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Title: Fire Refugia Function and Composition in Dry Mixed-Conifer Forests of Oregon’s Blue Mountains

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Contemporary fire effects are raising concerns about the resistance and resilience of dry mixed-conifer forests to large wildfires. Fire refugia – unburned or low-severity patches within fire perimeters – are understudied components of post-fire mosaics that may be key drivers of forest recovery following high-severity fire. Little is known about the capacity of dry mixed-conifer forests to regenerate forest following high-severity fire in Oregon’s Blue Mountains, and more broadly, there are significant knowledge gaps regarding the function and composition of fire refugia in dry forest ecosystems in the western United States. This thesis took advantage of a large natural experiment resulting from four large fires that burned in the Blue Mountains between 2000 and 2005. The primary objectives were to: (a) quantify post-fire conifer regeneration in stand-replacement patches and determine the influence of local- and landscape-scale refugial seed source pattern on post-fire forest regeneration, and (b) characterize fire refugia structure and composition, and compare understory plant communities in fire refugia to the higher-severity burned matrix.

Dry mixed-conifer forests in the Blue Mountains of Oregon show evidence of resilience to high-severity fire effects, 12 – 17 years post-fire. Seed sources that survived fire in refugia are critical drivers of post-fire forest regeneration in adjacent high-severity burned areas. In contrast to slow or absent post-fire forest recovery reported in dry forests in other regions, regenerating conifer seedlings were generally abundant in our study area: over 80% of plots in stand-replacement patches contained regenerating seedlings and the median seedling density across all

plots was 1100 seedlings ha^{-1}. Consistent with previous studies, we found that proximity to surviving seed source is a key driver of post-fire conifer regeneration. In addition, high-resolution maps of landscape fire refugia, developed using 1 meter aerial imagery, allowed us to provide novel insights into the influence of landscape patterns of surviving seed source on post-fire forest regeneration, and the additive effect of multiple seed sources contributing to a site's capacity to reestablish forest following high-severity fire. Although stand-replacement patches in our study fires have been largely converted from forests to shrublands 12 – 17 years post-fire, we did not find evidence of a competitive interaction between regenerating conifers and shrubs. In addition, many seedlings appear to have recently emerged above the shrub canopy, suggesting these sites have not been permanently "captured" by woody understory species.

Understory plant community composition in fire refugia and the higher-severity burned matrix was similar 12 – 17 years post-fire, despite substantial structural differences between refugia and stand-replacement patches. We found no evidence of differences between fire refugia and stand-replacement patches in species richness, diversity, or invasibility by exotic annual grasses. Although plant community composition was similar between plot types, we did identify several indicator species for fire refugia and stand-replacement patches, suggesting that differences between these plot types strongly influences the abundance of some plant species. Our findings highlight the capacity of understory plant communities in the Blue Mountains to recover following fire, and together with results from our seedling regeneration analysis, these results suggest that dry mixed-conifer forests in our study area are resilient to even high-severity fire effects. We anticipate that in the absence of subsequent disturbance (e.g., reburn), dry mixed-conifer forest in the Blue Mountains will recover following stand-replacement fire, provided adequate seed sources survived fire within refugia. Fire refugia in the Blue Mountains appear to be important primarily as remnant forest structure and as surviving seed sources essential for the reestablishment of trees in high-severity burned areas, rather than as "safe havens" for plant communities otherwise absent from the higher-severity burned matrix.

Understanding the drivers of forest resistance and resilience to landscape-scale disturbance is increasingly important in the context of accelerating global change. This thesis provides new insights into the composition and ecological function of dry mixed-conifer fire refugia in Oregon’s Blue Mountains, as well as the important role fire refugia play in supporting post-fire forest resilience. Studies like this one can contribute to a growing recognition that fire refugia are important, but perhaps underappreciated, components of post-fire landscapes. However, for the concept of fire refugia to gain lasting currency with scientists and managers, more research will be needed to understand the drivers, persistence, composition, and ecological functions of fire refugia across a diversity of forest ecosystems and fire regimes.

Fire Refugia Function and Composition in Dry Mixed-Conifer Forests of Oregon's Blue Mountains

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William Downing, Author

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TABLE OF CONTENTS

Page

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX FIGURES

LIST OF APPENDIX FIGURES (Continued)

LIST OF APPENDIX TABLES

Fire Refugia Function and Composition in Dry Mixed-Conifer Forests of Oregon’s Blue Mountains

CHAPTER 1 – INTRODUCTION

Recent fire activity is increasing concern about the capacity of some dry forest ecosystems to recover following high-severity fire. Historically, frequent fire in Pacific Northwest dry mixed-conifer forests produced low- to moderate-severity fire effects (Hessburg et al. 2005). However, a legacy of fire exclusion, grazing, and logging has significantly increased fire return intervals (Reilly et al. 2017) and transformed forest structure and composition (Hagmann et al. 2014, Merschel et al. 2014). These landscapes are now more vulnerable to high-severity effects when large fires do occur (Spies et al. 2006, Stephens et al. 2017), and contemporary fires regularly produce high-severity patch sizes that are larger than historical estimates (Reilly et al. 2017). Evidence is emerging that large disturbances may be pushing some forests beyond sustainability thresholds (Millar and Stephenson 2015), and historical reference conditions may not be useful for anticipating ecosystem responses to contemporary fires (Yocom-Kent et al. 2015, Johnstone et al. 2016). Some high-severity burned areas may be at risk of widespread tree recruitment failure, and conversion from forest to non-forest states, as a result of limited surviving seed source, unfavorable climatic conditions, and competing vegetation (Stephens et al. 2013, Tepley et al. 2017, Stevens-Rumann et al. 2018).

Dry forest ecosystems, particularly those already at the edge of their climatic tolerances, must retain a degree of resistance and resilience to disturbance in order to persist in the context of accelerating global change (Millar et al. 2007). Resistance is the capacity of a system to remain essentially unchanged by disturbance, and resilience is a system’s ability to recover from disturbance and return to a reference state (Grimm and Wissel 1997). Fire refugia, locations that burn less severely or less frequently than the surrounding landscape matrix (Gill 1975, Camp et al. 1997, Wood et al. 2011, Krawchuk et al. 2016), constitute the most fire-resistant portions of the forest landscape within fire perimeters. As locations where forest persists in a matrix of higher-severity fire effects, fire refugia contain seed sources and relatively intact forest structure that may be essential for post-fire resilience and recovery (Robinson et al. 2013, Landesmann and Morales 2018). However, little is known about fire refugia composition and function in dry mixed-conifer forests in the western United States. Identifying the drivers of post-fire forest recovery and developing a baseline understanding of the composition and ecological function of fire refugia are essential next steps for evaluating the resilience of dry mixed-conifer forests to fire in the Blue Mountains.

Fire in the Blue Mountains

Fire is a key disturbance process that historically produced a range of low- and mixed-severity effects in Pacific Northwest dry mixed-conifer forests and supported a heterogeneous landscape resilient to disturbance and variations in climate (Hessburg and Agee 2003, Hessburg et al. 2005, Stine et al. 2014). Settlers traveling on the Oregon Trail across the Blue Mountains en route to the Columbia River remarked on the open, park-like forests, and the near ubiquitous evidence of fire (Mutch et al. 1993). As her party ascended from the Grande Ronde valley towards Pendleton in 1853, Miss Rebecca Ketcham documented that, “the country all through is burnt over, so often there is not the least underbrush, but the grass grows thick and beautiful” (Wickman 1992). Lightning and indigenous peoples ignited fires that burned every 10 – 21 years on average in the southern Blue Mountains (Johnston et al. 2016) and slightly less frequently in the northern part of the range (Heyerdahl et al. 2001). Frequent fire maintained a mosaic of fire-tolerant forests, grasslands and shrublands (Hessburg and Agee 2003), and reduced the likelihood of high-severity fire by periodically consuming ground fuels and shrubs, elevating tree crown base-heights and limiting seedling recruitment (Agee 1993, Hessburg et al. 2005).

In the years since Ms. Ketcham traversed the Blue Mountains, post-settlement land use has profoundly changed dry mixed-conifer forests. Cattle grazing began with the arrival of the first settlers. By 1860 there were 200,000 cattle in Oregon and cattle grazing in the Blue Mountains reached its peak around 1900 (Hessburg and Agee 2003). Sheep largely supplanted cattle at the turn of century, with herds peaking in the 1930s and 1940s (Johnson 1994). By the turn of the century, grazing had significantly reduced the fine surface fuels primarily responsible for fire spread in the Blue Mountains. This change in fuel structure, in conjunction with a period of above average precipitation, likely caused the initial decrease in fire activity in the late 1800s (Irwin 1994, Heyerdahl et al. 2001).

Commercial timber harvest began in the 1860s to supply local demand from miners and homesteaders. Logging rapidly increased with the completion of the transcontinental railroad in 1884, which connected sawmills in the Blue Mountains to markets hungry for railroad ties and mine timbers (Robbins and Wolf 1994). For decades, timber companies targeted the largest and most profitable individuals, particularly ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud), in a practice known as “high-grading” (Hessburg and Agee 2003). The majority of accessible ponderosa pine was cut by the early 1960s and forest practices shifted away from selective harvest to clear-cutting. Timber harvest increased significantly in the 1960s and 1970s and subsequent replanting replaced low- and variable-density forests with dense, fir-dominated stands (Johnson 1994, Hessburg and Agee 2003).

As European settlement intensified, wildfire was increasingly perceived as a threat to livelihoods and infrastructure (Hessburg et al. 2015). The US Forest Service took over the administration of the newly created Blue Mountain Forest Reserves in 1906 and by the 1930s a network of guard stations, smokechasers, and fire lookouts were in place to rapidly identify and extinguish fires (Mosgrove 1980). Firefighting became increasingly effective after World War II with the expansion of federal firefighting programs and the widespread integration of new firefighting resources like smokejumpers, helicopters, and bulldozers (Pyne 1982). Today, approximately 98% of all wildfires in the U.S are quickly suppressed before they can grow large (Calkin et al. 2015).

The combined effects of grazing and fire suppression fundamentally altered the pre-settlement fire regime. Centuries of frequent fire in the Blue Mountains came to an abrupt end in the early 1900s (Heyerdahl et al. 2001, Johnston et al. 2016). Timber harvest and fire exclusion in eastern Oregon resulted in stand density increases of several orders of magnitude, a decrease in shrub and herbaceous understory, and an increase in vertical and horizontal fuel continuity (Agee 1996, Merschel et al. 2014). In dry mixed-conifer forests on the eastern slopes of the Oregon Cascades, mean tree abundance is more than four times higher than it was in the 1920s (Hagmann et al. 2014). Mean basal area doubled, favoring Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Dougl.) Lindl.), while the mean basal area for large ponderosa pines decreased by 30-50% (Hagmann et al. 2014). The shift from early-seral, shade intolerant species like ponderosa pine, to shade tolerant, late-seral species like grand fir, has allowed for the development of dense, homogenous stands no longer be capable of supporting the patterns of pre-settlement fire (Hessburg and Agee 2003).

Widespread changes to the periodicity of fire and the structure and composition of dry mixed-conifer forests in the Blue Mountains have led to concerns that contemporary fires are more severe than fires in the past. The overwhelming majority of fires are suppressed when they are small, but this success has come at a price; when fires do escape, it is often during extreme fire weather conditions that produce equally extreme fire behavior and effects. High-severity patches significantly larger than dendrochronological estimates are common in contemporary fires in Pacific Northwest dry mixed-conifer forests, especially during hotter and drier fire seasons (Reilly et al. 2017). The historical patterns of mixed-severity fire regimes are not well understood, and there is debate about the amount of high-severity fire effects in dry mixed-conifer forests prior to European settlement (Tepley and Veblen 2015, Yocom-Kent et al. 2015, Reilly et al. 2017). Dendrochronological research from the southern Blue Mountains indicates that fire effects in dry mixed-conifer forests were low-severity and relatively homogeneous, and that pre-settlement fire was not a prominent driver of differences in dry mixed-conifer forest composition or structure (Johnston et al. 2016). Others have argued that a combination of low- and mixed-severity fire regimes supported a heterogeneous forest landscape, characterized by a mosaic of open, patchy stands that frequently burned at low-severity, and mixtures of dense and open stands that burned during less frequent, mixed-severity fires (Spies et al. 2006, Hessburg et al. 2007). Reconstructions of dry mixed-conifer forests in the Pacific Northwest using early 20th century aerial photography indicate that ~20% of pre-settlement fire effects were high-severity (canopy mortality >70%), including high-severity patch sizes as large as 10,000 ha (Hessburg et al. 2007). In contrast, estimates of high-severity patch sizes from dendrochronological fire histories range from less than an acre in ponderosa pine forests, to 10 - 100 ha in Douglas-fir/grand fir forests (Wright and Agee 2004). Such discrepancies may be due in part to the wide range of variability in dry mixed-conifer forests and the difficulty of distinguishing the dendrochronological signal of mixed-severity fire regimes and patches of high-severity (Lentile et al. 2005, Hessburg et al. 2007).

The lack of data about historical high-severity fire effects in dry mixed-conifer forests makes it difficult to anticipate the resilience of these forests to contemporary large fires. This uncertainty is compounded by the novel structure and composition of today's dry mixed-conifer forests (Yocom-Kent et al. 2015), and changing environmental conditions that appear to be reducing the ability of forests to recover from severe disturbance (Stevens-Rumann et al. 2018). Human-caused climate change has driven an increase in burned area over the last several decades (Abatzoglou and Williams 2016) and this trend is expected to continue (Rogers et al. 2011). As early as the 1970s, researchers have warned that dry mixed-conifer forests in the Blue Mountains had become more susceptible to high-severity fire (Hall 1976). These isolated voices became a chorus in the early 1990s when several consecutive years of drought, insect outbreaks, and unusually severe fires prompted some to declare "a forest health problem of catastrophic proportions" (Mutch et al. 1993). Fire activity in the Blue Mountains is increasing (Dennison et al. 2014), and the climatic conditions that support large fire growth are predicted to be significantly more common in the region over the next century (Davis et al. 2017). Despite decades of concern about the resilience of dry mixed-conifer forests to high-severity fire in the Blue Mountains, and evidence that fire activity will only increase, little is known about capacity of these landscapes to recover following high-severity fire.

The resilience of dry forest ecosystems to high-severity fire depends on the capacity stand-replacement patches to regenerate forest. The mechanisms governing post-fire seedling regeneration are complex. Seed dispersal, microclimate, edaphic conditions, competitive interactions, and seed herbivory are just some of the factors that mediate seedling establishment and survival (Wiens 1976). The presence of surviving seed source is particularly important for seed obligate tree species like ponderosa pine, Douglas-fir, and grand fir, as these species are not capable of vegetative reproduction or producing serotinus cones (Donato et al. 2009, Chambers et al. 2016, Kemp et al. 2016). Because wind is the primary dispersal mechanism for conifers, dispersal distances vary with seed weight (Vander Wall 2003, Safford 2013), and numerous studies have observed lower densities of post-fire regenerating seedlings farther from surviving seed sources (e.g., Chambers et al. 2016, Kemp et al. 2016). Conifer seeds are important food sources for birds and rodents, and seed caching rodents can increase a ponderosa pine seed's dispersal distance by as much as 80 meters from the parent tree (Vander Wall 2003). Conifer seedlings commonly establish beyond documented seed rain distances following fire, suggesting secondary dispersal is an important mechanism for colonizing stand-replacement patches, at least in some locations (Shatford et al. 2007). After a seed reaches a site, seedbed conditions, plant composition, and environmental factors determine its chances of germination and survival (Burns and Honkala 1990). Ponderosa pine, Douglas-fir, and grand fir all readily establish on bare mineral soil in burned areas. However, seedlings must compete with other species that are well adapted for rapidly colonizing burned areas, including those that seed from the soil seedbank or re-sprout after fire. Fire promotes germination from below ground seed banks for several shrub species in Blue Mountain dry mixed-conifer forests, including greenleaf manzanita (*Arctostaphylos patula* Greene) and snowbrush ceanothus (*Ceanothus velutinus* Dougl. Ex Hook). These species flourish in high-severity patches were sunlight and belowground resources are plentiful. *Ceanothus* root nodules are nitrogen fixing and play an important role in nitrogen reaccumulation after fire, but a robust post-fire shrub response can decrease conifer seed germination and seedling growth (Zavitkovski et al. 1969, Burns and Honkala 1990). In some areas, shrub cover appears to facilitate seedling establishment and survival, with higher seedling densities associated with greater shrub cover. However, it is unclear whether this is a function of beneficial microclimatic buffering or simply underlying site productivity (Shatford et al. 2007, Collins and Roller 2013, Dodson and Root 2013).

Abiotic factors interact with the availability of surviving seed source and competing vegetation to mediate the pace and trajectory of post-fire forest succession. Mixed-conifer seedlings are vulnerable to heat and drought stress (Rother et al. 2015), and increased heat insolation may be an important factor limiting forest regeneration in patches without any surviving overstory trees, especially during hot and dry years after fire (Burns and Honkala 1990). North aspects and higher elevations can buffer seedlings from heat and drought stress, and promote higher rates of establishment and survival compared to more exposed landscape positions (Chappell and Agee 1996, Collins and Roller 2013, Dodson and Root 2013, Chambers et al. 2016). Other factors influencing seedling regeneration are more difficult to measure. The species-specific amount of surviving seed source contributing to a site, interannual variation in seed production, and fine scale variability in microclimate and site quality are difficult to quantify and compare between sites, and these factors are generally not accounted for in post-fire regeneration studies.

Considerable uncertainty exists regarding the ability of Blue Mountain dry mixed-conifer forests to return to a forested condition after severe fire, and results from studies in dry forests ecosystems elsewhere suggest that post-fire forest regeneration is highly variable across regions. Forests in the Klamath Siskiyou region were recovering rapidly in stand-replacement patches 2-19 years post-fire (Shatford et al. 2007, Donato et al. 2009, Crotteau et al. 2013), and natural regeneration in the Northern Rockies appears to be adequate to return dry mixed-conifer forests to pre-fire stand densities in all but the largest high-severity patches (Kemp et al. 2016). Ponderosa pine forests in Arizona and New Mexico were reported to be recovering slowly several decades after fire, but natural regeneration was expected to reestablish forest in even the largest stand-replacement patches within 50 years of fire (Haire and McGarigal 2010).

A less promising post-fire picture has emerged from dry mixed-conifer forests in other regions. In two recent studies in the Sierra Nevada Mountains, there were no regenerating conifer seedlings in 40 – 80% of sampled locations, 2 – 11 years after 19 large fires (Collins and Roller 2013, Welch et al. 2016). Seedlings were absent three years post-fire in stand-replacement patches in South Dakota’s Black Hills (Lentile et al. 2005), and seedling recruitment in the Hayman fire in Colorado was so poor in large, high-severity patches that some areas are not expected to return to a forested condition for decades or even centuries (Chambers et al. 2016). In the eastern Oregon Cascades, Meigs et al. (2009) reported that regeneration in high-severity burned ponderosa pine stands was virtually nonexistent 4-5 years following fire, and Dodson and Root (2013) reported that seedlings were absent in 1/3 of sample plots, 10 years post-fire. Widespread recruitment failure in parts of the Northern Rockies, attributed to hotter and drier weather consistent with projected climate warming, are raising concerns that dry forests already at the edge of their climatic tolerances are at risk of conversion to non-forest states by high-severity fire (Stevens-Rumann et al. 2018). The results of these studies, which provide evidence for both forest resilience and forest vulnerability to high-severity fire, highlight the difficulty of making generalizations about post-fire forest recovery in dry forest ecosystems, and demonstrate the importance of understanding the successional trajectories of burned areas in locations like the Blue Mountains in Oregon where these questions have not previously been addressed.

Fire refugia

Fire refugia are unburned or low-severity burned patches within fire perimeters that support ecosystem resilience by contributing important structural and biological heterogeneity to post-fire landscapes. In the context of this study, fire refugia are specifically identified as patches of surviving forest that did not experience stand-replacement fire effects. The capacity of forest to reestablish following severe wildfire is strongly influenced by the pattern of organisms and structures left behind by a fire event (Turner 2010). Together with environmental conditions and land management, biological legacies like fire refugia are essential components of forest resilience (Franklin et al. 2000, Johnstone et al. 2016, Landesmann and Morales 2018). Fire refugia buffer plant communities from high-severity fire (Camp et al. 1997, Hylander and Johnson 2010, Wood et al. 2011, Ouarmim et al. 2016), provide seed sources for the reestablishment of forest in adjacent high-severity burned areas (Landesmann and Morales 2018), and provide important faunal habitat otherwise absent from burned interiors (Gandhi et al. 2001, Robinson et al. 2013, Swan et al. 2016, Vanbianchi et al. 2017). As fire seasons grow longer, large fires become more frequent, and fire’s geographic distribution shifts (Krawchuk et al. 2009, Westerling 2016, Davis et al. 2017), a deeper understanding of the ecological function and composition of fire refugia will be increasingly important for anticipating ecosystem resilience to fire in the face of rapid global change (Meigs and Krawchuk 2018).

Recent fire refugia research is part of a broader effort to identify relatively ecologically stable locations that facilitate the persistence of biological communities. Refugia have traditionally been studied by paleontologists and biogeographers, with a focus on population dynamics during historical periods of significant temperature fluctuations, such as glaciation events. Refugia were places where biota could persist and eventually disperse from when conditions improved (Stewart et al. 2010, Keppel et al. 2012). Interest in refugia of all kinds is increasing (Ashcroft 2010), and the definition is evolving as the term is applied to a range of different processes, species, and scales. Contemporary applications have resulted in contradictions in usage and some argue the potential exists for conceptual dilution and ecological ambiguity (Ashcroft 2010). To distinguish refugia from short-lived phenomenon, some scientists suggest the term refugia should be reserved for evolutionary time scales (Mackey et al. 2012, Davis et al. 2013), and that the term 'refuge' should be substituted when examining shorter time scales of minutes and decades (Keppel et al. 2012). Others argue that a similar distinction should hold for spatial scales; refugia should refer to areas large enough to support small populations (c. 100 - 10000m^2 or larger), while the term refuge should apply to areas protected from exposure and disturbance, or individual shelters like rocks and nest boxes (Ashcroft 2010, Morelli et al. 2016).

Despite efforts to curtail its spatial and temporal scope, the refugia lexicon is increasingly resonant among scientists and conservationists. Interest in current and future refugia is driven in large part by concerns about the ecologically detrimental impacts of projected climate warming. In the western US, climate change is expected to result in significant range reductions for many species, and identifying areas that promote biological diversity and adaptive capacity is increasingly a priority (Loarie et al. 2008, Ashcroft et al. 2009). Climate change refugia, referred to variously as micro-fuges, microrefugia, holdouts and stepping-stones, are places sufficiently decoupled from the regional climate to allow species to persist in situ or to facilitate migration to suitable habitats (Dobrowski 2010, Mackey et al. 2012, Morelli et al. 2016, Mclaughlin et al. 2017). Climate change appears to be altering disturbance regimes (Abatzoglou and Williams 2016, Westerling 2016), and small populations that persist in climate change refugia may still be extirpated by high-severity disturbance events that precipitate rapid ecological change (Turner 2010, Mclaughlin et al. 2017). Locations buffered from the most severe effects of floods, droughts, and fires may function as important ecological anchors that allow for systems to cope with significant environmental change, especially if they overlap with climate change refugia (Sedell et al. 1990, Magoulick and Kobza 2003, Mclaughlin et al. 2017). Recent increases in fire activity are driving an interest in fire refugia in particular, although a consensus about how to refer to low-severity or unburned patches within fire perimeters remains somewhat elusive. Acknowledging there is significant variation with regards to scale, persistence, and underlying drivers, in the interest of simplicity we follow Krawchuk et al. (2016) and use the term "fire refugia” to include fire refuges, unburned forest islands, low-severity patches, fire skips, residuals, remnants, and fire shadows (Delong and Kessler 2000, Clarke 2002, Román-Cuesta et al. 2009, Wood et al. 2011, Dragotescu and Kneeshaw 2012, Robinson et al. 2013, Vanbianchi et al. 2017).

Fire refugia are the product of fire behavior, which is itself a function of weather, fuels, and topography. Topography, being the least temporally variable of these three drivers, is associated with fire refugia that persist through multiple fire events, and these persistent refugia may support the development of late-seral forest structure (Camp et al. 1997, Ouarmim et al. 2016) and protect long-lived, fire-sensitive species from lethal fire effects (Wood et al. 2011, Landesmann et al. 2015, Adie et al. 2017). The influence of topography also allows for some degree of predictability of fire refugia occurrence, although fires burning during extreme weather events appear to override topographic controls (Román-Cuesta et al. 2009, Leonard et al. 2014, Berry et al. 2015, Krawchuk et al. 2016, Kolden et al. 2017). Fire refugia can also be the product of stochastic factors like weather, fire suppression, and fuel conditions. These refugia may be more likely to “wink out” after repeated fires, although relatively few studies have examined fire refugia pattern dynamics across multiple fire events (Haire et al. 2017, Kolden et al. 2017).

Previous studies have identified multiple ecosystem functions associated with fire refugia in forest ecosystems. Numerous animal species rely on the relatively intact forest habitat within fire refugia during and after fire. Species like ground dwelling epigaeic beetles appear to be entirely dependent on refugial habitat within burn mosaics (Gandhi et al. 2001). Fire refugia also provide important food and cover resources for a variety of mammal species, including moose in Alaska (Gasaway and DuBois 1985), bears in Arizona (Cunningham et al. 2003), lynx in Washington (Vanbianchi et al. 2017), and rodents in Australia (Swan et al. 2016). Fire-sensitive plant species that occur in fire-prone environments are particularly reliant on fire refugia. In Patagonia, fire refugia allow for the survival of fire-sensitive cypress trees during fire, and cypress seed sources that survived in fire refugia are essential for the reestablishment of forest in nearby high-severity burned areas (Landesmann and Morales 2018). Fire-sensitive Tasmanian rainforest persists in a matrix of highly flammable moorland and sclerophyll forest by preferentially occupying fire refugia that are topographically buffered from fire effects (Wood et al. 2011). Rock outcroppings in fire-prone eucalypt forests function as fire refugia by reducing fire frequency and intensity, allowing seed obligate shrubs to outcompete the resprouting species that dominate adjacent, higher-severity burned areas (Clarke 2002). Despite a growing recognition that fire refugia are an important, but perhaps understudied (Kolden et al. 2012), component of post-fire mosaics, little is known about their composition and ecological function in dry forest ecosystems in the western United States.

