UC Davis
UC Davis Electronic Theses and Dissertations

Title
Understory Plant Community Responses to Post-fire Environments in the Sierra Nevada

Permalink
https://escholarship.org/uc/item/7v02701v

Author
Richter, Clark Joseph

Publication Date
2021

Peer reviewed|Thesis/dissertation

eScholarship.org
Powered by the California Digital Library
University of California

Understory Plant Community Responses to Post-fire Environments in the Sierra Nevada

By

Clark Joseph Richter
DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

Marcel Rejmánek

Hugh D. Safford

Malcolm P. North

Andrew Latimer

Committee in Charge

2021

Copyright © 2021 by Clark Richter
All rights reserved.

This is dedicated to my universe: Anna, Sadie & Hank

TABLE OF CONTENTS

ABSTRACT

Forests in the North American Mediterranean Climate zone (NAMCZ) are increasingly defined by novel disturbance regimes and manifestations of climate change. Many regions in the NACMZ, including the yellow pine/mixed-conifer (YPMC) forests of the Sierra Nevada, California, that historically experienced low to moderate intensity fire regimes are seeing increased area burned at high intensity resulting in high post-fire severity as a result of interactions between high fuel loads and climate warming with a number of negative ecological effects. It is important to understand species responses to the ecological disturbance of wildfire in this context, especially from the perspective of the understory plant community where the bulk of regional plant diversity is found and vital ecosystem functions take place. We examined understory plant responses across gradients of post-wildfire severity, shrub cover and a suite of other post-fire environmental features in over 400 plots of YPMC forests of the Sierra Nevada. We found a generally unimodal 'hump-shaped' relationship between local (alpha) understory plant diversity and fire severity. High severity burning resulted in lower local diversity and there was some indication of homogenization of the flora at the regional scale. Fire severity class, postfire litter cover, and annual precipitation were the best predictors of understory species diversity.

In the YPMC forests of the NAMCZ, shrub lifeforms tend to be promoted by high intensity fires, and the recent increase in the extent of high intensity burning is driving major changes in the spatial patterns of shrub-dominated vegetation. We further examined understory plant community response to shrub cover and demonstrated that understory plant species diversity and evenness decline as shrub cover increased while understory richness was less affected. We used structural equation modeling to better understand relationships among shrub cover, understory richness and diversity and other environmental variables. Our examinations of specific lifeforms and life history categories in the understory revealed that while many environmental factors influence richness, water availability, rock and shrub cover mostly determine diversity and evenness. Our research suggests that increases in post-fire severity in systems historically characterized by low to moderate intensity wildfire may lead to understory plant diversity losses. Anticipated increases in shrubfield area due to these changing wildfire regimes will also likely negatively impact native herbaceous plant species diversity. These findings collectively indicate that global patterns of increasing fire size and severity may have important implications for regional plant species biodiversity.

INTRODUCTION

Forest plant communities are shaped like all other ecosystems in the world by a suite of environmental drivers including ecological disturbance. In forest systems like the yellow pine/mixed conifer forests of the Sierra Nevada, wildfire is an important driver of plant community dynamics because of its interaction with climate and its landscape-scale influence (Oakley et al. 2003, Westerling et al. 2006, Knapp et al. 2012, van Mantgem et al. 2013). Climate change and its associated higher local temperatures and influence on precipitation are expected to greatly influence plant communities (Chase 2007, van Mantgem and Stephenson 2007) and fire regimes (Westerling et al. 2006, Taylor and Scholl 2012, Restaino and Safford 2018). In yellow pine/mixed conifer Sierra Nevada forests, the effects of climate change along with the legacy of past federal fire policy (Stephens and Ruth 2005) are largely responsible for heavier fuel loads, high understory tree density (Westerling et al. 2003, Brown et al. 2004, Liu et al. 2010) and novel wildfire regimes. The evidence is accumulating that the wildfire regimes of these Sierra Nevada forests and their associated plant communities are now defined by increasingly more widespread high post-fire severity (Miller et al. 2009, Safford and Van de Water 2014, Steel et al. 2015); the ecological characteristics of high severity post-fire sites often include profound changes in canopy cover and soil structure that have major influences on the recovering understory communities.

The response of a plant species to the post-fire environment is defined by a web of drivers including ecological features of the system, species specific adaptations and interactions with other species (Lloret et al. 2003, Wayman and North 2007, Laughlin and Fule 2008). During a wildfire, the consumptive effects of heat and oxidation remove living and dead plant biomass from the system (Sugihara et al. 2006). Some trees and fire-adapted plant species, depending upon the intensity of the fire, can resist these consumptive conditions and survive a wildfire intact (van Wagtendonk et al. 2018). However, most understory plant species are susceptible to wildfire and must regenerate under the present post-fire conditions (Maranon-Jimenez and Castro 2013, Wan et al. 2014). Some plant species, like those in the shrub genus *Ceanothus*, will either maintain seed banks that allow rapid regeneration post-fire or are induced to re-sprout from carbohydrate stores present underground (this is especially common amongst species of oaks in California) (Peterson and Reich 2001, Franklin 2010). Those that don't have seed banks or re-sprout after fire must disperse into the recently burned area. These species are therefore sensitive to the size of a burned area as well as the availability of biotic agents it may rely on for dispersal and the competitive and facilitative effects of other plant species (Haire and McGarigal 2010, Harvey and Holzman 2014). Depending upon the fire severity and associated plant responses or a site, there may or may not be any canopy cover remaining to moderate the amount of solar radiation that filters down into the understory, and this can favor certain plant species over others (He et al. 2012, Safford et al. 2012, Stevens et al. 2015). Understory plant species response to wildfire is therefore highly variable and understanding the dynamics and patterns of species diversity post-disturbance is consequently important for land managers and researchers working in fire-prone systems (Burkle et al. 2015, Myers et al. 2015).

The research in this dissertation seeks to provide a clearer picture of the implications of novel fire regimes for the understory plant communities of yellow pine/mixed conifer forests of the Sierra Nevada. The tireless work of field assistants, the adept recommendations of committee members and advisors, and the support of the US Forest Service allowed for extensive field surveys and resulted in a large sample of post-fire sites for hypothesis-testing and careful analysis. We examined patterns in species richness and diversity, compared the influences of severity-driven features in the post-fire environment, and determined the strength of plant-driven interactions on the recovering plant communities. We found that understory forest plant species are profoundly affected by ecological features associated with fire severity, and high severity sites are decidedly challenging places to grow. The dominant plant form in these sites are species of shrubs, and while they appear to greatly influence the recovering understory plant community, they are not the sole driver, and their influence varies depending on the life form and life history of the understory plant species. While there is yet work to do to better understand the consequences of novel fire regimes in places like the yellow pine/mixed conifer forests of the Sierra Nevada, our hope it to provide a benchmark for comparison as climate change, novel wildfire regimes and their myriad accompanying affects continue to influence the recovery of plant communities after ecological disturbances.

Literature Cited

Brown, T. J., B. L. Hall, and A. L. Westerling. 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: An applications perspective. Climatic Change 62:365–388.

Burkle, L. A., J. A. Myers, and R. T. Belote. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6:1–14.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences 104:17430–17434.

Franklin, J. 2010. Vegetation dynamics and exotic plant invasion following high severity crown fire in a southern California conifer forest. Plant Ecology 207:281–295.

Haire, S. L., and K. McGarigal. 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (Pinus ponderosa) in New Mexico and Arizona, USA. Landscape Ecology 25:1055–1069.

Harvey, B. J., and B. A. Holzman. 2014. Divergent successional pathways of stand development following fire in a California closed-cone pine forest. Journal of Vegetation Science 25:88–99.

He, T., J. G. Pausas, C. M. Belcher, D. W. Schwilk, and B. B. Lamont. 2012. Fire-adapted traits of Pinus arose in the fiery Cretaceous. New Phytologist 194:751–759.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Knapp, E. E., C. P. Weatherspoon, and C. N. Skinner. 2012. Shrub seed banks in mixed conifer forests of Northern California and the role of fire in regulating abundance. Fire Ecology 8:32–48.

Laughlin, D. C., and P. Z. Fule. 2008. Wildland fire effects on understory plant communities in two fire-prone forests. Canadian Journal of Forest Research 38:133–142.

Liu, Y., J. Stanturf, and S. Goodrick. 2010. Trends in global wildfire potential in a changing climate. Forest Ecology and Management 259:685–697.

Lloret, F., J. G. Pausas, and M. Vilà. 2003. Responses of Mediterranean Plant Species to different fire frequencies in Garraf Natural Park (Catalonia, Spain): field observations and modelling predictions. Plant Ecology 167:223–235.

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151–1156.

van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecology Letters 10:909–16.

Maranon-Jimenez, S., and J. Castro. 2013. Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. Biogeochemistry 112:519–535.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade mountains, California and Nevada, USA. Ecosystems 12:16–32.

Myers, J. A., J. M. Chase, R. M. Crandall, and I. Jiménez. 2015. Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. Journal of Ecology 103:1291–1299.

Oakley, B. B., M. P. North, and J. F. Franklin. 2003. The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub Ceanothus cordulatus. Plant and Soil 254:35–46.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914–927.

Restaino, C., and H. Safford. 2018. Fire and Climate Change. Pages 493–505 *in* J. W. van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, and K. E. Shaffer, editors. Fire in California's Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Safford, H. D., J. T. Stevens, K. Merriam, M. D. Meyer, and A. M. Latimer. 2012. Fuel treatment effectiveness in California yellow pine and mixed conifer forests. Forest Ecology and Management 274:17–28.

Safford, H. D., and K. P. Van de Water. 2014. Using Fire Return Interval Departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. PSW-RP-266. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:1–23.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stevens, J. T., H. D. Safford, S. Harrison, and A. M. Latimer. 2015. Forest disturbance accelerates thermophilization of understory plant communities. Journal of Ecology 103:1253–1263.

Sugihara, N. G., J. W. Van Wagtendonk, and J. Fites-Kaufman. 2006. Fire as an Ecological Process. Pages 58–74 *in* N. G. Sugihara, J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's Ecosystems. University of California Press, Berkeley, California, USA.

Taylor, A. H., and A. E. Scholl. 2012. Climatic and human influences on fire regimes in mixed conifer forests in Yosemite National Park, USA. Forest Ecology and Management 267:144–156.

van Wagtendonk, J. W. 2006. Fire as a Physical Process. Pages 38–57 *in* N. G. Sugihara, J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's Ecosystems. University of California Press, Berkeley, California, USA.

van Wagtendonk, J. W., J. Fites-Kaufman, H. D. Safford, M. North, and B. M. Collins. 2018. Sierra Nevada Bioregion. Pages 249–278 Fire in California's Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Wan, H. Y., A. C. Rhodes, and S. B. St Clair. 2014. Fire severity alters plant regeneration patterns and defense against herbivores in mixed aspen forests. Oikos 123:1479–1488.

Wayman, R. B., and M. North. 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. Forest Ecology and Management 239:32–44.

Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger. 2003. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society 84:595-+.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313:940–943.

CHAPTER 1

The local species diversity x fire severity relationship is hump-shaped in dry conifer forests

Background

Ecological disturbances shape and restructure abiotic resources and biotic communities (Pickett et al. 1989, Bond and Van Wilgen 1996, Meurant 2012). Humans have major influences on ecological disturbance processes, and disturbance regimes in particular can be greatly altered by human agency (Taylor and Scholl 2012, van Mantgem et al. 2013, Enright et al. 2014). Fire provides excellent examples of how human influences on disturbance regimes can have major impacts on ecosystem states and processes. Human presence usually increases fire occurrence in ecosystems leading to deleterious effects on species and ecosystem components and processes not adapted to or resilient to high fire frequencies (Bowman et al. 2011, McWethy et al. 2013). However, in some ecosystems humans have notably reduced natural fire frequencies. Examples of ecosystems affected in this way include grasslands, savannas, and oak and pine woodlands, which tend to support highly frequent, low severity fire carried principally in surface fuel layers dominated by herbaceous plants and litter and/or small-diameter woody fuels (Syphard et al. 2007, Safford and Van de Water 2014). In these types of fuel beds, fire can be easily ignited but also easily extinguished. In western North America, semi-arid forests dominated by fire resistant conifers like ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*P. jeffreyi*) are well-known examples of human-affected ecosystems. Since the early 20th century, many forested areas dominated by these and related species have experienced widespread ecosystem transformations as a result of a century or more of systematic fire suppression and exclusion by humans. Such fire exclusion typically leads to forest densifition, accumulation of dead woody material and surface litter, increases in the densities of fire-intolerant tree species, and a shift to a fire regime characterized by highly infrequent but very severe fire (Stephens and Ruth 2005, Van de Water and Safford 2011, Steel et al. 2015).

Such trends threaten the resilience of these forests because few species are adapted to regenerating after severe fire, which was comparatively rare before Euroamerican settlement of western North America (Welch et al. 2016, Tepley et al. 2017, Shive et al. 2018). The impacts of the changed fire regime on forest structure and the dominant tree species have been intensively studied (North et al. 2016, Safford and Stevens 2017, van Wagtendonk et al. 2018), however little is known about the effects of the changed fire regime on the shrubs and herbaceous plants that make up the forest understory. Western forests are decidedly poor in tree species, and most biota are found in the understory (Booth 1950, Peet 1978, Halpern and Spies 1995, Barbour et al. 2007). Understory plant species play crucial ecological roles in various ecosystem processes and services including nutrient cycling, soil hydrology, food and forage provision, pollination, and provision of animal habitat (Levine et al. 2003, Gilbert and Lechowicz 2004, Gilliam 2007, Kudo et al. 2008, Kuhn et al. 2011). Understory plant communities are also shaped by ecological disturbance, interactions with other plant species, and features of the biophysical environment (Bowman et al. 2009, Belote 2015, Burkle et al. 2015, Stevens et al. 2015, Werner et al. 2019).

Fire intensity is the amount of heat energy released during burning, and this is the most direct influence fire has on an ecosystem. Since actual heat flux is difficult to measure, an imperfect surrogate – fire severity – is usually used to measure fire’s impact to the ecosystem. Fire severity is a measure of the effect of fire intensity on the ecosystem driven by interactions between the fire’s heat, plant species adaptations, and environmental conditions (Keeley 2009). However, the same amount of energy input can severely impact certain ecosystems but barely affect others, so system recovery and reassembly may vary greatly depending on the severity of fire. Low severity sites may recover in an ‘auto-successional’ manner (e.g. Matthews et al. 2018) because while the post-fire system may differ initially in the distribution of fuel loads and some small-statured plant mortality; it is largely similar to or quickly returns to resemble the system it was before fire in terms of overstory species composition, seedbank diversity, nutrient, water and light availability, and so on (Turner et al. 1999, Wang and Kemball 2005). Low severity sites therefore exhibit a sort of system memory, whereas sites burning at high severity look and function dramatically differently from their pre-fire state (Sugihara et al. 2006, Shenoy et al. 2013). Features such as living overstory trees and viable seedbanks may be rare to non-existent in high severity sites post-fire and ecosystem-level characteristics like light infiltration to the understory, soil structure and nutrient availability are often decidedly altered (Wells et al. 1979, Certini 2005, van Wagtendonk 2006, Stevens et al. 2015).

Fire can increase forest heterogeneity (Collins and Stephens 2010), which can in turn increase species diversity (Harner and Harper 1976, Huston 1994), but progressively larger high severity burn patches may decrease habitat heterogeneity (Safford and Stevens 2017, Shive et al. 2018, Steel et al. 2018). Such homogenization of the postfire environment could have major effects on forest biodiversity (Lindner et al. 2010, Hessburg et al. 2016). A rich body of ecological theory posits a variety of potential diversity and disturbance severity relationships with the shape and amplitude of the diversity response varying based on factors like ecosystem productivity, the composition of the species pool, evolutionary feedbacks, and the type of disturbance (Grime 1977, Huston 1994, Safford et al. 2001, Safford and Mallek 2011, Hall et al. 2012). Previous research has examined understory community responses to prescribed fires in various North American forest types (Halpern 1989, Schoennagel et al. 2004, Wayman and

North 2007, Webster and Halpern 2010). However, such studies are nearly universally restricted to the lower half of the fire severity gradient because prescribed fires are almost always carried out under moderate weather and fuels conditions intended to preclude high severity burning. Such studies have mostly documented increasing plant species richness or diversity with increasing fire severity with the pattern in the upper half of the fire severity gradient left to the imagination.

Importantly, plant responses to fire severity could be contingent upon historical fire regimes. In a recent review, Miller and Safford (in review) summarized the ecological literature from the western US using only studies that included more than one fire severity class and unburned controls. They were able to locate 13 studies that included the full fire severity gradient. In these studies, they found that plant species richness responses to fire severity depended to a great extent on the historical (e.g., pre-Euroamerican arrival) disturbance regime of the ecosystem in question because it was a fundamental driver of species adaptations and the makeup of the species pool. For instance, in forest types historically defined by frequent, low to moderate severity fires (Fire Regime Group 1; Schmidt et al. 2002), species richness tended to be unimodal along the fire severity gradient (from unburned to high severity). In contrast, in moist, high elevation forests defined by infrequent, high severity fires (Fire Regime Groups IV and V), species richness tended to rise with fire severity (Miller and Safford, in review). However, further research is needed to clarify whether these patterns are generalizable.

