Shrub Response to Short vs. Long Disturbance Free Interval in Northern California Chaparral: A Fire and Fire Surrogate Study

Jameson N.P. Christiansen

ABSTRACT

The shrub dominated Northern California chaparral is a biodiverse ecosystem that is highly adapted to fire. Historical mean fire return intervals in these communities are estimated to have been relatively infrequent, with high severity, stand-replacing fires occurring every 30-70 years. However, this ecosystem has experienced significant anthropogenic alteration of its historic regime. Widespread fire suppression for the past century created an uncharacteristically long fire-free period followed by a recent dramatic increase in the number of fires burning through chaparral stands in short periods of time. It has been suggested that too infrequent fire occurrence may lead to change in plant community structure, while fire returning at too short of interval may lead to risk of type conversion to grassland vegetation. Yet few studies have tested these expectations in Northern California chaparral. To better understand the implications of disturbance regime variation in this ecosystem I resampled a network of research plots in Mendocino county's coast range chaparral. These plots were first established in 2001 and subsequently treated as part of a study observing the long-term disturbance effects of fire and mastication. A 2018 wildland fire event then burned both treated and control plots creating patches of short (<20 years) and long (> 60 year) disturbance return intervals respectively. Significant differences in growth and diversity were not detected between sites experiencing long vs. short disturbance free intervals or different initial treatments. This suggests that chaparral shrubs may have similar recovery trajectories and may be more resilient to variable disturbance intervals than previously feared.

KEYWORDS

fire return interval, mastication, prescribed fire, wildfire, fire regime

INTRODUCTION

Over recent decades in California, wildfire events have been increasing dramatically, both in size of fire area and frequency of event (Williams et al. 2019). California ecosystems have evolved with the influence of fire as an abiotic factor and are adapted to be resilient to specific regimes of fire recurrence (Sugihara et al. 2019). Humans have long influenced these fire regimes dating back to California's earliest inhabitants, indigenous people who stewarded fire on the landscape to promote ecosystem service benefits (Anderson 2019). Early in the 20th century, the relationship of people utilizing fire on the landscape abruptly ended and was replaced with policy strategies aimed toward complete fire suppression (Stephens and Sugihara 2019). In the contemporary era, those policies have been relaxed somewhat, allowing for some prescribed burning to maintain the landscape and some reintroduction of cultural burning practices by indigenous people, yet these burns are still highly constrained both by policy and practical limitations (Marks-Block and Tripp 2021, Quinn-Davidson and Varner 2011). Meanwhile, humankind has exerted further influence over fire regimes by altering climate systems. Anthropogenic climate change has made fire events in California more likely, by making drought conditions occur more frequently, which dries out vegetation and woody fuels, combined with the more frequent occurrence of fire weather conditions (Bowman et al. 2020, IPCC 2021). California's ecosystems must now respond to novel and challenging fire-promoting conditions, where the era of fire suppression has built up fuels and vegetation, followed by the era of climate change making these materials more likely to burn.

The focus of wildland fire research is often placed on the coniferous forested areas of California, while another important ecosystem, the highly fire prone California chaparral, receives less research focus (Calhoun et al. 2021). The California chaparral is a shrub dominated ecosystem. These shrubs feature sclerophyllous leaves and have branches that grow to form a continuous thicket of ground adjacent canopy (Barro and Conard 1991, Rundel 2018). Fires behave differently between these two ecosystems. In conifer forests fires may have varying levels of severity, from low intensity surface fires to high intensity crown fires (Agee 1998). In contrast, fires in the chaparral are primarily carried through the canopy. Here, high severity stand replacing fires are the norm (Keeley and Davis 2007). The time between fire events, referred to as the fire return interval, is an important metric characterizing fire regimes (Sugihara et al.

2019). Long ranging histories of fire return intervals are more readily observed in forested ecosystems, where fire scars, recorded in the tree rings of fire survivors, show evidence of prior events. Whereas in the chaparral, observations of past fire events are largely limited to records of fire perimeters from the modern era (Collins et al. 2019, Rundel 2018). This means that while much is known about how differing ranges of fire return interval affect California's forests, much less is known about how different timing between these disturbance events affect the chaparral.