This project builds on a growing body of literature examining the role of fire refugia in forest ecosystems by taking advantage of a large natural experiment resulting from four recent large wildfires that burned in Oregon's Blue Mountains 12 – 17 years prior to sampling. The primary objectives were to address key knowledge gaps regarding the composition of fire refugia and their influence on post-fire forest regeneration. Specifically, Chapter 2 examines the influence of fire refugia pattern on post-fire forest recovery in high-severity burned areas. This study surveyed 135 plots in stand-replacement patches across a gradient of fire refugia density to address three research questions: (1) How does post-fire conifer regeneration vary with local and landscape fire refugia pattern? (2) How do fire severity, understory vegetation, and environmental gradients influence post-fire conifer regeneration? (3) What are the temporal patterns of seedling establishment of ponderosa pine, one prominent conifer species in the community, following stand-replacement fire?

Chapter 3 focuses on the composition of fire refugia, and compares understory plant community composition in fire refugia to the higher-severity burned matrix. We used plant community data collected in 52 fire refugia and 135 stand-replacement patches plots to address three research questions: (1) Does plant community composition differ between fire refugia and stand-replacement patches? (2) Does plant community composition differ between unburned and low-severity burned fire refugia? (3) Are there plant species strongly associated with fire refugia or stand-replacement patches? We were particularly interested in determining whether fire refugia support fire-sensitive plant communities otherwise absent from the higher-severity burned matrix, as has been reported in other systems (e.g., Wood et al. 2011, Adie et al. 2017).

Chapter 4 provides a synthesis of the findings from Chapters 2 and 3. We discuss the implications of fire refugia for forest resilience, identify management implications, and propose topics for future research.

CHAPTER 2 – INFLUENCE OF FIRE REFUGIA PATTERN ON POST-FIRE FOREST RECOVERY IN OREGON’S BLUE MOUNTAINS

Introduction

Fire regimes in dry mixed-conifer forests in the American west are substantially departed from historical reference conditions, raising concern about forests’ capacity to regenerate after stand-replacement fire. The combined effects of fire suppression, logging, and grazing have significantly altered dry mixed-conifer forest structure and composition (Hagmann et al. 2013, Merschel et al. 2014), and fire return intervals are now estimated to be an order of magnitude longer than historical averages (Reilly et al. 2017). Substantial increases in stand densities and fuel continuity are resulting in uncharacteristically severe fire effects, particularly when large fires escape initial fire suppression efforts due to extreme fire weather conditions (Miller and Safford 2012, Stephens et al. 2013). Large, stand replacement-patches resulting from high-severity fire may be slow or unable to regenerate forest due to tree seed source limitations (Haire and McGarigal 2010, Chambers et al. 2016), although the influence of landscape patterns of surviving seed source on forest reestablishment are not well understood. Additionally, evidence is emerging that recent hotter and drier conditions, consistent with climate change, are increasing physiologically stressful conditions for reestablishing seedlings, and limiting the capacity of some forests to regenerate following high-severity fire (Donato et al. 2016, Tepley et al. 2017, Stevens-Rumann et al. 2018). Predicted increases in fire activity and climate warming are heightening concerns that high-severity fire effects will precipitate transformations of forests to grass- or shrub-dominated, alternative stable states (Stephens et al. 2013, Dobrowski et al. 2015, Rother et al. 2015, Coppoletta et al. 2016). Understanding the patterns and drivers of post-fire forest regeneration across the gradient of environmental variability that constitutes the range of dry mixed-conifer forests is important to evaluating the resilience of these forests to the effects of large fire events.

Fires create burn severity mosaics that include unburned and low-severity patches, referred to here as fire refugia, which are important for the ecological stability of forest ecosystems. Fire refugia can contribute heterogeneity to the post-fire landscape due to the fire-sensitive plant communities and late-successional forest structure they contain (Camp et al. 1997, Wood et al. 2011, Ouarmim et al. 2016), and by providing less-disturbed habitat where individuals and populations can persist during and after fire (Gandhi et al. 2001, Robinson et al. 2013, Swan et al. 2016). Fire refugia can also be important drivers of post-fire forest recovery because of the seed sources they provide to adjacent higher-severity burned areas (Landesmann and Morales 2018). In stand-replacement patches where fire has killed overstory trees, conifer regeneration relies on seeds dispersed from surviving trees in fire refugia or from seed sources outside the fire perimeter. Average dispersal distances are primarily a function of seed weight (Vander Wall 2003, Safford 2013) and numerous studies have reported that distance to nearest 'refugial' seed source is a key control on post-fire conifer regeneration (Donato et al. 2009, Harvey et al. 2016, Kemp et al. 2016, Owen et al. 2017). However, burn mosaics in forests are spatially complex, and multiple seed sources are likely to influence a site's capacity to regenerate forest. One-dimensional measures of distance to nearest seed source are unable to capture this complexity. Quantifying the landscape pattern of fire refugia in a way that accounts for the additive effect of multiple seed sources across the landscape may provide a more ecologically relevant metric for understanding variability in post-fire forest regeneration. Haire and McGarigal (2010) reported that scaled seed dispersal kernels, a landscape measure of surviving seed source pattern, were strong predictors of post-fire seedling abundance in southwestern ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud) forests. Their results suggest that the landscape pattern of refugial seed source may be an important, but underappreciated, driver of post-fire dry mixed-conifer forest recovery.

Abiotic and biotic factors interact with the availability of surviving seed source to mediate the pace and trajectory of post-fire forest succession. Conifer seedlings are vulnerable to heat and drought stress (Rother et al. 2015), and heat from insolation may be an important factor limiting post-fire seedling establishment in stand-replacement patches, especially during hot, dry years (Burns and Honkala 1990). North aspects, higher elevations, and shade from surviving trees can buffer seedlings from heat and drought stress, and promote higher rates of establishment and survival compared to more exposed landscape positions (Chappell and Agee 1996, Collins and Roller 2013, Dodson and Root 2013, Chambers et al. 2016). We anticipate that climatic and topographic variability results in heterogeneous seedling regeneration patterns in stand-replacement patches. Additionally, conifer seedlings must compete with other species that are well adapted for rapidly colonizing high-severity burned areas. A robust post-fire shrub response following high-severity fire in dry mixed-conifer forests is common (Powell 1994), and dense shrub cover can decrease conifer seed germination and seedling growth (Zavitkovski et al. 1969, Burns and Honkala 1990). However, shrub cover in stand-replacement patches may also ameliorate unfavorable environmental conditions, facilitating conifer establishment and survival in some cases (Shatford et al. 2007, Collins and Roller 2013). It remains unclear how shrub cover influences conifer germination and survival following high-severity fire across the range of dry mixed-conifer forests.

Prior studies of post-fire regeneration in dry forests of the western United States report widely divergent recovery trajectories. Seedlings were rapidly regenerating in the southern Cascades and Klamath-Siskiyou region 2 - 19 years after fire (Shatford et al. 2007, Donato et al. 2009, Crotteau et al. 2013), and in the Northern Rockies, Kemp et al. (2016) predicted that natural regeneration would be adequate to return landscapes to pre-fire stand densities in all but the largest high-severity patches, based on data collected 5 – 13 years post-fire. In southwest ponderosa pine forests, natural regeneration in stand-replacement patches was expected to reestablish forest within 50 years after fire, even in the areas farthest from refugial seed source (Haire and McGarigal 2010). In contrast, slow, or even absent regeneration has been reported in other regions. Conifer seedlings were not present in 40 – 80% of plots, 2 – 11 years post-fire in the Sierra Nevada Mountains and California Coast Range (Collins and Roller 2013, Welch et al. 2016), and seedlings were entirely absent in stand-replacement patches three years after a large fire in South Dakota’s Black Hills (Lentile et al. 2005). Conifer regeneration following the Hayman fire, Colorado’s largest on record, was so poor that Chambers et al. (2016) predicted that some stand-replacement patches would not return to a forested condition for decades or even centuries. Additionally, evidence is emerging that post-fire drought conditions, consistent with climate change, are decreasing forest resilience to high-severity fire effects and resulting in widespread regeneration failure (Stevens-Rumann et al. 2018). Some dry forests may be near a “tipping point,” as climate warming slows post-fire forest regeneration and increases fire activity. These locations may be unable to recover between fire events, resulting in extensive forest loss (Tepley et al. 2017). The results of these studies, which provide evidence for both forest resilience and forest vulnerability to high-severity fire, highlight the importance of understanding post-fire regeneration patterns across different geographic regions that contribute to the gradient of environmental variability in western forests.

In this study, we quantify conifer seedling regeneration in stand-replacement patches within four large fires that occurred in Oregon’s Blue Mountains to examine the influence of fire refugia pattern on forest reestablishment. Although there has been concern about the vulnerability of Blue Mountain forests to high-severity fire for decades (Hall 1976), their capacity to recover following stand-replacement fire effects is unknown. Fire activity in the Blue Mountains is expected to increase substantially as the climate warms in the coming decades (Rogers et al. 2011, Davis et al. 2017), and post-fire successional trajectories have important regional implications for long-term forest resilience. The Blue Mountains provide an opportunity to examine post-fire forest regeneration across broad temperature and precipitation gradients, and new methods for characterizing landscape-scale fire refugia pattern as estimates of seed source using high-resolution aerial imagery may offer novel insights into the key drivers of post-fire forest recovery. Focusing on landscapes that burned between 2000 and 2005 we asked: (1) How does post-fire conifer regeneration vary with local and landscape patterns of fire refugia, representing different scales of seed source availability for tree regeneration? (2) How do fire severity, understory vegetation, and environmental gradients influence post-fire conifer regeneration in conjunction with patterns of fire refugia? (3) What are the temporal patterns of seedling establishment of ponderosa pine, one prominent conifer species in the community, following stand-replacement fire? Based on our knowledge of post-fire regeneration dynamics in other dry forest ecosystems, we expected higher conifer regeneration densities in areas closer to surviving seed sources and in locations where more forest survived fire in refugia. We anticipated that seedling regeneration would be positively associated with fire severity (as a proxy for pre-fire biomass and site productivity), lower amounts of competing woody vegetation, higher elevations, and cooler, wetter climatic conditions. Lastly, we expected an initial pulse of post-fire ponderosa pine establishment followed by a gradual decrease in establishment as sites became fully occupied by competing woody vegetation.

Methods

Study region

The Blue Mountain ecoregion extends from central Oregon east to the Snake River Plain near the Idaho border, and north to the Columbia River in southeastern Washington (Figure 2.1). Composed of a series of small sub-ranges bisected by rugged river canyons, the Blue Mountains are topographically and biologically complex. The majority of precipitation falls in the winter as snow, and thunderstorms that ignite wildfires are common during warm, dry summers (Burns 1983). The Cascade Mountains to the west effectively block marine air masses from reaching the drier, southern portion of the range (Johnson and Clausnitzer 1992), while the Columbia River provides an ingress for these systems, resulting in a comparatively cooler and wetter climate in the northern Blue Mountains (Heyerdahl et al. 2001). The forested extent of the Blue Mountains spans broad environmental gradients: the 30-yr average maximum temperature in August ranged from 16°C to 34°C, and average minimum temperature in January ranged from -12°C to -1°C. The 30-yr average annual precipitation ranged from 20 to 180 centimeters (PRISM).

Dry mixed-conifer forests in the Blue Mountains occupy the warmer, drier portions of these climatic gradients, and are composed primarily of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and lesser amounts of western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Douglas var. latifolia). Grand fir and white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) hybridize across their ranges in Oregon (Ott et al. 2015), and we refer to their variants here as grand fir. Dry mixed-conifer forests in the Blue Mountains contain components of western juniper (*Juniperus occidentalis* Hook.) at hot and dry, lower elevation sites, and Engelmann spruce (*Picea engelmannii* Parry ex Englm) and subalpine fir (*Abies lasiocarpa* Hook) at the highest elevation sites.

Fire burned frequently in the Blue Mountains prior to fire exclusion beginning in the late 1800s. Pre-settlement fire return intervals in the southern Blue Mountains were between 10 to 21 years on average (Johnston et al. 2016), and slightly longer in the northern part of the range where the climate is cooler and wetter (Heyerdahl et al. 2001). Frequent historical fire produced a range of low- and mixed-severity effects that supported a heterogeneous landscape resilient to disturbance and variations in climate (Hessburg and Agee 2003, Hessburg et al. 2005, Stine et al. 2014). Contemporary fire return intervals for ponderosa pine and Douglas-fir/grand fir forests in the Pacific Northwest are now estimated to be 265 to 380 years, an order of magnitude longer than prior to fire exclusion, and the amount and scale of high-severity fire effects is widely considered outside the historical range of variability (Reilly et al. 2017).

Study design

We collected data in the summer of 2017 in 135 plots in four large fires that burned in the years 2000, 2002, and 2005, 12 – 17 years prior to sampling (Figure 2.1, C - E). We selected fires that burned primarily in designated roadless or wilderness areas to minimize the influence of pre- and post-fire management, and we avoided areas for which we had a record of pre- or post-fire timber harvest, fuels treatments, or tree replanting. All fires were lightning caused. We sampled exclusively in areas forested prior to fire that experienced 100% overstory mortality within our plots, along a gradient of landscape fire refugia pattern.

Fire refugia used to characterize landscape fire refugia patterns were identified as patches of surviving overstory tree canopy. In the context of this study, fire refugia represent potential seed sources for forest reestablishment, and landscape-scale fire refugia patterns characterize this feature in two dimensions. We mapped fire refugia using post-fire aerial imagery at 1 meter resolution from the National Agriculture Imagery Program (NAIP). Our processing follows Chambers et al. (2016), modified by collaborators in our research group as described in Walker et al. (in prep.) and summarized here. Aerial imagery provides a finer resolution compliment to widely used Landsat burn severity products, allowing us to accurately map the extent of fire refugia within fire perimeters. NAIP imagery was acquired for 2012 and 2014, resulting in images 7 to 14 years post-fire for our study fires. Images were classified with a maximum likelihood algorithm using training samples, to produce 1 meter resolution raster grids with two classes, “refugia” and “non-refugia” (Figure 2.1, C – F). Classified rasters were subsequently converted into polygons based on a simple rule set: all adjacent refugia were considered members of the same polygon; remaining polygons at a distance of 20 meters or less were aggregated; and holes less than 50 meters^2 were closed. The layers were edited manually, but to a limited degree, to remove any un-forested areas and to contain all tree canopies. The refugia polygon maps were validated using the source 1 meter NAIP imagery (total accuracy = 0.92 – 0.95, Cohen's kappa = 0.84 – 0.90) and ground-truthed using data collected in the field (total accuracy = 0.90 – 0.95, Cohen's kappa = 0.80 – 0.89).

The landscape pattern of fire refugia, referred to here as the landscape fire refugia density (FRD), was calculated from the refugia polygon maps described above. For each 1 meter pixel, FRD values were based on the amount of fire refugia cells within a 300 x 300 meter^2 moving window, using a distance-weighted density approach. Within the moving window, the value of each cell (1 = refugia, 0 = non-refugia) was divided by its distance from the focal cell. These values were then summed to produce the landscape FRD metric for each focal cell:

$$FRD = \sum_{i=1}^{n} 1/(d+1)$$

The result is a continuous metric ranging from zero in areas where fire refugia are absent, to approximately 1000 in areas saturated with fire refugia. The choice of window size was based on observed seed dispersal distances from prior studies - our 300 meter window size integrates seed source within 150 meters of the focal cell. Although Kemp et al. (2016) reported that the probability of seedling presence was low beyond 95 meters in similar forests in the Northern Rockies, studies in dry mixed-conifer forests in the Klamath-Siskiyou region reported that longer dispersal events (>95 meters) were common (Shatford et al. 2007, Donato et al. 2009). Based on these studies and others, and given the goal of quantifying refugial seed source at an ecologically relevant scale across the landscape, we felt that a 300 meter window size was a reasonable *a priori* estimate of the scale at which landscape fire refugia pattern influences post-fire tree regeneration. We refer to this NAIP-based metric as landscape FRD or landscape-scale refugial seed source.

We generated a population of random sample points stratified along the landscape FRD gradient for each study fire, focused on sites that experienced stand-replacement fire effects. We identified areas of stand-replacing/high-severity fire in the landscape using the Normalized Burn Ratio (dNBR) derived from 30 meter Landsat TM+ satellite imagery from the Monitoring Trends in Burn Severity (MTBS) project. From the dNBR products we constrained sampling to areas that experienced moderate/high or high-severity (>440 dNBR, Key and Benson 2006). We expected this constraint would exclude areas like grasslands, scree fields and bare ground that were not forested prior to fire. The dNBR constraint was not imposed in the case of our smallest study fire (Figure 2.1 F: Burnt Cabin, 800 ha), although sampling remained restricted to areas forested prior to fire that experienced stand-replacement fire effects based on assessments made in the field. We excluded all areas within 150 meters of fire perimeters and roads to minimize the influence of seed sources outside of the fire perimeter, and to avoid the locations most heavily impacted by fire suppression activities. To facilitate access, all sample sites were within one kilometer of a road or trail, and no further than three kilometers from a road.

Final site selection was made in the field based on four rejection criteria and a range of environmental criteria. We rejected plot locations if: (a) there was no evidence of forest prior to fire, (b) locations exhibited potentially confounding management histories, (c) surviving pre-fire trees (i.e., fire refugia) were present in the sample plot, or (d) the terrain was inaccessible or unsafe. Plot locations were separated by a minimum distance of 150 meters to reduce possible spatial autocorrelation. While abiotic gradients were not explicitly included in our stratification, we attempted to representatively sample the range of aspects and elevations available within each fire while attending to our other constraints.

Field data collection

Field data were collected from 5.64 meter radius circular plots (100 m^2) in areas that burned with stand-replacing effects. To characterize seedling regeneration we tallied all established post-fire tree seedlings within each plot according to species. To determine the structure and composition of regenerating seedlings, we recorded species identity, height, diameter at breast height (if height was >1.37 m) for the three individuals of each tree species closest to plot center. Seedlings were recorded as overtopped if they were growing beneath the shrub canopy and no part of the seedling had emerged above the shrub canopy. Emergent seedlings, defined as seedlings that germinated in the spring of the year of sampling, were excluded because we anticipated many would not persist through the growing season. Where ponderosa pine seedlings were present, we estimated establishment dates for the three seedlings closest to plot center by counting branch whorls.

We quantified plot structure and composition to provide context for the tree recruitment data. We recorded the species identity and diameter at breast height for all snags and downed trees that were present prior to fire and rooted in the plot, and converted these measurements into an estimate of pre-fire basal area. We relied primarily on bark color and texture to determine the species of dead trees, and a definitive determination was not always possible due to bark loss or decay. Elevation, aspect, slope position, and slope shape (flat, convex, or concave) were recorded for each plot. Canopy cover at plot center was measured at four cardinal directions using a convex spherical densitometer. We estimated percent ground cover of rock, gravel, bare soil, litter, downed wood, cryptogams, and plant base within each plot. Plant base was defined as the surface area occupied by living plant material at ground level. For all vascular plant species occupying greater than 0.25% of the plot area (25 cm^2) we recorded the species identity, maximum height, and estimated percent cover. Spatial locations were recorded for each plot using a handheld GPS (Garmin GPSMAP 64).

We measured the distance to the three closest living, pre-fire seed sources for each species observed in the plot. Distances were quantified using a laser rangefinder (TruPulse 200) from plot center. When seed sources for a particular species were beyond the range of the laser rangefinder (~500 meters) or not visible from plot center, we assigned a value of 600 meters to represent distances >500 meters in analyses. Metrics based on measurements of distance to seed source are referred to here as field-scale refugial seed source.

To validate ponderosa pine age estimates collected in our sample plots, we collected a sample of seedlings and cross-referenced whorl-based age with age based on growth rings. We opportunistically sampled seedlings outside of wilderness areas within all four fires. We cut 21 ponderosa pine seedlings at the root-shoot boundary and cross-sections from the samples were finely sanded until the cell structure was visible with a binocular microscope (AmScope, 45X). We counted the number of growth rings for each sample and compared these counts to our field-based, whorl-count age estimates. Our ultimate goal was to characterize temporal trends in ponderosa pine seedling establishment and identify relationships with annual climate conditions.

Climate environment

We collected existing, digital environmental data to characterize the climate space associated with each field plot. We calculated heat load to characterize the local microclimate for each plot location. Heat load is a unitless, continuous variable calculated by folding aspect along the southwest-northeast axis, which is then combined with slope and latitude to estimate the potential annual solar radiation a site receives (McCune and Keon 2002, Equation 3). We calculated mean annual temperature, mean annual precipitation, and mean annual climate moisture deficit (CMD) data for each plot to examine post-fire regeneration along climatic gradients. Data were acquired from Climate WNA, an application that allows users to download monthly climate data from moderate spatial resolution (800 x 800 meter) grids to point locations (Wang et al. 2016). We used Hargreaves CMD as an annual metric that is the sum of the monthly difference between reference evaporation and precipitation (Zhao et al. 2012). Climate data were acquired for 2000 to 2015 and averaged across years for each plot location to characterize the general contemporary climatology of each plot. We included climate data for post-fire years only, beginning with year of burn, to quantify the post-fire conditions experienced by regenerating seedlings. For example, climate data assigned to sample plots in the 747 fire, which burned in 2002, were averaged from the 2002 – 2015 data.

Data analysis

We generated summary statistics from our seedling data to characterize the amount and composition of conifer seedlings regenerating in stand-replacement patches. We calculated the percentage of plots occupied by each species to identify the most widespread regenerating species, and totaled seedling counts for each species to determine the most abundant regenerating species. In addition, we calculated the mean and median seedling densities for each conifer species across all sample plots. To understand the relationship of non-tree, woody vegetation with regenerating seedlings, we calculated the average height for each conifer species, the percentage of each species overtopped by shrubs, and the mean percent shrub cover. Lastly, we used boxplots to examine seedling densities across plots and among fires.

We used statistical models to examine the variability in post-fire conifer regeneration among plots as a function of refugial seed source (field- and landscape-scale), and site characteristics including: elevation, understory vegetation, fire severity, pre-fire basal area, and climate environment gradients. We fit generalized linear mixed models for ponderosa pine, Douglas-fir, and grand fir individually, as well as a model for all conifer species combined. The all-conifer model included our three focal species, as well as western larch, subalpine fir, Engelmann spruce, and western juniper. We considered both negative binomial and zero-inflated negative binomial models, and included a random effects term for fire to account for variability in seedling counts not otherwise explained by our fixed effects model parameters.

We identified the best subset of field- and landscape-scale refugial seed source metrics to parsimoniously represent surviving seed source contributing to post-fire regeneration in the study plots. We considered a number of different field-scale metrics of surviving seed source for inclusion in our models. For species-specific models, we considered minimum, median, and mean distance to nearest species-specific seed source. For the model including all conifer species, we considered minimum, median, and mean distance to surviving seed source of any species. We calculated mean and median distances to nearest seed source based on the distance to the three nearest surviving, pre-fire trees measured in the field. When fewer than three seed sources were visible, or one or more seed sources were beyond the range of the laser rangefinder, we averaged only measured distances and did not include the 600 meter placeholder value. When no seed sources were visible from plot center or within the range of the laser rangefinder, we substituted 600 meters for our distance metrics.

We fit each model with a single metric of surviving seed source from the field data, as well as a combined model including both a field-scale metric and landscape FRD. We compared all surviving seed source metrics based on ΔAIC (Akaike information criterion), relative to a null model. Models were fit for our three focal species, as well as all species combined.

To understand the spatial variability of post-fire conifer regeneration as a function of both abiotic and biotic factors, we combined the seed source metrics that explained the most variability in observed post-fire seedling abundance with our suite of site characteristics. Site characteristics considered for inclusion in our final models were chosen based on results from similar studies, as well as our own experience in the field. Data included refugial seed source (field- and landscape-scale), and site characteristics including: elevation, understory vegetation, fire severity, pre-fire basal area, and climate environment gradients. We examined all site characteristics for collinearity (Spearman's rho > 0.7), and removed temperature from the analysis because it was collinear with elevation. We selected elevation rather than temperature because we believed these data were more accurate and precise than the 800 x 800 meter, interpolated temperature data. Mean annual precipitation was collinear with CMD, and we chose to exclude precipitation in favor of CMD because it integrates both precipitation and temperature data. Exploratory plots provided some evidence of a non-linear relationship between observed seedling densities, and elevation and CMD gradients (Appendix 1). Species often respond to environmental gradients non-linearly (Whittaker 1960), especially across broad environmental gradients like the ones we sampled here. To account for what appeared to be a non-linear response, we included a quadratic term for elevation and CMD in our final models, in addition to linear terms. We tested for an interaction between shrub cover and CMD because we predicted that seedling recruitment might diminish in hotter, drier locations due to physiological stress, but that shrub cover could ameliorate those unfavorable climatic conditions. We tested the sensitivity of our models to the placeholder value of 600 meters for the field-scale refugia metric, which we included when a seed source for a particular species was either not visible from plot center or beyond the range of the laser range finder. We substituted larger values (1000, 2000 meters) to determine if parameter estimates or the statistical significance of our estimates changed substantially. Substituting larger values (1000, 2000 meters) did not significantly change parameter estimates ($\Delta < 0.001$) or the statistical significance of any parameter estimates.

Final statistical models including metrics of field- and landscape-scale refugial seed source and site characteristics were used to identify the key drivers of post-fire regeneration for our three focal species and all species combined. We evaluated the significance of model parameters based on p-values ($\alpha = 0.05$) and ΔAIC relative to a full model; these metrics pull from frequentist and information theoretic statistical perspectives and are closely related mathematically (Murtaugh 2014). We quantified the effect size of surviving seed source parameters to interpret the influence of fire refugia pattern of post-fire forest regeneration. All analyses were implemented using the R statistical program (ver. 3.4.0, R Core Team 2017). Model fitting and selection was performed using glmmTMB (Brooks et al. 2017) and model predictions were generated using lme4 (Bates et al. 2014).

To examine relationships between temporal trends in ponderosa pine seedling establishment and annual climate conditions we averaged annual CMD for each fire. For each year, we plotted CMD values and the number of ponderosa pine established, for each fire. We examined these plots to identify relationships between establishment dates and landscape-scale climate variability.

Results

Post-fire conifer regeneration was present in 83% of sampled plots. Regeneration densities varied by five orders of magnitude, ranging from 0 to 67800 stems ha^{-1}. The median seedling density for all plots was 1100 stems/ha^{-1} (Table 2.1). We documented 7,313 post-fire conifer seedlings. The most widespread species were ponderosa pine, grand fir, and Douglas-fir (Figure 2.2A), which were present in 61%, 54%, and 47% of plots, respectively, and these species accounted for 54% of recorded seedlings. Western larch and lodgepole pine were less widespread, occurring in 30% and 28% of plots, respectively. Both larch and lodgepole tended to regenerate at high densities when present and accounted for 39% of seedlings tallied (Figure 2.2B). The remaining 7% of seedlings consisted of western juniper, Engelmann spruce, subalpine fir, western white pine (*Pinus monticola* Dougl. Ex D. Don), and whitebark pine (*Pinus albicaulis* Engelm).

