 11, $p < 0.01$). Fires in serpentine sites had a significant association with conditions prior to the fire but showed no relationship with PDSI in the year of the fire. Serpentine sites showed a significant relationship

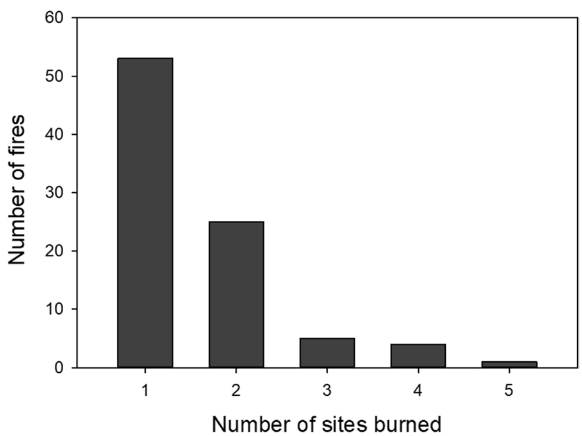

Fig. 8 The number of sites burned in each fire event between 1632–1885

with wet conditions (positive PDSI) five years prior to fire ($p < 0.05$), followed by strong drought conditions four years prior to the fire event ($p < 0.01$, Fig. 11.).

In years when fires were limited to a single site, we found no significant relationship between fire occurrence and PDSI. In contrast, more extensive fires (i.e., those recorded at more than one site), occurred in years that were drier than expected (Fig. 12).

Discussion

Despite clear differences in soil productivity, we did not detect consistent differences in mean FRI between serpentine and non-serpentine conifer forests. This similarity in fire frequency suggests that fire spread potential was similar in serpentine and non-serpentine sites, despite distinct differences in productivity, biomass accumulation, and fuel continuity. However, it is also important to recognize that these findings could, at least in part, be a function of sampling close to the edge of the serpentine soil contact zone, where fire spread from adjacent more productive forests might be more likely than the interior of large serpentine barrens, which generally have lower tree densities, more exposed rock, and discontinuous cover of grasses and shrubs.

The range of FRIs across our study area is comparable to those reported by other studies conducted in mixed conifer forests of the Sierra Nevada (Table 4). For example, Moody et al. (2006) used similar methods to derive median composite FRIs for non-serpentine mixed conifer forests on the Plumas National Forest that ranged between 5–15 years (using all scars) and 6–16.5 years (25% filter). The composite FRIs for serpentine sites in our study (median: 8–22.5 years) are also similar to those reported by Taylor and Skinner (2003) where documented median composite FRIs ranged from 8 to 15 years for mid-elevation Jeffrey pine sites growing on serpentine soils in the Klamath Mountains (Skinner et al. 2018). It is worth noting that fire-scar-based reconstructions