The shrub species of the California chaparral are fire adapted in such a way, that much of their reproduction is connected to fire events. Older stands of chaparral typically have a completely closed canopy, with little opportunity for growth in the understory (Christensen and Muller 1975). When a fire event occurs it typically will remove most of the canopy, allowing light to penetrate to the ground for the first time in decades. As the fires convert woody debris to ash, this re-introduces nutrients to the soils that were previously trapped in the canopy, further promoting new growth (Rundel and Parsons 1984). Chaparral species are characterized by three major methods of post-fire regeneration (Keeley 1991). One group is the obligate seeders that require the influence of fire to stimulate seeds to germinate. Buckbrush (*Ceanothus cuneatus*) is an example of a species with this life history. Obligate sprouters on the other hand have seeds that are less likely to survive a fire and will respond to fire primarily through basal resprouting. California Scrub Oak (*Quercus berberidifolia*) is an example of this feature, having acorns that take several years to mature and are likely to be damaged by fire. The third group is known as the facultative seeders. Species in this group may regenerate both by basal resprouting and by the fire promoted seed germination. Chamise (*Adenostoma fasciculatum)*, in an example of the success of this life history. With the ability to respond to fire either vegetatively through sprouting or sexually through seed germination, Chamise is the most prolific plant in the chaparral (Rundel et al. 1987, Hilbert 1987). These three types of post-fire regeneration work in concert with the timing between fires, with there being risk of seedlings being immature if fire returns too quickly, or risk of stand and seed senescence if fire return interval is too long (Keeley and Fotheringham 2000, Hilbert 1987). Much of the existing research on this topic has been conducted in the Southern California Chaparral. This study is, to the best of my knowledge, one of very few to explore fire regime variations in Northern California chaparral (Wilkin et al. 2017).

A research site in Northern California chaparral was established in 2001 as a long-term study to observe response to fire in this ecosystem (Potts et al. 2010). This site was then exposed to a range of treatments on the landscape, including prescribed burns over three different seasons, and mastication (shredding) over two seasons, which acts as a stand removing fire surrogate. Prior to these treatments, no stand replacing events are known on record, and the area was characterized as senescent. Seventeen years later in 2018, a wildland fire event occurred in the area, burning 19 of the 24 original plots. This created a situation where treated plots had only a short 15-17 year disturbance free interval prior to the wildfire event, while the untreated control plots had not seen disturbance in more than 70 years, a long interval. In this study I seek to better understand, how does shrub regrowth respond differently to short vs long intervals of time between stand replacing disturbance events. I investigated this topic by asking the following specific research questions:

(1): How does shrub diversity differ between short vs long intervals of time between fire disturbance events?

(2): How does shrub growth differ between short vs long intervals of time between fire disturbance events?

(**3):** Given that findings from the prior studies in this area found that the mastication treatment reduced shrub growth, will these differences remain after the entire area is exposed to a fire event?

METHODS

Site Description

To observe the response of shrubs to variable fire regimes, I surveyed chaparral sites that had been subjected to recent stand-replacing disturbance events. My study area is in Mendocino County coast range chaparral, approximately 50 km inland from the Pacific Ocean and 175 km north of San Francisco (39°N, 123°W), near Ukiah California, USA. This area experiences a characteristic Mediterranean climate, which includes hot dry summers, with most precipitation occurring over the mild winters (Deitch et al. 2017). With elevation ranging from 214 m to 305 m above sea level, the experimental plots are on steep (35% to 55%), south and west facing slopes. Soils are rocky, shallow, and mildly acidic, derived from weathered sandstone and shale

(Potts et al. 2010, Wilkin et al. 2017). The vegetation of these sites is dominated by *Adenostoma fasciculatum* (Chamise), with *Ceanothus cuneatus* (Buckbrush) and *Arctostaphylos* (Manzanita) species making up a more minor component of the plant community. The experiment sites are representative of Chamise chaparral, which occupies areas throughout the mountain ranges of California (Rundel 2018). The naturally occurring fire return interval of Chamise chaparral is estimated to be between 30-70 years (Stephens et al. 2007). Prior to treatment the plant community at our sites was nearly 100% shrub cover, an average height of 1-2 m, and over 65% of the overstory was composed of Chamise.