For three seedlings of each species in each plot, if present, we recorded height, and whether or not the seedling was overtopped by shrubs. A total of 1290 seedlings were measured. The mean height for all seedlings was 100 cm (SE = 0.03), with ponderosa pine, Douglas-fir, and grand fir seedlings shorter on average than western larch and lodgepole pine (Table 2.1). Shrubs overtopped 40% of measured seedlings, although the percentage overtopped varied considerably by species (Table 2.1). Seedlings classified as not overtopped by shrubs were either not growing in close proximity to shrubs, or had grown above the shrub canopy (Figure 2.3).

We sampled across broad environmental gradients. Plot locations ranged in elevation from 900 meters to 2140 meters (mean = 1600 meters), and CMD ranged from 340 to 720 (mean = 505). Average fire severity according to dNBR was 560 (152 – 966), and average pre-fire basal area was 17.4 (0 – 78) m^2 ha^{-1}. Average shrub cover was 54% (Figure 2.4B), and only one plot had 0% shrub cover. Average shrub height was 0.92 meters (± 0.07 SE), slightly lower than the average seedling height. *Ceanothus velutinus* and *C. sanguineus* were the dominant shrub species and occurred in 88% of plots, averaging 33% cover where present. Other common shrub genera included *Rosa spp*., *Arctostaphylos spp*., *Symphoricarpos spp*., *Salix spp*., and *Ribes spp*.

The availability of surviving seed source varied substantially surrounding stand-replacement patches in our study fires. The mean distance to nearest seed source recorded in the field was 53 meters, and distances ranged from six meters (just outside the 5.64 meter plot radius) to 600 meters (estimated, beyond the range of our laser rangefinder). According to our field data, mean distances to seed source for ponderosa pine, Douglas-fir, and grand fir were 119 meters, 98 meters, and 169 meters, respectively. Mean landscape FRD across all plots was 275, with a range of 0 (no refugia cells within 300 x 300 $meter^2$ window) to 750 (approximately 75% of cells classified as refugia within 300 x 300 $meter^2$ window). Field-based estimates of average distance to nearest seed source were similar to results inferred from our 1 meter resolution maps of fire refugia. The mean distance to nearest seed source (according to our fire refugia maps) within our study fires ranged from 67 meters (747 fire) to 120 meters (Hash Rock fire), and maximum distance to nearest seed source within our study fires ranged from 335 meters (747 fire) to 580 meters (Roberts Creek fire) (Walker et al. in prep). Appendix 1 includes a comparison of observed distance to nearest seed source values from the field and estimated distance to seed source values derived from our fire refugia maps.

We considered both negative binomial and zero-inflated negative binomial models because our seedling count data were highly right-skewed and counts varied by several orders of magnitude. Negative binomial models were ultimately chosen because they adequately accounted for the over-dispersion in the data (Appendix 1), and they performed as well as or better than the more complex, zero-inflated negative binomial models, according to AIC. We examined the scaled residuals from our models with variograms and bubble plots and did not detect evidence of residual spatial autocorrelation. We chose not to include lodgepole pine regeneration data in the all-conifer model because we expected this species would not be as dependent on refugial seed source because of its capacity to produce serotinus cones. Additionally, unlike other conifer species, many lodgepole pine seedlings established post-fire were already producing cones, and ongoing lodgepole regeneration did not appear reliant on trees that survived fire in refugia.

We identified mean distance to nearest seed source and landscape FRD for inclusion in our final statistical models of seedling recruitment based on our exploratory analysis of seed source metrics (Table 2.2). It was necessary to choose between the three strongly related distance variables: minimum, median, and mean distance to the three nearest seed sources identified in the field. These distance metrics were species-specific for our ponderosa pine, Douglas-fir, and grand fir models, but for the all species model they were based on the distance to seed source of any species. Landscape FRD was agnostic to species composition in fire refugia because aerial imagery did not allow us to discriminate between species. There was some evidence that mean distance to seed source explained more variability in the data than minimum and median distance in models of Douglas-fir regeneration, and we used this as the basis for choosing mean distance to seed source (hereafter, distance to seed source) as our field-scale metric of refugial seed source pattern. Ponderosa pine and Douglas-fir models that included both distance to nearest seed source and landscape FRD outperformed other models with a single seed source metric. For models of grand fir regeneration and all species combined, landscape FRD explained more of the variability in the regeneration data than field-scale distance to seed source alone (Table 2.2). Combined models (distance to seed source + FRD) represented substantial improvement over null models fit with only an intercept term for our three focal species and all species combined (Table 2.2). We considered both distance to seed source and landscape FRD important, complimentary sources of information about surviving seed source pattern, and we chose to include both in all of our final models.

Final models demonstrate spatial variability in post-fire regeneration as a function of both site characteristics and surviving seed source (Table 2.3). Field-based distance to seed source was negatively associated with seedling regeneration in all models, but was not significant (p-value > 0.05) in the case of grand fir (Figure 2.5). Landscape FRD was positively associated with post-fire conifer regeneration in all of our models, after accounting for distance to seed source, fire severity, elevation, CMD, heat load, pre-fire basal area, and shrub cover (Figure 2.5). Plots of observed seedling densities along distance to seed source and landscape FRD gradients are included in Appendix 1. We quantified the effect size of surviving seed source parameters by comparing model predictions for low (25th percentile of observed) and high (75th percentile of observed) values of distance to seed source and landscape FRD, while holding all other model parameters constant at their median values. In all four models, predicted seedling densities increased with landscape FRD, and decreased with distance to seed source (Table 2.4). The standard deviation of the random effect term, which we included to account for variation between fires, was 0, 0.57, 0.93, 0.92 for our ponderosa pine, Douglas-fir, grand fir, and all species models, respectively.

While surviving seed source was an important driver of post-fire regeneration in all of our models, the influence of site characteristics varied between models. Douglas-fir regeneration was positively associated with burn severity and negatively associated with heat load. Shrub cover was positively related with ponderosa pine regeneration, but was not associated with Douglas-fir, grand fir, or all species combined. We found evidence in all of our models of non-linear relationships between both elevation and CMD, and seedling regeneration. With the exception of a positive relationship between ponderosa pine regeneration and CMD, elevation and CMD were not associated with seedling densities in any models fit without squared terms for these parameters (Appendix 1). There was no evidence of an interaction between CMD and shrub cover for any species, and we did not include the interaction in final models.

To examine the temporal pattern of post-fire ponderosa pine regeneration after stand-replacing fire we estimated establishment dates for 327 ponderosa pine seedlings in the field using whorl-counts. Validation of establishment date estimates based on 21 seedling cross-sections demonstrated that we underestimated seedling age using whorls by an average of 2 years. We attempted to correct for bias in our estimates by subtracting two years from establishment dates, but acknowledge that there is significant uncertainty associated with these data. Our data show that regeneration is ongoing across all fires, as illustrated by Figure 2.7. The peak period of seedling establishment varied between fires, occurring as early as 5 years post-fire (Burnt Cabin and Roberts Creek) and as late as 11 years post-fire (747). Younger seedlings were more likely to be overtopped by shrubs than older seedlings. Overall, ponderosa pine seedling establishment shows no association with variability in annual climatic moisture deficit, although there is an increase in establishment in Burnt Cabin that coincides with a decline in moisture deficit in 2010. We chose not to pursue a formal analysis of the relationship between establishment dates and climate because of the uncertainty related to our seedling age estimates.

Discussion

Dry mixed-conifer forests in the Blue Mountains of Oregon show evidence of resilience to high-severity fire effects, 12 – 17 years post-fire. In contrast to slow or absent post-fire forest regeneration reported in dry forests in other regions (Collins and Roller 2013, Chambers et al. 2016, Welch et al. 2016), conifer seedlings in our study area were widespread, indicating that these forests have capacity to recover following stand-replacement fire effects. Our results demonstrate that seed sources that survived fire in refugia are critically important for post-fire forest recovery. Consistent with previous studies (Donato et al. 2009, Chambers et al. 2016, Harvey et al. 2016, Kemp et al. 2016, Owen et al. 2017), we found that proximity to surviving seed source is a key driver of post-fire conifer regeneration. Our high-resolution maps of landscape fire refugia pattern allowed us to provide novel insights into the importance of landscape patterns of surviving seed source, and the additive effect of multiple seed sources contributing to a site's capacity to regenerate forest. Although stand-replacement patches in our study fires have been largely converted from forests to shrublands 12 – 17 years post-fire, we did not find evidence of a competitive interaction between regenerating conifers and shrubs. In addition, many seedlings appear to have recently emerged above the shrub canopy, suggesting these sites have not been permanently "captured" by woody understory species (Savage and Mast 2005). Unlike other dry forest systems that appear to be transitioning to alternative, stable states following high-severity fire (Savage and Mast 2005, Coop et al. 2016, Tepley et al. 2017), we anticipate that in the absence of subsequent disturbance (e.g., reburn), dry mixed-conifer forest in the Blue Mountains will recover following stand-replacement fire, provided adequate seed sources survived fire within refugia. However, high-severity fire in our study resulted in substantial losses of mature forest structure that will take decades to be replaced, and it is not clear the degree to which regenerating forest in stand-replacement patches is representative of pre-fire forest composition.

This study contributes to a growing body of literature demonstrating the variability in post-fire forest regeneration among different dry forest ecosystems. Post-fire seedling densities in our study are consistent with previous research on early forest succession after high-severity fire in similar forest types in the Northwest. In the Klamath-Siskiyou region of Oregon, Donato et al. (2009) reported median seedling densities of 1721 – 1603 seedlings ha^{-1} two to four years post-fire, and Shatford et al. (2007) reported an average seedling density of 1694 ha^{-1}, 9 – 19 years post-fire. In the southern Cascades, median conifer seedling density in high-severity patches was 715 seedlings ha^{-1}, nine to 10 years after fire (Crotteau et al. 2013). Post-fire regeneration was even more rapid and robust in dry mixed-conifer forests in the Northern Rockies, where mean seedling densities were as high as 8153 seedlings ha^{-1}, five to six years post-fire (Kemp et al. 2016). We observed seedlings in over 80% of our study plots and a median seedling density across all plots of 1100 seedlings ha^{-1}, results that contrast sharply with other post-fire landscapes in parts of California and the Southern Rockies. Seedlings were present in less than half of sample plots two – 11 years post-fire in the northern Sierra Nevada Mountains (Collins and Roller 2013). Only 25% of plots contained seedlings 11 – 18 years post-fire in the Colorado Front Range and seedling densities in high-severity patches averaged just 118 seedlings ha^{-1} (Chambers et al. 2016). Our study, the first of its kind in the range of environmental conditions supported by the Blue Mountains of Oregon, highlights the importance of studying post-fire forest recovery across the range of dry forest ecosystems in the American west, and our results contribute to a growing recognition that variability between regions defies broad generalizations about the resilience of dry forests to high-severity fire effects (Collins and Roller 2013).

Large patches of high-severity fire in dry mixed-conifer forests are raising concerns that forest will be unable to regenerate in locations far from surviving seed sources. Observed declines in seedling abundance with increasing distance to seed source suggest that post-fire recovery in stand-replacement patches that are significantly larger than those within our study fires may be slow or unable to regenerate forest. Our models predicted a 28 – 43% decrease in seedling abundance, depending on species, when distance to seed source increased from the 25th percentile (average across models = 33m) to the 75th percentile (average across models = 135m) of observed values. Despite steep declines in regeneration with distance to seed source, widespread regeneration in our study area indicates that adequate seed source is present in most areas. Seedlings were absent in 23 of our study plots, but we failed to identify any distinguishing features of these plots, indicating that there are other factors limiting seedling germination and survival that we did not account for in this study. Plots that did not contain seedlings were relatively close to a surviving seed source (median distance to nearest seed source = 27 meters), indicating that seed availability was not the key constraint in most of these locations. Additionally, the area within stand-replacement patches far (>150m) from a refugial seed source was relatively small across our study fires, ranging between 3% (747 fire) to 13% (Hash Rock fire). Although we sampled relatively few locations (3 plots) that were very far (>300 meters) from a surviving seed source, we believe that our sampling reasonably approximated the distribution of distances to nearest seed source in our study area according to our NAIP-based fire refugia maps (Appendix 1) However, contemporary fires are capable of creating much larger stand-replacement patches than those within our study fires (Reilly et al. 2017, Walker et al. in prep). The pace of forest recovery we identified here may not be representative of larger stand-replacement patches in recent fires burning through dry mixed conifer forests reported elsewhere (Chambers et al. 2016, Haffey et al. 2018).

We have advanced research on the drivers of post-fire regeneration by providing evidence that the landscape pattern of surviving seed source is an important control on forest regeneration following high-severity fire. The positive association we found between post-fire seedling density and landscape FRD demonstrates that there is an additive effect of multiple seed sources contributing to a site's capacity to reestablish forest following fire: regeneration varies depending on the landscape pattern of surviving seed source, even when *distance* to seed source is held constant (Figure 2.6). Prior studies that relied solely on simpler, field-based metrics of distance to nearest, or several nearest, seed sources measured in the field, have provided important insights into post-fire regeneration dynamics. However, these studies fail to account for the spatial variability in the amount and pattern of surviving seed source across the broader landscape. Our high-resolution, NAIP-based maps demonstrate that the spatial patterns of fire refugia are complex. Distance to seed source metrics assume homogeneity in patches of surviving seed sources harbored in fire refugia, which in reality vary widely in size, shape, density, and composition. Fire refugia range from isolated groups composed of a small number of surviving individual trees surrounded by stand-replacement fire effects, to large, contiguous patches of surviving forest that form the borders of high-severity patches (Walker et al. in prep). Abundant seed dispersed from large, dense refugial patches may increase the probability of long-distance dispersal events (Shatford et al. 2007), while small, isolated refugia may influence regeneration in surrounding high-severity burned areas at comparatively smaller spatial scales.

Our ability to quantify fire refugia pattern had a number of limitations. For our field-based metrics, seed sources may have been closer than measured in the field when topography or individuals of other species obscured our view. Unlike our field-based distance to seed source metric, which was measured for each species, the methods we used to calculate landscape FRD did not differentiate between species – these were simply surviving tree canopies. Our capacity to model post-fire regeneration would almost certainly be strengthened if landscape FRD reflected the tree composition of fire refugia, but we are unaware of remote sensing products that would make this possible. Our landscape-scale seed source metric accounted for surviving forest within 150 meters of a plot location. However, we observed many seedlings farther than 150 meters from refugial seed sources, and in the future it may be more appropriate to quantify fire refugia landscape pattern at broader spatial scales (i.e. window sizes larger than 300 x 300 meter^2). We chose our window size based in part based on a previous study that found that seed dispersal kernels scaled at 60 – 100 meters were the strongest predictors of post-fire regeneration in ponderosa pine forest (Haire and McGarigal 2010). However, these results may not translate to more diverse, mixed-conifer forests, and to tree species like Douglas-fir and grand fir which have lighter seeds than ponderosa pine (Burns and Honkala 1990). Lastly, the aerial imagery used to map fire refugia was acquired 7 to 14 years post-fire, and we likely underestimated the amount of seed source present on the landscape in the years immediately following fire. Trees that survived fire, only to die prior to image acquisition, would not have been mapped as fire refugia.

While surviving seed source was an important driver of conifer seedling densities in all of our models, the importance of site characteristics varied between models. These results suggest that the amount and pattern of refugial seed source are the dominant controls on post-fire regeneration, rather than fire severity, environmental gradients, understory vegetation, or site productivity. Fire severity (dNBR) was not associated with ponderosa pine, grand fir, and all species seedling regeneration, perhaps because we restricted our sampling to stand-replacement patches. However, fire severity was positively associated with Douglas-fir regeneration, but we interpret this result as evidence that Douglas-fir regenerates at higher densities in more productive locations, also described by (Kemp et al. 2016). Stand-replacement fire in areas with dense pre-fire canopy will result in higher dNBR values compared to stand-replacement fire in areas with sparse pre-fire canopy (Miller and Thode 2007), so the positive association between Douglas-fir seedling abundance and fire severity may reflect site productivity (higher pre-fire biomass), rather than the direct influence of fire effects. This appears to be confirmed by the positive association between Douglas-fir and pre-fire basal area, a proxy for site productivity. Consistent with a similar study conducted in the Northern Rockies (Kemp et al. 2016), we found that Douglas-fir was also the only species strongly influenced by heat load. Douglas-fir is more sensitive than ponderosa pine to heat and drought stress (Rother et al. 2015), and our results suggest that in the Blue Mountains its capacity to regenerate is limited in landscape positions with high heat load. Based on previous studies (Chappell and Agee 1996, Dodson and Root 2013, Chambers et al. 2016), we expected conifer seedling abundance to increase with elevation and cooler, wetter climatic conditions (i.e., lower CMD). While we found evidence of non-linear relationships between seedling regeneration and both elevation and CMD, exploratory data plots of raw data were noisy; and model results did not provide evidence of a strong, linear association between post-fire seedling regeneration and either CMD or elevation, with the exception of a positive association between CMD and ponderosa pine. In all four of our models, polynomial terms indicate seedling abundance may have a convex response along the elevation gradient, indicating that seedling densities are highest at intermediate elevations, locations where regenerating seedlings may be buffered from both hot and cold temperature extremes, as found by Collins and Roller (2013). In contrast, our model results for CMD showed the opposite trend; seedling densities were lowest at intermediate CMD values (Appendix 1). To test if a small number of plots with high seedling densities were driving the relationship between with CMD, we removed the three plots with the highest seedling abundances from each model, but our model results from this reduced dataset were not meaningfully different. For both Douglas-fir and ponderosa pine, predicted seedling densities increased exponentially with increased CMD, indicating that these species regenerate more densely at hotter, drier locations. In addition, the "U-shaped" response along the CMD gradient may be partly the result of variability between fires. We observed relatively high seedling densities in the Burnt Cabin fire, which occupied the lower portion of the CMD gradient, and relatively high seedling densities in the 747 fire, which occupied the upper portion of the CMD gradient. It may also be the case that the resolution of available climate data may be too coarse (800 x 800 meters) to provide meaningful, interpretable results for a phenomenon like post-fire tree regeneration that is sensitive to factors operating at much finer spatial scales. These data may be better suited to identifying general climatic trends through time, rather than variability across the range of data we sampled in our study.

Widespread shrub cover in stand-replacement patches in our study area does not appear to limit post-fire conifer regeneration. We found no evidence of a competitive interaction between regenerating conifers and shrubs, and we found a positive association between ponderosa pine seedling abundance and shrub cover that may indicate a facilitative relationship. Numerous seedlings in our study area appear to have recently emerged above the shrub canopy, suggesting that a robust post-fire shrub response is compatible with the reforestation of stand-replacement patches in the Blue Mountains. Similar initial conversions to shrublands after fire have been observed in the Klamath-Siskiyou and Sierra Nevada mountains, and both positive (Shatford et al. 2007, Collins and Roller 2013), and negative (Welch et al. 2016, Tepley et al. 2017) associations between shrub cover and post-fire conifer regeneration have been reported. *Ceanothus*, the dominant shrub genus in our study area, requires scarification for its seeds to germinate and responds vigorously after high-severity fire (Conrad et al. 1985). *Ceanothus* has been shown to both suppress conifer establishment and growth (Zavitkovski et al. 1969) as well as facilitate seedling survival by ameliorating unfavorable post-fire environmental conditions (Wahlenberg 1930). It is possible that both of these mechanisms are at work in our system, but that the net effect of shrub cover on seedling regeneration is not substantial for grand fir, Douglas-fir, or all species combined.

Although forest is reestablishing in stand-replacement in our study area, it is not clear the degree to which regenerating seedlings represent pre-fire forest composition, or, importantly, historical forest composition. Unfortunately, we were unable to directly compare pre-fire forest composition to the composition of regenerating seedlings because bark loss and decay made it impossible to determine the species identity of all fire-killed tree within our plots. There is some evidence that conditions favor the establishment of more shade-tolerant trees species when shrubs like *Ceanothus* dominate burned sites for more than 15 years post-fire (Zavitkovski and Newton 1968, Crotteau et al. 2013). We did observe higher proportions of shade-tolerant seedlings overtopped by shrubs compared to shade-intolerant species: 38% of grand fir and 48% of Douglas-fire were overtopped by shrubs, in comparison to 25% of ponderosa pine and 12% of western larch. Additionally, data from a related study suggests that forest composition in fire refugia differs from the composition of regenerating seedlings; more western larch and lodgepole pine, and grand fir seedlings were regenerating in stand-replacement patches than would be expected based on the composition of surviving forest (Chapter 3). As a result of fire exclusion, infilling by grand fir is widespread across dry mixed-conifer forests in the Pacific Northwest (Hagmann et al. 2014, Merschel et al. 2014, Johnston 2017), and it is likely that pre-fire forest composition in our study area was departed from historical reference conditions because of the decades-long absence of frequent fire. Despite a reduction in grand fir basal area as a result of low-severity fire in refugia (Chapter 3), grand fir may still be overrepresented in surviving forest within fire perimeters, compared to historical estimates (Stine et al. 2014). The relative abundance of surviving grand fir seed source, in addition to its capacity to establish beneath the shrub canopy, could provide grand fir an advantage over species like ponderosa pine. Consequently, it is possible that regenerating seedlings do not reflect historical reference conditions, and that the transition towards grand fir dominance initiated by post-settlement fire exclusion is being reinforced by high-severity fire effects in our study area. However, additional research will be needed to determine the degree to which the composition of regenerating seedlings following high-severity fire in Pacific Northwest dry mixed-conifer forests resembles either pre-fire forest composition, or the composition of these forests prior to European settlement.

Ponderosa pine seedling establishment is ongoing in stand-replacement patches 12 – 17 years post-fire, even in areas dominated by shrubs. These results serve as an important reminder that reforestation of stand-replacement patches in dry forests can be a slow process that continues for decades (Haire and McGarigal 2010), and initial post-fire dominance by shrubs does not necessarily indicate an enduring vegetation type shift. The temporal patterns of regeneration we identified are consistent with previous studies conducted in ponderosa pine forests in the Southwest and South Dakota (Savage and Mast 2005, Haire and McGarigal 2010), and in dry mixed-conifer forests in the Klamath-Siskiyou region (Shatford et al. 2007), where a period of slow initial establishment was followed by a peak in regeneration. Other studies have reported a distinct regeneration pulse in the years immediately following fire (Bonnet et al. 2005, Donato et al. 2009, Tepley et al. 2017), but our data indicate that ponderosa pine seedlings either did not establish rapidly post-fire, or these early establishers did not survive to be recorded. A qualitative assessment of ponderosa pine seedling establishment dates and climatic moisture deficit did not identify a strong relationship, suggesting that ponderosa pine regeneration is constrained by factors other than landscape-scale climatic variability. In contrast, a recent meta-analysis of post-fire regeneration in the Northern Rockies found significant decreases in conifer regeneration during drier periods, leading the authors to conclude that climate warming may contribute to conversion to non-forest states following high-severity fire (Stevens-Rumann et al. 2018). The lack of an apparent relationship in our study may be a result of relatively low climatic variability during the post-fire time period; conditions may not have been hot and dry enough in the years following fire to significantly discourage ponderosa pine regeneration. In addition, ponderosa pine seed production is highly episodic, with good cone crops occurring only once every 4 to 6 years (Shepperd et al. 2006), and interannual variability in seed availability may obscure any climate signal present in our establishment data.

Management applications and conclusions

The strong influence of refugial seed source pattern on post-fire regeneration that we identified may inform potential management strategies. We sampled primarily in designated roadless and wilderness areas where post-fire management interventions like salvage logging and tree planting are either not feasible or not permitted. However, our findings suggest that managers interested in promoting natural forest regeneration should avoid actions during and after fire suppression that reduce or eliminate fire refugia from the post-fire landscape. Additionally, managers may find that investments in fuel treatments prior to fire, which increase forests' resistance to high-severity fire (Agee and Skinner 2005), may be a more effective use of limited resources than replanting in stand-replacement patches. In areas where replanting is a viable and desirable option, managers could leverage natural regeneration and target areas with little fire refugia in the surrounding landscape and far from refugial seed source.

This study provides evidence that fire refugia confer resilience to dry mixed-conifer forests following high-severity fire. As the areas least changed by a fire event, fire refugia promote forests' capacity to absorb and recover from significant fire induced change. Despite an increase in fire activity and a legacy of fire exclusion, dry mixed-conifer forests in the Blue Mountains are able to regenerate following high-severity fire effects, provided adequate seed sources survived fire in refugia. However, the degree to which the composition of regenerating forest will reflect that of the past remains uncertain. Fire refugia may serve additional ecosystem functions, such as facilitating the survival of fire-sensitive plant species (Wood et al. 2011), providing faunal habitat otherwise absent in burned landscapes (Robinson et al. 2013), and buffering post-fire microclimates (Delong and Kessler 2000). Additional research will be needed to broaden our understanding of the role of fire refugia in dry mixed-conifer forest ecosystems.

References

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research 35:37–47.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Burns, R. M. 1983. Silvicultural systems for the major forest types of the United States. Agricultural Handbook 445. USDA Forest Service, Washington, D.C., USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee mountains. Forest Ecology and Management 95:63–77.

Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. Forest Ecology and Management 378:57–67.

Chappell, C. B., and J. K. Agee. 1996. Fire severity and tree seedling establishment in Abies magnifica forests, Southern Cascades, Oregon. Ecological Applications 6:628–640.

Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecology 28:1801–1813.

Conrad, S. G., A. E. Jaramillo, J. Kermit Cromack, and S. Rose. 1985. The role of the genus Ceanothus in western forest ecosystems. USDA Forest Service General Technical Report, PNW-GTR-182. Pacific Northwest Research Station, Portland, OR, USA.

Coop, J. D., S. A. Parks, S. R. Mcclernan, and L. M. Holsinger. 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned southwestern landscape. Ecological Applications 26:346–354.

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.

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

Davis, R., Z. Yang, A. Yost, C. Belongie, and W. Cohen. 2017. The normal fire environment — Modeling environmental suitability for large forest wildfires using past , present , and future climate normals. Forest Ecology and Management 390:173–186.

Delong, S. C., and W. B. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131:93–106.

Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography 24:917–927.

Dodson, E. K., and H. T. Root. 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. Forest Ecology and Management 302:163–170.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains. Canadian Journal of Forest Research 39:823–838.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years afer the 1988 Yellowstone fires: A fire-catalyzed shif in lower treelines? Ecosphere 7:1–16.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera : Carabidae and Staphylinidae). Biological Conservation 102:131–141.