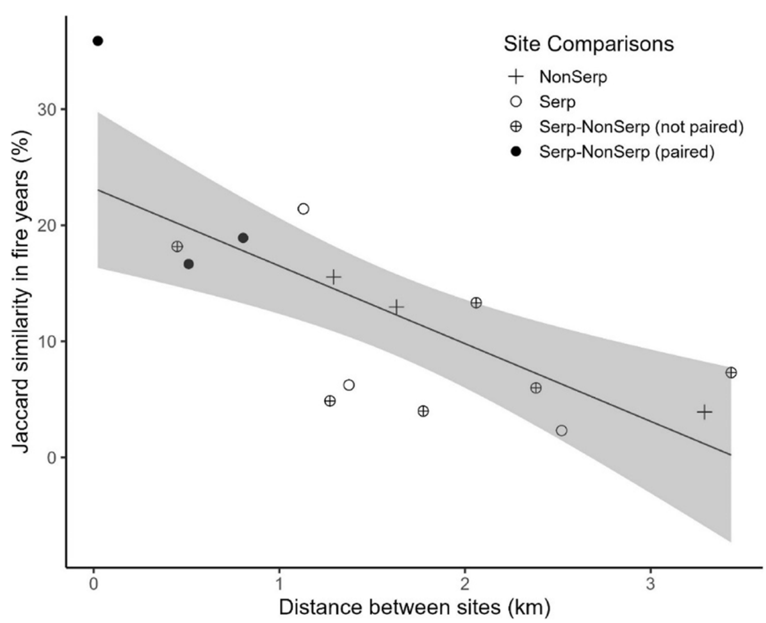

Fig. 9 Relationship between Jaccard similarity in shared fire events and the geographic distance between sites. Points represent pairwise comparisons between non-serpentine sites (NonSerp), serpentine sites (Serp), and serpentine and non-serpentine sites within a study pair and outside of a study pair

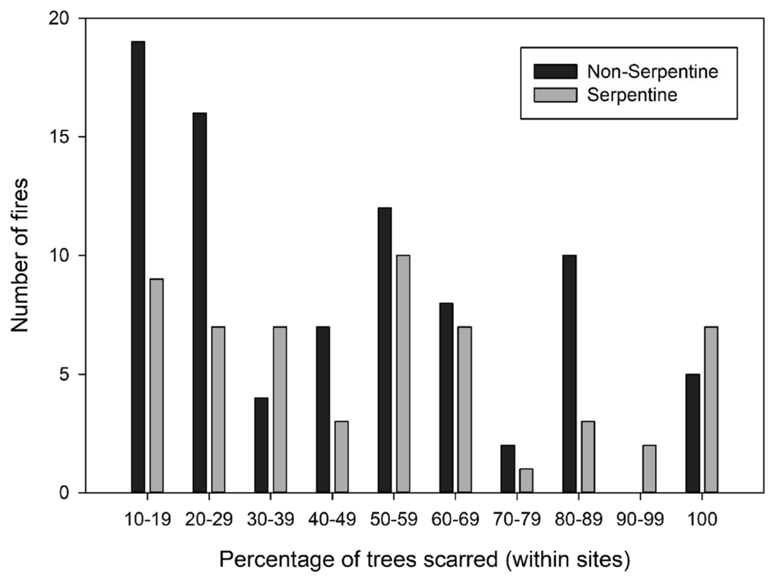

Fig. 10 The number of fires by the percentage of recording trees scarred within each of the six sampling sites. Values were weighted by the number of trees recording at the time of the fire

likely underestimate fire frequency due to a wide range of factors that influence tree scarring, such as fuel loading around the base of the tree, conditions at the time of the burn (e.g., wind, fuel moisture), topographic position of the tree, and the presence of previous scars or wounds (Baker and Ehle 2001; Collins and Stephens 2007; Farris et al. 2010; Stephens et al. 2010). Sampling intensity and sampling area can also influence FRI estimates, with more extensive sampling resulting in shorter composite FRIs as more fire events are captured (Stephens and Collins 2004; Baker and Ehle 2001). Taking these factors into consideration, historical fire frequency at our sites was likely greater than what we report here (see Table 4).

The highest proportion of scars in our study area were formed by fires that occurred between late-summer and early fall (Stephens et al. 2018), when tree growth had ceased for the season, similar to the seasonal timing reported for other studies in northern California (Taylor and Skinner 2003; Taylor and Beaty 2005; Fry and Stephens 2006; Moody et al. 2006; Gill and Taylor 2009; Vaillant and Stephens 2009; Stephens et al. 2023). The predominance of fires recorded in the latewood and dormant period was consistent among sites and between serpentine and non-serpentine soils (Fig. 4). This timing suggests that many fires in our study area likely occurred in the later part of the dry season and before the beginning of the wet season, as a result of ignitions from either lightning or cultural burning practices, at times when surface fuels were dry enough to promote fire spread (Moody et al. 2006; Stephens et al. 2023). The relatively high proportion of fires in the dormant season also includes the possibility that some Indigenous ignited fires could have occurred in the cooler months, when sunny conditions could have dried out surface fuels (Stephens et al. 2023).

