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Wilkin, Katherine Marie Johnston

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California forest and shrubland ecosystem changes in relation to fire, fuel hazard, and climate change

By

Katherine M Wilkin

A dissertation submitted in partial satisfaction of the requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Scott L. Stephens, Chair
Professor Nina Maggi Kelly
Professor David D. Ackerly

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ABSTRACT

Exploring climate change refugia, fuel hazard treatments, and restored fire regimes

By Katherine M Wilkin

Doctor of Philosophy in Environmental Science Policy and Management

University of California, Berkeley

Professor Scott L. Stephens, Chair

Fire is an integral ecological process, however fire's impacts have been dramatically altered by people. In this dissertation I researched how fire ecology use to work and the vulnerability of ecosystems to fuel hazard reduction treatments by using a combination of experiments and landscape scale natural experiments throughout California. One of the best places to understand past fire behavior are the Wildland Fire Use areas in Sierran mixed conifer where I revealed that a forests' environment, local-scale fire experiences, and regional fire experiences foster a rich, but sparse understory plant community. Throughout Yosemite National Park's mixed conifer zone I examined the fire ecology of climate change refugia which have unique fire occurrence and severity patterns in frequent-fire mixed conifer forests of California's Sierra Nevada: cold-air pool refugia have less fire and if it occurs, it is lower severity. In Northern California's chaparral I examined fuel hazard reduction treatments and found that mastication and fire each have negative, yet unique influences on plant communities and fuel hazards which warrant examining other methods to protect people from chaparral fires. Overall these studies allow greater insight into our ecosystems and may help managers make informed fire management decisions.

ACKNOWLEDGEMENTS

My parents lead me to believe that I had the intellect to be anyone or do anything that I wanted, which was to their detriment when I was a teenager. My journey to complete a doctorate began in elementary school when I played “Dr. Wilkin” to mimic my father and wore his fashionable hot pink doctoral gown. My sister, Beth, patiently listened to my lectures at our basement chalkboard. I pulled my first (and last!) all-nighter with my Grammy - we stayed up all night to watch her plant bloom, which it did less than once a decade. My family’s support allowed me to become curious and successful.

Beyond my family, supportive friends and mentors challenged me to think bigger and reach new goals – at The College of William & Mary (Dr. Randy Chambers, Dr. Timothy Roberts, Timothy Russell, Dr. Mellisa Pensa, Dr. Christina Sigur, Aurelie Croze, and Rachel Lewis), at The Nature Conservancy’s Disney Wilderness Preserve (Dr. Monica Folk, Sandy Woiak, and fellow Student Conservation Association interns), and at Yosemite National Park (Dr. Allison Colwell, Dr. George Jaramillo, and many others). Thank you!

Once at UC Berkeley, Dr. Scott Stephens, Dr. David Ackerly, Danny Fry, and Dr. Brandon Collins patiently helped me transform ideas into published manuscripts. Colleagues in the Stephens Lab, especially Dr. Anu Kramer and Carmen Tubbesing, helped refine ideas nearly every day. Dr. Lauren Ponisio taught me how to decipher statistics. Dr. Sara Knox, Dr. Kevi Mace, and soon-to-be-doctors Katy Seto, Lisa Kelley, and Ashton Wesner gave emotional support through the PhD journey. Thank you, thank you, and thank you!

Lastly, I would like to thank my husband, Josiah, for his steadfast love and support.

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CHAPTER 1

INTRODUCTION

Using science to inform management and policy − one of my primary goals as a scientist− requires pertinent applied science and effective communication with stakeholders from policy makers to the public. Therefore my focus at the University of California at Berkeley has been to develop as a well-rounded scholar including research, extension, and teaching. Throughout my academic and professional career, I have used many different avenues to work toward this end. My recent experience as a University of California Cooperative Extension Fellow stands out in this regard.

In Yosemite National Park, tourists are often drawn to the Valley to gain spectacular views of Yosemite Falls, Half Dome, Glacier Point, and to watch climbers scale El Capitan. But, there is much more to the park than these classic vistas. I took NPR reporter Amy Quinton see the parks' true marvel --- Yosemite's Illilouette Creek Basin (Quinton). Here, a natural experiment has occurred for the last 50 years where park managers let all lighting strike fires burn and it is a vision for what sound fire management could look like in California. The fires are allowed to blaze, smolder, and creep their way through the woods until they are extinguished naturally by winter precipitation; these lightning-ignited fires consume dry wood and small trees, thus starving future fires of fuel. These managed areas most closely resemble historical fire patterns in California forests. Together Amy and I saw how frequent fire shapes the landscape, creating a pattern of park-like forests, shrub fields, and fields of blackened snags with brilliant purple understories. These burned patches are relatively small and contribute to floral and pollinator diversity while moderating fire behavior (Collins *et al.* , Ponisio *et al.* , Wilkin, Ponisio, Fry, Collins, *et al.* 2016). The Illilouette's quilt-like plant patterns are in stark contrast to the aftermath of the 2013 Rim Fire, which left more than 12,000 contiguous hectares of blackened trees, devoid of seedlings to form future forests. During our three day journey, we traveled over 26 kilometers to investigate the Illilouette Creek Basin which gave the NPR listeners a vision of what good fire was like in California. Most importantly, the listeners learned how Californians could live more harmoniously with our environment by allowing some fires to burn and thus protecting both nature and people.

I believe that people and the environment are co-dependent, unfortunately many of our land management practices are not sustainable especially with climate change. I completed applied research in the wildland urban interface, restored areas, and the wilderness to understand historical fire ecology, and ecosystems vulnerability to land management and climate change. Specifically, I used ecosystem sciences to help answer, "How can we manage natural lands to be resilient to climate change induced fire and other compounded disturbances?" In my dissertation I revealed plant community and fuel patterns' relationship to disturbances and elucidated their mechanisms.

My collaborative work spanned chaparral fuel hazard reduction (Wilkin *et al.* 2015, Wilkin, Ponisio, Fry, Tubbesing, *et al.* 2016); pyrodiversity in a Wildland Fire Use Sierra mixed conifer forests in relation to fuels, understory plants, and pollinators (Collins *et al.* , Ponisio *et al.*); the vulnerability of climate change refugia to fire in the Sierra mixed conifer forests (Wilkin, Ackerly, *et al.* 2016), and how social relationships influence wildfire outcomes for people and property (Wilkin 2016). I was fortunate to build upon long-term studies from the Stephens Lab to understand the spatial and temporal complexities of plant communities in chaparral and the mixed conifer forests; I transformed historic data to archival standards and added complimentary data during three extensive field seasons. In addition, I completed a novel study using publically accessible spatial data. Throughout my career my research techniques have ranged from lab experiments to understand how seeds' germination responds to the heat and chemicals of fire (Wilkin *et al.* 2013), through common garden experiments in green houses and field experiments with experimental units ranging from one meter to two hectares to understand plant communities (Wilkin 2009, Wilkin *et al.* 2013, Wilkin *et al.* 2015, Wilkin, Ponisio, Fry, Tubbesing, *et al.* 2016), to landscape scale observational studies to understand how climate, plant communities, fire interact (Collins *et al.* 2016, Ponisio *et al.* 2016, Wilkin, Ackerly, *et al.* 2016, Wilkin, Ponisio, Fry, Collins, *et al.* 2016). My dissertation includes diverse, but interrelated chapters about fire ecology and management in California:

(1) Shrubland fire hazard reduction has drawbacks for biodiversity,

(2) Climate change refugia fire ecology and management, and

(3) Drivers of plant communities in arid forests with restored fire regimes.

Together these chapters enhance California's understanding of applied and basic fire science, and make the results relevant to scientists and land managers.

CHAPTER 2

SHRUBLAND FIRE HAZARD REDUCTION HAS DRAWBACKS FOR BIODIVERSITY

Abstract

Fuel reduction treatments, such as prescribed fire and mastication, are widely used to reduce fire hazard. These treatments help protect humans from wildfire, yet are not mutually beneficial for people and ecosystems especially in areas adapted to infrequent crown fire. Fire risk and plant biodiversity can be negatively related, wherein decreasing fire risk leads to fundamental shifts in plant communities. Short-term studies suggest land managers face an acute dilemma between protecting people or ecosystems. However, the long-term ecological trajectories and fire risks of fuel treatments are often poorly understood. Using a 13-year replicated experimental study, I evaluate how shrub cover, nonnative species invasion, native species diversity, and an obligate seeder responded to fuel treatments in California's northern chaparral. The fuel reduction treatments (fire/mastication) and their seasons (fall/winter/spring) had unique influences on plant communities. Untreated controls had continuous shrub canopy with no understory throughout the study. Mastication retarded recovery of shrubs more so than fire while increasing the number of nonnative plants, including nonnative annual grasses. Surprisingly, mastication also increased an uncommon shrub that is an obligate seeder. The season in which each treatment was applied also influenced these outcomes, but to a lesser magnitude than treatment type. Fall fire and mastication treatments resulted in delayed shrub recovery and more nonnative plants, nonnative annual grasses, and an obligate seeder shrub species than spring or winter fire treatments. Long-term shrub species composition had little correlation with short-term recruitment results. Based on the findings, I conclude that fire hazard reduction treatments change plant community composition and only reduce fuel hazard for approximately 10 years, warranting thorough consideration before implementation.

Keywords: California, chaparral, prescribed fire, mastication, fire/fire-surrogate

Introduction

Wildfires near the wildland urban interface (WUI) can cause large losses of human life and structures (Stephens, Adams, *et al.* 2009, Syphard *et al.* 2014). Additionally, wildfire losses and suppression costs are expected to increase with climate change (Westerling and Bryant 2008). Wildland fire risk reduction through fuel reduction is therefore a high priority for the WUI (Dicus and Scott 2006, Stephens, Adams, *et al.* 2009), yet can impact wildlife populations by, for example, shifting the composition of plant communities (Briese 1996, Merriam *et al.* 2006). In California's chaparral, fuel reduction treatments can facilitate the invasion of nonnative species in the short-term (<five years) (Merriam *et al.* 2006, Potts and Stephens 2009), but the long-term (> five years) ecological trajectory and fire risk of these treatments is poorly understood.

Fuel reduction may be detrimental to ecosystem health and species diversity, especially in chaparral (Keeley 2002). Chaparral constitutes 7% of California land area but it hosts more than one- quarter of the state's endemic flora and fauna— nearly half of which are endemic to chaparral (Keeley and Davis 2007). Chaparral, like most Mediterranean shrublands, is highly fire resilient and historically burned with high-severity, stand replacing events every 30 to 100 years (Keeley and Davis 2007). Historically, Native Americans burned chaparral to promote grasslands for textiles and food (Vale 2002). Though adapted to infrequent fires, chaparral plant communities can be exterminated by frequent fires and disturbances (Syphard *et al.* 2007, Pratt *et al.* 2013). Today, frequent accidental ignitions can convert chaparral from a native shrubland to nonnative annual grassland and drastically reduce species diversity, especially under global-change-type drought (Syphard *et al.* 2007, Pratt *et al.* 2013). As such, increased disturbances, like fuel reductions, may also extirpate chaparral.

Nonnative plant invasion can also create a positive feedback cycle: once nonnative plants are established, they increase fire frequency, which favors more nonnative plants (Brooks *et al.* 2004, Brennan and Keeley 2015). Changes in plant community structure also drive changes in habitat, negatively affecting wildlife including certain birds and small mammals (Lillywhite 1977, Longhurst 1978, Bleich and Holl 1982, Seavy *et al.* 2008). Therefore, all chaparral fuel reduction may threaten native flora and fauna. This is in contrast to frequent, low severity fire systems, such as many California forests, in which most fuel reduction treatments both reduce fuel hazard and restore native plant communities (Schwilk *et al.* 2009, Stephens, Moghaddas, *et al.* 2009).

In the WUI, managers often prefer mastication, in which heavy machinery chews up vegetation, because prescribed fire involves more regulatory and social barriers (Gill and Stephens 2009, Moritz *et al.* 2014). Mastication treatments require less technical expertise than prescribed fire and their application is not dependent upon being granted an air quality permits. Nearby residents may also be more comfortable with mastication near their property than high-intensity chaparral fire (Winter *et al.* 2002, Mayberry 2011). However, there are limitations to mastication: it is infeasible on steep slopes, costs more per hectare than fire, and cannot occur in winter when soils are softened from rain (Hartsough *et al.* 2008). Mastication also had conservation drawbacks in the short term, as it can promote nonnative plant invasion to a greater extent than fire because it kills more individuals and delays canopy closure longer, allowing more time for nonnatives to invade (Keeley *et al.* 2005).

Despite the disadvantages of mastication, prescribed fire can be controversial because it commonly occurs outside the historical fire season, i.e. in winter or spring rather than fall (Parker 1987). Winter and spring burns are advantageous for managers because they have higher fuel moisture, leading to lower rates of fire spread and thus lower potential for an escaped fire. Burning outside the fall wildfire season is also subject to fewer air quality restraints, and personnel and equipment are more available. However, winter and spring burns are of ecological concern because they may lead to shifts in plant communities due to lower germination of obligate fire seeders like *Ceanothus cuneatus* (buckbrush) and other rare herbs (Parker 1987, Parker 1987, Keeley 2002). Some attribute the lack of obligate fire seeders to the shortened growing season (Knapp *et al.* 2009), while others point to high soil moisture, which allows seeds to absorb water and become metabolically more active, causing them to be killed by steam or heat in lab experiments (Le Fer and Parker 2005). In contrast, others conclude that an indirect effect of season, namely decreased fire intensity driven by seasonal weather and fuel moistures, prevents fires from reaching temperatures necessary to scarify seeds (Knapp *et al.* 2009). Research on the influence of fire season on chaparral shrub composition, however, is sparse and contradictory; a lab study suggest a seasonal influence on obligate seeders (Le Fer and Parker 2005) while field studies do not suggest an influence on shrub composition (Dunne *et al.* 1991, Beyers and Wakeman 2000). Season may also play an important role in competition between natives and nonnatives; the timing of treatment may allow nonnatives to establish before natives begin to germinate or grow.

Broadly, I test the following hypothesis: in systems adapted to infrequent high severity fire, fire hazard reduction causes negative ecological consequences in the long term. I focus on two main questions:

(1) *Which fuel reduction treatment and season combination minimizes nonnative species invasion and persistence?*

(2) *Which fuel reduction treatment and season combination fosters native plant diversity and structure?*

To address these questions, I use a chaparral study in California's Interior Coast Range to evaluate changes in plant community over 13 years following fuel reduction treatments (fire or mastication), with a seasonal component (fall, winter, and spring; Table A1, Figure B1). To my knowledge, this is one of only a few replicated and long-term studies in Mediterranean shrublands with before-treatment measurements, controls, and two treatments applied across multiple seasons to address impacts on biodiversity and fire risk.

Methods

Study site

The study was conducted in northern California's Interior Coast Range chaparral, approximately 50 km inland from the Pacific Ocean and 175 km north of San Francisco near Ukiah, CA, USA (39°N, 123°W). Vegetation is chamise chaparral, ecologically similar to chaparral throughout California (Figure 1) (Keeley and Davis 2007). Soils are shallow, rocky, and moderately acidic, derived from weathered sandstone and shale. The study sites are 214 to 305 m above sea level on steep (25 to 55%), southern- and western-facing slopes. The region has a typical Mediterranean climate with hot, dry summers and cool, wet winters. (Potts and Stephens 2009, Potts *et al.* 2010).

Figure 1. South to west facing chamisal chaparral in the interior North Coast Range. This area had six adjoining experimental units including fire and mastication in spring and winter. Unit boundaries included the two-track road to the top, riparian area to the bottom, and drainages or ridges in between units. Photo: D. Fry

Study design

Late successional chaparral was chosen in areas where disturbances had been absent for at least 40 years. Experimental units were clustered in the University of California Hopland Research & Extension Center and at US Bureau of Land Management South Cow Mountain Recreational Area and on adjacent private land. The study area was divided into 24 experimental units of nearly two hectares each, including four replicates of each treatments and four untreated control units (Table A1, Figure 1, and B1). Fall treatments occurred in November, winter treatments occurred in January, and spring treatments occurred in April to early June (Table A1).

Study design was influenced by operational limitations. Mastication was limited to lower grade slopes for equipment maneuverability and safety. Prescribed fires required favorable weather conditions to safely burn and were completed over two years. Treatments were done from 2001 to 2003 (Table A1) and were assigned randomly to experimental units, with mastication limited to <35% slopes (Figure B1).

Prescribed fires were ignited with drip torches at the slope's base, creating upslope head fires. Given the nature of fire, these treatments had some heterogeneity. Mastication by a track bulldozer with a front mounted rotating toothed drum shredded aboveground biomass and left surface woody debris less than 5 cm deep and discontinuous (Figure 2). The debris ranged from 10 to 40 cm in length by 5 to 10 cm in width (Figure 3). Sub-surface soil and root systems were not disturbed by the masticator, but there may have been some soil compaction and surface damage to the lignotubers of resprouting shrubs. Treatment heterogeneity was minimal in mastication treatments since the equipment operator performed systematic passes through vegetation. Both fire and mastication reduced vegetation cover by 90 to 100%.

Figure 2. Fuel reduction treatments included prescribed fire, mastication, and a control (left to right). Photos: D. Fry, J. Potts, and K. Wilkin, respectively.

Figure 3. While the fuel reduction treatments reduced vegetation, mastication redistributed all of the shrub biomass to the ground creating a discontinuous layer of fuel (top left and bottom left) whereas fire consumed the fine materials and left larger diameter stems standing (top right and bottom right). Photos: J. Potts and D. Fry

Sample design

Prior to treatment, 15 randomly distributed permanent transects were installed and sampled within each experimental unit. Shrub, vine, and tree (as defined by (U.S.D.A. 2016)) species composition and cover were recorded continuously along each 15 m transect. Five understory plots 1.8m in radius were randomly established at transect endpoints and herbaceous plant counts were recorded at each. Burned and masticated treatments were measured prior to treatment, during the second and third summers after treatment, and in 2012. Untreated areas were measured once between 2001 and 2004 and again in 2012.

I used various components of the plant community to investigate my questions.

1. *Which fuel reduction treatment and season combination minimizes nonnative species invasion and persistence?* Nonnative species invasion was assessed using nonnative annual grasses, all nonnative understory plants and shrubs, and their ecological harmfulness ratings(Bell *et al.* 2015). Harmfulness ratings are from the California Integrated Pest Management program and are based on a combination of ecological impact, invasive potential, and current distribution.
2. *Which fuel reduction treatment and season combination fosters native plant communities?* Native plant community was assessed using shrub cover, shrub richness, and cover of the dominant obligate seeder, *Ceanothus cuneatus* (buckbrush).

Analysis

I constructed statistical models to represent my hypotheses for the drivers of chaparral succession after fuel treatments. Particularly, I examined how the different treatment and season combinations affected the trajectory of the plant community and how they differed from untreated communities. I used linear and generalized linear mixed effects models to test the significance of response variables between treatments, and to account for the repeated measurements at each transect or quadrant through time. (Bates 2014, Bates *et al.* 2014, Kuznetsova 2014). I examined the main effect of how each treatment-season combination changed through time and the interaction of treatment-season and years since treatment. I also included environmental variables that may influence the response of the plant. I included percent slope, solar radiation index (unitless) (Mccune and Keon 2002) and precipitation (cm), specifically survey year annual precipitation or precipitation one year post treatment based on growing season (August to July), as explanatory variables in the models (data from(U.C. Hopland Research & Cooperative Extension Center 2014). In addition, I modeled the effect of random variability between and within sites (experimental unit and sample unit) and land owner type (UC Hopland Research & Extension Center, BLM South Cow Mountain ORV, or private ranch) to account for repeated measure.

I was interested in whether the treatments and untreated areas different from one another for shrubs and understory plants (Equation 1 & 2)? I use the following equation to evaluate shrubs.

$$\textbf{Shrub Length Along Transect}\Big/\textbf{Transect Length} \sim$$

$$\textbf{Treatment} * \textbf{Years Since Treatment} +$$

$$\textbf{Treatment} + \textbf{Years Since Treatment} +$$

$$\textbf{Solar Radiation Index} + \textbf{Slope} +$$
$$\textbf{Management Type} + \textbf{Experimental Unit} + \textbf{Shrub Transect}$$

(Equation 1)

Where γ is the response variable, the control includes both untreated and pre-treatment measurements for shrubs, fixed effects are bolded, and random effects are plain text. The interaction between growing years and treatment enabled us to compare the trajectories of the shrub communities as they matured in the different treatments and untreated.

I evaluated understory plants with the following equation:

$$\textbf{Count of understory plants} \sim \textbf{Treatment} * \textbf{Years Since Treatment} +$$

$$\textbf{Treatment} + \textbf{Years Since Treatment} +$$

$$\textbf{Survey Year Precipitation} +$$

$$\text{Management Type} + \text{Experimental Unit}$$

(Equation 2)

Where γ is the response variable, the control includes both untreated and pre-treatment measurements for understory plants, fixed effects are bolded, and random effects are plain text. The interaction between growing years and treatment enabled us to compare the trajectories of the understory communities as they matured in the different treatments and untreated. The understory sample unit was not included in the analysis because of the sparse and variable counts at that scale. Rather, density was summarized at the experimental unit scale.

For models with plant count and their density as response variables I assumed Gaussian with square root transformation if needed or Poisson error depending on the dispersion of the data and model residuals (Table C1). For shrub cover and its proportion data, I assumed a binomial error distribution (Table C1). Some data required zero-inflated models (Fournier *et al.* 2012, Skaug *et al.* 2014). AIC was used to assess model fit, and model family with lowest AIC was chosen (Mazerolle 2016). All analyses were conducted in R 3.1.2 (R Development Core Team 2008).

Results

(1)Which fuel reduction treatment and season combination minimizes nonnative species invasion and persistence?

(1a) Nonnative annual grass density

Throughout the study period, untreated areas had significantly less nonnative annual grass density than the mastication treatment applied in the fall (P<0.001, Figure 4, Table D1). No other treatments had significantly different nonnative grass density than the untreated areas (P>0.08). Mastication applied in the fall had a mean of 360 nonnative annual grass individuals m^{-2} one year after treatment ($P<0.001$). In contrast, the untreated areas' mean number of nonnative grasses was less than 3 individuals per year throughout the study. Increased annual precipitation also increased nonnative annual grass density in all experimental units ($P<0.001$).

Between fire and mastication treatments, mastication treatments generally had greater nonnative annual grass density than fire treatments (Figure 4). All fire treatments each had a mean of less than 10 nonnative plants m^{-2} throughout the study. Fall and spring fires were similar to mastication treatments applied in the spring regarding nonnative annual grass density.

Season of application only had a significant influence on nonnative annual grass density within the mastication treatments. Mastication applied in the fall had a mean of 333 more nonnative annual grass individuals m^{-2} than spring mastication one year after treatment ($P<0.001$). Through time the difference persisted, but declined in magnitude. Ten years after treatment, fall mastication had 16 mean more nonnative annual grass individuals m^{-2} than spring mastication ($P=0.02$).

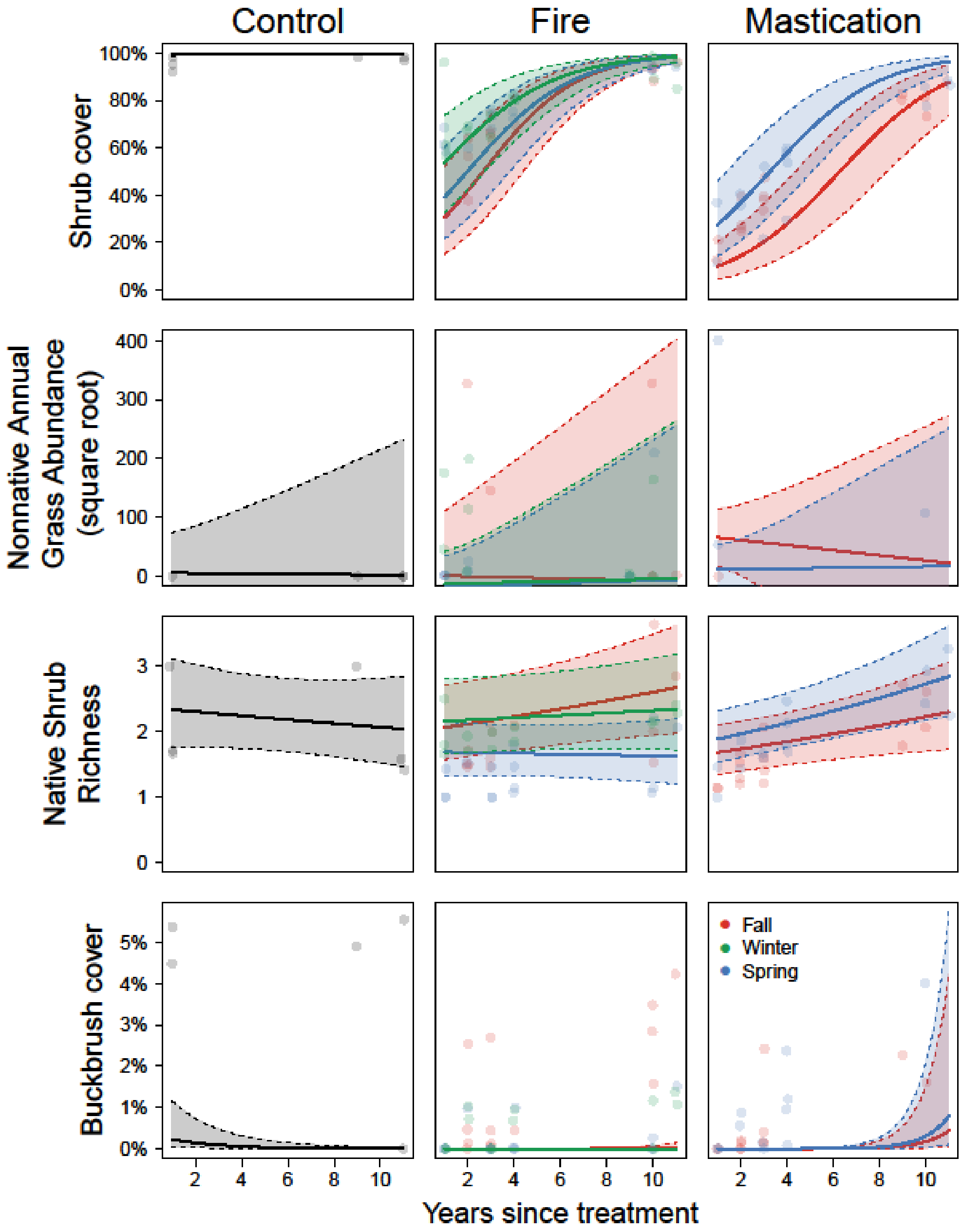

Figure 4. Responses to treatments and the control throughout the study for nonnative annual grass occurrence, shrub cover, shrub richness, and *Ceanothus cuneatu*s (buckbrush) cover. Nonnative annual grass estimates and standard error are based on the square root of the data. Curves represent the regression coefficients, shaded areas are the 95% confidence intervals, and points are experimental unit mean for each survey year.

(1b) Nonnative plant density by harmfulness rating

All shrubs were native, thus I report only understory nonnative herbaceous plants (Table G1). Untreated areas had fewer nonnative plants than mastication treatments throughout the study ($P<0.04$). Untreated areas had a mean between 17 and 25 total nonnative plants each year across an entire site (Figure 5), and fire treatments had similar densities of between 5 and 10 plants m^{-2}. Most of the nonnative plants in untreated areas and fire treatments did not have significant ecological impact ratings (Bell *et al.* 2015). In contrast, nonnative plants invaded and persisted after mastication treatments ($P<0.01$). Mastication applied in the spring had a mean of 83 individuals m^{-2} 10 years after treatment and fall mastication had a mean of 333 m^{-2}. Nonnative plants in masticated treatments also were more likely to be harmful to the ecosystem than both the untreated areas and fire treatments, although the most harmful plants did not persist, with mean density near zero 10 years after treatment ($P<0.01$).

Overall, mastication treatments had greater nonnative plant densities than fire treatments ($P<0.001$, Figure 5); only fall fire and spring mastication were marginally similar ($P<0.09$). In mastication treatments, nonnative plants invaded and persisted 10 years after treatment. Fall mastication treatments had fewer nonnative plants as time since treatment increased, although they still remained in higher density than in any other treatment ($P<0.001$). In contrast, nonnative plants in spring mastication treatments continued to increase 10 years after treatment ($P<0.001$).

There is a seasonal influence across treatments: both fall treatments had more mean nonnative plant individuals than spring treatments 10 years after treatment with about 10 to 100 times more for fire and mastication, respectively ($P<0.01$, Figure 5). Of the fire treatments, fall treatments had the most nonnative individuals, but still had 10 to 40 times fewer than mastication treatments 10 years after treatment ($P<0.01$).

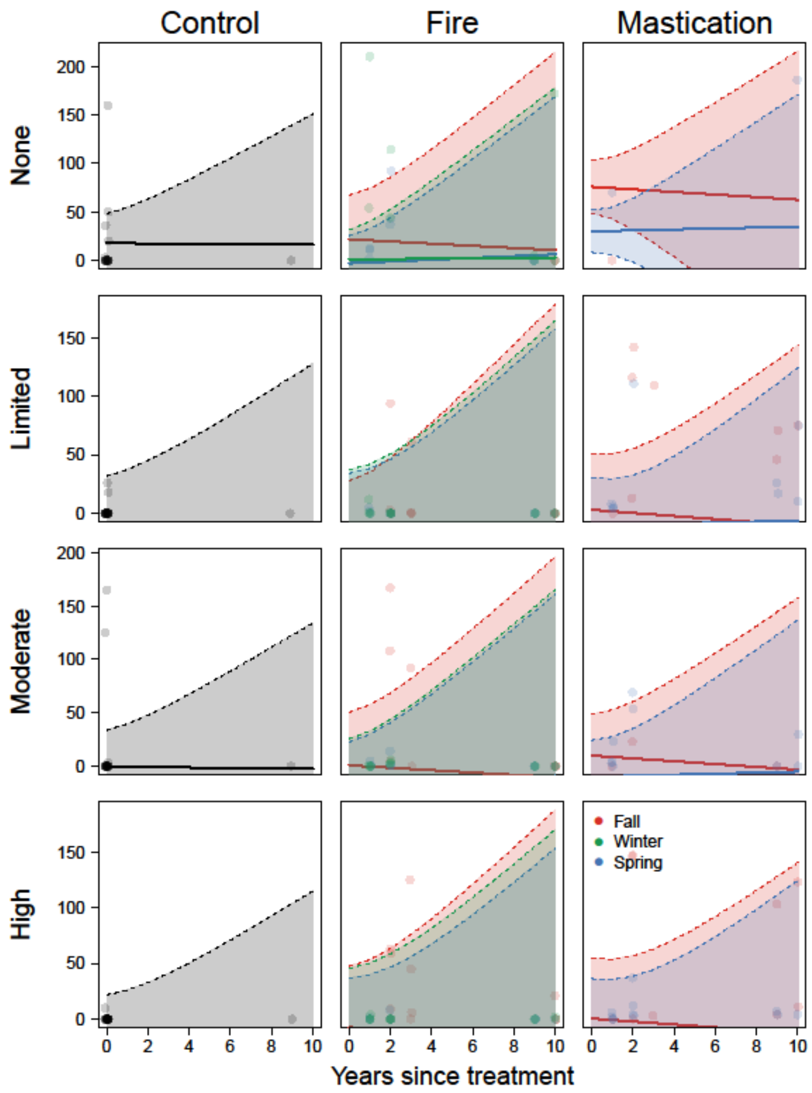

Figure 5. Responses to treatments and the control throughout the study for nonnative plants by Harmfulness rating from the California Integrated Pest Management (Bell *et al.* 2015). Estimates and standard error are based on the square root of the data. Curves represent the regression coefficients, shaded areas are the 95% confidence intervals, and points are experimental unit mean for each survey year. Harmfulness rating is from the California Integrated Pest Management and is based on a combination of ecological impact, invasive potential, and current distribution (Bell *et al.* 2015).