Study Design

To observe plant response to fire disturbance, late successional chaparral plots were established in 2001. The study area was spread between two distinct sites: one at University of California Hopland Research and Extension Center, and the other at US Bureau of Land Management South Cow Mountain OHV Recreational Area. Prior to treatment, no fire or large disturbance event had occurred on these sites in at least 50 years, with the plant community on sites being in a late successional state. The study area was divided into 24 experimental plots, with each plot area being approximately 2 ha. Plots were assigned to five different combinations of fuel removal technique and season of application, plus a control group. Each of these groups had four replicants each. The treatment types were prescribed fire performed in fall, winter, or spring, and mastication performed in fall or spring. Fall treatments occurred in November, winter treatments in January, and spring treatments from April through June. The treatments did impose some limitations to the study. To preserve roads and sensitive habitat, mastication could not be performed in winter, and had to be performed later in Spring than prescribed fire. Additionally, mastication equipment can only be safely operated on lower grade slopes (3% to 25%). Aside from limiting mastication to this range of slope, treatment types were randomly assigned. All fuel removal treatments resulted in a similar effect on vegetation cover, reducing it by 90% to 100%.

In mid-August of 2018, the River fire, a part of the 2018 Mendocino complex, burned 19 of the 24 experimental plots. These plots burned at high severity, removing most vegetation. Of the five plots that were outside the fire perimeter, two were fall mastication treatment type, plus one each of spring mastication, fall prescribed fire, and winter prescribed fire. This resulted in a situation where the four control plots were only treated with wildfire and had not experienced a prior disturbance event in greater than 70 years, a long disturbance free interval. The remaining 15 plots that had been treated between 15-17 years prior, a short interval. Of these, 10 had initially had the prescribed fire treatment, and 5 had mastication treatment, and all 15 later exposed to wildfire.

Sampling Regime

To measure shrub response to variation in disturbance regime, in 2021 after three years of post-fire growth, I measured the 19 plots that were within the river fire perimeter using the line transect method. Each plot was initially established containing fifteen line transects, each being 15 meters in length, which were randomly located and permanently installed. I measured shrubs by placing a measuring tape between transects posts and recording species composition and cover continuously as it intersected the line. Additionally, shrub height was also recorded at 3 m intervals on the line transect, including the 0 m and 15 m heights, for a total of 6 height recordings per transect.

Data Analysis

To evaluate the shrub response to these disturbance events, I used linear and generalized linear mixed effects models. I based model selection on the method that best normalized the data distribution or model residuals when data normalization was not possible. I evaluated all data sets at the sample transect scale (n = 274). To address the question of shrub diversity, I analyzed the metric of shrub species richness by treatment groups. Richness data was non-normally distributed, having a positive skew. I used a generalized linear mixed effects model to account for this, treatment groups paired with richness were the fixed effects, and plot units were the random effect. I tested Poisson, binomial, and Gaussian models and selected the Poisson model for having the most normal distribution of residuals. To analyze shrub growth by treatment group, I used the metric of percent shrub cover by transect. Percent shrub cover data was negatively skewed, however I was able to normalize using a square-root transformation. This allowed me to use linear mixed effect models to analyze this data. I used percent cover paired with treatment groups as the fixed effects, and the plot unit as a random effect. All analysis was performed in R version 4.1.2 (R Core Team 2020).

RESULTS

Shrub Diversity

I measured nineteen plots, ranging from eleven to fifteen transects per plot, for a total of 274 transects measured (Table 1). Although all of the plots were initially established with fifteen transects, in some plots I was only able to locate fourteen transects. Additionally, in the case of plots D and F, a portion of the plot was outside of the 2018 fire perimeter, leaving twelve and eleven transects respectively, within the fire perimeter. I did not include unburnt plots or transects in this study.

This data set has an uneven distribution of plots and transects across treatment groups. The smallest group of transects is the control/wildfire only plots which make up the short disturbance free interval group (n = 59). Mastication transects are close in number (n = 67). However, prescribed fire transects are far more numerous (n = 148). When the prescribed fire and mastication groups transects are combined to form the short interval group (n = 363), it makes for a large difference in sample size between long and short disturbance interval groups.

Table 1. Number of transects where each shrub species was observed. Transects are grouped by initial treatment, and plot. Bottom two rows show the number of species observed in each plot, followed by the total number of transects measured in each plot.