Haffey, C., T. D. Sisk, C. D. Allen, A. E. Thode, and E. Q. Margolis. 2018. Limits to ponderosa pine regeneration following large high-severity forest fires in the United States southwest. Fire Ecology 14:143–163.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern oregon cascade range, USA. Forest Ecology and Management 330:158–170.

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.

Hall, F. C. 1976. Fire and vegetaion in the Blue Mountains - Implications for land managers. Page Proceedings of the annual Tall Timbers fire ecology conference. Tall Timbers Research Station: 155-170, Tallahassee, Florida.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest United States forests, 1800-2000. Forest Ecology and Management 178:23–59.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. Ecology 82:660–678.

Johnson, C. G., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-T-036092. Pacific Northwest Research Station, Portland, OR, USA.

Johnston, J. D. 2017. Forest succession along a productivity gradient following fire exclusion. Forest Ecology and Management 392:45–57.

Johnston, J. D., J. D. Bailey, and C. J. Dunn. 2016. Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests. Ecosphere 7:1–19.

Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology 31:619–636.

Key, C. H., and N. C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. USDA Forest Service General Technical Report RMS-GTR-164-CD. Ogden, UT, USA.

Landesmann, J. B., and J. M. Morales. 2018. The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia. Plant Ecology 219:455–466.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research 35:2875–2885.

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

Merschel, A. G., T. A. Spies, and E. K. Heyerdahl. 2014. Mixed-conifer forests of central Oregon: Effects of logging and fire exclusion vary with environment. Ecological Applications 24:1670–1688.

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.

Murtaugh, P. A. 2014. In defense of P values. Ecology 95:611–617.

Ott, T. M., E. K. Strand, and C. L. Anderson. 2015. Niche divergence of Abies grandis-Abies concolor hybrids. Plant Ecology 216:479–490.

Ouarmim, S., L. Paradis, H. Asselin, Y. Bergeron, A. Ali, and C. Hély. 2016. Burning potential of fire refuges in the boreal mixedwood forest. Forests 7:246.

Owen, S. M., C. H. Sieg, A. J. Sánchez Meador, P. Z. Fulé, J. M. Iniguez, L. S. Baggett, P. J. Fornwalt, and M. A. Battaglia. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. Forest Ecology and Management 405:134–149.

Powell, D. 1994. Effects of the 1980s western spruce budworm outbreak on the Malheur National Forest in northeastern Oregon. USDA Forest Service Technical Report R6-FI&D-TP-12-94. Pacific Northwest Region Forest Insects and Disease Group, Portland, OR, USA.

PRISM. 2018. PRISM Climate Group, Oregon State University. http://www.prism.oregonstate.edu.

R Core Team. 2017. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. www.R-project.org. https://www.r-project.org/.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985-2010). Ecosphere 8.

Robinson, N. M., S. W. J. Leonard, E. G. Ritchie, M. Bassett, E. K. Chia, S. Buckingham, H. Gibb, A. F. Bennett, and M. F. Clarke. 2013. Refuges for fauna in fire-prone landscapes: Their ecological function and importance. Journal of Applied Ecology 50.

Rogers, B. M., R. P. Neilson, R. Drapek, J. M. Lenihan, J. R. Wells, D. Bachelet, and B. E. Law. 2011. Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. Journal of Geophysical Research: Biogeosciences 116:1–13.

Rother, M. T., T. T. Veblen, and L. G. Furman. 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Canadian Journal of Forest Research 45:1607–1616.

Safford, H. D. 2013. Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the bioregional assessment area, including the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests. Unpublished report. USDA Forest Service, Pacific Southwest Region, Vallejo, CA.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35:967–977.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry 105:139–146.

Shepperd, W. D., C. B. Edminster, and S. A. Mata. 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado Front Range. Western Journal of Applied Forestry 21:19–26.

Stephens, S. L., J. K. Agee, P. Z. Fule, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing forests and fire in a changing climate. Science 342:41–42.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Stine, P., P. Hessburg, T. Spies, M. Kramer, C. J. Fettig, A. Hansen, J. Lehmkuhl, K. O’Hara, K. Polivka, P. Singleton, S. Charnley, A. Merschel, and R. White. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. USDA Forest Service, General Technical Report, PNW-GTR-897. Pacific Northwest Research Station, Portland, Oregon, USA.

Swan, M., C. Galindez-Silva, F. Christie, A. York, and J. Di Stefano. 2016. Contrasting responses of small mammals to fire and topographic refugia. Austral Ecology 41:443–451.

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.

Wahlenberg, W. G. 1930. Effect of ceanothus brush on western yellow pine plantations in the northern Rocky Mountains. Journal of Agricultural Research 41:601–612.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:1–17.

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.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Wood, S. W., B. P. Murphy, and D. M. J. S. Bowman. 2011. Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. Journal of Biogeography 38:1807–1820.

Zavitkovski, J., and M. Newton. 1968. Ecological Importance of Snowbrush Ceanothus Velutinus in the Oregon Cascades. Ecology 49:1134–1145.

Zavitkovski, J., M. Newton, and B. El-Hassan. 1969. Effects of snowbrush on growth of some conifers. Journal of Forestry 67:242–246.

Figures and tables

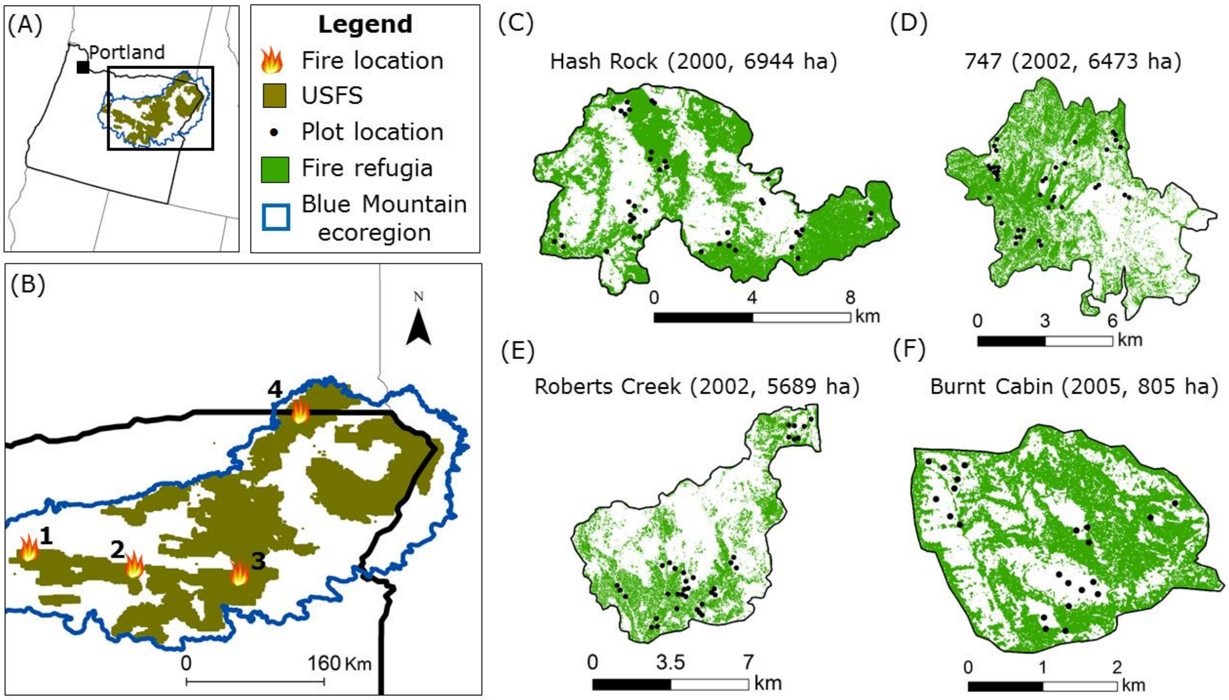


Figure 2.1. The study area and study fires in central and northeastern Oregon. (A) The study was performed in the Blue Mountains ecoregion. (B) All four study fires burned primarily on land managed by the US Forest Service (USFS). (C - F) Fire refugia within our four study fires, mapped using 1-m resolution aerial imagery, illustrate the complex spatial patterning of surviving forest, including areas where fire refugia are sparse and isolated, and locations where refugia are large and dense. Plots locations were located outside of fire refugia in areas that experienced stand-replacement fire effects.

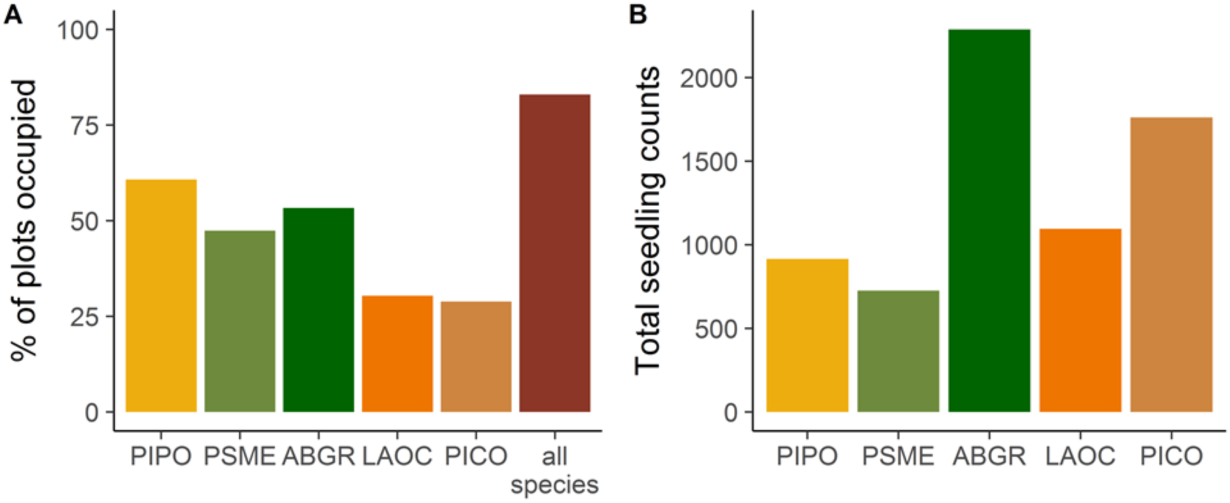


Figure 2.2. Percentage of plots occupied by regenerating conifer species, and the total seedling counts for common conifer species. Ponderosa pine (PIPO), Douglas-fir (PSME), and grand fir (ABGR) were the most widespread species regenerating in our study area (A), while grand fir was the most abundant (B). Western larch and lodgepole pine were regenerating densely where present, which accounts for their high total seedling counts compared to ponderosa pine and Douglas-fir.

Table 2.1. Observed seedling densities, mean seedling heights, and the proportion of seedlings overtopped by shrubs for common tree species. To represent the broader population of regeneration seedlings, these data were recorded for the three individuals of each species closest to plot center. Median density values of zero for several species are the result of fewer than ½ of sample plots containing regenerating seedlings of that species.

	Seedlings ha^{-1}			
Species	**median**	**mean ± SE**	**height (cm, ± SE)**	**% overtopped**
ponderosa pine	100	679 ± 19	0.90 ± 0.03	26
Douglas-fir	0	538 ± 15	0.66 ± 0.03	48
grand fir	100	1696 ± 43	0.61 ± 0.03	38
western larch	0	1305 ± 50	1.71 ± 0.09	12
lodgepole pine	0	811 ± 27	1.68 ± 0.08	6
all species	1100	5417 ± 107	1.03 ± 0.03	40

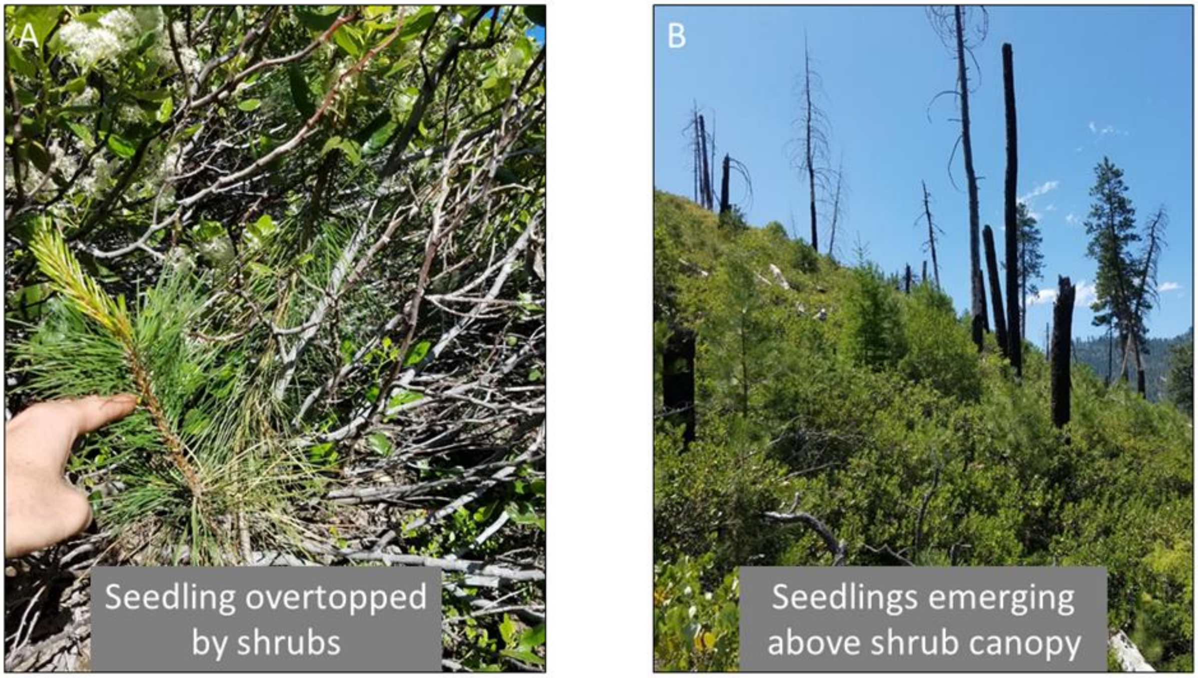


Figure 2.3. Photos of regenerating seedlings above and below the shrub layer. (A) Many post-fire seedlings in our study area were overtopped by shrubs, (B) while others appear to have recently emerged from the shrub canopy.

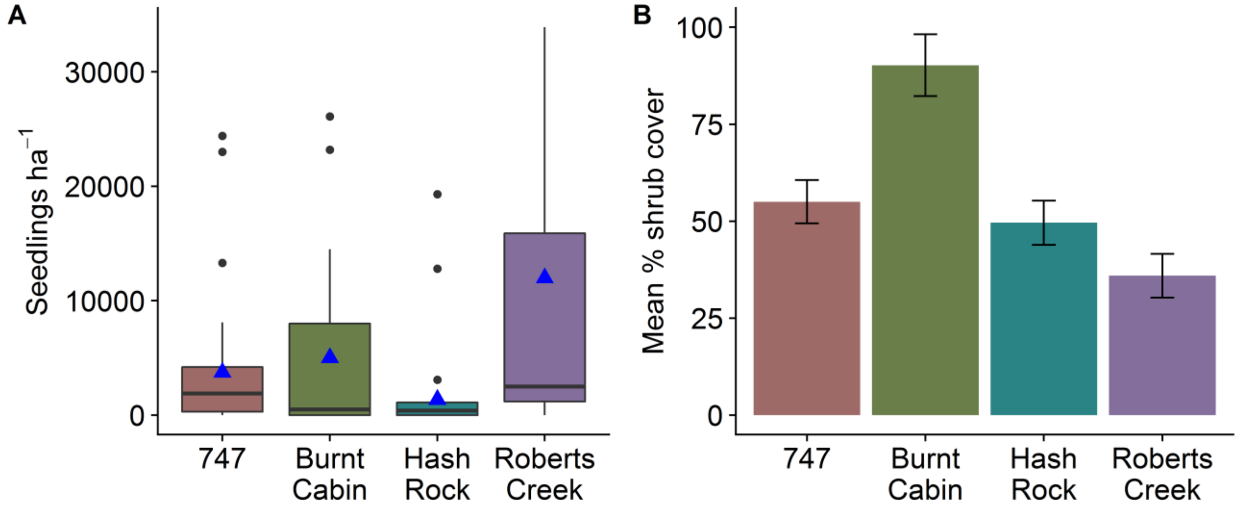


Figure 2.4. (A) Observed seedling densities and shrub cover in four study fires. Seedling densities varied substantially between plots and among fires. Blue triangles represent mean seedling densities among plots for each fire. Three plots in the Roberts Creek fire with seedling densities >40000 seedlings ha^{-1} were removed to improve the interpretability of figure A. Horizontal lines represent the median, with first and third quantiles flanking either side. Median seedling densities calculated among plots for each fire were >400 seedlings ha^{-1} in all four fires. (B) Shrub cover was 54%, on average, across all fires. Error bars represent the mean ± SE.

Table 2.2. Generalized linear mixed effects models of tree recruitment fit with seed source metrics considered for inclusion in our final models. All metrics represented substantial improvements over a null model with only an intercept term. Combined models (mean distance + FRD) explained more variability in seedling abundance data than field-based distance to seed source metrics alone, for ponderosa pine and Douglas-fir. There was little difference (Δ AIC = 1) between combined models and models with landscape FRD density alone for grand fir and all species combined.

	ponderosa pine		***Douglas-fir***		***grand fir***		***all species***	
Seedling density ~	*AIC*	*Δ AIC*	*AIC*	*Δ AIC*	*AIC*	*Δ AIC*	*AIC*	*Δ AIC*
mean distance + FRD	**662**	**37**	**549**	**40**	**748**	**31**	**1172**	**36**
landscape FRD	672	27	555	34	**747**	**32**	**1173**	**35**
mean distance	668	31	552	37	750	29	1179	29
median distance	669	30	555	34	749	30	1179	29
minimum distance	670	29	554	35	750	29	1179	29
null model	699	0	589	0	779	0	1208	0

Table 2.3. Parameter estimates, p-values, and Δ AIC values for variables included in negative binomial models of seedling regeneration. The Δ AIC for each parameter represents the difference in AIC between a reduced model (a model without the parameter) and a full model (all parameters included). Large Δ AIC values and small p-values indicate important drivers of post-fire seedling densities in our models. Statistically significant (p-value < 0.05) parameters are in bold. The Δ AIC values reported for squared parameters represent the difference in AIC between a reduced model without the linear and squared parameters, and a full model with both the linear and squared parameters.

	Ponderosa pine			***Douglas-fir***			***Grand fir***			***All species***		
Parameter	*Coef.*	*Δ AIC*	*p-value*	*Coef.*	*Δ AIC*	*p-value*	*Coef.*	*ΔAIC*	*p-value*	*Coef.*	*Δ AIC*	*p-value*
dist. to seed source	**-0.004**	**6**	**0.009**	**-0.007**	**6**	**0.012**	-0.002	1	0.199	**-0.007**	**5**	**0.004**
fire refugia density	**0.003**	**14**	**<0.001**	**0.004**	**10**	**<0.001**	**0.002**	**3**	**0.044**	**0.002**	**2**	**0.048**
burn severity	0.002	1	0.089	**0.003**	**4**	**0.019**	-0.0004	-2	0.80	-0.001	-1	0.380
elevation	3.77	-	0.324	0.36	-	0.935	**25.30**	**-**	**0.013**	**10.06**	**-**	**0.039**
elevation^2	**-9.68**	**10**	**<0.001**	**-8.37**	**5**	**0.002**	**-17.42**	**13**	**0.015**	**-12.15**	**19**	**<0.001**
moisture deficit	**10.34**	**-**	**<0.001**	0.84	-	0.79	1.71	-	0.75	5.87	-	0.21
moisture deficit^2	**7.58**	**21**	**0.004**	**8.47**	**8**	**<0.001**	**23.54**	**23**	**<0.001**	**10.52**	**20**	**<0.001**
heat load	0.59	-2	0.62	**-3.69**	**5**	**0.009**	-2.64	0	0.18	0.75	-1	0.51
basal area	0.003	-5	0.72	**0.032**	**5**	**0.002**	0.002	-2	0.90	-0.001	-2	0.89
shrub cover	**0.013**	**3**	**0.006**	0.007	-1	0.24	-0.005	-1	0.45	-0.005	-1	0.30

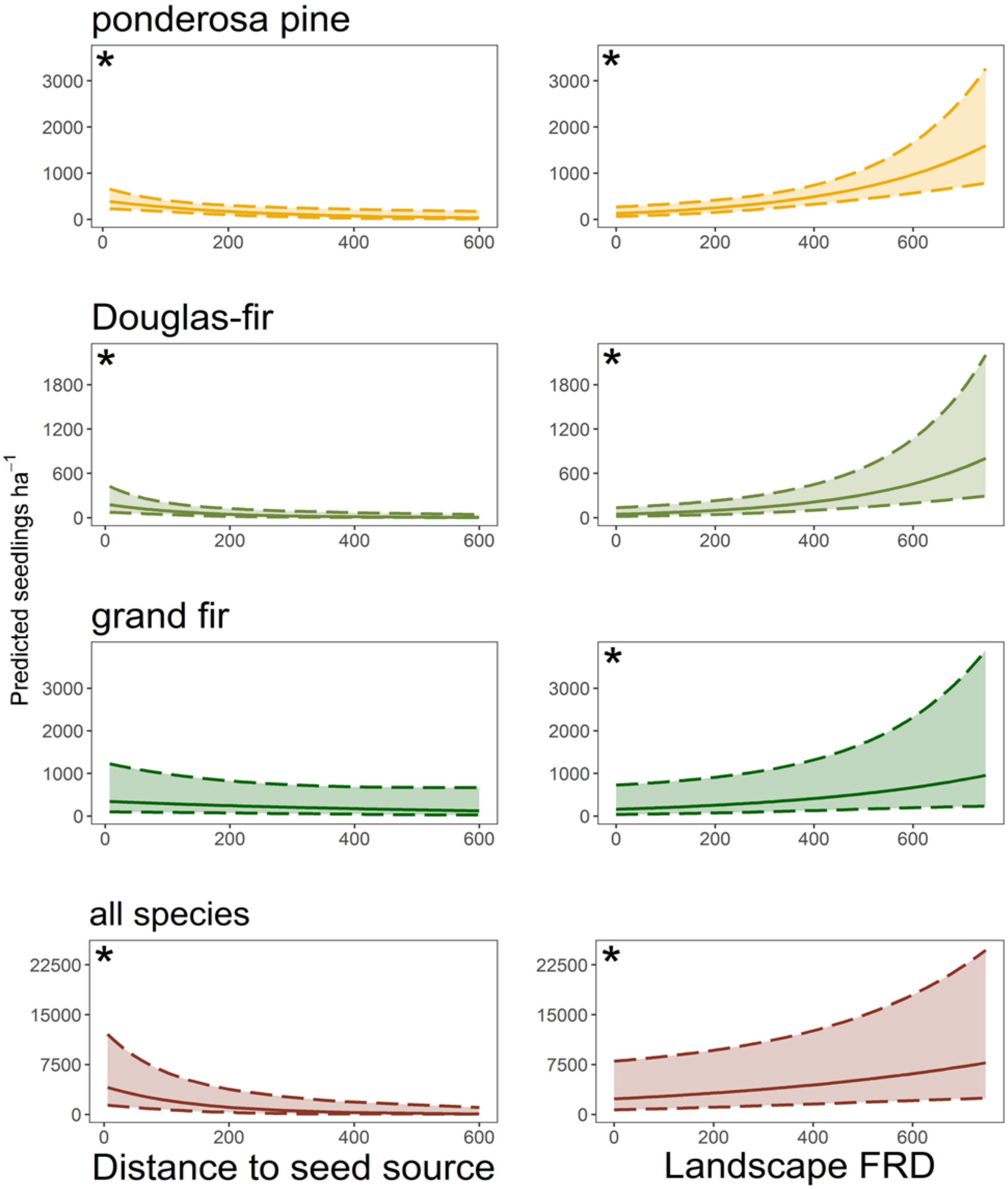
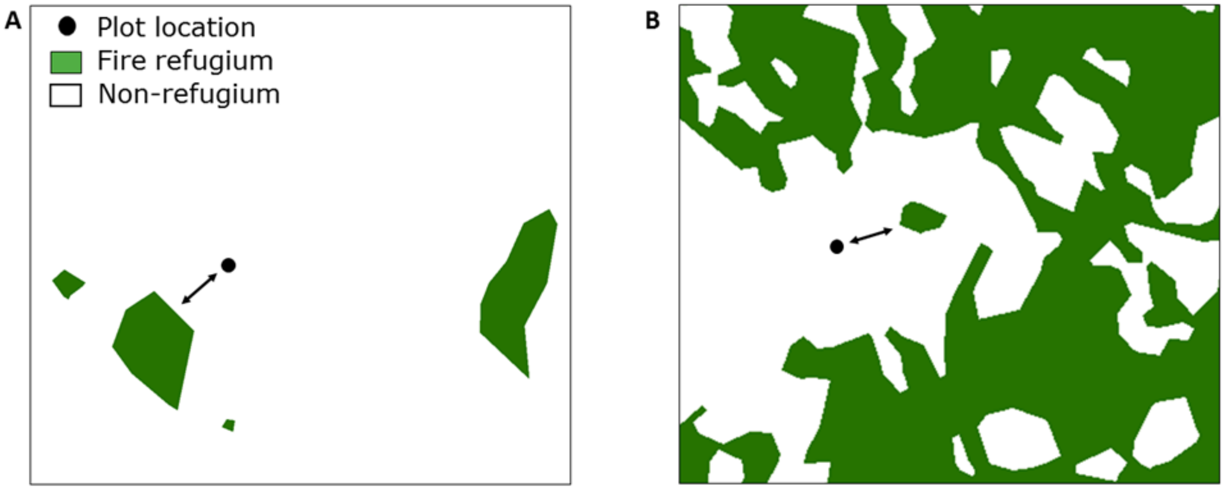


Figure 2.5. Predicted seedling densities along gradients of distance to seed source and landscape fire refugia density. Predicted seedling densities decreased with distance to seed source and increased with landscape FRD. Added variable plots represent the effect size of refugial seed source parameters, with all other variables held constant at median values. Dotted lines represent 95% confidence intervals. Note y-axis scales vary between each pair of plots due to significant variation in predicted seedling densities for different species. Stars denote statistically significant relationships between seed source metrics and post-fire seedling abundance.