More than half of the fires in our study area were recorded in only a single site, and a third were recorded by only a single tree within a site. Fires that burned beyond the boundary of a single site were most often recorded by sites in close proximity. Considering the relatively small size of our study area (approximately 2 km^2) and the close proximity of our paired sites, these findings suggest that, while frequent, historical fires may also have been relatively limited in extent. The finding that historical fires were unlikely to burn large portions of the study area in any given year may be due to the abrupt change in parent material and soil type, which have been shown to inhibit fire spread under normal climate conditions (Taylor and Skinner 2003). Scattered rock outcrops, perennial streams, and meadows, all of which occur within our study area, can also affect fire spread by breaking up fuel continuity. The frequency of locally limited fires, in combination with variation in topography and abrupt changes in soil type, would have historically resulted in a spatially diverse mosaic of vegetation types, sizes, and age classes (Hessburg et al. 2019). This pattern would have been self-reinforcing, as the patchwork of burns limited the extent of subsequent fires by influencing the abundance and availability of burnable fuel (Collins et al. 2009; Scholl and Taylor 2010; Ireland et al. 2012; Stephens et al. 2023).

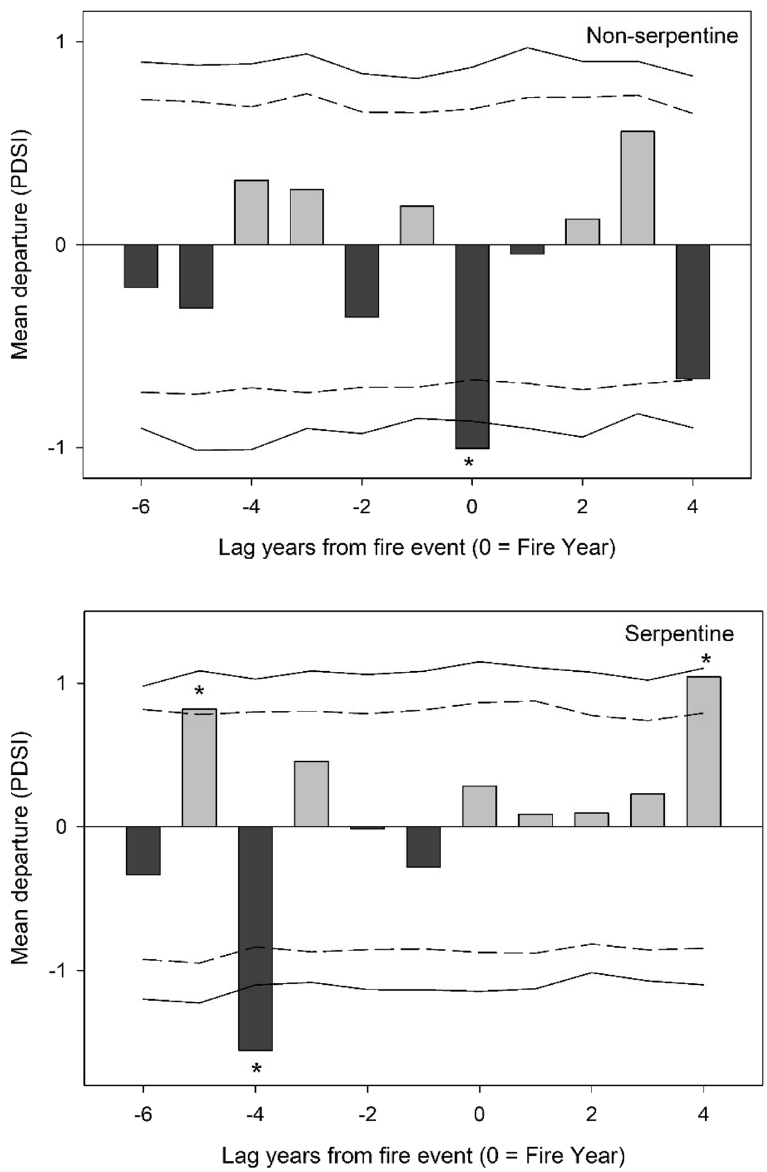

Fig. 11 Superposed epoch analysis (SEA) plots for Palmer Drought Severity Index (PDSI) in non-serpentine (top) and serpentine (bottom) sites. Light gray bars indicate wet/cool years and dark gray bars indicate dry/warm years. Dashed line indicates significance at the $p < 0.05$ level, solid line at the $p < 0.01$ level. Asterisk indicates significant ($p < 0.05$) departure from mean conditions

While it is difficult to distinguish between Indigenous and lightning-ignited fires using fire scars alone (Anderson 2005; Van Wagtendonk and Cayan 2008; Roos et al. 2019), a few lines of evidence suggest that the frequency of fires in our study area was substantively augmented by Indigenous ignitions. The constant promotion of fire, whether ignited by lightning or humans, has long been a major component of Mountain Maidu land stewardship (Dixon 1905; Kroeber 1925, Stephens et el. 2023). Frequent burning, often in relatively small patches, was used to reduce fuels, clear hunting grounds, and promote the growth of plants for food, medicine, and basketry (Dixon 1905; Kimmerer and Lake 2001; Stephens et al. 2023). In our study, the inclusion of all fire-scarred trees (C00) resulted in the shortest fire return intervals (median FRI: 4.5 to 12 years). Compared to other filtering methods, this method has been identified as being most effective at capturing smaller, more localized fires that may have been intentionally lit or tended (Roos et al. 2019). Most of the fires recorded in our study area also occurred at short intervals of less than 10 years, and many were less than 5 years (Fig. 6.). This fire interval is difficult to attribute

