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High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA

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ABSTRACT

Understanding how alternative vegetation types co-exist in a landscape is important in managing for biodiversity within an ecosystem. In California, mixed conifer forest is often interrupted by stands of shrubs known as montane chaparral. The development of chaparral stands following recent high severity or stand-replacing wildfires in mixed conifer forests has been well documented. Fire has been excluded from mixed conifer forests for over a century, and fuel loads are at historically high levels across much of this landscape. Despite contemporary post-fire research on mixed conifer forest, little is known about montane chaparral fire regimes or forest-chaparral dynamics in an ecosystem with a functioning fire regime. This study quantifies fire regimes in chaparral and adjacent forest and determines how chaparral responded to fire before fire exclusion in Lassen Volcanic National Park, California, a park that was never logged. Chaparral stems regenerated immediately after high severity fires in the 19th and early 20th century, and stem recruitment continued until the present. Fire return intervals in chaparral were longer than in adjacent forest (25 years vs. 11 years), and chaparral fires occurred during drier, potentially more extreme conditions. The apparent maintenance of stands of chaparral by less frequent, more severe fires suggests chaparral represents a self-reinforcing alternative stable state to forest. Following fire exclusion, chaparral stands gradually converted to forest as trees progressively invaded chaparral from the forest edge. Forest developing in chaparral is denser and more fir-enriched than the adjacent forest, similar to the understory that develops beneath a pine overstory following fire exclusion. Replacement of chaparral by forest reduces mixed conifer forest landscape diversity. However, the mixture of shrubs and trees in long unburned former chaparral is likely to burn with high severity effects in a subsequent fire. Since chaparral is also establishing in recent, very large high severity burn patches, chaparral extent may be expanding in the new configuration. If the decades needed for trees to invade from forest at the edge of severe burns exceed the fire return interval, chaparral may emerge as an alternative stable state to forest. Consequently, developing management strategies to increase resilience of mixed conifer forests to altered fire regimes is a pressing management challenge.

1. Introduction

A key premise of ecosystem management is that the maintenance of spatial and temporal heterogeneity in ecosystem structure is important for ecosystem function (Christensen, 1997). In many forested ecosystems, recurring fire is an ecological process that acts to create and maintain heterogeneity by consuming live and dead vegetation and altering vegetation structure and composition at both stand and landscape scales (Romme, 1982; Agee, 1993; Perry et al., 2011). The effects of fire on vegetation structure and forest fuels can be remarkably diverse and strongly influence the type and rate of post-fire vegetation development which may also influence subsequent fire-vegetation interactions (e.g. Thompson et al., 2007; Collins et al., 2009; Odion et al., 2010). For example, in frequently burned (e.g. 5–25 years) dry-conifer forests of western North America, fire-vegetation interactions create a forest mosaic that is self-limiting with respect to fire. Where fuel is consumed by one fire, subsequent fires will not occur until sufficient fuels accumulate again (Taylor and Skinner, 2003; Collins et al., 2009; Scholl and Taylor, 2010; Parks et al., 2014). In some forest types, the effects of fire may include the establishment of alternative vegetation types followed by self-reinforcing fire-vegetation interactions in subsequent fires. For example, anthropogenic fires have resulted in forests converting to shrub and

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grasslands, particularly in island ecosystems such as Hawaii, Madagascar, and New Zealand (see Bond et al., 2005). In temperate forests, high severity or stand-replacing fire may initiate shrublands that tend to burn severely in subsequent fires (Thompson et al., 2007; Odion et al., 2010; Collins et al., 2009; van Wagtendonk et al., 2012; Parks et al., 2014). Changes in fire frequency have also been shown to alter vegetation type in forests in as diverse locations as the American Southeast (Myers, 1985) and Southwest (Fishbein et al., 1994), southern France (Trabaud and Galti, 1996), New Caledonia (Perry and Enright, 2002) and South America (Paritsis et al., 2015). Fire regime differences in the fire-maintained alternative stable states are at least partially the result of differences in the structure, abundance, and flammability of fuel, and post-fire rates of fuel accumulation (Myers, 1985; Trauernicht et al., 2012; Paritsis et al., 2015).

In dry pine and mixed-conifer forests of the Sierra Nevada and southern Cascade Range of California, patches of shrub-dominated vegetation are interspersed within a forest that historically exhibited a high degree of fine scale spatial heterogeneity. There is strong and abundant evidence that frequent low and moderate severity fires, fires where aboveground vegetation consumption and post-fire mortality were minimal to moderate (Keeley, 2009), and self-limiting fire-forest-structure interactions maintained the fine scale spatial heterogeneity in forest structure over time and over wide areas (Bonnicksen and Stone, 1982; Taylor, 2000, 2010; Beaty and Taylor, 2007; Scholl and Taylor, 2010). Spatially explicit dendroecological reconstructions of the pre-fire-exclusion forest structures demonstrate that forests were multi-aged and typically composed of small overlapping patches (100–1500 m^2) of similar-aged trees (Beaty and Taylor, 2007; Scholl and Taylor, 2010; Taylor, 2010). Embedded in these forest landscapes were stands of shrubs, or montane chaparral (hereafter chaparral), ranging in size from tens to hundreds of hectares (Bolsinger, 1989; Skinner and Chang, 1996; Nagel and Taylor, 2005; Skinner and Taylor, 2006; Beaty and Taylor, 2008). On sites capable of supporting trees, chaparral is thought to be a fire-maintained alternative stable state to forest (Odion et al., 2010). Chaparral shrubs are fire-adapted and rapidly establish after fire by re-sprouting following top-kill or establishing from seed from a long-lived seed bank in the soil (Kauffman and Martin, 1991; Keeley, 1991; Knapp et al., 2012). Once established, they impede tree seedling establishment and growth, slowing forest development (Conard and Radosevich, 1982b; Conrad and Sparks, 1993; McDonald and Fiddler, 1995; Nagel and Taylor, 2005; Beaty and Taylor, 2008; Collins and Roller, 2013). Moreover, chaparral shrubs regenerate immediately post-fire and continue to produce stems for decades or even centuries, promoting long term shrub persistence (e.g. Wilken, 1967; Biswell, 1974; Nagel and Taylor, 2005; Duren and Muir, 2010).

Some large chaparral stands are known to have established after intense 19th and 20th century logging and burning promoted shrub establishment by reducing tree cover and seed source (Sudworth, 1900; Leiburg, 1902; Biswell, 1974; Wilson and Agnew, 1992; Skinner and Taylor, 2006). However, historical chaparral-forest dynamics and chaparral fire regimes have been little studied (Skinner and Chang, 1996; Van de Water and Safford, 2011). Although chaparral fire regimes are poorly known, there is some evidence that the frequency of fire is lower and more variable than in adjacent forest (Nagel and Taylor, 2005). This may be related to lower rates of dead fuel production and a higher proportion of moist live fuels in chaparral than in forests that may impede fire spread through chaparral under moderate weather conditions (Skinner and Chang, 1996; Nagel and Taylor, 2005).

Exclusion of fire for a century or more in mixed conifer forests has significantly increased forest density, basal area, live and dead fuels, and the proportion of fire intolerant species compared to forests before fire exclusion (Parsons and DeBenedetti, 1979; Beaty and Taylor, 2007; North et al., 2007; Scholl and Taylor, 2010; Taylor et al., 2014). Exclusion of fire may also have contributed to the conversion of chaparral to forest observed on sites throughout the Sierra Nevada and southern Cascades (Vankat and Major, 1978; Gruell, 2001; Beaty and Taylor, 2001, 2008; Nagel and Taylor, 2005; Skinner and Taylor, 2006; Bekker and Taylor, 2010). Exclusion of fire from mixed conifer forests appears to have reduced heterogeneity not only within forest stands but also across the forest landscape.