In this study, we examine plant community responses to fire severity in dry conifer forests that occupy more than 1.7 million km^2 of the United States (Schmidt et al. n.d.) and are the site of the most notable increases in fire size and fire severity over the last three decades in the lower 48 States (Safford and Van de Water 2014, Steel et al. 2018). Such dramatic changes in fire regimes at continental scales may pose major threats to the ecosystems affected and the services they provide. In this paper, we seek to generate more robust documentation of the relationship between plant species diversity and fire severity in Fire Regime Group I forests in the western US and provide an independent test of the patterns reported by Miller and Safford (in review). Working in eight burned areas in yellow pine and mixed conifer (YPMC) forests of the Sierra Nevada, California, we asked two principal questions: (1) How does understory plant species diversity (alpha and gamma) vary along the entire fire severity gradient; and (2) How does fire severity influence the rate of species turnover on the landscape (beta diversity). Under (1), we hypothesized that local (alpha) diversity would exhibit a "hump-shaped" pattern across the fire severity spectrum with low diversity in unburned and high severity classes and higher diversity in low and moderate severity classes. Under (2) we expected to find high species turnover among plots in low and moderate severity classes and less difference between plots in unburned and high severity classes.

Methodology

Study sites

We sampled eight burned areas (hereafter "fires") in YPMC forests of the Sierra Nevada, California (Figure 1.1; Table 1.1). YPMC forests are the most widespread forest type in the Sierra Nevada, occurring above oak woodlands and mixed evergreen forest and below red fir forests, generally at elevations between 500 m and 2000 m. They are dominated by the yellow pines (ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson] and Jeffrey pine [*P. jeffreyi* Balf.]); white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.); sugar pine (*P. lambertiana* Douglas); incense cedar (*Calocedrus decurrens* (Torr.) Florin); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*); and a number of hardwood species, most notably black oak (*Quercus kelloggii* Newberry) and canyon live oak *(Quercus chrysolepis* Liebm.) (Safford and Stevens 2017). The climate is Mediterranean with warm, dry summers and cold, wet winters. Most of the YPMC forest falls within the Cwb climate zone of Köppen, where the mean temperature of the warmest month is below 22°C, at least 3x more rain falls in the wettest month than in the driest month, and the proportion of rain to snow is >1:1 (Safford and Van de Water 2014).

Sample collection and processing

We chose fires that were of sufficient size to permit location of ≥10 randomly located plots in each of six fire severity classes. We conducted field sampling at least five years post-fire. We located potential plot locations through a stratified random process based on fire severity estimates using satellite RdNBR (relative differenced Normalized Burn Ratio) measures (Miller and Thode 2007, Miller et al. 2009). We used ArcGIS software to overlay a 400 x 400-meter grid across each fire area and potential plot centers were located at grid nodes. Within each fire severity class in the imagery, at least 10 potential sites were sampled in the field in each fire, but final sample sizes varied due to discrepancies between image and field-based severity assessments and vegetation type mismatches. We used circular, 405 m^2 (1/10 acre) study plots following the Forest Service's Common Stand Exam protocol (*USDA Forest Service Region 5 - Common Stand Exam Field Guide* 2012). To characterize fire severity in the field, we assessed scorch heights, torch heights and existing vegetation, and we binned study plots into six fire severity classes (Table 1.2), from Welch et al. (2016). We made ocular estimates of cover for all plant species in each study plot and gave any species with less than 1% cover a "trace" designation. We identified plants using *The Jepson Manual* (Baldwin et al. 2018). We also recorded environmental data including elevation, slope, aspect, total overstory cover, litter depth and litter cover. Time since fire was derived by subtracting the year of burning from the year of sampling, but because unburned controls were also included, time since last fire for these plots as well as total number of fires over the last 110 years for every plot were extracted from the US Forest Service Pacific Southwest Region Fire Return Interval Departure GIS database (Safford and Van de Water 2014). We used the Basin Characterization Model (Flint and Flint 2007, 2014) to extract climatic water deficit and mean annual precipitation estimates and generated estimates of heat load and potential direct incident radiation for our plot locations using latitude, aspect and slope (McCune and Keon 2002, McCune 2007).

Diversity indices

Alpha diversity was measured as local species richness (mean number of species per 405 m^2 plots), and the per plot means of the antilogarithm Shannon diversity index (focus on rare species, cover as abundance), inverse Simpson index (focus on abundant species, cover as abundance), and Pielou's evenness (cover as abundance), based on formulas from Pielou (1984) and Ludwig and Reynolds (1988). Data from the eight fires were pooled for these analyses.

Beta diversity was measured as Jaccard dissimilarity (1-J) between plots within each fire severity class in each fire. The overall means from the eight mean 1-J measures were also calculated for each fire severity class and then pooled into unburned, low severity (class 1), moderate severity (classes 2 and 3), and high severity (classes 4 and 5).

Gamma diversity for each severity class was calculated using averaged rarefied richness from the vegan package (Oksanen et al. 2018) in R statistical software (R Development Core Team 2013). We used 4 as the minimum sample size, and we excluded Bassetts from the analysis because of especially low plot numbers in severity classes 3 and 4.

Statistical analyses

All data were tested for normality and heteroscedasticity of residuals and data transformations were applied if necessary. One-way ANOVAs were conducted to examine differences in diversity indices, evenness and dissimilarity among fire severity classes using GraphPad Prism 8.01 software (Motulsky et al. 2021). Tukey multiple-comparison tests were employed after ANOVAs when there were statistically significant differences among fire severity classes.

To determine which species were most characteristic in the understory vegetation of a given fire severity class, two-way indicator species analysis (TWINSPAN) was used in PC-ORD (McCune and Mefford 1999).

To examine the influence of fire severity and other environmental factors on our observed diversity metrics, we used restricted maximum likelihood linear mixed-effects models from the lme4 package (Bates et al. 2014) in R statistical software (R Development Core Team 2013). For each dependent variable (species richness, Antilog Shannon diversity index (AS), Simpson's diversity index (SI) and Pielou's evenness (PE)), we created a full model including our main effect (fire severity; 0-5) and a suite of other environmental variables including year, elevation, slope, aspect, total overstory cover, litter depth, litter cover, time since last fire, number of fires, climatic water deficit, mean annual precipitation, heat load, and potential direct incident radiation as well as interactions between fire severity and litter cover, litter depth and overstory cover. Fires were included as a random blocking variable in all of the models. Prior to analysis we determined whether a polynomial term should be used in each model by examining the diversity metrics across fire severity. Ultimately, a 2nd order polynomial was applied to fire severity for the curved pattern of species richness while no polynomial was applied for AS, SI, and PE because they exhibited linear relationships. After running the full model, non-significant predictors were eliminated and the model re-run.

Results

Species diversity measures

In our pooled analyses, all of our measures of diversity and evenness showed notable differences across fire severity classes. (Figure 1.2 and 1.4). Species richness showed significant differences ($F_{5,623}$=6.292, p<0.0001) between unburned controls ("0") and fire severity classes 2 (p=0.034), 3 (p<0001), and 4 (p=0.023), between fire severity class 1 and class 3 (p=0.003), and between fire severity class 3 and class 5 (p=0.002; Figure 1.2). Patterns of the diversity vs severity relationship varied somewhat among fires. As an example, we show the richness x severity relationship for each fire in Figure 1.3. Five of the fires showed peaks in richness at moderate severity ('hump'-shaped relationships), and one fire each showed a positive plateau (Freds), a negative trend (Bassett's), and no relationship (Pendola) (Figure 1.3).

The two diversity indices and evenness all showed the same general pattern: similar (or slightly rising) diversity from unburned to fire severity class 3, then a major drop in the high severity classes 4 and 5. We show the Simpson's and Pielou's indices in Figure 1.4 (Antilog Shannon diversity indices – nearly identical pattern to Simpson's – were also significantly different across fire severity classes at p<0.0001).

Mean gamma diversity (as rarefied richness) displayed a 'hump-shaped' relationship with fire severity (Figure 1.5) similar to that of alpha diversity. While unburned controls were not significantly different from the highest severity class (5), their gamma diversity was decidedly lower than understory communities in low to moderate severity (2: p=0.016, 3: p<0.0001, and 4: p=0.0005). Overall, understory communities in severity class 3 showed significantly higher gamma diversity than plots anywhere else along the spectrum (p<0.0001 for all).

The average species dissimilarity among plots in our unburned class was higher than in any of the burned classes (Figure 1.6). Dissimilarity dropped slightly at higher severities, and when blocked as with gamma diversity the highest values were found in the unburned and low severity classes, medium values in the moderate severity classes, and lowest values in the high severity classes. However, our analyses did not reveal any of these fire severity blocks to be statistically significant from each other.

Species indicator analyses

Analysis of the dataset with TWINSPAN derived three conifer tree species (*Pinus ponderosa, P. lambertiana, Calocedrus decurrens*; present in the understory as seedlings) as reliable indicators (P <0.05) for the unburned, low and low-moderate severity classes. The fire-stimulated shrubs *Ceanothus integerrimus* and *C. cordulatus* were significant indicators of high-moderate and high severity burning.

Influence of fire severity and environmental variables on diversity indices

A small set of environmental variables (fire severity, time since last fire, elevation, litter cover, litter depth, overstory cover and mean annual precipitation) were significant predictors of understory plant species richness, diversity, and evenness but varied depending on the particular index (Table 1.3). Fire severity (unimodal relationship with richness, negative with the other dependent variables) and litter cover (mostly negative relationship, but marginally significant positive relationship with richness) were the only two predictor variables that appeared in all of our models. Mean annual precipitation (negative relationship with the dependent variables) appeared in the models for richness and diversity; overstory cover (positive relationship) appeared in the models for diversity and evenness (Table 1.3). Time since last fire was negatively related to diversity, wherein older fires were less diverse. Higher elevations supported lower species richness overall. In the model for richness, there was a significant interaction between elevation and precipitation, such that at lower elevations, richness declined with increasing precipitation while at higher elevations greater precipitation led to more understory species. Year of sampling helped to explain some of the differences in richness between fires but did not prove to be an important predictor of the relationships between richness, diversity, or evenness and fire severity. Our best model for species richness explained 61% of the variance, and our best Shannon index model explained 50%; models for the two other diversity measures did not account for a majority of the variance in the dependent variables (Table 1.3).

Discussion

Across our eight study fires, understory plant species richness and gamma diversity were highest in moderate fire severity classes and lowest in the unburned and high severity classes. Our other diversity and evenness measures showed similar but less accentuated patterns. These findings generally correspond to the unimodal ‘hump-shaped’ relationship between diversity and disturbance described in the theoretical literature for ecosystems of moderate levels of ecosystem productivity (Connell 1978, Huston 1994, Hall et al. 2012). Higher levels of postfire diversity in areas burned at moderate severity were also found in dry forests by DeSiervo et al. (2015) and Stevens et al. (2015), and there is evidence that this may be a general pattern for forests adapted to frequent, low severity fire (Miller and Safford, in review). Our results thus further confirm the generality of the ‘hump-shaped’ diversity vs fire severity pattern in FRG I forests. The pattern of fire increasing understory species diversity in ecosystems that have at least some evolutionary history with fire is very well documented in the literature (Romme 1982, Cowling et al. 1996, Pausas and Ribeiro 2017). The drop in diversity at high levels of severity in YPMC forests (and other similar ecosystems adapted to frequent, low and moderate severity fire) is likely due to a number of factors: (1) there is a general lack of species with adaptations to survive and/or regenerate (e.g., fire-cued germination, serotiny) after high severity fire in communities adapted to primarily low severity fire regimes (Grubb 1977, Denslow 1985, Keeley and Safford 2016); (2) those relatively few species in the Sierra Nevada that do respond positively to high intensity fire include a group of widespread, highly competitive shrubs (mostly in the genus *Ceanothus*) that rapidly dominate high severity burn patches and competitively exclude conifer seedlings and many herbaceous species (Bohlman et al. 2016, Welch et al. 2016); and (3) the altered (warmer, drier) environmental conditions associated with severely burned sites can filter out species adapted to more mesic habitat conditions, especially in regions with hot, dry summers like California (Stevens et al. 2015, Keeley and Safford 2016, Miller and Safford, in review).

Both theoretical and empirical evidence suggest that high severity disturbances should generally homogenize biota, because relatively few species can survive such conditions (Connell 1978, Huston 1994, Grime 2006); such an effect should be exaggerated in ecosystems with little evolutionary exposure to high severity disturbance. We found evidence for this effect, as diversity and evenness measures all dropped in the high severity classes, and our beta and gamma diversity measures were also low in the high severity classes. On the other end of the fire severity spectrum, unburned forest plots also tended to support lower levels of alpha diversity and the overall species pool (gamma diversity) was similarly low in the high severity plots. Dry forests that have experienced long-term fire exclusion (75% of YPMC forests in California have not experienced a single fire in >100 years; Steel et al. 2015) are typically dominated by dense canopies of shade-tolerant conifers and thick layers of surface litter where little light reaches the forest floor and understory diversity is typically low (North et al. 2016, Safford and Stevens 2017). When such long unburned forests are burned at low to moderate severity, our results suggest that plant species richness and diversity benefit, at both the local (alpha) and regional (gamma) scale. Where such forests burn at high severity – which is increasingly more likely under contemporary fuel and climate conditions (Steel et al. 2015, Safford and Stevens 2017, Restaino and Safford 2018) – plant richness does not benefit and diversity and evenness (i.e., taking into account abundance relationships) decline.

While fire is often perceived as a driver of heterogeneity, and this was true for moderate severity fire, we also observed relatively high beta diversity in unburned areas. Our unburned plots are necessarily found mostly around the perimeter of the sampled fires and are thus separated by notably more distance than the plots in other severity classes. We suspect this is inflating species turnover between plots in the unburned class. We are adding more fires to our dataset in the next few field seasons and we plan to carry out an analysis of the influence of inter-plot distances on beta diversity using this expanded dataset.

Our findings highlight that shifting fire regimes could cause substantial decreases in both forested area and plant diversity over coming decades. Areas burned at higher levels of fire severity in dry forests support fewer plant species, lower levels of diversity, lower evenness, and less dissimilarity across the landscape. Thus, the shift from the historical high frequency/low severity fire regime (FRG I) to the modern low frequency/high severity fire regime (FRG III and IV) is reducing both local and landscape-level plant diversity. Under current fire patterns in dry forests, the landscape area dominated by low-diversity high-severity burn patches/shrub fields is increasing rapidly and often transitions to persistent shrublands (Miller and Safford 2012, Mallek et al. 2013, Steel et al. 2015, 2018). Because montane chaparral is characterized by a different natural fire regime (low frequency/high severity) than YPMC forest, re-entry of fire into these shrub fields generally kills tree seedlings and saplings that have colonized since the original burn. Under climate change and a continuation or acceleration of current fire trends, there is a real possibility that large portions of the Sierra Nevada landscape could get caught in a feedback-loop, threshold-type dynamic that prevents recovery of former forest in many high severity burn patches (Coppoletta et al. 2016, Tepley et al. 2017, Dettinger et al. 2018, Restaino and Safford 2018). This could have major effects – not necessarily all negative – on plant and animal diversity and composition (McKenzie et al. 2004, Mallek et al. 2013, Bohlman et al. 2016, White et al. 2016, Miller et al. 2018).

Fire severity and litter cover consistently predicted patterns in all of our richness, diversity, and evenness measures. We discussed severity in depth above. As expected, higher litter cover led to lower understory diversity, but had a marginally significant positive relationship with species richness. We suspect this is due to litter cover's interactions with other variables in the regression especially fire severity (which had reversing relationships with species richness in the low and high severity classes) and time since last fire. Higher precipitation was associated with lower understory richness, diversity, and evenness, most likely because precipitation is closely correlated with vegetation productivity in semi-arid areas (Fites-Kaufman et al. 2007) and recovery of woody plants and canopy closure is much higher in burned wet areas than in burned dry areas. In a similar fashion, older fires supported fewer understory species, most probably because post-fire shrub response has driven down herbaceous diversity in these sites (Bohlman et al. 2016). The positive relationship between overstory cover and understory diversity and evenness is likely due to the reduction in shrub cover that occurs as tree canopies expand, as well as the general amelioration of evaporative stress. In the Sierra Nevada forests we sampled, even in unburned plots canopy cover >60% is relatively rare and increasing tree cover to about 40-50% total cover in burned sites and low cover unburned sites can facilitate the coexistence of understory (and epiphytic) species from plant lineages adapted to both mesic and xeric habitats (Stevens et al. 2015, Miller et al. 2018).

Management Implications

The post-fire successional trajectory of dry forests in a major management concern as climates continue to warm, dry seasons get drier, and the probability of short-interval reburns become more common. Severely burned areas in low and middle elevation California forests are at high risk of (semi)permanent conversion to shrubs in the event of another high severity fire before forest cover has been able to re-establish (Coppoletta et al. 2016, Tepley et al. 2017). Taken in concert with other recent studies from California (e.g., DeSiervo et al. 2015, Stevens et al. 2015, Bohlman et al. 2016, Welch et al. 2016, Steel et al. 2018), our data show that the conversion of large areas of Sierra Nevada forest to shrublands by way of high severity burning is likely to have a negative effect on plant species diversity.