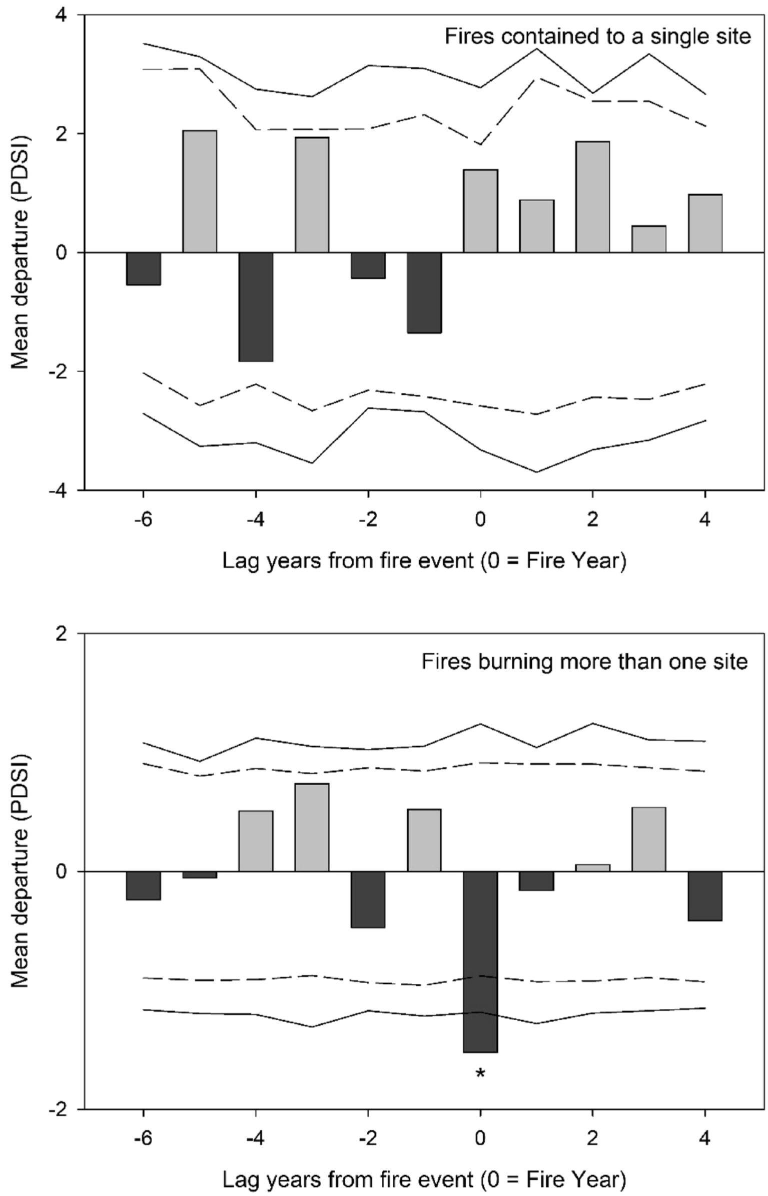

Fig. 12 Superposed epoch analysis (SEA) plots for Palmer Drought Severity Index (PDSI) for fires that burned a single site (top) and fires that burned more than one site (bottom). Light gray bars indicate wet/cool years and dark gray bars indicate dry/warm years. Dashed line indicates significance at the $p < 0.05$ level, solid line at the $p < 0.01$ level. Asterisk indicates significant ($p < 0.05$) departure from mean conditions

to lightning fires alone, which would require both frequent strikes and an available fuel bed, the latter of which can be a limiting factor in frequently burned areas or in low-productivity sites where fuel accumulation is slower (Van Wagtendonk and Cayan 2008; Stephens et al. 2023). Unfortunately, we did not have the sampling depth to investigate how land use changes (e.g., the decline in Native American populations after 1850) may have affected fire frequency in our study area. However, several fire history studies have documented a reduction in fire frequency and increase in fire extent following the decline in Native American populations and disruption of cultural burning (Fry and Stephens 2006; Gill and Taylor 2009; Skinner et al. 2009; Taylor et al. 2016).