> "High: These species have severe ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to high rates of dispersal and establishment. Most are widely distributed ecologically.
>
> Moderate: These species have substantial and apparent—but generally not severe—ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to

high rates of dispersal, though establishment is generally dependent upon ecological disturbance. Ecological amplitude and distribution may range from limited to widespread.

Limited: These species are invasive but their ecological impacts are minor on a statewide level or there was not enough information to justify a higher score. Their reproductive biology and other attributes result in low to moderate rates of invasiveness. Ecological amplitude and distribution are generally limited, but these species may be locally persistent and problematic.

None: available information indicates that the species does not have significant impacts at the present time." (Bell *et al.* 2015).

(2)Which fuel reduction treatment and season combination foster native plant communities?

(2a) Shrub cover

Untreated areas had persistently and significantly higher shrub cover than all fire and mastication treatments throughout the study ($P<0.001$, Figure 4, Table F1). Fuel reduction treatments greatly reduced shrub cover and then shrub cover in treated areas increased at greater rates than in untreated areas ($P<0.001$). By about 10 years after treatment, all fire and mastication treatments rebounded to only 2% and 12% less cover than the untreated areas, respectively ($P<0.001$).

Between fire and mastication treatments, mastication treatments generally resulted in lower shrub cover than fire (Figure 4). Ten years after treatments, areas with mastication applied in the fall had the lowest shrub cover compared to other treatments: fall fires, spring fire, and spring mastication had 8 to 10% more shrub cover than fall mastication ($P<0.001$).

The season of application within each treatment had significant effects on shrub cover (Figure 4). Within both fire and mastication treatments, fall treatments had lower shrub cover than spring treatments one year after treatment (by 18 and 10%, respectively), but the differences narrowed by 10 years after treatment to 8%, and 2%, respectively ($P< .001$ and 2%, $P<0.03$). All treated areas increased shrub cover at similar rates throughout the study with mean estimates between 3 and 7% yr^{-1}.

(2b) Native shrub richness

Untreated areas had greater shrub richness than fall mastication treatments and spring fires one year after treatment ($P<0.04$, Figure 4, Table F1). The untreated areas had a richness mean of two shrub species per transect whereas the fall mastication and spring fire treatments had a mean of 1.6 species per transect. Through time, mastication treatment species richness increased, and by 10 years after treatment mastication treatments become similar to the untreated areas ($P<0.04$). In contrast, spring fire treatment species richness remained lower than the untreated areas throughout the study. Fall fires and winter fires had similar species richness to the untreated areas throughout the study ($P>0.3$).

Between fire and mastication treatments, there were few significant differences in shrub species richness (Figure 4, Table F1). Mastication applied in the fall had slightly more species, about 0.3 species on average, than winter fires one year after treatment ($P<0.03$). Mastication applied in the spring had a slightly lower rate of species accumulation through time than spring fires (only about 0.05 species/year, $P<0.01$).

(2c) Dominant obligate seeder shrub cover

The untreated areas had significantly more buckbrush cover than fire and mastication after treatment (P<0.001, Figure 4, Table F1). Through time, the cover of buckbrush decreased in the untreated areas, whereas it increased slightly in burned areas and it increased by a larger magnitude in mastication treatments (P<0.001). A decade after treatment, buckbrush cover in masticated treatments had between 0.44 and 0.79% greater mean cover than in fire treatments and the untreated areas (P<0.001). In contrast, fire treatments still had ten times less cover than the untreated areas; all fire treatments had less than 0.01% mean buckbrush cover a decade after treatment (P<0.001).

Season also influenced buckbrush cover within fire treatments: fall fire treatments had more cover than spring (P<0.001) and these differences marginally increase through time (P<0.09, Figure 4, Table F1). In contrast, there was no seasonal differences within mastication treatments.

Discussion

The results demonstrate that chaparral fuel treatments involve trade-offs at three decision points (Figure 6): *(1) Should managers treat or accept fuel hazard?* If treatments occur, *(2) Should fire or mastication be used?* and *(3) In what season should treatments occur?* I discuss these questions and illuminate concerns managers could consider when planning fire hazard reduction.

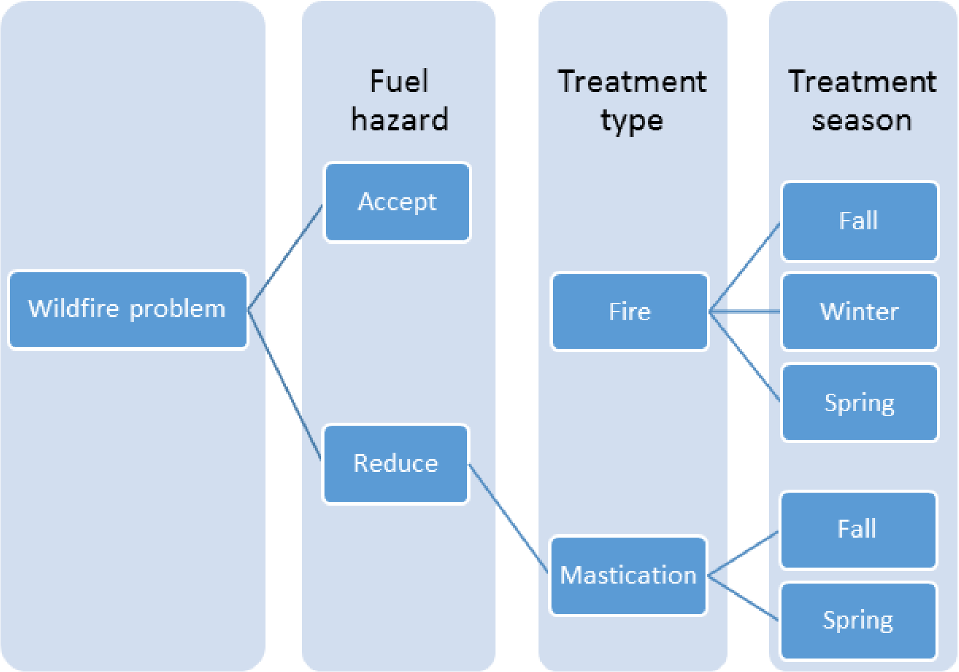

Figure 6. Managers have three decision points to consider when asked to reduce fuel hazard in chaparral.

1. Should managers treat or accept fuel hazard?

About 10 years after treatment, the shrub cover and correspondingly the fuel load in areas that were burned or masticated differ from untreated areas. Untreated areas had nearly continuous shrub canopy dominated by chamise with infrequent buckbrush and *Arctostaphylos* spp. throughout, with little to no understory. This continuous shrub cover is important for wildlife because it provides perches for birds while also protecting birds and small mammals from birds of prey (Lillywhite 1977, Longhurst 1978, Bleich and Holl 1982, Seavy *et al.* 2008). Nonnative annual grasses were rare and restricted to shrub gaps or roadsides.

Fire and mastication treatments had lower shrub cover than the untreated areas and higher densities of herbaceous plants, including nonnative plants and grasses. Although the differences between treatments and untreated diminished through time, burned areas have a mean of 4% less shrub cover than untreated and masticated areas had between 4 and 12% less cover than untreated areas (depending on the season of treatment) 10 years post treatment.

To maintain fuel hazard reduction, it is likely that retreatment will be needed every ten to twenty years, especially in the fire treatments. Retreatment would leave areas more vulnerable to nonnative plant invasion, and newly recruited shrubs may not have deposited a robust soil seed bank yet for their replacement. Fire and mastication treatments still had lower shrub species richness and buckbrush cover than untreated areas, and both of these differences would likely be exacerbated if treatments reoccurred soon. Particularly when dealing with repeat treatments, persistent nonnative plants, including annual grasses, would likely increase quickly if another treatment occurred. The results suggest that the reduction of fire hazard in chaparral can be detrimental to native plant biodiversity. Therefore, these treatments should be applied carefully and other wildfire risk reduction strategies may need to be considered.

2. Should fire or mastication be used?

Burned area shrub cover rebounded to pre-treatment levels quicker than that of fall mastication treatments. Fire treatments had a mean of more than twice as much shrub cover than masticated treatments two years after treatment. These large differences between treatment types diminished through time, but lesser differences persisted. In contrast, mastication treatments had greater nonnative plants and grasses. Consequently, fire may be a preferred treatment for avoiding nonnative plant invasion, including nonnative annual grasses, whereas mastication may be preferred for short-term woody fuel load reduction.

Shrub regrowth differences between treatments may relate to the disturbance responses of shrubs, their soil seed banks, and deer browsing. Shrubs resprouted aggressively after all treatments. The masticator may have killed some shrubs by damaging their burls whereas fire top-killed shrubs, allowing them to resprout (Figure 3, B2). Fire also stimulated more seedlings than mastication (Potts *et al.* 2010) and nutrients are often enhanced immediately post fire (Debano and Conrad 1978). All of the resprouting shrubs and seedlings were browsed by black tail deer (*Odocoileus hemionus*) (Figure B2) (Potts *et al.* 2010). Three years after the treatment the herbivory effects were still present: shrubs excluded from deer browse were about 10 cm taller than nearby open-grown shrubs in both treatments (Potts *et al.* 2010). While both treatments had statistically similar live shrub height, dead shrub skeletons provided some physical protection from herbivory from the burned plant skeletons (Figure 3, B2). These difference probably led to lower shrub cover for mastication compared to fire treatments throughout the study.

Slower shrub recovery in masticated treatments may have created space where herbs became established, including nonnative annual grasses. Fire treatments had low nonnative annual grass presence, low nonnative species richness, and no noxious weeds present despite their close proximity to maintained fuel breaks, which are known to be weed highways (Merriam *et al.* 2006). In contrast, mastication treatments generally were not placed next to fuel breaks, yet they had high nonnative grass presence, high nonnative plant richness, and noxious weeds present.

In masticated treatments, nonnative plants, including nonnative annual grasses, invaded and persisted for at least 10 years post-treatment, creating a shrub-grass matrix. There can be direct negative consequences of increasing nonnative annual grasses, including increased flammability and even extirpation of native plants (Keeley 2000, Beyers 2004, Merriam *et al.* 2006, Syphard and Keeley 2015). Chaparral's rich flora that emerges after fire can be out-competed by nonnative annual grasses (Keeley *et al.* 1981, Beyers 2004). These grasses are much more likely to ignite than shrubs, and grass incursion in chaparral can lead to increased fire frequency (Cione *et al.* 2002, Brooks *et al.* 2004). Nonnative annual grasses increase fuel continuity between natural areas and homes, increase how quickly fire spreads, and lengthen the fire season by drying earlier than native species. Thus, nonnative annual grass invasion and persistence in chaparral is detrimental to people and biodiversity in the WUI (Mack and D'antonio 1998, Brooks *et al.* 2004, Dickens and Allen 2014). The nonnative annual grass density was not consistent across years in this study, but rather varied with annual precipitation (Figure E1). Nonnative annual grasses decreased during drought years and increased when there is above average rainfall.

Some of the plant species that can accumulated in masticated areas were desired by managers. For example, buckbrush, a native shrub that is an obligate seeder and preferred deer browse (Biswell 1989), had greater cover in masticated treatments than fire treatments. While differences in buckbrush cover between fire and mastication treatments were only about 1% or less, this may be biologically significant given that buckbrush is widespread but uncommon and important as deer forage (Bleich and Holl 1982). The majority of buckbrush seeds are cued by heat shock (Keeley 1987), but post-fire seedlings found early in this study (Potts *et al.* 2010) did not catalyze long-term cover. Rather, mastication likely promoted buckbrush because competitive resprouters like chamise were repressed, allowing the non-fire cued seedlings to prosper (Biswell 1961, Keeley 1987, Wilkin *et al.* 2013). Future research is needed to understand the mechanisms by which fire-cued species respond to mastication.

3. In what season should treatments occur?

Burns outside of the natural fire season are safer and easier to implement for managers, but may have unintended consequences because of seasonal differences in plant physiology, plant competition, and treatment efficacy (Knapp *et al.* 2009). The seasonal differences in plant regrowth after fire are sometimes attributed to soil moisture, wherein imbibed seeds' are more susceptible to heat (Le Fer and Parker 2005). However, in this study soil moistures were statistically similar across seasons immediately prior to treatments (Potts and Stephens 2009) likely because fall and winter burns were only completed after a drying period following rainfall. Therefore seasonal differences in surface soil moistures were minimized. Other physiological processes also occur in association with seasonal drought, including reduced water potential in mature shrubs and reduced carbohydrate storage in lignotubers, which may leave plants more susceptible to disturbance by reducing resources needed for resprouting (Pratt *et al.* 2013).

Another possible driver of seasonal differences is fire intensity (Knapp *et al.* 2009). There is reason to believe that fire behavior could have been unique in each season (Stephens *et al.* 2008) – live fuel moistures were greater in the spring than in the fall or winter for fire treatments (Potts and Stephens 2009). My data support a seasonal difference in regrowth across both treatments. Fall treatments in general have the lowest shrub cover while winter and spring treatments have higher shrub cover. Surprisingly, these differences tend to persist between fire and mastication treatments. Thus, fire intensity alone cannot explain the differences in shrub cover, and thus fall treatments in general may have lower shrub cover due to plant physiology or competition. Fewer shrubs may resprout after both fall treatments because of a combination of harsh environment and low storage and availability of resources such as carbohydrates or water (Pratt *et al.* 2013). These cover differences are not supported by early trends in seedling densities; at two and three years post treatment both fall treatments had the greatest seedling densities (Potts *et al.* 2010).

Buckbrush cover did not follow early trends in seedling density (Potts *et al.* 2010). Despite being an obligate seeder with fire-stimulated seeds (Keeley 1987, Schwilk 2003), it had the highest cover with mastication, not fire, 10 years after treatment. In contrast, three years post treatment fall fire treatment had greater seedling densities with about two buckbrush seedlings m^{-2}, which is more than twice as many as all other treatments and seasons (Potts *et al.* 2010). However, in mastication treatments, the soil seed bank may continue to be stimulated by solar heat because of sparse shrub cover (Baskin and Baskin 1998). Additionally, seedlings in masticated areas had less competition from resprouters such as chamise.

Conclusion

Land managers are challenged to simultaneously protect people from fire and protect ecosystems from harmful effects of fuel reductions. A decade after treatments, mastication and prescribed fire treatments had unique ecological responses. Masticated treatments had higher densities of nonnative species, especially annual grasses, and lower shrub cover than prescribed fire treatments. Fire treatments had little to no buckbrush, an obligate seeder and important deer browse. Lastly, the long-term plant community response did not follow the short-term response for shrub cover and seedling densities as suggested by Potts and Stephens (2009) and Potts et al (2010) showing that long-term studies, like ours, are needed to understand these dynamics. My results show that methods to reduce human vulnerability from fire other than fuel reduction treatments, such as improved land-use planning and adopting more FireWise building practices, should be considered in combination with strategic fuel reduction (Mutch *et al.* 2011, Fire Wise Communities 2012, Moritz *et al.* 2014).

These results should be applied cautiously throughout Mediterranean shrublands because of possible differences in fire behavior, climate, and plant communities between Northern California's chaparral and other Mediterranean regions. Fire behavior can have limited response to fuel reduction treatments in areas like Southern California where chaparral fires are driven by Foehn winds (Keeley 2002). Foehn winds fosters fires that are nearly unstoppable, though fuel reductions may facilitate safer firefighting and evacuations. Fuel reduction treatments are more successful in areas with limited Foehn-wind-driven fires such as Central and Northern California (Moritz *et al.* 2010). Southern California also has more frequent and severe drought, which drives higher shrub mortality after fuel reduction treatment, and these trends decrease along a latitudinal gradient northward (Pratt *et al.* 2013). Local climates and plant varieties may cause the seemingly similar dominant plants across California's chaparral to respond to treatments differently. Despite regional differences, my findings expand upon results from other studies in California's chaparral (Beyers and Wakeman 2000, Keeley 2000, Keeley 2002, Keeley 2004, Merriam *et al.* 2006, Perchemlides *et al.* 2008, Brennan and Keeley 2015) and can be used in combination with local studies to aid in fuel hazard reduction planning.

Mastication promotes nonnative species invasion and persistence in chaparral 10 years after treatment. Shrubs are excluded by nonnative annual grasses if they don't colonize the site early on, and this is exacerbated by drought (Keeley 2004, Pratt *et al.* 2013). Despite these negative effects, there is a significant benefit to mastication: treatment longevity diminishes the potential for loss of people or structures because it reduces fuel load and the need for more frequent treatments. However, increased grass fuels can extend the season in which fire can ignite and spread.

Managers must carefully weigh the trade-offs between treatment options, including the location and extent of fuel treatments, desires of their surrounding communities for fire risk reduction (Toman *et al.* 2011), cost, preserving native ecosystems, increasing flammability, and decreasing fire severity. Questions remain about chaparral's longer-term succession after fuel reduction treatments, especially repeated treatments. Shrubs regrow after treatments and treatments need to be repeated to remain effective at reducing fire risk near residential communities. Treatment intervals may vary but they will inevitably be shorter now than historical fire intervals. Altering fire regimes by increasing disturbance frequencies will leave these ecosystems vulnerable to possible adverse effects such as vegetation type conversion and species composition changes. Due to these strong trade-offs and concerns for biodiversity, I recommend that land-use planners reduce the amount of WUI in chaparral to decrease the need for managers to make acute decisions between the needs of people and biodiversity (Moritz *et al.* 2014).

Summary of Management Implications:

Prescribed fire

- Generally fosters long-term native plant diversity and community structure
- Reduces fire hazard for a shorter time than mastication and requires more frequent treatments
- Decreases certain native shrubs, such as the obligate seeder buckbrush

Mastication

- Fosters native shrub species, but nonnative understory species invade and persist
- Reduces fuel load more than fire, but may also increase fire frequency due to highly flammable and abundant annual grasses
- Increases certain native shrubs, such as the obligate seeder buckbrush

Season of treatment

- Season influences shrub cover, nonnative annual grass presence, and buckbrush to a lesser extent than treatment type:
  - Fall treatments slow shrub recovery more than winter and, even more so, spring treatments
  - Fall treatments promote greater nonnative plants and nonnative annual grass density than other seasons
  - Fall fire treatments increase the preferred dear browse buckbrush. Within mastication treatments, season does not influence buckbrush outcomes.

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CHAPTER 3

CLIMATE CHANGE REFUGIA FIRE ECOLOGY AND MANAGEMENT

Abstract

Early climate change forecasts warned of widespread species extinctions. As scientists have probed more deeply into species responses, a more nuanced perspective emerged indicating that some species may persist in microrefugia (refugia), including in mountainous terrain. Refugia are habitats that buffer climate changes and allow species to persist in—and to potentially expand under—changing environmental conditions. While climate and species interactions in refugia have been noted as sources of uncertainty, land management practices and disturbances, such as wildland fire, should also be considered when assessing any given refugium. My landscape scale study suggests that cold-air pools, an important type of small-scale refugia, have unique fire occurrence, frequency, and severity patterns in frequent-fire mixed conifer forests of California's Sierra Nevada: cold-air pool refugia have less fire and if it occurs, it is lower severity. Therefore, individuals and small populations are less likely to be extirpated by fire. Active management, such as restoration and fuels treatments for climate change adaptation, may be required to maintain these distinctive and potentially important refugia.

Keywords: mixed conifer forest, arid forests, fire ecology, fire management, refugia, climate change, vulnerability

Introduction

Early models of climate change impacts predicted widespread species extinctions as the rate of climate change outpaced the ability of plants and animals to migrate and track suitable climate (Walther *et al.* 2002, Root *et al.* 2003, Thomas *et al.* 2004). Subsequent investigations suggest a more nuanced perspective, indicating that while species extinctions may still be dramatic, some species are likely to persist in microrefugia (refugia) especially in mountainous terrain (Petit *et al.* 2002, Taberlet and Cheddadi 2002, Petit *et al.* 2003, Loarie *et al.* 2009, Dobrowski 2011, Keppel *et al.* 2011, Keppel and Wardell-Johnson 2012). As the ice sheets retreated following the last ice age, these refugia are believed to have played an integral role in the rapid expansion of many species by providing source propagules for rapid species migration (Taberlet *et al.* 1998, Willis and Whittaker 2000, Petit *et al.* 2002, Taberlet and Cheddadi 2002, Petit *et al.* 2003, Willis and Niklas 2004, Pearson 2006).

Many studies have sought to define refugia based on biological (Keppel *et al.* 2011) or climatic (Dobrowski 2011) evidence. Keppel *et al.*'s (2011) biological definition of refugia is "habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions." Dobrowski *et al.*, (2011) describe refugia as locations where extant climates (temperature and available water) are maintained during periods of climate change. Together they form a holistic definition, a habitat that buffers climate and allows species to persist in and to potentially expand from in response to changing environmental conditions. Refugia with relictual species, such as a disjunct southern population persisting from past large-scale populations during a past ice age, may or may not continue to function as refugia with climate change and changing disturbance regimes. Here, I focus on the importance of fire regimes as a component of potential refugia during periods of climate change. For fire sensitive species, landscape locations with reduced fire frequency or severity will serve as refugia with distinct disturbance regimes. Here I address the question of how some refugia in montane ecosystems may buffer both climate change and fire disturbance, with the potential to maintain species through episodes of climate change.

Refugia have attracted attention as important conservation areas (Groves *et al.* 2012, Keppel and Wardell-Johnson 2012), however the full range of conservation threats in these areas, including wildfire, have not been fully explored. Keppel and Wardell-Johnson (2012) highlight how refugia play a potentially important role in climate buffering and may offer *in situ* conservation benefits in the face of climate change and its biological effects (Keppel and Wardell-Johnson 2012). I expand 'climate change and its biological effects' to explicitly include ecological processes such as fire. In addition, I consider the importance of land management practices because of how policies, such as fire suppression, have drastically changed fire frequency and severity patterns in many forests (Miller *et al.* 2012). Climate, species interactions, ecological processes, and land management combine to create conservation challenges and opportunities for individual refugia (Figure 7).

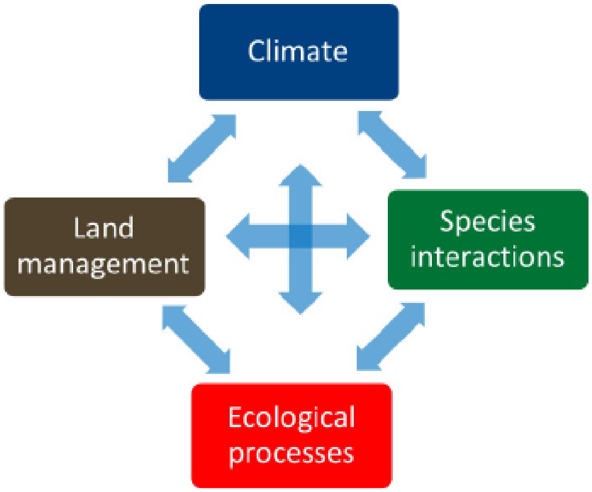

Figure 7. Refugia ecology is complex and affected by climate, land management, species interactions, ecological processes, and their interactions.

Fire is one example of a changing ecological process. Fire frequency and severity are changing world-wide due to land management (Anderson 2005, Trouet *et al.* 2010, Falk *et al.* 2011, Miller *et al.* 2012, Stephens *et al.* 2014) and climate change (Swetnam 1993, Westerling and Bryant 2008, Trouet *et al.* 2010, Moritz *et al.* 2012). Refugia populations are at a greater risk from changing fire patterns (Moritz *et al.* 2012) due to their predisposition to local extinction because of their small, isolated nature, especially if the plants are fire avoiders (Rowe 1983). Fire could alter species occurrence directly by killing vegetation or indirectly by altering vegetation's moderating effect on climate (Rambo and North 2009, Ford *et al.* 2013) and the selection pressures on vegetation (Bond and Keeley 2005). In more extreme cases fire can locally extirpate plants if fires are more frequent (Keeley *et al.* 1999), less frequent (Menges and Hawkes 1998), or more severe than historical fire regimes (Collins and Roller 2013). Some define refugia as areas with complete absence of fire (Nordén *et al.* 2014); however in arid regions with frequent fire, a reduction in frequency or severity may also create distinct conditions that serve as biological refugia for some taxa.

In this paper I focus on cold-air pool refugia (CAPs), a particular example of climatic refugia occurring in mountainous regions including my study region in the Sierra Nevada of California (Dobrowski 2011). CAPs have lower temperatures and more frequent minimum temperatures, below any chosen threshold. And maximum temperatures are also lower, with fewer days exceeding certain thresholds. CAPS often have greater moisture availability than their surrounding landscape, due to reduced evaporative demand and water accumulation into low-lying areas (Lundquist *et al.* 2008, Dobrowski *et al.* 2009). While overall temperatures are warming, the weather patterns that produce cold-air pooling at a landscape scale are projected to increase, so the frequency and duration of cold-pools may increase in the Sierra Nevada with climate change (Daly *et al.* 2010, Pepin *et al.* 2011). Alternatively, if the weather patterns that produce cold-air pooling decrease, CAPs may warm at a greater rate than the landscape, yet still have lower average temperatures than the landscape. Overall CAPs have and will likely continue to have cooler and moister climates that their surrounding landscape although the magnitude of these differences is uncertain.

Plants respond to environmental conditions within CAPs and these sites often have plants characteristically found at higher elevations or latitudes. Similar climatic refugia forests are known as frost hollows in Quebec's boreal temperate forests (Dy and Payette 2007) and cove forests in southern Appalachia especially in Great Smoky Mountain National Park (Shanks 1954). Another well-known example is subalpine fir (*Abies lasiocarpa*), which descend more than 300 m into river valleys with cold-air pools in Idaho (Daubenmire 1980, Axelrod 1998). In a more visually extreme case, the subalpine tree line is inverted due to cold-air pooling where mixed conifer forests grow above subalpine treeless regions on Mt. Hotham in Australia (Wearne and Morgan 2001). In the White Mountains of California, bristlecone pine are expanding downhill into local cold-air pools as temperatures warm (Millar *et al.* 2015). Lesser known examples in the CAPs of Yosemite National Park in California include the Merced Grove, with disjunct distributions of species more characteristic of the Pacific Northwest, such as mountain lady's slipper (*Cypripedium montanum*) and Old-man's-beard Lichen (*Alectoria sarmentosa*), growing together with Sierran species. These areas are dominated by ponderosa pine (*Pinus ponderosa*) intermingled with sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), and mountain hemlock (*Tsuga mertensiana*) with western hazelnut (*Corylus cornuta*) and mountain dogwood (*Cornus nuttallii*) in the understory (Colwell 2012) (Figure 2). As the climate changes and species ranges shift, we may see different species become restricted to CAPs, and the fate of the examples noted here are unknown.

Figure 8. Refugia where species retreated to after the last ice age, such as regions of Yosemite National Park’s Merced Giant Sequoia Grove, that have cooler climates with disjunct species characteristic of the Pacific Northwest such as *Alectoria sarmentosa* (Witch’s hair lichen) pictured here. Yosemite National Park has used prescribed fires to protect areas from large, nearly unstoppable fires such as the catastrophic Rim Fire in 2013. Photo by Martin Hutten.

Fire refugia and climate change refugia are similar, but they are also distinct. These refugia share some topographical similarities, and are both often associated with cooler, wetter places on the landscape (Eberhart and Woodard 1987, Camp *et al.* 1997, Dobrowski 2011). Fire refugia are areas where fire has been excluded (Ouarmim *et al.* 2014) whereas climate change refugia are areas that buffer climate change and the fire regime may be dramatically or subtlety different than the surrounding landscape (Dobrowski 2011). Both likely have distinct fire regimes from their surrounding areas, although the magnitude may be different.

CAPs have unique climates and plants and they may serve as *in situ* conservation opportunities in the face of climate change. However, little is known about CAPs' fire ecology and risk. Therefore, I investigate the fire ecology of CAPs. Specifically I ask:

1. Do cold-air pools have similar fire frequency as their surrounding landscape?
2. If fires occur, do cold-air pools have similar fire severity patterns as their surrounding landscape?

Methods

Study Site

The study was conducted in mixed conifer forests in central California's Sierra Nevada Range within Yosemite National Park (37.8499° N, 119.5677° W), approximately 240 km inland from the Pacific Ocean. Historical fires were frequent and burnt every 6 to 15 years (Collins and Stephens 2007, Scholl and Taylor 2010). Fire suppression occurred from the late 1800s to the mid-1900s. Beginning in the 1970s, fire patterns were allowed to return to historical patterns, as lightning strike fires were allowed to burn freely through nearly one-third of the study area and prescribed fires occurred over a large area as well (Swetnam 1993, Collins and Stephens 2007, Scholl and Taylor 2010). A large fire deficit persists for more than two-thirds of my study area. Vegetation is mixed conifer forest co-dominated by fire resilient species including ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), and red fir (*Abies magnifica*), and scattered meadows and shrublands. The study region is from 1000 to 2600 m elevation and has hot, dry summers followed by cold, snowy winters.

Study Design

All spatial data were projected to a common projection and coordinate system of UTM, NAD83, Zone 11N in ArcGIS 10.2 (ESRI, Redlands CA, USA). Relevant spatial data was compiled from private and public sources, including predicted location of CAPs (based on methodology of (1, 2)), fire history polygons from 1930 until 2012 (3, 4), and Relative differenced Normalized Burn Ratio (RdNBR) fire severity categories based on changes in tree cover from 1984 to 2012 (5, 6) (Figure 3). Predicted CAP values included absent (no cold-air pooling occurs), marginal (areas with no clear signal for cold-air pooling due to topography and weather patterns and present (areas with potential for cold-air pooling to occur). The predicted CAPs are areas with potential to pool cold-air and there is variation in the frequency and duration of cold-air pooling. CAPs include areas with short and infrequent cold-air pooling that have similar climate and fire history to the surrounding area that are false-positives for climate change refugia. Conversely, areas predicted to lack CAPs may have CAPs present and thus represent false-negatives from the modeling procedure. The raw RdNBR range exceeded true differences in fire severity, and was -34,000 to 20,000. I limited the RdNBR range to -150 to 940, to better describe true differences (6, 7).