Both forest and fire management practices can have major effects on the occurrence and outcome of fire in FRG I forests in the western United States. Long-term fire suppression in these fire-dependent ecosystems has greatly reduced fire occurrence but ironically increased the probability that the outcomes of fire will be ecologically negative when they occur (Steel et al. 2015). Restoration of low tree stem densities and low fuel loadings in FRG I forests by managers can greatly increase forest resilience to fire and drought and benefit a suite of forest conditions, ecological processes, and biota (Schwilk et al. 2009, Stevens et al. 2014, Hanberry et al. 2015, Winford et al. 2015). However, the spatial footprint of active management will continue to be limited by economic, ecological, social, and political factors. Restoration of low and moderate severity fire as an ecological process has the potential to positively affect much larger landscapes (North 2012, Mallek et al. 2013). In FRG I ecosystems like the forests we studied in California, resilience to rapidly changing environmental conditions will be best promoted by a multifaceted approach that combines strategic forest thinning with a major expansion of prescribed burning and managed wildland fire under moderate weather conditions.

Figures & Tables

Figure 1.1: Locations and areas of fires included in this study.

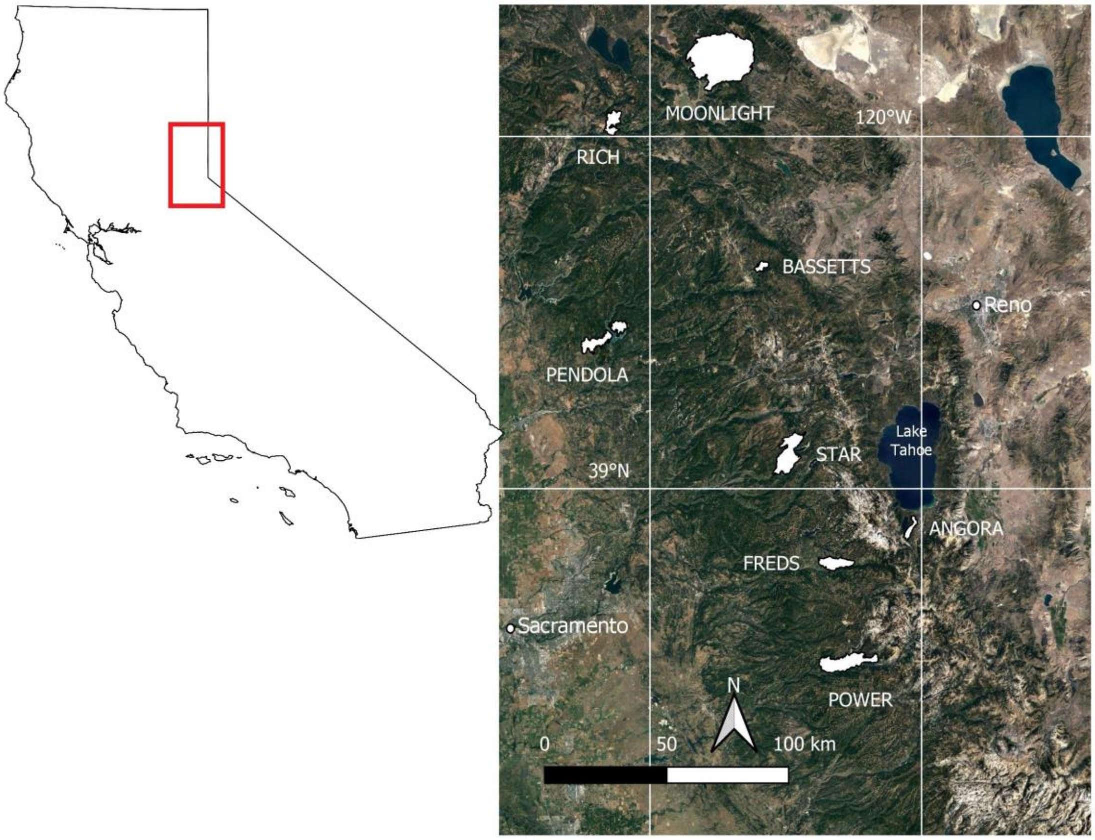


Table 1.1: Details of fires sampled including years of ignition and sampling, elevation range and number of plots surveyed for each fire.

Fire Name	**Fire Abbv.**	**Burn Year**	**Size (ha)**	**Year of Sampling**	**Years Since Fire**	**Elevation range (m)**	**Severity**					
							0	**1**	**2**	**3**	**4**	**5**
							# of Plots					
Angora	ANG	2007	1,220	2015	8	1905–2251	29	7	14	14	16	15
Bassetts	BAS	2006	939	2015	9	2129-2741	6	18	2	1	1	6
Freds	FRD	2004	3,298	2013	9	1291-2090	10	14	10	2	7	5
Moonlight	MNL	2007	26,595	2014	7	1488-2167	10	6	12	17	15	20
Pendola	PEN	1999	4,753	2011	12	598-966	17	17	13	9	10	25
Power	PWR	2004	6,987	2014	10	1003-2294	11	13	23	19	26	24
Rich	RCH	2008	2,703	2013	5	967-1943	38	8	31	20	22	11
Star	STA	2001	6,817	2015	14	1616-2456	0	10	7	4	2	13
				Total	-	-	121	93	112	86	99	119
				Means/Range	9	1377-2114	15	12	14	11	12	15

Table 1.2: Fire severity classification used for ground-truthing remotely-sensed severity estimates (from Welch et al. (2016)).

Fire Severity Class **(designation)**	**Description**	**% Basal Area Mortality**
0; unburned	Unburned	0
1; low	Lightly burned, no significant overstory mortality, patchy spatial burn pattern, groups of surviving shrubs/saplings	0-25
2; low-moderate	Lightly burned, isolated overstory mortality, most saplings/shrubs dead	25-50
3; high-moderate	Moderately burned, mixed overstory mortality, understory mortality burned to the ground	50-75
4; high	High intensity, significant proportions (75-100%) of overstory killed, dead needles remaining on trees one year later	75-90
5; high	High intensity burn, total/near total mortality of overstory, most needles consumed in fire	>90

Table 1.3: Linear mixed-effects models for predicting species richness, antilog Shannon diversity index, Simpson diversity index, and Pielou’s evenness.

<table>
<tr><th colspan="2">Dependent variable</th><th>Fixed effects</th><th>Coefficient</th><th>SE</th><th>t value</th><th>p-value</th></tr>
<tr><td colspan="2" rowspan="7">Species Richness</td><td>(Intercept)</td><td>0.959</td><td>0.110</td><td>8.706</td><td><0.001</td></tr>
<tr><td>Fire severity^2</td><td>-0.007</td><td>0.002</td><td>-3.272</td><td>0.001</td></tr>
<tr><td>Elevation</td><td>-0.402</td><td>0.187</td><td>-3.606</td><td>0.032</td></tr>
<tr><td>Litter depth</td><td>-0.181</td><td>0.054</td><td>-3.355</td><td><0.001</td></tr>
<tr><td>Litter cover</td><td>0.044</td><td>0.023</td><td>1.896</td><td>0.058</td></tr>
<tr><td>Mean annual precipitation</td><td>-0.888</td><td>0.147</td><td>-6.035</td><td><0.001</td></tr>
<tr><td>Elevation* precipitation</td><td>0.869</td><td>0.257</td><td>3.386</td><td><0.001</td></tr>
<tr><td>R^2</td><td>AIC</td><td>Random effects</td><td>Variance</td><td colspan="3" rowspan="2"></td></tr>
<tr><td>0.61</td><td>-570.44</td><td>Fire ID (Intercept)</td><td>0.009</td></tr>
<tr><td colspan="2" rowspan="6">Antilog Shannon Diversity Index</td><td>(Intercept)</td><td>0.933</td><td>0.086</td><td>10.846</td><td><0.001</td></tr>
<tr><td>Fire severity</td><td>-0.015</td><td>0.005</td><td>-3.036</td><td>0.003</td></tr>
<tr><td>Time since last fire</td><td>-0.118</td><td>0.043</td><td>-2.765</td><td>0.006</td></tr>
<tr><td>Overstory cover</td><td>0.080</td><td>0.027</td><td>2.926</td><td>0.004</td></tr>
<tr><td>Litter cover</td><td>-0.045</td><td>0.023</td><td>-1.936</td><td>0.053</td></tr>
<tr><td>Mean annual precipitation</td><td>-0.283</td><td>0.087</td><td>-3.253</td><td>0.001</td></tr>
<tr><td>R^2</td><td>AIC</td><td>Random effects</td><td>Variance</td><td colspan="3" rowspan="2"></td></tr>
<tr><td>0.50</td><td>-574.68</td><td>Fire ID (Intercept)</td><td>0.013</td></tr>
<tr><td colspan="2" rowspan="6">Simpson’s Diversity Index</td><td>(Intercept)</td><td>-0.753</td><td>0.035</td><td>-21.49</td><td><0.001</td></tr>
<tr><td>Fire severity</td><td>-0.006</td><td>0.002</td><td>-2.741</td><td>0.006</td></tr>
<tr><td>Time since last fire</td><td>-0.049</td><td>0.019</td><td>-2.557</td><td>0.003</td></tr>
<tr><td>Overstory cover</td><td>0.037</td><td>0.012</td><td>3.018</td><td>0.003</td></tr>
<tr><td>Litter cover</td><td>-0.024</td><td>0.010</td><td>-2.317</td><td>0.021</td></tr>
<tr><td>Mean annual precipitation</td><td>-0.087</td><td>0.037</td><td>-2.315</td><td>0.023</td></tr>
<tr><td>R^2</td><td>AIC</td><td>Random effects</td><td>Variance</td><td colspan="3" rowspan="2"></td></tr>
<tr><td>0.40</td><td>-1423.314</td><td>Fire ID (Intercept)</td><td>0.002</td></tr>
<tr><td colspan="2" rowspan="4">Pielou’s Evenness</td><td>(Intercept)</td><td>0.465</td><td>0.040</td><td>11.551</td><td><0.001</td></tr>
<tr><td>Fire severity</td><td>-0.019</td><td>0.009</td><td>-2.115</td><td>0.032</td></tr>
<tr><td>Overstory cover</td><td>0.122</td><td>0.044</td><td>2.799</td><td>0.005</td></tr>
<tr><td>Litter cover</td><td>-0.103</td><td>0.037</td><td>-2.751</td><td>0.006</td></tr>
<tr><td>R^2</td><td>AIC</td><td>Random effects</td><td>Variance</td><td colspan="3" rowspan="2"></td></tr>
<tr><td>0.28</td><td>-567.22</td><td>Fire ID (Intercept)</td><td>0.004</td></tr>
</table>

Figure 1.2: Species richness of all fires combined across fire severity classes. Means with different letters are significantly different from each other (Tukey test, p<0.05).

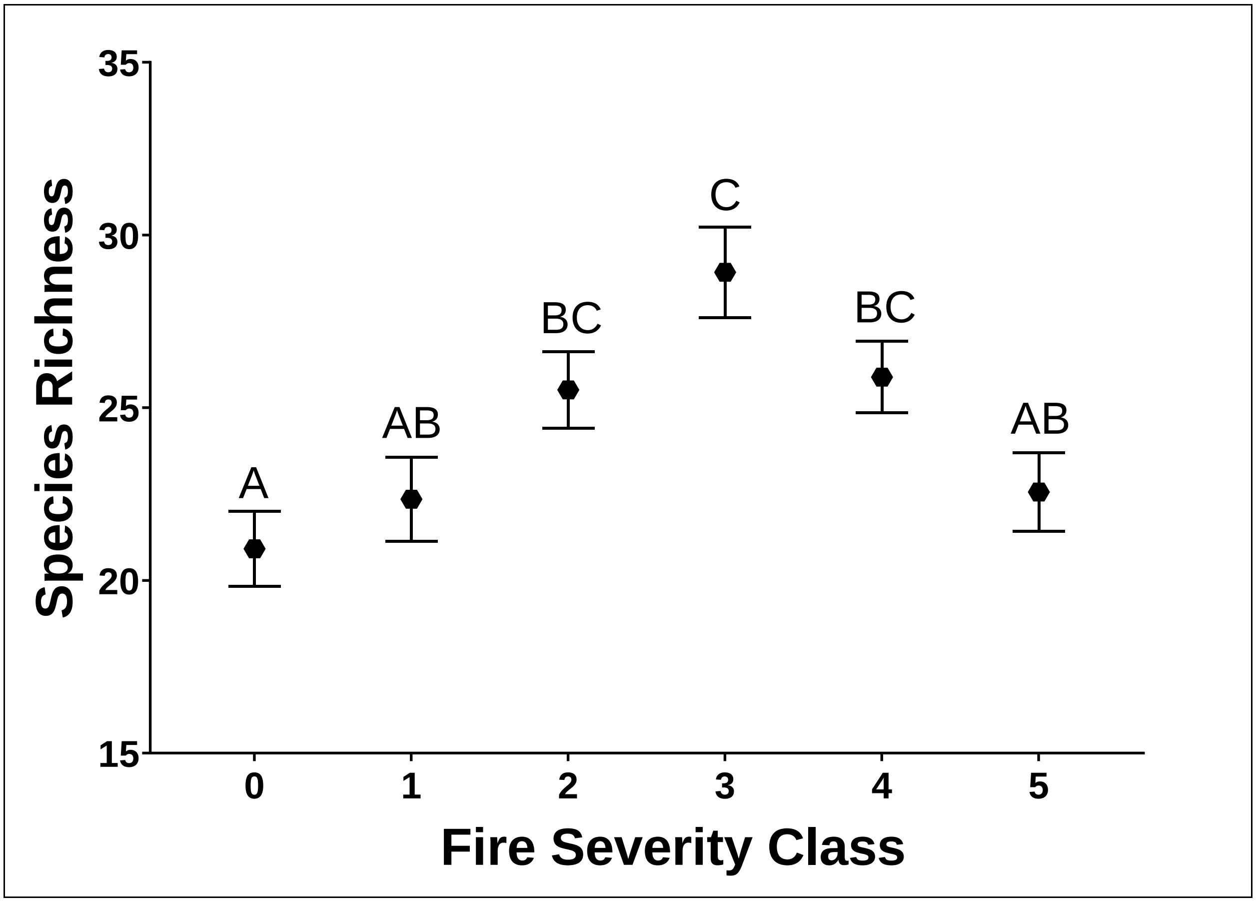


Figure 1.3: Plant species richness versus fire severity relationships for the eight fires we studied.

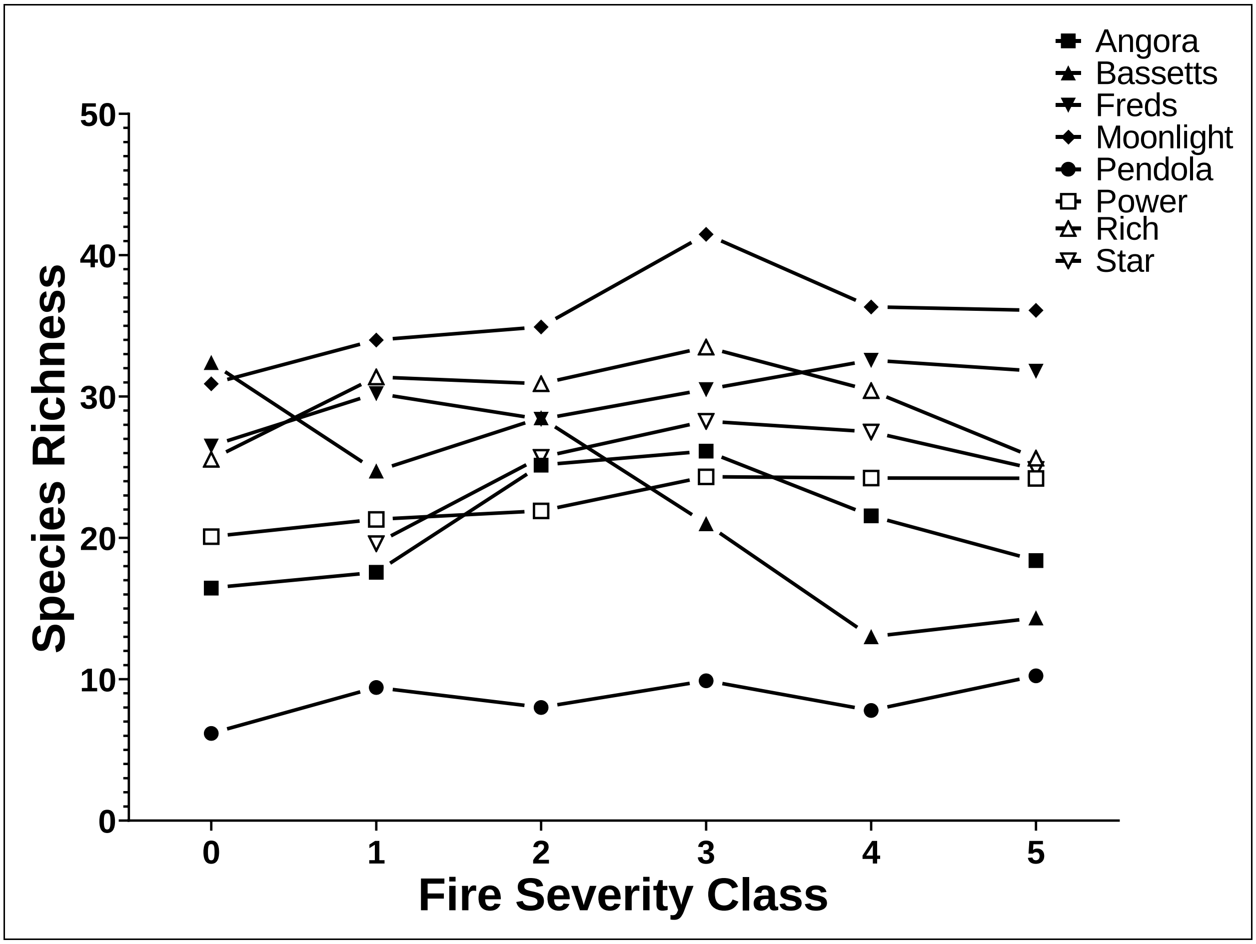


Figure 1.4: A: Simpson diversity index of all fires combined across fire severity classes (overall ANOVA $F_{5,623}$=7.914, p<0.0001). B: Pielou’s evenness of all fires combined across fire severity classes (overall ANOVA $F_{5,623}$=12.75, p<0.0001). Means with different letters are significantly different from each other (Tukey test, p<0.05).