Table 2.4. Effect size of distance to seed source and landscape fire refugia density on predicted post-fire conifer seedling abundance. Percentiles (PCTL) reflect observed distance to seed source and landscape FRD values, and vary between models. Predicted seedlings ha^{-1} decrease with distance to seed source and increase with landscape FRD.

	Predicted Seedlings ha^{-1} *(Distance to seed source)*			**Predicted Seedlings ha^{-1} *(landscape FRD)***		
Species	**25th PCTL**	**75th PCTL**	**% decrease**	**25th PCTL**	**75th PCTL**	**% increase**
ponderosa pine	490 (*35 m*)	300 (*136 m*)	39 %	280 (*90*)	610 (*420*)	118 %
Douglas-fir	140 (*39 m*)	80 (*116 m*)	43 %	65 (*90*)	200 (*420*)	208 %
grand fir	300 (*45 m*)	215 (*239 m*)	28 %	185 (*90*)	415 (*420*)	127 %
all species	3800 (*14 m*)	2900 (*50 m*)	24%	2600 (*90*)	4600 (*420*)	77 %



Distance to seed source = **70** meters
Fire refugia DWD = **90** (25th percentile)
Predicted PIPO seedlings ha^{-1} = **280** (95% CI 160 – 500)

Distance to seed source = **70** meters
Fire refugia DWD = **420** (75th percentile)
Predicted PIPO seedlings ha^{-1} = **610** (95% CI 400 – 935)

Figure 2.6. Density of regenerating seedlings varied with the landscape pattern of surviving seed source, even when distance to seed source is held constant. Our models predict substantially higher seedling densities in locations with high fire refugia density (B) than in locations with low refugia density (A). In both A and B, distance to seed source is held constant at 70 meters, the observed median value for ponderosa pine. Landscape FRD is 90 (25th percentile) in panel A, and 420 (75th percentile) in panel B. The difference in predicted ponderosa pine seedling densities is 118%.

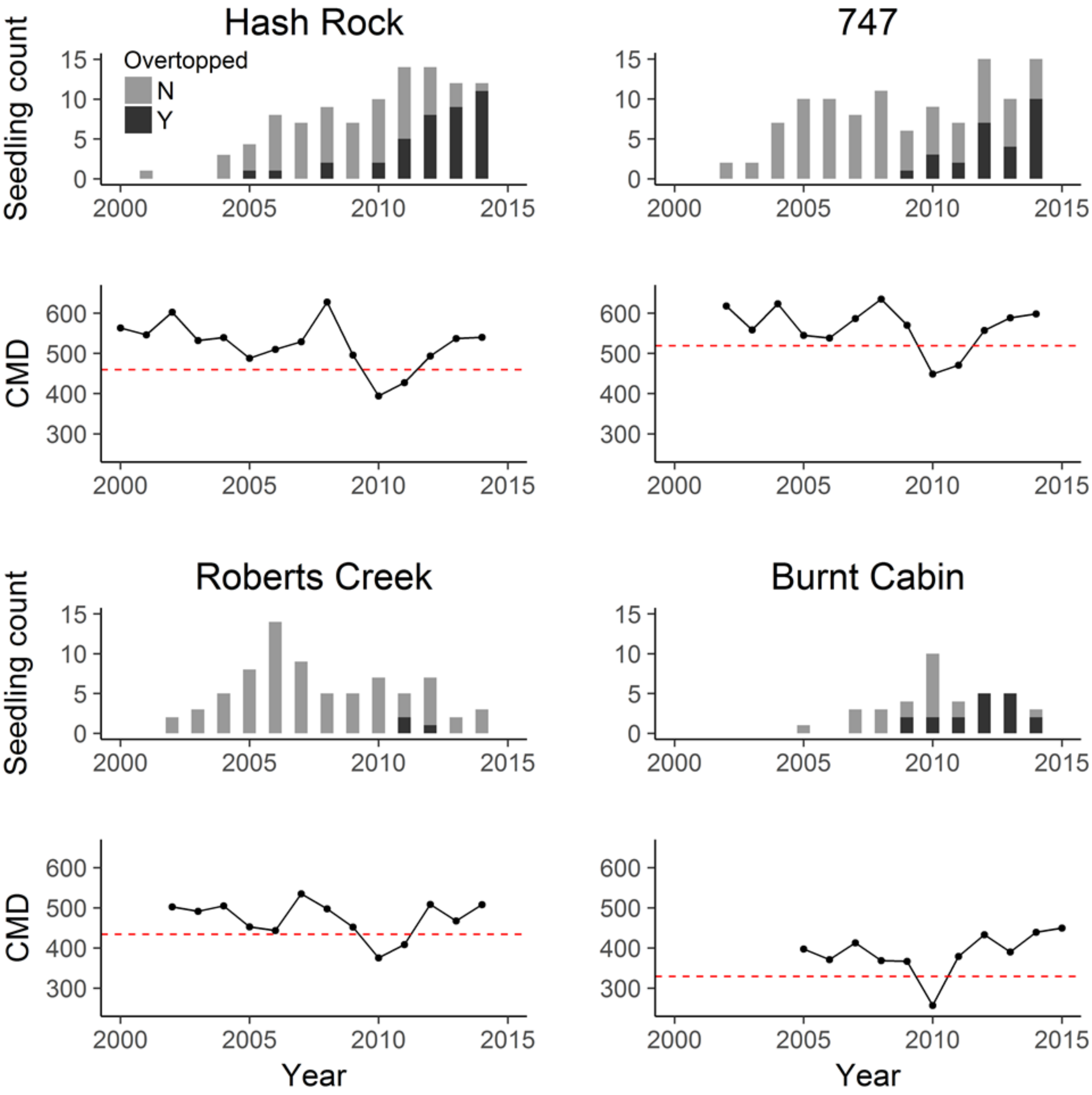


Figure 2.7. Ponderosa pine seedling establishment dates and annual climatic moisture deficit. Ponderosa pine seedling recruitment is ongoing in stand-replacement patches across our study area. There does not appear to be a strong association between seedling establishment and climate moisture deficit (CMD). Seedlings overtopped by shrubs are represented with black, and seedlings that have emerged above the shrub canopy or were not growing in close proximity to shrubs are represented with grey. Plots of seedlings established each year and mean annual CMD are paired for each fire. CMD was averaged across plots for each fire to characterize landscape-scale climatological trends. Two years were subtracted from seedling establishment dates to attempt to correct for the bias of field-based estimates based on whorl-counts. Red dotted line represents the 30-yr average, annual climate moisture deficit for each fire area.

CHAPTER 3 - PLANT COMMUNITY COMPOSITION IN POST-FIRE DRY MIXED-CONIFER FORESTS OF OREGON'S BLUE MOUNTAINS: IS FIRE REFUGIA COMPOSITION DIFFERENT FROM THE HIGHER-SEVERITY BURNED MATRIX?

Introduction

Fire is a globally important disturbance process that interacts with topography, fuels, and weather to create mosaics of burn severity. Burn severity patterns are changing in dry mixed-conifer forests (Hessburg et al. 2005, Reilly et al. 2017), raising questions about the resistance and resilience of these landscapes to contemporary fire effects. Relatively little is known about plant composition following recent large fires in dry mixed-conifer forests, or the degree to which fire refugia - unburned or low-severity burned patches within fire perimeters - support understory plant communities otherwise absent from the higher-severity burned matrix. Dry mixed-conifer forests in the Pacific Northwest were historically composed of low-density stands subject to frequent, low-intensity fire, but tree density and fuel loads have increased substantially due to logging and fire exclusion (Hagmann et al. 2014, Merschel et al. 2014, Johnston et al. 2016). Although high-severity fire effects were a component of pre-European fire regimes (Hessburg et al. 2007), contemporary fires in Pacific Northwest dry mixed-conifer forests now regularly produce stand-replacement patches that are larger than historical estimates (Reilly et al. 2017). Recent research following high-severity fire in dry mixed-conifer forests has focused primarily on post-fire forest regeneration, driven in part by concerns that stand-replacement patches may be unable regenerate forest because a lack of surviving seed sources and unfavorable climatic conditions (e.g., Chapter 2, Chambers et al. 2016, Stevens-Rumann et al. 2017). Comparatively little attention has been paid to fire refugia (Kolden et al. 2012), and even less to understory plant communities, which directly or indirectly sustain much of the floristic and faunistic diversity in Pacific Northwest forests (Halpern and Spies 1995). To better understand the effects of contemporary burn mosaics on the biodiversity of dry forest ecosystems there is need for a baseline characterization of the structure and composition of fire refugia that persist through contemporary fire events, and an understanding of whether fire refugia support understory plant communities absent from the higher-severity burned areas.

Recent research on fire refugia is part of a broader effort to identify relatively ecologically stable locations that may be important drivers of ecosystem resilience in the context of rapid global change. Refugia have been traditionally studied by paleontologists and biogeographers, with a focus on population dynamics during historical periods of significant temperature fluctuations such as glaciation events. However, interest in contemporary refugia is increasing (Ashcroft 2010), particularly as “safe havens” in the context of anthropogenic climate change and its biological effects (Keppel et al. 2012). The refugia framework has been broadened to include not only climate change, but ecological processes associated with climate, like wildfire (Wilkin et al. 2016). Fire refugia can be generally defined as locations that burn less frequently or less severely than the surrounding landscape (Gill 1975, Wood et al. 2011, Krawchuk et al. 2016). Here, we identify fire refugia specifically as locations within fire perimeters where overstory trees survived large fire events. As the most fire-resistant components of the forest landscape during a fire event, fire refugia constitute the remaining, intact forest structure within fire perimeters, in a landscape matrix that has been largely converted to an early-successional state by high-severity fire.

The ecological importance of fire refugia for particular plant species during and after fire is in part a function of species’ life-history traits. Many species in fire-prone ecosystems possess adaptive traits that provide fitness advantages in the context of a given fire regime (Rowe 1983), and these traits influence post-fire successional trajectories in spatially heterogeneous burn mosaics (Turner et al. 1997, Haire and McGarigal 2008). Species that resprout or produce seed banks are well adapted to survive and reestablish following high-severity fire (Keeley et al. 2011, Airey Lauvaux et al. 2016), and these species would be unlikely to depend on fire refugia to persist in burned areas. In contrast, species that are easily killed by fire, or that require surviving seed sources to regenerate, tend to rely on low-severity or unburned areas to avoid and/or survive fire and to recolonize high-severity burned areas (Chapter 2, Wood et al. 2011, Chambers et al. 2016, Adie et al. 2017). In some forest ecosystems, fire refugia promote the persistence of fire-sensitive plant communities and late-successional forest structure, including old, conifer-dominated stands in mixedwood boreal forests (Ouarmim et al. 2016), fire-sensitive Tasmanian rainforest in a matrix of more fire-tolerant moorland and sclerophyll forest (Wood et al. 2011), and islands of Afrotemporate forest surrounded by frequent-fire grasslands in South Africa (Adie et al. 2017). Although research on fire refugia in forests has focused primarily on overstory tree communities, there is some indication that fire refugia may also promote the persistence of fire-sensitive understory plant communities. Fire-sensitive bryophyte species survive in unburned and low-severity patches in spruce forest following fire (Hylander and Johnson 2010, Barbé et al. 2017), and obligate-seeder shrub species in coastal areas of Australia are largely confined to fire refugia where competition with resprouters is less acute (Clarke 2002). However, little is known about the composition of fire refugia in dry forests in the western United States, or the degree to which fire refugia promote the persistence of understory plant communities in these landscapes otherwise absent from the higher-severity matrix.

Previous studies in dry forest ecosystems report contrasting results regarding the influence of fire severity on post-fire plant composition and diversity. Donato et al. (2009) reported no significant differences in understory composition or diversity between stand-replacement patches and unburned controls two years post-fire in the Klamath-Siskiyou region. In contrast, DeSiervo et al. (2015) found that plant species diversity in the northern Sierra Nevada mountains peaked at moderate fire severity five years post-fire, and reported some evidence that fire severity influenced plant community composition, although less strongly than elevation or soil type. There was no significant difference in native plant diversity along a gradient of fire severity two years post-fire in ponderosa pine forests in northern Arizona, although exotic species cover and diversity was substantially higher in high-severity patches (Crawford et al. 2001). These studies indicate that there is important geographic variability in plant community responses to fire in dry forest ecosystems, and they highlight the need to address key knowledge gaps within the gradient of conditions supporting dry mixed-conifer forests.

In this study, we characterize fire refugia composition and compare understory plant communities in fire refugia to the higher-severity burned matrix within dry mixed-conifer landscapes of Oregon's Blue Mountains. We recognize that "understory" is something of a misnomer in the context of stand-replacement fire effects, where the overstory forest has been killed by fire. However, in the absence of a widely accepted alternative, we use the term “understory” to refer to the plant communities that do not constitute overstory forest. Specifically, we asked (1) Does understory plant community composition differ between fire refugia and stand-replacement patches? (2) Does understory plant community composition differ between unburned and low-severity burned fire refugia? (3) Are there plant species strongly associated with fire refugia or stand-replacement patches? We were particularly interested in determining whether fire refugia support plant communities that differ significantly from the higher-severity burned landscape, as has been reported in other systems (e.g., Wood et al. 2011, Adie et al. 2017). If strong compositional differences exist, it would suggest that fire refugia are critical landscape elements that support the persistence of fire-sensitive plant communities. In contrast, compositional similarities between fire refugia and stand-replacement patches would indicate that understory plant communities in the Blue Mountains are resilient to high-severity fire effects, and that fire refugia are important primarily as locations where relatively intact forest structure persists and as surviving seed sources that contribute to tree regeneration in nearby high-severity burned areas (Chapter 2), rather than as “safe havens” for particular plant communities.

Methods

Study region

The Blue Mountain ecoregion extends from central Oregon east to the Snake River Plain near the Idaho border, and north to the Columbia River in southeastern Washington (Figure 3.1). Composed of a series of small sub-ranges bisected by rugged river canyons, the Blue Mountains are topographically and biologically complex. The majority of precipitation falls in the winter as snow, and thunderstorms that ignite wildfires are common during warm, dry summers (Burns 1983). The Cascade Mountains to the west effectively block marine air masses from reaching the drier, southern portion of the range (Johnson and Clausnitzer 1992), while the Columbia River provides an ingress for these systems, resulting in a comparatively cooler and wetter climate in the northern Blue Mountains (Heyerdahl et al. 2001). The forested extent of the Blue Mountains spans broad environmental gradients: the 30-yr average maximum temperature in August ranged from 16°C to 34°C, and average minimum temperature in January ranged from -12°C to -1°C. The 30-yr average annual precipitation ranged from 20 to 180 centimeters (PRISM).

Dry mixed-conifer forests in the Blue Mountains occupy the warmer, drier portions of these climatic gradients, and are composed primarily of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and lesser amounts of western larch (*Larix occidentalis*) and lodgepole pine (*Pinus contorta*). Grand fir and white fir (*Abies concolor*) hybridize across their ranges in Oregon (Ott et al. 2015), and we refer to their variants here as grand fir. Dry mixed-conifer forests in the Blue Mountains contain components of western juniper (*Juniperus occidentalis*) at hot and dry, lower elevation sites, and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at the highest elevation sites. Common herbaceous species include *Achillea millefolium, Calamagrostis rubescens, Bromus carinatus, Fragaria vesca, Arnica cordifolia,* and *Carex geyeri*. Shrub species common in our study area include *Ceanothus velutinus, Symphoricarpos albus, Rosa gymnocarpa,* and *Mahonia repens*.

Fire burned frequently in the Blue Mountains prior to fire exclusion beginning in the late 1800s. Pre-settlement fire return intervals in the southern Blue Mountains were between 10 to 21 years on average (Johnston et al. 2016), and slightly longer in the northern part of the range where the climate is cooler and wetter (Heyerdahl et al. 2001). Frequent historical fire produced a range of low- and mixed-severity effects that supported a heterogeneous landscape resilient to disturbance and variations in climate (Hessburg and Agee 2003, Hessburg et al. 2005, Stine et al. 2014). Contemporary fire return intervals for ponderosa pine and Douglas-fir/grand fir forests in the Pacific Northwest are now estimated to be 265 to 380 years, an order of magnitude longer than prior to fire exclusion, and the amount and scale of high-severity fire effects is widely considered outside the historical range of variability (Reilly et al. 2017).

Study design

We collected field data in the summer of 2017 in 187 plots located within four large fires that burned 12 – 17 years prior to sampling (Figure 3.1). We selected fires that burned primarily in designated roadless or wilderness areas to minimize the influence of pre- and post-fire management, and we avoided areas for which we had a record of pre- or post-fire timber harvest, fuels treatments, or tree replanting. All fires were lightning caused.

Fire refugia were identified as patches of surviving overstory tree canopy and mapped using post-fire aerial imagery from the 1 meter resolution National Agriculture Imagery Program (NAIP). NAIP imagery was acquired for 2012 and 2014, 7 to 14 years post-fire. Methods for mapping fire refugia are described in Chapter 1 and Walker et al. (in prep.). Sampling was stratified along a fire refugia density gradient. Fire refugia density was calculated for each 1 meter pixel inside the fire perimeter based on the sum of fire refugia cells within a 300 x 300 meter^2 moving window divided by their distance to the focal cell. This study design supported Chapters 1 and 2 objectives and provided sample locations along a gradient ranging from neighborhoods with larger, denser fire refugia patches where surviving trees were the dominant landscape feature, to neighborhoods with fewer, smaller, fire refugia patches where the dominant landscape feature was stand-replacement fire effects.

We generated a population of random sample points stratified along the fire refugia density gradient in both fire refugia and stand-replacement patches. We identified areas of stand-replacement/high-severity fire in the landscape using the Normalized Burn Ratios (dNBR) derived from 30 meter Landsat TM+ satellite imagery from the Monitoring Trends in Burn Severity (MTBS) project. From the dNBR products we constrained sampling to areas that experienced moderate/high – high-severity (>440 dNBR, Key and Benson 2006). We expected this constraint would exclude areas like grasslands, scree fields and bare ground that were not forested prior to fire. The dNBR constraint was not imposed in the case of our smallest study fire (Figure 3.1 F: Burnt Cabin, 800 ha). However, sampling in stand-replacement patches remained restricted to areas forested prior to fire based on assessments in the field. We excluded all areas within 150 meters of fire perimeters and roads to avoid the locations most heavily impacted by fire suppression activities. To facilitate access, all sample plots were within 1 kilometer of a road or trail and no further than 3 kilometers from a road.

Final plot selection was made in the field based on three rejection criteria and a range of environmental criteria. We rejected plot locations if: (a) there was no evidence of forest prior to fire in stand-replacement patch plots, (b) locations exhibited potentially confounding management histories, or (c) the terrain was inaccessible or unsafe. In the rare event that a plot was misidentified according to our NAIP-based maps (i.e., plot identified as refugia, but no residual trees present), we sampled the plot and categorized it appropriately (refugium or stand-replacement patch) based evidence in the field. Plot locations were separated by a minimum distance of 150 meters to reduce possible spatial autocorrelation. While abiotic gradients were not explicitly included in our stratification, we attempted to representatively sample the range of aspects and elevations available within each fire while attending to our other constraints..

Data collection

We sampled vegetation inside of 100 m^2 circular sample areas for 52 fire refugia plots and in 135 stand-replacement plots. We recorded the percent cover for all vascular plant species occupying >0.25 $meter^2$. Cover values were recorded as the midpoint of eight cover ranges: 0.5% (0.25 – 1%), 2.5% (1 – 5%), 7.5% (5 – 10%), 17.5% (10 – 25%), 29% (25 – 33%), 41.5% (33 – 50 %), 62.5% (50 – 75%), 87.5% (>75%). Voucher samples for all species were collected within plots and species identities were confirmed by Richard Halse, Oregon State University Botany and Plant Pathology Department. In some cases we were unable to identify individuals to the species level because of the lack of developed flowers or fruits. These individuals were classified to the family or genus level when possible, or recorded as unknown by lifeform (e.g., “unknown forb”) when further identification was not possible. To characterize fire refugia overstory tree composition, we recorded the species identity and diameter at breast height for all live and dead trees rooted within fire refugia plots. Because we were primarily interested in plant communities within large fire perimeters, we did not sample unburned controls outside of fire perimeters.

At each sample plot we recorded elevation, aspect, slope, and distance to nearest surviving pre-fire tree. To determine if fire refugia plots were unburned or experienced some degree of fire effects in the most recent fire, we recorded any evidence of fire (e.g., bole scorch, charred coarse woody debris).

We used spatial data archives of mean annual temperature and precipitation for each plot location to support analyses examining understory plant community composition along climatic gradients. Data were acquired from Climate WNA, an application which allows users to download monthly climate data from moderate spatial resolution (800 x 800 meter) grids to point locations (Wang et al. 2016). We acquired climate data from the year of burn to 2015, and averaged across years to characterize the general post-fire climatology of each plot location. In addition, we calculated heat load to characterize the plot-level microclimate. Heat load is a unitless continuous variable calculated by folding aspect along the southwest-northeast axis, which is then combined with slope and latitude to estimate the potential annual solar radiation a location receives (McCune and Keon 2002, Equation 3).

Analysis

We used a combination of univariate and multivariate analyses to compare observations from our three plot types: stand-replacement patches, low-severity burned fire refugia, and unburned fire refugia. We compared estimates of tree, shrub and herbaceous cover to identify differences in structural attributes between fire refugia and stand-replacement patches. Additionally, we tested for differences in species diversity between stand-replacement patches, low-severity burned refugia, and unburned refugia. Diversity metrics included species richness and Shannon’s diversity. Richness was a count of the number of species recorded in each plot. Shannon’s diversity is a widely used measure of species diversity that integrates information on abundance to dampen the effects of rare species relative to raw measures of species richness, making it relatively stable with sample size (Whittaker 1972). A one-way ANOVA was used to test for significant differences among plot types. Two invasive grass species, cheatgrass (*Bromus tectorum*) and ventenata (*Ventenata dubia*), were common in parts of our study area, and we compared their frequency of occurrence in fire refugia and stand-replacement patches to determine if invasibility differed between fire refugia and high-severity burned areas.

We used a suite of multivariate tools to examine plant communities and their variability among plot types. We assessed observations from stand-replacement patch plots in comparison to all fire refugia plots combined (unburned and low severity refugia), then derived a reduced community matrix including only the fire refugia plots to determine if understory plant communities differed between low-severity burned fire refugia and unburned fire refugia. We made several adjustments to the plant abundance data to prepare our community matrix for multivariate analyses. First, we removed cover data for all overstory trees (>5 meters in height). The 5 meter threshold eliminated the data strongly associated with the criteria we used to classify fire refugia (patches of surviving overstory trees), while preserving the data for regenerating tree seedlings in stand-replacement patches and understory trees in fire refugia. The resulting data represented understory plant communities. To decrease the influence of hyper-dominant species on the interpretation of the structure of the community dataset and to emphasize differences in species composition (relative proportions of species), we relativized columns by species maximum in (McCune and Grace 2002). Because we were interested in detecting the relationships between community composition and environmental gradients, relationships that are often diluted by the noise produced by rare species in the data, we removed species that occurred in fewer than 5% of plots. Outlier analysis was performed using PC-ORD 7.02 (McCune and Mefford 2011) using the Bray-Curtis distance measure on the relativized datasets, after rare species and overstory tree data were removed. Outliers were identified as sample units that had an average distance from other sample units more than two standard deviations from the grand mean of distance among sample units.

We used Multi-response Permutation Procedures (MRPP) to test for differences in understory plant community composition in fire refugia and stand-replacement patches, and unburned fire refugia and low-severity burned fire refugia. MRPP is a nonparametric method for testing the hypothesis of no difference between a priori groups that does not rely on assumptions of multivariate normality (Mielke et al. 1981). MRPP generates a p-value: the likelihood of getting a delta (weighted mean within-group distance) as extreme or more extreme than the observed delta, given the distribution of possible deltas (McCune and Grace 2002). MRPP also reports an A statistic, a measure of effect size, which describes within-group homogeneity compared to random expectation (McCune and Grace 2002). MRPP analyses were conducted in R (ver. 3.4.0, R Core Team 2017) with the vegan package (Oksanen et al. 2017).

Non-metric multidimensional scaling (NMS) was used to graphically examine community relationships and evaluate community variability along environmental gradients. We compared observations between fire refugia and stand-replacement patch plots, as well as low-severity burned and unburned fire refugia plots. NMS is often the method of choice for graphical representations of community relationships (Clarke 1993) for a number of reasons. NMS avoids assumptions of linear relationships among variables, preserves the structure of community data in ordination space, and is compatible with multiple distance measures and relativizations (McCune and Grace 2002). We graphed NMS ordinations with sample units ordinated in species space, and overlaid biplots of environmental gradients to identify key drivers of community composition. Variables included in the environmental matrix were fire, elevation (in meters), heat load, distance to nearest surviving pre-fire tree, plot type (stand-replacement patch, low-severity burned refugia, unburned refugia), fire severity (dNBR), mean annual temperature, mean annual precipitation, and the total percent cover for three vegetation strata (tree, shrub, herbaceous). We chose to include strata totals in the environmental matrix to examine how community composition varied along gradients of abundance by lifeform. While a similar analysis of post-fire plant community composition included strata totals in the community matrix (Coop et al. 2016), doing so has the potential to significantly distort the structure of community datasets and may lead to unsupported inferences. A discussion of the implications of data relativizations and the inclusion of strata in the community matrix can be found in Appendix 3. NMS was conducted with the vegan package in R using Bray-Curtis dissimilarity.

The presence of surviving pre-fire trees in fire refugia plots allowed us to use tree cover data to partition fire refugia plots into more homogeneous groups using cluster analysis. We were interested in determining if unburned fire refugia were associated with a particular overstory forest composition. Additionally, we anticipated that increased homogeneity within groups delineated in the cluster analysis would improve our ability to identify compositional differences between unburned and low-severity burned fire refugia, if such differences existed. Cluster analysis was performed in PC-ORD with Euclidean distance and Ward’s method.

We used indicator species analysis (ISA) to describe species relationships to fire refugia and stand-replacement patch plot types. ISA combines species’ relative abundance with frequency of occurrence in different groups. The indicator value of a species is the product of two components, “exclusivity” and “fidelity”. Exclusivity is the probability that a plot belongs in the assigned category, given that the species occurs in that plot. Fidelity is the probability of encountering the species in a plot based on its assigned category (Cáceres and Legendre 2009).

The indicator value (IV) of a species is maximum (100) when all individuals of a species occur in a single group, and when the species occurs in all plots within that group (Dufrêne and Legendre 1997). Monte Carlo randomizations were used to test the hypothesis that IVs were higher than would be expected by chance. Indicator species analyses was performed in R with the indicspecies package (Cáceres and Legendre 2009) with 999 randomizations in the Monte Carlo test. In addition, we used information derived from the US Fire Effects Information System (www.feis-crs.org/feis/) to assign life-history traits to each indicator species to determine if certain fire-adaptive traits where associated with fire refugia and stand-replacement patches.