Fire return intervals in the serpentine and non-serpentine sites in our southern-most study pair were significantly longer (median composite FRI: 16–22.5 years) than the FRIs documented in the other two pairs of sites (median composite FRI: 6–9 years; Table 2). Although we were not able to explicitly test this, anecdotally, the six

Table 4 Fire return interval estimates from comparable fire history studies in mixed conifer forest in the northern and central Sierra Nevada. *NSN* northern Sierra Nevada, *CSN* central Sierra Nevada, *C00* composite using all fire scars, *C25* composite of fires that scarred 25% of sample, *PFRI* point (individual tree) estimate

Location	Time period	# Sites (sample area)	Method	Mean FRI (years)[a]	Median FRI (years)[a]	Study
NSN (Plumas NF)	1775–1849	11	C00	8.2	7.7	Moody et al. 2006
		(0.3–2 ha)	C25	17.2	10.2	
NSN (Diamond Mnts)	1525–1900	34	C00	12.1	10.4	Gill and Taylor 2009
		(9–36 ha)	PFRI	19.8	17.7	
NSN (Sagehen EF)	1700–2006	5	C00	7.9	5.6	Vaillant and Stephens 2009
		(0.6–3.5 ha)	C25	17.8	8.5	
CSN (Lake Tahoe)	1700–1875	1	C00	4	3	Beaty and Taylor 2008
		2000 ha[b]				
CSN (Blodgett Forest)	1750–1900	6	PFRI	14.6	11.3	Stephens and Collins 2004
		(9–15 ha)				
CSN (Yosemite NP)	1575–1849	1	C00	1.2	1	Scholl and Taylor 2010
		(2125 ha)[b]	C25	10.7	9	

[a] Values represent the grand mean when FRI estimates were presented for multiple sites