	Control Plots				Fire Plots										Mastication Plots					Total
Shrub Species	**6**	**9**	**P**	**Q**	**2**	**4**	**5**	**7**	**C**	**E**	**J**	**K**	**L**	**O**	**1**	**8**	**A**	**D**	**F**	
Adenostoma fasciculatum	15	14	15	15	15	15	15	15	15	15	14	15	15	14	14	15	15	12	11	274
Arctostaphylos canescens				1																1
Arctostaphylos glandulosa		5	3	5	9		3	3		4	3	1	1	3	1	4	4	3		52
Arctostaphylos manzanita			5		1		2	1								1				10
Arctostaphylos stanfordiana			6			2	4	1										2	1	16
Baccharis pilularis	3				1								1		3					8
Ceanothus cuneatus cuneatus	1	12	12	11	13	11	10	14	5	12	11	12	6	13	6	7	6	11	3	176
Ceanothus foliosus		1	9	7	3		1						1	3		3	1	2	2	33
Cercocarpus betuloides			1	2					1				3							7
Eriodictyon californicum	1	4	3	5	4	6	2	12	7		9	9	4	14	3	2	1			86
Garrya fremontii								1						1						2
Heteromeles arbutifolia	3					1	2	4	6	1			8	5	1	2			1	34
Lepechinia calycina						2														2
Lotus scoparius	6				3	2	9	4							10	8				42
Mimulus aurantiacus	7	5			8			6												26
Pickeringia montana									3											3
Quercus berberidifolia			1	1	1		1						2			1	4	2	2	15
Quercus durata durata		1	2		1				1								1	5	1	12
Toxicodendron diversilobum			2	1					1	2			2	1	1		1	1	1	13
Plot Richness	**7**	**7**	**11**	**9**	**11**	**7**	**10**	**10**	**8**	**5**	**4**	**4**	**10**	**8**	**8**	**9**	**8**	**8**	**8**	**19**
Total Transects per Plot	**15**	**14**	**15**	**15**	**15**	**15**	**15**	**15**	**15**	**15**	**14**	**15**	**15**	**14**	**14**	**15**	**15**	**12**	**11**	**274**

In my surveys I observed nineteen distinct shrub species. Mean shrub species richness per transect were similar between groups (Fig. 1). The control/long interval group had a mean richness of 3.14. The prescribed fire group had a mean richness of 3.05, mastication group's mean was the lowest at 2.61, and when these two groups were combined to form the short interval group the mean was 2.91. The generalized linear mixed effects model did not show any significant difference in species richness between groups. No difference was found between fire ($p = 0.81$), mastication ($p = 0.16$), or Long and Short DFI ($p = 0.51$).

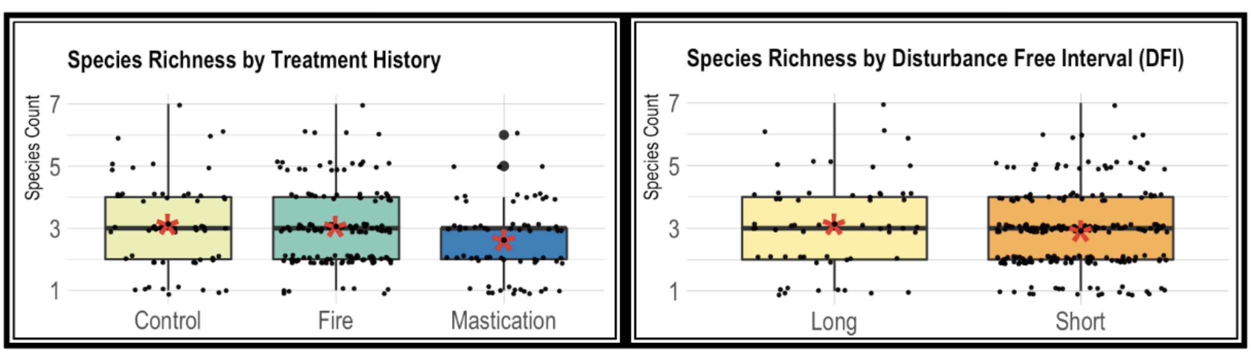

Figure 1. Boxplots of shrub species richness by transect. Left graph is grouped by initial treatment, control (n = 59), prescribed fire (n = 148), and mastication (n = 67). Right graph shows this data regrouped, with the control plots representing a long disturbance interval (n = 59). Fire combined with mastication groups represent the short interval (n = 215). Mean shrub species richness is displayed with a red star.