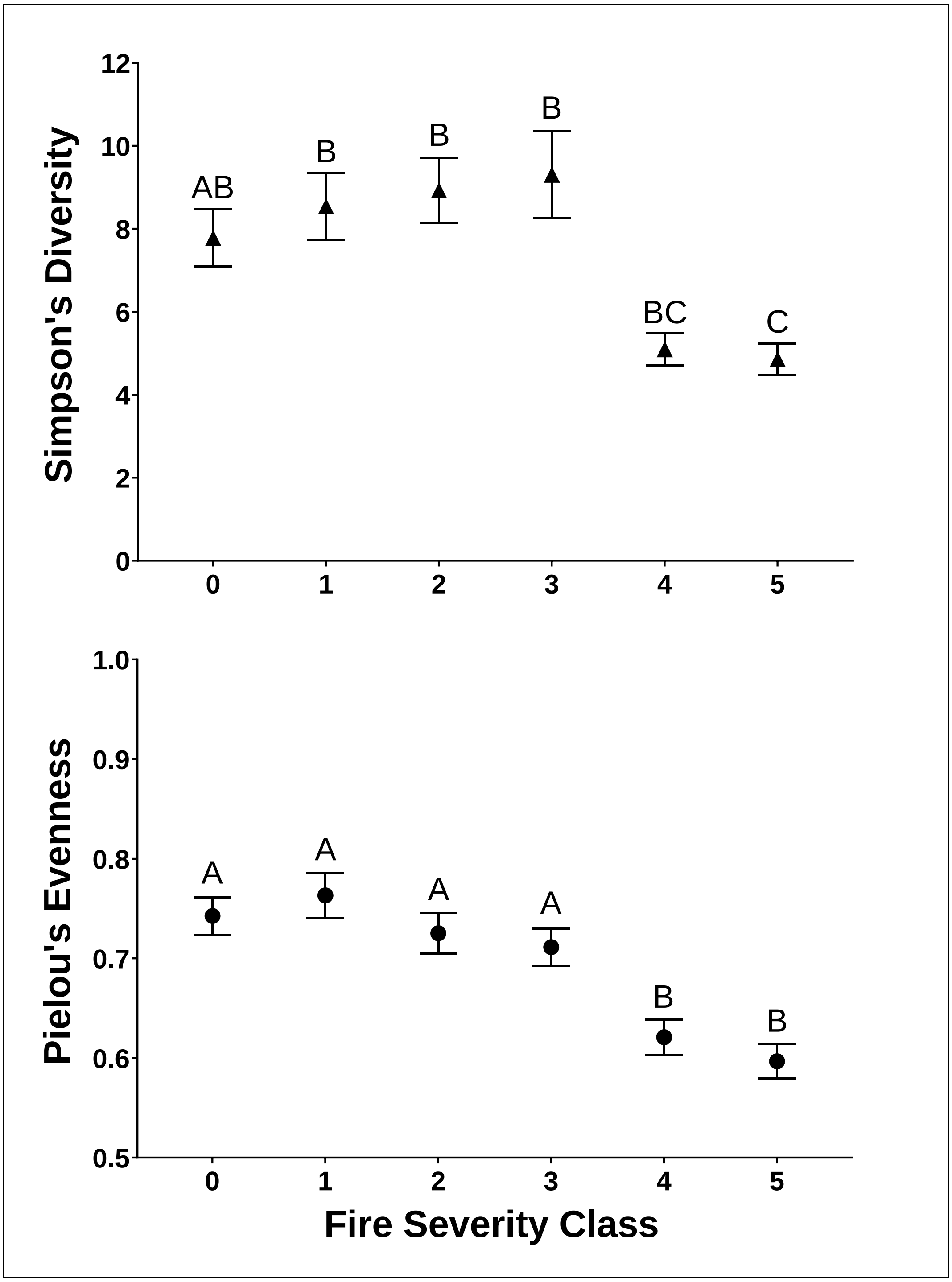


Figure 1.5: Gamma diversity as rarefied richness for all fires combined across fire severity classes (overall ANOVA $F_{5,33}$=27.06, $p<0.0001$). Means with different letters are significantly different from each other (Tukey test, $p<0.05$).

Figure 1.6: Dissimilarity for all fires combined and blocked into Unburned (Fire Severity Class 0); Low (Fire Severity Class 1); Moderate (Fire Severity Class 2 & 3) and High (Fire Severity Class 4 & 5).

Literature Cited

Baldwin, B. G., D. J. Keil, S. Markos, B. D. Mishler, R. Patterson, T. J. Rosatti, and D. H. Wilken. 2018. The Digital Jepson Manual: Vascular Plants of California, Thoroughly Revised and Expanded. http://ucjeps.berkeley.edu/eflora/.

Barbour, M. G., T. Keeler-Wolf, and A. A. Schoenherr. 2007. Terrestrial Vegetation of California. University of California Press, Berkeley, California, USA.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1:1–23.

Belote, R. T. 2015. Contemporary patterns of burn severity heterogeneity from fires in the Northwestern US.

Bohlman, G. N., M. North, and H. D. Safford. 2016. Shrub removal in reforested post-fire areas increases native plant species richness. Forest Ecology and Management 374:195–210.

Bond, W., and B. Van Wilgen. 1996. Fire and Plants. Chapman & Hall, London, UK.

Booth, W. E. 1950. Flora of Montana. The Research Foundation at Montana State College, Bozeman, Montana, USA.

Bowman, D. M., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D’antonio, R. DeFries, F. H. Johnston, J. E. Keeley, and M. A. Krawchuk. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

Bowman, D. M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D’Antonio, R. S. DeFries, J. C. Doyle, and S. P. Harrison. 2009. Fire in the Earth system. Science 324:481–484.

Burkle, L. A., J. A. Myers, and R. T. Belote. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6:1–14.

Certini, G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143:1–10.

Collins, B. M., and S. L. Stephens. 2010. Stand-replacing patches within a “mixed severity” fire regime: quantitative characterization using recent fires in a long-established natural fire area. Landscape Ecology 25:927–939.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Cowling, R. M., P. W. Rundel, B. B. Lamont, M. K. Arroyo, and M. Arianoutsou. 1996. Plant diversity in Mediterranean-climate regions. Trends in Ecology & Evolution 11:362–366.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. Pages 307–324 *in* A. Pickett and P. S. White, editors. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida, USA.

DeSiervo, M. H., E. S. Jules, and H. D. Safford. 2015. Disturbance response across a productivity gradient: postfire vegetation in serpentine and nonserpentine forests. Ecosphere 6:1–19.

Dettinger, M., H. Alpert, J. J. Battles, J. Kusel, H. Safford, D. Fougeres, C. Knight, L. Miller, and S. Sawyer. 2018. Sierra Nevada summary report. California’s Fourth Climate Change Assessment. California Energy Commission/Natural Resources Agency.

Enright, N. J., J. B. Fontaine, B. B. Lamont, B. P. Miller, and V. C. Westcott. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. Journal of Ecology 102:1572–1581.

Fites-Kaufman, J. A., P. Rundel, N. Stephenson, and D. A. Weixelman. 2007. Montane and Subalpine Vegetation of the Sierra Nevada and Cascade ranges. Pages 456–501 *in* M. Barbour, T. Keeler-Wolf, and A. A. Schoenherr, editors. Terrestrial Vegetation of California. University of California Press, Berkeley, California, USA.

Flint, A. L., and L. E. Flint. 2007. Application of the basin characterization model to estimate in-place recharge and runoff potential in the Basin and Range carbonate-rock aquifer system, White Pine County, Nevada, and adjacent areas in Nevada and Utah. U.S. Geological Survey Scientific Investigations Report 2007-5099.

Flint, L., and A. Flint. 2014. California basin characterization model: a dataset of historical and future hydrologic response to climate change. https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html.

Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences 101:7651–7656.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57:845–858.

Grime, J. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist:1169–1194.

Grime, J. P. 2006. Plant Strategies, Vegetation Processes, and Ecosystem Properties. 2nd edition. John Wiley & Sons, Chichester, UK.

Grubb, P. J. 1977. The maintenance of species richness in plant communities - the importance of the regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52:107–145.

Hall, A. R., A. D. Miller, H. C. Leggett, S. H. Roxburgh, A. Buckling, and K. Shea. 2012. Diversity–disturbance relationships: frequency and intensity interact. Biology Letters 8:768–771.

Halpern, C. B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70:704–720.

Halpern, C. B., and T. A. Spies. 1995. Plant Species Diversity in Natural and Managed Forests of the Pacific Northwest. Ecological Applications 5:913–934.

Hanberry, B. B., R. F. Noss, H. D. Safford, S. K. Allison, and D. C. Dey. 2015. Restoration is preparation for the future. Journal of Forestry 113:425–429.

Harner, R. F., and K. T. Harper. 1976. The role of area, heterogeneity, and favorability in plant species diversity of pinyon-juniper ecosystems. Ecology 57:1254–1263.

Hessburg, P. F., T. A. Spies, D. A. Perry, C. N. Skinner, A. H. Taylor, P. M. Brown, S. L. Stephens, A. J. Larson, D. J. Churchill, and N. A. Povak. 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. Forest Ecology and Management 366:221–250.

Huston, M. A. 1994. Biological Diversity: the Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18:116–126.

Keeley, J., and H. D. Safford. 2016. Fire as an Ecosystem Process. Pages 27–45 *in* H. A. Mooney and E. S. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Kudo, G., T. Y. Ida, and T. Tani. 2008. Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89:321–331.

Kuhn, T. J., H. D. Safford, B. E. Jones, and K. W. Tate. 2011. Aspen (Populus tremuloides) stands and their contribution to plant diversity in a semiarid coniferous landscape. Plant Ecology 212:1451.

Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings. Biological sciences / The Royal Society 270:775–81.

Lindner, M., M. Maroschek, S. Netherer, A. Kremer, A. Barbati, J. Garcia-Gonzalo, R. Seidl, S. Delzon, P. Corona, and M. Kolström. 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259:698–709.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical Ecology: a Primer on Methods and Computing. John Wiley & Sons, Chichester, UK.

Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4:1–28.

van Mantgem, P. J., J. C. B. Nesmith, M. Keifer, E. E. Knapp, A. Flint, and L. Flint. 2013. Climatic stress increases forest fire severity across the western United States. Ecology Letters 16:1151–1156.

Matthews, J. A., J. L. Hill, S. Winkler, G. Owen, and A. E. Vater. 2018. Autosuccession in alpine vegetation: testing the concept on an altitudinal bioclimatic gradient, Jotunheimen, southern Norway. Catena 170:169–182.

McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. Journal of Vegetation Science 18:751–754.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.

McCune, B., and M. J. Mefford. 1999. Multivariate Analysis of Ecological Data. MjM Software Design, Cleveland, Ohio, USA.

McKenzie, D., Z. Gedalof, D. L. Peterson, and P. Mote. 2004. Climatic change, wildfire, and conservation. Conservation Biology 18:890–902.

McWethy, D., P. Higuera, C. Whitlock, T. Veblen, D. Bowman, G. Cary, S. Haberle, R. E. Keane, B. Maxwell, and M. McGlone. 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. Global Ecology and Biogeography 22:900–912.

Meurant, G. 2012. The ecology of natural disturbance and patch dynamics. Academic Press, San Diego, California, USA.

Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113:645–656.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. Fire Ecology 8:41–57.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Miller, J. E., H. T. Root, and H. D. Safford. 2018. Altered fire regimes cause long-term lichen diversity losses. Global Change Biology 24:4909–4918.

Motulsky, H., P. Spannard, and R. Neubig. 2021. GraphPad Prism (version 9). GraphPad Software Incorporated, San Diego, California, USA.

North, M. 2012. Managing Sierra Nevada Forests. PSW-GTR-237. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

North, M., B. M. Collins, H. Safford, and N. L. Stephenson. 2016. Montane Forests. Pages 553–577 *in* H. Mooney and E. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. vegan: Community Ecology Package.

Pausas, J. G., and E. Ribeiro. 2017. Fire and plant diversity at the global scale. Global Ecology and Biogeography 26:889–897.

Peet, R. K. 1978. Forest vegetation of the Colorado Front Range: Patterns of species diversity. Vegetatio 37:65–78.

Pickett, S., J. Kolasa, J. Armesto, and S. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136.

Pielou, E. C. 1984. The Interpretation of Ecological Data: a Primer on Classification and Ordination. John Wiley & Sons, Chichester, UK.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Restaino, C., and H. Safford. 2018. Fire and Climate Change. Pages 493–505 *in* J. W. van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, and K. E. Shaffer, editors. Fire in California’s Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Safford, H. D., and C. R. Mallek. 2011. Disturbance and diversity in low-productivity ecosystems. Pages 249–472 *in* S. Harrison and N. Rajakaruna, editors. Serpentine: the Evolution and Ecology of a Model System. University of California Press, Berkeley, California, USA.

Safford, H. D., M. Rejmánek, and E. Hadač. 2001. Species pools and the “hump-back” model of plant species diversity: an empirical analysis at a relevant spatial scale. Oikos 95:282–290.

Safford, H. D., and J. T. Stevens. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. PSW-GTR-256. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Safford, H. D., and K. P. Van de Water. 2014. Using Fire Return Interval Departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. PSW-RP-266. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Schmidt, K. M., J. P. Menakis, and Hardy. (n.d.). Development of coarse-scale spatial data for wildland fire and fuel management.

Schoennagel, T., D. Waller, M. Turner, and W. Romme. 2004. The effect of fire interval on post-fire understory communities in Yellowstone National Park. Journal of Vegetation Science 15:797–806.

Schwilk, D. W., J. E. Keeley, E. E. Knapp, J. McIver, J. D. Bailey, C. J. Fettig, C. E. Fiedler, R. J. Harrod, J. J. Moghaddas, K. W. Outcalt, C. N. Skinner, S. L. Stephens, T. A. Waldrop, D. A. Yaussy, and A. Youngblood. 2009. The national Fire and Fire Surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecological Applications 19:285–304.

Shenoy, A., K. Kielland, and J. F. Johnstone. 2013. Effects of fire severity on plant nutrient uptake reinforce alternate pathways of succession in boreal forests. Plant Ecology 214:587–596.

Shive, K., H. Preisler, K. Welch, H. Safford, R. J. Butz, K. O’Hara, and S. L. Stephens. 2018. Scaling stand-scale measurements to landscape-scale predictions of forest regeneration after disturbance: the importance of spatial pattern. Ecological Applications 28:1626–1639.

Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. The changing landscape of wildfire: burn pattern trends and implications for California’s yellow pine and mixed conifer forests. Landscape Ecology 33:1159–1176.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:1–23.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stevens, J. T., H. D. Safford, S. Harrison, and A. M. Latimer. 2015. Forest disturbance accelerates thermophilization of understory plant communities. Journal of Ecology 103:1253–1263.

Stevens, J. T., H. D. Safford, and A. M. Latimer. 2014. Wildfire-contingent effects of fuel treatments can promote ecological resilience in seasonally dry conifer forests. Canadian Journal of Forest Research 44:843–854.

Sugihara, N. G., J. W. Van Wagtendonk, and J. Fites-Kaufman. 2006. Fire as an Ecological Process. Pages 58–74 *in* N. G. Sugihara, J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's Ecosystems. University of California Press, Berkeley, California, USA.

Syphard, A. D., V. C. Radeloff, J. E. Keeley, T. J. Hawbaker, M. K. Clayton, S. I. Stewart, and R. B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications 17:1388–1402.

