FIRE AND THE PERSISTENCE AND DECLINE OF MONTANE CHAPARRAL IN MIXED CONIFER FORESTS IN THE SOUTHERN CASCADES, LASSEN VOLCANIC NATIONAL PARK, CA

A Thesis in

Ecology

by

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Abstract

Stands of montane chaparral are an integral component of the mixed conifer forest in the Cascade Mountains of northern California. In this region, chaparral stands found on sites that could support trees are thought to have established following high severity fire. The exclusion of fire for over a century may have allowed trees to invade chaparral. The conversion of chaparral to forest has reduced chaparral in the mixed conifer landscape. This study investigated the timing and spatial dynamics of chaparral and tree establishment in six chaparral stands in Lassen Volcanic National Park, California. Findings include that the oldest chaparral established after a fire event and were older than most trees in the stand. The chaparral were multi-aged, indicating continued resprouting in the absence of fire. Tree density (trees hectare\(^{-1}\)) was higher closer to the forest edge than further into the chaparral, suggesting gradual tree invasion from the forest. *Pinus jeffreyi* were older at the forest edge than further into the chaparral while *Abies concolor* and *Abies magnifica* showed no relationship between age and distance from forest edge. Fir density was higher in invaded chaparral than in the surrounding forest. In three recent wildfires in the Park, historically chaparral dominated areas burned with more high severity compared to forest vegetation. Characterization of the dynamics of montane chaparral can contribute to our understanding of the historic importance of high severity fire to forest landscape heterogeneity. This study demonstrates that most trees in the chaparral have established since fire suppression was implemented and that wildfires have the potential to restore tree-invaded chaparral.
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Chapter 1

Introduction

Vegetation heterogeneity and disturbance

The geographic distribution of plant species and communities is shaped by consistent environmental conditions such as temperature (i.e. elevation), moisture, and soil characteristics (Whittaker 1956; Gosz 1992) and by episodic disturbance events. In forest ecosystems, disturbances including fires, windstorms, and insect attacks have been shown to affect the structure, composition, and distribution of tree, shrub, and herbaceous cover (Romme 1982; Veblen 1991; Foster & Boose 1992). Greater understanding of the relationships between vegetation patterns and disturbance patterns may aid efforts to restore, manage, and predict potential future changes in forest ecosystems (Covington 2000).

Land managers with the National Park Service are especially interested in understanding the characteristics of pre-Euro-American settlement landscape heterogeneity and disturbance regimes in order to implement the NPS mandate to restore and support forests in their natural condition and preserve the wildlife therein. In much of the western US, a critical aspect of restoring pre-settlement conditions is determining how fire disturbance functioned as an ecosystem process before fire suppression efforts initiated in the early 20th century largely removed fire from the landscape (Parsons & Landres 1998).
Vegetation heterogeneity and fire

Fire-vegetation interactions can be difficult to define because of a two-way relationship in which fire influences species distribution and abundance patterns while vegetation type also influences fire characteristics (Peterson 2002; van Wagtendonk & Fites-Kaufman 2006; Fites-Kaufman et al. 2007). Multiple factors combine to create the fire regime at a given location. Fire regime refers to a summary of fire occurrence and effects, including the frequency, extent, seasonality, and severity of fire. Some of the variation in fire regimes can be explained by environmental gradients. For example, in warmer, drier areas, fires tend to be more frequent and less severe than in cooler, wetter areas. In the Smoky Mountains of Tennessee, fires historically occurred most frequently on southern aspects and at high elevations and least frequently on northern aspects at low elevation. Pine trees were most prevalent on southerly sites and hardwoods on northern sites (Harmon 1982). Forest composition also influences fire characteristics because tree species vary in their rate of production of live fuels and deposition of dead fuels and in fuel flammability (Bond & van Wilgen 1996). In the Colorado Front Range, fire characteristics result from an interaction of vegetation patterns as well as weather, fuels, and topography. The absence of Gambel oak (*Quercus gambelii*) a shrub species, at low elevations in the northern Front Range is thought to result in a lower incidence of high severity fires compared to sites where Gambel oak is present(Kaufmann et al. 2006).
**Mixed conifer forest heterogeneity and fire**

The coniferous forests of northern California are one type of fire evolved ecosystem. These forests are extensive, around 6 million ha, and considered ecologically and economically important. In these forests, temperature and precipitation gradients are major environmental determinants of the distribution of forest cover, and fire was historically the most ubiquitous and frequent natural disturbance (Parker 1991).

The fire regime of the mid-montane conifer forests is thought to have been a mixed severity regime (Fites-Kaufman et al. 2007; Bekker & Taylor 2010). Mixed severity regimes are complex and have high variability across space and time, making them difficult to characterize. Severity patterns may be controlled by fuels, weather, and topography to degrees that are event specific (Agee 2005). The mixed nature of the fire severity in these forests is thought to be particularly important to the creation and maintenance of heterogeneity in vegetation structure and composition at both stand and landscape scales. Variation in fire severity creates a heterogeneous vegetation pattern because a given fire may exhibit a continuum of severity from low to high across its extent. The resulting effects include a range from almost no change in the forest canopy to total canopy mortality. The high severity component of the fire regime can be especially difficult to elucidate because the fire may destroy fire scarred trees, the main evidence of the previous fire history (Agee 2005; Kaufmann et al. 2006; Perry et al. 2011).

In the southern Cascades, historical reconstructions of fire patterns from fire scarred trees and age class analyses indicate how the mixed severity fire regime varied with elevation, slope, aspect, and vegetation gradients in several locations. Fire records from lower elevation dry pine forests indicate mostly low severity fires, while higher,
mesic fir forest fire records and age structures suggest greater variability in severity.

Compared to the central and southern Sierra Nevada, in the southern Cascades, mixed conifer forest fires generally occurred later in the growing season and high severity patches were a more regular component. High severity burns were detected at all slope positions and in some upper slopes comprised the majority of burned area (Beatty & Taylor, 2001; Bekker & Taylor 2010).

Mixed conifer forests and fire suppression

A century of fire suppression has resulted in changes in forest structure and composition. Low and mid-elevation coniferous forests that historically burned on the order of a few decades or less have become more dense with more small, shade-tolerant, fire-intolerant species (Parsons & DeBenedetti 1979; Taylor 2000; Scholl & Taylor 2010). Less is known about the effects of fire suppression on shrubs and herbaceous species. However, comparisons of current conditions with historical photographs and descriptions suggest that the denser, more homogenous fire suppressed forests have fewer canopy gaps and less understory light. The shadier environments likely support sparser shrub and grass cover overall and a reduced extent of interspersed open shrub and grass dominated patches (Skinner 1995; Gruell 2001; Fites-Kaufman et al. 2007).

Montane chaparral vegetation and mixed-conifer forests

Some treeless areas dominated by fire dependent shrubs, called montane chaparral remain throughout the mid and high elevation forests (Fites-Kaufman et al. 2007). Montane chaparral patches are thought to be created by high severity fire (Chappell & Agee 1996; Beatty & A.H. Taylor 2007; van Wagendonk et al. 2012).
Logging is also known to lead to the establishment of chaparral (MacDonald & Fiddler 2010). However, early surveyors documented large areas of chaparral within mixed-conifer forests, some of which existed before settlement period logging and burning activities began (Leiberg 1902).

**Montane chaparral persistence and fire**

Although research on the role of fire in the establishment and maintenance of montane chaparral has not been extensive, most montane chaparral species are known to exhibit life history traits that allow them both to survive high severity fires and persist between fire events (Keeley 1991, 1992; Conard & Reed 2003). Keeley (1991) identified three syndromes of chaparral response to fire; obligate seeders which produce long-lived fire stimulated seeds, obligate resprouters that resprout from adventitious buds after fire, and facultative seeders that exhibit both traits. Chaparral seedlings and resprouts are able to establish in the first post-disturbance growing season. Seedlings grow rapidly and tend to occur at high densities (Keeley 1991). Two genera common in southern Cascade chaparral stands are *Arctostaphylos* and *Ceanothus*. Green leaf manzanita, *Arctostaphylos patula*, is a facultative seeder while *Ceanothus* species are obligate seeders. *Ceanothus* seeds can remain viable in the soil for more than 200 years and germinate following heat scarification (Conard & Radosévich 1982; Conard & Reed 2003).

Chaparral seeds not only remain viable for many years but are also widely distributed in the forest. Recent studies in the mixed conifer forest have shown that chaparral seeds persist in the seed bank in locations with little or no live chaparral
Ceanothus seeds appear to be ubiquitous and abundant and Arctostaphylos seeds common. The Ceanothus seeds occur in densities on the order of 100s of seeds m$^{-2}$. Arctostaphylos average around 30 seeds m$^{-2}$. A substantial portion of the seeds are buried at depths (6-10cm) that should enable them to survive a fire. The presence of chaparral seeds at sites with no live chaparral could indicate that chaparral is now less abundant than in the past. Or, animals may disperse seeds to forested sites where live chaparral is not present. Chaparral would then potentially be able to colonize following the creation of a large enough forest canopy gap (Knapp et al. 2012).