Shrub Growth

In my survey area the most abundant shrub was Adenostoma fasciculatum (chamise). This shrub was found on all 274 transects. Percent transect cover for Adenostoma fasciculatum ranged from a minimum of 2%, to maximum of 100%, with a mean cover of 65%. The second most abundant species was Ceanothus cuneatus (buckbrush). I observed this species in every plot unit, and in 64% of the transects. On the transects where I found buckbrush, percent cover ranged from a minimum of 0.001% to a maximum of 49%, with a mean cover of 10%. Only one transect had 100% shrub cover. All other transects had some sections of the length where no shrubs intersected the line. The percent cover with no shrub had a mean of 26%, a median of 23%, and a range from zero to 91.7%. I used the inverse of no shrub measurements, as a measure of total cover for each transect. This yielded a mean value of 74%, a median of 77%, and a range of 8.3% to 100% of shrub cover across all transects.

Mean shrub cover was similar between disturbance interval groups, with long at 75% and short at 73% (Fig. 2). Shrub cover data was negatively skewed, and I normalized it using a square-root transformation. I used a linear mixed effects (LME) model to analyze the transformed data which reported no significant difference between long and short interval groups ($F_{1,15} = 0.21$, $p = 0.65$).

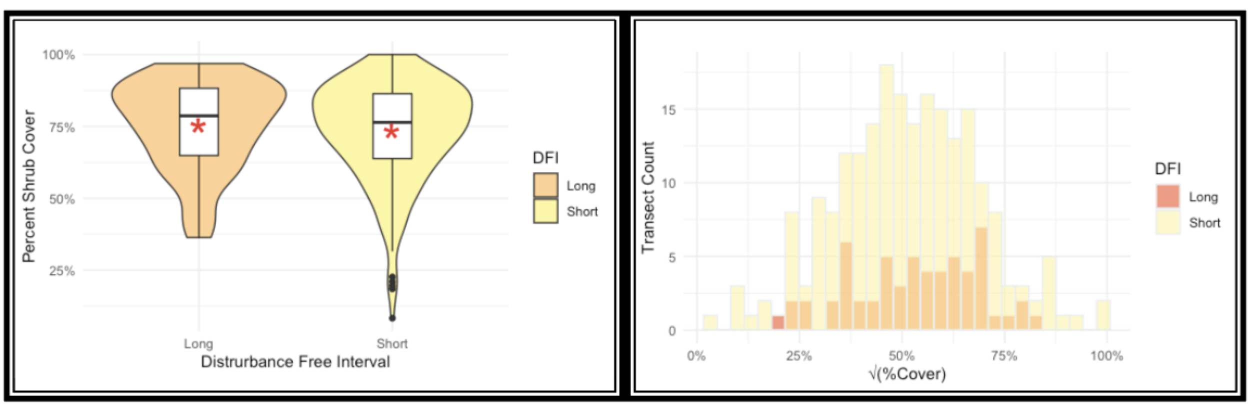

Figure 2. Transect distribution of percent shrub cover by disturbance free interval (DFI). Violin plot shows mean values with a red star, for long interval (n= 59) mean is 75% and for short interval (n = 215) mean is 73%. Histogram shows this transect shrub cover data normalized using square root transformation.

Percent cover showed only a minor difference between transects initially treated with prescribed fire or mastication. The fire plots had a higher mean of 76% cover as compared to a mean cover of 68% in masticated transects (Fig. 3). The small difference between treatment groups was found to be non-significant by an LME analysis of square root transformed data ($F_{1,13} = 1.74$, $p = 0.21$).