[b] FRI calculated for entire study area

sites in our study area occur at relatively similar elevations, slopes, and aspects (see Table 1) and the three pairs were selected to reduce variation in these attributes. One potential explanation for the shorter FRIs in pairs 1 and 2 may be their close proximity to large meadow complexes and creeks. The four trees with extremely short intervals (intervals of 2 and 3 years) were situated less than 200 m from the edge of large meadows. During the drier parts of the year, the continuity of flammable fuels in these habitats could have provided connectivity with other parts of the landscape, collecting fire from adjacent areas and facilitating fire spread to surrounding uplands. The shorter FRIs near the edges of meadows may also have been an indicator of Indigenous burning (Anderson and Carpenter 1991; Anderson and Moratto 1996; Kimmerer and Lake 2001; Anderson 2005). Native Americans in this region used periodic burning in and around meadows to discourage the encroachment of conifers, maintain and promote edible plants, and improve forage for wildlife (Kimmerer and Lake 2001; Anderson 2005).

Climate exerted a strong influence on fire occurrence and extent in our study area, but the specific relationship between climatic conditions and fire activity differed between serpentine and non-serpentine sites. Fires in more productive non-serpentine sites were strongly associated with drought conditions in the year of the fire (Fig. 11). This coincides with a number of other studies in northern California mixed conifer forests that have also found that historical fires were correlated with significantly drier conditions (Moody et al. 2006; Taylor et al. 2008; Skinner et al. 2009). Drought conditions in the year of the fire would have created highly favorable conditions for fire spread, such as low fuel moisture, high air temperatures, and low relative humidity.

Fire occurrence in our serpentine sites was limited more by preceding climatic conditions than moisture in the year of the fire. In serpentine sites, fires were preceded by a significantly wet year, followed by a substantially dry year, 5 and 4 years prior to the fire (Fig. 11). These antecedent wet conditions would have produced more abundant and continuous herbaceous fuels, while a subsequent dry year would have allowed those fuels to cure, increasing the potential for fire spread in future years (Margolis et al. 2022; Roos et al. 2022). While the mechanism behind this wet-then-dry connection to fire occurrence is fairly well established, the longer preceding lag (4–5 years) and lack of a strong fire year signal for our serpentine sites is somewhat puzzling. Skinner et al. (2008) found a similar 5-year lag with wet conditions leading to more fire occurrence in the Jeffrey pine-mixed conifer forests of the northern Baja, Mexico, but this was also connected to a strong drought signal for fire years. Skinner et al. (2008) posited that the longer lag with wet years may have been connected to needle cast, for which the wetter conditions allowed for greater needle production, that was then cast 4–6 years later, resulting in greater fuel continuity. A similar mechanism may be responsible for fire occurrence on our serpentine sites, which are also dominated by Jeffrey pine. Alternatively, this longer preceding lag could be connected with understory plant growth, perhaps perennial forbs and shrubs if the understory was similar to what exists now, which are slower to respond than grasses. Regardless of the specific mechanism for increased fuel production and continuity, the lack of a drought signal for fire years suggests that these serpentine sites may be somewhat unique in that flammability is not a major limiting factor.

The difference in fire–climate patterns on and off serpentine soils suggests that fire regime attributes in our study area varied in response to interactions between top-down climatic controls and bottom-up site conditions. Soil productivity indirectly affects fire cycles by directly influencing the amount of biomass that is available to burn (Pausas and Bradstock 2007). Compared to more productive sites, forests growing on serpentine soils have substantially lower biomass, slower growth rates, and a more open and heterogenous structure (Kruckeburg 1984; Safford and Harrison 2008; Safford and Mallek 2010). However, widely spaced trees in serpentine stands can also increase both light and wind near the soil surface, resulting in faster drying of surface fuels and higher potential for wind-driven fires (Safford and Mallek 2010; Bigelow and North 2012). These open forests were historically dominated by Jeffery pine, which produces a well-aerated, flammable, long-needle litter layer that is also conducive to fire spread (Fonda et al. 1998). Taken together, these factors suggest that under normal climate conditions, serpentine sites had suitable environmental conditions for fire spread (i.e., higher surface temperatures and wind speeds) but were dependent on canonical patterns of wet and dry years to produce sufficient understory fuels for fires to more easily spread.