In contrast, recent wildfires in long fire-excluded forests may be leading to an expansion of chaparral vegetation. There is considerable evidence that increases in area burned and area burned at high severity in mixed conifer forests of the Sierra Nevada and Cascade Range in recent decades are mainly due to a large increase in fuels caused by fire exclusion, although climate warming has also contributed (Westerling et al., 2006; Miller et al., 2009; Miller and Safford, 2012; van Wagtendonk et al., 2012; Mallek et al., 2013; Harris and Taylor, 2015). Chaparral shrubs establish well in forests burned at high severity, and consequently chaparral extent is likely increasing as a result of more high severity fire (Collins and Roller, 2013). Moreover, in large severely burned areas, subsequent fires within a decade or two tend to burn again at high severity, reinforcing the switch from forest to chaparral caused by an initial high severity fire (Wilken, 1967; Bock and Bock, 1977; Thompson et al., 2007; Stephens and Collins, 2010; Odion et al., 2010; van Wagtendonk et al., 2012). An improved understanding of chaparral-forest dynamics and chaparral-fire interactions is needed to understand historical forest landscape heterogeneity and to develop strategies for restoring heterogeneity and fire resilience in mixed conifer forests that have been highly altered by fire suppression, logging, and other human activities over the last century.

In this study, we identify the fire history and regeneration dynamics of trees and chaparral shrubs in a mixed conifer forest landscape in the southern Cascade Range that has never been logged. We hypothesize that chaparral had a fire regime distinct from the surrounding mixed conifer forest and was maintained by fires that removed most or all of the forest vegetation. Given the differences in structure and fuel characteristics between forest and chaparral, we expected chaparral to burn less frequently and at higher severity, i.e. with a greater proportion of the vegetation consumed or killed by each fire compared to adjacent forest. We also quantified the conversion of chaparral to forest by comparing change in the extent of forest and chaparral in pairs of aerial photographs taken decades apart. We expected the timing of forest expansion into chaparral to correspond with the onset of fire exclusion and forest in former chaparral to be enriched in shade tolerant trees compared to adjacent forest. We expected forest expansion into chaparral to be distance dependent because of higher long-term seed rain near the forest edge.

2. Methods

2.1. Study area

Montane chaparral stands were studied in a mixed conifer forest landscape in Lassen Volcanic National Park (LVNP) in the southern Cascade Range, California (Fig. 1). LVNP is a volcanic plateau punctuated by high volcanic peaks, and elevations range from 1600 to 3200 m. Conifer forest is the dominant vegetation type, and species composition varies with elevation (Parker, 1991; Taylor, 2000). Mixed conifer forest occurs between 1700 and 2300 m and is comprised mainly of Jeffrey pine (*Pinus jeffreyi*) and white fir (*Abies concolor*), but incense cedar (*Calocedrus*

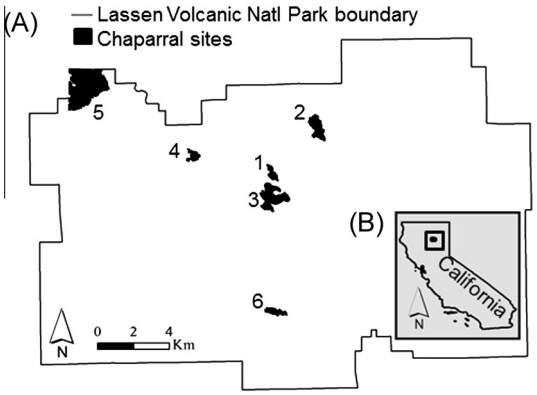

Fig. 1. (A) Location of the six sampled chaparral stands, Lassen Volcanic National Park in the southern Cascades, California, USA. 1. Bear, 2. Cluster, 3. Hat, 4. Raker, 5. Table, 6. Warner. (B) Area of detail.

decurrens), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), and Ponderosa pine (*Pinus ponderosa*) may be locally abundant. Stands of montane chaparral are interspersed with forests in the mixed conifer forest landscape. Shrub dominants include greenleaf manzanita (*Arctostaphylos patula*) and snowbrush (*Ceanothus velutinus*) with chokecherry (*Prunus emarginata*) and bush chinquapin (*Chrysolepis sempervirens*) often present. Chaparral tends to occupy steeper slopes and more xeric aspects and slope positions (Pinder et al., 1997).

The climate of LVNP is Mediterranean with hot, dry summers and cold, wet winters. At Manzanita Lake (in LVNP at 1800 m elevation), average monthly minimum and maximum temperatures range from −6.6 °C to 5.0 °C in January and from 7.5 °C to 26.1 °C in July, respectively (WRCC, 2015). Annual average precipitation is 104 cm with high inter-annual variability. Most precipitation (>80%) falls as snow between November and April.

Fire was a ubiquitous disturbance in LVNP forests prior to fire suppression, and the length of fire return intervals have been strongly correlated with elevation and forest type (Taylor, 2000). Native American tribes that used LVNP seasonally are known to have set fires to promote production of particular plant species and to flush game (Schulz, 1954). Euro-Americans began arriving in 1850, and parts of LVNP were grazed by their cattle and sheep between 1870 and 1905 (Strong, 1973; Taylor, 1990). In 1905, the area became part of the Lassen National Forest Reserve, and LVNP was established in 1916 following the eruptions of Mt Lassen (Strong, 1973). A policy of suppressing fire was implemented in 1905, and fire frequency in LVNP forests declined dramatically after this date (Taylor, 2000).

2.2. Field sampling

2.2.1. Forest and chaparral structure and composition

We selected six chaparral stands in the mixed conifer zone in LVNP using the following criteria: (1) they were discrete with few trees or bare areas visible within their perimeters in 1941 aerial photographs, (2) there was no record of fire between 1941 and 2011, (3) they were >5 ha in size, and (4) they could be reached by foot travel in <1.5 h.

Vegetation at each of the six chaparral sites was divided into three zones identified in 1941 and 2005 aerial photographs: (1) an open zone where shrubs remain dominant, (2) an infill zone where trees have replaced shrubs between 1941 and 2005, (3) a forest zone adjacent to the chaparral stand. At each site, three transects were established from the forest through the infill and open zones. Transect lengths varied from 150 to 500 m. Twelve evenly spaced plots with four plots in each zone were established along each transect. The distance from the forest edge was recorded. Vegetation at each point was sampled in a 50 m^2 circular plot. The abundance of shrubs (live and dead) and trees ($\geqslant$ 5 cm) was estimated by cover class (0, >0–5%, 5–25%, 25–50%, 50–75%, 75–100%). Tree seedlings (0.5–1.5 m) and saplings (>1.4 m tall, <5 cm dbh) were also counted by species.

Establishment dates of shrubs in the chaparral stands were determined by collecting ground-level cross-sections from the two largest (i.e. greatest basal diameter) greenleaf manzanita stems using a handsaw in each open zone plot. This approach assumes larger diameter shrubs are older; an assumption supported by age-diameter relationships reported for other chaparral species (Keeley, 1992). Stem cross-sections were sanded to a high polish, and their annual growth rings were counted beneath a binocular microscope.