Taylor, A. H., and A. E. Scholl. 2012. Climatic and human influences on fire regimes in mixed conifer forests in Yosemite National Park, USA. Forest Ecology and Management 267:144–156.

Tepley, A. J., J. R. Thompson, H. E. Epstein, and K. J. Anderson-Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Global Change Biology 23:4117–4132.

Turner, M. G., W. H. Romme, and R. H. Gardner. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. International Journal of Wildland Fire 9:21–36.

USDA Forest Service Region 5 - Common Stand Exam Field Guide. 2012. . USDA Forest Service, http://www.fs.fed.us/nrm/fsveg/index.shtml.

Van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. Fire Ecology 7:26–58.

van Wagtendonk, J. W. 2006. Fire as a Physical Process. Pages 38–57 *in* N. G. Sugihara, J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's Ecosystems. University of California Press, Berkeley, California, USA.

van Wagtendonk, J. W., J. Fites-Kaufman, H. D. Safford, M. North, and B. M. Collins. 2018. Sierra Nevada Bioregion. Pages 249–278 Fire in California's Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Wang, G. G., and K. J. Kemball. 2005. Effects of fire severity on early development of understory vegetation. Canadian Journal of Forest Research 35:254–262.

Wayman, R. B., and M. North. 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. Forest Ecology and Management 239:32–44.

Webster, K. M., and C. B. Halpern. 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. Ecosphere 1:1–27.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7:1–29.

Wells, C. G., R. E. Campbell, L. F. DeBano, C. E. Lewis, R. L. Fredriksen, E. C. Franklin, R. C. Froelich, and P. H. Dunn. 1979. Effects of fire on soil: a state-of-knowledge review. GTR-WO-7. USDA Forest Service, Denver, Colorado, USA.

Werner, C. M., D. J. N. Young, H. D. Safford, and T. P. Young. 2019. Decreased snowpack and warmer temperatures reduce the negative effects of interspecific neighbors on regenerating conifers. Oecologia in press.

White, A. M., P. N. Manley, G. L. Tarbill, T. W. Richardson, R. E. Russell, H. D. Safford, and S. Z. Dobrowski. 2016. Avian community responses to post-fire forest structure: implications for fire management in mixed conifer forests. Animal Conservation 19:256–264.

Winford, E., J. Stevens, and H. Safford. 2015. Effects of fuel treatments on California mixed-conifer forests. California Agriculture 69:150–156.

CHAPTER 2

High postfire shrub cover negatively impacts plant diversity in yellow pine and mixed conifer forests of the North American Mediterranean climate zone

Background

After an ecological disturbance, community recovery and reassembly are driven by a suite of interacting biotic and abiotic forces and the severity of the perturbation (Noble and Slatyer 1977, Cornwell and Ackerly 2009, Prach and Walker 2020). As an example, wildfire occurs in many ecosystems around the globe and alters local abiotic and biotic features through modifications to ecosystem structure, nutrient availability, and species populations, among other things (Bond and Van Wilgen 1996, Bowman et al. 2009, Turner 2010, Gongalsky et al. 2020). Like other ecological disturbances, fire has been modified by human activities and the changing climate (Dale et al. 2001, Collins et al. 2011, Crockett and Westerling 2018). A classic example of human modification of the fire regime is the case of temperate dry conifer forests in the western United States. Here, long-term human suppression of fires (Stephens and Ruth 2005) is having major effects on the ecology of forest ecosystems that once supported highly frequent, low severity fires, including increases in stand density and fuel accumulation, changing plant communities, and altered recovery trajectories after disturbance (Agee 1993, van Wagtendonk et al. 2018, Lydersen et al. 2019, Richter et al. 2019). These changes in fire regime include a dramatic shift toward much more infrequent and consequently – largely due to fuels accumulation - much more severe fires (Miller et al. 2009b, Steel et al. 2015). This trend is changing fire-driven selective pressures in temperate, seasonally dry conifer forests from ones favoring fire resisting species adapted to low severity disturbance to ones favoring species that are resilient to high severity disturbance (Mallek et al. 2013, Keeley and Safford 2016, Miller and Safford 2020, Rodman et al. 2020).

Species of the latter group include many of the shrub species found in the "montane chaparral" vegetation of the North American Mediterranean climate zone (NAMCZ), which is comprised of most of California and portions of neighboring Oregon, Nevada, and Baja California, Mexico. In many NAMCZ ecosystems, montane chaparral regeneration after fire is enhanced by interactions between reduction of competition and tree shading, increased nutrient or water availability, and fire stimulation of regeneration, including by re-sprouting or fire-induced germination response (Malanson and O'Leary 1982, Keeley 1986, Seligman and Henkin 2000, Crotteau et al. 2013). After high severity burning, montane chaparral can come to dominate the postfire landscape, where it may strongly influence community reassembly and recovery (Show and Kotok 1924, Kauffman and Martin 1991). In ecosystems like yellow pine (*Pinus ponderosa*, *P. jeffreyi*) or mixed conifer (collectively "YPMC") forests, fast-growing montane chaparral shrubs can play both facilitative and competitive roles, with the direction and strength of their ecological influences varying depending on characteristics of the site itself. Where the system is particularly stressful due to limited resources, shrubs may play the role of facilitators and contribute to the total soil nitrogen pool or reduce soil evaporation (St John and Rundel 1976, Blaser et al. 2013). Where conditions are less stressful and resources are in greater abundance, they may act in a more competitive role (Harvey et al. 1987, Messina et al. 1990, Zhang et al. 2006, Greene et al. 2007).

Research on the influence of montane chaparral after fire in YPMC forests has historically been dominated by considerations of conifer plantation growth and survival in postfire shrubfields (e.g. Oliver 1984, 1990, McDonald and Abbott 1997, Zhang et al. 2013). In recent years, montane chaparral influences on conifer regeneration in unplanted YPMC forests have begun to receive more attention (Welch et al. 2016, Shive et al. 2018, Tubbesing et al. 2020). Other recent studies have investigated montane chaparral connections to postfire fuel dynamics and subsequent high severity reburns (Coppoletta et al. 2016, Lydersen et al. 2019), and the effects of climate warming and snow cover on shrub-conifer seedling interactions (Werner et al. 2019). The biodiversity impacts of forest transitions to montane chaparral have received much less attention, and almost all studies of plant diversity in postfire shrubfields have focused on the effects of postfire management activities in and near planted conifer stands (e.g. DiTomaso et al. 1997, McGinnis et al. 2010, Kayes et al. 2011, Bohlman et al. 2016, Zhang et al. 2016).

Previous research has thus left a major information gap: what is the relationship between postfire shrub response and the overall diversity of the plant community in unmanaged and unplanted sites? Here we report on the results of a study of understory plant community response to postfire shrub cover in seven wildfire sites in YPMC forest in the Sierra Nevada of California. None of our sites were managed or planted after fire. We hypothesized that interspecific competition by shrubs after severe fire drives declines in understory plant richness and diversity with increasing shrub cover. In keeping with the established relationship between shrub cover and high severity fire, we therefore expected to find the lowest richness and diversity in high severity burn sites.

Methodology

Study site and plot locations

Our study sampled sites across the fire severity spectrum in seven areas burned by wildfire in YPMC forests of the Sierra Nevada, California, which is in the northeastern portion of the NAMCZ. These forests supported high frequency, low to moderate severity fire regimes before Euroamerican settlement in the mid-19th century, but under fire suppression policies the fire regime today includes less frequent but much more severe fire when it occurs (Mallek et al. 2013, Steel et al. 2015, Safford and Stevens 2017). In California, YPMC forest types are widespread and dominate the Sierra Nevada landscape between 500m and 2000m elevation. Common tree species are the yellow pines (ponderosa pine [*Pinus ponderosa* Lawson & C. Lawson] and Jeffrey pine [*P. jeffreyi* Balf.]); white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.); sugar pine (*P. lambertiana* Douglas); incense cedar (*Calocedrus decurrens* (Torr.) Florin); Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*); and several hardwood species, most notably black oak (*Quercus kelloggii* Newberry) and canyon live oak *(Quercus chrysolepis* Liebm.) (Safford and Stevens 2017). Generally, the climate is Mediterranean with warm, dry summers and cold, wet winters. Most YPMC forest falls within the Cwb climate zone of Köppen with average temperatures below 22°C, at least 3x as much rain in the wettest months as in the driest months; the water content proportion of rain to snow is >1:1 in most YPMC forests in the NAMCZ (Safford and Van de Water 2014).

All fires were sampled at least 5 years after fire and were between 1000m and 2300m in elevation. Within each fire we selected potential plot locations through a stratified random process based on the US Forest Service classification of fire-caused basal area mortality:

https://www.fs.usda.gov/detailfull/r5/landmanagement/resourcemanagement/?cid=STELPRDB5362659. These classifications are based on satellite-collected RdNBR (relative differenced Normalized Burn Ratio). They are calibrated to extensive field data and use objective thresholds for fire severity class definition (Miller and Thode 2007, Miller et al. 2009a). We used GIS software to overlay a 400 x 400-meter grid across each fire area and potential plot centers were located at grid intersections. The distribution of plots also follows Richter et al., (2019); within each fire severity class in the imagery at least 10 sites were sampled in the field in each fire, but final sample sizes varied due to accessibility issues, and mismatches between image- and field-based severity assessments and vegetation typing. To characterize fire severity in the field, we assessed scorch heights, torch heights and vegetation mortality and binned plots into six fire severity classes (Table 2.1) following the inverse of the National Park Service scale of severity (Service 2003) also used by (Welch et al. 2016).

Sampling protocol

We conducted our vegetation sampling in circular, 405 m^2 (1/10 acre) plots, using a variation of the Forest Service Common Stand Exam protocol (*USDA Forest Service Region 5 - Common Stand Exam Field Guide* 2012). We sampled the total of 424 plots and recorded a total of 645 vascular plant species. We made visual estimates of cover percentage and recorded modal height for all lifeforms (trees, shrubs, forbs and graminoids) in each plot. All plant species were identified in the field or lab using Baldwin et al. (2012). We gave any species with less than 1% cover a “trace” designation. We used the 10-year averaged Normalized Difference Vegetation Index (NDVI) as our index of pre-fire site productivity. NDVI is a remotely-sensed vegetation index derived from Landsat imagery that has been used in many other wildfire studies (Burgan et al. 1996, Illera et al. 1996, Chuvieco et al. 2004, Escuin et al. 2008); we used code developed in the Google Earth Engine (Gorelick et al. 2017) to extract maximum reflectance data for our plots the year before the fire occurred, and we then calculated NDVI in R by using the intensities of the red and infrared range (R Development Core Team 2013).

Cover and Diversity Analyses

Normal distribution and heteroscedasticity were tested for all variables, and where necessary square root transformation was used to meet statistical assumptions. Mean tree and shrub lifeform cover across fire severity class were examined with a one-way ANOVA GraphPad Prism version 9 (Motulsky et al. 2021). Bonferroni multiple comparison tests were used to compare mean tree to shrub cover in each fire severity class.

We quantified understory plant diversity in our plots using three metrics (species richness, Shannon's diversity, and Pielou's evenness). Species richness was the total number of species per 405 m^2 plot. Shannon's diversity index (H', focuses on rare species, cover as abundance) and Pielou's evenness index (J, cover as abundance) were based on formulas from Pielou (1984) and Ludwig and Reynolds (1988). The total understory data were also segregated into the following lifeform and life history categories: native species, exotic species, woody species, herbaceous species, nitrogen-fixing species, perennial and annual species. Per plot values for richness, Shannon's diversity and Pielou's evenness for each lifeform and life history category were likewise calculated as above.

Linear regression analyses were performed in GraphPad Prism version 9 (Motulsky et al. 2021) to examine the relationship between shrub cover and total understory richness, Shannon's diversity and Pielou's evenness. To examine the influence of a suite of environmental variables on our segregated lifeform/life history categories, we used multiple linear regressions models in

GraphPad Prism version 9 (Motulsky et al. 2021). The suite of environmental variables included fire severity, shrub cover, rock (non-growing) cover (assessed in the field) as well as those calculated later: NDVI productivity (see methodology above), and climatic water deficit (extracted using the Basin Characterization Model (Flint and Flint 2014)). After running the full model, non-significant predictors were eliminated and all predictors whose variance inflation factors were above 4 were eliminated and the models re-run.

Structural Equation Modeling

In order to test our hypothesized relationships about the drivers of understory plant richness and diversity, we constructed a structural equation model (SEM) (Grace 2006). SEM's analytic approach has proven effective at elucidating complex cause and effect relationships in natural systems, and its capacity to evaluate both direct and indirect relationships makes it especially suitable for our study (Miller et al. 2018). In keeping with Grace's (2006) recommended SEM approach, we first created a "meta-model" by considering a priori knowledge to identify a suite of potential mechanisms that may be driving biotic patterns in our system. Total overstory cover, shrub cover, NDVI, species richness and Shannon's diversity index were all treated as endogenous variables while fire severity was the sole exogenous variable.

We used the piecewiseSEM package (Lefcheck 2016) in R (R Development Core Team 2013) that allows for multiple linear mixed models to be combined into structural equation models. We ran both linear and quadratic models for each path but in all cases the linear relationships were stronger so we do not report the quadratic results. Square-root transformations were applied to total overstory cover and shrub cover to better meet model assumptions, and fire severity (using the inverse NPS model from Welch et al. 2016) was treated as a continuous variable in keeping with the recommendations of Grace (2006).

Results

Lifeform cover by severity class

Tree cover declined (R^2=0.37, $p<0.0001$) with increasing fire severity while shrub cover increased (R^2=0.19, $p<0.0001$) (Figure 2.2). The differences between cover means of these two lifeforms were statistically significant ($p<0.0001$) across the severity gradient except for moderate severity (class 3).

Diversity indices by shrub cover

Understory plant species richness declined marginally with increasing shrub cover, but amount of variation explained was very low (not shown; R^2=0.0042, p=0.0815). We found stronger negative relationships among shrub cover and diversity indices that involved community evenness: Shannon's diversity index declined significantly with increasing shrub cover (Figure 2.3a; R^2=0.2111, $p<0.0001$) as did community evenness (Pielou's index) (Figure 2.3b; R^2=0.3067, $p<0.0001$).

Life form & Life history by environmental variables

We examined how the richness of various lifeforms and life history categories responded to a suite of environmental factors including shrub cover using multiple linear regressions. All regression models for richness were highly significant (Table 2.2). Overall, all richness regressions included at least three predictors; most included 4 or 5 predictors and one lifeform model included the full suite of environmental variables as significant predictors. Native species richness was the strongest regression model according to R^2. Richness of nitrogen-fixing and exotic species were the weakest models, but all models explained between 19.4% and 31% of the variance (Table 2.2). Where it was included in the final model (exotic, woody, herbaceous, and annual species), productivity (NDVI max) was by far the most important independent variable. Productivity was positively related to woody plant richness, but negatively related to exotic, herbaceous, and annual plants (which all greatly overlap in their species set). Fire severity was a component of five of the seven models for richness, where it was always the top or second-ranked predictor (but it was not statistically significant in the native plants model); in the models the effect of fire severity on richness was always positive. CWD, shrub cover, and rock cover were the only predictor variables in every model. Shrub cover was negatively related to richness of all groups except woody plants and N-fixing plants (some of which are shrubs), and CWD was negatively related to richness of all groups except woody plants (Table 2.2). Rock cover was the most important independent variable in the perennial plants model, but although it fell among the top two or three predictors in some of the other models it tended not to be a major player. Higher elevations supported higher richness of all groups but exotics (where elevation was not a component of the final model), but the effect size of elevation was minimal.

Multiple regression models for Shannon's diversity ("SD"; Table 2.3) were generally defined by fewer predictors than species richness models, and model performance was more variable as well; model R^2 ranged from 0.067 to 0.343. Although all the models were highly significant, the variance explained by the models for exotic species, N-fixers, and annual plants was low. CWD was a component of all of our SD models, as with richness it was positively related to SD for all groups but woody plants. Shrub cover, rock cover, and elevation were in five of the final models. Shrub cover was a negative predictor of SD in all models (Table 2.3). Rock cover was positively related to SD for four models but was a negative predictor of SD for exotic plants; elevation was a weak positive predictor in all cases. Fire severity was in four models and was the most important variable in all four. Productivity, which was a very strong predictor of richness in four of the seven groups, was not in any of the final models for SD (Table 2.3).

Our multiple regression models for Pielou's evenness ("PE"; Table 2.4) were even more variable in variance explained than SD. Our overall strongest model was the model for PE of native plants ($R^2 = 0.370$), while our weakest model overall was for PE of annual plants ($R^2 = 0.032$). Shrub cover was in four of the seven models, always with a negative coefficient, and rock cover, elevation, CWD, and fire severity appeared in three models; fire severity was always the most important predictor variable in the models it appeared in. CWD was the only independent variable in the annual plants model, and the only significant predictor in the exotic plants model.