We found little overlap in the timing of fires between serpentine and non-serpentine sites, suggesting that fires were often asynchronous. When fires did cross the boundary between serpentine and non-serpentine sites, they were often associated with more extensive fire years (i.e., fires recorded in two or more sites) that occurred during drier than normal conditions. There were 5 years (1729, 1776, 1782, 1829, 1843) when fires were recorded in four or more sites, and all occurred in years with lower PDSI. Several of these years were also identified as regional fire years by studies synthesizing multiple individual fire history reconstructions (Swetnam and Baisan 2003; Trouet et al. 2010; Taylor et al. 2016). According to Taylor et al. (2016), 1829 is the most highly recoded fire year in the entire Sierra Nevada, with evidence of burning as far north as southwestern Oregon (Metlen et al. 2018). These findings suggest that the abrupt boundary between soil types in our study area may have acted like a filter to fire spread, containing fires under normal climate conditions, while allowing fires to spread across the gradient of soil productivity in drier years (Taylor and Skinner 2003).

Conclusion

As the push to increase the pace and scale of fire reintroduction gains momentum, it is important for managers to have reliable information about how fire regime attributes vary in response to local site conditions, as well as more broadscale changes in climate. In our study, fine-scale variation in historical fire frequency and timing was linked to both bottom-up and top-down controls, which interacted to influence the quantity, continuity, and availability of fuels. Fires in our more productive sites were strongly associated with drought conditions in the year of the fire, while fires in our less productive serpentine sites were limited more by fuel amount and availability. In these less productive systems, the capacity for fire spread appeared to be strongly dependent on a cycle of wet and dry conditions in the years preceding the fire to produce sufficient fuels for fires to more readily spread.

The fire scars in our study area recorded a history of frequent, low severity fire at all of our sites and a distinct lack of fire after the beginning of the twentieth century. This dramatic decline in fire frequency has been documented in mixed conifer forests throughout California (Safford and Stevens 2017; Bohlman et al. 2021) and is likely due to a variety of contributing factors including the removal of Mountain Maidu populations and disruption of cultural practices (Stephens et al. 2023), as well as the onset of organized fire suppression on federal lands in the early 1900s (Stephens and Ruth 2005). This marked decrease in fire frequency also follows a period of intensive livestock grazing that peaked in the late-1800s that could have broken up the continuity of grass and herbaceous fuels across the landscape and reduced the potential for fire spread (Swetnam and Baisan 2003; Norman and Taylor 2005; Taylor et al. 2016).

Forest changes in the absence of fire have been well documented for more productive mixed conifer forests in the Sierra Nevada (Parsons and Debenedetti 1979; Collins et al. 2011; Knapp et al. 2013; Stephens et al. 2015). Significant increases in tree density, shifts in species composition, and reduced structural diversity have occurred at both the stand and landscape scale (Safford and Stevens 2017). Similar changes in forest structure have been documented in fire-excluded forests growing on serpentine soils, but these changes often occur over much longer time periods due to slower growth rates (Sahara et al. 2015). These changes, in combination with the findings from this study, suggest that frequent, low severity fire was a fundamental component of mixed conifer forests growing on and off of serpentine soils. Understanding how historical fire regime attributes varied in response to both local and broadscale conditions can help managers more effectively define desired conditions, develop management objectives, and identify management strategies for fire reintroduction and forest restoration projects in the Sierra Nevada and elsewhere.

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Authors' contributions
MC, SS, BC, and EK designed the study and collected field samples. CA prepared and dated fire scar samples. MC and HF completed the data analysis. MC wrote the manuscript, with contribution from all authors.

Availability of data and materials
The datasets used during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests
The authors declare that they have no competing interests.

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