Once chaparral has established, the ability to persist in the absence fire may differ among species. Although Arctostaphylos species require severe disturbance for initial establishment, a study of 12 chaparral lower elevation sites ($\leq 1200$m) throughout California with 56 to 120 years since fire indicated that chaparral regeneration was continuous (Keeley 1992). Arctostaphylos and Ceanothus both depend on fire for initial germination. Virtually no new Arctostaphylos and Ceanothus plants germinated more than 2 years after fire events, but Arctostaphylos continued to develop new sprouts as evidenced by multiple stems of varying ages. Arctostaphylos was able to remain dominant and productive on sites with 100 years since fire. In contrast, Ceanothus species, which grow rapidly after initial establishment and have higher light requirements and less drought resistance than other shrub species, appeared to be succeeded by more tolerant shrubs with increasing time since fire (Keeley 1992).

Alternative models of the importance of fire to the persistence of chaparral are that chaparral communities: 1. are fixed in place and tend to reestablish after successive high severity fires or 2. are created by high severity fire events and undergo succession
to forest or grassland as part of a shifting mosaic. There is support for both the fixed in
place and shifting mosaic models of chaparral persistence. Chaparral patches are
hypothesized to establish after high severity fire events generated by extreme weather
conditions in locations that were previously forested (Wilken 1967; Bolsinger 1989; Nagel
& Taylor 2005) or by recurring high fire severity promoted by self-reinforcing effects of
established shrub vegetation (Stephens & Collins 2010; Odion et al. 2010; van
Wagendonk et al. 2012) and topographic parameters, such as steep slope (Beaty
&Taylor 2001; Taylor & Skinner 2003). The persistence time of chaparral in some
locations may be related to site characteristics that influence fire patterns. In more
moderate terrain, individual chaparral stands may be more transient, establishing after a
high severity fire but gradually replaced by forest (Swedberg 1973; Nagel & Taylor,
2005). In highly incised terrain such as in the Klamath Mountains (Taylor & Skinner,
1998; 2003), and the Cascade Range (Beaty & Taylor, 2001), chaparral may be relatively
fixed in topographic locations that tend to burn at high severity consistently (Nagel &
Taylor, 2005; Stephens & Collins 2010).

The fire regime of montane chaparral has not been well characterized
(Van de Water & Safford 2011). Because fuel accumulation in chaparral is slower than in
forests, chaparral may serve as a fire break until fuel accumulation and/or weather
conditions are sufficient to generate extreme fire behavior (Skinner & Chang 1996). Fire
return intervals were found to be longer and more variable in montane chaparral than
the adjacent forest types. Nagel and Taylor (2005) found that in the Lake Tahoe Basin
mean point fire return interval for chaparral stands (28 years, range 16-40) was twice as
long as the mixed conifer forest (12 years, range 2-47) (Taylor & Beatty 2008). In
chaparral dominated areas of the Sierra Nevada, once a stand began to burn, the full extent was likely to burn. The severity seemed to be both driven and constrained more by the vegetation type than by topography or weather (Stephens & Collins 2010). Burn severity in chaparral tends to be higher than surrounding forest (Odion et al. 2010).

Montane chaparral and fire suppression

Fire suppression over the last century may have facilitated tree encroachment into chaparral. This may have happened as trees gradually invaded from the forest or as suppressed trees that co-established with chaparral emerged above the chaparral canopy. The replacement of chaparral with forest has been observed in the Klamath (Skinner 1995), Cascades (Bekker & Taylor 2001) and Sierra Nevada Mountains (Conard & Radosevich 1982; Nagel & Taylor 2005). In the Lake Tahoe Basin, Nagel & Taylor (2005) found that from 1939 to 2000, an average of 60% of chaparral patches were replaced by forest. Some of the trees had established at the same time as the oldest chaparral while most established after chaparral (Nagel & Taylor, 2005).

Tree regeneration and high severity fire

Post-fire tree regeneration in high severity fire areas is likely to be limited by seed source proximity and the seedling tolerance for site conditions including low moisture availability. Seed source and seedling tolerance characteristics are different for different tree species. Red fir (Abies magnifica A. Murr) and white fir (Abies concolor Gord. & Glend.) regeneration after fire is negatively associated with distance to seed source. In the decades after a fire, densities of seedlings and saplings are higher in low and
moderate severity burns than high severity burns (Chappell & Agee 1996; Peirce & Taylor 2011). In contrast, Jeffrey pine (Pinus jeffreyii Grev. & Balf.) seedlings are more numerous in high severity patches (Swedberg 1973; Peirce & Taylor 2011) and may benefit from seed caching by rodents (Pierce & Taylor 2011; Briggs 2009). Pines may be better able to tolerate the harsh post-severe-fire site conditions and co-establish with chaparral more readily than fir (Swedberg 1973). Once successfully established, seedlings of all species appear to grow more rapidly on open high severity sites than lower severity sites with more forest cover (Chappell & Agee 1996).

**Tree regeneration and chaparral canopy**

After the chaparral canopy has developed, it can act to both aid and retard seedling establishment. Seedlings may benefit from the protection offered by chaparral but will grow slowly as long as they are beneath the canopy. Seedlings establishment is better beneath chaparral cover than in the open but growth is better where there are no chaparral. The microenvironment beneath Ceanothus has a lower light level, soil temperature, and water potential but higher air temperature than nearby open environments (Conard & Radosevich 1982).

There are species differences in tolerance of chaparral canopy conditions. Pine seedling growth declines as chaparral cover increases (Shainsky & Radosevich 1986). Fir species can achieve maximum photosynthesis at lower light levels than Ceanothus. This trait is consistent with their ability to establish beneath Ceanothus and eventually overtop the chaparral (Conard & Radosevich 1982). Seedling growth limitation is most strongly
attributed to water stress caused by the superior ability of chaparral species to capture soil moisture (Shainsky & Radosevich 1986).

In the chaparral stand, the time it takes for an initial cohort of seedlings to grow above the chaparral canopy may create a lag period in tree encroachment. When a tree eventually emerges above the chaparral canopy into the light, it undergoes a release. Above the shrub canopy, annual growth is about two times greater than that of conspecifics still growing beneath the shrubs (Conard & Radosevich 1982). Once trees get above the canopy, the rate of infilling might increase due to a combined effect of the tree shade on chaparral vigor and development of local seed source on the establishment of new trees (Nagel & Taylor 2005).
Chapter 2

Research Objectives

This study investigates chaparral and tree establishment in the southern Cascades in areas within mixed conifer vegetation that appear chaparral dominated in 1941 aerial photographs. An increased understanding of the timing of montane chaparral establishment with respect to past fire disturbance and the conversion of chaparral to forest will help to better characterize the high severity component of the mixed conifer fire regime as well as the changes in vegetation that have occurred since fire suppression.

The questions addressed include:

1. Within the historical chaparral extent, did the chaparral and trees establish following the most recent fire event?

   If chaparral-dominated stands result from high severity fire events, then I expect the trees and chaparral within the historic extent of the stands to have established after the last fire. In contrast, in the adjacent forest where fire severity was lower and trees probably survived multiple fires, many trees should have establishment dates preceding the last fire date.

2. Does tree age distribution, density, and composition in former chaparral dominated stands indicate progressive tree invasion of chaparral? Do shade intolerant pine species show different invasion patterns than shade tolerant firs?

   From comparison of 1941 and 2005 aerial photographs, it appears as though chaparral vegetation established before the trees. Then, trees invaded. Alternatively, trees and chaparral may have established simultaneously with trees remaining
suppressed and hidden beneath the chaparral canopy for several decades before emerging above the chaparral.

I expect that in chaparral, the trees are multi-aged and tree density decreases with distance from forest edge, reflecting progressive invasion of trees from the forest rather than a pulse of co-establishment with chaparral. However, I expect differences in the establishment patterns of shade-intolerant pine and shade-tolerant fir species. Because pine seedlings better tolerate open, dry conditions and are typically more numerous in high severity burn areas, I expect more pines to have established in the years immediately post-fire. I also expect pines to be less likely to establish in the light-limited conditions that result from chaparral understory combined with invading tree overstory. If pines are better able to establish sooner after fire, they should be older than the fir. Because fir can survive in the light-limited conditions beneath the chaparral canopy and because increased fir density in the fire suppressed surrounding forest may have increased fir seed source relative to pine, I would expect tree composition in former chaparral to be enriched for fir compared to the surrounding forest.

3. Does an increase in tree canopy cover correlate with decline in chaparral cover or does chaparral appear to decline in the absence of tree invasion?

Trees may be able to establish in former chaparral vegetation because the chaparral declines when the stems that established after the fire senesce. However, because some of the chaparral dominated areas in 1941 photographs are still chaparral dominated in 2005, I expect that the chaparral stems are multi-aged and will continue to resprout in the absence of fire. I expect that if chaparral decline results from shading
from overstory trees, live chaparral cover will decrease with increasing tree canopy cover.