Results

Fire refugia identified for the purposes of this study are distinct from stand-replacement patches in composition and structure by virtue of the criteria used to map them: fire refugia are where overstory trees persist, stand-replacement patches are areas where all trees were killed by fire (Figure 3.2A, 3.2B). The percentage of area classified as fire refugia by our NAIP-based analysis ranged from 33% in the Roberts Creek fire, to 60% in the Burnt Cabin fire, with an average of 45% across all fires. The remainder of the landscape was primarily forest that experienced complete overstory mortality, although some areas were not forested prior to fire (grasslands, rock, etc.). Within these landscapes we surveyed 187 plots, resulting in 135 stand-replacement patches (SRP) and 52 fire refugia (Refugia) plots. Within the sample of fire refugia we identified seven fire refugia plots that contained no evidence of fire (Unburned), with the remaining showing evidence of low severity surface fire (Low-severity).

A dominant feature of the post-fire landscape is the difference in tree cover between fire refugia and stand-replacement patches (Figure 3.2C). However, when considering tree cover as a metric that integrates both overstory and understory trees, the magnitude of the difference in overall tree cover between plot types is reduced by relatively high densities of regenerating conifer seedlings in stand-replacement patches (median = 1100 seedlings ha^{-1}; Chapter 1). Shrub cover was substantially higher on average in stand-replacement patch plots (mean = 53.8, SE = 38.7) than in fire refugia plots (mean = 15.7, SE = 21.4), and herbaceous cover was similar between fire refugia and stand-replacement patches (Figure 3.2D, 3.2E).

The most common overstory tree species in fire refugia were grand fir, Douglas-fir, and ponderosa pine (Figure 3.3). A substantial proportion of grand fir and Douglas-fir basal area consisted of trees that were dead at the time of sampling. Although we were unable to definitively identify mortality agents, most dead trees appeared to have been killed by surface fire in refugia. Dead trees were smaller on average (diameter at breast height, DBH) than trees alive at the time of sampling for the three most common species in our study area (Figure 3.3B), and surviving grand fir trees were smaller on average (22.6 cm, SE = 17.2) than both Douglas-fir (41.6 cm, SE = 22) and ponderosa pine (41.2, SE = 28).

We identified a total of 293 plant species; 220 occurred in fire refugia plots and 245 occurred in stand-replacement patch plots. Species richness and diversity were similar between plots types. Average species richness (Figure 3.4) across all plots was 19.5 (range = 1 – 46 species), and there was no significant difference (one-way ANOVA, F = 0.06, p = 0.9) in species richness between stand-replacement patches (19.6, SE = 0.7), low-severity fire refugia (19.4, SE = 1.1), and unburned fire refugia (18.6, SE = 2.9). Average Shannon's diversity was 1.8 (range = 0 – 3.27) for all plots. There was no evidence of a difference (F = 0.15, p = 0.8) between stand-replacement patches (1.8, SE = 0.05), low-severity fire refugia (1.8, SE = 0.09), and unburned fire refugia (1.7, SE = 0.23).

We observed exotic invasive annual grasses in 52 study plots, and focused analyses on two common species, cheatgrass and ventenata. Cheatgrass was present in 11 fire refugia plots and 36 stand-replacement patch plots, and average cover was low in plots where it was present (mean = 4%, range = 0.5 – 29% cover). We found no evidence of a difference between the percentage of fire refugia (21%, SE = 6%) and stand-replacement patch plots (27%, SE = 4%) occupied by cheatgrass ($\chi^2_{df=1}$ = 0.349, p = 0.55). Ventenata was present in 19 plots and cover was low on average in plots were it occurred (mean = 8%, range = 0.5 – 29% cover). There was no difference in the percentage of refugia (12%, SE = 5%) and stand-replacement patch plots (10%, SE = 3%) that contained ventenata ($\chi^2_{df=1}$ = 0.014, p = 0.91).

The most abundant species present in the understory of fire refugia, in decreasing order from the most abundant, were *Carex geyerii, Abies grandis, Ceanothus velutinus, Calamagrostis rubescens,* and *Arnica cordifolia*. The most abundant species in stand-replacement patches were similar: *C. velutinus, C. rubescens, C. geyerii, Ceanothus sanguineus,* and *Pinus contorta*. A complete list of all species can be found in Appendix 2. The removal of species that occurred in fewer than 5% of plots resulted in 84 species remaining in our multivariate analyses. We identified one outlier that did not contain any plant cover data after overstory tree data were removed, and this plot was not included in further analysis.

Multivariate analyses of understory plant communities did not identify strong compositional differences between understory plant communities in fire refugia and stand-replacement patches, 12 – 17 years post-fire. Multi-response permutation procedures provided some evidence of a difference in composition between fire refugia and stand-replacement patch plots ($p < 0.001$), but the effect size was very small ($A = 0.025$), indicating substantial heterogeneity within groups and overlap between groups. The NMS ordination of fire refugia and stand-replacement patch plots resulted in a two-dimensional solution with a final stress of 0.28 (Figure 3.2A). The environmental gradient most strongly associated with axis 1 was mean annual precipitation ($R^2 = 0.33$). Axis 2 was most strongly associated with mean annual temperature ($R^2 = 0.27$) and elevation ($R^2 = 0.29$). Fire severity (dNBR) was weakly related to axis 1 ($R^2 = 0. 11$). The remaining environmental gradients were not strongly associated with either axis ($R^2 < 0.15$), including distance to refugium. NMS ordination results are consistent with the low effect size (A) detected with MRPP analysis; fire refugia and stand-replacement patch plots do not appear to occupy distinct portions of species space.

Although understory plant communities were similar in fire refugia and stand-replacement patch plots, ISA analysis identified a small number of statistically significant indicator species. Eight species were associated with stand-replacement patches, and seven associated with fire refugia (Figure 3.5B, Table 3.1). Indicator values were lower on average ($t = 2.2$, $p = 0.05$) for refugial species (mean = 18.9, SE = 8.8) than those associated with stand-replacement patches (mean = 34, SE = 17.5). Additionally, the species with the highest indicator values (IV > 60, *C. velutinus, Epilobium angustifolium, C. rubescens*) were all associated with stand-replacement patches. The primary driver of comparatively low indicator values for fire refugia indicator species was low species “fidelity.” These species were not present in most fire refugia plots, although they did occur primarily in fire refugia (high “exclusivity”).

Multivariate analyses of plant community composition in unburned and low-severity burned fire refugia did not identify substantial differences between these plot types. According to MRPP, there was little evidence of a difference between unburned (n = 7) and low-severity burned (n = 44) fire refugia (p = 0.06, A = 0.004). Non-metric multidimensional scaling produced a two dimensional solution with a final stress of 0.22. An ordination of fire refugia plots in species space indicated that unburned fire refugia occupied a subset of fire refugia species space (Figure 3.3), but we acknowledge our capacity for drawing inference about the composition of unburned fire refugia is limited by our small sample size. Axis 1 was associated with elevation ($R^2 = 0.30$) herbaceous cover ($R^2 = 0.44$), and mean annual temperature ($R^2 = 0.34$). Axis 2 was associated with mean annual precipitation ($R^2 = 0.24$). Fire severity was weakly associated with axis two ($R^2 = 0.11$), and no other variables were strongly related with either axis ($R^2 < 1.5$). Unburned fire refugia were associated with lower mean annual temperatures, higher precipitation, and lower herbaceous cover.

Cluster analysis, which we used to divide fire refugia plots into more homogenous groups based on conifer tree cover data, resulted in two “forest types.” Rank abundance values indicated that the first group was dominated by ponderosa pine and Douglas-fir, while the second group was dominated by grand fir. Six out of seven unburned refugia plots were assigned to the grand fir group. Because conifer tree data were used in the cluster analysis to delineate forest types, we compared low-severity and unburned fire refugia in the grand fir group using only non-conifer vegetation cover data. Despite constituting a more homogenous sample, there was no evidence of a difference between unburned fire refugia plots (n = 6) and low-severity burned fire refugia plots (n=11) in grand fir dominated stands (MRPP, p = 0.77).

Discussion

Understory plant community composition in fire refugia and stand-replacement patches was similar 12 – 17 years post-fire, despite substantial structural differences between plot types. We found no evidence of differences among plot types in species richness, diversity, or invasibility by exotic annual grasses. Although plant community composition was similar between plot types, we did identify several indicator species for fire refugia and stand-replacement patches, suggesting that differences between these plot types strongly influence the abundance of some plant species. We did not find evidence of a difference between understory plant community composition in unburned and low-severity burned fire refugia. Our findings highlight the capacity of understory plant communities in the Blue Mountains to recover following fire, and suggest that dry mixed-conifer forests in our study area are resilient to even high-severity fire effects. Fire refugia in the Blue Mountains appear to be important primarily as remnant forest structure and as surviving seed sources essential for the reestablishment of trees in high-severity burned areas (Chapter 2). Neither unburned fire refugia nor low-severity refugia contained distinct communities of fire-sensitive plant species otherwise absent from the higher-severity burned matrix. Frequent fire in Blue Mountain dry mixed-conifer forests prior to European settlement may have functioned as a coarse filter that largely prevented truly fire-sensitive species from occupying the broader landscape (Keeley et al. 2011), resulting in a contemporary flora that is highly fire-resilient (Donato et al. 2009).

Fire had a profound effect on forest structure in our study area. More than half of the area within our study fires did not contain overstory forest following fire, and much of the high-severity burned landscape has been temporarily converted from forest to an early-seral, shrub-dominated state. Conifer seedlings were regenerating in over 80% of our stand-replacement patch plots (Chapter 2), but it will likely require many decades, and the absence of subsequent disturbance (e.g., reburn), for regenerating forest to approximate the relatively intact forest structure present in fire refugia. Additionally, there is some indication that forest regenerating in stand-replacement patches is not representative of surviving forest in fire refugia. Regenerating lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and grand fir were more abundant in stand-replacement patches than we would expect based on the composition of fire refugia (Chapter 2). However, our data provide little insight into which seedlings will eventually recruit into the overstory, and evaluating the long-term impacts of high-severity fire on forest composition was outside the scope of this study.

Low-severity surface fire appears to have substantially reduced small, Douglas-fir and grand fir basal area in fire refugia, and these fire effects may have important implications for the resistance of fire refugia to future fire events. Fire exclusion and resultant infilling of dry forests by relatively shade tolerant species like Douglas-fir and grand fir have raised concerns about the increasing risk of high-severity fire in Pacific Northwest dry forests (Hagmann et al. 2013, Merschel et al. 2014). Prescribed fire and thinning treatments designed to mimic historical, low-severity fire regimes by removing surface fuels, reducing tree densities, and retaining fire-resistant trees, have been shown to decrease wildfire severity (Agee and Skinner 2005, Finney et al. 2005). In our study fires, low-severity fire effects in fire refugia may have resulted in stand structure more similar to historical reference conditions, and reductions in ladder fuels and fuel continuity could promote the persistence of remnant forest in fire refugia during subsequent fire (Coppoletta et al. 2016, Kolden et al. 2017). In contrast, unburned fire refugia may more vulnerable to high-severity fire effects in future fires (Kolden et al. 2017). It is possible that these patchy and relatively rare areas of unburned forest, which miss one or more fire return intervals and accumulate more fuel than the surrounding landscape, were responsible for the rare, high-severity fire effects observed in the fire history record.

For species that rely on relatively intact forest habitat, structural differences between fire refugia and the surrounding higher-severity burned matrix may be a critical driver of habitat selection within fire perimeters. Large mammal species like lynx, black bears, and moose preferentially occupy fire refugia inside large fire perimeters where cover and food resources are more abundant (Gasaway and DuBois 1985, Cunningham et al. 2003, Vanbianchi et al. 2017). Seeds produced by mature conifer trees are an important food source for seed-cacheing jays, nutcrackers, and rodents (Vander Wall 2003), and these seed sources are also critical for re-populating tree communities in nearby patches of high-severity fire. Within fire perimeters, this seed resource is available only within fire refugia until regenerating conifers begin producing cones. However, similarities in understory plant composition between fire refugia and stand-replacement patches suggest that species that do not depend on intact forest canopy, and rely instead primarily on understory plant communities for food, shelter, or nesting, are unlikely to be confined to fire refugia.

Similarities in understory plant community composition between fire refugia and stand-replacement patches indicate that these communities are relatively resilient to high-severity fire effects. Community composition varied most strongly along environmental gradients of temperature and precipitation, rather than with fire severity (dNBR) or between plot types (fire refugia, stand-replacement patches). There was a statistically significant difference between the community composition of fire refugia and stand-replacement patches, but NMS ordination demonstrated that the difference was subtle and that plant communities in fire refugia are not distinct from those in stand-replacement patches. It is possible that stronger compositional differences existed between fire refugia and stand-replacement patches in the years immediately post-fire and that the strength of these differences has declined as more time has passed. Additionally, the strong influence of site characteristics (elevation, temperature, and precipitation), rather than fire effects, may be a function of sampling across the broad environmental gradients of the region, and stronger compositional differences between fire refugia and stand-replacement patches may exist within narrower ranges of these environmental gradients. However, we did not have an *a priori* basis for organizing our data into more homogeneous groups; for example, cluster analysis based on pre-fire overstory tree composition was not possible for all plots due to our inability to definitively determine the species identity of all fire-killed trees in stand-replacement patches 12 - 17 years after fire.

Rapid compositional recovery of highly disturbed forest ecosystems has been reported in other parts of the northwestern United States. In Northern Rockies spruce-fir forests, understory plant communities strongly resembled pre-fire assemblages within as little as one growing season after fire (Doyle et al. 1998). Understory plant communities in Douglas-fir forests in western Oregon were significantly different between undisturbed and severely disturbed sites (logged and subsequently burned) five years following disturbance (Dyrness 1973), but had largely returned to their pre-fire composition 21 years post-treatment (Halpern 1988). These studies were conducted in more mesic forests where infrequent, high-severity fire effects were likely an important feature of pre-European fire regimes (Agee 1993). In contrast, dry forests in the Blue Mountains no longer support their historical fire regimes; frequent-fire has been excluded by fire suppression, and high-severity fire effects appear to be more prevalent than they were historically (Merschel et al. 2014, Johnston et al. 2016, Reilly et al. 2017). Compositional similarities between fire refugia and stand-replacement patches in our study suggest substantial ecosystem resilience to high-severity fire, which is perhaps unexpected in a system so severely departed from its historical disturbance regime (Keeley et al. 2011). However, our results are consistent with a similar study in the Klamath Siskiyou region where pre-European fire return intervals of 12 - 19 years are comparable to those documented in the Blue Mountains (Taylor and Skinner 1998). Donato et al. (2009) reported that the composition of high-severity burned plots was similar to unburned controls two growing seasons after fire, and the authors concluded that a long history of recurrent fire, including some proportion of stand-replacement fire, resulted in a native biota that is highly adaptive to a range of fire effects.

The results of our indicator species analysis demonstrate that the abundance of a small number of species in our study area is strongly influenced by differences between fire refugia and stand-replacement patches. Indicator species' life-history traits generally support their association with either fire refugia or stand-replacement patches. Fire refugia indicator species are primarily fire-sensitive, obligate seeders, while species associated with stand-replacement patches resprout, produce long-lived seed banks, or are early-seral specialists that require high light conditions to establish. Grand fir, the strongest fire refugia indicator species, is fire-sensitive when young, and readily regenerates beneath intact forest canopy. We encountered seedling densities as high as 73,900 stems ha^{-1} inside fire refugia plots, substantially higher than regeneration densities observed in stand-replacement patches (Chapter 2). Another refugia indicator species, *Hieracium albiflorum*, a perennial herb with a shallow root system easily killed by fire (Doyle et al. 1998), has also been associated with volcanic refugia following the Mount St. Helens eruption (Fuller and Del Moral 2003). Two fire refugia indicator species are associated with locations that may reduce their exposure to fire. *Sedum stenopetalum*, a flowering perennial herb in the stonecrop family, and *Juniperus occidentalis*, are often found on rock outcrops and gravely benches (Mason 2001), locations that may offer partial protection from fire (Young and Evans 1981). Not all fire refugia indicator species possess functional traits that would suggest an association with fire refugia. *Poa secunda*, a native perennial grass, and *Balsamorhiza sagittata*, a perennial forb, are capable of resprouting, are highly resistant to fire, and generally increase after fire (Powell 1994, Youngblood et al. 2006, Rau et al. 2008). Shrub cover was substantially lower on average (14 - 15%) in plots with *Poa secunda* and *Balsamorhiza sagittata*, compared to plots where these species were absent (45%), and a possible explanation for why these two species were classified as fire refugia indicator species may be that strong interspecific competition with woody species in stand-replacement patches reduced their cover in those areas relative to fire refugia.

Species strongly associated with stand-replacement patches had higher indicator values on average than species associated with fire refugia, and these species possess life-history traits well suited to high-severity burned environments. *Ceanothus velutinus* and *Arctostaphylos patula* produce long-lived, ground-stored seeds that require heat to germinate, and both species are capable of resprouting following fire (Conrad et al. 1985, Agee 1993). *Epilobium angustifolium*, a perennial forb, *Calamagrostis rubescens*, a native perennial grass, and willows (*Salix spp*.) are all highly effective off-site colonizers following high-severity fire and they all have the capacity to resprout from rhizomes or root crowns after being top-killed (Stickney 1990, Powell 1994). Two conifer species, lodgepole pine and western larch, were identified as stand-replacement patch indicator species. Although sensitive to fire, lodgepole pine can rapidly recolonize stand-replacement patches due to its serotinus cones, which open when exposed to heat from fire, but are retained in tree crowns as a canopy seedbank where they are protected from high-severity effects. Cone serotiny is spatially highly variable, but even non-serotinus individuals can promote rapid regeneration in high-severity patches via wind-dispersed seed (Baker 2009). Western larch readily regenerates in high light environments produced by high-severity fire effects, although it relies exclusively on light, windborne seeds to reproduce (Powell 1994). Both of these tree species were more common in stand-replacement patches than we would expect based on the composition of surviving forest in fire refugia, but in the absence of pre-fire forest composition data, we are unable to determine the degree to which regenerating seedlings are representative of pre-fire forest composition.

Our results provide only weak evidence that fire refugia in our study area promote the persistence of fire-sensitive plant communities otherwise absent from the higher-severity burned matrix, as has been reported in studies in other forest ecosystems (Wood et al. 2011, Adie et al. 2017). The lack of strong community differences between fire refugia and stand-replacement patches could be attributed to the fact that we did not specifically target fire refugia associated with topographic features that predictably moderate fire effects. In contrast, studies conducted in

Patagonia, Australia, and South Africa reported that fire-sensitive tree and shrub species were associated with fire refugia in sparsely vegetated areas or near rock outcrops that decrease fire intensity and frequency (Clarke 2002, Landesmann et al. 2015, Adie et al. 2017). Long lived, fire-sensitive plant species like Alaska yellow cedar (*Callitropsis nootkatensis*) and mountain mahogany (*Cercocarpus ledifolius*) do occur in some parts of the Blue Mountains and there is some indication that these species are associated with topoedaphic features that support persistent fire refugia where fire burns less frequently or severely than the surrounding landscape (Frenkel 1974, Dealy 1975). However, additional research is needed to determine if the locations where these species occur are in fact fire refugia, and whether their understory composition is distinct from the surrounding landscape matrix.

Consistent with other studies in Pacific Northwest dry forests, we found no evidence of a difference in species richness and diversity among plots types, suggesting fire severity is not a strong driver of understory plant diversity in our study area. Donato et al. (2009) reported no differences in plant species richness or diversity between unburned controls and high-severity burned areas two years post-fire in the Klamath-Siskiyou region. Similarly, Kerns et al. (2006) reported no differences in richness or diversity between unburned controls, low-severity fire (spring burn), and higher-severity fire (fall burn) in the Blue Mountains. Relationships between species diversity and disturbance are a source of continued, vigorous debate among ecologists (Fox 2013, Sheil and Burslem 2013), and additional research is needed to understand the ecological implications of high-severity disturbance in mixed-conifer forests. Early-seral forests like those created by high-severity fire are important landscape elements associated with high species diversity in some ecosystems (Swanson et al. 2011, Campbell and Donato 2014, Hutto et al. 2016). However, there are concerns that stand-replacement fire effects pose a threat to biodiversity in frequent-fire forests where high-severity fire was not a substantial component of pre-European fire regimes (Haire and McGarigal 2008, Coop et al. 2016). Our results demonstrate that neither fire refugia nor stand-replacement patches in our study area are either particularly species rich, or species poor, and compositional similarities between our plot types provide little evidence that high-severity fire results in significant losses of biodiversity. However, we recognize that high-severity fire resulted in substantial losses of mature forest structure within our fire perimeters, and that short-interval reburn, should it occur in stand-replacement patches in our study area, has the capacity to significantly alter understory plant communities (Donato et al. 2009) and reinforce shifts towards non-forested states (Coop et al. 2016, Coppoletta et al. 2016).

Our data provide some indication that post-fire mosaics that contain both stand-replacement patches and fire refugia promote higher landscape-scale plant diversity than one patch type alone. All of the common species included in our multivariate analysis (species present in > 5% of plots) occurred in both fire refugia and stand-replacement patch plots. However, 48 of the excluded rare species were present only in fire refugia, and 77 rare species were present only in stand-replacement patches (Appendix 2). These species constituted approximately 40% of the species sampled, and although they were not widespread components of understory communities in our study area, their presence may indicate that a gradient of fire effects, including both fire refugia and stand-replacement patches, promotes plant diversity at a landscape scale (Perry et al. 2011, Burkle et al. 2015).

We found no evidence of a difference between fire refugia and stand-replacement patch plot types in the occurrence cheatgrass and ventenata, two exotic annual grass species of concern in parts of our study area. Increased cheatgrass densities have been associated with higher-severity prescribed fire effects and canopy gaps in the Blue Mountains (Kerns et al. 2006), but very little is known about the biology and response to disturbance of ventenata, a relative newcomer to the Pacific Northwest (Wallace et al. 2015). Ventenata has been primarily described in grassland and sagebrush ecosystems (Wallace et al. 2015, Jones et al. 2018), but our data demonstrate that it is expanding into dry forests in the Blue Mountains, even into the roadless and wilderness areas we primarily sampled. Both experimental and observational studies have demonstrated that disturbance intensity increases the invasibility of native plant communities (Burke and Grime 1996, Crawford et al. 2001, Kerns et al. 2006), and in the absence of pre-fire data we were unable to distinguish between exotic grass populations that were present prior to fire and those that established after fire, or if exotic grass cover increased following fire. However, similar frequency of occurrence of ventenata and cheatgrass in our plot types suggests that fire refugia are not immune to invasive grass establishment following surface fire, and high-severity fire effects do not appear to substantially increase the invasibility of dry mixed-conifer forests in our study area.

We did not identify strong compositional differences between understory plant communities in unburned and low-severity burned fire refugia. The NMS ordinations, however, demonstrated that unburned fire refugia were associated with higher elevations and precipitation, as well as lower temperatures and herbaceous cover. Despite the fact that all of our refugia plots contained persistent canopy according to both field observations and our NAIP-based maps, burn severity, as measured by dNBR, varied significantly within our refugia sample (mean = 205, range = -51 – 811). However, burn severity did not appear to be a strong driver of understory plant composition in fire refugia. While our ability to definitely identify unburned islands was limited because of the amount of time that has elapsed since fire, we did encounter locations within fire perimeters that exhibited no evidence of recent fire effects, some as large as several hectares in size. The small sample size of unburned refugia plots and our experience in the field indicate that unburned fire refugia constitute a relatively small proportion of the area within large fire perimeters in the Blue Mountains, which is consistent with post-fire observations in other dry forest systems (Campbell et al. 2007).

Our cluster analysis assigned six out of seven unburned fire refugia plots to the grand fir group rather than the ponderosa pine/Douglas-fir group. Although grand fir is sometimes referred to as a fire-intolerant species (Camp et al. 1997, Youngblood et al. 2008), these results should not necessarily be taken as evidence that unburned patches were characteristic of grand fir stands historically. Johnston et al (2016) reported that grand fir stands in the southern Blue Mountains burned nearly as frequently as ponderosa pine stands prior to European settlement. However, the clustering of unburned plots in grand fir stands may indicate that contemporary surface fire effects are patchier in grand fir stands than in stands dominated by ponderosa pine and Douglas-fir. Grand fir needles are considerably shorter than ponderosa pine needles, and grand fir leaf litter may constitute a more compact, less flammable fuel bed that discourages the spread of low-intensity fire, compared to ponderosa pine leaf litter (de Magalhães and Schwilk 2012). Additionally, it is possible that in more productive sites where grand fir is dominant, fire exclusion and resultant increases in tree density have more rapidly reduced the herbaceous, fine fuels that historically propagated low-severity fire (Hessburg et al. 2005).

The lack of strong compositional differences between unburned and low-severity burned fire refugia may provide support for the use of satellite remote sensing methods commonly used to map fire refugia. Fire refugia are frequently identified as low-severity or unburned patches based on dNBR and related metrics from Landsat imagery (e.g., Krawchuk et al. 2016). However, these remote sensing methods are unable to reliably differentiate between unburned and low-severity burned patches (Kolden et al. 2012, Meddens et al. 2016). Based on our results, combining unburned and low-severity burned patches into a “refugia” group may be a reasonable approach depending on the taxa or ecological process of interest. However, the difference between truly unburned patches and patches that experienced low-severity fire effects may be important for species other than understory plants, including epigaeic beetles (Gandhi et al. 2001), fire-sensitive bryophytes (Hylander and Johnson 2010) and some rodent species (Swan et al. 2016). Additionally, it is possible that important compositional differences between burned and unburned refugia did exist in the years immediately post-fire but since have lapsed as plant communities converge toward similar compositions. It also may be the case that some or all of the sites we identified as unburned did in fact experience some degree of fire effects, the evidence of which was not apparent at the time of sampling.

Conclusions

Our results provide novel insights into the structure and composition of fire refugia in Blue Mountain dry mixed-conifer forests. Fire refugia are ecologically important as locations where relatively intact forest structure persists, and as seed sources that contribute to post-fire forest recovery in stand-replacement patches (Chapter 2, Landesmann and Morales 2018). By definition, there are strong and unequivocal differences in physical structure between fire refugia and stand-replacement patches, but these differences do not appear to extend to the composition of understory plant communities. The similarities in the community composition of common understory plant species we observed between fire refugia and stand-replacement patches provide little evidence that high-severity fire effects in the Blue Mountains result in unacceptable losses of biota and ecological communities, as has been suggested in other dry forest systems (Coop et al. 2016). However, stand-replacement fire effects in our study area did result in substantial losses of mature forest structure, and post-fire forest recovery in these high-severity burned areas depends on seed sources that survived fire in refugia, particularly in locations far from intact forest outside of fire perimeters. It is possible that the low-severity fire effects we observed in fire refugia resulted in more fire-resistant stand structure, but the persistence of fire refugia through multiple fire events remains poorly understood (Kolden et al. 2017). Ideally, the baseline understanding of fire refugia composition and structure provided by this study will support future investigations into the functions, persistence, and vulnerability of these important landscape elements.