Structural Equation Model

We developed and refined two SEMs: one for understory plant species richness (model p-value = 0.27) and the other for Shannon's diversity index (model p-value = 0.96). In the richness model, shrub cover and total overstory cover were significant negative direct predictors while NDVI was a significant positive direct predictor; fire severity class exerted an overall negative indirect effect on richness via shrub and total overstory cover (Figure 2.4). The Shannon's understory plant diversity model showed a similar structure, although productivity was missing in this model. As above, fire severity had a significant indirect effect on understory diversity via shrub and total overstory cover (Figure 2.5). Both of these models were consistent with our hypothesized relationships among shrub cover, total overstory cover, fire severity and the understory community along with NDVI (our productivity index) in the Shannon's diversity index model. The final richness model explained 58% of variation in understory plant species richness (10% by direct effects), 31% of variation in shrub cover (26% by direct effects), and 47% of total overstory cover (31% by direct effects). The Shannon's diversity model explained 48% of understory SD (19% by direct effects), 31% of variation in shrub cover (26% by direct effects), and 47% of total overstory cover (31% by direct effects).

Discussion

After severe burning, forested landscapes in the NAMCZ are often dominated by dense shrubfields (Leiberg 1902, Show and Kotok 1924, Wilken 1967, Oakley et al. 2006, Welch et al. 2016, Lydersen et al. 2019). We predicted that high shrub cover in post-fire landscapes would drive declines in understory plant richness and diversity, and that overall plant richness and diversity would be lowest in severely burned forests, since the hottest fires generally result in the densest shrubfields. Our analyses generally supported these hypotheses, but with some nuances.

We found that shrub cover on its own was only a marginally significant driver of understory plant richness. However, our multiple regression models did a much better job of explaining variance in richness, and shrub cover and fire severity (a driver of shrub cover and overstory cover) were the two most important drivers of native plant richness; this lifeform encompasses the vast majority of our species. In fact, shrub cover was the only predictor variable found in every richness model, and its effects were negative in all cases but for woody plants (not surprising, since shrubs were the most common woody plants) and N-fixers, many of which are also shrubs. Shrub cover was also an important driver of Shannon diversity and evenness, where it was always under a negative coefficient and mostly in first or second position behind fire severity.

Our SEM models help to explain the relationship of fire severity to species richness and diversity. In the regression analysis, fire severity had a direct positive relationship with richness primarily through the fact that any fire at all drove increases in species numbers over the unburned condition. However, the SEM showed how severity's overall relationship with plant richness is mediated through its influences on shrub and overstory cover. Fire severity was positively related with shrub cover – due to its stimulation of postfire shrub regeneration – but negatively related with overstory cover, while both cover variables were negative drivers of richness. Summing the SEM pathways between fire severity and richness, the negative relationship between severity and richness accounted for about 43% of the variance in richness, and the positive relationship (directly through overstory cover) explains about 15%. The SEM for Shannon's diversity showed the same general pattern.

In temperate forest systems like those of our NAMCZ sites, the bulk of plant diversity is found in the understory plant community (Whigham 2004, Kuhn et al. 2011, Richter et al. 2019, Miller and Safford 2020). In burned areas, high postfire shrub cover exerts a strongly negative influence on plant diversity, and such conditions are most common in areas that burn at high severity (i.e., where much of the prefire tree canopy is killed) (Miller and Safford 2012, Lydersen et al. 2019). High postfire shrub cover also reduces tree recruitment, especially in large high burn severity patches that exceed the typical dispersal distances of NAMCZ conifers (Welch et al. 2016, Shive et al. 2018, Steel et al. 2018). Recent research has also better defined the risks that extensive high severity burning poses for key wildlife species (e.g. Jones et al. 2016, Kramer et al. 2021, Stillman et al. 2021). Overall, modern patterns and trends in wildfire size and severity in the NAMCZ pose significant challenges to the resilience of forest ecosystems and the species they support (Stephens et al. 2018, North et al. 2019, Dove et al. 2020, Safford et al. in press).

Our analyses also investigated the relationships of other variables with richness and diversity. Climatic water deficit (CWD) was not generally a strong predictor of richness and diversity, but it was the only independent variable that appeared in every one of our models for richness and SD, and it occurred in three of the PE models. Higher CWD was indicative of greater water availability, and we found that CWD was positively related to richness and diversity in every model in which it occurred, excepting the models for the woody species group which appear to benefit from less water availability. Elevation and rock cover were also important predictor variables and occurred in many models. Elevation was always positively related to richness and diversity except for the exotic plant group, whose species numbers generally decrease at higher elevations. Our index of productivity (NDVI) was a minor driver of plant richness but was not related to diversity; this was somewhat unexpected considering how closely diversity and productivity have been tied elsewhere (Burkle et al. 2015). However, we also found productivity was a strong predictor only for the richness of certain lifeforms (herbaceous, annual, woody and exotic plant species) in our multiple regression models. The lack of relationship of other species richness in the understory to productivity is potentially driving down its influence on the full understory community in the SEM.

Several broad patterns emerged when we separated the understory community into life form and life history categories. The most prominent was that understory plant richness, regardless of life form and life history category, is influenced by many environmental factors. Most life form and life history diversity and evenness models were defined by fewer variables. The presence or absence of an understory plant species after a fire is a function of many interacting elements of the system, and of these many elements, post-fire severity class is a notably strong predictor, likely because many understory species in the NACMZ system are not well-adapted to high severity fire (Bohlman et al., 2016; Keeley and Safford 2016; Tepley et al., 2017; Steel et al., 2018; Richter et al., 2019). The influence of fire severity was particularly evident in our richness models for exotic, herbaceous, and nitrogen plant species; these lifeforms include a significant portion of the understory community. Of note, shrub cover was a negative predictor for nearly all lifeform richness models with the exception of woody, nitrogen fixers. Most *Ceanothus* species fit this description.

Most of our lifeform/life history diversity and evenness models identified only a few environmental predictors: water availability (indicated as climatic water deficit), space to grow (rock cover) and shrub cover. Across most lifeform and life history categories, shrub cover served as a negative predictor of diversity and evenness. We did not examine below-ground competition for water, but there is previous research that found strong evidence of such competition for water among shrubs and other plant species (Rejmánek and Messina 1989, McDonald and Fiddler 2010), and shrubs will often fill competitive roles when their stature and ability to intercept and outcompete other plants for water and other nutrients grants them an advantage (Harvey et al. 1987, Messina et al. 1990, Greene et al. 2007, Bohlman et al. 2016). Shrub dominance in post-fire sites after high severity burning in the NAMCZ is a function of their capacity for rapid resprouting and/or copious germination from abundant seed banks (Schlesinger and Gill 1978, Barro and Conard 1991, Nagel and Taylor 2005, Burge et al. 2011, Bohlman et al. 2016). By germinating and growing quickly early in the post-fire successional sequence these shrubs may be acting as inhibitors for most lifeforms, (or “edificators” *senso* Braun-Blanquet and Pavillard 1922); they limit the ability for most lifeforms to grow and survive. There is also evidence, however, that situations in which resources like water and light are limiting, shrubs may play the role of facilitators (St John and Rundel 1976, Southon et al. 2012, Blaser et al. 2013) and benefit some species by increasing the availability of nitrogen – especially shrubs in the genus *Ceanothus* (Oakley et al. 2003). Their role as facilitators has also been found to extend to fauna (Wiens and Rotenberry 1981, Klug and Jackrel 2010).

Montane chaparral and related shrub types have always been a feature of the NAMCZ landscape, but the evidence is that the spatial patterns of shrub occurrence have changed from one dominated by fine-scaled heterogeneity and relatively small shrub patches scattered across the landscape to one dominated by coarse-grained, large and contiguous shrubfields (Safford and Stevens 2017). Although the mean annual area of YPMC and related forests burned by wildfires continues to be far below the pre-Euroamerican settlement (EAS) mean (Safford and Van de Water 2014), annual burned area has been rising over the last few decades. Perhaps more importantly, the area of montane forest burning under high severity conditions has greatly increased to the point that the total area burned at high severity in a year is greater on average than before EAS (Mallek et al., 2013; Steel et al., 2018; Williams et al. in review). Under the warming climate, and with no change to forest and fire management policies, this pattern will continue (Restaino and Safford 2018, Moreira et al. 2020). These novel wildfire regimes are defined by increases in area burned, fire severity and high-severity patch size, and they are likely to increase the extent of shrubfields and homogenize ecological conditions on large landscapes (Miller and Safford 2012, Mallek et al. 2013, Lauvaux et al. 2016, Tubbesing et al. 2020a). In the absence of subsequent fire these states may persist for 30-60 years or more (Russell et al. 1998, Nagel and Taylor 2005, Knapp et al. 2012), but the recurrence of fire before the succession of the site to forest has the potential to increase the area in the NAMCZ dominated by shrubs and potentially make them permanent parts of the landscape (Leiberg 1902, Coppoletta et al. 2016, Tepley et al. 2017, Lydersen et al. 2019) as the shrubfields replace themselves with repeated high severity fire (Knapp et al. 2012, Coppoletta et al. 2016, Guiterman et al. 2018, Landesmann et al. 2021). Our work here better elucidates the implications of such state persistence for the understory plant community.

Applications & Management

Long-term and widespread shrubfield persistence has the potential to decrease plant diversity and conifer regeneration (Welch et al. 2016, Tepley et al. 2017) in YPMC forests in the NAMCZ. The potential benefits of shrub control to the diversity of the native understory plant community have been established (e.g., DiTomaso et al. 1997, Bohlman et al. 2016, Zhang et al. 2016). Adaptive fire management like prescribed burns and wildland fire use can go a long way towards promoting historic fire regimes by reducing the likelihood of high severity burn area and frequency (Moritz and Stephens 2008, Hessburg et al. 2016). Presumably, doing so would also reduce the area dominated by shrubs after fire, but it is still important to acknowledge the diverse role that shrubs may play in these systems and the fact that active fire management demands a lot of resources beyond the time and money necessary for establishing such projects across such a large landscape as the temperate dry forests of the Sierra Nevada. There is a need to find an equilibrium in the ecosystem benefits afforded by forest and montane chaparral cover and the goals of high understory plant species diversity. A balance in management tactics to promote both ideals would ideally aim to restore the natural range of variation, but these must be associated and tempered for changing climate (Restaino and Safford 2018). Our hope is that this research can provide yet more incentive towards this undertaking, not only for the potential benefits to tree regeneration, but for the greater diversity of understory plant communities.

Figures & Tables

Figure 2.1: Fire locations.

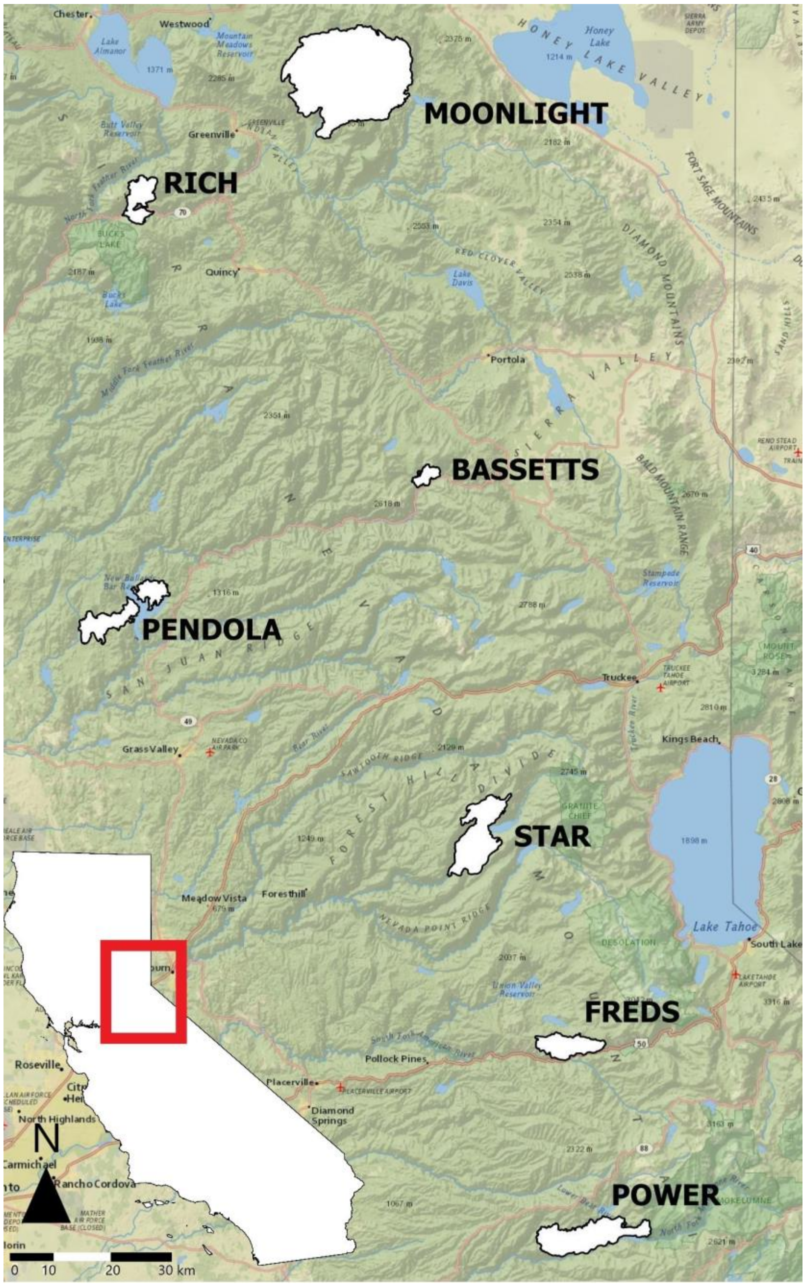


Table 2.1: Distribution of plots by fire severity class

	Fire Severity Class						**Total # of plots**
	0	1	2	3	4	5	
# of plots	64	77	79	63	66	75	424

Figure 2.2: Dominant lifeform cover (trees and shrubs) across fire severity class. Asterisks indicate significant differences (p<0.001) between tree and shrub cover means in individual severity classes.

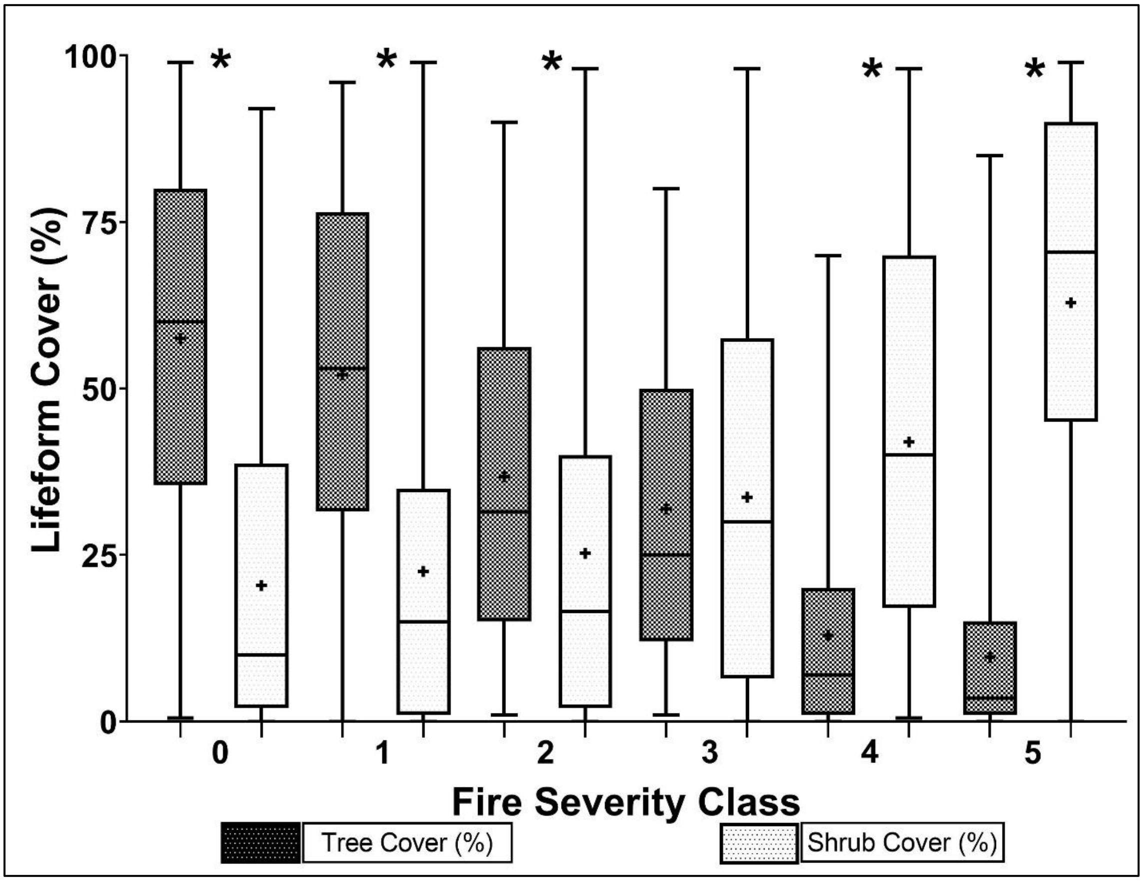


Figure 2.3: Linear regression analysis of Shannon's diversity index (a) and Pielou's evenness (b) in relation to shrub cover.