Spatial data was clipped with a USGS 10 meter Digital Elevation Model to restrict it to the mixed conifer zone (8). Spatial autocorrelation of raster data (cold-air pools, fire occurrence, and fire frequency) was reviewed the "variogram" function from the "usdm" package in R 3.1.2 (9, 10). Spatial autocorrelation was visually determined to be negligible when variance plateaued. Cold-air pool variance plateaued near 1000 m (Figure H1). Fire severity variance plateaued between 40 and 120 m depending on the specific fire (N=72).

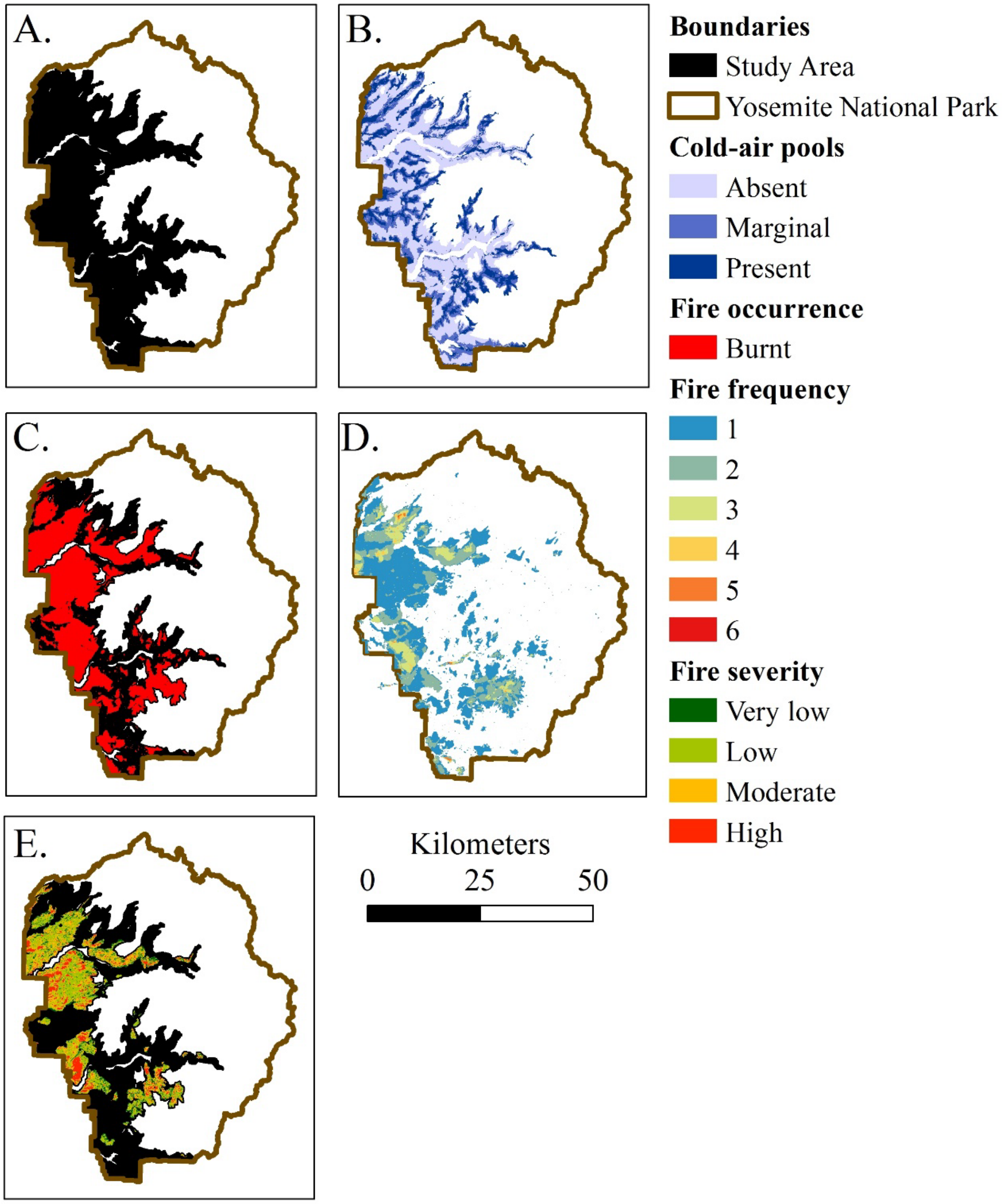

Figure 9. (**A**) The study area included mixed conifer forests of Yosemite National Park from 1000 to 3600 m in elevation, which encompassed about 170,000 ha. (**B**) Predicted cold-air pools

(CAPs) followed drainages and had a semi-regular pattern throughout the study area. The study area was dominated by areas without CAPs (100,000 ha) followed by areas with marginal CAPs (40,000 ha), and lastly CAPs (30,000 ha); (**C**) Fires have occurred through about 60% study area from 1930 to 2012; (**D**) Areas within the study area have burnt up to 6 times; (**E**) Fire severity distribution from 1984 to 2012 was dominated by low severity followed by moderate severity fires. Fire severity area included: very low severity 16,000 ha, low severity 44,000 ha, moderate severity 28,000 ha, and high severity 12,000 ha.

Analysis

I conducted analyses in R 3.1.2 (9) with the "nmle" package to incorporate spatial autocorrelation (11). I constructed statistical models to test if cold-air pools are related to fire (Eq 3).

$$\gamma \sim \text{Cold air pool (Eq 3)}$$

> Where $\boldsymbol{\gamma}$ is the response variable, either fire frequency (0 to 6) or fire severity (RdNBR: -150 to 940 (6, 7)). Cold-air pool categories include absent, marginal, and present.

For fire frequency, I modeled generalized least square models with the "gls" function. For fire severity, I modeled linear mixed effect with the "lme" function. I accounted for repeated measures from multiple fires (N=72) and their severities with random factors, including point identify and fire year. To reduce computational time, I subsampled 2,500 samples without replacement from a 100 m grid (N>100,000). I computed models with all available correlation structures, and compared then with Akaike information criterion (AIC). Then, I selected the model with the lowest AIC, and confirmed that the model residuals met assumptions. The best models had an exponential correlation structure and a nugget was present.

Results

CAPs had significantly less frequent fire than their surrounding landscape including areas with no CAPs ($P < 0.000$), and here was 25% reduction in fire occurrence from areas without CAPs to CAPs. Areas with marginal CAPs also had significantly less frequent fire than areas without CAPs ($P < 0.0002$), and there was a 10% reduction in fire occurrence ($P < 0.0001$). Areas without CAPs had 0.70+/-0.1 fire frequency, marginal CAP areas had 0.59+/-0.1 fire frequency, and CAPs areas had 0.52+/-0.1 fire frequency.

CAPs had significantly lower fire severity than areas without CAPs ($P < 0.006$), they had a 10% reduction in RdNBR. CAPs had low severity fire with RdNBR of 306 +/- 18. Marginal CAPs had moderate severity fire with an RdNBR of 325 +/-15. Areas without CAPs had moderate severity fire with an RdNBR of 340 +/-16. Areas with marginal CAPs were similar to areas with CAPs and without outs ($P = 0.16$ and $P = 0.18$ respectively).

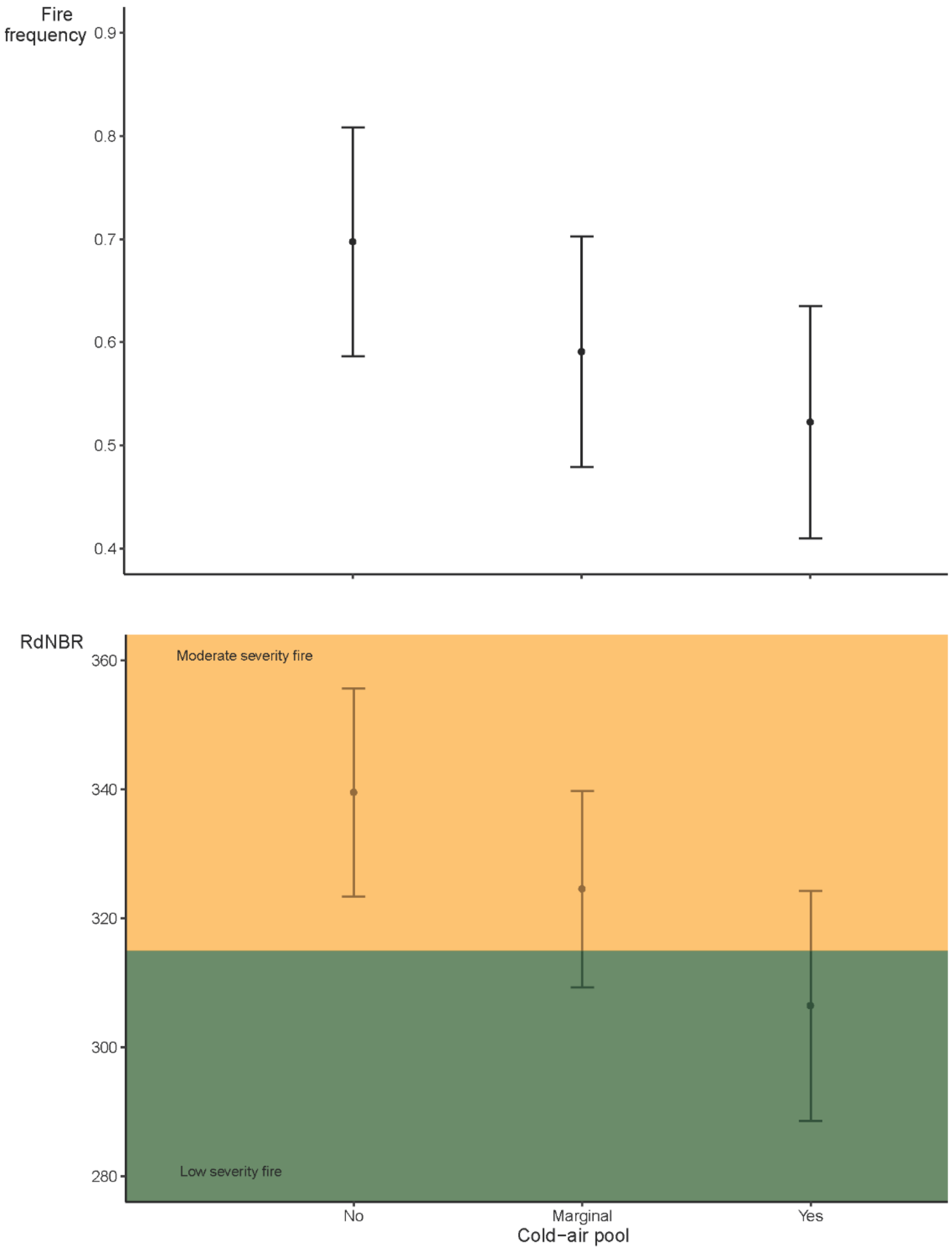

Figure 10. **(Top)** Model estimates for fire frequency with standard error grouped by their CAP level where dots represent the average and the bars are the standard error. **(Bottom)** Model estimates for fire severity with standard error grouped by their CAP level where dots represent the average and the bars are the standard error. Fire severity classification breakpoints include enhanced greenness, <-150; no change detected, -150 to 68; low severity, 69–315; moderate severity,316–640; high severity, >641 (6)). These classes correlate to the change in canopy cover and tree basal area whereby very low and low severity fires have between 0 and 25% change, moderate severity fires have between 26 and 75% change, and high severity fires have more than 76% change in canopy cover and tree basal area (12).

Discussion

CAP refugia had significantly different fire patterns from the surrounding landscape likely due to a combination of their vegetation, topography, or microclimate. Refugia in rugged terrain separated by fire barriers such as rock or water are more likely to have decreased fire occurrence than their surrounding terrain through these bottom-up controls (Heyerdahl *et al.* 2001). Other refugia may lack a physical barrier to fire, but their distinct microclimates can influence fire behavior. CAPs may have direct effects on fire behavior (temperature, wind, and fuel moisture) as well as indirect effects mediated through vegetation and fuel characteristics (amount and size distribution of fuel, fuel continuity, fuel moisture, forest structure, and relative humidity) (Brown 1974). These effects are realized as reducing fire energy (commonly called intensity) and change in dominant vegetation (commonly called severity), and in some cases even reducing fire extent if the fire self-extinguishes (Figure 11).

The interaction between CAPs and fire may be influenced by diurnal patterns because drivers of fire behavior vary diurnally including temperature, wind, and humidity. CAPs may be cooler in the evening and morning but reach similar maximum daytime temperatures as surrounding areas, but fire effects may be lessened by higher humidity and residual fuel moisture (Brown 1974, Fosberg *et al.* 1981, Lundquist *et al.* 2008). Overall, my analysis demonstrates that the unique climate and topographic placement of CAPs reduce fire frequency and intensity and thus, quite possibly, fire's ability to impact these ecosystems.

The interaction between CAPs and fire may be moderated by effects of season and weather on fire behavior. Historically fuel moisture would have been lower in fall due to seasonal drought and thus there may have been an increase in fire occurrence and severity. Climate change may magnify this trend because extreme fire weather (hot, dry and windy weather) is becoming more common, which allows fires to grow rapidly and reach unprecedented fire intensity and size (Collins 2014). As fire behavior becomes more extreme, bottom-up controls such as microclimate, topography, and fire barriers are weaker (Heyerdahl *et al.* 2001). If fire becomes driven by extreme events such as drought, high winds, or in extreme cases where the combination of weather, topography and fuels catalyze fire-generated weather phenomena such as plume-dominated fires, then historic fire barriers of refugia may no longer function (Figure 4) (Turner *et al.* 1999). This was evident in the 2013 Rim Fire, which burned over 100,000 ha, impacting a noticeable portion of my study area (Lydersen *et al.* 2014). Refugia that historically have had physical and climatic barriers to fire may be more susceptible to high-severity mega-fires becaue they produce effects well outside of desired ranges (Stephens *et al.* 2014).

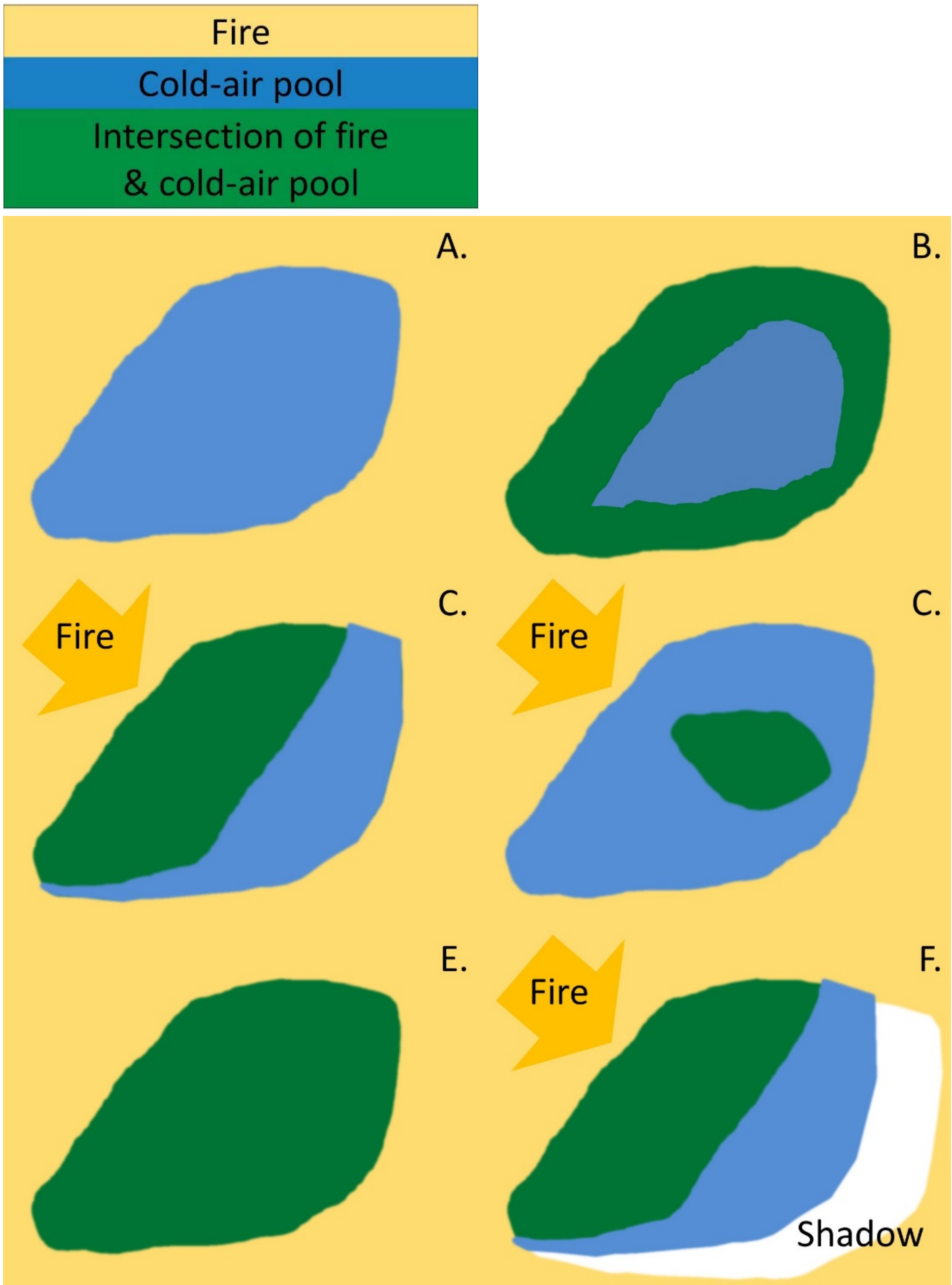

Figure 11. The interaction of fire and CAPs may be dependent upon fire behavior including the fire's direction, magnitude, and intensity. The yellow background indicates where fire occurred and the golden arrows indicate the fire's direction of movement. (**A**) Fires which move slowly (low magnitude) and release little energy (low intensity) may respond quickly to a refugium's microenvironment and not penetrate the CAP, whereas (**B**) fires with high magnitude and intensity may respond slowly to a CAP (burn a buffer around the perimeter); (**C**) and/or a larger region near the flame front; (**D**) create a spot fire ignites within the CAP which grows especially during dry windy conditions; or (**E**) can burn the entire CAP. (**F**) There also may be a CAP fire shadow where a reduction in fire extent or severity occurs because of its proximity to a CAP and the subsequent reduction in fire presence or severity.

Implications for management

More than 100 years of fire suppression fostered dense tree stands with ladder fuels including small trees reaching from the forest floor to its' canopy. Today's mixed conifer forests are more susceptible to high severity fire than ever before (Stephens *et al.* 2013). There is a consensus that we need to reduce tree density and fuels to make forests resilient to climate-change induced disturbances (Millar *et al.* 2007, Collins *et al.* 2009, Schwilk *et al.* 2009). While prescribed fire and mechanical fuel reduction treatments may have short-term effects on the inhabitants of refugia, the long-term lack of fire exacerbates climate change's increasing disturbance threats to biodiversity, including increased fire frequency and severity (Westerling *et al.* 2003, Westerling and Bryant 2008).

Refugia, especially in arid regions like Yosemite National Park have greater moisture, fuel production, and historically lower fire risk than the surrounding landscape (Lundquist *et al.* 2008, Dobrowski 2011, Van De Water and North 2011). However, refugia fire risk is likely increasing due to the combination of fire suppression and climate change induced extreme fires. Refugia commonly occur in riparian areas, which were heavily altered by fire suppression resulting in extraordinary amounts of fuel (more than five times greater than historic levels), leaving them uncharacteristically susceptible to high severity fire that might be quite detrimental to biodiversity (Van De Water and North 2011). As climate becomes drier, these fuels have reduced moisture and are thus available to burn for a larger portion of the year (Batllori *et al.* 2013). These additional fuels can contribute to more severe fires.

High-severity fire risk could be mitigated with prescribed fire, mechanical treatments, or managed wildfire within the CAP and at the landscape level (Stephens *et al.* 2010). Fuel reduction could have unintended consequences, since trees moderate climate. Trees filter solar radiation, providing a buffer between CAPs and the atmosphere; removing trees can increase surface temperatures 10 to 40°C (Ford *et al.* 2013). Oddly, fire suppression which increases tree density may have also made CAPs climates cooler. To reduce the potential to increase temperatures dominant trees should be preserved in fuel treatments (Agee and Skinner 2005). Nonetheless, managers must understand the trade-offs for refugia management and thresholds between reducing fire risk and altering the very environment that they wish to protect.

Stand-replacing fires surrounding CAPs are also of concern because large-scale high severity fires can kill many trees within the CAP air shed and in doing so may also change the local climate. Killing trees that moderate the temperature and soil moisture in the greater air shed may reduce the cold-air source and thus the frequency and duration of cold-air pooling. Trees likely have strong biological feedback on climate in gentle sloping environments because there are not strong topographical drivers of cold-air movement. Steeper slopes have faster cold-air run-off and trees likely play a smaller role here. Fuel and restoration treatments could be completed in areas surrounding CAPs to protect cold-air sources from severe fire. As before, caution is needed when applying fuel treatments because trees moderate temperature and minimizing these impacts will be a higher priority with climate change.

Conclusions

Conservation planners are advised that their "highest priority (is) to reduce negative edge effects and improve *in situ* management of existing habitat patches" (Oliver *et al.* 2012). Refugia do exactly this, allowing *in situ* management of habitat patches (Oliver *et al.* 2012). Refugia are complex habitats influenced by species interactions, climate, and fire that interact with one another. For that reason, protecting the land associated with refugia is not sufficient to protect the biological and physical properties of refugia; *additional management actions are necessary*. Many of these actions, like strategic fuel treatments or managed wildfire, are already recommended for both forest restoration and climate change adaptation (Millar *et al.* 2007, Stephens *et al.* 2010). Refugia are also susceptible to disturbances, and redundancy on the landscape is necessary to utilize this conservation strategy. Actions to manage refugia are similar to manager’s current tool kits for conservation, but the need for these actions in refugia may be an additional incentive to complete them. Managers will be asked to make decisions about refugia without understanding their full ecological complexity and they must understand that refugia are not static.

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CHAPTER 4

DRIVERS OF UNDERSTORY PLANT COMMUNITIES IN MIXED CONIFER FORESTS WITH LONG RESTORED FIRE REGIMES

Abstract

Fire suppression in western North America has caused large changes in forests, their understory plant communities, and a potential decline in plant biodiversity. I sought to understand past understory communities and their drivers in an arid mixed conifer forests with long restored fire regimes. This expansive and long-term study utilized natural experiments which were part of Wildland Fire Use program, including the Illilouette Basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park. The Wildland Fire Use areas began in the 1970s when the National Parks allowed lighting strike fires to burn and thus restored fire regimes. These fires reduced fuels and performed other ecosystem restoration functions such as opening canopies which foster the re-development of diverse forest understories. Understory plant communities were influenced by a combination of forest structure, environmental, plot-scale fire experience, and regional-scale fire experience within 50 and 75 meters. There were seven distinct plant communities which could explained by forest structure, elevation, local fire experience, and the diversity of regional-scale fire, also called pyrodiversity − the diversity of fire size, severity, season, and frequency. Broad community metrics (cover, richness Simpson diversity, and evenness) were also influenced by some of the same variables, and distinct ones as well. Canopy cover, an indirect measure of restoring mixed severity fire which reduces tree canopy as a process, influenced plant communities. As canopy covered increased from 0 to 100%, understory plant cover decreased 7%, Simpson diversity decreased 0.09, and evenness decreased 0.11. Plant cover also influenced burn severity and number of times burnt, although to a lesser degree. Richness was increased by moisture, soil texture, and pyrodiversity. Based on my study, restoring mixed severity fire regimes can lead to an overall reduction of canopy cover and unique fire experiences within 50 and 75 m which in turn fosters diverse understories.

Introduction

Fire suppression has dramatically altered forests adapted to frequent, mixed severity fire. Historically fire was a keystone ecological process that consumed and recycled nutrients, altered community composition and assembly, and selected for fire-resilient species (Bond and Keeley 2005). Diversity, including in understory plant communities, has been negatively impacted by fire suppression (Tilman and Lehman 2001). Specific pathways for fire suppression to negatively influence plant communities include, but are not restricted to changes in light and moisture on the forest floor (Battles *et al.* 2001, North *et al.* 2005). Fire suppressed forests are homogenized and densified creating nearly continuous canopy cover (Larson and Churchill 2012). These forests also have more shade-tolerant trees and denser canopies which together block light to the forest floor and increase competition for water and nutrients (Kilgore 1973, Minnich *et al.* 1995, Bouldin 1999). The combination of many years since fire and additional trees also dramatically increases litter on the forest floor which may either enhance moisture, physically block plants, or a combination of the two (Parsons and Debenedetti 1979, North *et al.* 2005). While the mechanisms of how fire suppression influences plant communities are well understood, the historical range of plant communities and their drivers in forests with historic natural fire regimes are poorly understood.

More than 1.8 million hectares of mixed conifer forests in the Sierra Nevada have been negatively affected by fire suppression (Allen-Diaz 1988). There is a growing body of literature about Sierran mixed conifer forest understories. The modern forests are speciose due to the forest understory (Fites and Holst 1994, Shevock 1996), but they likely had greater richness. Studies have described plant communities (Potter 1998) and investigated the effects on the environment of fire suppression (North *et al.* 2005), timber management (Battles *et al.* 2001), forest restoration and fuel hazard reduction (Collins, Moghaddas, *et al.* 2007), and climate change (Hurteau and North 2008). Together, these studies suggest light and moisture are important for the understory plant communities, and that nonnative plants are uncommon. Some studies seek to understand the role of fire in understories, but they have limited applicability because they study prescribed fired that are only monitored for a few years (Huisinga *et al.* 2005, Collins, Moghaddas, *et al.* 2007, Hurteau and North 2008). As a result, there is a research gap for mixed conifer forest understories − how do understories respond to frequent wildland fire in the long-term. As such, I investigate understory plant communities in forests with restored fire regimes and restored forest structures and broadly ask*: What are the structure and composition of understory plant communities in forests with restored fire regimes? What factor are responsible for variation in these factors?*

Many ecologists have investigated how individual species and local communities respond to fire although there is great variation (Turner *et al.* 2003, Chase 2007). Often this work is focused on one or possibly two aspects of a fire regime (Saxon 1984, Martin and Sapsis 1992, Knapp and Keeley 2006, Parr and Andersen 2006, Clarke 2008). For example, large, high severity fires homogenize microenvironments and select for disturbance tolerant species across the landscape (Pausas and Verdú 2008). In contrast, mixed severity fire increases a forest's mosaic and its microenvironments which selects for species with a wide variety of traits. Mixed severity fires may influence diversity by increasing alpha diversity or species richness, whereby there are more niches for species to inhabit (Perry *et al.* 2011), beta diversity whereby species turnover increases between unique habits while species richness remains the same throughout the region, or a combination of both.

Others have noted the importance of pyrodiversity or how the extent, frequency, season, or severity interact to foster biodiversity (Martin and Sapsis 1992). Fire may create unique niches in space and time, alter competition, and create a new baseline in severe cases (Martin and Sapsis 1992, Bond and Keeley 2005) (Figure 12, Table 1). Few studies include pyrodiversity because there are few natural areas with restored fire regimes (and thus pyrodiversity) and because it is difficult to quantify; therefore singular fire variables are included in a multivariate analysis and these do not explain the diversity of fire experiences (Van Wagtendonk 2007). My other recent study demonstrates that pyrodiversity enhanced pollinator diversity, plant diversity, and pollinator-plant interactions (Ponisio *et al.* 2016). I build upon earlier results by using a longer term data set with repeated measures and by expanding the definition of the plant community to include all types of plants. This is one of the first studies to consider the long-term effect of pyrodiversity on the entire plant community including trees, shrubs, and herbaceous plants.

Table 1. Mechanisms that could influence both natural selection and species favored in community assembly in an active fire regime (Martin and Sapsis 1992).

Fire regime characteristics	**Mechanism of selection**
Severity	kills or releases seed bank and vegetation
Extent	alters dispersal capabilities of species
Season	alters potential colonizers and species response to the disturbance
Frequency	selects for climax or early successional species, and resistance or resilient species
Compounded disturbances	Fire in combination with other disturbances such as disease (beetle outbreak or fungal infection) or weather (drought or severe wind)

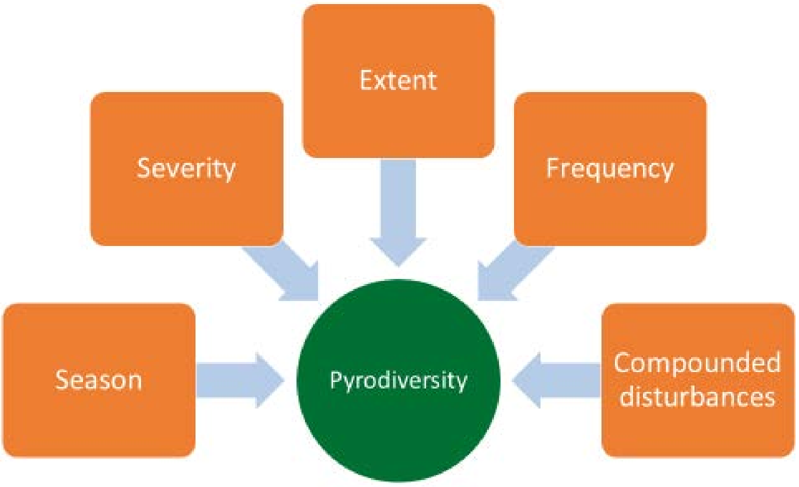

Figure 12. Martin and Sapsis (1992) hypothesize that fire diversity, also called pyrodiversity, fosters biodiversity.

Fire may burn similar vegetation in dramatically different patterns due to daily, weekly, and seasonal weather (Rothermel 1972, Littell *et al.* 2009, Dillon *et al.* 2011, Thode *et al.* 2011). Daily weather influences temperature, relative humidity, and wind, and is also related to topography (Holden and Jolly 2011). Often in the morning temperatures are low, relative humidity is high, and wind is low, so fire intensity is also subdued. In contrast, late afternoons are characterized by warmer temperatures, lower humidity, and local winds blowing upslope. Areas which burn during the afternoon often have greater fire intensity, and thus increased fire severity. In addition, there are differences in temperature and humidity based on aspect. At the weekly scale, there may be extreme heat or wind, and fronts where relative humidity does not recover at night which cause the fire to increase in intensity. These daily differences seasonal weather influence moisture, and how fuel burns (Heyerdahl *et al.* 2001, Littell *et al.* 2009). For example, a forest with saturated soils and high herbaceous cover in the early season may not carry a surface fire when water is present. However, once the site is dry in the late season, a surface fire may carry through the herbaceous cover, and sometimes cause trees to torch due to dense fuel and fuel ladders. In these ways and others, fire may dramatically alter vegetation and shift plant community boundaries.

Fire may also burn similar vegetation in similar patterns because both are responding to environmental factors (Thode *et al.* 2011). Montane chaparral communities with continuous shrub fields often arise on the steepest slopes with thin soils embedded within *Pinus jeffreyi* (Jeffrey pine) woodlands. The combination of continuous shrub fuel and steep slopes also promote high severity fires (Dillon *et al.* 2011). In contrast, *Pinus jeffreyi* (Jeffrey pine) woodlands most often burn at low to moderate severity with limited high severity fire (Thode *et al.* 2011). These distinct plant communities near one another also have unique fire patterns which influence pyrodiversity at the landscape level (Dillon *et al.* 2011, Thode *et al.* 2011).