References

Adie, H., D. J. Kotze, and M. J. Lawes. 2017. Small fire refugia in the grassy matrix and the persistence of Afrotemperate forest in the Drakensberg mountains. Scientific Reports 7:1–10.

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Airey Lauvaux, C., 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.

Ashcroft, M. B. 2010. Identifying refugia from climate change. Journal of Biogeography 37:1407–1413.

Barbé, M., N. J. Fenton, and Y. Bergeron. 2017. Are post-fire residual forest patches refugia for boreal bryophyte species? Implications for ecosystem based management and conservation. Biodiversity and Conservation 26:943–965.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Burkle, L. A., J. A. Myers, R. T. Belote, and D. P. C. Peters. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6.

Burns, R. M. 1983. Silvicultural systems for the major forest types of the United States. Agricultural Handbook 445. USDA Forest Service, Washington, D.C., USA.

Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90:3566–3574.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee mountains. Forest Ecology and Management 95:63–77.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

Campbell, J. L., and D. C. Donato. 2014. Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. Forest Ecology and Management 324:172–178.

Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. Forest Ecology and Management 378:57–67.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clarke, P. J. 2002. Habitat islands in fire-prone vegetation: Do landscape features influence community composition? Journal of Biogeography 29:677–684.

Conrad, S. G., A. E. Jaramillo, J. Kermit Cromack, and S. Rose. 1985. The role of the genus Ceanothus in western forest ecosystems. USDA Forest Service General Technical Report, PNW-GTR-182. Pacific Northwest Research Station, Portland, OR, USA.

Coop, J. D., S. A. Parks, S. R. Mcclernan, and L. M. Holsinger. 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned southwestern landscape. Ecological Applications 26:346–354.

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.

Crawford, J. A., C. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in Pinus ponderosa forests in northern Arizona. Journal of Vegetation Science 12:261–268.

Cunningham, S. C., W. B. Ballard, L. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, central Arizona. Wildlife Society Bulletin 31:786–792.

Dealy, J. E. 1975. Ecology of Curlleaf Mountain-Mahogany (Cercocarpus ledifolius Nutt.) in Eastern Oregon and Adjacent Areas. Oregon State University, Corvallis, OR, USA. 161 . Thesis.

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.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.

Doyle, K., D. Knight, D. Taylor, W. Barmore, and J. Benedict. 1998. Seventeen years of forest succession following the Waterfalls Canyon fire in Grand Teton National Park, Wyoming. International Journal of Wildland Fire 8:45.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57–69.

Finney, M. A., C. W. McHugh, and I. C. Grenfell. 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. Canadian Journal of Forest Research 35:1714–1722.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28:86–92.

Frenkel, R. 1974. An isolated occurrence of Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) in the Aldrich Mountains, Central Oregon. Northwest Science 48.

Fuller, R. N., and R. Del Moral. 2003. The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. Journal of Vegetation Science 14:637–644.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera : Carabidae and Staphylinidae). Biological Conservation 102:131–141.

Gasaway, W. C., and S. D. DuBois. 1985. Initial response of moose to a wildfire in interior Alaska. The Canadian Field Naturalist 99:135–140.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern oregon cascade range, USA. Forest Ecology and Management 330:158–170.

Haire, S. L., and K. McGarigal. 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. Southwestern Naturalist 53:146–161.

Halpern, C. B. 1988. Early successional pathways and the resistence and resilience of forest communities. Ecology 69:1703–1715.

Halpern, C., and T. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:913–934.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: Inferences from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. Ecology 82:660–678.

Hutto, R. L., R. E. Keane, R. L. Sherriff, C. T. Rota, L. A. Eby, and V. A. Saab. 2016. Toward a more ecologically informed view of severe forest fires. Ecosphere 7:1–13.

Hylander, K., and S. Johnson. 2010. In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. Journal of Vegetation Science 21:1099–1109.

Johnson, C. G. 1994. Forest health in the Blue Mountains: A plant ecologist’s perspective on ecosystem processes and biological diversity. USDA Forest Service, General Technical Report, PNW-GTR-339. Pacific Northwest Research Station, Portland, Oregon, USA.

Johnson, C. G., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-T-036092. Pacific Northwest Research Station, Portland, OR, USA.

Johnston, J. D., J. D. Bailey, and C. J. Dunn. 2016. Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests. Ecosphere 7:1–19.

Jones, L. C., N. Norton, and T. S. Prather. 2018. Indicators of ventenata (Ventenata dubia) invasion in sagebrush steppe rangelands. Invasive Plant Science and Management 11:1–9.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16:406–411.

Keppel, G., K. P. Van Niel, G. W. Wardell-Johnson, C. J. Yates, M. Byrne, L. Mucina, A. G. T. Schut, S. D. Hopper, and S. E. Franklin. 2012. Refugia: Identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21:393–404.

Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. Season and severity of prescribed burn in ponderosa pine forests: Implications for understory native and exotic plants. Ecoscience 13:44–55.

Key, C. H., and N. C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. USDA Forest Service General Technical Report RMS-GTR-164-CD. Ogden, UT, USA.

Kolden, C. A., J. A. Lutz, C. H. Key, J. T. Kane, and J. W. van Wagtendonk. 2012. Mapped versus actual burned area within wildfire perimeters: Characterizing the unburned. Forest Ecology and Management 286:38–47.

Kolden, C., T. Bleeker, A. Smith, H. Poulos, and A. Camp. 2017. Fire effects on historical wildfire refugia in contemporary wildfires. Forests 8:400.

Krawchuk, M. A., S. L. Haire, J. D. Coop, M.-A. Parisien, E. Whitman, G. W. Chong, and C. Miller. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7(12).

Landesmann, J. B., J. H. Gowda, L. A. Garibaldi, and T. Kitzberger. 2015. Survival, growth and vulnerability to drought in fire refuges: Implications for the persistence of a fire-sensitive conifer in northern Patagonia. Oecologia 179:1111–1122.

Landesmann, J. B., and J. M. Morales. 2018. The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia. Plant Ecology 219:455–466.

Mason, G. 2001. Guide to plants of the Wallowa Mountains of northeastern Oregon. University of Oregon Press, Eugene, OR, USA.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, USA.

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. 2011. PC-ORD. Multivariate analysis of ecological data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.

Meddens, A. J. H., C. A. Kolden, and J. A. Lutz. 2016. Detecting unburned areas within wildfire perimeters using Landsat and ancillary data across the northwestern United States. Remote Sensing of Environment 186:275–285.

Merschel, A. G., T. A. Spies, and E. K. Heyerdahl. 2014. Mixed-conifer forests of central Oregon: Effects of logging and fire exclusion vary with environment. Ecological Applications 24:1670–1688.

Mielke, P. W., K. J. Berry, and G. W. Brier. 1981. Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. Monthly Weather Review 109:120–126.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, H. Wagner, and M. J. Oksanen. 2017. Vegan: community ecology package. R Package Version 2. 4-6.

Ott, T. M., E. K. Strand, and C. L. Anderson. 2015. Niche divergence of Abies grandis-Abies concolor hybrids. Plant Ecology 216:479–490.

Ouarmim, S., L. Paradis, H. Asselin, Y. Bergeron, A. Ali, and C. Hély. 2016. Burning potential of fire refuges in the boreal mixedwood forest. Forests 7:246.

Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703–717.

Powell, D. 1994. Effects of the 1980s western spruce budworm outbreak on the Malheur National Forest in northeastern Oregon. USDA Forest Service Technical Report R6-FI&D-TP-12-94. Pacific Northwest Region Forest Insects and Disease Group, Portland, OR, USA.

PRISM. 2018. PRISM Climate Group, Oregon State University. http://www.prism.oregonstate.edu.

R Core Team. 2017. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. www.R-project.org. https://www.r-project.org/.

Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central Great Basin. Rangeland Ecology and Management 61:169–181.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985-2010). Ecosphere 8.

Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135–154 in R. W. Wein and D. A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystems. Wiley, New York.

Sheil, D., and D. F. R. P. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: A response to Fox. Trends in Ecology and Evolution 28:571–572.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Stickney, P. F. 1990. Early development of vegetation following holocaustic fire in northern Rocky Mountain forests. Northwest Science 64:243–246.

Swan, M., C. Galindez-Silva, F. Christie, A. York, and J. Di Stefano. 2016. Contrasting responses of small mammals to fire and topographic refugia. Austral Ecology 41:443–451.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-sucessional reserve, Klamath Mountians, Califorina, USA. Forest Ecology and Management 44:1–17.

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park 67:411–433.

Vanbianchi, C. M., M. A. Murphy, and K. E. Hodges. 2017. Canada lynx use of burned areas: Conservation implications of changing fire regimes. Ecology and Evolution:2382–2394.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34.

Wallace, J. M., P. L. S. Pavek, and T. S. Prather. 2015. Ecological characteristics of Ventenata dubia in the intermountain Pacific Northwest. Invasive Plant Science and Management 8:57–71.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:1–17.

Whittaker, A. R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Wilkin, K. M., D. D. Ackerly, and S. L. Stephens. 2016. Climate change refugia, fire ecology and management. Forests 7.

Wood, S. W., B. P. Murphy, and D. M. J. S. Bowman. 2011. Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. Journal of Biogeography 38:1807–1820.

Young, J. A., and R. A. Evans. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34:501–506.

Youngblood, A., K. L. Metlen, and K. Coe. 2006. Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. Forest Ecology and Management 234:143–163.

Youngblood, A., C. S. Wright, R. D. Ottmar, and J. D. McIver. 2008. Changes in fuelbed characteristics and resulting fire potentials after fuel reduction treatments in dry forests of the Blue Mountains, northeastern Oregon. Forest Ecology and Management 255:3151–3169.

Figures and tables

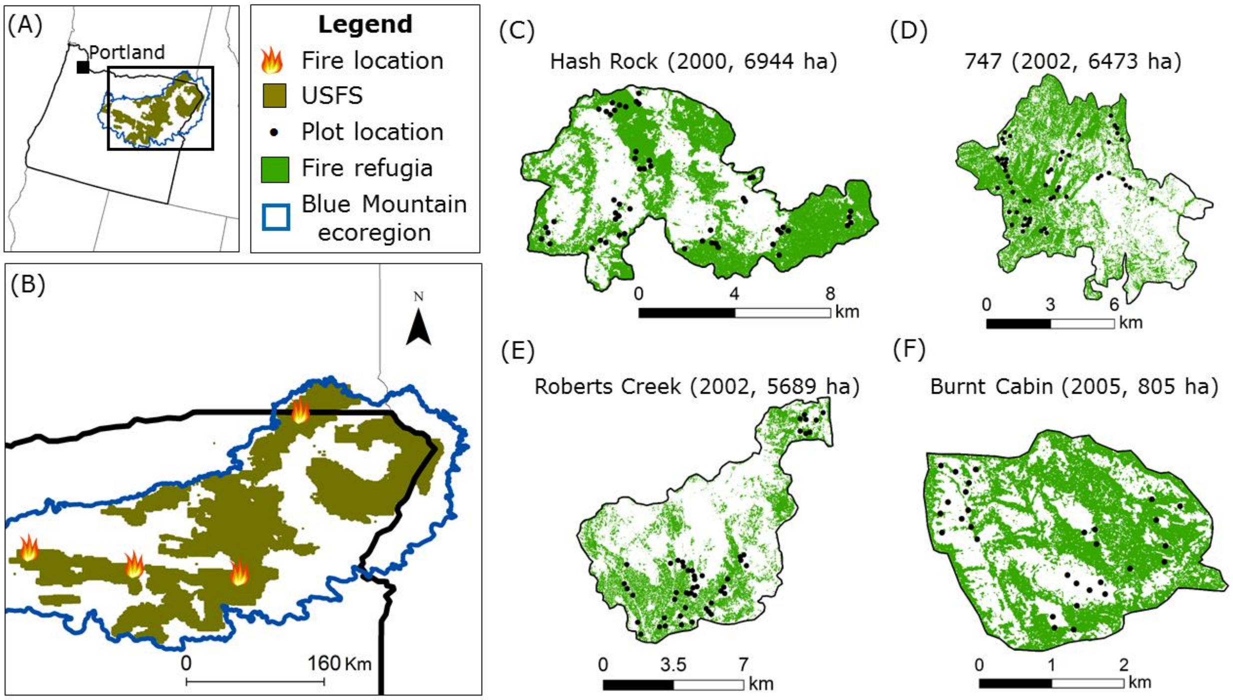


Figure 3.1. The study area and study fires in central and northeastern Oregon. (A) The study was performed in the Blue Mountains ecoregion. All study fires burned between 2000 and 2005, primarily on land managed by the US Forest Service (USFS). (C) – (F) Fire refugia within our four study fires, mapped using 1 meter resolution aerial imagery (see methods section in Chapter 1 for details). Sample plots, shown using black dots, were located in fire refugia where overstory trees survived fire, and in stand-replacement patches were all overstory trees were killed by fire.

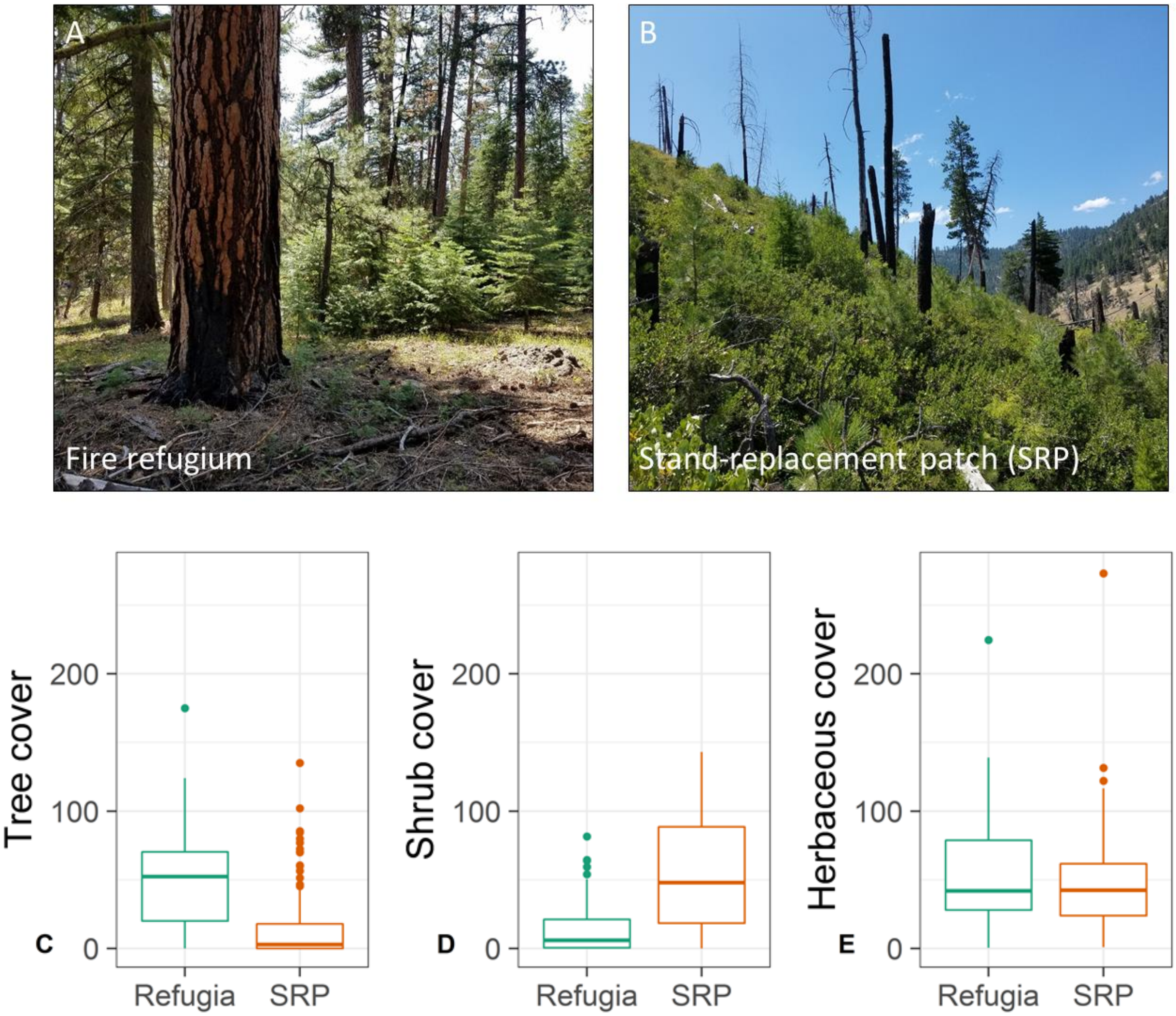


Figure 3.2. Photos of a fire refugium plot and a stand-replacement patch plot. Boxplots representing a comparison of tree, shrub, and herbaceous cover between fire refugia and stand-replacement patch plots. Photos demonstrate substantial structural differences between fire refugia (Refugia, A) and stand-replacement patches (B) as a function of how we classified the post-fire landscape (surviving overstory trees present, or not). Boxplots represent a comparison of tree (C), shrub (D) and herbaceous (E) cover between fire refugia and stand-replacement patch (SRP) plots, prior to removing overstory tree data from the analysis. Cover values can sum to >100 where species overlap in space. Here, tree cover includes all sizes from seedlings and saplings to overstory dominants. Indicator species present in the fire refugia plot (A) include *Abies grandis*, *Osmorhiza berteroi* and *Hieracium albiflorum*. Indicator species present in the stand-replacement plot (B) included *Ceanothus velutinus*, *Calamagrostis rubescens*, *Larix occidentalis*, *Salix spp*., and *Epilobium angustifolium*.

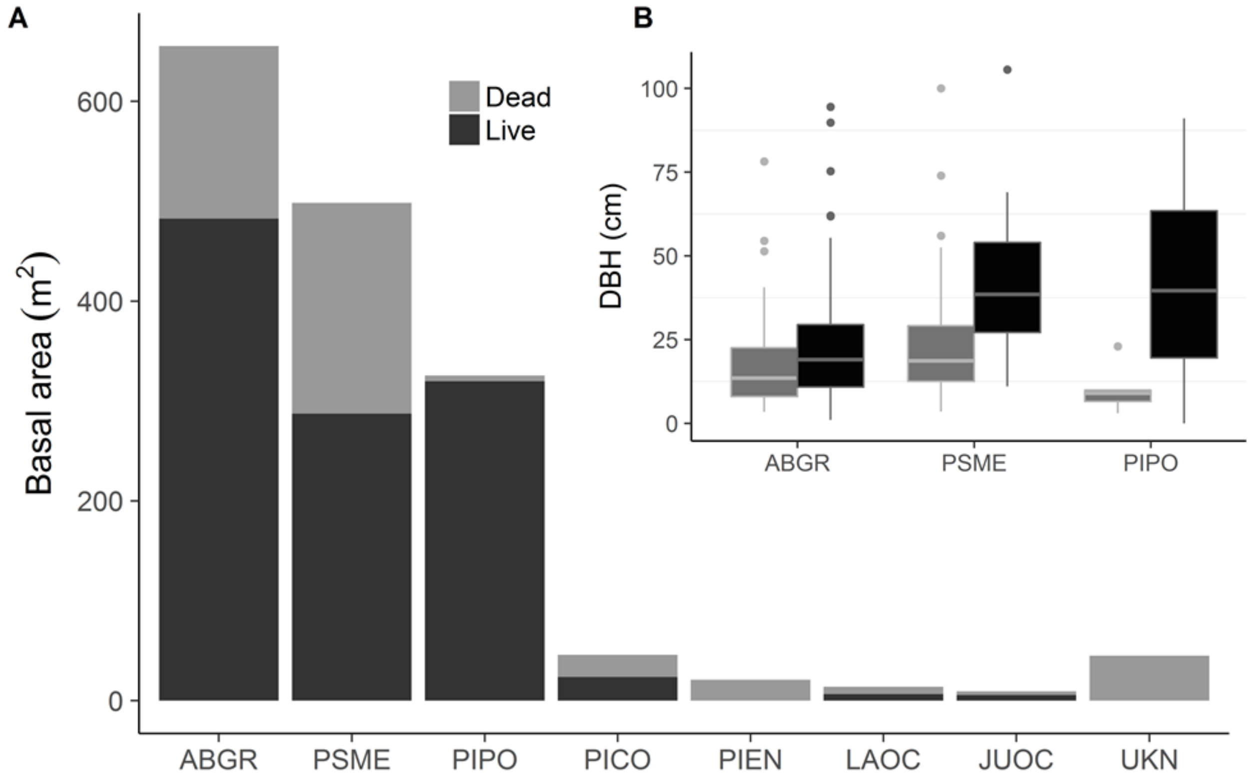


Figure 3.3. Overstory tree composition in fire refugia and size distributions of common species. (A) Overstory tree composition in fire refugia was dominated by grand fir (ABGR), Douglas-fir (PSME), and ponderosa pine (PIPO). Substantial proportions of grand fir and Douglas-fir basal area were dead at time of sampling. Lodgepole pine (PICO), Engelmann spruce (PIEN), western juniper (JUOC), and western larch (LAOC) constituted only a small proportion of the total overstory basal area within fire refugia. We were not able to determine the species identity of some dead trees due to decay or bark loss and these individuals were classified as “unknown” (UKN). (B) Surviving trees in fire refugia were larger in diameter (breast height, DBH) than trees dead at time of sampling, particularly for Douglas-fir and ponderosa pine.

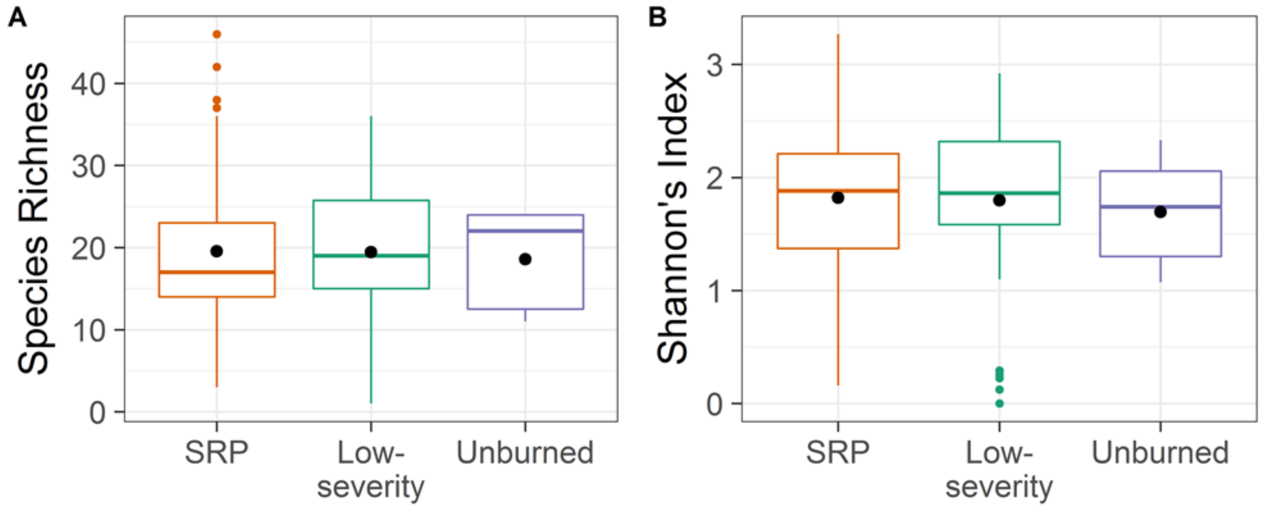


Figure 3.4. Boxplots of species richness and diversity among stand-replacement patches, low-severity burned fire refugia, and unburned fire refugia plots. Species richness (A) and diversity (B) were similar among stand-replacement patches (SRP), low-severity burned fire refugia (Low-severity), and unburned fire refugia (Unburned). Horizontal lines represent the median, with first and third quantiles flanking either side. Black points represent mean values.

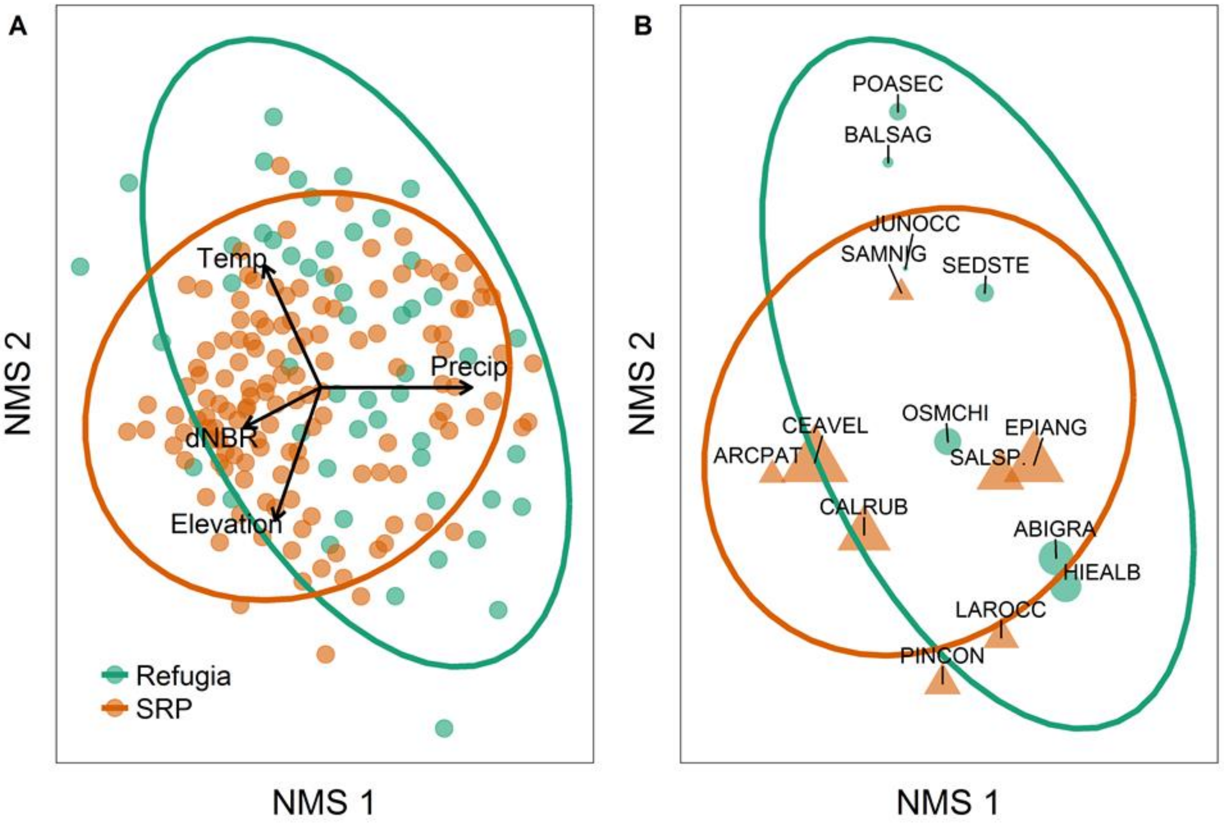


Figure 3.5. NMS ordinations of fire refugia and stand-replacement patch plots, and indicator species. (A) Understory plant communities in fire refugia (Refugia, green) and stand-replacement patches (SRP, orange) occupy similar portions of species space. Arrowed lines indicate the strength and direction of correlations with environmental variables. Ellipses represent 95% confidence intervals for refugia and stand-replacement patch plots types. (B) Indicator species associated with stand-replacement patches (triangles) had higher indicator values on average than species associated with fire refugia (circles). Symbol sizes are scaled to represent the indicator value for each species. Table 3.1 provides species names and functional traits for all species represented in panel B.