Trees were sampled in each plot using the point-centered-quarter technique, a plotless technique for determining density (Mueller-Dombois and Ellenberg, 1974). The distance and diameter of the nearest tree in each quarter was measured and recorded by species. In forest zone plots, two size classes of trees were sampled in each quarter: (1) an understory tree (5 cm–35 cm dbh), and (2) an overstory tree (>35 cm dbh). This provided a sample of trees that likely established both before (overstory) and after (understory) fire suppression based on extensive fire history and tree establishment dates in LVNP forests (Taylor, 2000; Scholl and Taylor, 2010; Taylor et al., 2014). The distance and tree diameter measurements were used to calculate tree density (trees ha^{-1}) and average basal area (m^2 ha^{-1}) from arithmetic mean tree diameter for pine and fir species in the open, infill, forest understory, and forest overstory at each site. Each tree was cored to the pith at a height of 30 cm above the ground. Cores were sanded to a high polish, and the annual growth rings were cross-dated using standard techniques (Stokes and Smiley, 1996). The date of the innermost ring was assigned as the tree age.

To compare the initial growth conditions of tree seedlings beneath forest and chaparral, we measured variation in annual radial growth by counting the number of rings cm^{-1} from the pith along the length of each tree cored to pith. Presumably, trees establishing in an open post-fire environment would show more rapid initial growth than those that established beneath a shrub canopy. Later, as trees overtop the shrub canopy, they may begin to reduce shrub vigor. Consequently, we tested for an association between total tree canopy cover (%) and live and dead shrub cover (%) in each stand using a non-parametric correlation coefficient (Spearmans r_s).

Seed dispersal and tree recruitment from forest edge into burned areas or other clearings follow a negative exponential function for the first several hundred meters (Greene and Johnson, 1996). To explore whether forest expansion into chaparral showed a similar pattern, we used linear regression to test the strength of a linear, quadratic (density^2), and negative exponential relationships between distance from the 1941 forest edge and tree density. Since the distance-tree density relationship could be expected to vary with site conditions (e.g. time since fire, slope, aspect, etc.), site was added as an interaction, allowing the slope of distance-tree density relationship to vary by site, using the lm function in the stats package component of R (R Core Team, 2014).

Replacement of chaparral by forest at each site was also quantified using change evident between aerial photographs taken in 1941 and 2005. We geo-referenced the 1941 aerial photographs to the USGS 2005 digital orthophoto quarter quads in a GIS using a minimum of 30 control points to establish an RMS error of <8 m. Tone and texture on the photographs were used to distinguish forest from chaparral and delinate chaparral extent. Only the center portions of the historic photographs were used

in analysis, because the center is likely to be less distorted. We repeated the mapping of chaparral on 2005 digital orthophotos and calculated the change in chaparral and forest extent between 1941 and 2005.

2.2.2. Chaparral fire dates and fire return intervals

Identifying fire dates in chaparral is difficult because evidence of fire in the form of fire scarred trees or stand structure may be destroyed by subsequent high severity chaparral fires. However, trees that survive but are damaged by fire may exhibit abrupt declines in radial growth, and fire scarred trees at the forest edge or in small forest islands within a chaparral stand may contain a record of multiple chaparral fires (Skinner and Chang, 1996; Nagel and Taylor, 2005). The date of the most recent fire that presumably initiated establishment of or perpetuated the existence of chaparral stands was identified using variation in radial growth of old trees (>250 years) in or on the edge of the chaparral stands. Cores were extracted from five trees at each site, sanded to a high polish, and cross-dated using standard dendrochronological techniques (Stokes and Smiley, 1996). The date of the last fire was identified as the first year of a 50% decline (suppression) or increase (release) in mean ring width for a period of five years or more compared to the previous five years.

To determine if fire return intervals in chaparral were different than in adjacent forest, we identified trees with external fire scars growing within or on the edge of the largest chaparral stand we studied (Table) and two nearby chaparral stands (Manzanita Lake). Partial cross-sections were removed with a chainsaw (Arno and Sneck, 1977), and the GPS location of each sample was recorded. A total of thirty trees, including sugar pine ($n = 3$), and Jeffrey pine ($n = 27$) were sampled in chaparral, and ten Jeffrey pine trees were sampled in adjacent old forest (>250 years). Cross-sections were sanded to a high polish and cross-dated using standard dendrochronological techniques (Speer, 2010). The year of each tree ring with a fire scar lesion was recorded as a fire date. Fire scar sampling was not conducted at the other sites because they were in the Wilderness portion of LVNP where chainsaw use is restricted.

Time spans of trees and their using a re-scar dates were compiled into fire history charts using program FHAES (Brewer et al., 2015). We compared FRI in chaparral and forest in several ways. We calculated the mean per tree FRI and filtered composite FRIs (any sample scarred, 10% or more of samples scarred, 25% or more of samples scarred) for all samples in chaparral and forest and then tested for differences using a Students t-test. We also compared the shapes of FRI distributions from chaparral and forest using a Kolmogorov–Smirnov test.

3. Results

3.1. Site characteristics

The median area of the six chaparral stands was 69 ha (range, 25–350 ha) and the median site elevation was 2081 m (range, 1907–2230 m) (Table 1). Stands occurred mainly on drier slope aspects (southerly) and on moderate to steep slopes. Fires occurred in the late 1800s except for the Table site, which burned in 1918 (Table 1). Comparison of aerial photos taken in 1941 and 2005 show the appearance of trees in former chaparral vegetation (Fig. 2). From 32% to 88% of chaparral in 1941 was converted to forest by 2005 (Table 1). Live greenleaf manzanita and snowbush cover was highest (mean = 51%, 42%) in the open zone, lowest (mean = 3%, 2 %) in the forest zone, and intermediate (mean = 10%, 12%) in the infill zone (Table 2). These trends were consistent among all sites.

Table 1
Site characteristics of six sampled chaparral stands, Lassen Volcanic National Park, California, USA.

Site	1941 Stand extent (ha)	2005 Forest infill	Transect elev	Aspect	Slope	Most recent fire
1. Bear	25	48	2084–2169	W/SW	8	1891
2. Cluster	69	83	1950–2121	N/NW	8	1889
3. Hat	120	78	2169–2291	SE	24	1864
4. Raker	68	88	2023–2267	SE	24	1873
5. Table	350	32	1718–2096	E/SE	6	1918
6. Warner	31	61	1840–2035	S	28	1876

Tree density and basal area varied by species, vegetation zone, and site (Table 3). White fir was proportionately most abundant in the infill zone and had the largest population and the highest basal area except in the forest overstory at Hat and Raker. White fir density and basal area are greater at Table than at other sites, while pine density and basal area were highest at Raker. Forest developing in chaparral was denser and more enriched in fir compared to adjacent forest (understory and overstory). Average tree density in the infill zone was ca. twofold greater than in the forest understory and ca. fivefold greater than in the forest overstory. The few pines growing in the chaparral (open, infill) were larger than the fir, and this was reflected in the proportionally high basal area of pine in the open zone despite a much higher density of fir. In contrast, in the infill zone and forest understory, fir basal area was greater than pine ($P < 0.05$, Kruskal–Wallis). Fir species comprise $\geqslant$90% of the saplings and seedlings in all zones (Table 4).