I broadly asked, how does fire with unique areas burnt, severities, and frequencies (hereafter referred to as pyrodiversity) and the environment influence plant communities across spatial and temporal scales? Specifically my goals were to:

(1) Describe plant communities that develop in frequent fire upper montane mixed conifer forests,

(2) Understand the most important environmental and fire gradients that influence plant communities through space and time, and

(3) Infer if pyrodiversity influences understory plant species richness and diversity, and determine the scale at which pyrodiversity is important.

Methods

Study Site

The best proxies for historic mixed conifer forests in the Sierra Nevada are National Park Service Wilderness areas, including Illilouette Creek basin in Yosemite and Sugarloaf valley in Kings Canyon National Parks (Figure 13) (Collins, Kelly, *et al.* 2007, Collins and Stephens 2007, Collins and Stephens 2007, Collins *et al.* 2009, Stephens *et al.* 2010) hereafter referred to as Illilouette and Sugarloaf. Based on tree-ring and remotely sensed data analysis reconstructions, the historic fire regime predominantly consists of frequent fires with low and moderate severity fire, and small patches of high severity fires (Collins *et al.* 2009, Collins and Stephens 2010). Fire suppression began in the late 1800s and remained until the early 1970s when the parks adopted a “let burn” management strategy (Van Wagtendonk 2007). In 1970 Illilouette had nearly continuous forests (Figure 14) and it is likely Sugarloaf also had a similar forest structure. Since the early 1970s, fires reduced fuels and performed other ecosystem restoration functions such as reducing canopy cover, which may foster the re-development of diverse forest understories (Collins & Stephens 2007) (Figure 15A, B, C, D, E, F, G, and H). Today the mixed conifer forests in Illilouette Creek and Sugarloaf Creek basins are interspersed with wet meadows, dry meadows, riparian forests, and shrublands. Forests are dominated by Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus contorta* ssp. *murrayana)*, white fir (*Abies concolor*), and red fir (*Abies magnifica*). These basins are reasonable historical representations of forests despite 100 years of fire suppression because the study areas are large, have intact watersheds, and have not been harvested. Most importantly, these areas were the first that allowed lightning-ignited fires to burn in California which has resulted in self-limiting fires and heterogeneous forest structures (Collins and Stephens 2007, Collins *et al.* 2009, Collins and Stephens 2010).

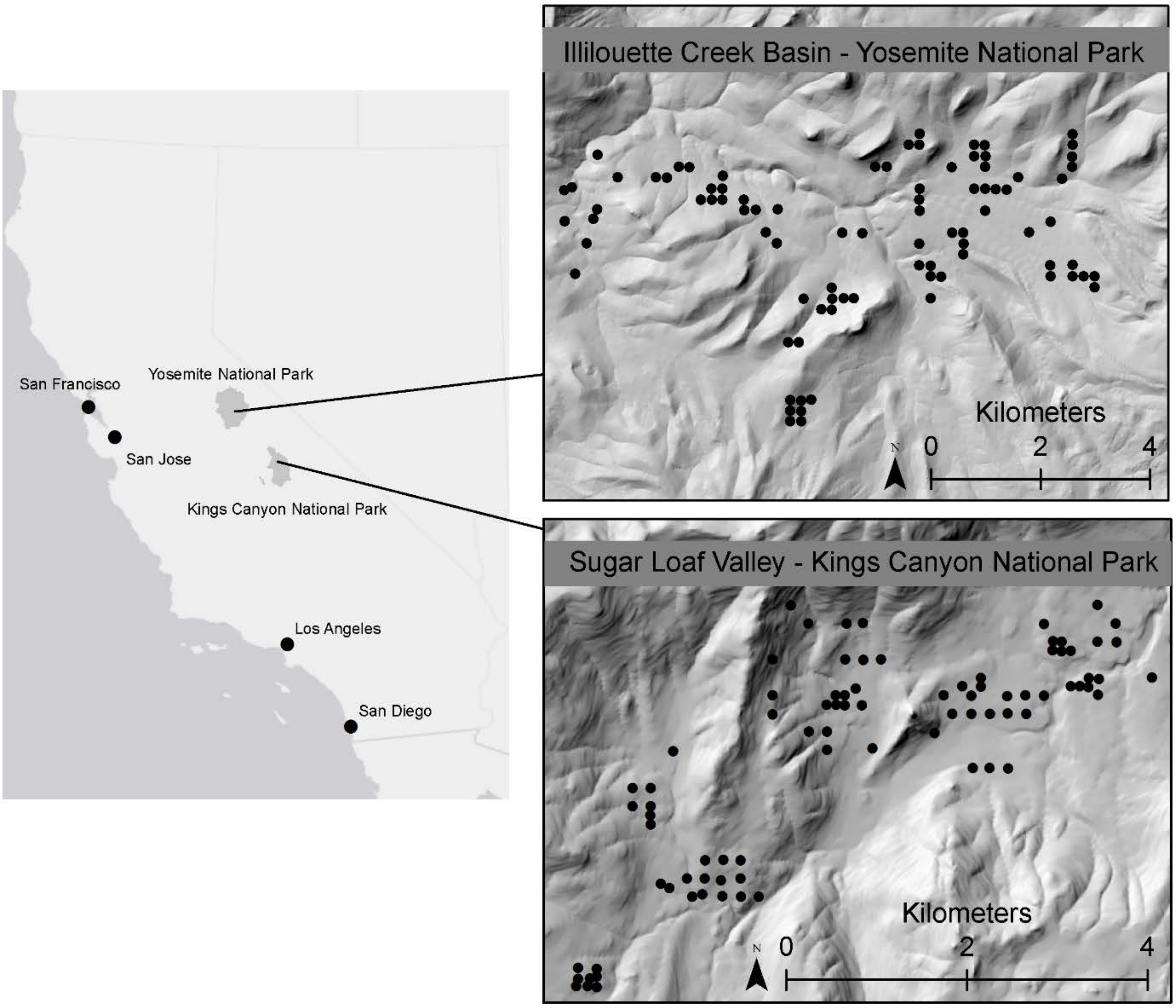

Figure 13. The study took place in California's Sierra Nevada in two wilderness areas with long-established natural fire programs: Yosemite National Park's Illilouette Creek Basin and Kings Canyon National Park's Sugarloaf Valley.

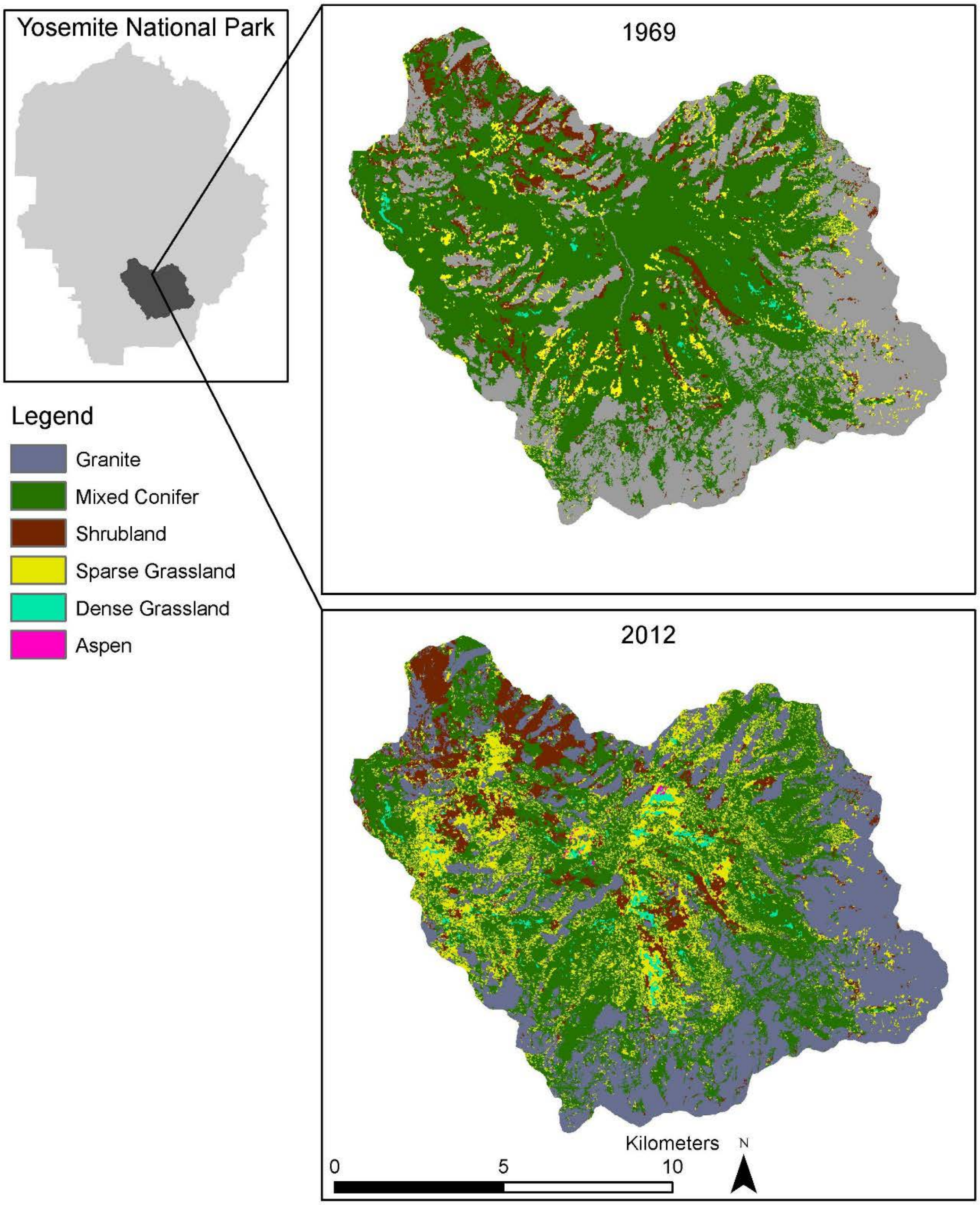

Figure 14. The Illilouette was dominated by forests in 1969 before the “Let it Burn” program began. After 40 years of frequent fire the nearly continuous mixed conifer forest is reduced in acreage and is discontinuous. Now there is greater frequency and acreage of sparse grasslands, dense grasslands, shrubs, and aspen. Images from 1969 are aerial photographs and images from 2012 are National Agriculture Imagery Product (NAIP). (Gabrielle Boisrame prepared photos and delimited plant communities in eCognition.)

Figure 15. Yosemite National Park's Wildland Fire Use Program fostered a mosaic of forest structures with unique plant communities. Within its 16,000 hectares, the Illilouette Creek Basin has (left to right, top to bottom) (A) spectacular displays of California goldenrod (*Solidago californica*) in what was a lodgepole pine forest (*Pinus contorta*) [by Scott Stephens], (B) park-like-forests with sparse shrubs [by Josiah Johnston], (C) open shrub fields in a previous Jeffrey pine (*Pinus jeffreyi*) and red fir stand (*Abies magnifica*) [by Kate Wilkin], (D) park-like-forests with native grasses [by Kate Wilkin], (E) habitat for California's native grasses like California brome (*Bromus carinatus*) [by Kate Wilkin], (F) areas with strong seedling recruitment [by Kate Wilkin], (G) sand barrens [by Lauren Ponisio], and (H) striking fields of purple lupines (*Lupinus polyphyllus*) set off by blackened pines [by Kate Wilkin].

The study area is along an elevation gradient from 1400 to 3000 m on the surrounding ridges. The study area's climate has cool, moist winters, and warm, generally dry summers (Table I1 and I2, Figure I1). Monthly climate normals (1981-2010) for January minimum temperatures range from 0 to -8 °C, whereas monthly climate normals (1981-2010) for July maximum temperatures range from 24 to 31 °C (Arguez *et al.* 2010). Precipitation varies with elevation and historically has been predominantly snow near 100-500 cm (Table I2, Figure I1,(Arguez *et al.* 2010).

Sample Design

Field Data

Based on watershed boundaries for Illilouette Creek and Sugarloaf Creek the basins are 16,200 and 12,300 ha, respectively. Sampling was not conducted across the entirety of both basins due to foot travel and field crew time limitations. Instead, sampling was focused where the greatest range of burn frequencies (since onset of the natural fire programs) could be captured in contiguous areas. Based on these limitations, plots occur between 2000 and 2500 m. in elevation with convex hull polygons around the field plot locations that were about 1500 and 600 ha in Illilouette and Sugarloaf, respectively. We chose plot locations using a 200 m systematic grid overlaid on two strata: burn frequency since onset of the natural fire program (0-4) and dominant tree genus (*Pinus*, *Abies*). In Sugarloaf a 100 m grid was used for two stratum combinations due to limited available area. The goal was to sample a minimum of five plots in each burn frequency-dominant tree genus combination. A total of 117 field plots were established in 2002 (65 in Illilouette, 52 in Sugarloaf). We sampled plots in 2002 and most plots were resampled in either 2012 or 2013. We added plots from the 200 m grid to improve inference about high severity fire in 2012 and 2013 including 16 plots each in Illilouette and Sugarloaf. In total there were 258 samples including 113 plots with repeated measurements (226 samples) and 32 plots that we sampled once (32 samples). These plots represent a chronosequence of post-fire succession from one year post-fire through more than 30 years post-fire, burned up to four times, and had varied fire severities; 30 plots burned in between sampling periods. Therefore, these plots are an excellent source for post-fire succession research.

Plots followed common forest inventory methods (Figure I1). Circular plots had a 12.62 m radius and covered 0.05 hectare. All trees above 10 cm in diameter at breast height (DBH) had their diameter and species recorded. We measured understory cover with two point-intercept transects which intersected at plot center and extended to the plot boundary along cardinal directions. The understory transects had 208 total hits with 104 hits each for the 0-0.5 m and 0.5 to 2 m strata. We recorded species lists through timed-area search of up to one-hour, or ceased if no new species had been found for 15 minutes. W measured litter depth, to the nearest centimeter, six times per plot in association with Brown's fuel transects (Brown 1974). We measured canopy cover with a densitometer at 25 gridded points within the plot. We determined soil texture with the "feel method" by holding a small sample of soil in your hand, adding water, and then trying to form a ball and ribbon with the mixture (Thien 1979). Potential soil texture categories include sand, loamy sand, sandy loam, silt loam, loam, sandy clay loam, silty clay loam, clay loam, sandy clay, silty clay, and clay.

We calculated understory cover based on the point-intercept data. Richness was based on the species area search. Simpson diversity was calculated with Vegan based on the point-intercept data (Dixon and Palmer 2003, Oksanen *et al.* 2007). Evenness was calculated as E_{var} which is adjusted for species richness (Smith and Wilson 1996). The number of unseen species was calculated with “specpool” in Vegan based on species area search (Dixon and Palmer 2003, Oksanen *et al.* 2007).

Spatial Data

All spatial data were projected to a common project and coordinate system of NAD 83 UTM 11N in ArcGIS 10.2 (ESRI, Redlands CA, USA). Spatial data was compiled from public and private sources, including average Climatic Water Deficit from 1981 to 2010 (Flint *et al.* 2014); solar radiation index (Mccune and Keon 2002); slope derived from USGS DEM; fire progression (Van Wagtendonk 2012); and Relative differenced Normalized Burn Ratio (RdNBR) fire severity categories based on changes in tree cover which is available for fires occurring from 1984 to 2012 (Miller and Thode 2007, Miller 2012). Fire severity values included very low (RdNBR < 69), low (69 < RdNBR < 315), moderate (316 < RdNBR < 640), and high (RdNBR ≥ 641). Fire severity classes correlate to the mean change in canopy cover and tree basal area whereby very low and low severity fires have between 0 and 15% change, moderate severity fires have between 16 and 89% change, and high severity fires have more than 90% change in canopy cover and tree basal area (Miller *et al.* 2009).

To understand the regional effect of pyrodiversity on plant communities, Lauren Ponisio and I created a pyrodiversity index, where we quantified the diversity of the fire histories in relation to fire frequency, age, extent and severity experienced in an area (Miller and Thode 2007, Miller 2012, Yosemite National Park 2012). Fire season is a component of fire history that we did not directly consider. In Illilouette there was, however, limited variability in fire season within any one fire, and most fires occurred in different months (Van Wagtendonk 2012). In addition, fire season data does not exist for Sugarloaf. Based on the Illilouette fires, we believe that season is also indirectly included with each fire.

Following Ponisio (2016), we estimated pyrodiversity and first evaluated the uniqueness of the fire history of each 30x30 m raster cell (Figure 16). First we created categories of fire severity within a fire (Miller 2012). For each raster cell, we then used the sequence of fires and the severity of each of those fires to define unique fire histories. There are more than 300 unique fire histories throughout both study sites. A raster layer for pyrodiversity was then calculated as Simpson’s diversity, functional dissimilarity, functional divergence, and functional richness of fire history categories around each plot. Simpson’s diversity describes the richness and abundance of fire experiences. Functional divergence describes different fire experiences within the buffer − as differences increase so does functional divergence. Functional richness is a count of the unique fire experiences within the buffer. Functional dissimilarity is similar to the Bray-Curtis dissimilarity index and calculates the proportion of fire experiences that are not shared.

We then calculated the weighted pyrodiversity score and transformed fire characteristics, mainly the year the fire occurred and its severity, into traits for each pixel and then used a functional dispersion metric to calculate the diversity of fire “traits” (see supplements in (Ponisio *et al.* 2016)). The fire histories of each raster cell were thus weighted based on the similarity of fire traits. For example, a low severity pixel in the same fire would be more similar to a moderate severity pixel than to a high severity pixel. Fire traits were also weighted by the number of years since the fire occurred to account for the variety of fire ages. We quantified the weighted diversity of fire history for 25, 50, 75, 100, 250, and 500 m buffers around each plot (Tscharntke *et al.* 2005). Preliminary analysis was used to identify the pyrodiversity index and scale at which pyrodiversity influenced plant communities, and these results were used for further analysis (Equations J1 and J2, and Tables J1, J2, and J3).

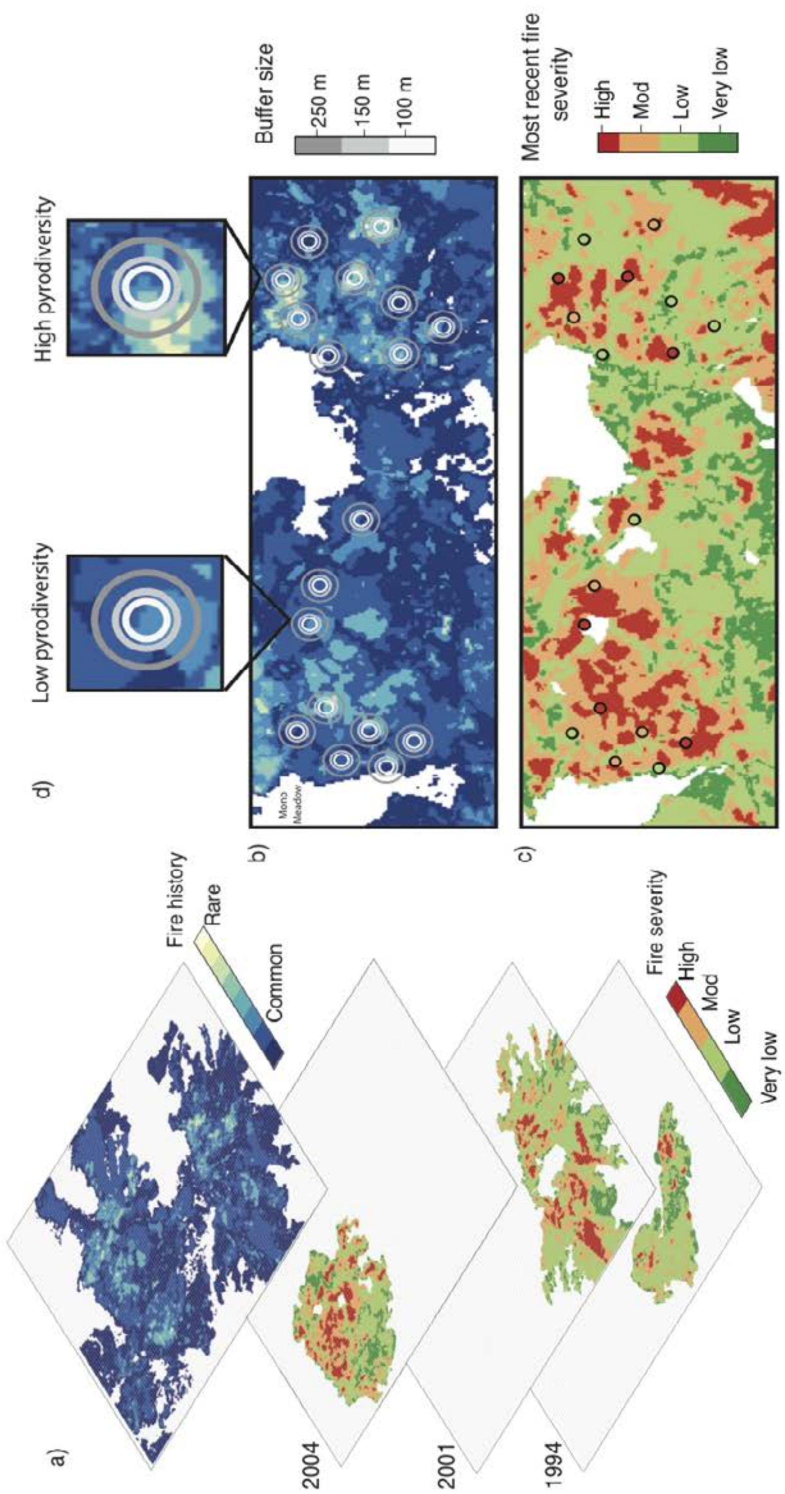

Figure 16. Representation of the method used to estimate pyrodiversity. A) Each 30x30 m raster cell is assigned a fire history classification based on the fires and severities it experienced (three representative fires depicted). B) The diversity of fire histories, either weighted for the similarity of fire history or unweighted, is calculated within buffers around the monitoring sites. C) The severity of the most recent fire is also included as a possible interaction with pyrodiversity. D) An example of sites with relatively low and high pyrodiversity measured as the diversity of unique fire histories at different buffer sizes. In the low pyrodiversity example, the pyrodiversity was estimated as 0.2, 0.5, and 0.7 within the 100, 150, and 250 m buffers, respectively. In the high pyrodiversity example, the pyrodiversity was estimated as 0.7, 0.8, and 0.8 in buffers of increasing diameter. Within a buffer, the number of different fire history categories ranged from 1 to 23. Some buffers overlapped areas did not burn during the time period for which we have burn history data (i.e., Mono Meadow, large rocky outcrops and fires that occurred before 1984). Those areas were assigned their own fire history category. From Ponisio 2016.

Analysis

What is the structure and composition of the fine-scale plant communities, and their drivers?

I explored how plant species assembled as communities. I used the species area search data and excluded rare species, those that occurred on less than 5% of the plots, which left 75 species in the analysis. The number of K-mean clusters was determined with an automated gap analysis using the Cluster package's "clusGAP" function with potential clusters ranging from one to 100, and tested with 1000 Monte Carlo bootstrap iterations (Tibshirani *et al.* 2001, Jain 2010, Maechler *et al.* 2016). The plots were assigned to the K-means clusters with the Cluster package's "kmeans" function. Explanatory variables were explored with a tree analysis in "rpart" (Therneau *et al.* 2015), including environmental variables (elevation, slope, CWD, TWI, heat load, canopy cover, litter depth, soil texture), fire history of site (time since fire, number of times burnt, and most recent burn severity), regional fire history (functional richness, functional divergence, and functional dissimilarity at buffered distances (Figure 16)), and forest structure including number of trees and tree basal area (total basal area of trees, and basal area of lodgepole pine, Jeffrey pine, white fir and red fir). The tree was pruned to avoid overfitting data, and tree size selected to minimize the cross-validated error.

What is the structure of the overall plant community, and its drivers?

I constructed statistical models to represent my hypotheses for the drivers of plant communities. I used generalized linear mixed effects models to test the significance of several independent variables on each response variable (Bates *et al.* 2014, Bates *et al.* 2014, Kuznetsova 2014). Model dispersion and residuals were reviewed and fit assumptions. All analyses were conducted in R 3.1.2 (R Development Core Team 2008). I examined the main effect of plot-based fire attributes (time since fire, most recent fire severity, and number of times burnt). In addition, I examined the interaction of time since fire and most recent burn severity at the plot scale. Other environmental variables that may influence the response of the plant communities were included. Lastly, to account for repeated measures I included site identity (park and plot) and survey year as random variates. I am interested in the combination of fire and environmental variables which influence plant communities. I used the following equation to evaluate understory cover and evenness (Equation 4):

y ~

Time since fire +
Most recent fire severity +
Time since fire * Most recent fire severity +
Number of times burnt +

Plot-based
fire
experience

Canopy cover +
Average litter depth +
Climatic Water Deficit (CWD) +
Soil texture +
Slope percent +

Environment

Park + Plot + Survey year

Random effect

Where y is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities.

To address if pyrodiversity begets biodiversity, I examined the main effect of plot-based fire attributes and regional pyrodiversity attributes, and their interactions, on diversity metrics including plant richness and Simpson's diversity. Characters of the most recent fire were explanatory variables because fire severity and time since fire can have strong effects on the plant communities that develop after fire (Turner *et al.* 1999, Wang and Kemball 2005, Swanson *et al.* 2010). In preliminary tests, individual models tested the main effect of one pyrodiversity metric, and its interaction with time since fire and most recent burn severity at all spatial scales (Equation J1, J2; Table J1, J2). The models' AIC values were compared to one another and the model with the lowest AIC value had its pyrodiversity metric and scale used in further analysis. Functional divergence of fire within 50 meters of plot was evaluated for richness and functional richness within 100 meters of plot was evaluated for Simpson diversity. Other environmental variables that may influence the response of the plant were included such as canopy cover, average litter depth, CWD, soil texture, and slope percent. I used the following equation to evaluate richness and diversity (Equation 5):

$y \sim$

Time since fire +
Most recent fire severity +
Pyrodiversity +
Time since fire ∗ Pyrodiversity +
Most recent fire severity ∗ Pyrodiversity +
Number of times burnt +

Plot-based fire experience & Pyrodiversity

Canopy cover +
Average litter depth +
Climatic Water Deficit (CWD) +
Soil texture +
Slope percent +

Environment

Park + Plot + Survey year

Random effect

Where γ is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities.

For models with density as response variables I assumed Gaussian with square root transformation if needed or Poisson error depending on the dispersion of the data and model residuals (Table J3). Model selection was completed whereby full and reduced models were compared. Reduced models included all combinations of variables with one to six variables in the model. AIC values were compared, and the model with the lowest AIC is presented (Mazerolle 2016). Marginal R^2 was calculated as the proportion of variance explained by fixed factors alone and conditional R^2 was calculated as the proportion of variance explained by both fixed and random factors (Nakagawa and Schielzeth 2013, Lefcheck 2015). Random effects were dropped from R^2 calculations if their variance and standard deviation were zero, and are noted as such in the results.

Results

What is the composition of the plant communities?

Today the landscape has closed to open forests interspersed with open shrublands, wet meadows, dry meadows, and continuous shrublands. While the dominant forest trees are Jeffrey pine, lodgepole pine, white fir, and red fir, other common trees include Sugar Pine (*Pinus lambertiana*), quaking aspen (*Populus tremuloides*), and western juniper (*Juniperus occidentalis*). Open forest stands often have sparse understories of bunch grasses, forbs, and shrubs. The understory included forbs such as Brewer's lupine (*Lupinus breweri* var. *breweri*), dogbane (*Apocynum androsaemifolium*), broad leaf lupine (*Lupinus latifolius* var. *columbianus*); shrubs such as ceanothus (*Ceanothus cordulatus*), greenleaf manzanita (*Arctostaphylos patula*), chinquapin (*Chrysolepis sempevirens*), and snowberry (*Symphoricarpos mollis*); graminoids such as western needle grass (*Achnatherum occidentale* ssp. *occidentale*) and big squirreltail grass (*Elymus multisetus*); and ferns such as western bracken fern (*Pteridium aquilinum* var. *pubescens*). The dominant montane chaparral shrubs include whitethorn ceanothus (*Ceanothus cordulatus*), green leaf manzanita (*Arctostaphylos patula*), and pine mat manzanita (*Arctostaphylos nevadensis*).

Illilouette had 298 plant species in 146 plots while Sugarloaf had 172 plant species in 116 plots. In total, there were 379taxa identified including 11 tree species, 47 shrub species, 38 graminoid species, 275 forb species, and two epiphytes. The unseen species model suggests that an additional 400 plant species were not encountered within my study region, however that is likely an overestimate because only 675 plant species are known within the heavily studied park (Yosemite National Park 2002). No nonnative plants occurred in 2002, and only eleven plots had nonnative plants during resampling (Table 2). Despite low understory cover, the understory is a surprisingly rich community (Figure 17A, B). Simpson diversity was moderately high throughout the study area (Figure 17C). Evenness was often high suggesting that plants were more likely to have even abundance rather than have a few dominant plants (Figure 17D).

Table 2. Nonnative plants found from 2011 through 2013 including the park in which they were found, their habit and life span based on USDA Plants, species name, California Integrated Pest Management Harmfulness Rating (Bell *et al.* 2015), and the number of plots where they occurred.