4. In recent wildfires, have areas where chaparral vegetation was historically present burned with higher severity than areas where chaparral was absent?

In the topographically incised landscape of the southern Cascades, because of feedbacks among vegetation, terrain, and fire behavior, I would expect a greater portion of chaparral vegetation to be fixed in place and prone to self-reinforcing high severity fire than may be the case in less topographically varied terrain. If chaparral exhibits self-reinforcing fire behavior, I expect that areas that supported chaparral in 1941 will burn with higher severity than non-chaparral areas.
Chapter 3

Study Site Description

Lassen Volcanic National Park

LVNP is 42,900 ha in size and lies at the southern end of the Cascade Range. The elevation ranges from 1,600 to 3,200 m. The landscape is largely forested and the distribution of forest dominants is strongly influenced by elevation and moisture (Taylor 1990, 2000; Parker 1991). The low elevation forests are dominated by ponderosa pine (Pinus ponderosa) and Jeffery pine (Pinus jeffreyi). Montane forests that occur at higher elevation are mixed conifer mainly Jeffrey pine and white fir (Abies concolor) but incense cedar (Calocedrus decurrens), sugar pine (Pinus lambertiana), and Douglas fir (Pseudotsuga menziesii) can be locally abundant. Upper montane forests that cover the most area in the park are dominated by red fir (A. magnifica var. magnifica), white fir, and western white pine (P. monticola). Lodgepole pine (P. contorta spp. murrayana) occurs in low lying depressions that are moist and are characterized by cold air drainage. Subalpine forests are dominated by mountain hemlock (Tsuga mertensiana) and whitebark pine (Pinus albicaulis) (Pinder et al. 1997). The climate is Mediterranean with hot, dry summers and cold, wet winters. Average monthly temperatures at Manzanita Lake, California (in LVNP at 1800 m elevation), range from -6.6 °C minimum and 5.0 °C maximum in January to 7.5 °C and 26.1 °C in July (WRCC 2009). Annual average precipitation is 104 cm with high inter-annual variability. Most precipitation (>80%) falls as snow between November and April and annual maximum snowpack depth (usually in April or May) has ranged from 1.6 to 8.4m with an average of 4.6m.
Montane Chaparral in Lassen Volcanic National Park

A 1997 vegetation assessment of LVNP found that montane chaparral covered 6% of the park. Distribution of the chaparral species *Arctostaphylos patula* (Greene) and *Ceanothus velutinus* (Doug.ex Hook), on steeper slopes and more xeric aspects and slope positions is consistent with dependency on fire (Pinder et al. 1997). From the 1941 aerial photographs, within the park boundary, 111 chaparral-dominated areas were identified with a total extent of 5630 ha. A comparison of chaparral extent in 1941 aerial photos of LVNP with 2005 aerial photos shows that in 64 years around 68% of 1941 chaparral dominated area has filled in with trees.
Chapter 4

Methods

Site selection

From the 111 chaparral-dominated stands visible on geo-referenced 1941 aerial photographs, stands (Figure 4.1) were selected using the following criteria:

1) the stand has not burned since the onset of fire suppression in 1905 (Taylor 2000), with the exception of the Table Mountain wildfire that occurred in 1918 (74 of 111 stands)

2) the extent is greater than 5 hectares (60 of the 74 remaining stands)

3) in 1941, the chaparral appears continuous with minimal pockets of trees or bare expanses (17 of the 60 stands)

4) in 2005 aerial photographs, trees have not completely filled in and some visible chaparral-dominated area remains (12 of the 17 stands).

Two additional criteria that did not deselect any of the 12 stands were that the site appeared to be edaphically suited to tree growth and that the vegetation map of the LVNP created in 1935 by A. Wieslander designated the stand as dominated by either *Archtostaphylos patula* or *Ceanothus velutinus*. Eight of the 12 potential stands were determined to be accessible (within a one day hike and near to water source if overnight camping was necessary). Six were sampled (Figure 4.2). The sampled stands varied in size on 1941 aerial photos, the percentage tree infilling by 2005, and in elevation, slope, and aspect. The 1941 sizes ranged from 25 ha to over 350 ha. There is no obvious relationship between 1941 size and amount of tree invasion by 2005. It is likely that
multiple factors including time since last fire and elevation, slope, and aspect influence the rate and pattern of tree infilling.

Figure 4.1: Map of the 1941 extent of chaparral dominated vegetation in Lassen Volcanic National Park, CA.( Note: Stands meeting all study criteria are shown outlined in thick black.)

Figure 4.2: Map of chaparral-dominated (A.patula and C. velutinus) stands selected for sampling in Lassen Volcanic National Park, CA.
Community composition

In order to characterize tree and chaparral establishment, the historic chaparral extent was divided into two zones from the 2005 aerial photograph: 1) an infill zone, formerly chaparral but now invaded by trees with chaparral no longer visible and 2) a chaparral zone with sparse tree invasion where chaparral is still visible (See Figure 4.3). The zones are defined as Forest: forested in 1941 and 2005, Infill: chaparral in 1941 but trees in 2005, and Chaparral: chaparral in 1941 and 2005.

![Diagram of sampling zones](image)

Figure 4.3: An example of the three sampling zones along transects using aerial photographs from 1941 and 2005 at Table Mountain in Lassen Volcanic National Park, CA.

At each site, three transects were established that ran from the surrounding forest zone through the former chaparral which is now filled with trees, the infill zone, and into the chaparral zone. Twelve evenly spaced points were established on each transect with four points in each zone (forest, infill, chaparral). The length of transects varied (150m-500m) among and within sites based upon the width of the infill and chaparral zones. Sample points were marked with a GPS and the slope, slope position, and aspect recorded.
Each sample consisted of an 8m diameter circular plot. To characterize the floristic composition and structure in each plot, ocular estimates were made of grasses, forbs, live chaparral by species, dead chaparral to species when possible, and tree canopy as well as rock, bare ground and litter by cover class (0, >0-5%, 5-25%, 25-50, 50-75%, 75-100%). The number of seedlings (0.5m – 1.4m height) and saplings by species (>1.4m height, < 5cm dbh) was recorded.

**Tree age structure**

The timing and spatial pattern of tree and chaparral establishment was investigated by determining the age structure and composition of trees and chaparral at the sample points on each transect. Tree (dbh >5cm) structure and composition was sampled using the point-quarter technique (Mueller-Dombois & Ellenberg 1974). In the forest zone, in order to capture both the understory that is likely to have established since the last fire as well as the forest overstory of pre-suppression trees, two size classes of trees were selected for sampling. The nearest live tree in each quarter that was >5cm but <35 cm (understory) was sampled as well as the nearest tree that was >35cm (overstory). To determine the timing of tree establishment, all sampled trees were cored to the pith with an increment borer at 30 cm above the ground.

In the laboratory, tree ages at four of the six sites \(n = 758\) were estimated by cross-dating each tree ring series with a nearby tree ring chronology from Lemon Canyon and using the inner most ring as an estimate of tree age (Stokes & Smiley 1996). Since all the cores were taken from living trees, the method of cross-dating described by Yamaguchi (1990) where narrow and wide rings in each core are recorded in a list.
fashion was used. Most cores included the center but not the pith (81%). For cores that did not include the pith, years were added using ring annuli following the method described by Applequist (1958). For incomplete cores, \([n = 32]\), the missing core length was estimated by subtracting actual core length from a theoretical core length determined from the tree diameter. For the missing length, the number of remaining rings was predicted using the average number of rings per centimeter for the first 6 cm of growth based on cores that reached the pith (Table 3-1). The number of missing rings was added to the observed ring count to estimate age of the tree using the following formula:

\[
\text{Age of incomplete core} = ([\text{core length}_\text{theo}\text{cm} - \text{core length}_\text{act}\text{cm}] \times \text{inner core growth rate in rings cm}^{-1}) + \text{observed ring count}
\]

Table 4.1: Species specific average number of rings cm\(^{-1}\) for the inner 6 cm of tree cores.

This was used to estimate the number of rings (years) to add to reach pith age to account for the calculated missing length on cores that did not reach curvature.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rings cm(^{-1}) forest</th>
<th>Rings cm(^{-1}) chaparral</th>
<th>Sample size ((n)) for/chap</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABCO &amp; ABMA</td>
<td>7.4</td>
<td>6.9</td>
<td>43/61</td>
</tr>
<tr>
<td>PIJE</td>
<td>11.1</td>
<td>8.5</td>
<td>7/8</td>
</tr>
</tbody>
</table>

This method is viable for cores that are missing small inner portions. Because trees that establish beneath chaparral are likely to show different early growth patterns than trees not beneath chaparral, separate regressions were developed for trees in the chaparral and forest zones.
Age estimates for trees that were missing more than a few centimeters of core (i.e. mostly hollow at DBH, \( n = 7 \) or for missing cores \( n = 4 \)) were developed using regression equations of age as a function of DBH from cores that reached pith (Appendix A).