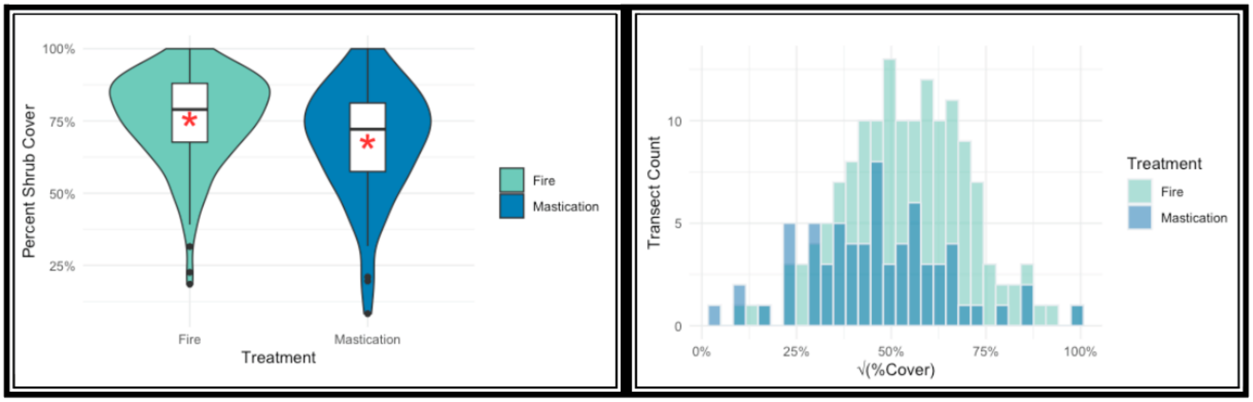

Figure 3. Transect distribution of percent shrub cover by initial treatment. Violin plot shows mean values with a red star, for prescribed fire (n = 148) mean is 76% cover and for mastication (n = 67) mean is 68%. Histogram shows this transect shrub cover data normalized using square root transformation.

DISCUSSION

My research found that the post-fire recovery of Northern California chaparral was remarkably similar, between areas that had been recently disturbed, versus those that had not seen a stand replacing event in a great while, and that differences between initial treatment of prescribed fire or mastication, had little impact on stand recovery. Older models of chaparral succession were based on intermediate disturbance theory, believing that post-fire recovery could be negatively impacted by immaturity risk if fire recurrence was too frequent, or senescence risk if fire was too infrequent (Keeley et al. 2005). Contrary to what I would expect in an idealized intermediate disturbance model, mean shrub species richness was similar, as was mean percent shrub cover, regardless of time since prior disturbance. Between the two different treatments initially used in this study, prescribed fire and mastication, only minor differences in effect remained between these treatments after the area experienced a wildfire event. This indicates that mastication is indeed an appropriate surrogate for fire in this ecosystem, despite differences in nutrient cycling and higher plant mortality of mastication treatment.

Shrub Species Richness

My study found mean shrub species richness to be similar between short and long disturbance free interval groups. Although my short interval (15-17 years) was outside the estimated fire return interval for this ecosystem (30-70 years), it may not have been short enough for immaturity risk to filter out obligate seeding species. Findings from Southern California chaparral show that extirpation of obligate seeders occurs when fires return with less than 5 years of recovery time, and that the range of 5-15 years was enough time for seed banks to recover (Keeley et al. 2005). My findings agree with this by showing that seed bank was equally well developed between long and short disturbance interval chaparral, as mean shrub richness was maintained between these groups.

The finding that shrub species richness was similar between short and long intervals challenges the idea of senescence risk forcing extirpation of species from this ecosystem. For early researchers of chaparral succession, it was common to consider this ecosystem to be rejuvenated by fire. It was believed that old stands of chaparral, deprived of fire, declined to a state of senescence where both productivity and species diversity was reduced (Vogl 1982). This idea has since fallen out of favor. Research performed on chaparral stands that ranged from 56 to 120 without fire events, found that greater stand age did favor some species and life histories over others, but did not result in an overall change in species richness (Keeley 1992). My results agree with the argument against the prior view of senescent chaparral, by showing that post-fire species richness is similar in both older and younger stands of chaparral.

Shrub Growth by Disturbance Free Interval

I found that shrub growth measured in percent cover was remarkably similar between short and long interval groups. Short fire return interval can be a major driver of type conversion from shrub dominated chaparral to grassland, however the short interval in my study may not have been short enough to capture this phenomenon. A study in Southern California chaparral showed the importance of short fire return intervals in promoting type conversion but found that this risk occurs in the less than 15 year range (Syphard et al. 2019). My results agree with this study by confirming that the 15-17 year range disturbance interval is similar to older growth chaparral in its resilience to type conversion.

Considering my results that regrowth was similar between short and long disturbance intervals, it is interesting to consider the potential differences in fuel build up and fire severity. Older stands of chaparral should have a substantially larger buildup of fuel, as both live and dead branch material build up in the canopy, and as litter builds in the understory. Research from Southern California confirms that older stands of chaparral do indeed burn with higher severity, but they found that this increased severity had a relatively small influence on post-fire recovery when compared to other effects (Keeley et al. 2008). This is another example of a potential senescence risk, that in this ecosystem does not appear to be accurate and may have been derived from how we understand fire behavior in forested ecosystems (Halsey and Syphard 2015). My results do agree with this understanding by showing that despite having a much longer buildup of fuels in older sections of chaparral, the recovery of shrub cover was similar to sections that had been more recently disturbed.