Park	Habit	Life span	Species	CA-IPM Rating	Plot count
Sugarloaf	forb	perennial	*Taraxicum officinale*		1
Illilouette	forb	annual	*Lactuca serriola*		3
	forb	perennial	*Hypocharis radiata*		1
	forb	perennial	*Taraxicum officinale*		1
	forb	perennial	*Tragopogon dubius*		3
	grass	annual	*Bromus tectorum*	High	3

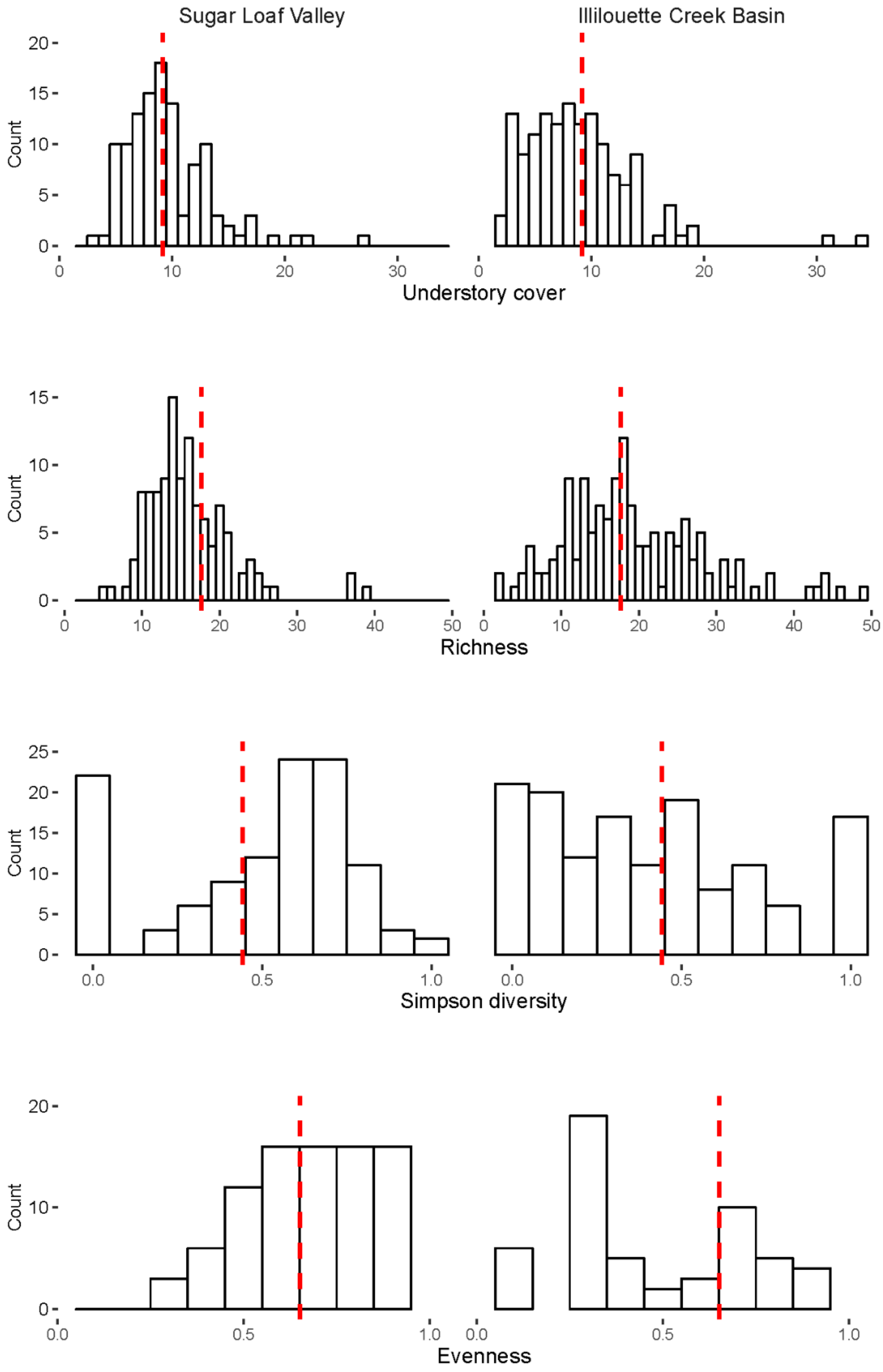

Figure 17. After 40 years of managed fire, plant community response variables (including understory cover, Simpson diversity, and evenness from point-intercept data; and richness from species-area-search) ranged across the study sites. Each histogram has a mean indicated with a dotted red line.

What is the structure and composition of the fine-scale plant communities, and their drivers?

Seven plant community clusters are identified and can be differentiated based on broad location (Illilouette or Sugarloaf), environment (elevation), fire history of site (time since fire), regional fire history (functional divergence within 50 m and Simpson diversity within 75 m), and the basal area (m^2/ha) of lodgepole pine and Jeffrey pine (Table 3, Figure 18 and 19).

Table 3. Qualitative K-mean cluster descriptions based on the inner quartiles for broad location, local fire experience, forest structure, understory communities, and environment (Figures K1, K2, K3, and K4). Fire severity data is restricted to fires after 1984 when RdNBR is available.

Cluster	**Qualitative description**
1	These plots are restricted to Sugarloaf's lower elevations. The plots have burnt one to two times and it has been 20 to 40 years since fire which were often low to moderate severity fires. The overstory is dominated by pines and lodgepole pine is restricted to less than < 8.3 m^2/ha which were most often many small trees, such as a DBH of 20 cm, rather than a few larger trees. The understory has 8 to 10% understory cover dominated by graminoids with some herbs. Shrubs are rare or not present. These plots also have the greatest CWD.
2	These plots are generally restricted to Illilouette. The plots have burnt one to two times with the most recent fire and had very low to low severity fires during the past 15 to 20 years. The overstory is mostly white fir with an understory cover dominated by shrubs which range from continuous to discontinuous in the plot. Few herbs present and the plots generally have low species richness. Graminoids are rare or not present.
3	Plots are from both study sites. The plots have burnt one to two times and the most recent fire had low to moderate severity fire during the past 15 to 20 years. The overstory is dominated by lodgepole pine and white fir. The plots have the highest cover and greatest richness of all plots. The understory cover of shrubs and herbs is up to 8% each, and graminoids have up to 4%.
4	These plots are restricted to Illilouette and may not have burnt, or burnt up to two times and the most recent fire had very low to low fire severity during the past 5 to 100 years. The overstory is fir with some Jeffrey pine with the sparsest understory of all clusters. The understory cover is dominated by shrubs with very low cover of herbs. Graminoids are rare or not present.
5	Plots are from both study sites. Plots burnt one to two times with the most recent fire having low to moderate severity fire during the past 20 to 30 years. Overstory is dominated by white fir and Jeffrey pine is subdominant. The understory is dominated by discontinuous to continuous shrub fields. The understory has low herb cover and graminoids are rare.
6	These plots are generally restricted to Sugarloaf. Plots burnt one to two times with the most recent fire having moderate severity during the past 10 to 30 years ago. The overstory is pine and white fir with up to a 3% cover each of shrubs, herbs, and graminoids.
7	These plots are generally restricted to Illilouette. Plots burnt one to two times with the most recent fire having low to moderate severity fire during the past 5 to 15 years. The overstory is Jeffrey pine and white fir with an understory cover dominated by herbs with infrequent shrubs and graminoids.

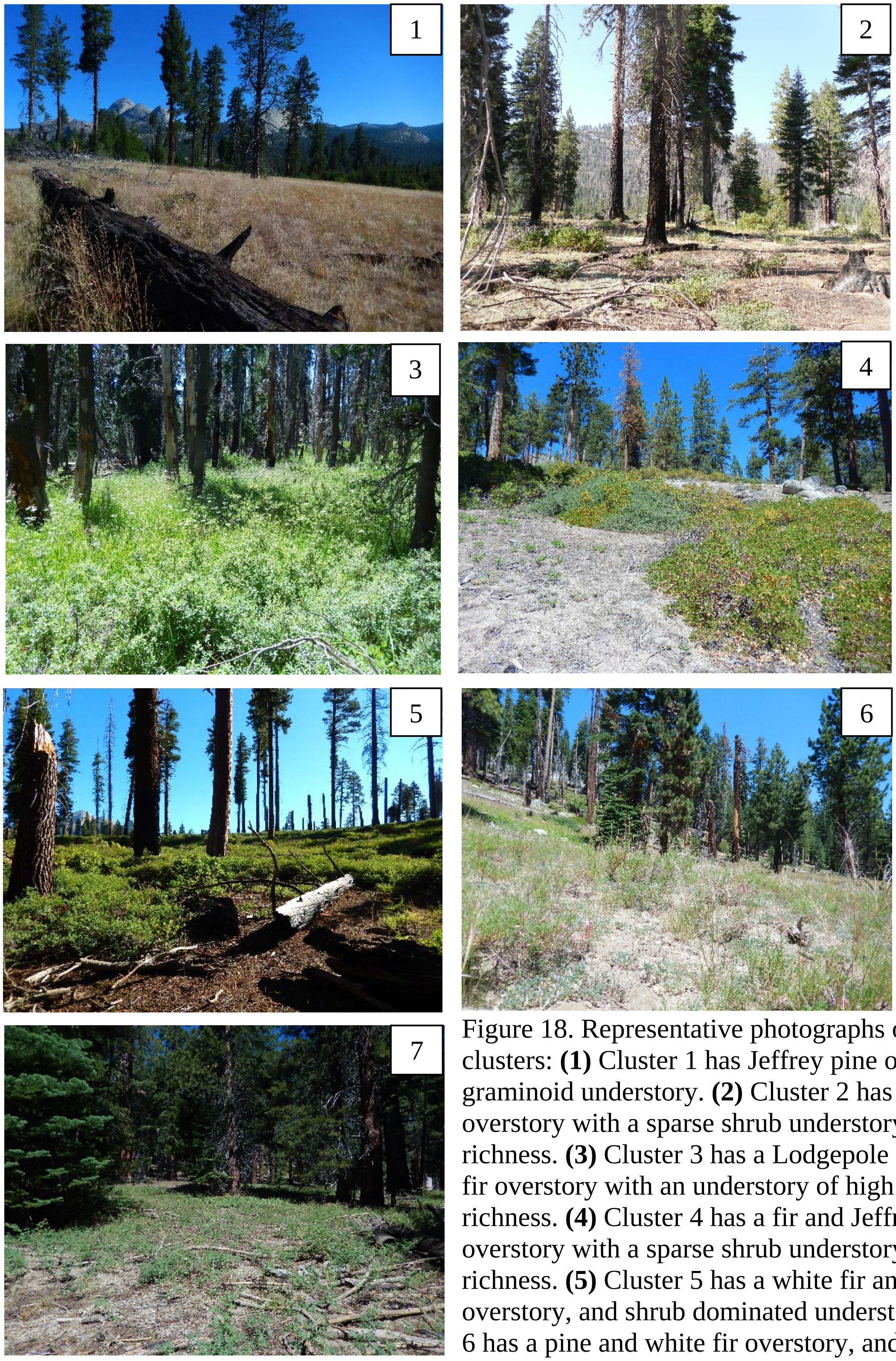

Figure 18. Representative photographs of K-mean clusters: **(1)** Cluster 1 has Jeffrey pine overstory with graminoid understory. **(2)** Cluster 2 has a white fir overstory with a sparse shrub understory of low richness. **(3)** Cluster 3 has a Lodgepole pine and white fir overstory with an understory of high cover and richness. **(4)** Cluster 4 has a fir and Jeffrey pine overstory with a sparse shrub understory of moderate richness. **(5)** Cluster 5 has a white fir and Jeffrey pine overstory, and shrub dominated understory. **(6)** Cluster 6 has a pine and white fir overstory, and low, even understory cover of shrubs, herbs, and graminoids. **(7)** Cluster 7 has a Jeffrey pine and white fir overstory with herb dominated understory of moderate richness.

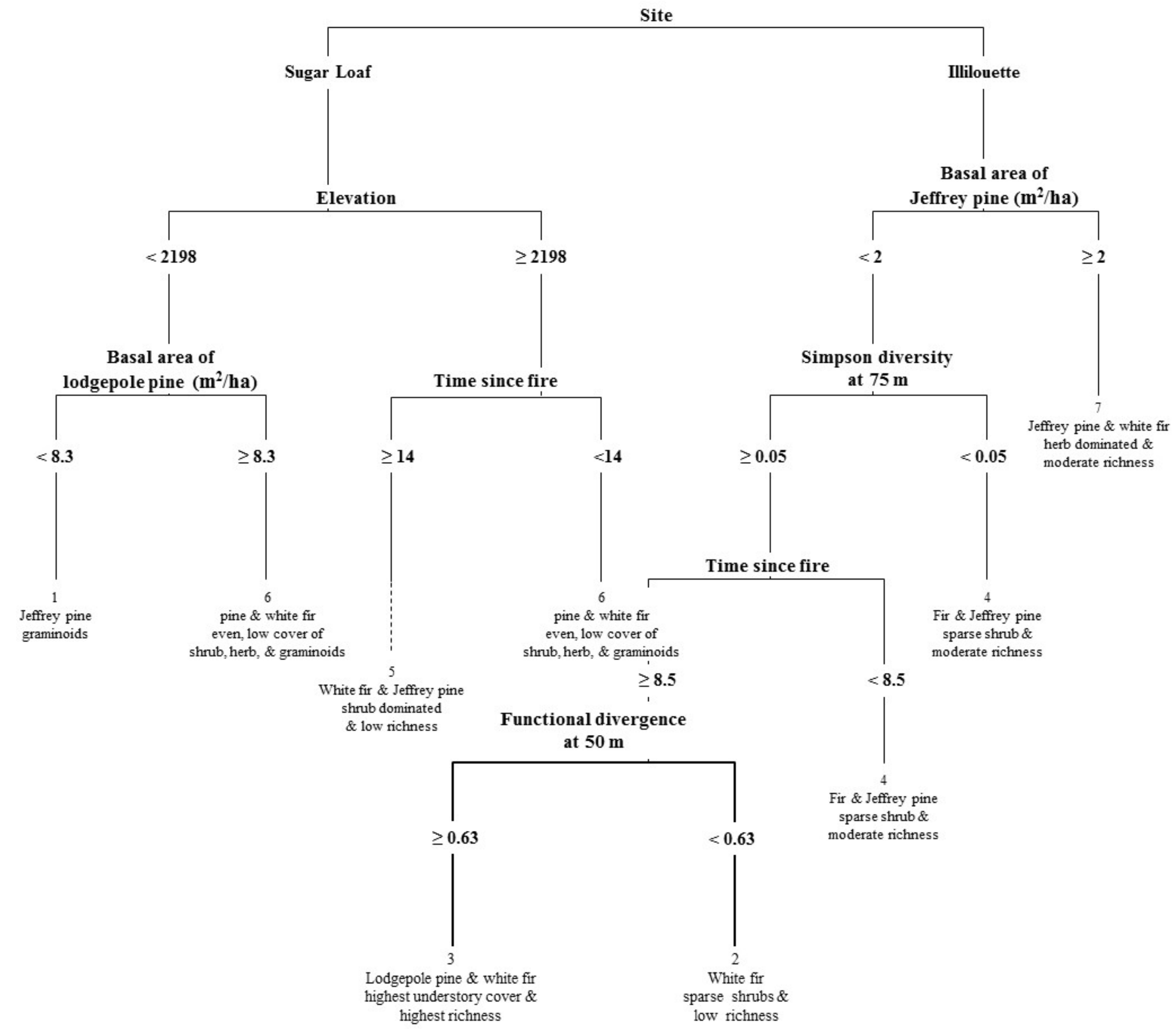

Figure 19. Pruned classification tree explores the relationships between understory clusters broad locations, the environment, local fire experience, regional fire experience, and the forest structure. Each cluster has a brief plant community description with tree species based on basal area and understory based on richness and cover of shrubs, herbs, and graminoids as defined by USDA PLANTS.

What is the structure of the overall plant community, and its drivers?

Understory cover was significantly influenced by environmental and fire variables including canopy cover ($P < 0.001$), number of times burnt ($P < 0.01$), and burn severity ($P < 0.03$) (marginal R^2: 0.11, conditional R^2: 0.63, Figure 18). Increase in mean canopy cover from 0 to 100% decreased understory cover 7%. Increase in mean number of times burnt from 0 to 4 decreased cover 1%. Low and moderate severity fires had 1% mean greater plant cover than other fire severities, and all other fire severities had similar plant cover.

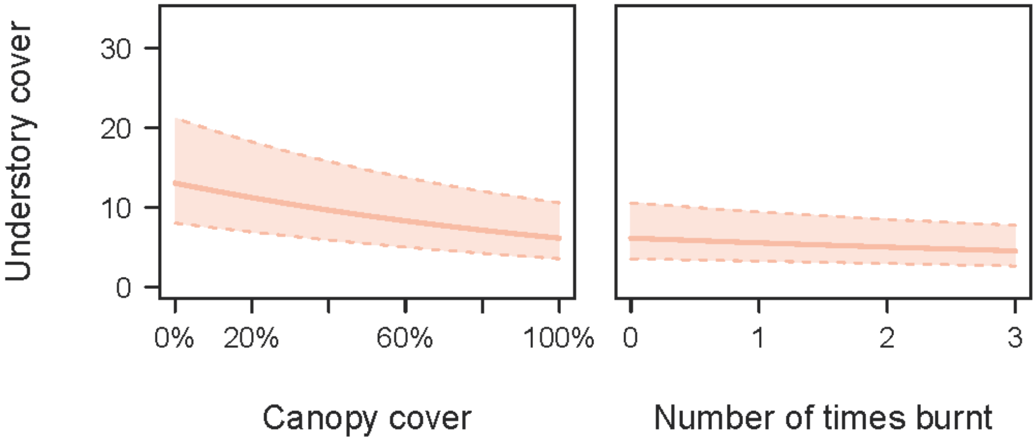

Figure 18. Understory cover response to canopy cover and the number of times burnt throughout the study. Understory cover response to burn severity is not depicted because of a small effect size, understory cover is predicted to change less than 1%. Curves represent the regression coefficients and shaded areas are the 95% confidence intervals.

Richness was significantly influenced by environment, plot-based fire experience, and local pyrodiversity (marginal R^2: 0.19, conditional R^2: 0.70). Specifically, richness was significantly influenced by CWD ($P < 0.01$), soil ($P < 0.001$), and the interaction between burn severity and functional divergence of fire within 50 meters of the plot ($P < 0.03$) (Figure 19). Increase in mean water deficit from 360 to 620 CWD decreased richness by six species. On average, sites with sandy loam soils had six to seven additional species than sites with loam or sands with 95% confidence intervals +/- 13 species. Sites with sandy loam and sandy clay loam soils had similar richness. If plots had a recent moderate severity fire, then there is an interaction where the increase in mean functional divergence from zero to 0.8 increased richness more than 21 species. Other fire severities did not influence the response of richness to functional divergence.

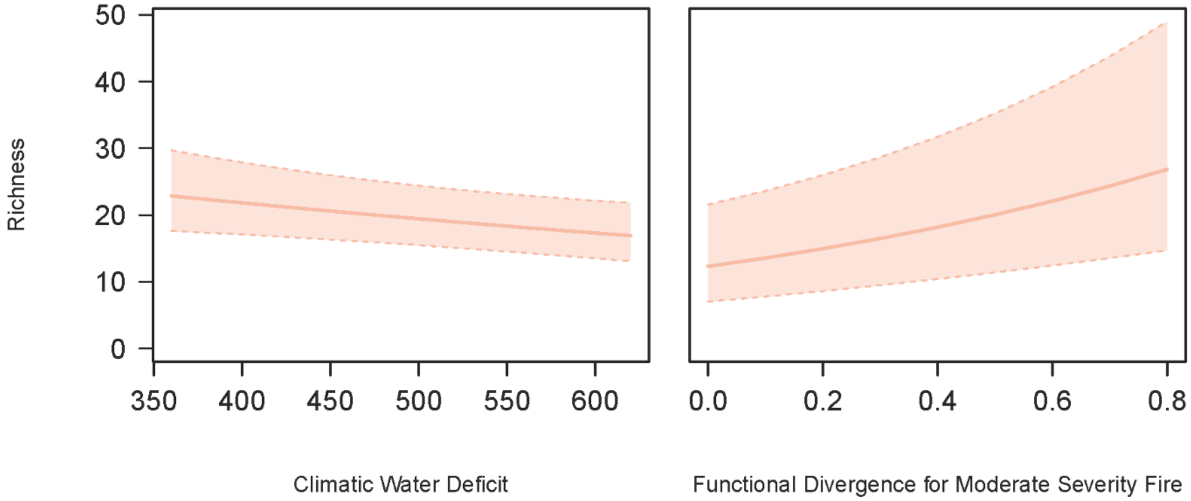

Figure 19. Richness response to Climatic Water Deficit (CWD) and the interaction between burn severity and functional divergence throughout the study. The interaction between burn severity and functional divergence is significant fire severity, although only moderate severity fires have a pattern different from the control and only the curve for moderate severity fires is graphed. Richness response to soils is not depicted because of small effect size. Curves represent the regression coefficients and shaded areas are the 95% confidence intervals.

Simpson diversity is only influenced by canopy cover ($P < 0.001$, marginal R^2: 0.14, conditional R^2: 0.33, Figure 20). Increase in mean canopy cover from 0 to 100% decreased Simpson diversity by 0.08, which is 8% of variation in the Simpson diversity index. There is a positive relationship between canopy cover and diversity: as the canopy cover decreases, diversity decreases.

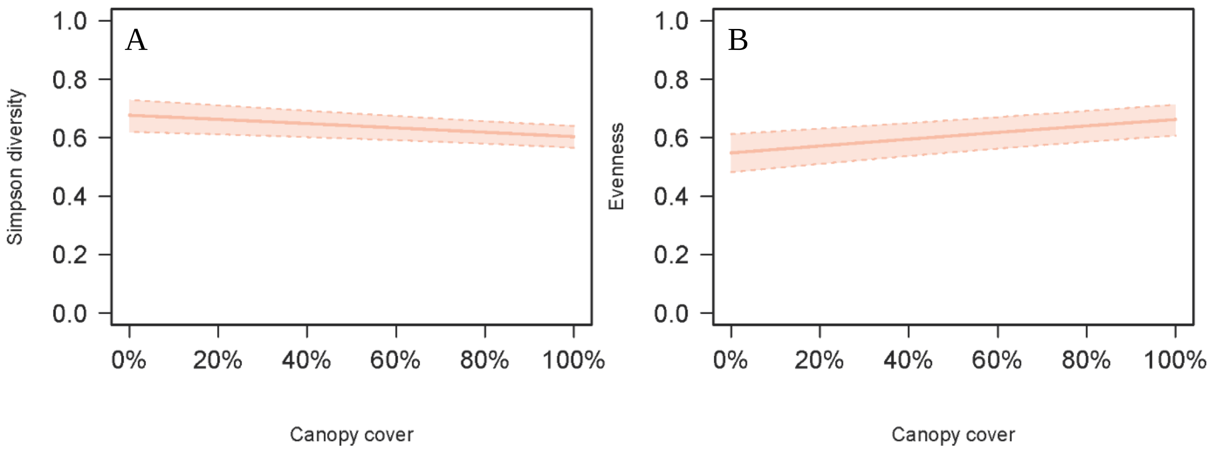

Figure 20A. Simpson diversity response to canopy cover throughout the study. Curves represent the regression coefficients and shaded areas are the 95% confidence intervals.

Figure 20B. Evenness response to canopy cover throughout the study. Curves represent the regression coefficients and shaded areas are the 95% confidence intervals.

Evenness is only influenced by canopy cover ($P < 0.001$, plot dropped as a random effect to calculate R^2, marginal R^2: 0.07, conditional R^2: 0.28, Figure 20). Increase in mean canopy cover from 0 to 100% increases evenness 0.11, which is a 13% change. As canopy cover increased, evenness increased and there is less variation between the cover of the species and a few plants are less likely to be dominant.

Discussion

Plant communities were influenced by unique combination of environmental, forest structure, and fire characteristics. Plant community clusters had distinct influences from the broad plant community characters such as cover, richness, Simpson diversity, and evenness. The clusters were influenced by park, local fire experience (time since fire), regional-scale fire experience (functional divergence within 50 m of the plot and Simpson diversity within 75 m of the plot), environment (elevation), and the basal area of Jeffrey pine and lodgepole pine. In contrast, most overall plant community characters (cover, Simpson diversity, and evenness) were strongly influenced by canopy cover. Richness was influenced by the environment, plot-scale fire experience including burn severity, and regional experience including function divergence within 50 m of the plot.

The cluster and regression tree analyses describe broad trends for distinct plant communities and their explanatory variables. The tree breaks are important explanatory variables although most are not steadfast rules. For example, sites appear to have distinct clusters and distinct explanatory variables which highlight the floristic differences between the central and southern Sierra (Potter 1998, Baldwin *et al.* 2012). While these sites are distinct, they do share many species and some clusters have high proportions from both sites, such as clusters 3 and 5. The predominantly

Illilouette based clusters were influenced by time since fire of 8.5 years which is similar to the length of time before this area will burn again (Collins *et al.* 2009). The Sugarloaf clusters were also influenced by time since fire although 14 years was significant. The Illilouette clusters were influenced by regional-scale fire experience, and the Sugarloaf clusters were not explicitly influenced by region-scale fire experience although a high proportion of Sugarloaf plots occurred in Illilouette cluster 6 which was influenced by regional-scale fire experience at two breakpoints. In contrast, only one cluster, cluster 1, is restricted to one site and the explanatory variables breaks have high affinity. Cluster 1 is restricted to the lower elevations of Sugarloaf. Elevation is commonly thought to be important due to a combination of temperature, snow amounts, and fire regimes (Table I2, Figure I1 and L1, Caprio and Lineback 2002)), and surprisingly the Illilouette clusters, which cover the same elevation range albeit at a higher latitude, were not sensitive to elevation. Elevation could also be a surrogate for other explanatory variables because elevation is also clearly distinct for cluster 1. The region where cluster 1 plots occur may be ecologically distinct because of deep, sandy soils with large, widely spaced Jeffrey pines. Overall the cluster and regression tree analyses describe unique plant communities and their explanatory variables, but do not necessarily capture factors most important for explaining variation in plant diversity, including richness, Simpson diversity, or evenness.

Canopy cover is indirectly related to frequent mixed severity fire (Figure 2) (Collins, Moghaddas, *et al.* 2007). Nearly all fires reduce canopy cover (Kane *et al.* 2014). High, moderate, and even low severity fires kill trees. All fires also reduce sub-canopy trees, shrubs, and lower limbs on canopy trees (Kane *et al.* 2013). While fires stimulate pine seedlings, frequent fires do often kill seedlings before they reach maturity especially when they are under the crown of a mature tree (Moghaddas *et al.* 2008). Canopy cover was the only significant influence on the plant community especially for Simpson diversity and evenness, and it also had the largest effect on understory cover. While canopy cover decreased Simpson diversity, evenness, and cover, it did not influence clusters. Therefore, reducing canopy cover does not inherently change the plant community, but it enhances it. Canopy cover is also an important factor for understory communities in forests managed for timber, and mechanical management techniques may be used to the enhance understory plant communities (Battles *et al.* 2001).

Richness was influenced by the interaction of pyrodiversity within 50 m of the plot and the most recent burn severity. The influential pyrodiversity metric was functional divergence within 50 m of the plot which describes extremely different fire experiences such as an area with repeated high severity fire adjacent to an area that has only had one low severity fire. These areas could be at the intersection of different environmentally driven plant communities such as lush, moist seeps embedded within drier forest. In this example, differences in moisture increased fuel loads which in turn influenced fire behavior and the subsequent functional divergence. Another example could be a fire's behavior derived from weather including changes in temperature, wind and relative humidity which create a matrix of high and low severity fire patches and unique fire derived plant communities are near to one another (Collins and Stephens 2010). Or, these areas could also have a combination of environmental and fire driven plant communities.

Regional-scale fire diversity is important for plant communities in montane mixed conifer forests in the Sierra Nevada with historic frequent and mixed-severity fire (Collins and Stephens 2007). The scale of regional fire experiences which influences plant communities for this study is lower than my previous work, 50 and 75 m compared to 150 m (Ponisio *et al.* 2016). The difference may have arisen because the current study includes comprehensive, long-term data across two sites whereas the previous work used a small subset of plots (18 of 149 plots sampled for two sequential years) and subset of plants which pollinators visit in Illilouette. It appears that small scale pyrodiversity (50 to 75 m) is important for plants and a slightly larger scale of pyrodiversity (150 m) is important for pollinators and plant-pollinator interactions. Additional research is needed to determine the important scale of pyrodiversity for other taxa in this system.

Based on a review of models and concepts, Roberts and Gilliam (1995) predict that maximum diversity for forests at the landscape scale occurs under historic disturbance regimes, while intermediate disturbances catalyze the greatest diversity at the patch scale. My study sites had a restored fire regime during the last 40 years that was similar to the period before fire suppression (Collins and Stephens 2007, Miller and Aplet 2016) which suggests that we've examined the maximum diversity for this system. This contemporary "reference" landscape provides an important and detailed description of the plant communities and their variation in relationship to climate and disturbances. However, there may be limitations to broad inferences from my study because sites have unique locations and fire regimes that were restored more than 40 years ago (Collins and Stephens 2007). Ultimately, this study complements historical forest reconstruction studies and is the most in-depth description of "reference" understories that I know. I can also interpret my results in relationship to the intermediate-disturbance hypothesis whereby local species richness reaches its maximum when disturbances are neither too rare nor too frequent (Connell 1978, Sousa 1984). Interestingly, disturbance frequency, measured by the number of times burnt, did not influence richness, Simpson diversity, or evenness. Further research is needed to compare these sites with their historical range of fire frequency to those that have less or more fire due to human interactions. For example, this system has allowed fires to express themselves and some niches within my study region are less likely to burn and therefore a poor comparison for the intermediate-disturbance hypothesis.

There are novel stresses on our plant communities including climate change and invasive species (Stephenson and Millar 2012). Sierra Nevada montane forests have nonnative plants present, however they've had limited frequency and impact in the past even with disturbances such as timber harvest, mechanical fuel reduction, fire, grazing, or in combination (Battles *et al.* 2001, Keeley *et al.* 2003, Collins, Moghaddas, *et al.* 2007, Kane *et al.* 2010). I also found that nonnative plants were rare, although there is a non-significant trend of increasing nonnative plant frequency. No nonnative plants were detected in plots in 2002, however nonnative plants were detected in 11 plots during the most recent surveys during 2011, 2012, and 2013. Of most concern is cheat grass (*Bromus tectorum*) because it can invade quickly and dramatically alter ecosystems (Bell *et al.* 2015). Cheat grass was restricted to major trails in 2002 in Illilouette (Yosemite National Park 2016) and expanded into three of my monitoring plots by 2013. The other nonnative plants had limited ability to outcompete native plants and alter the ecology. These plants are wind-dispersed and include prickly lettuce (*Lactuca serriola*), yellow salsify (*Tragopogon dubius*), common dandelion (*Taraxicum officinale*), and hairy cat's ear (*Hypocharis radiate*) in order of decreasing frequency (Bell *et al.* 2015). Climate change will provide more hospitable habitat for nonnative plants, while the wind, visitors, and wildlife will continue to disperse seeds (Dukes and Mooney 1999, Hellmann *et al.* 2008). Frequent fire will also leave these ecosystems more vulnerable to nonnative plant invasion (Keeley *et al.* 2003). In addition, there could be a positive feedback between fire and cheat grass at my study sites; fire will create colonization opportunities for cheat grass and cheat grass will promote fire by producing continuous, highly flammable fuel (D'antonio and Vitousek 1992, Brooks *et al.* 2004).

Despite having wilderness protection and restored fire regimes, these systems are being influenced by novel threats and it is important to continue monitoring them.

Conclusion

There are many management strategies which restore historical forests and promote forests resilient to climate change, including managed wildland fire, prescribed fire, mechanical treatments, and a combination these processes (Millar *et al.* 2007, Stephens *et al.* 2010, Stephenson and Millar 2012). These forest management techniques could be enhanced because we understand how historical fire regimes (including frequency, severity, season, and patch size) fostered diverse, resilient forests (Stephens *et al.* 2013). Based on the findings, I recommend reducing tree canopy cover throughout Sierran mixed conifer forests, and when possible fostering unique fire experiences within 50 to 75 m of one another to support diverse understory plant communities.