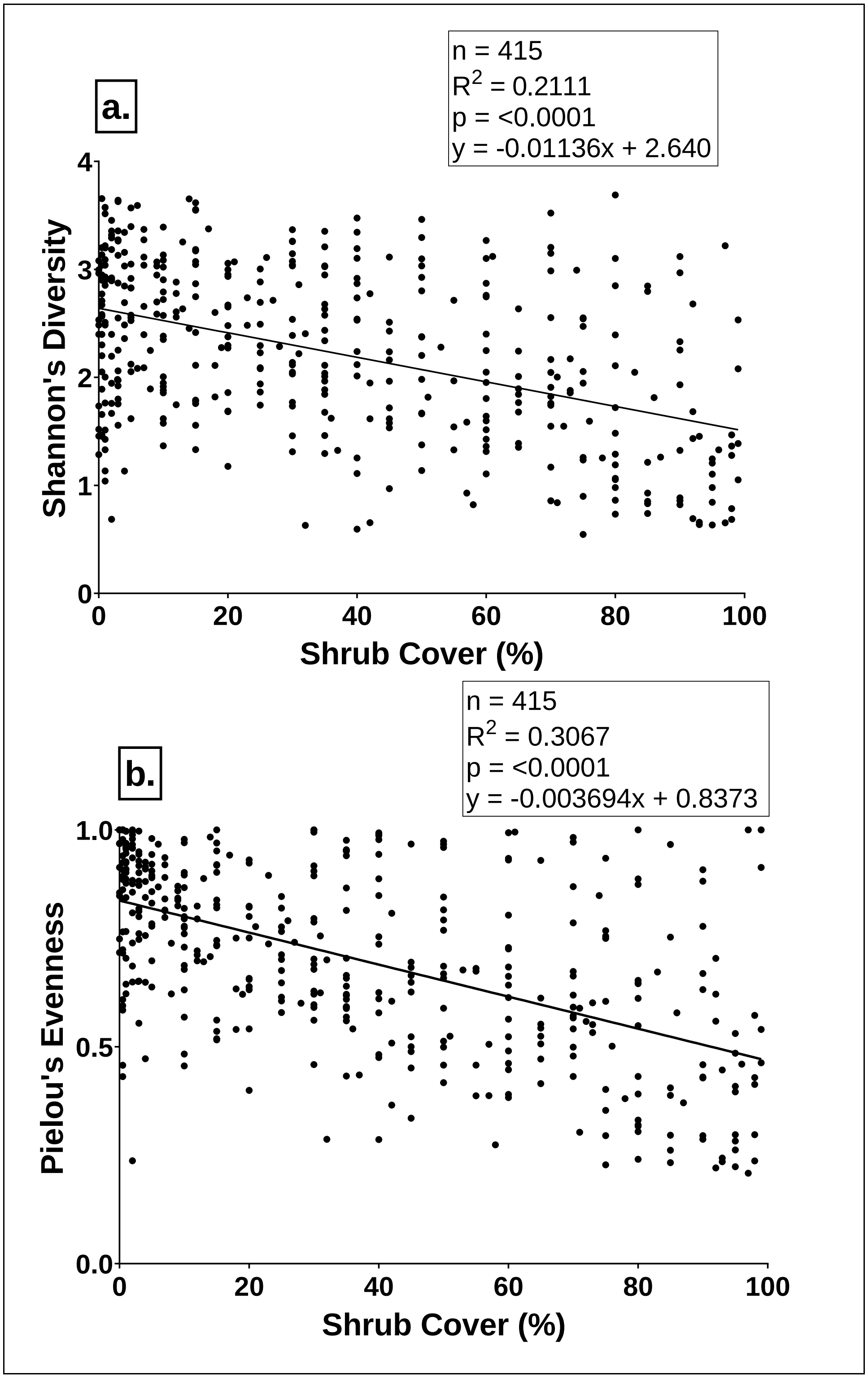


Table 2.2: Multiple linear regressions for lifeform/life history categories (species richness).

Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	
Exotic Plants	Fire Severity	0.3779	0.06343	<0.0001	**Model R^2:** 0.187 **Model p-value:** <0.0001 **AICc:** 626.5
	Productivity	-2.88	0.905	0.0016	
	Climatic Water Deficit	0.00694	0.0009638	<0.0001	
	Rock Cover	-0.01569	0.004905	0.0015	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2916 **Model p-value:** <0.0001 **AICc:** 1740
Native Plants	Shrub Cover	-0.04653	0.01259	0.0002	
	Elevation	0.01222	0.000959	<0.0001	
	Climatic Water Deficit	0.02035	0.003975	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2563 **Model p-value:** <0.0001 **AICc:** 822.4
Woody Plants	Shrub Cover	0.01324	0.004370	0.0026	
	Productivity	4.556	1.280	0.0004	
	Elevation	0.002022	0.000365	<0.0001	
	Climatic Water Deficit	-0.006999	0.001372	<0.0001	
	Rock Cover	-0.01682	0.006228	0.0072	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2845 **Model p-value:** <0.0001 **AICc:** 1773
Herbaceous Plants	Fire Severity	0.7063	0.2698	0.0092	
	Shrub Cover	-0.07753	0.01434	<0.0001	
	Elevation	0.01128	0.001012	<0.0001	
	Climatic Water Deficit	0.03433	0.004168	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.1941 **Model p-value:** <0.0001 **AICc:** -73.9
Nitrogen-fixing Plants	Fire Severity	0.1525	0.03056	<0.0001	
	Shrub Cover	0.003478	0.001609	0.00312	
	Elevation	0.0003881	0.0001106	0.0005	
	Climatic Water Deficit	0.001610	0.0004575	0.0005	
	Rock Cover	-0.008964	0.002117	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2809 **Model p-value:** <0.0001 **AICc:** 1562
Perennial Plants	Shrub Cover	-0.03396	0.01085	0.0019	
	Elevation	0.009328	0.0008158	<0.0001	
	Climatic Water Deficit	0.007473	0.003414	0.0292	
	Rock Cover	0.03643	0.03643	0.0191	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2748 **Model p-value:** <0.0001 **AICc:** 1107
Annual Plants	Fire Severity	0.6888	0.1325	<0.0001	
	Shrub Cover	-0.02228	0.00688	0.0013	
	Productivity	-5.201	1.84	0.0049	
	Elevation	0.002836	0.0005335	<0.0001	
	Climatic Water Deficit	0.01907	0.001957	<0.0001	
	Rock Cover	-0.02161	0.009103	0.00181	

Table 2.3: Multiple linear regressions for lifeform/life history categories (Shannon's Diversity).

Lifeform/Life History	Parameters	Coefficient	SE	p-value	**Model R^2:** 0.056 **Model p-value:** 0.0006 **AICc:** -265.9
Exotic Plants	Climatic Water Deficit	0.00123	0.00035	0.0006	
	Rock Cover	-0.00307	0.00154	0.0481	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.2559 **Model p-value:** <0.0001 **AICc:** 323.8
Native Plants	Shrub Cover	-0.02316	0.002361	<0.0001	
	Elevation	0.0006909	0.000178	0.0001	
	Climatic Water Deficit	0.001732	0.000743	0.0202	
	Rock Cover	0.01597	0.003367	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.206 **Model p-value:** <0.0001 **AICc:** -580.1
Woody Plants	Shrub Cover	-0.006907	0.0007748	<0.0001	
	Elevation	0.0001364	-0.000059	0.0211	
	Climatic Water Deficit	-0.0006806	0.0002461	0.0059	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.300 **Model p-value:** <0.0001 **AICc:** -291.8
Herbaceous Plants	Elevation	0.00105	0.00009	<0.0001	
	Climatic Water Deficit	0.00301	0.00035	<0.0001	
	Rock Cover	0.00552	0.00157	0.0005	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.043 **Model p-value:** 0.0036 **AICc:** -674.6
Nitrogen-fixing Plants	Fire Severity	0.02119	0.01139	0.0639	
	Elevation	0.00012	0.00005	0.0129	
	Climatic Water Deficit	0.00052	0.00019	0.0061	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.334 **Model p-value:** <0.0001 **AICc:** -355.5
Perennial Plants	Shrub Cover	-0.0115	0.00101	<0.0001	
	Elevation	0.00046	0.00007	<0.0001	
	Rock Cover	0.00786	0.00145	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.11 **Model p-value:** <0.0001 **AICc:** -247.7
Annual Plants	Fire Severity	0.06061	0.02238	0.0071	
	Climatic Water Deficit	0.00188	0.00032	<0.0001	

Table 2.4: Multiple linear regressions for lifeform/life history categories (Pielou's evenness).

Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.0363 **Model p-value:** 0.0019 **AICc:** -433.5
Exotic Plants	Climatic Water Deficit	0.00018	0.000259	0.0019	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.37 **Model p-value:** <0.0001 **AICc:** -1382
Native Plants	Fire Severity	-0.01767	0.00599	0.0034	
	Shrub Cover	-0.003368	0.0003204	<0.0001	
	Rock Cover	0.002455	0.0004179	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.294 **Model p-value:** <0.0001 **AICc:** -1180
Woody Plants	Shrub Cover	-0.004321	0.0003626	<0.0001	
	Rock Cover	0.001763	0.0005452	0.0013	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.053 **Model p-value:** <0.0001 **AICc:** 427.5
Herbaceous Plants	Elevation	0.0009111	0.0001969	<0.0001	
	Climatic Water Deficit	0.00292	0.0008194	0.0004	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.036 **Model p-value:** 0.0035 **AICc:** -589.6
Nitrogen-fixing Plants	Elevation	0.0001584	0.00005639	0.0053	
	Climatic Water Deficit	0.0006795	0.0002151	0.0017	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.356 **Model p-value:** <0.0001 **AICc:** -1353
Perennial Plants	Fire Severity	-0.01956	0.006209	0.0017	
	Shrub Cover	-0.003346	0.0003321	<0.0001	
	Rock Cover	0.002448	0.0004331	<0.0001	
Lifeform/Life History	**Parameters**	**Coefficient**	**SE**	**p-value**	**Model R^2:** 0.032 **Model p-value:** 0.0008 **AICc:** -751.6
Annual Plants	Climatic Water Deficit	0.00052	0.0001534	0.0008	

Figure 2.4: Refined structural equation model for understory plant species richness in postfire landscapes. Line thickness represents the strength of relationships (based on standardized path coefficients). The ♀ symbol indicates paths that are marginally significant (p = 0.06), *** paths were highly significant (p<0.001), * paths were moderately significant (p = 0.01), and NS indicates non-significant paths. Conditional R^2 values (R^2_c) represent the combined explanatory power of fixed and random effects.

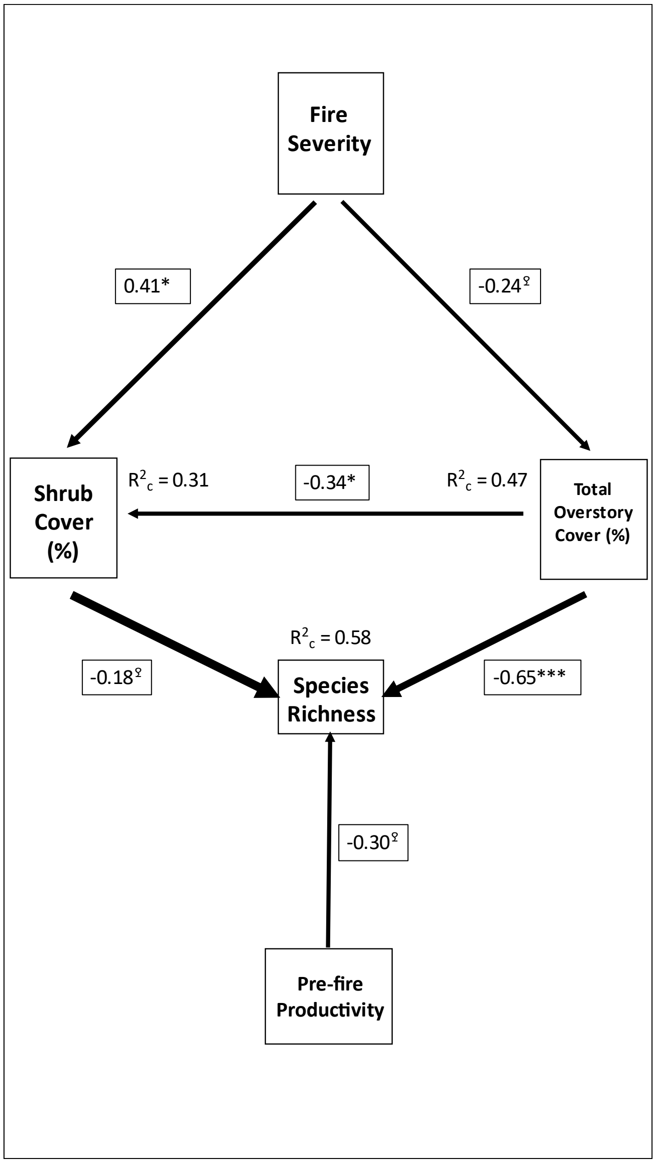
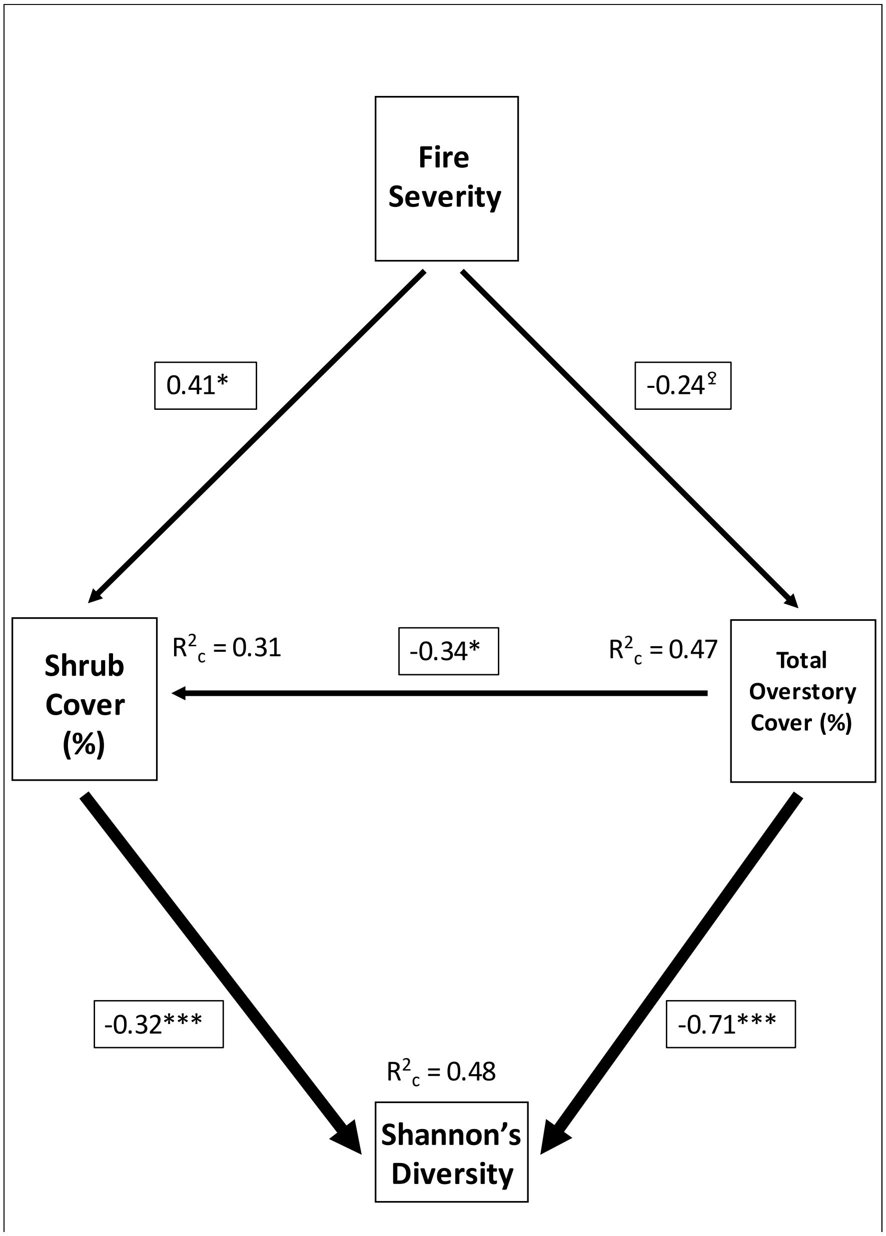


Figure 2.5: Refined structural equation model for understory plant species diversity (Shannon's index) in postfire landscapes. Line thickness represents the strength of relationships (based on standardized path coefficients). The Ձ symbol indicates paths that are marginally significant (p = 0.06), *** paths were highly significant (p<0.001), * paths were moderately significant (p = 0.01), and NS indicates non-significant paths. Conditional R^2 values (R^2_c) represent the combined explanatory power of fixed and random effects.



Literature Cited

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington D.C.