3.2. Fire history

Thirty-eight fires between 1527 and 1926 CE were recorded in the 30 fire scar samples in the three adjacent chaparral stands (Fig. 3A and C). The mean number of scars per tree was 6 scars (SD ± 2). The mean per tree fire return interval (FRI) of the samples was 28 years (±17.2 years). For fires that scared at least 25% of the samples ($n = 16$), the mean composite FRI was 25 years (±20.7 years), and the mean FRI for fires that scarred trees in all three sites was 32 years (range, 28–46 years). The most widespread fire occurred in 1918 and was recorded in 25 trees. Five other years with widespread fire in chaparral were 1741, 1783, 1815, 1843, and 1889.

In forest adjacent to chaparral, sixty-three fires were recorded between 1524 and 1919 (Fig. 3 B and D). The mean number of scars per tree was 16 scars (±3 scars). The mean per tree FRI was 12 years (±9.3 years). Fires ($n = 29$) that scarred at least 25% of the samples had a composite mean FRI of 11 (±7.3 years). The composite FRI distribution for forest and chaparral were different ($P < 0.001$, Kolmogorov–Smirnov two-sample) with more long intervals for chaparral than forest. The median per tree FRI for samples in chaparral (25.9 years) was also longer than for forest (12.7 years) ($p > 0.001$, Kruskal Wallis H Test).

3.3. Chaparral age structure

Ninety-seven percent of the aged greenleaf manzanita established or resprouted after the last fire. Stems were present in multiple age classes indicating recruitment was not limited to the immediate post-fire period (Fig. 4). At the two sites with the most recent fires (Fig. 4, Bear, Table), there were some shrub stems that dated to before the last fire. At sites with fires in the 1860s and 70s (Fig. 5 Hat, Raker, Warner) the earliest detected sprouting dates were 10–30 years after the last fire.

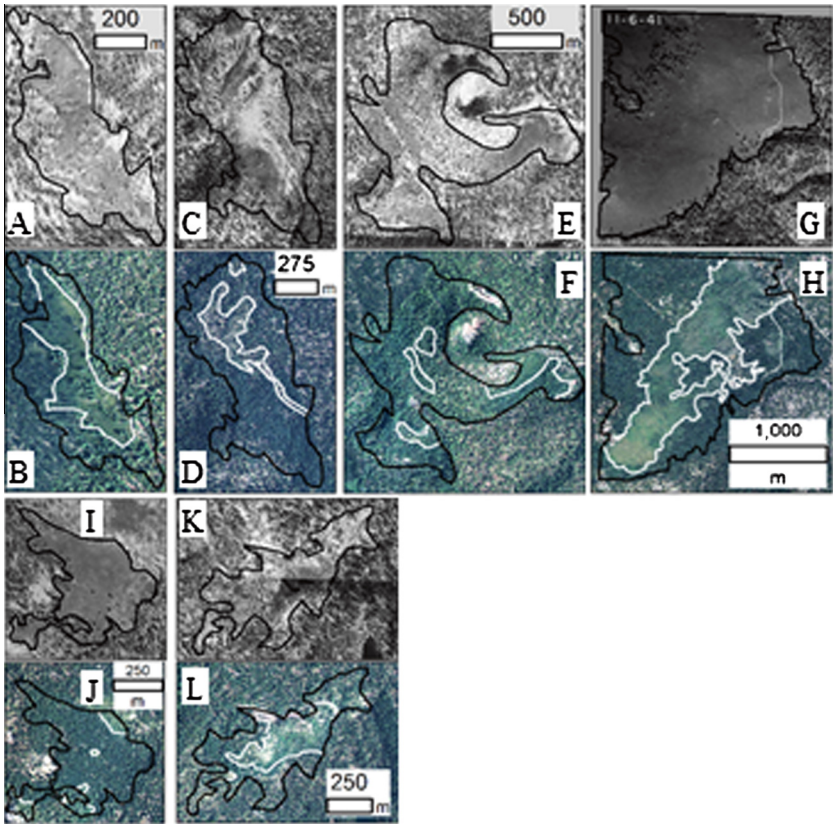

Fig. 2. Extent of the six sampled chaparral stands from aerial photographs taken in 1941 and 2007 in Lassen Volcanic National Park, California, USA. The 1941 forest boundary is outlined in black and the 2007 boundary in white. (A) Bear 1941, (B) Bear 2007, (C) Cluster 1941, (D) Cluster 2007, (E) Hat 1941 (F) Hat 2007, (G) Table 1941, (H) Table 2007, (I) Raker 1941, (J) Raker 2007, (K) Warner 1941, (L) Warner 2007.

3.4. Tree encroachment

There were consistent patterns of tree establishment among sites (Figs. 4–6). Trees began to establish 10–30 years after the last fire with peak establishment occurring a few decades after initial establishment. Because we report tree ages uncorrected for age at coring height, trees in open and infill zones may be years to decades older than the age reported, and thus trees may have established more rapidly after the fire (cf. Discussion). Peak establishment in the infill zone occurred two decades earlier than the peak in the open zone (Fig. 6b and c). The age structures of fir and pine in the infill and open zones were broadly unimodal (Figs. 4, 6b and c). Populations of pine and fir were multi-aged. Trees in the forest overstory established >100 years before the fires that initiated chaparral, and the population of overstory trees was multi-aged (Fig. 6e). In contrast, >90% of forest understory trees established after the last fire with peak establishment four decades later (Fig. 6d). Also, tree establishment in all zones drops off rapidly in recent decades, but this may be a sampling artifact since tree seedlings and saplings were not aged. Individuals in these size classes probably established in the last 50 years.

Forest expansion into chaparral reduced chaparral extent. The area of chaparral evident in the aerial photographs declined between 1941 and 2005. On average, the area of chaparral in a stand declined by 65% (range 32–88%) (Fig. 1).

There was evidence of distance-dependent infilling of forest into chaparral (Fig. 7). A negative exponential relationship between distance from the forest edge and tree density fit the data ($r^2 = 0.44$, $p < .001$) better than a linear ($r^2 = 0.28$, $p < .001$) or quadratic relationship ($r^2 = 0.39$, $p > .05$ for 3 sites). For all sites, except Cluster, ($r^2 = 0.05$), the r^2 was $\geqslant 0.3$. Pines, mainly Jeffrey pine, established earlier (were older) nearer to and later (were younger) farther from the forest edge ($p > 0.05$) (Fig. 8). However, distance from the 1941 forest edge explained only 19% of the variance in tree age. For fir species, the age-distance regression was not significant ($p > 0.05$).

Trees that established in chaparral had lower initial growth rates than trees that established in adjacent forest. Initial tree growth rates in chaparral averaged 15 rings cm^{-1} (SE = ±0.6 rings cm^{-1}) with a range of averages of 10–18 rings cm^{-1} among sites while forest trees had average initial growth rates of 10 rings cm^{-1} (SE = ±0.5 rings cm^{-1}), with a range of averages from 9 to 14 rings cm^{-1} among sites (Fig. 9). After 25–30 years, chaparral trees reached 4–5 cm diameter at 30 cm, and began to grow faster than forest trees of the same diameter, probably because their crowns emerged from the shrub canopy.

Development of a tree canopy above chaparral had a detrimental effect on the shrubs. There was a negative relationship between tree canopy cover and shrub abundance. The negative association was strongest for greenleaf manzanita (Spearmans $r_s = -0.73$, $p < 0.001$) and snowbrush (Spearmans $r_s = -0.50$ $p < 0.001$), and weaker for bush chinquapin (Spearmans $r_s = -0.30$ $p < 0.05$). There was also a weak association between tree canopy cover and cover of dead greenleaf manzanita ($r_s = 0.24$, $p < 0.05$).