Trees that establish beneath chaparral grow slowly initially because of intense competition with the chaparral (Conard & Radosevich 1982). For chaparral and infill zone trees, an additional number of years were added to the pith years to account for the time it takes for a tree growing beneath chaparral to reach 30cm. To estimate the number of years it takes to grow to 30cm, seedlings (fir \( n = 21 \), pine \( n = 4 \)) near 30cm in height found growing beneath chaparral were cut at the base. A cross-section from the base was sanded and the rings counted to determine the seedling age. From the 25 trees, an estimate the number of years that it takes for a tree to reach 30cm was found by a linear regression of seedling age by height. Firs were estimated to be 15 years old at 30cm and pines 17 years old (Appendix B). For trees in the forest zone, no correction was made to account for growth from tree establishment to coring height.

**Chaparral age structure**

Keeley (1992) found that many California chaparral species produce annual growth rings that can be used to estimate stem age. At the selected stands, the dominant species were *Archtostaphylos patula* and *Ceanothus velutinus*. The age of the oldest chaparral stems may indicate when the chaparral patch was last burned. After fire, *A. patula* either resprout from below ground lignotubers or establish from seed. Nagel and
Taylor (2005) successfully aged *A. patula* cross-sections from chaparral patches in the Lake Tahoe Basin.

At each site, the date chaparral established was estimated from cross sections collected from the two largest *A. patula* in each of the circular plots in the chaparral zone. This sampling scheme assumes that the large diameter stems represent the oldest individuals, which is supported by age-diameter relationships for other chaparral species (Keeley 1992). The chaparral stem cross-sections were collected as close to the ground as possible with a handsaw.

In the laboratory, *A. patula* stem cross-sections were sanded to a high polish for ring count determination. The cross-sections had distinguishable annual growth rings. The rings were counted as an estimate of stem age. Since chaparral cross sections were not cross dated, estimated ages were grouped into 10-year ages classes to minimize interpretation error from a few missing or false rings.

**Fire disturbance**

The fire return interval in the montane chaparral patches may be different than in the surrounding forest. In the Tahoe Basin, the mean point FRI for chaparral was 28 years, about twice that of the surrounding forest (12 years) (Beatty and Taylor, 2007; Nagel & Taylor, 2005). Because chaparral patches are often generated by high severity fire, much of the fire history evidence is consumed by fire. However, surviving old trees in or near the chaparral patches may have responded to fire events with abrupt changes in radial growth, either suppressions or releases (Arno & Sneck 1977; Abrams and Nowacki 1992; Brown & Swetnam 1994).
In order to try to date the most recent fire that may have generated the conditions for shrub establishment, I used radial growth variation in tree cores from older trees (>150 years) that survived on the edges of the chaparral patches or in the nearby forest on the transects. To target trees with the greatest potential to have evidence in tree-ring patterns and lesions, 1941 aerial photos were used to identify locations of historical trees near or within the chaparral patch. I searched these areas for old trees. Up to five old trees in or around each chaparral patch transect were cored at dbh in order to supplement the transect sample of forest trees. The species, dbh, fire damage evidence, and GPS location of each cored tree were recorded.

Cores extracted from the old trees were sanded to a high polish, and visually cross-dated using standard dendrochronological techniques (Stokes & Smiley 1996). Dates of fires were inferred from radial growth variation identified by measuring the cross-dated cores. The starting year of periods of sudden growth decline, defined as a 100% change in mean ring width for a period of five years or more compared to the previous five years, were identified as years that could represent the date of the last fire.

**Recent wildfire severity**

To investigate whether areas that contained chaparral in 1941 were more likely to burn at higher severity than non-chaparral, I examined burn severity class data from National Monitoring Trends in Burn Severity (MTBS) Severity Mosaics (mtbs.gov) for 3 wildfires that burned in LVNP since 1984. Fire severity classes are based on methods currently used by the US Forest Service for post-fire burn severity mapping efforts. Burned areas are classified from 1- unburned/low to 4 - high severity in 30X30m pixels.
The fires were the Badger (475ha; 1984), Huffer (930ha; 1997), and Bluff (820ha portion; 2004). For the Bluff Fire, only the portion that did not previously burn in the 1987 Snag Complex was used in the analysis.

A 1ha grid was super-imposed on each wildfire. From the 1941 aerial photographs, each grid cell was assigned a historic vegetation category of forest, chaparral, mixed forest/chaparral, or other according to the majority of the vegetation in the cell. The mix forest/chaparral category was assigned when both chaparral and trees were present but neither could be considered dominant. The number of 30mX30m pixels in each of four fire severity classes was summed by vegetation category. For each fire, chi-squared goodness of fit test was performed to compare forest vegetation fire severity distribution to the chaparral vegetation distribution.
Chapter 5

Results

Site characteristics

The size and topographic characteristics of the six study stands are given in Table 5.1. Table Mountain is the largest stand (350 ha) with the lowest elevation (1700-2100m), gentlest slope (mean=6%), the least amount of infilling (32%) and most recent fire date (1918). The earliest fire (1862) was at the second largest (120ha) and highest elevation site, South Hat Mountain (Hat), (2170-2300m), which has been reduced in size by ca. 80%. Only slightly steeper than Table, the slopes of transects at Cluster Lake (Cluster) and Bear Lake (Bear) were, on average, 8 degrees. Slopes at Hat, Raker Peak, and Warner average 25 degrees. All sites are southerly in aspect, except Cluster which faces north to northwest. The Table Mountain fire date was recorded by park staff (1918) while fire date for the three other sites was inferred from tree growth suppressions (Figure 5.1).
Tree and chaparral establishment

Tree ages from the tree core data and chaparral ages from cross-sections are reported for four of the six sites: Raker Peak, Hat Mountain, Table Mountain, and Warner Valley. In Figures 5.2 and 5.3, tree and chaparral ages from all sites are combined by zone. Establishment decade is plotted as years since the last fire. In the forest, many trees, mostly overstory, pre-dated the most recent fire. In the infill and chaparral zones, the chaparral and all except for a few trees established after last fire.

Table 5.1: Site characteristics of chaparral stands in Lassen Volcanic National Park, CA USA.

<table>
<thead>
<tr>
<th>Site</th>
<th>1941 Extent</th>
<th>2005 Forest Infill</th>
<th>Transect Elevation Range (meters)</th>
<th>Aspect</th>
<th>Slope</th>
<th>Most Recent Fire</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>hectares</td>
<td>percent</td>
<td>min</td>
<td>max</td>
<td></td>
<td>degrees</td>
</tr>
<tr>
<td>Bear</td>
<td>25</td>
<td>48%</td>
<td>2084</td>
<td>2169</td>
<td>W to SW</td>
<td>8</td>
</tr>
<tr>
<td>Warner</td>
<td>31</td>
<td>61%</td>
<td>1840</td>
<td>2035</td>
<td>S</td>
<td>28</td>
</tr>
<tr>
<td>Raker</td>
<td>68</td>
<td>88%</td>
<td>2023</td>
<td>2267</td>
<td>SE</td>
<td>24</td>
</tr>
<tr>
<td>Cluster</td>
<td>69</td>
<td>83%</td>
<td>1950</td>
<td>2121</td>
<td>N to NW</td>
<td>8</td>
</tr>
<tr>
<td>S.Hat</td>
<td>120</td>
<td>78%</td>
<td>2169</td>
<td>2291</td>
<td>SE</td>
<td>24</td>
</tr>
<tr>
<td>Table</td>
<td>350</td>
<td>32%</td>
<td>1718</td>
<td>2096</td>
<td>E to SE</td>
<td>6</td>
</tr>
</tbody>
</table>

*Cores from these sites have not been cross-dated.*

Figure 5.1: The number of old trees (>150 yr) growing near chaparral stands that showed growth suppressions. Suppression is defined at least 5 yrs of ring width measuring less than half the width of the previous 5 yrs, in year indicated. Gray filled bars show the year identified as most recent fire. a. Raker Peak, fire 1873, b. Hat Mountain, fire 1863, c. Warner Valley, fire 1895.
Among sites (Figures 5.4 & 5.5), the time between the estimated fire date and initial tree establishment varied. At two sites, Table Mountain and Warner, the earliest establishment occurred immediately after the fire whereas at Hat Mountain and Raker, there are 1-2 decades between the fire and tree establishment. At Warner Valley and Table Mountain one or two trees in the montane chaparral pre-dated the last fire.