Baldwin, B. G., D. H. Goldman, D. J. Keil, R. Patterson, T. J. Rosatti, and L. A. Vorobik. 2012. The Jepson Manual: Vascular Plants of California. University of California Press.

Barro, S. C., and S. G. Conard. 1991. Fire effects on California chaparral systems: an overview. Environment International 17:135–149.

Blaser, W. J., J. Sitters, S. P. Hart, P. J. Edwards, and H. O. Venterink. 2013. Facilitative or competitive effects of woody plants on understorey vegetation depend on N-fixation, canopy shape and rainfall. Journal of Ecology 101:1598–1603.

Bohlman, G. N., M. North, and H. D. Safford. 2016. Shrub removal in reforested post-fire areas increases native plant species richness. Forest Ecology and Management 374:195–210.

Bond, W., and B. Van Wilgen. 1996. Fire and Plants. Chapman & Hall, London, UK.

Bowman, D. M., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D’Antonio, R. S. DeFries, J. C. Doyle, and S. P. Harrison. 2009. Fire in the Earth system. Science 324:481–484.

Braun-Blanquet, J., and J. Pavillard. 1922. Vocabulaire de Sociologie Vegetale. Montpellier.

Burgan, R. E., R. A. Hartford, and J. C. Eidenshink. 1996. Using NDVI to assess departure from average greenness and its relation to fire business. General Technical Report, US Department of Agriculture, Forest Service, Intermountain Research Station.

Burge, D. O., D. M. Erwin, M. B. Islam, J. Kellermann, S. W. Kembel, D. H. Wilken, and P. S. Manos. 2011. Diversification of Ceanothus (Rhamnaceae) in the California Floristic Province. International Journal of Plant Sciences 172:1137–1164.

Burkle, L. A., J. A. Myers, and R. T. Belote. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6:1–14.

Chuvieco, E., D. Cocero, D. Riano, P. Martin, J. Martınez-Vega, J. de la Riva, and F. Pérez. 2004. Combining NDVI and surface temperature for the estimation of live fuel moisture content in forest fire danger rating. Remote Sensing of Environment 92:322–331.

Collins, B. M., R. G. Everett, and S. L. Stephens. 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Cornwell, W. K., and D. D. Ackerly. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. Ecological Monographs 79:109–126.

Crockett, J. L., and A. L. Westerling. 2018. Greater temperature and precipitation extremes intensify Western US droughts, wildfire severity, and Sierra Nevada tree mortality. Journal of Climate 31:341–354.

Crotteau, J. S., J. M. Varner III, and M. W. Ritchie. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. Forest Ecology and Management 287:103–112.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, and C. J. Peterson. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience 51:723–734.

DiTomaso, J., E. Healy, D. Marcum, G. Kyser, and M. Rasmussen. 1997. Post-fire herbicide sprays enhance native plant diversity. California Agriculture 51:6–11.

Dove, N. C., H. D. Safford, G. N. Bohlman, B. L. Estes, and S. C. Hart. 2020. High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. Ecological Applications 30.

Escuin, S., R. Navarro, and P. Fernandez. 2008. Fire severity assessment by using NBR (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) derived from LANDSAT TM/ETM images. International Journal of Remote Sensing 29:1053–1073.

Flint, L., and A. Flint. 2014. California basin characterization model: a dataset of historical and future hydrologic response to climate change. https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html.

Gongalsky, K. B., A. S. Zaitsev, D. I. Korobushkin, R. A. Saifutdinov, K. O. Butenko, F. T. de Vries, K. Ekschmitt, M. I. Degtyarev, A. Y. Gorbunova, and N. V. Kostina. 2020. Forest fire induces short-term shifts in soil food webs with consequences for carbon cycling. Ecology Letters.

Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sensing of Environment.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press.

Greene, D. F., S. E. Macdonald, S. Haeussler, S. Domenicano, J. Noel, K. Jayen, I. Charron, S. Gauthier, S. Hunt, and E. T. Gielau. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research 37:1012–1023.

Guiterman, C. H., E. Q. Margolis, C. D. Allen, D. A. Falk, and T. W. Swetnam. 2018. Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of northern New Mexico. Ecosystems 21:943–959.

Harvey, A. E., M. F. Jurgensen, M. J. Larsen, and R. Graham. 1987. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. Canadian Journal of Forest Research 17:58–62.

Hessburg, P. F., T. A. Spies, D. A. Perry, C. N. Skinner, A. H. Taylor, P. M. Brown, S. L. Stephens, A. J. Larson, D. J. Churchill, and N. A. Povak. 2016. Tamm review: management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. Forest Ecology and Management 366:221–250.

Illera, P., A. Fernandez, and J. A. Delgado. 1996. Temporal evolution of the NDVI as an indicator of forest fire danger. International Journal of remote sensing 17:1093–1105.

Jones, G. M., R. J. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery. 2016. Megafires: an emerging threat to old-forest species. Frontiers in Ecology and the Environment 14:300–306.

Kauffman, J. B., and R. E. Martin. 1991. Factors influencing the scarification and germination of three montane Sierra-Nevada, California, USA Shrubs. Northwest Science 65:180–187.

Kayes, L. J., K. J. Puettmann, and P. D. Anderson. 2011. Short-term bryoid and vascular vegetation response to reforestation alternatives following wildfire in conifer plantations. Applied Vegetation Science 14:326–339.

Keeley, J. E. 1986. Resilience of Mediterranean shrub communities to fires. Pages 95–112 Resilience in Mediterranean-type ecosystems. Springer.

Keeley, J., and H. D. Safford. 2016. Fire as an Ecosystem Process. Pages 27–45 *in* H. A. Mooney and E. S. Zavaleta, editors. Ecosystems of California. University of California Press, Berkeley, California, USA.

Klug, P. E., and S. L. Jackrel. 2010. Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. Oecologia 162:803–813.

Knapp, E. E., C. P. Weatherspoon, and C. N. Skinner. 2012. Shrub seed banks in mixed conifer forests of Northern California and the role of fire in regulating abundance. Fire Ecology 8:32–48.

Kramer, A., G. M. Jones, S. A. Whitmore, J. J. Keane, F. A. Atuo, B. P. Dotters, S. C. Sawyer, S. L. Stock, R. J. Gutiérrez, and M. Z. Peery. 2021. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management 479.

Kuhn, T. J., H. D. Safford, B. E. Jones, and K. W. Tate. 2011. Aspen (Populus tremuloides) stands and their contribution to plant diversity in a semiarid coniferous landscape. Plant Ecology 212:1451.

Landesmann, J. B., F. Tiribelli, J. Paritsis, T. T. Veblen, and T. Kitzberger. 2021. Increased fire severity triggers positive feedbacks of greater vegetation flammability and favors plant community-type conversions. Journal of Vegetation Science 32.

Lauvaux, C. A., C. N. Skinner, and A. H. Taylor. 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. Forest Ecology and Management 363:74–85.

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Leiberg, J. B. 1902. Forest conditions in the northern Sierra Nevada, California. US Government Printing Office.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical Ecology: a Primer on Methods and Computing. John Wiley & Sons, Chichester, UK.

Lydersen, J. M., B. M. Collins, M. Coppoletta, M. R. Jaffe, H. Northrop, and S. L. Stephens. 2019. Fuel dynamics and reburn severity following high-severity fire in a Sierra Nevada, USA, mixed-conifer forest. Fire Ecology 15:43.

Malanson, G. P., and J. F. O’Leary. 1982. Post-fire regeneration strategies of Californian coastal sage shrubs. Oecologia 53:355–358.

Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4:1–28.

McDonald, P. M., and C. S. Abbott. 1997. Vegetation trends in a 31-year-old ponderosa pine plantation: effect of different shrub densities. Res. Pap. PSW-RP-231. Albany, CA: US Department of Agriculture, Forest Service ….

McDonald, P. M., and G. O. Fiddler. 2010. Twenty-five years of managing vegetation in conifer plantations in northern and central California: results, application, principles, and challenges. Gen. Tech. Rep. PSW-GTR-231. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station. 87 p 231.

McGinnis, T. W., J. E. Keeley, S. L. Stephens, and G. B. Roller. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. Forest Ecology and Management 260:22–35.

Messina, J. J., M. Rejmanek, and A. Franklin. 1990. Interference between seedlings and shrubs and conifers is competition for water, the most important interaction. Bulletin of the Ecological Society of America 71:252–252.

Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009a. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment 113:645–656.

Miller, J. D., and H. Safford. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. Fire Ecology 8:41–57.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009b. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade mountains, California and Nevada, USA. Ecosystems 12:16–32.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

Miller, J. E. D., and H. D. Safford. 2020. Are plant community responses to wildfire contingent upon historical disturbance regimes? Global Ecology and Biogeography.

Miller, J. E., H. T. Root, and H. D. Safford. 2018. Altered fire regimes cause long-term lichen diversity losses. Global Change Biology 24:4909–4918.

Moreira, F., D. Ascoli, H. Safford, M. A. Adams, J. M. Moreno, J. M. Pereira, F. X. Catry, J. Armesto, W. Bond, and M. E. González. 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. Environmental Research Letters 15.

Moritz, M. A., and S. L. Stephens. 2008. Fire and sustainability: considerations for California's altered future climate. Climatic Change 87:265–271.

Motulsky, H., P. Spannard, and R. Neubig. 2021. GraphPad Prism (version 9). GraphPad Software Incorporated, San Diego, California, USA.

Nagel, T. A., and A. H. Taylor. 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. The Journal of the Torrey Botanical Society 132:442–457.

Noble, I., and R. Slatyer. 1977. Post-fire succession of plants in Mediterranean ecosystems [Eucalyptus]. USDA Forest Service General Technical Report WO.

North, M. P., J. T. Stevens, D. F. Greene, M. Coppoletta, E. E. Knapp, A. M. Latimer, C. M. Restaino, R. E. Tompkins, K. R. Welch, and R. A. York. 2019. Tamm Review: Reforestation for resilience in dry western US forests. Forest Ecology and Management 432:209–224.

Oakley, B. B., M. P. North, and J. F. Franklin. 2003. The effects of fire on soil nitrogen associated with patches of the actinorhizal shrub Ceanothus cordulatus. Plant and Soil 254:35–46.

Oakley, B. B., M. P. North, and J. F. Franklin. 2006. Facilitative and competitive effects of a N-fixing shrub on white fir saplings. Forest Ecology and Management 233:100–107.

Oliver, W. W. 1984. Brush reduces growth of thinned ponderosa pine in northern California. US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experimental Station. 172.

Oliver, W. W. 1990. Spacing and shrub competition influence 20-year development of planted ponderosa pine. Western Journal of Applied Forestry 5:79–82.

Pielou, E. C. 1984. The Interpretation of Ecological Data: a Primer on Classification and Ordination. John Wiley & Sons, Chichester, UK.

Prach, K., and L. R. Walker. 2020. Comparative Plant Succession Among Terrestrial Biomes of the World. Cambridge University Press.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rejmánek, M., and J. J. Messina. 1989. Predicting conifer growth reduction from the analysis of neighborhood weed competition. Pages 11–25 Proceedings of the 10th Annual Forest Vegetation Management Conference, Redding, California, USA.

Restaino, C., and H. Safford. 2018. Fire and Climate Change. Pages 493–505 *in* J. W. van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, and K. E. Shaffer, editors. Fire in California’s Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Richter, C., M. Rejmánek, J. E. Miller, K. R. Welch, J. Weeks, and H. Safford. 2019. The species diversity x fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. Ecosphere 10.

Rodman, K. C., T. T. Veblen, R. A. Andrus, N. J. Enright, J. B. Fontaine, A. D. Gonzalez, M. D. Redmond, and A. P. Wion. 2020. A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. Journal of Ecology:313–326.

Russell, W. H., J. McBride, and R. Rowntree. 1998. Revegetation after four stand-replacing fires in the Lake Tahoe basin. Madrono:40–46.

Safford, H. D., R. J. Butz, G. Bohlman, M. Coppoletta, B. Estes, S. E. Gross, K. E. Merriam, M. D. Meyer, N. Molinari, and A. Wuenschel. (n.d.). Fire ecology of the North American Mediterranean-climate zone. Page *in* B. M. Collins and C. H. Greenberg, editors. Fire Ecology and Management of US Forestested Ecosystems: Past, Present and Future.

Safford, H. D., and J. T. Stevens. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. PSW-GTR-256. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Safford, H. D., and K. P. Van de Water. 2014. Using Fire Return Interval Departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. PSW-RP-266. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Schlesinger, W. H., and D. S. Gill. 1978. Demographic studies of the chapparal shrub Ceanothus-megacarpus in the Santa-Ynez Mountains of California, USA. Ecology 59:1256–1263.

Seligman, N. G., and Z. Henkin. 2000. Regeneration of a dominant Mediterranean dwarf-shrub after fire. Journal of Vegetation Science 11:893–902.

Service, U. N. P. 2003. Fire Monitoring Handbook. Fire Management Program Center, National Interagency Fire Center, Boise, ID.

Show, S. B., and E. I. Kotok. 1924. The role of fire in the California pine forests.

Southon, G. E., E. R. Green, A. G. Jones, C. G. Barker, and S. A. Power. 2012. Long-term nitrogen additions increase likelihood of climate stress and affect recovery from wildfire in a lowland heath. Global Change Biology 18:2824–2837.

St John, T. V., and P. W. Rundel. 1976. The role of fire as a mineralizing agent in a Sierran coniferous forest. Oecologia 25:35–45.

Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. The changing landscape of wildfire: burn pattern trends and implications for California’s yellow pine and mixed conifer forests. Landscape Ecology 33:1159–1176.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:1–23.

Stephens, S. L., B. M. Collins, C. J. Fettig, M. A. Finney, C. M. Hoffman, E. E. Knapp, M. P. North, H. Safford, and R. B. Wayman. 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. BioScience 68:77–88.

Stephens, S. L., and L. W. Ruth. 2005. Federal forest-fire policy in the United States. Ecological Applications 15:532–542.

Stillman, A. N., T. J. Lorenz, P. C. Fischer, R. B. Siegel, R. L. Wilkerson, M. Johnson, and M. W. Tingley. 2021. Juvenile survival of a burned forest specialist in response to variation in fire characteristics. Journal of Animal Ecology.

Tepley, A. J., J. R. Thompson, H. E. Epstein, and K. J. Anderson-Teixeira. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Global Change Biology 23:4117–4132.

Tubbesing, C. L., R. A. York, S. L. Stephens, and J. J. Battles. 2020a. Rethinking fire-adapted species in an altered fire regime. Ecosphere 11.

Tubbesing, C. L., D. J. N. Young, R. A. York, S. L. Stephens, and J. J. Battles. 2020b. Forest succession in an altered fire regime: the role of shrub neighborhood dynamics. Ecosphere.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

USDA Forest Service Region 5 - Common Stand Exam Field Guide. 2012. . USDA Forest Service, http://www.fs.fed.us/nrm/fsveg/index.shtml.

van Wagtendonk, J. W., J. Fites-Kaufman, H. D. Safford, M. North, and B. M. Collins. 2018. Sierra Nevada Bioregion. Pages 249–278 Fire in California's Ecosystems. 2nd edition. University of California Press, Berkeley, California, USA.

Welch, K. R., H. D. Safford, and T. P. Young. 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7:1–29.

Werner, C. M., D. J. Young, H. D. Safford, and T. P. Young. 2019. Decreased snowpack and warmer temperatures reduce the negative effects of interspecific competitors on regenerating conifers. Oecologia 191:731–743.

Whigham, D. F. 2004. Ecology of woodland herbs in temperate deciduous forests. Annual Review of Ecology, Evolution, and Systematics:583–621.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–42.

Wilken, G. C. 1967. History and fire record of a timberland brush field in Sierra Nevada of California. Ecology 48:302.

Zhang, J., W. W. Oliver, and M. D. Busse. 2006. Growth and development of ponderosa pine on sites of contrasting productivities: relative importance of stand density and shrub competition effects. Canadian Journal of Forest Research 36:2426–2438.

Zhang, J., R. F. Powers, W. W. Oliver, and D. H. Young. 2013. Response of ponderosa pine plantations to competing vegetation control in Northern California, USA: a meta-analysis. Forestry 86:3–11.

Zhang, J., D. H. Young, W. W. Oliver, and G. O. Fiddler. 2016. Effect of overstorey trees on understorey vegetation in California (USA) ponderosa pine plantations. Forestry 89:91–99.

ACKNOWLEDGEMENTS

I am grateful to my advisors Marcel Rejmánek and Hugh Safford for all of their comments, edits, and support throughout this undertaking, as well as my other committee members Andrew Latimer and Malcolm North for their recommendations. Many thanks to the field technicians who tirelessly assisted with field data collection: Chris Preston, Marcel Safford, Allyson Ayalon, Jake Albino, Michelle Rampula, Paul Excoffier, Jacob Macdonald and Gabina Bohlman. Jesse Miller provided his expertise on many of these statistical analyses, and the fabulous members of the Safford Lab extended emotional and technical support when and where it was needed. I extend my appreciation as well to Jon Lefcheck for his help with the SEM (and his piecewiseSEM package). Funding came from the USDA Forest Service Pacific Southwest Region and the Eldorado National Forest.