4. Discussion

Montane chaparral in LVNP was compositionally similar to chaparral stands in the Sierra Nevada, Klamath Mountains, and other locations in the southern Cascades (Conard and Radosevich, 1982a; Skinner and Chang, 1996; Nagel and Taylor, 2005; Skinner et al., 2006; Fites-Kaufman et al., 2007; Duren and Muir, 2010).

Table 2
Mean cover (%) of live chaparral by zone in six sampled chaparral stands, Lassen Volcanic National Park, California, USA. Abbreviations: *A. patula* = *Arctostaphylos patula*, *C. semp.*=*Chrysolepis sempervirens*, *C. velut.* = *Ceanothus velutinus*, *P. emarg.* = *Prunus emarginata*. See Table 1 for site conditions.

Site (species)	Open	Infill	Forest
	Mean Cover (%)		
Bear			
C. semp.	3	6	1
A. patula	76	17	8
C. velut.	32	9	3
Cluster			
C. semp.	3	0	3
A. patula	42	9	6
C. velut.	65	0	0
Hat			
C. semp.	27	25	0
A. patula	63	11	3
C. velut.	41	14	0
Raker			
C. semp	23	44	11
P. emarg.	24	4	0
A. patula	54	13	0
C. velut.	48	37	0
Table			
C. semp.	45	18	4
P. emarg.	4	0	0
A. patula	22	1	0
C. velut.	28	4	4
Warner			
C. semp.	29	12	0
P. emarg.	21	2	0
A. patula	47	9	0
C. velut.	39	9	3
All Sites			
C. semp.	22	18	3
P. emarg.	10	1	0
A. patula	51	10	3
C. velut.	42	12	2

Table 4
Mean sapling (<5 cm dbh and >1.4 m tall) and seedling (0.3–1.4 m tall) density of fir (white and red fir) and pine (Jeffrey and lodgepole pine) species by zone for six sampled chaparral stands Lassen Volcanic National Park, California, USA.

Zone	Saplings (ha^{-1})		Seedlings (ha^{-1})	
	Fir	Pine	Fir	Pine
Open	58	4	157	0
Infill	105	3	196	0
Forest	95	10	137	2

In our sites, chaparral was a mixture of greenleaf manzanita, snowbrush, bush chinquapin, and chokecherry. Each of these species has life history traits that promote persistence or rapid establishment and growth after severe fire and lead to site dominance. Species of *Ceanothus* (snowbrush), greenleaf manzanita, and chokecherry can establish from seed in a long-lived soil seed bank and some (e.g., snowbrush) require heat scarification for germination (Stewart, 1978; Conard et al., 1985; Weatherspoon, 1985, 1988; Keeley, 1991; Kauffman and Martin, 1991; Knapp et al., 2012). Each species can also sprout vigorously when top-killed by fire (Skinner and Taylor, 2006).

The historical fire return interval in chaparral was not the same as the fire return interval in surrounding forest. The mean FRI in chaparral was twice as long as in nearby forest with a mean per tree FRI of 28 years vs. 12 years for forest. The composite FRI distribution for chaparral was more variable and skewed to the right (i.e. had longer intervals compared to forest). These differences suggest that, at least in some locations, chaparral may represent an alternative stable state to forest, maintained by repeated high severity fires with greater variability in time between fires. The longer FRI in chaparral is probably related to differences in flammability caused by the structure and composition of fuels. Dead fuel accumulation is slower in chaparral than in forest (Skinner and Chang, 1996; Thompson and Spies, 2009; Perry et al., 2011). The combination of minimal surface fuel and high live fuel moisture

Table 3
Density and basal area (BA) for fir and pine trees ($\geqslant$5 cm) by zone in six sampled chaparral stands, Lassen Volcanic National Park, California, USA. Understory trees were 5 cm–35 cm dbh and overstory forest trees were >35 cm dbh.

Site	Zone	Total	Tree density (trees ha^{-1})			Mean BA (m^2 m^{-1})		
			Fir	Pine	Fir:Pine	Fir	Pine	Fir:Pine
Bear	Open	111	92	19	4.8	2.7	4.2	0.6
	Infill	449	430	19	23	23.1	2.5	9.3
	Understory	245	153	92	1.7	10.1	2.7	3.7
	Overstory	119	74	40	1.8	32.2	16.3	2.0
Cluster	Open	209	165	43	3.8	9.0	5.2	1.7
	Infill	546	511	34	15.0	36.1	4.0	9.0
	Understory	409	358	51	7.0	8.0	1.3	6.0
	Overstory	90	71	19	3.8	29.6	6.1	4.9
Hat	Open	132	123	9	13.7	11.6	0.8	14.1
	Infill	559	547	12	47.0	39.6	0.2	180.3
	Understory	197	122	75	1.6	2.3	2.2	1.0
	Overstory	84	37	47	0.8	10.6	14.6	0.7
Raker	Open	70	37	33	1.1	4.5	3.1	1.4
	Infill	318	186	133	1.4	20.8	16.2	1.3
	Understory	448	353	95	3.7	10.4	2.0	5.3
	Overstory	137	98	39	2.5	21.9	22.8	1.0
Table	Open	237	217	20	11.0	20.1	1.0	20.1
	Infill	1078	1045	34	31.0	86.2	1.1	75.4
	Understory	475	475	0	NA	17.0	0.0	NA
	Overstory	149	129	20	6.3	39.7	16.2	2.5
Warner	open	167	139	28	5.0	15.7	5.0	3.2
	Infill	558	465	93	5.0	41.6	15.6	2.7
	Understory	132	106	26	4.1	4.1	0.7	5.6
	Overstory	88	62	26	2.4	15.2	8.9	1.7

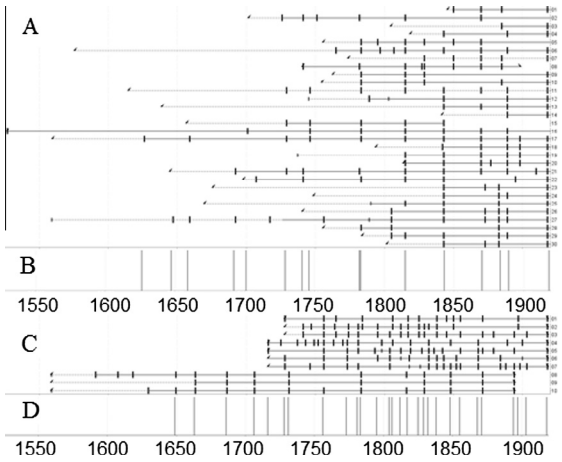

Fig. 3. Fire occurrence between 1525 and 1920 for 3 chaparral stands and surrounding forest in Lassen Volcanic National Park, California, USA. In chaparral (A) and forest (C), the record of individual trees are represented by horizontal lines and dates of fire scars are represented by filled vertical bars. Injuries not attributed to fire are indicated by open vertical bars. The triangular hash mark indicates the earliest year for each sample. Composite fire scar diagrams for chaparral (B) and forest (D) are shown below individual samples for each vegetation type. Each line represents the year of a fire that scarred at least 25% of the samples.