Initial establishment of the *Arctostaphylos patula* stems with respect to fire at individual sites showed some differences. At Raker and Table chaparral, (Figures 5.4a & 5.5a) the oldest *A. patula* were as old as the oldest trees. At Hat and Warner chaparral (Figures 5.4e & 5.5e), several trees had earlier establishment dates than the oldest *A. patula*. This may be an artifact of missing rings in the cracked and rotten stems. As the *A. patula* stems age, parts of the stems die and crack while other parts remain alive. Determining the age of chaparral cross-sections was also complicated by the presence of cracks, breaks, and rotten portions that could not be counted. These occurrences varied by site. At Table Mountain 17% of samples had breaks or rot, whereas at Hat and Raker the value was 36% and at Warner it was 43%. For the stems in the oldest age class, cracks and breaks, not rot, were the most common problem (1 of the 3 stems in oldest class at Table contained cracks, 3 of 4 at Raker, 1 of 3 at Hat, none at Warner). Additionally, cross-sections were collected from the lowest portion of the stem that was accessible with a handsaw (15-30 cm above the base) rather than at ground level. Because of the partial disintegration of the stems with age and the sampling height, it is likely that the ages are an underestimate.
*A. patula* had a range of age classes indicating that recruitment was not limited to the period immediately after the fire. In the open zone conditions, *A. patula* are able to resprout for over 100 years after fire.
Establishment decade with respect to decade of the last fire (0)

Figure 5.2:  Age distributions of trees that established in the decades before (decade <0) and after (decade >0) the most recent severe fire in the a. overstory (>35cm) and b. understory (>5cm; <35cm) in the forest surrounding four chaparral stands in Lassen Volcanic National Park, CA.

Solid bars are pine species, *Pinus jeffreyi* and *Pinus contorta*, open bars are fir, *Abies magnifica* and *Abies concolor*. 
Figure 5.3: Age distributions of trees >5cm that established in a. infill zone and b. chaparral zone of four chaparral stands in Lassen Volcanic National Park, CA.

Establishment shown by decade with respect to the decade of the most recent severe fire (year = 0). Solid bars are pine species, Pinus jeffreyi and Pinus contorta, open bars are fir, Abies magnifica and Abies concolor, and checkered bars are chaparral Archtostaphylos patula.
Figure 5.4: Age distributions of trees >5cm that established in each decade by zone in Raker and Hat chaparral stands in Lassen Volcanic National Park, CA.

Pine species, *Pinus jeffreyi* and *Pinus contorta*, are solid bars, fir, *Abies magnifica* and *Abies concolor*, are open bars, and chaparral *A. patula* are checkered bars. Understory includes forest zone trees >5cm and <35cm. Overstory includes forest zone trees >35cm. Fire date indicated with the arrow. **a-d.** Raker Peak zones. **e-h.** Hat Mountain zones.
Figure 5.5: Age distributions of trees >5cm that established in each decade by zone in Table and Warner chaparral stands in Lassen Volcanic National Park, CA.

Pine species, *Pinus jeffreyi* and *Pinus contorta*, are solid bars, fir, *Abies magnifica* and *Abies concolor*, are open bars, and chaparral *A. patula* are checkered bars. Understory includes forest zone trees >5cm and <35cm. Overstory includes forest zone trees >35cm. Fire date indicated with the arrow. **a-d.** Table Mountain zones. **e-h.** Warner Valley zones.
Tree age

Tree populations were multi-aged. In the forest understory, infill and chaparral, the fir age distributions were broadly unimodal. At all sites and zones with more than a few pines, pine distribution was also unimodal. The seeming lack of recent recruits is a sampling artifact since seedlings and saplings were not aged. They probably represent trees that established in the last 50 years.

The peak of tree establishment in the forest understory (Figure 5.2b) occurs 2 to 3 decades sooner after the fire than the peak in the chaparral vegetation (Figure 5.3b). Trees in both infill and chaparral zones established more recently than the forest overstory trees (p<0.05, Kruskal-Wallis). Chaparral zone trees established more recently than infill at both Raker and Table (p<0.05, Kruskal-Wallis). However, at Hat and Warner, the ages of chaparral and infill trees were similar (p<0.05, Kruskal-Wallis).

A linear regression of establishment date in years since fire as a function of distance from forest edge found that pine species, mainly Pinus jeffreyi, but not firs established earlier nearer the forest edge and more recently further from the forest edge (Figure 5.6). The correlation for pines is R=.42 (p<.001, R^2=0.16) whereas firs show no relationship (p=0.22). Examining establishment more broadly, pines established earlier than firs in infill and chaparral zones (p<0.05, Kruskal-Wallis two sample). The mean year of pine establishment in each zone was 17 years before fir (range of individual site means 9-30yrs).
Figure 5.6: Establishment date for trees (>5cm) in years after most recent fire as a function of distance in meters from forest edge into chaparral in four chaparral stands in Lassen Volcanic National Park, CA. Pine species, *Pinus jeffreyi* and *Pinus contorta*, are closed circles, (R=.42, p<.001, R²=0.16). Fir, *Abies magnifica* and *Abies concolor*, are open circles (p=0.22).

In the chaparral zones, the initial radial growth as measured by the number of rings per centimeter of invading trees was slower than in the forest (Figure 5.7a). At diameters above 3 centimeters, chaparral trees grew more rapidly than forest trees as indicated by the fewer rings per centimeter at larger diameters. This increase presumably corresponds to tree emergence above shrub the canopy. At all sites except Table (Figure 5.7 b), early tree growth in chaparral was slower than in the forest. Seedlings growing in the montane chaparral also showed slow growth, taking more than 20 years to reach 0.5m in height.
Figure 5.7: Average (±SE) number of rings per centimeter from inner portion of trees (>5cm) cored to pith in Lassen Volcanic National Park, CA. 
  a. from four chaparral stands and surrounding forest. b. from each of four chaparral stands and surrounding forest zones.

Tree density

A plot of tree density (trees ha⁻¹) as a function of distance from forest edge into chaparral showed an apparent exponential decline. In order to explore this relationship using a generalized linear model with distance from forest edge as a predictor and tree
density as an outcome variable, density and distance were log transformed and tested for normality. The QQ plot looked normal and there was no obvious trend in the residuals. Density was found to be a negative function of distance where \( \ln(\text{density}) = 8.709 - 0.610(\ln(\text{distance})) \). The model explains 20% of the variance. Because tree density is not expected to be uniform among stands but rather to vary based upon stand characteristics such as time since fire, slope, and aspect, stand was tested as a random effect in a second model. Stand as a random effect allowed the slope of the distance density relationship to vary. For all stands, the relationship between distance from edge and density was negative and significant. Figure 5.8 shows the plots of density as a function of distance by stand. The random stand effect model was significantly better than the fixed effects model by ANOVA (\( p < 0.001 \)) and explained 44% of the variance (Appendix C). In the forest, tree infilling does not show this spatial pattern. From forest-chaparral edge into the forest, there is no apparent relationship between distance and tree density (\( p = 0.30 \)).
Figure 5.8: Generalized linear model of ln(tree density in trees ha\(^{-1}\)) as a function of ln(distance from forest edge m) with chaparral stand as a random effect for six chaparral stands in Lassen Volcanic National Park, CA. (p<0.001, R\(^2\)=0.44). See Appendix C for stand level slope and intercept values.

By zones, the density in the infill zone (547 trees ha\(^{-1}\)) is about twice the forest understory density (272 trees ha\(^{-1}\)) and slightly greater than forest density (421 tree ha\(^{-1}\)) where forest density represents the nearest four trees at a forest point >5cm (Table 5.2).

By site, time since fire does not seem to be the only factor limiting tree invasion. Both the densest infill (1078 trees ha\(^{-1}\)) and chaparral zones (92 trees ha\(^{-1}\)) occurred at Table Mountain, the most recently burned site where almost all the trees have established since the 1918 fire. Table Mountain is the lowest elevation, gentlest sloping site. The lowest infill density (318 trees ha\(^{-1}\)) and chaparral density (70 trees ha\(^{-1}\)) was at Raker Peak, where the fire was in 1873.
Tree composition

The forest in all zones at all sites is dominated by fir, mostly white fir (*A. concolor*). While there was considerable variation among sites, there were some consistent patterns. Pine relative density is lower in both chaparral and infill zones than in the forest overstory. Since fire suppression, a greater number of trees ha\(^{-1}\), larger trees, and more fir have established in former chaparral areas (infill zone) than in the forest understories. Except at Raker Peak, tree density (trees ha\(^{-1}\)) and basal area were higher in the infill zones than in the forest understory (Table 5.2). Raker Peak may be a particularly harsh site, better suited to pines. It has the pine highest relative basal area and overall tree zone tree density is lower than at other sites.