Shrub Growth by Initial Treatment

Prior studies on this site found that mastication plots resulted in reduced shrub growth when compared to areas treated with prescribed fire. My results show that these effects have continued somewhat but not to a statistically significant degree. If reduced shrub growth was only due to higher shrub mortality in mastication treatments, the following wildfire treatment may have simply allowed damaged patches time necessary to reestablish. However, this may not be the full explanation. A recent study in Northern California chaparral confirmed that mastication treatments resulted in reduced shrub growth, and that fifteen years later this reduced growth remained (Martorano et al. 2021). Another factor to consider is that the seeds of some shrub species have increased rates of germination in the presence of factors unique to fire such as high heat and smoke exposure (Wilkin et al. 2013). It is possible that my observation of the reduced effect of mastication is due to the re-establishment of fire cued seedlings.

My results did show that shrub growth was greater in areas that had an initial treatment of prescribed fire, than those treated with mastication. I had expected the opposite, that shrub growth may have been reduced in plots that had burned twice, due to potential nutrient losses. In mature chaparral there is poor availability of nutrients in the soil, with most of the nutrients in this system stored in the plant tissues of the canopy (Christensen 1973). Fire events can rapidly release these nutrients, but some amount is lost during the event to volatilization, and further losses occur in the following seasons due to erosion (DeBano and Conrad 1978). As plant material slowly decomposes in situ, mastication treated areas would not suffer these same nutrient losses (Potts et al. 2010). My findings suggest that chaparral areas are resilient to the nutrient losses of repeated fires, while benefiting from the rapid release of nutrients fire provides.

Limitations

There are some important limitations to my research. The quasi-controlled nature of this study was prompted by an unplanned wildfire event, which established the disturbance intervals based on the date this event occurred. Additionally, this made for an uneven distribution of treatments across plots, allowing the smaller groups of long interval and masticated plots to be over-represented when compared to the larger prescribed fire and short interval groups. It would be more ideal to study a wider range of disturbance intervals especially in the important short interval spread from 3 to 17 years. It would also be better to have treatment groups more even in sample size. Another issue has been the difficulty in determining what disturbance events may have occurred on this location prior to the 70 year record we have on the site. I can say that prior to treatments in 2001 the area had been disturbance free for more than 50 years, but only because the record ends there, not because I know of any specific disturbance event. If there is truly a senescence pressure on old growth chaparral, it is possible that all the plots had been conditioned by this pressure prior to initial treatments.

Future Directions

I am looking forward to continuing to explore the data from this study area. In the topic of shrub diversity, I would like to perform analysis on how species evenness is impacted by disturbance interval groups. I also would like to explore individual species relationships with this factor, to see if any species were excluded in any treatment groups. I am also interested in incorporating the data from the initial study in this area for comparison. Studies from Southern

California chaparral found that lack of precipitation was the second most influential factor leading to type conversion (Syphard et al. 2019). I would like to explore how this area of chaparral may have recovered differently in the early 2000's when precipitation was more regular, as compared to the post 2018 growing seasons that I observed, which have been more drought exposed. Further understanding of the combined impact of fire and drought could be important as California continues into an era where both factors are likely to occur more frequently than in the past.

Broader implications

This research provides evidence that although chaparral plant species are highly adapted to the presence of fire, they are also resilient to wide variations in fire recurrence. Land managers may prevent fires from entering chaparral areas without concern that they are forcing the landscape into a state of senescence. Where regular fuel removal treatments are required to protect nearby features, managers may have some confidence that this ecosystem will remain resilient to treatments recurring after fifteen years have passed. When mastication is chosen to remove fuels, this technique can result in reduced shrub growth, but reintroduction of fire can lessen these effects. It is important to note that the California chaparral is not a fuel limited system, rather it is ignition limited (Keeley and Fotheringham 2001). In the era of climate change, it is expected that ignitions will occur more frequently leading to large areas of chaparral burning (Davis and Michaelsen 1995). It will be important to protect this biodiverse ecosystem to limit fire events to recurrences greater than fifteen years to avoid species extirpation and ecosystem type conversion.

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