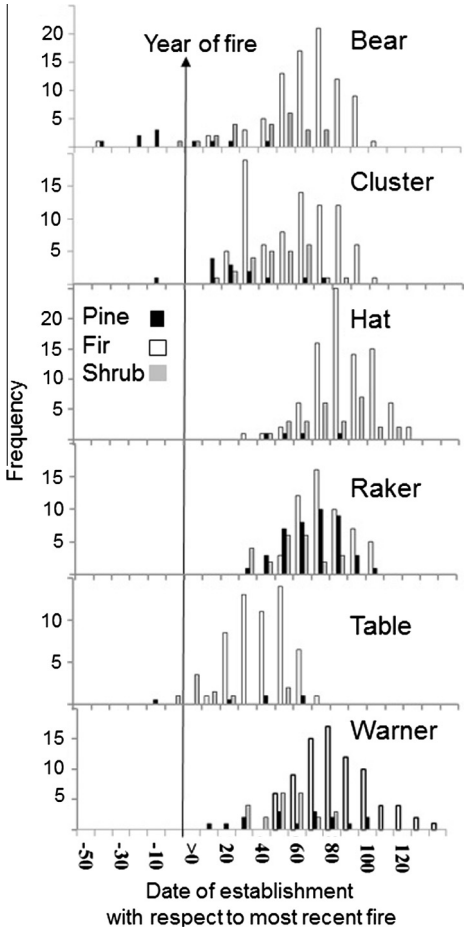

Fig. 4. Dates of establishment with respect to date of the last fire for pine (filled bars), fir (open bars), and greenleaf manzanita (shaded bars) in six sampled montane chaparral stands, Lassen Volcanic National Park, California, USA. The last fire is shown as year 0 and indicated by the arrow.

in chaparral would retard fire spread under moderate weather conditions. Under such conditions, fires carried by the fine surface fuels in mixed conifer forests may stop spreading when they reach

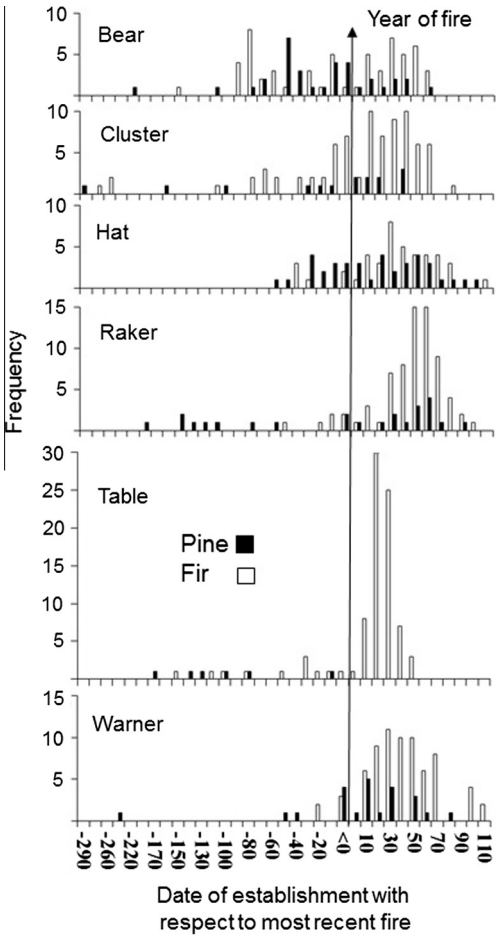

Fig. 5. Dates of establishment of understory (5 cm–35 cm dbh) and overstory (>35 cm) forest zone trees with respect to the last fire for pine (filled bars) and fir (open) in six sampled montane chaparral stands, Lassen Volcanic National Park, California, USA. The last fire is shown as year 0 and indicated by the arrow.

chaparral (Weatherspoon and Skinner, 1995; Perry et al., 2011). Our chaparral FRI estimate may be too short, since fire scarred trees on the edges of chaparral stands may also have recorded some fires that burned only the adjacent forest but not the chaparral. Generally, the years with widespread chaparral fires were very dry which would increase flammability and fire spread and would tend to increase fire severity. Five of the six widespread fire years for chaparral occurred during severe droughts (Palmer Drought Index $\leqslant -3.0$, Gridpoint 35) (Cook et al., 2004). Our results suggest chaparral dominance was facilitated by generally longer, more variable FRIs that tended to produce higher severity fires frequently enough to kill most encroaching conifers. Further, the smaller sample size ($n = 10$) of trees in the forest may underestimate the frequency of fires in the closed canopy forest.

The chaparral-forest, fire-mediated vegetation dynamic is not unique. Several other shrub dominated vegetation types burn with higher severity and a different (often shorter) fire return interval than the surrounding forest vegetation. In the western US, one study found Gambel oak fire return interval to be about 100 years while the surrounding pinyon-juniper forest has a 400 year rotation of stand-replacing fire (Floyd et al., 2000). In the Mediterranean, maquis shrubland burns with a 10–20 year return while the pine forest burns at 50–100 year intervals (Trabaud, 1994). Perhaps most similar to the chaparral mixed-conifer dynamic, Florida sandhill forest burns much more frequently (every 1–5 years) and less intensely than adjacent sandpine scrub (10–45 years) which can serve as a fire break (Myers, 1985, 1990). Each of these

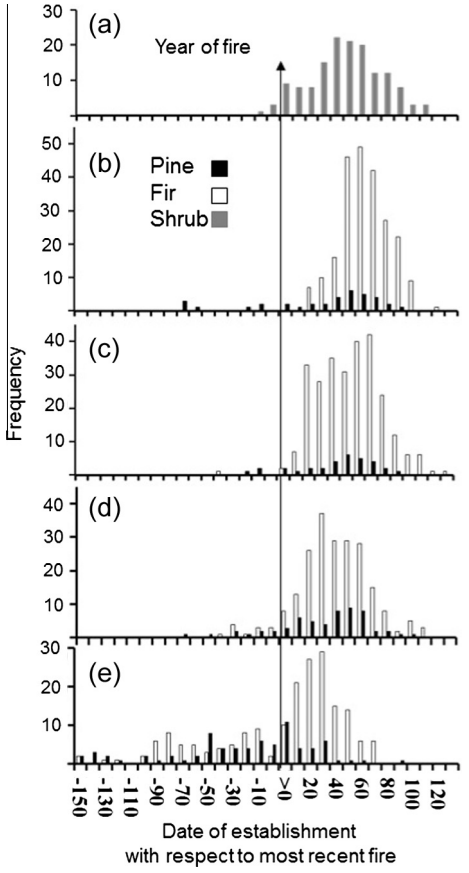

Fig. 6. Dates of establishment combined by zone for (a) open zone greenleaf manzanita (shaded bars), (b) open zone pine (filled bars) and fir (open bars) (c) infill zone pine and fir (d) forest understory (5 cm–35 cm dbh) pine and fir and (e) forest overstory (>35 cm dbh) pine and fir with respect to the last fire in six sampled chaparral stands, Lassen Volcanic National Park, California, USA. The last fire was in year 0 and is indicated by the arrow.

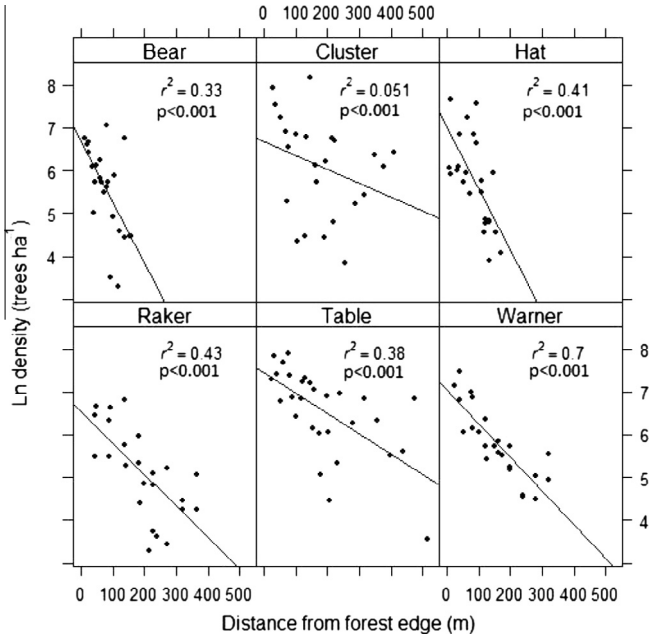

Fig. 7. Tree density (log-transformed) in montane chaparral as a function of distance from the forest edge determined from 1941 aerial photographs in six stands in Lassen Volcanic National, California, USA (r^2 = 0.44).