When data from all sites are combined (Table 5.3), the forest composition in the infill zone has a lower pine density than the forest understory. In the chaparral and infill zones, even though firs outnumber pines, the mean tree basal area (m\(^2\) tree\(^{-1}\)) of pines is about 3 times that of the firs. In the chaparral zone and the forest overstory, the pine basal area (m\(^2\) ha\(^{-1}\)) was similar to that of firs (P>0.05, Kolmogorov-Smirnov two sample). In contrast, in the infill zone and forest understory fir basal area was greater than pine (P<0.05, Kolmogorov-Smirnov two sample). In the plots, fir species comprised at least 90% of the sapling and seedling component (Table 5.4).
Table 5.2: Density (trees ha\(^{-1}\)) and basal area (m\(^2\)tree\(^{-1}\)) for fir (Abies concolor and A. magnifica) and pine (Pinus jeffreyi and P. contorta) trees (>5cm) where understory includes forest trees >5cm and <35cm and overstory trees are >35cm dbh. Shown by zone in six chaparral stands in Lassen Volcanic National Park, CA USA.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Zone</th>
<th>Tree Relative Density</th>
<th>Tree Density (trees ha(^{-1}))</th>
<th>Mean Tree BA (m(^2)tree(^{-1}))</th>
<th>Relative Total BA</th>
<th>Mean Total BA (m(^2)ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Fir</td>
<td>Pine</td>
<td>Fir</td>
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<tr>
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</tr>
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<td>chaparral</td>
<td>83</td>
<td>17</td>
<td>139</td>
<td>28</td>
<td>167</td>
</tr>
<tr>
<td></td>
<td>infill</td>
<td>83</td>
<td>17</td>
<td>465</td>
<td>93</td>
<td>558</td>
</tr>
<tr>
<td></td>
<td>understory</td>
<td>80</td>
<td>20</td>
<td>106</td>
<td>26</td>
<td>132</td>
</tr>
<tr>
<td></td>
<td>overstory</td>
<td>71</td>
<td>29</td>
<td>62</td>
<td>26</td>
<td>88</td>
</tr>
</tbody>
</table>
Table 5.3: Mean density (trees ha⁻¹) and basal area (m²tree⁻¹) for fir (Abies concolor and A. magnifica) and pine (Pinus jeffreyi and P. contorta) trees (>5cm) by zone for six chaparral stands in Lassen Volcanic National Park, CA USA.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Fir</th>
<th>Pine</th>
<th>Tot</th>
<th>Fir Relative Density</th>
<th>Pine Relative Density</th>
<th>Mean Tree BA (m²tree⁻¹)</th>
<th>Total BA (m²ha⁻¹)</th>
<th>Relative Total BA</th>
</tr>
</thead>
<tbody>
<tr>
<td>chaparral</td>
<td>110</td>
<td>27</td>
<td>136</td>
<td>80%</td>
<td>20%</td>
<td>0.04</td>
<td>4.9ns</td>
<td>61%</td>
</tr>
<tr>
<td>Infill</td>
<td>482</td>
<td>65</td>
<td>547</td>
<td>88%</td>
<td>12%</td>
<td>0.09</td>
<td>42.6*</td>
<td>72%</td>
</tr>
<tr>
<td>forest (nearest 4 trees)</td>
<td>324</td>
<td>97</td>
<td>421</td>
<td>77%</td>
<td>23%</td>
<td>0.08</td>
<td>25.3*</td>
<td>69%</td>
</tr>
<tr>
<td>understory (&gt;5cm &amp; &lt;35cm)</td>
<td>213</td>
<td>58</td>
<td>272</td>
<td>79%</td>
<td>21%</td>
<td>0.03</td>
<td>7.4*</td>
<td>82%</td>
</tr>
<tr>
<td>overstory (&gt;35cm)</td>
<td>75</td>
<td>32</td>
<td>107</td>
<td>70%</td>
<td>30%</td>
<td>0.32</td>
<td>24.1ns</td>
<td>64%</td>
</tr>
</tbody>
</table>

Table 5.4: Mean sapling (<5cm dbh and >1.4m height) and seedling density (<1.4m height) for fir (Abies concolor and A. magnifica) and pine (Pinus jeffreyi and P. contorta) species by zone for six chaparral stands in Lassen Volcanic National Park, CA USA.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Fir</th>
<th>Pine</th>
<th>Fir Sapling Density (saplings ha⁻¹)</th>
<th>Fir Saplings Relative Density</th>
<th>Pine Sapling Density</th>
<th>Pine Saplings Relative Density</th>
<th>Fir Seedling Density (seedlings ha⁻¹)</th>
<th>Pine Seedlings Relative Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>chaparral</td>
<td>58</td>
<td>4</td>
<td>93%</td>
<td>7%</td>
<td>157</td>
<td>0</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td>Infill</td>
<td>105</td>
<td>3</td>
<td>97%</td>
<td>3%</td>
<td>196</td>
<td>0</td>
<td>100%</td>
<td>0%</td>
</tr>
<tr>
<td>forest</td>
<td>95</td>
<td>10</td>
<td>91%</td>
<td>9%</td>
<td>137</td>
<td>2</td>
<td>98%</td>
<td>2%</td>
</tr>
</tbody>
</table>

Chaparral composition

At all sites, in the chaparral zone plots, the most frequent chaparral species was *Arctostaphylos patula* (greenleaf manzanita) most often codominant with *Ceanothus velutinus* (snowbrush ceanothus) both fire tolerant, shade intolerant species and to a lesser extent with *Chrysolepis sempervirens* (bush chinquapin) which is not fire tolerant (Appendix D). In the chaparral zone, the mode of cover for each of live and dead
A. patula and live C. velutinus was 16%. A. patula cover exceeded 25% at 42% of plots while C. velutinus cover was > 25% at 33% of plots.

Chaparral cover declined from the infill to the forest. About 96% of chaparral plots contained live chaparral whereas in the infill zone, only 60% of plots contained some live chaparral and only 36% in the forest (Table 5.5). Although live A. patula was uncommon in the infill and nearly absent from the forest, there was evidence of past occupation. Some 66% of infill plots contained A. patula skeletons while 24% of forest plots contained skeletons. Live A. patula was less frequent than C. velutinus and C. sempervirens in infill and forest zone.
Table 5.5: Presence of live and dead chaparral species *A. patula* and *C. velutinus* in plots by zone for six chaparral stands in Lassen Volcanic National Park, CA USA. (sample size n=72 chaparral, 76 infill, 72 forest plots)

<table>
<thead>
<tr>
<th>Species</th>
<th>Chaparral (n=72)</th>
<th>Infill (n=76)</th>
<th>Forest (n=72)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Arctostaphylos patula</em></td>
<td>67</td>
<td>27</td>
<td>7</td>
</tr>
<tr>
<td>DEAD <em>A. patula</em></td>
<td>55</td>
<td>49</td>
<td>17</td>
</tr>
<tr>
<td><em>Ceanothus velutinus</em></td>
<td>63</td>
<td>20</td>
<td>2</td>
</tr>
<tr>
<td>DEAD <em>C. velutinus</em></td>
<td>53</td>
<td>25</td>
<td>1</td>
</tr>
</tbody>
</table>

There was a negative association between chaparral cover and tree canopy cover for the three dominant chaparral species. *Arctostaphylos patula* had a stronger negative association with canopy cover (Spearman’s $r_s$=-0.73, p<0.001) than did *C. velutinus* (Spearman’s $r_s$=-0.50 p<0.001) and *C. sempervirens* (Spearman’s $r_s$=-0.30 p<0.05). The association between tree canopy cover and *A. patula* skeletons was weakly positive (Spearman’s $r_s$= 0.24, p<0.05). Because *A. patula* is the only chaparral for which dead stems are easily identifiable to species, correlations with other dead chaparral species were not tested.

**Recent fire severity patterns in chaparral vegetation**

The presence of dead chaparral ground fuels in forests that have established in former chaparral areas combined with topographic characteristics may predispose the former chaparral areas to burn at higher severity than surrounding forest vegetation. Areas that were historically chaparral burned with more high severity than forests. For all three recent wildfires, the chaparral had larger (p<0.001, chi squared goodness of fit) portions burned at the two higher severity classes than did the forest vegetation (Table 5.6). However, areas identified as chaparral vegetation in 1941 also burned at lower
severity. In both the Bluff and Huffer fires, even though there was more high severity burn in chaparral and forest-chaparral mix than in the forest, over half of the chaparral vegetation burned at lower severity (classes 1 and 2). Only in the Badger fire did majority of the chaparral area burn at higher severity (classes 3 and 4).

Table 5.6: Percentage of area burned in each of four NMTBS severity classes in 3 recent (1984-2004) wildfires for three vegetation categories, chaparral, forest and mixed forest and chaparral, derived from a 1 ha grid imposed on 1941 aerial photographs of burn area in Lassen Volcanic National Park, CA USA. *indicates statistically different (p<0.001)

<table>
<thead>
<tr>
<th>Fire Severity</th>
<th>Class</th>
<th>Bluff</th>
<th>Huffer</th>
<th>Badger</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chaparral*</td>
<td>Forest*</td>
<td>Mixed</td>
<td>Chaparral*</td>
</tr>
<tr>
<td>no change</td>
<td>1</td>
<td>40%</td>
<td>22%</td>
<td>31%</td>
</tr>
<tr>
<td>low</td>
<td>2</td>
<td>32%</td>
<td>59%</td>
<td>40%</td>
</tr>
<tr>
<td>moderate</td>
<td>3</td>
<td>21%</td>
<td>18%</td>
<td>22%</td>
</tr>
<tr>
<td>high</td>
<td>4</td>
<td>6%</td>
<td>1%</td>
<td>7%</td>
</tr>
</tbody>
</table>

Appendices E-G show aerial photographs, vegetation classification, and burn severity maps for each fire. For each of the fires and for all fires combined, the tables in Appendix H show the percentage of pixels of each severity class by fire for each of the three vegetation classifications.
Chapter 6

Discussion

Tree invasion

At all sites, tree invasion has occurred since the date of the last fire. Growth suppressions (3 sites) and one known fire date recorded by forest staff (1 site) indicate that the last fires in the montane chaparral occurred between 1862 and 1918. Jeffrey pine and red and white fir began establishing immediately or soon after the last fire and have continued to the present. As trees emerged above the shrub canopy, live chaparral declined, and dead chaparral increased. This resulted in a transition from the chaparral dominated cover that is visible in 1941 photographs to forest vegetation with some remnant chaparral skeletons. Significant tree invasion following fire suppression has been found in other montane chaparral sites (Gruell 2001; Nagel & Taylor, 2004).