Acknowledgments

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CONCLUSION

My collaborative work spanned chaparral fuel hazard reduction (Wilkin *et al.* 2015, Wilkin, Ponisio, Fry, Tubbesing, *et al.* 2016); pyrodiversity in a Wildland Fire Use Sierra mixed conifer forests in relation to fuels, understory plants, and pollinators (Collins *et al.* , Ponisio *et al.*); the vulnerability of climate change refugia to fire in the Sierra mixed conifer forests (Wilkin, Ackerly, *et al.* 2016), and how social relationships influence wildfire outcomes for people and property (Wilkin 2016). I was fortunate to build upon long-term studies from the Stephens Lab to understand the spatial and temporal complexities of plant communities in chaparral and the mixed conifer forests; I transformed historic data to archival standards and added complimentary data during three extensive field seasons. In addition, I completed a novel study using publically accessible spatial data. Throughout my career my research techniques have ranged from lab experiments to understand how seeds' germination responds to the heat and chemicals of fire (Wilkin *et al.* 2013), through common garden experiments in green houses and field experiments with experimental units ranging from one meter to two hectares to understand plant communities (Wilkin 2009, Wilkin *et al.* 2013, Wilkin *et al.* 2015, Wilkin, Ponisio, Fry, Tubbesing, *et al.* 2016), to landscape scale observational studies to understand how climate, plant communities, fire interact (Collins *et al.* 2016, Ponisio *et al.* 2016, Wilkin, Ackerly, *et al.* 2016, Wilkin, Ponisio, Fry, Collins, *et al.* 2016). My dissertation includes diverse, but interrelated chapters about fire ecology and management in California:

1. Shrubland fire hazard reduction has drawbacks for biodiversity,
2. Climate change refugia fire ecology and management, and
3. Drivers of plant communities in arid forests with restored fire regimes.

Together these chapters enhance our understanding of fire in California. I demonstrate that fire and fuel hazard reduction is not always good or bad, but rather fire and fuel hazard reduction have nuanced effects on biodiversity and fuel hazards depending on the ecosystem, site history, and treatments. These results affirm the need for continued applied and basic fire science research.

As I move forward in my career, I will continue collaborating on applied projects for complex and controversial environmental issues which cross disciplines and stakeholder groups. A project that exemplifies my future research agenda is Shrubland fire hazard reduction has drawbacks for biodiversity, which examined the long-term effects of both prescribed fire and mastication completed in different seasons (Wilkin *et al.* 2015, Wilkin, Ponisio, Fry, Tubbesing, *et al.* 2016). This is a much needed study for a contentious issue in California which will directly impact up to two million people's fire hazard and nearly 600,000 hectares of chaparral. Our results were timely and incorporated into Cal Fire's proposed Vegetation Management Plan. This research supports land managers who must make difficult decisions where they must simultaneously protect human communities from fire and protect chaparral, e.g. an area of extremely high biodiversity, from fire hazard reduction treatments.

Managers must carefully weigh the trade-offs between the desire of their constituents for fire hazard reduction, cost, preserving native systems, increasing flammability, and decreasing fire severity. Research, such as my project, is integral to sound management decisions. Consequently, communicating this research to managers effectively is essential to policy implementation. To this end, I co-led a field trip, Natural and social trade-offs of reducing chaparral fire hazard, for the Northern California Prescribed Fire Council, to communicate our results stakeholders. Participants left the field trip with an integrated understanding of fire-hazard reduction natural and social trade-offs, but still had unanswered questions. Therefore I organized the Northern California Chaparral Summit to address their concerns this past spring. The summit included a wide range of stakeholders speaking about their research and management plans, a field trip, and a discussion to build consensus about when, how, what, and where fire hazard reduction should be applied. Since, managers have contacted me about potential modifications to their mastication projects and a study which builds up on our earlier results – how does partial or selective mastication buffers along fuel break roads influence biodiversity and fire behavior. This future study is part of an iterative cycle where scientists and stakeholders generate applied research ideas to inform best management practices and policy.

My goal is to incorporate more students and stakeholders in generating applied research including how to implement the best management practices so that we can make policy recommendations together. After completing my PhD at University of California at Berkeley, I strive to be a scientist where I participate in transdisciplinary research to inform land management policies, teach future land managers and scientists, and bridge the gap between science and management. Together these activities will help transform land management. Now more than ever collaborative and innovative solutions are needed, and I look forward to being part of the solution.

APPENDIX

Appendix A. Climate and treatment time periods for Shrubland fire hazard reduction has drawbacks for biodiversity

Table A1. Fuel reduction treatments were completed over three seasons. Spring mastication treatments were conducted later than spring fire treatments because roads were not dry enough for masticator access. There was no winter mastication treatment because masticators damage seasonally wet roads and slopes.

Fuel reduction	Season	Treatment dates
Fire	Fall	November 3-20
	Spring	March 31-3 April
	Winter	January 8-18
Mastication	Fall	November 3-20
	Spring	April 23-June 2
Control	No treatment	

Appendix B. Site and treatment description for Shrubland fire hazard reduction has drawbacks for biodiversity

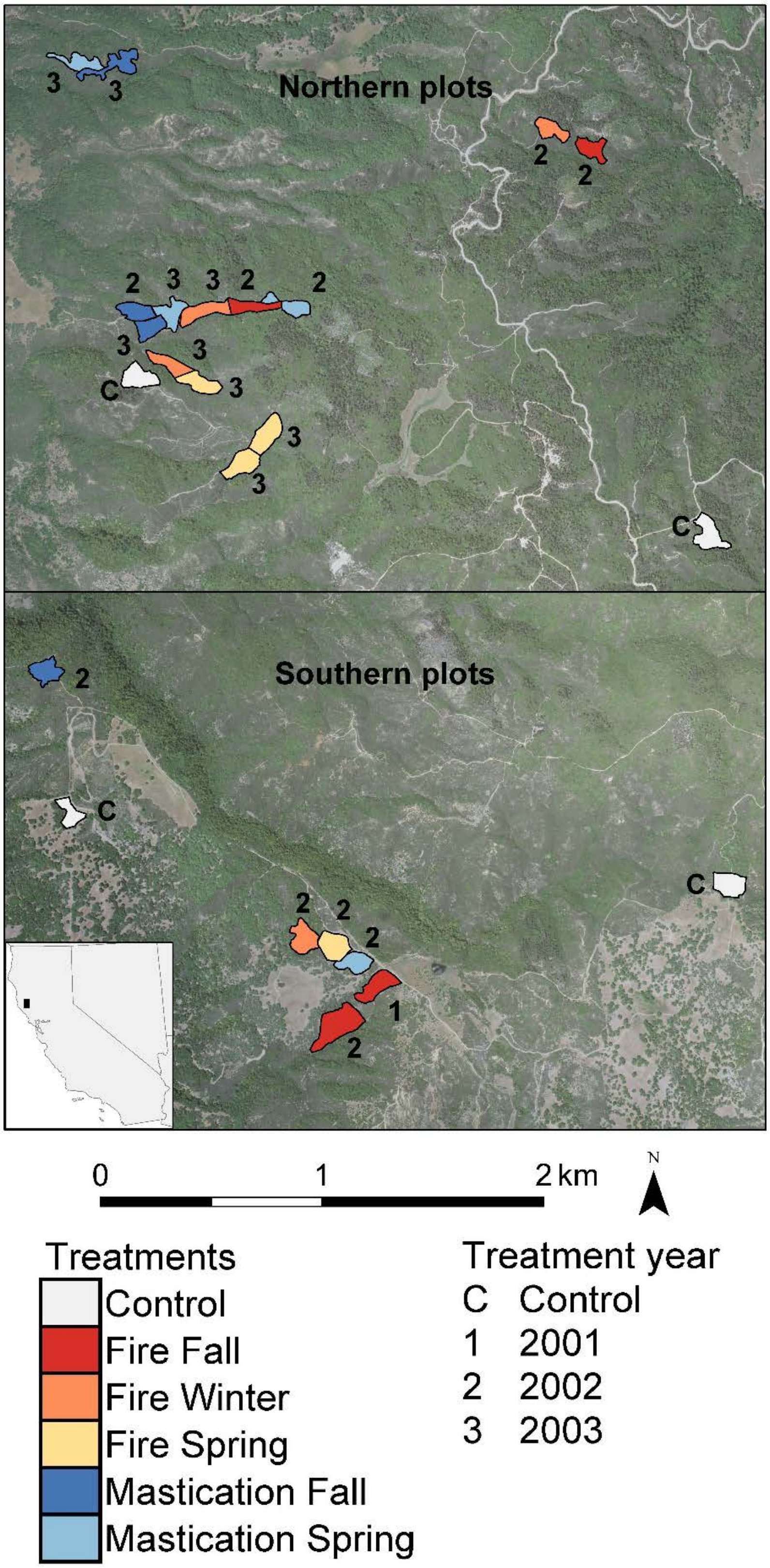


Figure B1. Treatment type, season, and year were distributed across both northern and southern study regions. The southern units were located at the UC Hopland Research and Extension Center and the northern units were mostly located at BLM's South Cow Mountain OHV Recreation Area. Two other northernmost units were located on adjacent private lands.

Figure B2. Exclosures had more chamise resprouts than the surrounding area nine months after mastication in plot 1 (top). Despite shrub height being significantly different in exclosures, exclosures had similar cover to their surrounding environment and browsing did not influence shrub cover (Potts *et al.* 2010). The differences in shrub cover and height diminished by two and a half years after treatment (Higginbottom *et al.*).

Appendix C: Model selection for Shrubland fire hazard reduction has drawbacks for biodiversity

Table C1. Statistical model types and specifications were tailored for each data set. Generalized linear models fit all data best. Asterisks (*) indicates both square root transformation and zero-inflated model.

Question		Response variable	Model family	Data
1A	Nonnative plants	Non-native grass occurrence	Gaussian *	Count
1B	Nonnative plants	Nonnative species occurrence	Gaussian *	Count
2A	Native plants	Nonnative species occurrence	Binomial	Proportion
2B	Native plants	Native shrub richness	Poisson	Species counted
2C	Native plants	Buckbrush cover	Binomial	Proportion

Appendix D. P-value and coefficient tables

Table D1. Shrub cover model estimates with standard error and p-value for the main effects and interaction (treatment by years since treatment). Different letters depict significant differences in shrub cover at α ≤ 0.05. Numbers depict marginal significant levels 0.05 ≤ α ≥ 0.10. Significance codes: ‘***’ <0.001, ‘**’ <0.01, ‘*’ <0.05, ‘.’< 0.1. Estimates, standard errors, and p-values are rounded to the nearest 100th. P-value of “0” implies p-value < 0.001.

			Control	Fire Fall	Fire Winter	Fire Spring	Mastication Fall	Mastication Spring
Main effect	Intercept		6.05+/-0.23 ***	0.94+/-0.27 ***	1.66+/-0.27 ***	1.19+/-0.28 ***	-0.65+/-0.27 0.02 *	0.61+/-0.27 0.03 *
	Years since treatment		0.6+/-0.18 ***	1.84+/-0.14 ***	1.5+/-0.13 ***	1.67+/-0.13 ***	1.55+/-0.14 ***	1.6+/-0.13 0 ***
	Control	A						
	Fire fall	B	-5.11+/-0.31 ***					
	Fire winter	C	-4.39+/-0.3 ***	0.73+/-0.34 0.03 *				
	Fire spring	BC	-4.86+/-0.32 ***	0.26+/-0.36 0.47	-0.47+/-0.36 0.19			
	Mastication fall	D	-6.7+/-0.31 ***	-1.59+/-0.35 ***	-2.32+/-0.34 ***	-1.85+/-0.35 ***		
	Mastication spring	BD	-5.44+/-0.29 ***	-0.33+/-0.35 0.35	-1.06+/-0.35 ***	-0.59+/-0.37 0.12	1.26+/-0.36 ***	
	slope		0.08+/-0.09 0.4	0.08+/-0.09 0.4	0.08+/-0.09 0.4	0.08+/-0.09 0.4	0.08+/-0.09 0.4	0.08+/-0.09 0.4
	solar radiation index		0.13+/-0.13 0.33	0.13+/-0.13 0.33	0.13+/-0.13 0.33	0.13+/-0.13 0.33	0.13+/-0.13 0.33	0.13+/-0.13 0.33
Treatment * Years since treatment	Control	A						
	Fire fall	B1	1.24+/-0.22 ***					
	Fire winter	1C	0.9+/-0.22 ***	-0.34+/-0.19 0.08 .				
	Fire spring	BC	1.07+/-0.22 ***	-0.17+/-0.19 0.36	0.17+/-0.18 0.36			
	Mastication fall	BC	0.95+/-0.22 ***	-0.29+/-0.2 0.15	0.05+/-0.19 0.79	-0.12+/-0.19 0.54		
	Mastication spring	BC	1+/-0.22 ***	-0.25+/-0.19 0.19	0.09+/-0.18 0.6	-0.07+/-0.18 0.69	0.04+/-0.19 0.82	

Table D2. Nonnative annual grass abundance model estimates with standard error and p-value for the main effects and interaction (treatment by years since treatment). Estimates and standard error are based on the square root of the data. Different letters depict significant differences in shrub cover at α ≤ 0.05. Numbers depict marginal significant levels 0.05 ≤ α ≥ 0.10. Significance codes: ‘***’ <0.001, ‘**’ <0.01, ‘*’ <0.05, ‘.’< 0.1. Estimates, standard errors, and p-values are rounded to the nearest 100th. P-value of “***” implies p-value < 0.001.

			Control		Fire Fall		Fire Winter		Fire Spring		Mastication Fall		Mastication Spring	
			Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P
	Intercept		41.06+/-11.16	***	36.46+/-17.03	0.03 *	20.72+/-15.72	0.19	15.42+/-15.75	0.33	104.98+/-17.5	***	45.68+/-15.04	***
	Years since treatment		-0.39+/-9.26	0.97	-0.87+/-2.55	0.73	0.96+/-2.61	0.72	1.27+/-2.99	0.67	-4.33+/-2.54	0.09 .	0.57+/-2.28	0.8
Main effect	Control	A1B												
	Fire fall	ABC	-4.6+/-16.35	0.78										
	Fire winter	1C	-25.64+/-14.74	0.08 .	-15.73+/-13.03	0.23								
	Fire spring	AC	-20.33+/-14.93	0.17	-21.04+/-13.3	0.11	-5.31+/-12.25	0.67						
	Mastication fall	D	63.94+/-17.17	***	68.54+/-15.31	***	84.26+/-14.59	***	89.58+/-15.28	***				
	Mastication spring	B	4.62+/-14.6	0.75	9.22+/-13.4	0.49	24.95+/-12.45	0.05 *	30.26+/-12.95	0.02 *	-59.31+/-13.76	***		
	survey year precipitation		8.82+/-6.76	0.19	8.82+/-6.76	0.19	8.83+/-6.76	0.19	8.82+/-6.76	0.19	8.83+/-6.76	0.19	8.82+/-6.76	0.19
Treatment * Years since treatment	Control	ABC												
	Fire fall	ABC	-0.49+/-9.89	0.96										
	Fire winter	AD	1.65+/-10.02	0.87	1.83+/-2.49	0.46								
	Fire spring	A1	1.34+/-9.9	0.89	2.14+/-2.87	0.46	0.31+/-2.88	0.91						
	Mastication fall	B1	-3.95+/-9.93	0.69	-3.46+/-2.4	0.15	-5.29+/-2.4	0.03 *	-5.6+/-2.87	0.05 .				
	Mastication spring	CD	0.95+/-9.83	0.92	1.44+/-2.24	0.52	-0.39+/-2.24	0.86	-0.7+/-2.72	0.8	4.9+/-2.1	0.02 *		

Table D3. Nonnative occurrence model estimates with standard error and p-value for the main effects and interactions (treatment by years since treatment and harmfulness rating by treatment). Estimates and standard error are based on the square root of the data. Different letters depict significant differences in shrub cover at $\alpha \leq 0.05$. Numbers depict marginal significant levels $0.05 \leq \alpha \geq 0.10$. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.'< 0.1. Estimates, standard errors, and p-values are rounded to the nearest 100th. P-value of "0" implies p-value < 0.001. Harmfulness rating is from the California Integrated Pest Management and is based on a combination of ecological impact, invasive potential, and current distribution (Bell *et al.* 2015). The base harmfulness rating in these models is "None".

"High: These species have severe ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to high rates of dispersal and establishment. Most are widely distributed ecologically.

Moderate: These species have substantial and apparent—but generally not severe—ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to high rates of dispersal, though establishment is generally dependent upon ecological disturbance. Ecological amplitude and distribution may range from limited to widespread.

Limited: These species are invasive but their ecological impacts are minor on a statewide level or there was not enough information to justify a higher score. Their reproductive biology and other attributes result in low to moderate rates of invasiveness. Ecological amplitude and distribution are generally limited, but these species may be locally persistent and problematic.

None: available information indicates that the species does not have significant impacts at the present time." (Bell *et al.* 2015)

Table D3 continued.

				Control		Fire Fall		Fire winter		Fire spring		Mastication Fall		Mastication Spring	
				Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P
Main effect		Intercept		34.84+/-5.97	***	38.81+/-9.5	***	18.03+/-8.69	0.04 *	14.12+/-8.89	0.11	92.94+/-9.2	***	47.06+/-7.79	***
		Years since treatment		-0.16+/-5.96	0.98	-1.12+/-1.53	0.46	0.2+/-1.59	0.9	0.92+/-1.95	0.64	-1.33+/-1.27	0.3	0.48+/-1.15	0.68
		Control													
		Fire fall		3.97+/-10.55	0.71										
		Fire winter		-16.82+/-9.8	0.09 .	-20.79+/-9.78	0.03 *								
		Fire spring		-20.72+/-9.88	0.04 *	-24.69+/-10.1	0.01 *	-3.91+/-9.53	0.68						
		Mastication fall		58.09+/-10.42	***	54.12+/-10.06	***	74.9+/-9.56	***	78.81+/-9.98	***				
		Mastication spring		12.21+/-9.22	0.19	8.25+/-9.32	0.38	29.02+/-8.75	***	32.93+/-9.14	***	-45.88+/-8.62	***		
		Limited		4.3+/-3.52	0.22	4.3+/-3.52	0.22	4.3+/-3.52	0.22	4.3+/-3.52	0.22	4.3+/-3.52	0.22	4.3+/-3.52	0.22
		Moderate		-32.44+/-10.04	***	-32.81+/-9.38	***	-17.65+/-10.16	0.08 .	-16.42+/-11.9	0.17	-72.91+/-6.89	***	-40.97+/-6.29	***
		High		-18.4+/-8.23	0.03 *	-21+/-7.81	0.01 **	-16.86+/-8.51	0.05 *	-15.41+/-8.19	0.06 .	-65.92+/-7.09	***	-39.95+/-6.83	***
		Survey precipitation		-35.91+/-14.28	0.01 *	-29.2+/-7.66	***	-15.49+/-11.98	0.2	-19.94+/-12.33	0.11	-75.36+/-7.09	***	-46.13+/-6.61	***
Treatment * Years since treatment		Control	AB												
		Fire fall	AB	-0.96+/-6.09	0.87										
		Fire winter	AB	0.37+/-6.1	0.95	1.33+/-1.75	0.45								
		Fire spring	AB	1.08+/-6.22	0.86	2.04+/-2.11	0.33	0.71+/-2.14	0.74						
		Mastication fall	A1	-1.17+/-6.02	0.85	-0.21+/-1.41	0.88	-1.53+/-1.45	0.29	-2.24+/-1.87	0.23				
		Mastication spring	B1	0.64+/-6	0.91	1.6+/-1.37	0.24	0.28+/-1.41	0.84	-0.44+/-1.84	0.81	1.81+/-0.95	0.06 .		
Treatment * Harmfulness rating	Limited	Control	AB												
		Fire fall	AB	-0.38+/-13.75	0.98										
		Fire winter	A1	14.77+/-14.2	0.3	15.14+/-13.82	0.27								
		Fire spring	A1	16.02+/-15.41	0.3	16.39+/-15.12	0.28	1.23+/-15.62	0.94						
		Mastication fall	C	-40.47+/-12.17	***	-40.1+/-11.64	***	-55.26+/-12.28	***	-56.49+/-13.75	***				
		Mastication spring	B1	-8.54+/-11.84	0.47	-8.16+/-11.29	0.47	-23.32+/-11.95	0.05 .	-24.55+/-13.46	0.07 .	31.94+/-9.33	***		
	Moderate	Control	AB												
		Fire fall	A1	-2.6+/-11.33	0.82										
		Fire winter	A	1.54+/-11.84	0.9	4.14+/-11.54	0.72								
		Fire spring	A	2.99+/-11.57	0.8	5.59+/-11.31	0.62	1.44+/-11.81	0.9						
		Mastication fall	C	-47.52+/-10.84	***	-44.92+/-10.55	***	-49.06+/-11.08	***	-50.51+/-10.82	***				
		Mastication spring	B1	-21.54+/-10.66	0.04 *	-18.95+/-10.37	0.07 .	-23.08+/-10.91	0.03 *	-24.54+/-10.67	0.02 *	25.97+/-9.84	0.01 *		
	High	Control	AB												
		Fire fall	A1	6.72+/-16.17	0.68										
		Fire winter	A	20.41+/-18.66	0.27	13.7+/-14.21	0.34								
		Fire spring	A1	15.97+/-18.52	0.39	9.26+/-14.44	0.52	-4.47+/-17.16	0.79						
		Mastication fall	C	-39.45+/-15.93	0.01 *	-46.16+/-10.44	***	-59.88+/-13.92	***	-55.42+/-14.21	***				
		Mastication spring	B1	-10.22+/-15.7	0.51	-16.94+/-10.11	0.09 .	-30.64+/-13.67	0.02 *	-26.19+/-13.96	0.06 .	29.23+/-9.69	***		

Table D4. Shrub species richness model estimates with standard error and p-value for the main effects and interaction (treatment by years since treatment). Different letters depict significant differences in shrub cover at α ≤ 0.05. Numbers depict marginal significant levels 0.05 ≤ α ≥ 0.10. Significance codes: ‘***’ <0.001, ‘**’ <0.01, ‘*’ <0.05, ‘.’< 0.1. Estimates, standard errors, and p-values are rounded to the nearest 100th. P-value of “***” implies p-value < 0.001.

			Control		Fire Fall		Fire Winter		Fire Spring		Mastication Fall		Mastication Spring	
			Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P
Main effect	Intercept		0.77+/-0.14	***	0.61+/-0.09	***	0.68+/-0.08	***	0.44+/-0.09	***	0.44+/-0.09	***	0.44+/-0.09	***
	Years since treatment		-0.01+/-0.02	0.45	0.03+/-0.01	0.02 *	0.01+/-0.01	0.48	0+/-0.01	0.77	0.03+/-0.01	0.01 *	0.04+/-0.01	***
	Control	AB1												
	Fire fall	ACD	-0.16+/-0.17	0.33										
	Fire winter	A2C	-0.1+/-0.17	0.55	0.06+/-0.12	0.59								
	Fire spring	2E	-0.33+/-0.17	0.04 *	-0.17+/-0.13	0.18	-0.23+/-0.13	0.07 .						
	Mastication fall	ED	-0.37+/-0.17	0.03 *	-0.21+/-0.13	0.11	-0.27+/-0.12	0.03 *	-0.04+/-0.13	0.76				
	Mastication spring	1CE	-0.27+/-0.16	0.1 .	-0.11+/-0.13	0.41	-0.17+/-0.12	0.17	0.06+/-0.13	0.6	0.1+/-0.12	0.39		
	slope		-0.05+/-0.03	0.07 .	-0.05+/-0.03	0.07 .	-0.05+/-0.03	0.07 .	-0.05+/-0.03	0.07 .	-0.05+/-0.03	0.07 .	-0.05+/-0.03	0.07 .
	solar radiation index		0.03+/-0.03	0.34	0.03+/-0.03	0.34	0.03+/-0.03	0.34	0.03+/-0.03	0.34	0.03+/-0.03	0.34	0.03+/-0.03	0.34
Treatment * Years since treatment	Control	A1												
	Fire fall	12B	0.04+/-0.02	0.06 .										
	Fire winter	A	0.02+/-0.02	0.31	-0.02+/-0.02	0.27								
	Fire spring	A2	0.01+/-0.02	0.67	-0.03+/-0.02	0.09 .	-0.01+/-0.02	0.5						
	Mastication fall	B	0.04+/-0.02	0.04 *	0.01+/-0.02	0.75	0.02+/-0.02	0.17	0.04+/-0.02	0.06 .				
	Mastication spring	B	0.05+/-0.02	0.01 **	0.02+/-0.02	0.33	0.03+/-0.02	0.03 *	0.05+/-0.02	0.01 **	0.01+/-0.02	0.56		

Table D5. Ceanothus cuneatus (buckbrush) cover model estimates with standard error and p-value for the main effects and interaction (treatment by years since treatment). Different letters depict significant differences in shrub cover at α ≤ 0.05. Numbers depict marginal significant levels 0.05 ≤ α ≥ 0.10. Significance codes: ‘***’ <0.001, ‘**’ <0.01, ‘*’ <0.05, ‘.’< 0.1. Estimates, standard errors, and p-values are rounded to the nearest 100th. P-value of “***” implies p-value < 0.001. Winter fire models would not compute for buckbrush likely because buckbrush is extremely uncommon and, if present it has very low cover.

			Control		Fire Fall		Fire Spring		Mastication Fall		Mastication Spring	
			Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P	Est +/- SE	P
Main effect	Intercept		-7.27+/-0.45	***	-12.44+/-0.61	***	-15.19+/-0.7	***	-12.04+/-0.61	***	-11.68+/-0.58	***
	Years since treatment		-1.69+/-0.36	***	1.71+/-0.41	***	0.65+/-0.48	0.18	3.39+/-0.44	***	3.51+/-0.38	***
	Control	A										
	Fire fall	BC	-5.17+/-0.67	***								
	Fire winter	B	-5.94+/-0.68	***	-0.77+/-0.75	0.3						
	Fire spring	E	-7.93+/-0.76	***	-2.76+/-0.84	***						
	Mastication fall	C	-4.78+/-0.68	***	0.4+/-0.8	0.62	3.15+/-0.89	***				
	Mastication spring	C	-4.41+/-0.63	***	0.76+/-0.77	0.33	3.51+/-0.86	***	0.36+/-0.75	0.63		
	slope		0.05+/-0.26	0.86	0.05+/-0.26	0.86	0.05+/-0.26	0.86	0.05+/-0.26	0.86	0.05+/-0.26	0.86
	solar radiation index		-0.06+/-0.25	0.81	-0.06+/-0.25	0.81	-0.06+/-0.25	0.81	-0.06+/-0.25	0.81	-0.06+/-0.25	0.81
Treatment * Years since treatment	Control	A										
	Fire fall	1	3.41+/-0.54	***								
	Fire winter	1B	2.35+/-0.55	***	-1.06+/-0.58	0.07 .	0+/-0.63	1				
	Fire spring	1B	2.35+/-0.6	***	-1.06+/-0.63	0.09 .						
	Mastication fall	C	5.09+/-0.57	***	1.68+/-0.6	***	2.74+/-0.65	***				
	Mastication spring	C	5.21+/-0.53	***	1.8+/-0.56	***	2.86+/-0.61	***	0.12+/-0.57	0.83		

Appendix E. Precipitation and response variables for Shrubland fire hazard reduction has drawbacks for biodiversity

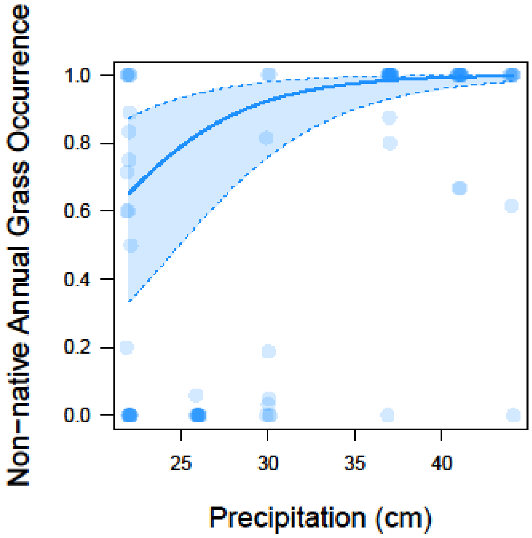


Figure E1. Non-native annual grass occurrence significantly increases with survey year precipitation for fire and mastication treatments (control data not included in this graphic). Precipitation amounts beyond 38 cm are confounded by the number of years since treatment; these high precipitation years only occurred two to three years post treatment. Precipitation less than 38 cm was dispersed across all years since treatment. Curves represent the fit regression coefficients, the shaded area represents 95% confidence intervals, and points represent an experimental unit mean for each survey year.

Appendix F. Shrub cover by species for Shrubland fire hazard reduction has drawbacks for biodiversity

Table F1. Shrub species list with an ecological description of each plant and its average cover with standard error by treatment type and its season of application, and years since treatment. Notably all species measured were native to California. The list includes endemism to California or chaparral, and the plants response to fire whether an individual survives the fire by resprouting, a population survives through seedlings, or a combination of the two. These calculations average across four experimental units for each treatment and its season of application that each have fifteen 15-meter transects where shrub cover and composition were measured. The average cover can exceed 100% because shrubs overlap one another. Nine, 10, and 11 years since treatments were merged into one year since treatment, 10. Asterisks (*) were used where standard errors cannot be calculated because the species only present once.