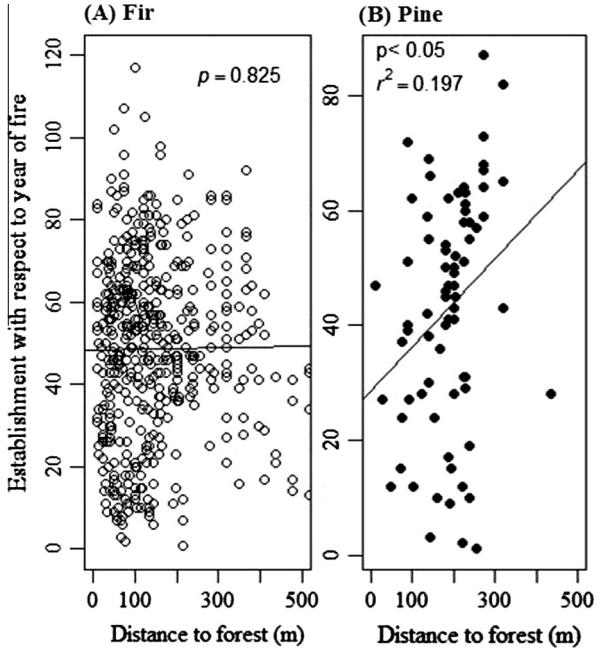

Fig. 8. Establishment date for trees (>5 cm dbh) in years after most recent fire, year 0, as a function of distance from the 1941 forest edge determined from aerial photographs in sampled chaparral stands in Lassen Volcanic National Park, California, USA. (A) Fir species are open circles. (B) Pine species are filled circles.

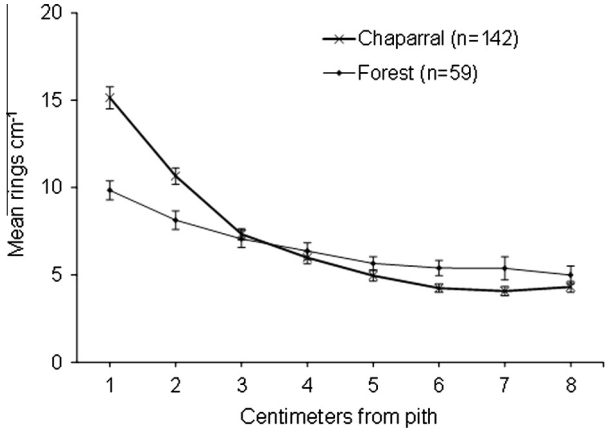

Fig. 9. Mean number of annual growth rings cm^{-1} (±SE) from the pith for cores from trees (>5 cm dbh) in sampled chaparral stands and adjacent forest in Lassen Volcanic National Park, California, USA.

ecosystems has undergone changes related to shifting fire patterns caused by human activities, climate change, or interactions between the two. In the Mediterranean, increases in fire frequency and severity are leading to an expansion of shrubs and overall decreased landscape heterogeneity (Trabaud and Galti, 1996; Mouillot et al., 2002). In contrast, with fire exclusion in the western and southeastern US, pinyon-juniper and sandpine scrub vegetation are expanding, invading the more fire prone vegetation (Myers, 1985; Floyd et al., 2000).

The age of the oldest aboveground stems of shrubs and encroaching trees generally corresponded with the dates of fires identified in each chaparral stand. This is a strong indicator that the stands persisted through or were initiated by high severity fires during the late 19th and early 20th century. The lag between fire dates and shrub sprouting for the oldest fires may be an artifact of missing rings in the oldest manzanita stems. In the largest

stems, the inner portions were frequently cracked rendering the rings uncountable. Additionally, cross-sections were collected from the lowest accessible portion (15–30 cm above the base) of each shrub rather than at ground level. Our shrub ages probably underestimate actual shrub age because of the sampling height above the stem base and the partial disintegration of some stems with age. Pulsed post-fire shrub and tree establishment after 19th and 20th century fires has been documented in other montane chaparral stands in the Sierra Nevada (Wilken, 1967; Nagel and Taylor, 2005; Crotteau et al., 2013; Collins and Roller, 2013), in interior chaparral in southwestern Oregon (Duren and Muir, 2010), in foothill woodland chaparral in California (Keeley, 1991), and in Gambel oak in southwestern Colorado (Floyd et al., 2000).

Shrub sprouting in chaparral was not confined to an initial post-fire period. On average, chaparral stems occurred in eight ten-year age-classes in each stand, indicating that shrub populations are multi-aged and that sprouting or recruitment continues during fire free periods. Multi-aged populations of other fire-dependent chaparral shrub species have been documented in montane chaparral in the Sierra Nevada (Nagel and Taylor, 2005), California foothill chaparral (Keeley, 1992) and interior chaparral in southwestern Oregon (Duren and Muir, 2010). Sprout recruitment is responsible for rejuvenating the shrub canopy in foothills chaparral (Keeley, 1992), and periodic germination of seed from either a plant or soil seed bank is thought to be responsible for recruitment of interior chaparral species in southwestern Oregon during fire-free periods (Duren and Muir, 2010). We did not observe chaparral shrub seedlings on our sites, nor did Nagel and Taylor (2005) in the Sierra Nevada, suggesting that sprouting is the primary mechanism for maintaining shrub dominance during fire-free periods.

Tree establishment also began soon after fire dates and continued for decades resulting in a vegetation conversion from chaparral to forest. Like shrub populations, tree populations were multi-aged. Initial establishment was slow and typically peaked five or more decades after the fire. In the seedling stage, trees growing with chaparral experience intense competition that impedes tree regeneration and growth (e.g. Conard and Radosevich, 1982a; McDonald and Fiddler, 2010). Overall, white fir was the most frequent colonizer of chaparral, and white fir initial growth beneath chaparral was slow. On average, white fir seedlings (n = 10) in LVNP took 27 years (±5 years) to grow to a height of 50 cm. Slow initial growth of trees has been observed in chaparral in the northern Sierra Nevada (Nagel and Taylor, 2005). Once trees emerge from the shrub canopy their growth rate increases significantly, and they begin to cast shade. Shading reduced shrub cover and vigor promoting replacement of chaparral by forest. The chaparral stands we studied have been fire-free for >95 years, and area of chaparral has declined by 65%, on average. Replacement of chaparral by forest has also been observed elsewhere in the southern Cascades and northern Sierra Nevada (Wilken, 1967; Nagel and Taylor, 2005).