Tree establishment data suggests some variation in fire severity in the chaparral and forest by stand. In some stands one or two trees in the montane chaparral pre-date the last fire. These fires may have been patchy with a few trees surviving within the high severity matrix. In the stands where surrounding forest understory tree establishment was delayed for several decades post-fire, the forest may have supported a patchy understory of chaparral immediately after the fire, slowing tree recruitment.

Tree age, density and early growth patterns of in the chaparral stands suggest that invasion occurs gradually from the forest rather than concurrently with chaparral establishment. Trees in the chaparral zone were younger than infill zone trees in two stands while in two stands there was no statistical difference in trees age by zone. One of these, Hat Mountain, also had the shortest transects, 150m in length. They may be too
short to detect age differences. At the other stand, Warner Valley, aerial photographs suggest that some tree invasion could have occurred from islands of trees that established within the chaparral. This may result in more complex spatial age pattern.

Consistent with gradual tree infilling of chaparral from the adjacent forest, tree density (trees ha⁻¹) is highest near the historic forest-chaparral boundary and declines exponentially with distance into the tree and chaparral zones. Greene and Johnson (2002) found that in recently burned areas, seedling recruitment patterns followed the negative exponential seed dispersal curves from the forest edge. Montane chaparral stands occur within the mixed conifer matrix where there is a high likelihood that seeds from nearby trees will regularly disperse into the chaparral (Bock and Bock, 1977; Conard & Radosevich, 1982).

The slow initial growth in rings per centimeter of trees establishing in the chaparral supports the idea that most trees established beneath the chaparral rather than simultaneously after the last fire. The period of intense competition lasted about 20 to 30 years and was followed by a substantial increase in radial growth to a rate more rapid than forest trees. An exception to slow growth occurred at the Table site. At this site, the infill is so dense that more of the sampled trees may have established after chaparral was already in substantial decline. Eventually, after several decades, trees that established under the chaparral will emerge, grow more rapidly, and create tree canopy that increasingly competes with chaparral for light.

There were proportionally less pine in the chaparral and infill compared to the surrounding historic forest. In the chaparral stand, pine generally established before fir. Pine may be more successful early in the invasion process while fir become dominant
over time. If seeds disperse into chaparral, seedling persistence will be limited by ability to survive the micro-conditions. Site conditions in chaparral stands are likely to change with time since fire. Immediate post-fire conditions will lack shade. In high severity fire sites, Jeffrey pine has been found to be initially more successful than fir (Bock and Bock 1977; Pierce and Taylor 2010). Several years after fire, sites are likely to have become heavily shaded by chaparral. Once chaparral canopy is established, fir are likely to be better at persisting beneath chaparral. White fir are less affected by shade and have been shown to establish at similar densities in areas with very different canopy covers (Stephens and Fry, 2005).

The higher pine than fir basal area in the chaparral zone could be consistent with pines establishing earlier than firs and able to grow rapidly in an open environment upon overtopping the shrub canopy. However, once some level of tree canopy is in place, pines seem to be outcompeted by firs, as indicated by the tree zone and understory zone where firs so outnumbered pines that fir basal area was greater than pine.

In the chaparral, pine but not fir were older nearer the forest edge than more interior in the chaparral. Successful pine establishment may depend on a nearby seed source for there to be enough seedlings that some survive the shady conditions. While Jeffrey pines can produce cones at 8 years old, most cones producers are over 18m tall which at these sites would make them at least 40 years old (Burns 1990). Pines may gradually infill whenever new seed trees establish within the chaparral. The progressive invasion by pine may also reflect the role of rodents in successful seed dispersal. Briggs et al. (2009) found that small mammals, especially chipmunks, cache Jeffrey pine seeds
in microsites where they are more likely to produce seedlings. Rodents do not typically transport seeds more than 40m from the source tree (Vander Walls, 2002) and may be reluctant to venture far into an open chaparral stand.

In this study, fir seedlings under chaparral grew only slightly faster than pine, but there were far fewer pines. The ratio of fir saplings to pine saplings in chaparral was nearly the same as in the post fire-suppression forest understory, about 9:1. However, as more trees gradually emerged above the chaparral and a fir dominated forest established, pines seemed to become increasingly infrequent. In the forested former chaparral stands, the seedling ratio was around 30 fir:1 pine. The greater success of fir in invading chaparral may be both because of a larger seed source and greater seedling tolerance of shaded site conditions.

**Chaparral establishment**

Our finding that chaparral stands established after the last fire recorded in nearby tree growth suppressions is similar to other findings of other studies (Floyd et al. 2000; Nagel and Taylor 2005) and suggests that the chaparral stands were initiated by high severity fire. At all study stands, the age distributions of the *A. patula* coincide with establishment after the last fire. The age structure of chaparral species has been used to date past fires in other chaparral communities. In the northern Sierra Nevada, Nagel and Taylor (2005) found that pulses of *A. patula* establishment occurred after fire in montane chaparral. Keeley (1992) used ring counts from several chaparral species to identify the time since last fire for foothill woodland chaparral communities. In
southwestern Colorado, Floyd et al. (2000) aged Gambel oak (*Quercus gambelii*) stems to
determine the decade of the most recent fire in petran chaparral.

At three sites, there were 1 to 4 decades between the estimated fire date and the
establishment of the oldest chaparral sampled. Fires at these sites were older (115, 137 &
148 years before present). In the Sierra Nevada, Nagel & Taylor (2005) found *A. patula* as
old as 150 years whereas the oldest collected in this study were 110 years old. It may be
that chaparral cross sections were collected higher above the base, that cracks in the
sections obscure several decades of rings, or that in some stands the oldest stems were
not sampled. Floyd et al. (2000) found that as time since fire increased in Gambel oak
stands, the original postfire cohort became less recognizable because new stems replaced
dying post-fire resprouts. In our scheme, we selected the largest chaparral within each
plot which may not have been the oldest stems within a stand.

We did find that stands of *A. patula* were multi-aged, indicating continuous
recruitment of new stems. In lower elevation chaparral communities, some stands
unburned for over a century showed little evidence of senescence or successional
replacement by trees (Keeley 1992). Resprouting shrub species have been shown to
recruit new sprouts even in the long-term absence of fire (Nagel & Taylor, 2005; Floyd et
al. 2000). The multi-age structure suggests that suitable site conditions including
sufficient light availability rather than fire are required for montane chaparral
regeneration. In the forest and invaded chaparral, live *A. patula* was less common than
*C. velutinus* and *C. sempervirens* and may be more sensitive to tree infilling.
Chaparral abundance and recent high severity fire

In LVNP, in recent wildfires, more high severity fire, likely to generate optimum conditions for montane chaparral, did occur more frequently in areas that were dominated by chaparral in 1941 than in areas that were historically forested. As land managers seek to restore pre-suppression forest structure and composition, there is an interest in how much high severity fire to expect and accept. Although fires in mixed conifer forests are described as being primarily low to moderate in severity (Kilgore and Taylor 1979; Bonnicksen & Stone 1982; Skinner & Chang 1996), fire history studies indicate that high severity fire may also be a significant component of fire regime (Bekker & Taylor 2001; Beaty & Taylor 2001). In the Sierra Nevada, wildfires in mixed conifer forests that have been returned to a more natural fire regime, typically consist of around 15% high severity burn. When high severity fire occurs within existing chaparral vegetation, it seems to be constrained by the extent of the chaparral (Stephens and Collins 2010). In Lassen, this pattern was especially strong in the Badger Fire, where the majority of the former chaparral burned at high severity but almost none of the forest did. This result suggests that in some locations, chaparral may be self-reinforcing and reestablish in the same location after successive high severity fires. In other places, where former chaparral burned with low severity, the chaparral may be part of a shifting mosaic that has become forested until the time that severe weather condition created more extreme fire behavior.

We did not compare the topographic characteristics of high and low severity burns within chaparral or within the fire extent. However, topographic features are strong predictors of high severity fire in more incised, drier terrain (Beaty and Taylor
The locations of some historical chaparral stands may reflect recurring patterns of topographically influenced high severity fire. The patterns of fire severity that occur in a forest with chaparral skeleton understory are largely uncharacterized. Whether forests with dead chaparral understories are more likely to burn with high severity than those without chaparral has not been extensively evaluated (Odion et al. 2010). These results suggest that some contemporary high severity fire may represent a return to historical vegetation patterns that have been obscured by vegetation changes caused by fire exclusion.