F1 Continued

		Treatment	Control		Fire Fall									
		Growing seasons since treatment	0		0		2		3		4		10	
Scientific name	**Endemism**	**Response to fire**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**
Adenostoma fasciculatum Hook. & Arn.	CA & Chaparral	seed & sprout	57	4	63	3	51	2	62	2	64	4	63	4
Arctostaphylos Adans. sp.	None	NA					1	<1	<1	<1	1	1		
Arctostaphylos canescens Eastw.	CA & Chaparral	sprout	7	*	13	9								
Arctostaphylos glandulosa Eastw. ssp. *glandulosa*	CA	seed & sprout	13	2	11	3	7	5	5	4	11	*	4	1
Arctostaphylos manzanita Parry ssp. *glaucescens*	CA	seed	12	3	11	2								
Arctostaphylos stanfordiana Parry ssp. *stanfordiana*	CA & Chaparral	seed	16	4	10	3							2	1
Baccharis pilularis *DC.*	None	seed			7	3	4	<1	7	2	10	*	7	3
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Chaparral	seed	12	2	21	2	4	2	3	2	2	<1	7	1
Ceanothus foliosus C. Parry	CA	seed							1	*	10	*	14	8
Cercocarpus montanus Raf. var. *glaber* (S. Watson) F.L. Martin	None	sprout	9	3					2	*				
Ericameria arborescens (A. Gray) Greene	CA	unknown	10	9									14	3
Eriodictyon californicum (Hook. & Arn.) Torr.	CA	seed & sprout											8	*
Garrya elliptica Lindl.	None	unknown	3	*									5	1
Garrya fremontii Torr.	None	seed & sprout					6	2						
Grossulariaceae	None	unknown							3	*			1	*
Heteromeles arbutifolia (Lindl.) M. Roem.	CA	sprout											2	*
Mimulus aurantiacus (W. Curtis) Jeps. ssp. *aurantiacus*	None	sprout	6	3	17	9	11	5	5	1	5	<1	14	7
Pickeringia montana Nutt. ex Torr. & A. Gray	CA	sprout			13	*	6	*	6	*			8	*
Quercus berberidifolia Liebm.	CA	sprout	15	4										
Quercus durata Jeps. var. *durata*	CA & Chaparral	sprout	25	10										
Quercus wislizeni A. DC.	CA	sprout												
Rhamnus crocea Nutt.	CA	sprout			5	*								
Toxicodendron diversilobum (Torr. & A. Gray) Greene	None	seed & sprout	16	9									8	3
Umbellularia californica (Hook. & Arn.) Nutt.	CA	seed & sprout												
		Total average cover	**201**		**171**		**90**		**94**		**103**		**158**	

F1 Continued

		Treatment	Fire Spring											
		Growing seasons since treatment	0		1		2		3		4		10	
Scientific name	Endemism	Response to fire	Avgerage	SE	Avgerage	SE	Avgerage	SE	Avgerage	SE	Avgerage	SE	Avgerage	SE
Adenostoma fasciculatum Hook. & Arn.	CA & Chaparral	seed & sprout	60	4	58	2	49	4	67	3	68	2	50	5
Arctostaphylos Adans. sp.	None	NA					11	5						
Arctostaphylos canescens Eastw.	CA & Chaparral	sprout												
Arctostaphylos glandulosa Eastw. ssp. *glandulosa*	CA	seed & sprout	7	5	7	*	15	3	15	*	13	<1	15	5
Arctostaphylos manzanita Parry ssp. *glaucescens*	CA	seed									10	*	14	5
Arctostaphylos stanfordiana Parry ssp. *stanfordiana*	CA & Chaparral	seed	21	6			10	*					7	*
Baccharis pilularis *DC.*	None	seed	35	*			11	6			1	<1	14	9
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Chaparral	seed	18	2			8	<1			3	2	6	2
Ceanothus foliosus C. Parry	CA	seed												
Cercocarpus montanus Raf. var. *glaber* (S. Watson) F.L. Martin	None	sprout												
Ericameria arborescens (A. Gray) Greene	CA	unknown					1	*					8	*
Eriodictyon californicum (Hook. & Arn.) Torr.	CA	seed & sprout												
Garrya elliptica Lindl.	None	unknown	2	*							37	1	7	5
Garrya fremontii Torr.	None	seed & sprout			13	*			13	*				
Grossulariaceae	None	unknown									13	*	29	*
Heteromeles arbutifolia (Lindl.) M. Roem.	CA	sprout												
Mimulus aurantiacus (W. Curtis) Jeps. ssp. *aurantiacus*	None	sprout			22	10			24	6	24	7	24	9
Pickeringia montana Nutt. ex Torr. & A. Gray	CA	sprout												
Quercus berberidifolia Liebm.	CA	sprout					6	*			5	*	35	*
Quercus durata Jeps. var. *durata*	CA & Chaparral	sprout												
Quercus wislizeni A. DC.	CA	sprout												
Rhamnus crocea Nutt.	CA	sprout												
Toxicodendron diversilobum (Torr. & A. Gray) Greene	None	seed & sprout											9	4
Umbellularia californica (Hook. & Arn.) Nutt.	CA	seed & sprout												
		Total average cover	**142**		**101**		**110**		**119**		**174**		**218**	

F1 Continued

		Treatment	**Fire Winter**											
		Growing seasons since treatment	**0**		**1**		**2**		**3**		**4**		**10**	
Scientific name	**Endemism**	**Response to fire**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**
Adenostoma fasciculatum Hook. & Arn.	CA & Chaparral	seed & sprout	55	4	54	2	54	3	62	3	60	4	51	5
Arctostaphylos Adans. sp.	None	NA					18	6	1	1	1	<1		
Arctostaphylos canescens Eastw.	CA & Chaparral	sprout					14	11			4	*		
Arctostaphylos glandulosa Eastw. ssp. *glandulosa*	CA	seed & sprout	17	5			10	2			10	4	4	1
Arctostaphylos manzanita Parry ssp. *glaucescens*	CA	seed	17	11							38	11	20	5
Arctostaphylos stanfordiana Parry ssp. *stanfordiana*	CA & Chaparral	seed	25	6	20	4	70	6					24	7
Baccharis pilularis *DC.*	None	seed												
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Chaparral	seed	19	3	29	12	5	2			4	2	5	2
Ceanothus foliosus C. Parry	CA	seed					1	1			<1	*	11	4
Cercocarpus montanus Raf. var. *glaber* (S. Watson) F.L. Martin	None	sprout	5	1	5	2			6	1			11	3
Ericameria arborescens (A. Gray) Greene	CA	unknown												
Eriodictyon californicum (Hook. & Arn.) Torr.	CA	seed & sprout												
Garrya elliptica Lindl.	None	unknown											2	1
Garrya fremontii Torr.	None	seed & sprout			1	<1	1	*						
Grossulariaceae	None	unknown	4	*			4	*	1	*	10	*	1	*
Heteromeles arbutifolia (Lindl.) M. Roem.	CA	sprout												
Mimulus aurantiacus (W. Curtis) Jeps. ssp. *aurantiacus*	None	sprout	9	2	10	3	7	3	10	2	10	4	11	3
Pickeringia montana Nutt. ex Torr. & A. Gray	CA	sprout	4	1	2	<1	6	2	5	2	10	3	7	1
Quercus berberidifolia Liebm.	CA	sprout	1	*	10	*			1	*			6	*
Quercus durata Jeps. var. *durata*	CA & Chaparral	sprout					5	1					7	1
Quercus wislizeni A. DC.	CA	sprout							3	*	3	<1		
Rhamnus crocea Nutt.	CA	sprout												
Toxicodendron diversilobum (Torr. & A. Gray) Greene	None	seed & sprout	3	*									5	2
Umbellularia californica (Hook. & Arn.) Nutt.	CA	seed & sprout			2	*							1	*
		Total average cover	**159**		**133**		**196**		**89**		**150**		**166**	

F1 Continued

		Treatment	Mastication Fall									
		Growing seasons since treatment	0		1		2		3		10	
Scientific name	Endemism	Response to fire	Avgerage	SE	Avgerage	SE	Avgerage	SE	Avgerage	SE	Avgerage	SE
Adenostoma fasciculatum Hook. & Arn.	CA & Chaparral	seed & sprout	61	4	16	3	27	2	36	2	65	3
Arctostaphylos Adans. sp.	None	NA										
Arctostaphylos canescens Eastw.	CA & Chaparral	sprout									<1	*
Arctostaphylos glandulosa Eastw. ssp. *glandulosa*	CA	seed & sprout	13	2	5	<1	7	2	8	3	8	4
Arctostaphylos manzanita Parry ssp. *glaucescens*	CA	seed	13	3								
Arctostaphylos stanfordiana Parry ssp. *stanfordiana*	CA & Chaparral	seed	9	5							5	3
Baccharis pilularis *DC.*	None	seed					1	<1	1	1	7	3
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Chaparral	seed	14	2			1	<1	3	1	8	2
Ceanothus foliosus C. Parry	CA	seed					4	*	14	9	9	3
Cercocarpus montanus Raf. var. *glaber* (S. Watson) F.L. Martin	None	sprout									1	*
Ericameria arborescens (A. Gray) Greene	CA	unknown									10	*
Eriodictyon californicum (Hook. & Arn.) Torr.	CA	seed & sprout										
Garrya elliptica Lindl.	None	unknown									1	*
Garrya fremontii Torr.	None	seed & sprout										
Grossulariaceae	None	unknown										
Heteromeles arbutifolia (Lindl.) M. Roem.	CA	sprout										
Mimulus aurantiacus (W. Curtis) Jeps. ssp. *aurantiacus*	None	sprout	4	*							3	*
Pickeringia montana Nutt. ex Torr. & A. Gray	CA	sprout									4	*
Quercus berberidifolia Liebm.	CA	sprout			6	5	5	1	5	2	6	2
Quercus durata Jeps. var. *durata*	CA & Chaparral	sprout					4	2	3	<1	23	*
Quercus wislizeni A. DC.	CA	sprout										
Rhamnus crocea Nutt.	CA	sprout										
Toxicodendron diversilobum (Torr. & A. Gray) Greene	None	seed & sprout										
Umbellularia californica (Hook. & Arn.) Nutt.	CA	seed & sprout										
		Total average cover	**112**		**26**		**50**		**71**		**151**	

F1 Continued

		Treatment	Mastication Spring											
		Growing seasons since treatment	0		1		2		3		4		10	
Scientific name	**Endemism**	**Response to fire**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**	**Avgerage**	**SE**
Adenostoma fasciculatum Hook. & Arn.	CA & Chaparral	seed & sprout	55	4	21	3	34	3	31	3	44	2	58	3
Arctostaphylos Adans. sp.	None	NA	3	2			7	7	1	<1	1	<1		
Arctostaphylos canescens Eastw.	CA & Chaparral	sprout	14	2									9	7
Arctostaphylos glandulosa Eastw. ssp. *glandulosa*	CA	seed & sprout	8	3			5	4	5	*	3	1	4	1
Arctostaphylos manzanita Parry ssp. *glaucescens*	CA	seed	20	5							1	*		
Arctostaphylos stanfordiana Parry ssp. *stanfordiana*	CA & Chaparral	seed	16	5									9	1
Baccharis pilularis *DC.*	None	seed									<1	*	2	1
Ceanothus cuneatus (Hook.) Nutt. var. *cuneatus*	Chaparral	seed	19	3			6	1	<1	<1	2	1	12	2
Ceanothus foliosus C. Parry	CA	seed					2	*			2	2	6	3
Cercocarpus montanus Raf. var. *glaber* (S. Watson) F.L. Martin	None	sprout	15	*										
Ericameria arborescens (A. Gray) Greene	CA	unknown												
Eriodictyon californicum (Hook. & Arn.) Torr.	CA	seed & sprout												
Garrya elliptica Lindl.	None	unknown												
Garrya fremontii Torr.	None	seed & sprout												
Grossulariaceae	None	unknown												
Heteromeles arbutifolia (Lindl.) M. Roem.	CA	sprout												
Mimulus aurantiacus (W. Curtis) Jeps. ssp. *aurantiacus*	None	sprout	13	12			5	3			9	3	15	11
Pickeringia montana Nutt. ex Torr. & A. Gray	CA	sprout			6	*			8	*	6	*	14	*
Quercus berberidifolia Liebm.	CA	sprout			10	4	10	3	17	6	11	2	16	2
Quercus durata Jeps. var. *durata*	CA & Chaparral	sprout					8	3			24	11	7	2
Quercus wislizeni A. DC.	CA	sprout												
Rhamnus crocea Nutt.	CA	sprout												
Toxicodendron diversilobum (Torr. & A. Gray) Greene	None	seed & sprout	10	*									18	7
Umbellularia californica (Hook. & Arn.) Nutt.	CA	seed & sprout												
		Total average cover	**172**		**37**		**76**		**63**		**103**		**171**	

Appendix G. Nonnative plants for Shrubland fire hazard reduction has drawbacks for biodiversity

Table G1. Nonnative understory species list with life history and form from USDA Plants, and nonnative plant harmfulness rating from CA-IPM. For each treatment and its season of application, the average plant count is calculated across four experimental units that each have five 5-m^2 plots where understory plants were counted by species. Years since treatments nine, 10, and 11 are merged into a year since treatment, 10, for this table. Asterisks (*) were used where standard errors cannot be calculated because the species only present once. Blank space indicates a plant was not present. CA-IPM harmfulness ratings include:

“High: These species have severe ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to high rates of dispersal and establishment. Most are widely distributed ecologically.

Moderate: These species have substantial and apparent—but generally not severe—ecological impacts on physical processes, plant and animal communities, and vegetation structure. Their reproductive biology and other attributes are conducive to moderate to high rates of dispersal, though establishment is generally dependent upon ecological disturbance. Ecological amplitude and distribution may range from limited to widespread.

Limited: These species are invasive but their ecological impacts are minor on a statewide level or there was not enough information to justify a higher score. Their reproductive biology and other attributes result in low to moderate rates of invasiveness. Ecological amplitude and distribution are generally limited, but these species may be locally persistent and problematic.

None: available information indicates that the species does not have significant impacts at the present time.” (Bell *et al.* 2015)

Table G1 Continued

	Treatment	Control		Fire Fall								Fire Spring								Fire Winter							
	Growing seasons since treatment	0		0		2		3		10		0		2		3		10		0		2		3		10	
Scientific name	Life history, form, and ranking	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE
Aira caryophyllea L.	Annual / Graminoid	140	38	30	20	107	43	80	21	93	83	2	*	40	19	205	87	61	38			70	63	14	7	36	31
Anagallis arvensis L.	Annual & Biennial / Herb					9	*	41	24					1	<1												
Anthriscus caucalis M. Bieb.	Annual / Herb					7	*																				
Avena fatua L.	Annual / Graminoid / Moderate																										
Brachypodium distachyon (L.) P. Beauv.	Annual / Graminoid / Moderate							2	*																		
Briza maxima L.	Annual / Graminoid / Limited																										
Briza minor L.	Annual / Graminoid																										
Bromus hordeaceus L.	Annual / Graminoid / Limited			20	*	1	<1	3	1													1	*				
Bromus rubens L.	Annual / Graminoid / High					16	8	19	11	21	*			1	*	8	*					4	*			2	*
Carduus pycnocephalus L.	Annual / Herb / Moderate																										
Centaurea melitensis L.	Annual & Biennial / Herb / Moderate					50	48	60	45					2	1	1	*										
Centaurea solstitialis L.	Annual / Herb / High																										
Cerastium glomeratum Thuill.	Annual / Herb							1	<1													1	*				
Crassula tillaea Lester-Garland	Annual / Herb					13	11															2	*				
Cynosurus echinatus L.	Annual / Graminoid / Moderate							1	*																		
Dactylis glomerata L.	Perennial / Graminoid / Limited			3	2																						
Erodium brachycarpum (Godr.) Thell	Annual / Herb															1	*										
Erodium cicutarium (L.) L'Hér. ex Aiton ssp. *cicutarium*	Annual & Biennial / Herb / Limited							1	*																		
Galium L. sp.	Annual / Herb															2	<1										
Galium murale (L.) All.	Annual / Herb																										
Galium parisiense L.	Annual / Herb	50	*			79	59	21	13					7	4	2	<1	11	4			2	1	40	39	5	1
Gastridium phleoides (Nees & Meyen) C.E. Hubbard	Annual / Graminoid	30	*			67	26	67	28					15	6	109	76	14	11			177	89	180	106		
Holcus lanatus L.	Perennial / Herb / Moderate																										
Hypochaeris glabra L.	Annual / Herb / Limited					13	11	2	1					1	<1							3	1	1	*		
Lactuca saligna L.	Annual & Biennial / Herb															2	*					4	<1				
Lactuca serriola L.	Annual & Biennial / Herb					3	1	1	<1					1	<1	1	<1					3	1				
Logfia gallica (L.) Coss. & Germ.	Annual / Herb	14	7	50	<1	93	35	95	29	11	8	33	*	7	2	52	16	25	24	50	*	17	15	8	2		
Phalaris aquatica L.	Perennial / Graminoid / Moderate					1	*																				
Piptatherum miliaceum (L.) Coss.	Annual & Perennial / Graminoid / Limited					2	1	6	*													4	*				
Poaceae (annual)	Annual / Graminoid	2	*			7	3	12	8					8	2	20	13					6	2	6	3		
Polypogon monspeliensis (L.) Desf.	Annual / Graminoid / Limited							39	*																		
Senecio vulgaris L.	Annual & Biennial / Herb					2	1	1	<1					1	*									1	*		
Sonchus asper (L.) Hill	Annual / Herb					2	<1	1	*					2	*							2	<1				
Taeniatherum caput-medusae (L.) Nevski	Annual / Graminoid / High							6	*					1	*												
Tolpis barbata (L.) Gaertn.	Annual / Herb					3	1	3	2																		
Torilis arvensis (Huds.) Link	Annual / Herb / Moderate					5	3	8	6							1	*					1	*				
Trifolium dubium Sibth.	Annual / Herb					3	*																				
Trifolium hirtum All.	Annual / Herb / Limited					1	<1	1	*					1	*												
Verbascum thapsus L.	Biennial / Herb / Limited																										
Vulpia bromoides (L.) Gray	Annual / Graminoid	14	5			59	33	4	1	25	20	20	*	7	6	11	7					55	34	5	3	48	33
Vulpia myuros (L.) C.C. Gmel.	Annual / Graminoid / Moderate	1	*	63	13	120	103	84	47					2	1	8	7			3	*			3	1		
	All nonnative understory plants	97	27	35	9	56	12	52	9	33		18	9	11	3	67	19	31	14	27	24	39	15	28	13	26	13

Table G1 Continued

	Treatment	Mastication Fall								Mastication Spring							
	Growing seasons since treatment	0		2		3		10		0		2		3		10	
Scientific name	Life history, form, and ranking	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE	Average	SE
Aira caryophyllea L.	Annual / Graminoid	150	21	551	107	574	85	107	24	239	25	164	43	372	71	137	28
Anagallis arvensis L.	Annual & Biennial / Herb			20	19	4	2	2	*			8	1	6	4	5	3
Anthriscus caucalis M. Bieb.	Annual / Herb																
Avena fatua L.	Annual / Graminoid / Moderate			3	*									2	*		
Brachypodium distachyon (L.) P. Beauv.	Annual / Graminoid / Moderate							83	*								
Briza maxima L.	Annual / Graminoid / Limited					5	*										
Briza minor L.	Annual / Graminoid					7	*							1	*		
Bromus hordeaceus L.	Annual / Graminoid / Limited			38	16	51	48	19	5	1	*	2	1	10	5	14	10
Bromus rubens L.	Annual / Graminoid / High			76	40	78	50	27	11	10	*	3	1	5	2	58	54
Carduus pycnocephalus L.	Annual / Herb / Moderate					1	*					1	*				
Centaurea melitensis L.	Annual & Biennial / Herb / Moderate			2	1	5	2	13	4					2	1		
Centaurea solstitialis L.	Annual / Herb / High			11	*												
Cerastium glomeratum Thuill.	Annual / Herb	2	*	7	6					7	*	4	3	356	*		
Crassula tillaea Lester-Garland	Annual / Herb			1	<1							8	3			4	*
Cynosurus echinatus L.	Annual / Graminoid / Moderate			4	1							1	<1	4	1		
Dactylis glomerata L.	Perennial / Graminoid / Limited	5	1														
Erodium brachycarpum (Godr.) Thell	Annual / Herb			3	*											7	*
Erodium cicutarium (L.) L'Hér. ex Aiton ssp. *cicutarium*	Annual & Biennial / Herb / Limited													1	*		
Galium L. sp.	Annual / Herb			8	7			47	34	1	*			1	*		
Galium murale (L.) All.	Annual / Herb							5	3							8	3
Galium parisiense L.	Annual / Herb	4	3	36	20	75	42	24	10			95	87	5	3	12	3
Gastridium phleoides (Nees & Meyen) C.E. Hubbard	Annual / Graminoid	19	4	95	31	360	88	10	3	22	9	16	12	83	39	11	6
Holcus lanatus L.	Perennial / Herb / Moderate			1	<1	1	*										
Hypochaeris glabra L.	Annual / Herb / Limited			10	2	70	32	50	20			2	<1	50	14	17	12
Lactuca saligna L.	Annual & Biennial / Herb			4	1							1	<1	3	1		
Lactuca serriola L.	Annual & Biennial / Herb			2	<1	4	1					1	<1	6	1		
Logfia gallica (L.) Coss. & Germ.	Annual / Herb	37	13	240	54	632	135	18	6	40	11	36	18	84	17	21	4
Phalaris aquatica L.	Perennial / Graminoid / Moderate																
Piptatherum miliaceum (L.) Coss.	Annual & Perennial / Graminoid / Limited																
Poaceae (annual)	Annual / Graminoid			21	10	1	*	1	*			4	2	3	1		
Polypogon monspeliensis (L.) Desf.	Annual / Graminoid / Limited																
Senecio vulgaris L.	Annual & Biennial / Herb			1	<1	1	*					1	<1	4	1		
Sonchus asper (L.) Hill	Annual / Herb	2	*	2	*	2	1					1	<1	4	2		
Taeniatherum caput-medusae (L.) Nevski	Annual / Graminoid / High			7	5									1	<1		
Tolpis barbata (L.) Gaertn.	Annual / Herb																
Torilis arvensis (Huds.) Link	Annual / Herb / Moderate			7	3	22	11					2	1	9	6		
Trifolium dubium Sibth.	Annual / Herb																
Trifolium hirtum All.	Annual / Herb / Limited			21	*												
Verbascum thapsus L.	Biennial / Herb / Limited											1	*	1	*		
Vulpia bromoides (L.) Gray	Annual / Graminoid	54	33	270	70	166	48	253	68			179	78	234	52	123	26
Vulpia myuros (L.) C.C. Gmel.	Annual / Graminoid / Moderate	80	15	51	15	219	128	163	72	71	17	2	1	97	35	97	45
	All nonnative understory plants	90	11	155	21	245	31	90	16	124	16	62	14	99	13	75	11

Appendix H. Statistical background for Climate change refugia fire ecology and management

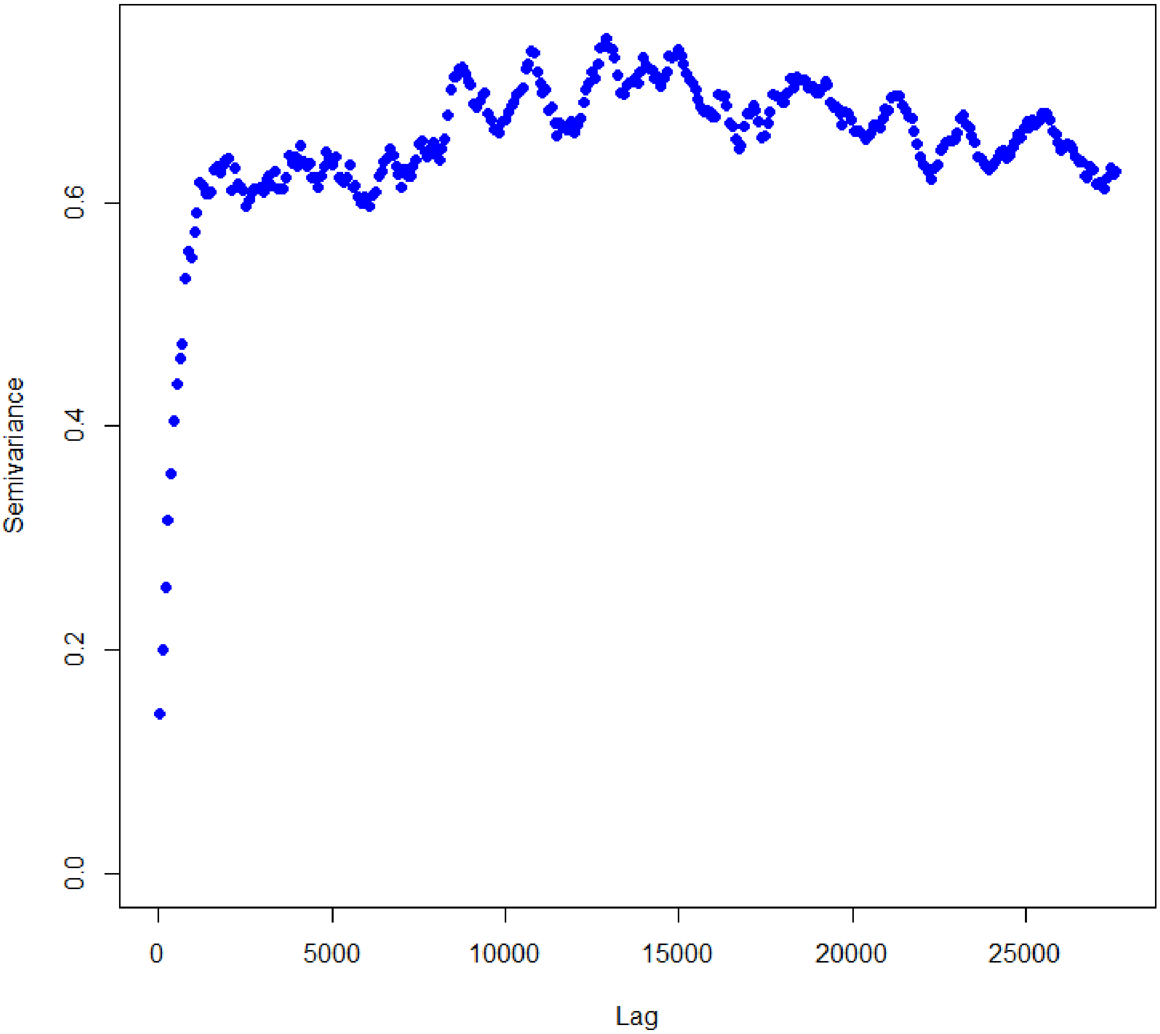


Figure H1. Cold-air pool spatial autocorrelation for the 83 m cell raster was assessed with a variogram with its neighborhood defined as the 30 closest pixels. The semivariance plateaued near 1000 m and data is not spatially autocorrelated beyond this distance.

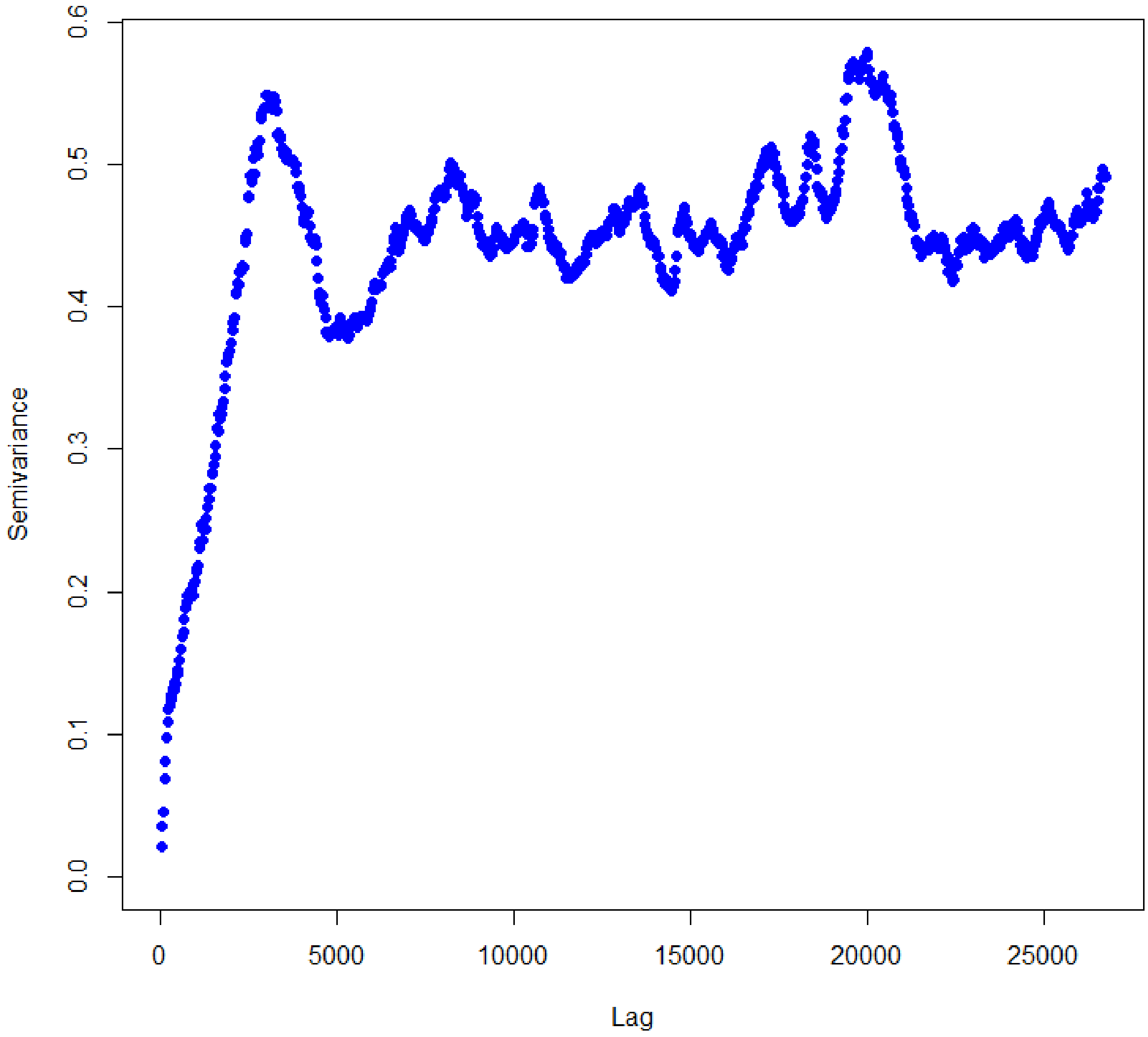


Figure H2. Fire frequency data spatial autocorrelation for the 30 m cell raster was assessed with a variogram with its neighborhood defined as the 30 closest pixels. The semivariance plateaued near 3000 m and data is not spatially autocorrelated beyond this distance.

Appendix I. Climate

Climate data

Table I1. NOAA weather stations near study sites within their elevation range and with monthly climate normals (1981-2010).