Nearby trees provide the seed source for conversion of chaparral to forest. Density of seed from wind-dispersed species like the conifers in LVNP declines exponentially with distance from a forest edge (Greene and Johnson, 2000). Consequently, tree seed rain would be higher at the forest-chaparral edge than in the interior of a chaparral stand. The negative association between tree density and distance from the forest edge we identified is consistent with a higher probability of tree establishment with higher seed rain. At one site, Cluster, the relationship was particularly weak. This is the only site with a northern aspect and likely experiences different wind patterns and moisture conditions than the other sites. Chaparral stands that become established in large patches of recent high severity fires in mixed conifer forests (e.g. Miller et al., 2009; Potter, 2014) may be slow to return to a forested state because of long distances to a tree seed source. These large patches may remain vulnerable to successive high-severity fires that would perpetuate the chaparral and inhibit return to forest.

There was a difference in the temporal pattern of establishment of white fir and Jeffrey pine within chaparral, and this is likely related to seed characteristics. There was no distance-dependent relationship between the forest edge and ages of white fir, but there was for Jeffrey pine. White fir of various ages were present at all distances along transects while Jeffrey pine were older near the original forest-chaparral edge and younger at the leading edge of forest advancing into chaparral. Jeffrey pine has heavier seeds (mean weight = 123 mg) than white fir (mean weight = 34 mg), which would more strongly concentrate Jeffrey pine seeds near the historic forest edge. The progressive pattern of invasion by pine may also reflect secondary seed dispersal by rodents and successful seedling establishment from seed caches near the historic forest edge. Small mammals, particularly chipmunks (*Tamias* spp.), cache Jeffrey and ponderosa pine seeds in microsites that are more favorable for seedling establishment than non-directed microsites (Vander Wall, 1993; Fiehler, 2007; Briggs et al., 2009). Future forest establishing in very large chaparral stands created by recent high severity fire (e.g. Collins and Roller, 2013; Crotteau et al., 2013) may be especially depauperate of pine.

Forest establishing in chaparral is enriched in fir compared to adjacent forest. The establishment, growth, and survival of tree seedlings can be strongly influenced by the abundance of shrubs and other plants that grow in a forest understory and can act as an ecological filter influencing overstory species composition (e.g. George and Bazzaz, 1999). In chaparral, establishment of shade-intolerant Jeffrey pine is much lower than shade tolerant fir, and Jeffrey pine establishment decreased with time since fire. The ratio of fir to pine saplings in the open zone is similar to the forest understory and threefold higher than in the infill zone. These data demonstrate the differential influence of chaparral shrubs on the composition of tree regeneration. The ecological filtering effect of chaparral on tree species composition is also evident in other locations in the southern Cascades and Sierra Nevada where forest is replacing chaparral (e.g. Bekker and Taylor, 2001; Beaty and Taylor, 2001; Nagel and Taylor, 2005; Skinner et al., 2006). The dense, fir enriched forest established in place of former chaparral may be prone to burn with high severity in the next fire, potentially leading to the re-establishment of chaparral.

4.1. Management implications

It remains a challenge to quantify precisely the proportion of the mixed conifer forest landscape that was occupied by chaparral and potentially burned with high severity effects before fire exclusion. However, modeling studies provide some insights. Broadly, the percentage of mixed conifer burned area that experienced high severity fire effects is estimated to have been around 2–8% during the presettlement period (Mallek et al., 2013). It is likely these areas of high intensity fire consisted of small patches of a few hectares (Skinner and Chang, 1996) and were more common at particular topographical locations, especially upper, south-facing slopes (Beaty and Taylor, 2001, 2008; Taylor and Skinner, 1998). Managers seeking to restore historical forest conditions and fire regimes can use topographic settings (e.g. Hessburg et al., 2007; Underwood et al., 2010; Harris and Taylor, 2015) to identify appropriate locations in and proportions of the landscape that would have been prone to burn with high severity effects and were likely dominated by montane chaparral during the presettlement period. These locations could be designated hot spots, expected to support montane chaparral and allowed to burn at high severity if surrounding fuel conditions permit.

Shrubs are not restricted to forest-free areas created by high severity fire or harsh site conditions. They occur locally in the

forest understory where gaps in the forest canopy increase light to the forest floor (Knapp et al., 2013). Nineteenth century photographs, general land office survey records, and early 20th century forest surveys consistently document the presence of chaparral shrubs in the forest understory (e.g. Sudworth, 1900; Knapp et al., 2012, 2013). In contemporary forests, chaparral shrubs are much less abundant or even absent because of shading from the large numbers of fire intolerant tree species (e.g. white fir) that have established in the forest understory due to suppression of frequent low severity fire (Skinner and Chang, 1996; Taylor, 2000; Scholl and Taylor, 2010; Knapp et al., 2012, 2013). Where restoration of historical structure is a management goal, the creation of small gaps within the forest should be considered, in addition to larger shrub-dominated patches.

There is potential for chaparral to increase above historical levels as a result of higher fuel loads as a legacy of fire suppression, the extreme weather conditions under which current uncontrolled wildfires often burn, and continued increases in temperature and extreme weather events due to anthropogenic climate change (Lenihan et al., 2008; Collins and Skinner, 2014; Collins, 2014). In contemporary mixed conifer forests, high fuel loads including increased understory tree density and ladder fuels due to fire suppression are strongly contributing to a disproportionately large areas burned at high severity in recent wildfires (Collins and Stephens, 2007; Miller and Safford, 2012; van Wagtendonk et al., 2012; Mallek et al., 2013). For example, in the 2013 Rim Fire, high severity fire effects occurred in over 40% of the total area burned (105,000 ha), with some high severity patches in mixed conifer forest exceeding 5000 ha (Steel et al., 2015). Chaparral shrubs seed banks are widely distributed throughout the mixed conifer forest (Knapp et al., 2012) and can germinate after severe fire, resulting in a vegetation shift from forest to chaparral (Collins and Roller, 2013). Consequently, the area occupied by large chaparral patches is likely to increase as severe fires increase. There is evidence of rapid chaparral establishment in formerly forested areas after recent high severity fires (Crotteau et al., 2013). Once chaparral is established, recurrent fires will tend burn at high severity, thus reinforcing chaparral dominance and reducing forest regeneration (Collins and Roller, 2013; Coppoletta et al., in press; Coop et al., in press). If the decades needed for trees to re-establish from seeds from forest at the chaparral edges exceed the new fire return interval, chaparral may emerge as an alternative stable state to forest.

Many managers are concerned with restoring and maintaining biodiversity and heterogeneity at the stand and landscape scale. For mixed conifer forests, developing management strategies to increase the resilience to altered fire regimes is also a pressing management challenge (Collins and Skinner, 2014). Similar dynamics to the interplay between fire, montane chaparral, and forest we describe are likely to occur across dry forest ecosystems with a history of fire suppression or high levels of anthropogenic fire. Here heterogeneity has declined while fuel loads create vulnerability to extreme fire events that may cross tipping points between alternative stable states of forest and non-forest vegetation (Coop et al., in press; Pausas and Keeley, 2014). Our results suggest a landscape approach to managing with fire, giving particular attention to local terrain and identifying historically forested locations that may be vulnerable to high severity fire given current fuel loads and projected climate conditions. These areas are likely steeper slopes and higher topographic positions and may be adjacent to the historical high severity burn areas and montane chaparral stands. Restorative prescribed burns conducted under mild conditions and strategically placed fuel breaks with aggressive thinning and surface fuels reduction may help protect forests against future stand-replacing fires. With these strategies, managers may be able to reestablish and maintain historically consistent forest heterogeneity, including stands of montane chaparral, while mitigating against potential type conversion of mixed conifer forest to chaparral over wide areas by large, severe wildfires.

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