Former chaparral areas also burned at lower severity. Some former chaparral stands may have been a transient feature on the landscape, the result of extreme weather conditions during a fire event. Given time for tree infilling and moderate weather conditions during subsequent fires, some chaparral locations might return to a more stable forested state (Odion et al. 2010).

Some higher severity fire also occurred in areas that were historically forested. As a result of fire exclusion, contemporary forests with higher fuel loads than historic forests may burn at higher severity than they did in the past. Longer time since fire and greater departure from fire return interval have been associated with greater proportions of high severity fire (Collins et al., 2007; vanWagtendonk et al. 2012). Climate changes and more extreme weather may also increase high severity fire. Miller et al. (2009) found that the mean size of the stand replacing component of wildfires in northern California doubled from the late 1980s to the late 2000s. They attributed the increase to secular changes in temperature and precipitation.
High severity fire in mixed conifer forest is not just a recent phenomenon. In addition to the landscape-scale loss of chaparral documented by this and other studies, chaparral has also declined as a component of the forest understory wherever larger gaps in the canopy were created by fine scale heterogeneity in fire severity. Along the transects, chaparral was uncommon in the forest understory. This is likely also a result of fire suppression increases in tree density and reduction in light availability on the forest floor. In the Klamath Mountains, Skinner (1995) found that fire suppression practices have caused a reduction in the size of existing forest openings and the formation of new ones. Knapp et al. (2012) found large seed banks of *Ceanothus* and *Arctostaphylos* in long unburned forests that had little or no live chaparral in the understory. *Ceanothus* seeds were found at almost all sites. *Arctostaphylos* were most common in fir forests where fires were less frequent and probably included more forest openings created by high severity fire (Knapp et al. 2012).

The ubiquity of chaparral seeds suggests that chaparral has the potential to establish where suitable conditions are created and offers additional evidence that high severity fire was part of the historical regime. It is possible that seeds are present because most places within the forest experienced high severity fire at some time in the past. However, because tree infilling has occurred in chaparral stands and in forest understory, fuel structure has become more homogenous at both stand and landscape levels. With potential for climatic changes and more frequent extreme weather combined with fewer natural fuel breaks to dampen fire behavior, high severity fire and montane chaparral could become more widespread than in the past. In wildfires in Yosemite National Park, high severity fire in forests led to the establishment of montane
chaparral. Subsequent fires, a decade or more later, tended to reburn with high severity, maintaining chaparral (vanWagtendonk et al. 2012). There is the potential for high severity fire and therefore montane chaparral to increase within the forest in a self-reinforcing pattern reversing the decline of chaparral in unburned forest.
Chapter 7

Conclusions

In LVNP, the montane chaparral stands that are visible in 1941 aerial photographs likely established in the last severe fire to burn the surrounding forest, dated to between 1862 and 1918. Fire suppression has caused large scale replacement of montane chaparral with mixed conifer forest. In 2005 photographs, most chaparral stands are greatly reduced in size. The ages of trees within the chaparral indicate gradual infilling by a multi-aged tree population that established after the last fire, mostly since fire-suppression was implemented in 1905. The chaparral populations also established after the last fire and in open areas have continued to resprout.

As a result of tree infilling, the structure and composition of the mixed conifer forests has become more homogenous at the landscape scale. A lower percentage of live chaparral cover is associated with increased tree canopy cover. In the infill, even though pines establish earlier and have larger basal area per tree than fir, the relative density of fir is higher than it is in the forest.

An understanding of the dynamics of montane chaparral and high severity fire within the forest matrix may be useful to managers charged with orchestrating prescribed burns and managing wildfires with the goal of restoring forest heterogeneity to historic levels. The historical presence of chaparral is an indication that high severity fire was part of the fire regime of the southern Cascades. The high infill tree density, understory of dead chaparral, and steepness of terrain may predispose some former chaparral areas to a self-reinforcing pattern of repeated high severity fire. Recent wildfires have burned in historical chaparral with a greater amount of high severity than
in surrounding forest. It may be possible to restore chaparral and landscape heterogeneity with the reintroduction of high severity fire.
Appendix A
Linear regressions of tree age as a function of diameter at breast height for pines (Pije & Pico) and firs (Abma & Abco) from trees cored to pith in Lassen Volcanic National Park CA.

Abco & Abma
Age as function of DBH

\[ y = 0.9686x + 49.972 \]
\[ R^2 = 0.5196 \]

Pije & Pico
Age as a function of DBH

\[ y = 1.5401x + 50.5 \]
\[ R^2 = 0.5661 \]
Appendix B

Ages of Abco and Pije seedlings growing beneath chaparral canopy in Lassen Volcanic National Park, CA

\[ y = 49.986x \]
\[ R^2 = 0.479 \]
\[ y = 55.462x \]
\[ R^2 = 0.9022 \]
Appendix C

Generalized linear model R output for tree density (trees ha⁻¹) as a function of distance(m) from forest edge with stand as a random factor

(\text{formula} = \ln{\text{density}} \sim \ln{\text{distance}}:\text{stand}, \text{data} = \text{densitydata})

Coefficients:

\begin{center}
\begin{tabular}{lrrrr}
 & Estimate & Std. Error & t value & Pr(>|t|) \\
(Intercept) & 9.69443 & 0.43506 & 22.283 & < 2e-16 *** \\
ln.distance:standBear & -0.98880 & 0.10923 & -9.053 & 9.76e-16 *** \\
ln.distance:standCluster & -0.72401 & 0.09206 & -7.864 & 8.49e-13 *** \\
ln.distance:standRaker & -0.90125 & 0.09021 & -9.991 & < 2e-16 *** \\
ln.distance:standSouthHat & -0.92894 & 0.10673 & -8.703 & 7.36e-15 *** \\
ln.distance:standTableMtn & -0.64070 & 0.09041 & -7.087 & 5.89e-11 *** \\
ln.distance:standWarner & -0.80721 & 0.09423 & -8.566 & 1.61e-14 *** \\
\end{tabular}
\end{center}

Residual standard error: 0.8245 on 142 degrees of freedom
Multiple R-squared: 0.4655, Adjusted R-squared: 0.4429
F-statistic: 20.61 on 6 and 142 DF, p-value: < 2.2e-16

Adding random slope for stand is significant as indicated by the significant difference between model 1 and model 2.

Analysis of Variance Table
Model 1: ln.density ~ ln.distance
Model 2: ln.density ~ ln.distance:stand
\begin{tabular}{llllll}
Res.Df & RSS & Df & Sum of Sq & F & Pr(>F) \\
1 & 147 & 143.124 & & & \\
2 & 142 & 96.528 & 5 & 46.596 & 13.709 6.412e-11 *** \\
\end{tabular}
Appendix D

Presence of live and dead chaparral species in plots (sample size = n) by zone for six chaparral stands in Lassen Volcanic National Park, CA USA.

<table>
<thead>
<tr>
<th>Species</th>
<th>Table</th>
<th>Raker</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chaparral (n=12)</td>
<td>Infill (n=16)</td>
</tr>
<tr>
<td>Arctostaphylos patula</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Ceanothus velutinus</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Chrysolepsis sempervirens</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>Prunus emarginata</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>DEAD A. patula</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>DEAD C. velutinus</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>DEAD C. sempervirens</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Bear</th>
<th>Cluster</th>
<th>Hat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chaparral (n=12)</td>
<td>Infill (n=12)</td>
<td>Forest (n=12)</td>
</tr>
<tr>
<td>Arctostaphylos nevadensis</td>
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Appendix E


A. Bluff Fire perimeter superimposed on the 1941 aerial photo mosaic, B. the assigned vegetation type in 1 ha grid, green = forest, purple = chapparal, pink= mixed forest & chaparral C. Bluff fire rNDBR severity map, D.clip of severity class in forest – dominated vegetation in 1941, E. the severity class in 1941 mixed forest/chaparral vegetation, F. the severity class in 1941 chaparral dominated vegetation.
Appendix F

A. Huffer Fire perimeter superimposed on the 1941 aerial photo mosaic, B. the assigned vegetation type in 1 ha grid, green = forest, purple = chaparral, pink = mixed forest & chaparral C. Huffer fire rNDBR severity map, D. clip of severity class in forest-dominated vegetation in 1941, E. the severity class in 1941 mixed forest/chaparral vegetation, F. the severity class in 1941 chaparral dominated vegetation.
Appendix G


A. Badger Fire perimeter superimposed on the 1941 aerial photo mosaic, B. the assigned vegetation type in 1 ha grid, green = forest, purple = chaparral, pink = mixed forest & chaparral C. Badger fire rNDBR severity map, D. clip of Badger severity class in forest–dominated vegetation in 1941, E. the Badger severity class in 1941 mixed forest/chaparral vegetation, F. the Badger severity class in 1941 chaparral dominated vegetation.
Appendix H

Percentage of burn in NMTBS severity classes in 30X30m pixels by historical vegetation type.


![Bar chart a.](image1)

![Bar chart b.](image2)

![Bar chart c.](image3)