Study Site	NOAA name	Comment	Latitude	Longitude	Elevation (m)
Sugar Loaf Basin	Grant Grove		36.7394	-118.9631	2012
Sugar Loaf Basin	Lodgepole		36.6044	-118.7325	2053
Illilouette Creek Basin	South Entrance Station		37.5075	-119.6336	1566
Illilouette Creek Basin	Yosemite Park Headquarters	Yosemite Valley	37.7500	-119.5897	1209
Illilouette Creek Basin	Yosemite Village 12W	Crane Flat Lookout	37.8833	-119.3500	2638

Table I2. Annual precipitation and snow calculated from monthly climate normal for each weather stations. Yosemite Park Headquarters and Yosemite Village 12W both had significant snow throughout the year, but it was not recorded. Monthly climate normals were computed for the 30 year period from 1981 to 2010. (Arguez *et al.* 2010)

NOAA name	Elevation (m)	Snow (cm)	Precipitation (cm)
Grant Grove	2012	457	107
Lodgepole	2053	554	115
South Entrance Station	1566	90	95
Yosemite Park Headquarters	1209	Not recorded	104
Yosemite Village 12W	2638	Not recorded	106

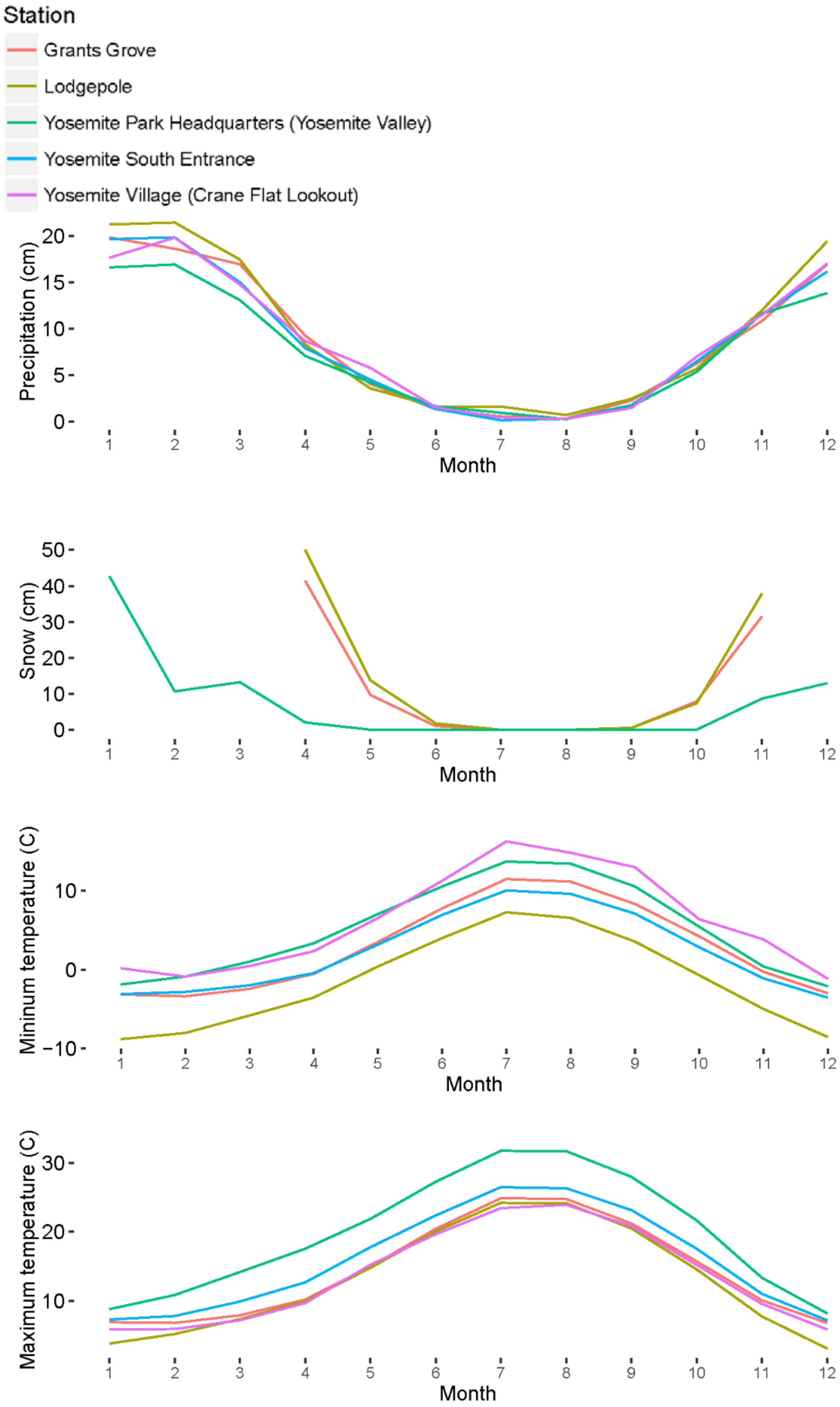


Figure I3. Monthly climate normals computed for the 30 year period from 1981 to 2010 for precipitation, snow, minimum temperature, and maximum temperature (Arguez *et al.* 2010).

Appendix J. Plot layout for Drivers of understory plant communities in mixed conifer forests with long restored fire regimes

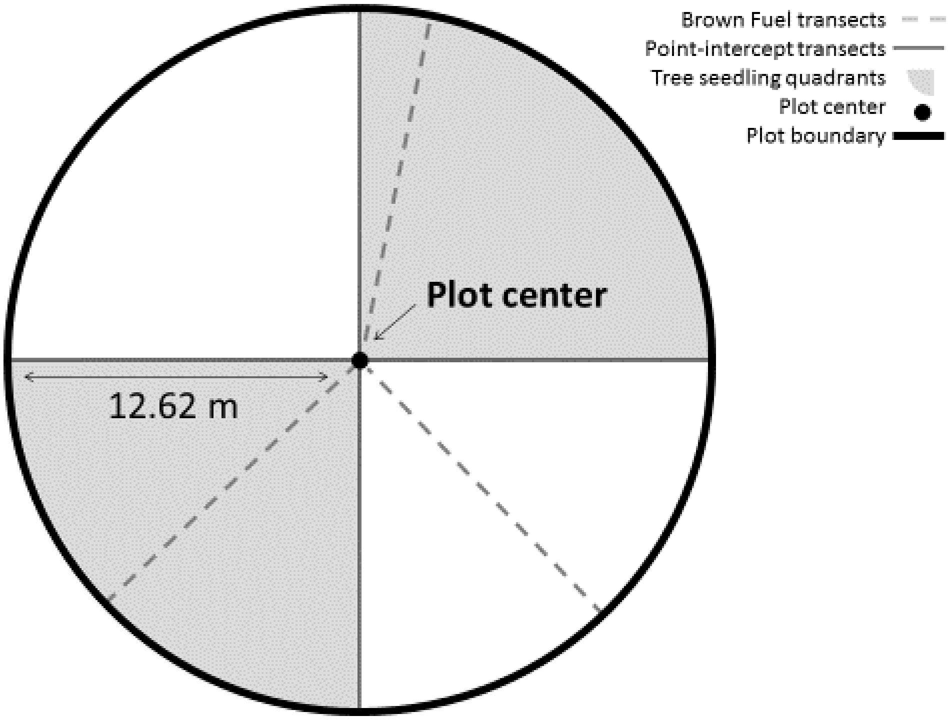


Figure J1. Circular plots had a 12.62 m radius and covered 0.05 acre. Trees were inventoried, including alive and dead trees greater than 10 cm DBH, measured at DBH, and identified to species. Seedlings were inventoried in two quadrants and counted by size classes per species. Understory cover was assessed with two point-intercept transects intersected at plot center and extended to the plot boundary along cardinal directions. Species lists were recorded through timed-area search of up to one-hour, or if no new species had been found within 15 minutes. Dead and down woody fuels were estimated from three 12.62 m Brown Fuel transects originated at plot center and extended to the plot boundary along random azimuths. Canopy closure was assessed with a moosehorn at 25 gridded points within the plot. Soil texture was assessed with the “feel method” (Thien 1979).

Appendix K. Statistical methods for Drivers of understory plant communities in mixed conifer forests with long restored fire regimes

I tested the main effect of pyrodiversity metrics, time since fire, and most recent burn severity together at many buffers around plot center including 25, 50, 75, 100, 250, and 500 m. We used the following equation (Equation K1)

$$\left.\begin{array}{c} y \sim \\ \textbf{Time since fire} + \\ \textbf{Most recent fire severity} + \\ \textbf{Simpson diversity} + \\ \textbf{Functional richness} + \\ \textbf{Functional dissimilarity} + \\ \textbf{Functional divergence} + \end{array}\right\} \begin{array}{l} \text{Plot-based} \\ \text{fire} \\ \text{experience \&} \\ \text{Pyrodiversity} \end{array}$$

$$\left.\text{Park} + \text{Plot} + \text{Survey year}\right\} \text{Random effect}$$

Where γ is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities.

I also tested the main effect of each pyrodiversity metric individually, and their interaction with time since fire and most recent burn severity at many buffers around the plot center including 25, 50, 75, 100, 250, and 500 m. I used the following equation (Equation K2):

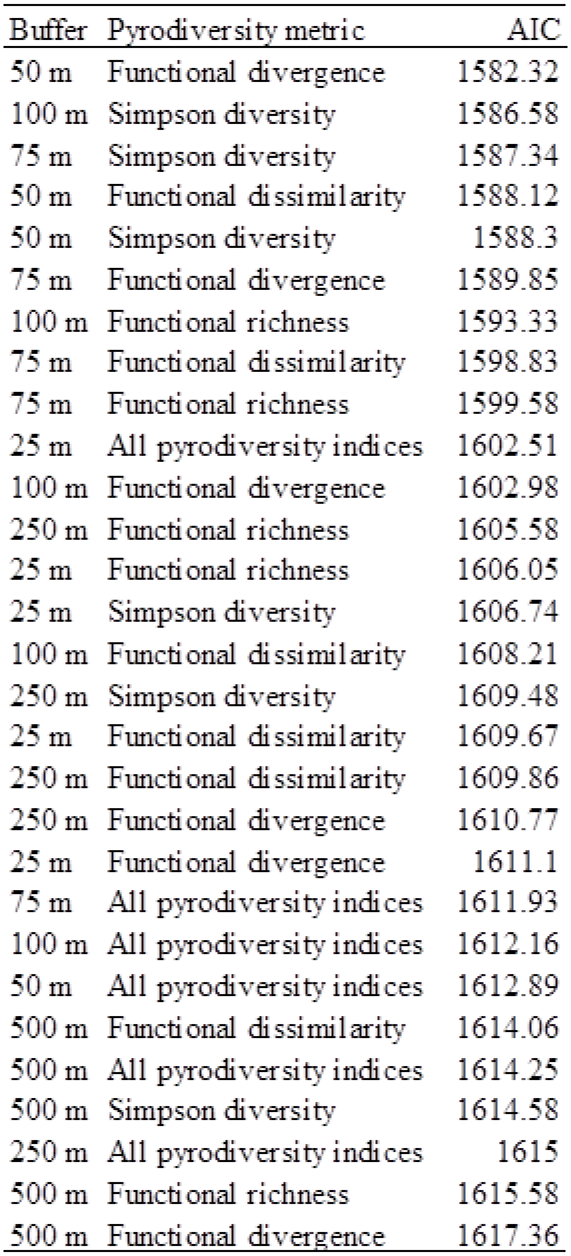
$$y \sim$$

$$\left.\begin{array}{c} \textbf{Time since fire} + \\ \textbf{Most recent fire severity} + \\ \textbf{Pyrodiversity} + \\ \textbf{Time since fire} * \textbf{Pyrodiversity} + \\ \textbf{Most recent fire severity} * \textbf{Pyrodiversity} + \end{array}\right\} \begin{array}{l} \text{Plot-based} \\ \text{fire} \\ \text{experience \&} \\ \text{Pyrodiversity} \end{array}$$

$$\left.\text{Park} + \text{Plot} + \text{Survey year}\right\} \text{Random effect}$$

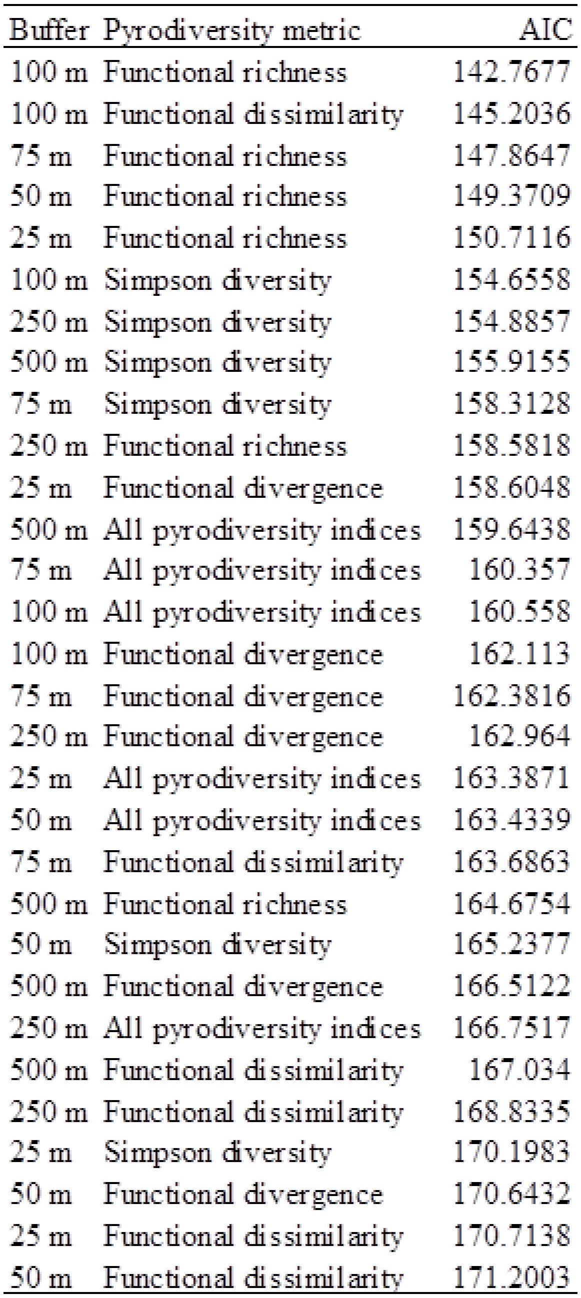
Where γ the response variable, fixed effects is are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities.

Table K1. Pyrodiversity metric models describing plant richness in order of increasing AIC values. “All pyrodiversity indices” used Equation K1. Models with specific pyrodiversity metric listed used Equation J2.



Buffer	Pyrodiversity metric	AIC
50 m	Functional divergence	1582.32
100 m	Simpson diversity	1586.58
75 m	Simpson diversity	1587.34
50 m	Functional dissimilarity	1588.12
50 m	Simpson diversity	1588.3
75 m	Functional divergence	1589.85
100 m	Functional richness	1593.33
75 m	Functional dissimilarity	1598.83
75 m	Functional richness	1599.58
25 m	All pyrodiversity indices	1602.51
100 m	Functional divergence	1602.98
250 m	Functional richness	1605.58
25 m	Functional richness	1606.05
25 m	Simpson diversity	1606.74
100 m	Functional dissimilarity	1608.21
250 m	Simpson diversity	1609.48
25 m	Functional dissimilarity	1609.67
250 m	Functional dissimilarity	1609.86
250 m	Functional divergence	1610.77
25 m	Functional divergence	1611.1
75 m	All pyrodiversity indices	1611.93
100 m	All pyrodiversity indices	1612.16
50 m	All pyrodiversity indices	1612.89
500 m	Functional dissimilarity	1614.06
500 m	All pyrodiversity indices	1614.25
500 m	Simpson diversity	1614.58
250 m	All pyrodiversity indices	1615
500 m	Functional richness	1615.58
500 m	Functional divergence	1617.36

Table K2. Pyrodiversity metric models describing plant Simpson diversity in order of increasing AIC values. “All pyrodiversity indices” used Equation K1. Models with specific pyrodiversity metric listed used Equation J2.



Buffer	Pyrodiversity metric	AIC
100 m	Functional richness	142.7677
100 m	Functional dissimilarity	145.2036
75 m	Functional richness	147.8647
50 m	Functional richness	149.3709
25 m	Functional richness	150.7116
100 m	Simpson diversity	154.6558
250 m	Simpson diversity	154.8857
500 m	Simpson diversity	155.9155
75 m	Simpson diversity	158.3128
250 m	Functional richness	158.5818
25 m	Functional divergence	158.6048
500 m	All pyrodiversity indices	159.6438
75 m	All pyrodiversity indices	160.357
100 m	All pyrodiversity indices	160.558
100 m	Functional divergence	162.113
75 m	Functional divergence	162.3816
250 m	Functional divergence	162.964
25 m	All pyrodiversity indices	163.3871
50 m	All pyrodiversity indices	163.4339
75 m	Functional dissimilarity	163.6863
500 m	Functional richness	164.6754
50 m	Simpson diversity	165.2377
500 m	Functional divergence	166.5122
250 m	All pyrodiversity indices	166.7517
500 m	Functional dissimilarity	167.034
250 m	Functional dissimilarity	168.8335
25 m	Simpson diversity	170.1983
50 m	Functional divergence	170.6432
25 m	Functional dissimilarity	170.7138
50 m	Functional dissimilarity	171.2003

Table K3. Model family and transformation for each response variable.

Response variable	Model family	Transformation
Cover	Poisson	None
Richness	Poisson	None
Simpson diversity	Gaussian	Square root
Evenness	Gaussian	None

Appendix L. Plant community cluster descriptions

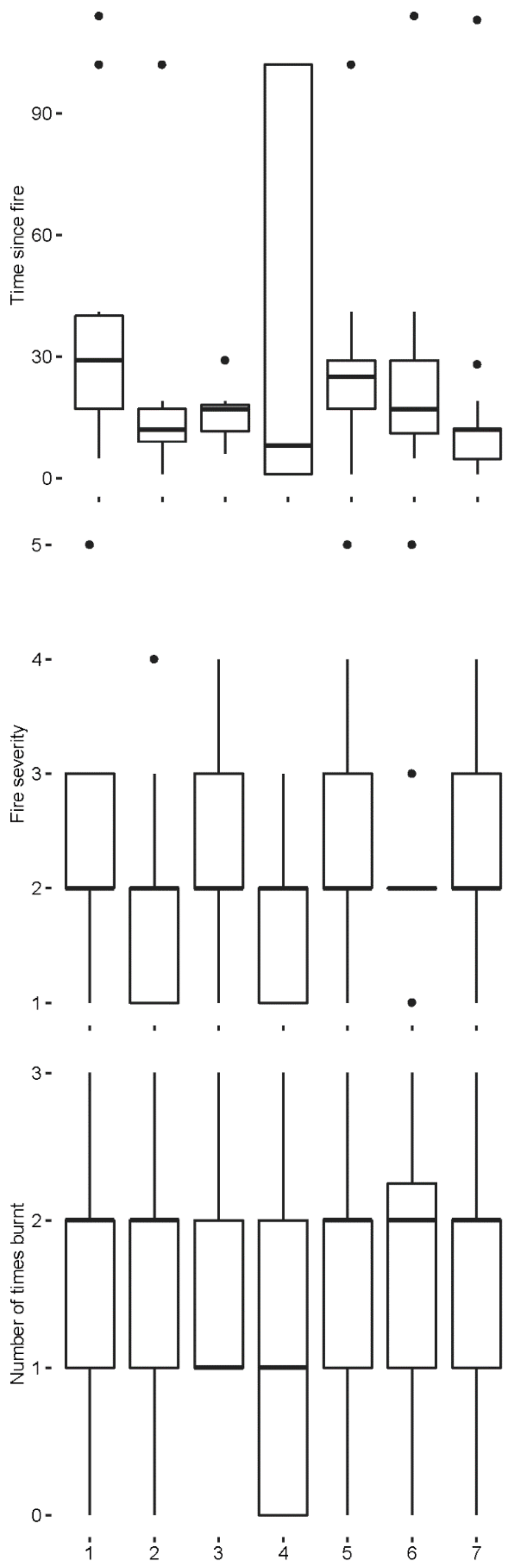


Figure L1. Site fire variables include time since fire, fire severity (0: No fire, 1: Very low severity, 2: Low, 3: Moderate, and 4: High), and burn frequency. Each boxplot has a median indicated with a bold line, first and third quartiles indicated with a box, 95% confidence interval indicated with whiskers, and outliers indicated with points.

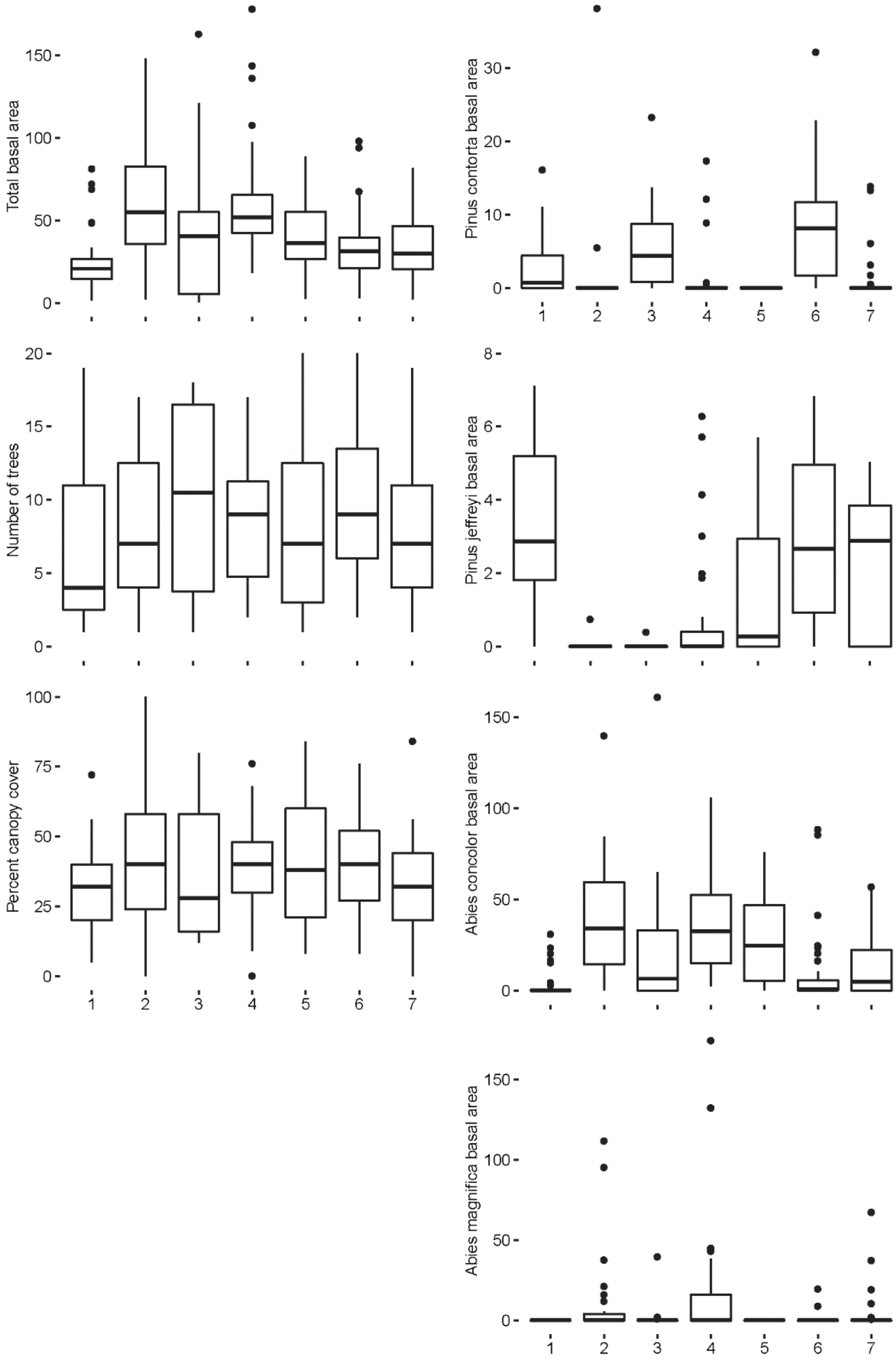


Figure L2. Forest structure data includes total basal area (m^2/ha), number of trees, percent canopy cover, and basal area (m^2/ha) of dominate trees including *Pinus contorta* (lodgepole pine), *Pinus jeffreyii* (Jeffrey pine), *Abies concolor* (white fir), and *Abies magnifica* (red fir). Each boxplot has a median indicated with a bold line, first and third quartiles indicated with a box, 95% confidence interval indicated with whiskers, and outliers indicated with points.

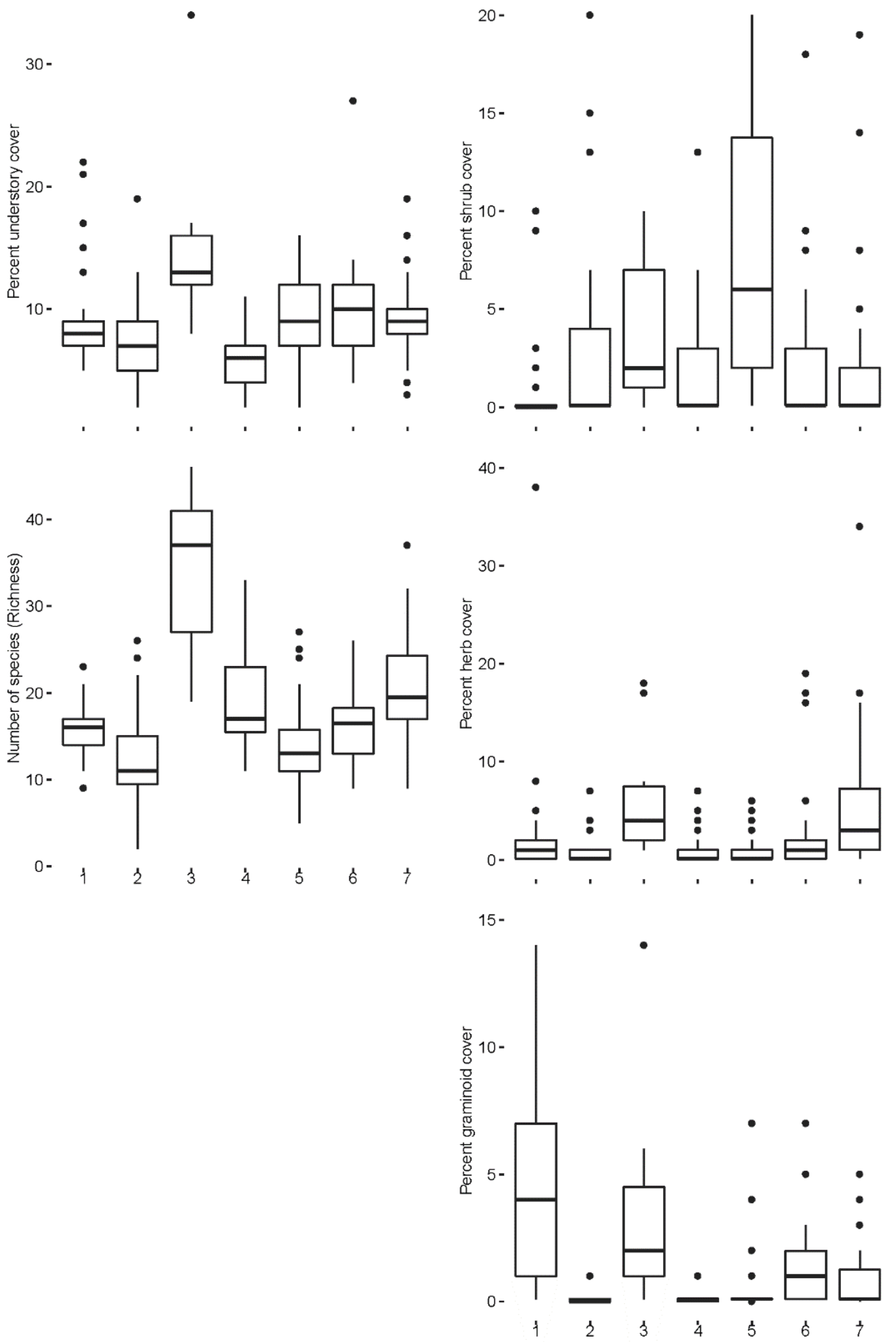


Figure L3. Understory community data includes total cover, species richness, shrub cover, herb cover, and graminoid cover. Functional group (shrub, herb, graminoid) is based on USDA Plants Database (U.S.D.A. 2016). Plant cover can exceed 100% because of the two understory strata (0 to 0.5m and 0.5 to 2m). Each boxplot has a median indicated with a bold line, first and third quartiles indicated with a box, 95% confidence interval indicated with whiskers, and outliers indicated with points.

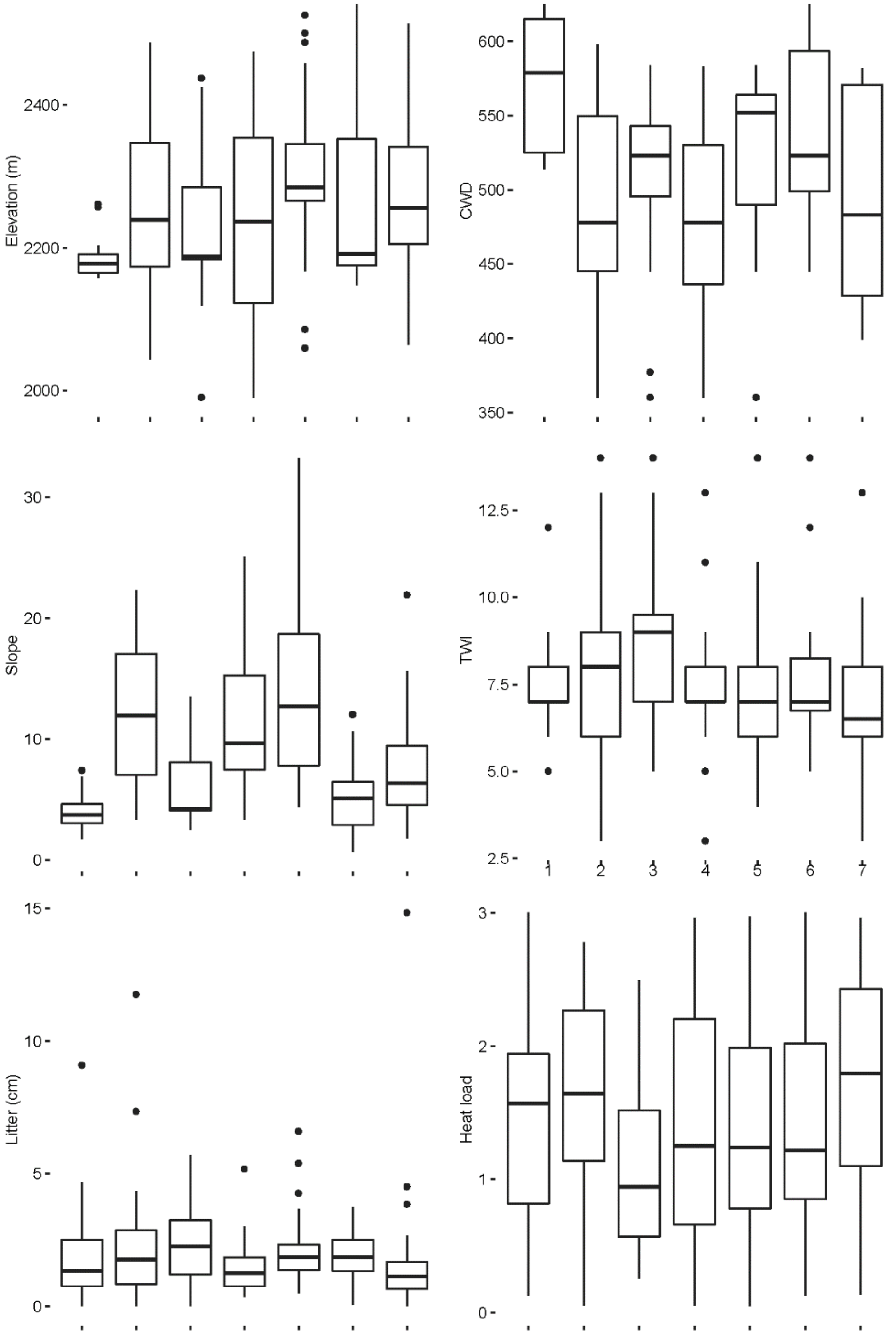


Figure L4. Environmental variables include elevation (m), percent slope, litter depth (cm), CWD, TWI, and heat load. Each boxplot has a median indicated with a bold line, first and third quartiles indicated with a box, 95% confidence interval indicated with whiskers, and outliers indicated with points.

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