Table 3.1. Indicator species associated with stand-replacement patch and fire refugia plots. The ISA identified eight species associated with stand-replacement patch (SRP) plots and seven species associated with fire refugia (Refugia) plots. Exclusivity is the probability that a plot belongs in the assigned category, given that the species occurs in that plot. Fidelity is the probability of encountering the species in a plot based on its assigned category. Species possess life-history traits (e.g., obligate seeders, resprouters) that generally support their classification. Grand fir is categorized as both fire sensitive and fire resistant (●/○) because published literature indicates that the species is fire sensitive when young, but relatively resistant to low-severity fire when mature.

Species	**ID**	**Group**	**Exclusivity**	**Fidelity**	**IV**	**p-value**	**Obligate seeder**	**Resprouter**	**Seed banker**	**Fire sensitive**
Ceanothus velutinus	CEAVEL	SRP	0.88	0.73	64	0.001	○	●	●	○
Epilobium angustifolium	EPIANG	SRP	0.85	0.61	52	0.006	○	●	○	○
Calamagrostis rubescens	CALRUB	SRP	0.75	0.56	42	0.005	○	●	○	○
Salix spp.	SALSP.	SRP	0.78	0.44	35	0.009	○	●	○	○
Pinus contorta	PINCON	SRP	0.89	0.27	24	0.025	●	○	●	●
Larix occidentalis	LAROCC	SRP	0.86	0.27	23	0.027	●	○	○	○
Arctostaphylos patula	ARCPAT	SRP	0.99	0.17	17	0.03	○	●	●	○
Sambucus nigra cerulea	SAMNIG	SRP	0.93	0.17	16	0.038	○	●	○	○
Abies grandis	ABIGRA	Refugia	0.69	0.49	43	0.039	●	○	○	●/○
Hieracium albertinum	HIEALB	Refugia	0.81	0.35	29	0.004	●	○	○	●
Osmorhiza berteroi	OSMBER	Refugia	0.76	0.31	24	0.050	●	○	○	●
Sedum stenopetalum	SEDSTE	Refugia	0.67	0.24	16	0.036	●	○	○	●
Poa secunda	POASEC	Refugia	0.86	0.14	15	0.006	○	●	○	○
Balsamorhiza sagittata	BALSAG	Refugia	0.80	0.14	12	0.011	○	●	○	○
Juniper occidentalis	JUNOCC	Refugia	0.92	0.12	11	0.010	●	○	○	●

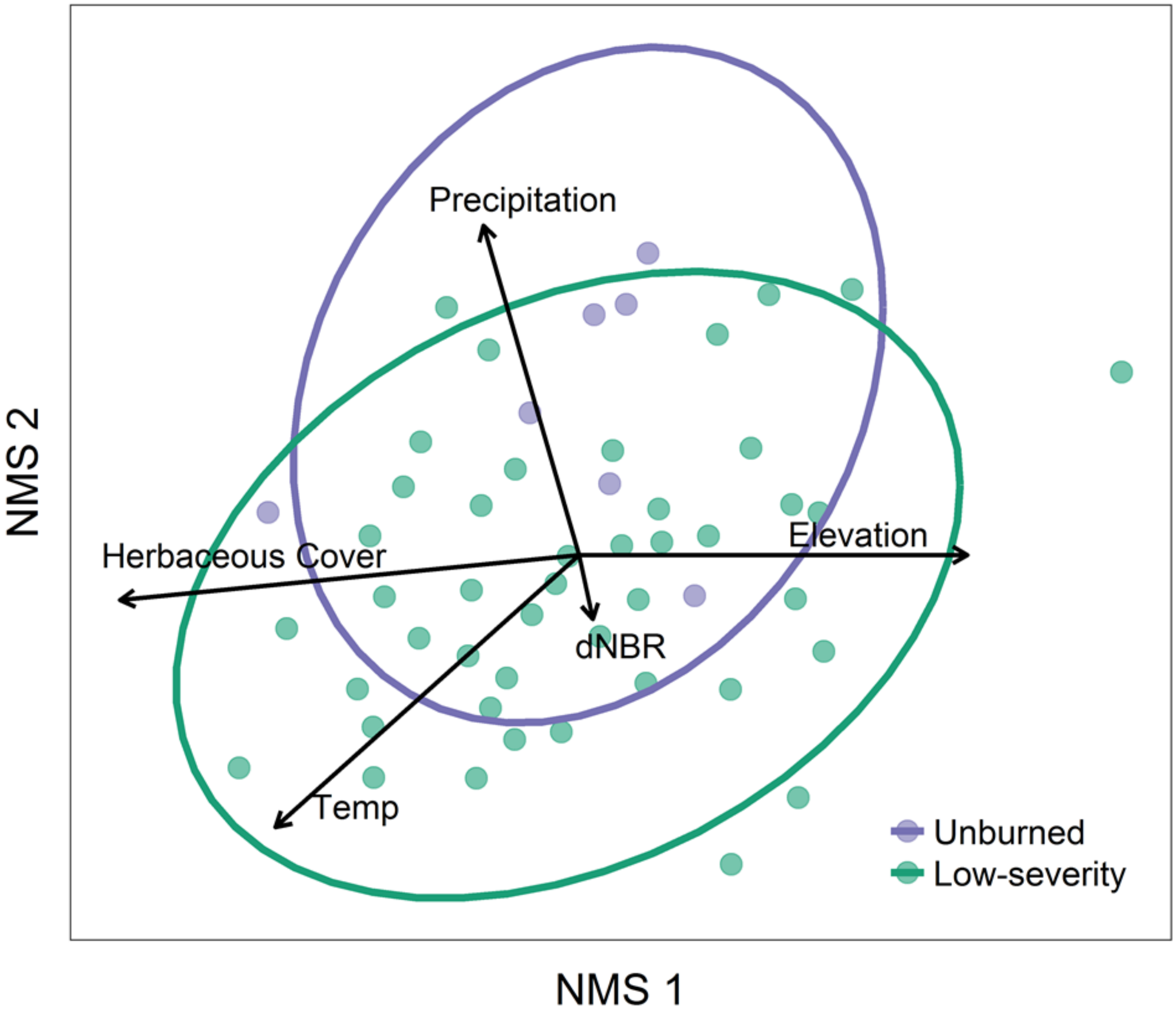


Figure 3.6. NMS ordination of fire refugia plots. The ordination demonstrates overlap between unburned and low-severity burned fire refugia plots. There does not appear to be strong compositional differences between plot types. Lines indicate the strength and direction of correlations with environmental variables and dots represent sample plots.

CHAPTER 4 - CONCLUSION

Understanding the drivers of forest resistance and resilience to landscape-scale disturbance is increasingly important in the context of accelerating global change. This thesis provides novel insights into the composition and ecological function of dry mixed-conifer fire refugia in Oregon's Blue Mountains. Fire refugia constitute the most fire resistant portions of the forest landscape during a fire event, and seed sources that survived fire in refugia are key drivers of forest resilience in stand-replacement patches. Our findings demonstrate that although fire periodicity and forest structure are significantly departed from historical reference conditions, dry mixed-conifer forests in the Blue Mountains remain relatively resilient to high-severity fire effects and retain the capacity to regenerate forest in stand-replacement patches. The results of our understory plant community analysis provide additional evidence of post-fire forest resilience. We found that despite substantial structural differences between fire refugia and stand-replacement patches, there was little evidence of a difference between the understory plant community composition between plot types, indicating that understory plant communities can recover even in severely burned areas.

While dry mixed-conifer forests in our study area show clear signs of resilience to high-severity fire, results from similar studies suggest that dry forest ecosystems elsewhere may be approaching a "tipping point" as a result of increasing fire activity and changing climatic conditions (Tepley et al. 2017). Some dry forests are experiencing post-fire recruitment failures and conversions to non-forest states as a result of inadequate refugial seed sources, post-fire drought, and short-interval reburn (Collins and Roller 2013, Chambers et al. 2016, Coop et al. 2016, Coppoletta et al. 2016, Tepley et al. 2017, Stevens-Rumann et al. 2018). In the Blue Mountains, the climatic conditions that support the growth of large fires are predicted to be substantially more common in future (Davis et al. 2017), and it is certainly possible that the post-fire forest resilience we documented here could be compromised by larger stand-replacement patches devoid of surviving seed source, hotter and drier post-fire climatic conditions, and reburn. In 2017, the Desolation fire reburned a substantial portion of previously high-severity burned area in the 2000 Hash Rock fire (one of our four study fires). The Desolation fire reburned locations where we observed many seedlings regenerating beneath the shrub canopy, and fire in these shrub-dominated areas likely resulted in significant seedling mortality. Reburns may also erode patches of forest that survived the previous fire in refugia, decreasing the amount of available seed source and slowing post-fire forest recovery. Studies in New Mexico and the northern Sierra Nevada suggest that reburn is already reinforcing transitions towards non-forested states by favoring resprouting species and limiting seedling recruitment (Coop et al. 2016, Coppoletta et al. 2016). Although the potential certainly exists for a similar post-fire successional trajectory in our study area, additional research will be necessary to determine the ecological impacts of reburn in the Blue Mountain dry mixed-conifer forests.

A key knowledge gap regarding fire refugia in forest ecosystems is their persistence through multiple fire events. We found evidence that surface fire effects in refugia may have increased the likelihood that these areas will persist as refugia during future fires by reducing ladder fuels and stand densities. However, in this study we were unable to differentiate between transient fire refugia that formed as a function of stochastic factors (e.g., weather, fire suppression) or persistent fire refugia that survive multiple fire events (Meddens et al. 2018, in review). Certain topographic positions appear to promote the formation of fire refugia, and because topography is less temporally variable than fuels and weather, these refugia may be more likely to persist through more than one fire event (Wood et al. 2011, Leonard et al. 2014, Berry et al. 2015, Krawchuk et al. 2016). Locations where disturbance refugia and climate refugia overlap may be essential for the maintenance of biodiversity in some regions, and identifying persistent fire refugia will be essential for fire refugia researchers to contribute substantively to conservation planning and management.

We did not find evidence that fire refugia in our study area support fire-sensitive plant communities otherwise absent from the higher-severity burned matrix. However, these results should not be taken as evidence that fire-sensitive plant species do not rely on fire refugia anywhere in the Blue Mountains. Long lived, fire-sensitive species are associated with fire refugia in other forest ecosystems (Wood et al. 2011, Landesmann et al. 2015, Adie et al. 2017), and there may be locations in the Blue Mountains that are decoupled from the broader, landscape fire regime which allow for the persistence of truly fire-sensitive species. One possible example is a small (five ha) grove of Alaska yellow cedar (*Callitropsis nootkatensis*) in the southern Blue

Mountains. Located on a steep, north-facing slope, along the margins of a perennial spring-fed creek, the grove lies approximately 220 km east of the species' main population, and is presumed to be a relict from cooler and wetter conditions during the Pleistocene (Frenkel 1974). In 2006, the grove burned in the 6000 ha Shaketable fire. Despite very low grand fir (*Abies grandis* (Dougl.) Lindl.), western larch (*Larix occidentalis* Nutt.), and ponderosa pine (*Pinus ponderosa* Dougl. Ex Loud) mortality in the stand, we estimate that over 90% of the cedar were killed by fire (W. Downing, unpublished data). A recent study by Johnston et al. (2016) reported pre-settlement fire return intervals in the southern Blue Mountains were 10 – 21 years on average. Their study includes data collected as close as 5 kilometers from the cedar grove. Significant cedar mortality from low-intensity fire in 2006 presents something of a mystery: how has the grove survived in a landscape where such fire behavior was historically frequent and widespread? A potential explanation may be that the grove occupies a persistent fire refugium that did not burn as frequently as the surrounding landscape. Initial results from a fire history reconstruction in the grove may indicate that fire did not affect the grove as frequently as other locations in the southern Blue Mountains (W. Downing, unpublished data). Although a conclusive determination will require the collection of additional data, this remnant population of Alaska yellow cedar appears to have persisted in the Blue Mountains in a location that provides both a favorable microclimate as well as well as some degree of protection from frequent fire. Locations like the cedar grove, which appear to have been historically decoupled from both regional climate trends and an unfavorable disturbance regime, may provide important insights into the capacity of at-risk populations to persist in the context of rapid global change. However, the effects of the 2006 Shaketable fire suggest that even refugia that supported populations for centuries or millennia may be at risk of "winking out" as climate and disturbance regimes continue to depart from reference conditions.

The results of this project have several implications for land managers. Managers interested in accelerating or supplementing natural regeneration in stand-replacement patches could target areas where the surrounding landscape contains little or no refugial seed source. In addition, managers seeking to promote natural forest regeneration may choose to avoid actions both during fire suppression, like non-essential burnout operations, and after, like salvage logging, which reduce or eliminate fire refugia from the post-fire landscape. Perhaps the most effective use of management resources would be to accelerate the pace and scale of fuel treatments prior to fire to increase the resistance of forests to high-severity fire (Agee and Skinner 2005, Finney et al. 2005). Thinning and prescribed burning to restore historical forest structure and reduce fuel loads could increase the amount of forest that survives in fire refugia within large fire perimeters. Reburns are occurring in previously high-severity burned areas in the Blue Mountains, and managers may choose to support future research to determine the effects short-interval, repeated fire. If evidence emerges that reburn in the Blue Mountains reinforces shifts to non-forested states, and managers are interested in minimizing forest loss, it may be appropriate to aggressively suppress new fires that have the potential to reburn previously high-severity burned areas. In contrast, managers may choose to allow these short-interval fires to burn in order to facilitate the transition of dry forests already at the edge of their climatic tolerances towards non-forest vegetation better suited to projected climate conditions.

Interest in refugia generally, and fire refugia in particular, is increasing in the context of rapid global change. However, not all fire ecologists have universally embraced the concept of fire refugia or agreed upon its definition (Meddens et al. 2018, in review). Studies like this one can contribute to a growing recognition that fire refugia are important, but perhaps underappreciated, components of post-fire landscapes. For the concept of fire refugia to gain lasting currency with scientists and managers, more research will be needed to understand the drivers, persistence, composition, and functions of fire refugia across a diversity of forest ecosystems and fire regimes.

BIBLIOGRAPHY

Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proceedings of the National Academy of Sciences of the United States of America 113:11770–11775.

Adie, H., D. J. Kotze, and M. J. Lawes. 2017. Small fire refugia in the grassy matrix and the persistence of Afrotemperate forest in the Drakensberg mountains. Scientific Reports 7:1–10.

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

Agee, J. K. 1996. Fire in the Blue Mountains: a history, ecology, and research agenda. Pages 119–145 in R. G. Jaindl and T. M. Quigley, editors. Search for a solution: sustaining the land, people, and economy of the Blue Mountains. American Forests.

Agee, J. K., and C. N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96.

Airey Lauvaux, C., 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.

Ashcroft, M. B. 2010. Identifying refugia from climate change. Journal of Biogeography 37:1407–1413.

Ashcroft, M. B., L. A. Chisholm, and K. O. French. 2009. Climate change at the landscape scale: Predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. Global Change Biology 15:656–667.

Barbé, M., N. J. Fenton, and Y. Bergeron. 2017. Are post-fire residual forest patches refugia for boreal bryophyte species? Implications for ecosystem based management and conservation. Biodiversity and Conservation 26:943–965.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67.

Berry, L. E., D. A. Driscoll, J. A. Stein, W. Blanchard, S. C. Banks, R. A. Bradstock, and D. B. Lindenmayer. 2015. Identifying the location of fire refuges in wet forest ecosystems. Ecological Applications 25:2337–2348.

Bonnet, V. H., A W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research 35:37–47.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Burkle, L. A., J. A. Myers, R. T. Belote, and D. P. C. Peters. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. Ecosphere 6.

Burns, R. M. 1983. Silvicultural systems for the major forest types of the United States. Agricultural Handbook 445. USDA Forest Service, Washington, D.C., USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Cáceres, M. De, and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90:3566–3574.

Calkin, D. E., M. P. Thompson, and M. a. Finney. 2015. Negative consequences of positive feedbacks in US wildfire management. Forest Ecosystems 2:1–10.

Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee mountains. Forest Ecology and Management 95:63–77.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emission from a large wildfire in Oregon, United States. Journal of Geophysical Research: Biogeosciences 112:1–11.

Campbell, J. L., and D. C. Donato. 2014. Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. Forest Ecology and Management 324:172–178.

Chambers, M. E., P. J. Fornwalt, S. L. Malone, and M. A. Battaglia. 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. Forest Ecology and Management 378:57–67.

Chappell, C. B., and J. K. Agee. 1996. Fire severity and tree seedling establishment in Abies magnifica forests, Southern Cascades, Oregon. Ecological Applications 6:628–640.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clarke, P. J. 2002. Habitat islands in fire-prone vegetation: Do landscape features influence community composition? Journal of Biogeography 29:677–684.

Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecology 28:1801–1813.

Conrad, S. G., A. E. Jaramillo, J. Kermit Cromack, and S. Rose. 1985. The role of the genus Ceanothus in western forest ecosystems. USDA Forest Service General Technical Report, PNW-GTR-182. Pacific Northwest Research Station, Portland, OR, USA.

Coop, J. D., S. A. Parks, S. R. Mcclernan, and L. M. Holsinger. 2016. Influences of prior wildfires on vegetation response to subsequent fire in a reburned southwestern landscape. Ecological Applications 26:346–354.

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.

Crawford, J. A., C. A. Wahren, S. Kyle, and W. H. Moir. 2001. Responses of exotic plant species to fires in Pinus ponderosa forests in northern Arizona. Journal of Vegetation Science 12:261–268.

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

Cunningham, S. C., W. B. Ballard, L. Monroe, M. J. Rabe, and K. D. Bristow. 2003. Black bear habitat use in burned and unburned areas, central Arizona. Wildlife Society Bulletin 31:786–792.

Davis, J., A. Pavlova, R. Thompson, and P. Sunnucks. 2013. Evolutionary refugia and ecological refuges: Key concepts for conserving Australian arid zone freshwater biodiversity under climate change. Global Change Biology 19:1970–1984.

Davis, R., Z. Yang, A. Yost, C. Belongie, and W. Cohen. 2017. The normal fire environment — Modeling environmental suitability for large forest wildfires using past , present , and future climate normals. Forest Ecology and Management 390:173–186.

Dealy, J. E. 1975. Ecology of Curlleaf Mountain-Mahogany (Cercocarpus ledifolius Nutt.) in eastern Oregon and adjacent areas. Oregon State University, Corvallis, OR, USA. 161. Thesis.

Delong, S. C., and W. B. Kessler. 2000. Ecological characteristics of mature forest remnants left by wildfire. Forest Ecology and Management 131:93–106.

Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends in the western United States, 1984-2011. Geophysical Research Letters 41:2928–2933.

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.

Dobrowski, S. Z. 2010. A climatic basis for microrefugia: The influence of terrain on climate. Global Change Biology.

Dobrowski, S. Z., A. K. Swanson, J. T. Abatzoglou, Z. A. Holden, H. D. Safford, M. K. Schwartz, and D. G. Gavin. 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Global Ecology and Biogeography 24:917–927.

Dodson, E. K., and H. T. Root. 2013. Conifer regeneration following stand-replacing wildfire varies along an elevation gradient in a ponderosa pine forest, Oregon, USA. Forest Ecology and Management 302:163–170.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009a. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath–Siskiyou Mountains. Canadian Journal of Forest Research 39:823–838.

Donato, D. C., J. B. Fontaine, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2009b. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. Journal of Ecology 97:142–154.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. Regeneration of montane forests 24 years afer the 1988 Yellowstone fires: A fire-catalyzed shif in lower treelines? Ecosphere 7:1–16.

Doyle, K., D. Knight, D. Taylor, W. Barmore, and J. Benedict. 1998. Seventeen years of forest succession following the Waterfalls Canyon fire in Grand Teton National Park, Wyoming. International Journal of Wildland Fire 8:45.

Dragotescu, I., and D. D. Kneeshaw. 2012. A comparison of residual forest following fires and harvesting in boreal forests in Quebec, Canada. Silva Fennica 46:365–376.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology 54:57–69.

Finney, M. A., C. W. McHugh, and I. C. Grenfell. 2005. Stand- and landscape-level effects of prescribed burning on two Arizona wildfires. Canadian Journal of Forest Research 35:1714–1722.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in Ecology and Evolution 28:86–92.

Franklin, J. F., D. Lindenmayer, J. A. Macmahon, A. Mckee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. Conservation Biology in Practice 1:8–16.

Frenkel, R. 1974. An isolated occurrence of Alaska-cedar (Chamaecyparis nootkatensis (D. Don) Spach) in the Aldrich Mountains, Central Oregon. Northwest Science 48.

Fuller, R. N., and R. Del Moral. 2003. The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. Journal of Vegetation Science 14:637–644.

Gandhi, K. J. K., J. R. Spence, D. W. Langor, and L. E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera : Carabidae and Staphylinidae). Biological Conservation 102:131–141.

Gasaway, W. C., and S. D. DuBois. 1985. Initial response of moose to a wildfire in interior Alaska. The Canadian Field Naturalist 99:135–140.

Gill, M. A. 1975. Fire and the Australian flora: A review. Australian Forestry 38:4–25.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334.

Haffey, C., T. D. Sisk, C. D. Allen, A. E. Thode, and E. Q. Margolis. 2018. Limits To Ponderosa Pine Regeneration Following Large High-Severity Forest Fires in the United States Southwest. Fire Ecology 14:143–163.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. Forest Ecology and Management 304:492–504.

Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern oregon cascade range, USA. Forest Ecology and Management 330:158–170.

Haire, S., J. Coop, and C. Miller. 2017. Characterizing spatial neighborhoods of refugia following large fires in northern New Mexico, USA. Land 6:19.

Haire, S. L., and K. McGarigal. 2008. Inhabitants of landscape scars: Succession of woody plants after large, severe forest fires in Arizona and New Mexico. Southwestern Naturalist 53:146–161.

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.

Hall, F. C. 1976. Fire and vegetaion in the Blue Mountains - Implications for land managers. Page Proceedings of the annual Tall Timbers fire ecology conference. Tall Timbers Research Station: 155-170, Tallahassee, Florida.

Halpern, C. B. 1988. Early successional pathways and the resistence and resilience of forest communities. Ecology 69:1703–1715.

Halpern, C., and T. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:913–934.

Harvey, B. J., D. C. Donato, and M. G. Turner. 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Global Ecology and Biogeography 25:655–669.

Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest United States forests, 1800-2000. Forest Ecology and Management 178:23–59.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., D. J. Churchill, A. J. Larson, R. D. Haugo, C. Miller, T. A. Spies, M. P. North, N. A. Povak, R. T. Belote, P. H. Singleton, W. L. Gaines, R. E. Keane, G. H. Aplet, S. L. Stephens, P. Morgan, P. A. Bisson, B. E. Rieman, R. B. Salter, and G. H. Reeves. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. Landscape Ecology 30:1805–1835.

Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: Inferences from landscape patterns of forest structure. Landscape Ecology 22:5–24.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: A multiscale example from the interior west, USA. Ecology 82:660–678.

Hutto, R. L., R. E. Keane, R. L. Sherriff, C. T. Rota, L. A. Eby, and V. A. Saab. 2016. Toward a more ecologically informed view of severe forest fires. Ecosphere 7:1–13.

Hylander, K., and S. Johnson. 2010. In situ survival of forest bryophytes in small-scale refugia after an intense forest fire. Journal of Vegetation Science 21:1099–1109.

Irwin, L. 1994. Effects of long-term grazing by big game and livestock in the Blue Mountains forest ecosystem. USDA Forest Service, General Technical Report, PNW-GTR-325. Pacific Northwest Research Station, Portland, Oregon, USA.

Johnson, C. G. 1994. Forest health in the Blue Mountains: A plant ecologist's perspective on ecosystem processes and biological diversity. USDA Forest Service, General Technical Report, PNW-GTR-339. Pacific Northwest Research Station, Portland, Oregon, USA.

Johnson, C. G., and R. R. Clausnitzer. 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERW-T-036092. Pacific Northwest Research Station, Portland, OR, USA.

Johnston, J. D. 2017. Forest succession along a productivity gradient following fire exclusion. Forest Ecology and Management 392:45–57.

Johnston, J. D., J. D. Bailey, and C. J. Dunn. 2016. Influence of fire disturbance and biophysical heterogeneity on pre-settlement ponderosa pine and mixed conifer forests. Ecosphere 7:1–19.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mock, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369–378.

Jones, L. C., N. Norton, and T. S. Prather. 2018. Indicators of ventenata (Ventenata dubia) invasion in sagebrush steppe rangelands. Invasive Plant Science and Management 11:1–9.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16:406–411.

Kemp, K. B., P. E. Higuera, and P. Morgan. 2016. Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. Landscape Ecology 31:619–636.

Keppel, G., K. P. Van Niel, G. W. Wardell-Johnson, C. J. Yates, M. Byrne, L. Mucina, A. G. T. Schut, S. D. Hopper, and S. E. Franklin. 2012. Refugia: Identifying and understanding safe havens for biodiversity under climate change. Global Ecology and Biogeography 21:393–404.

Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. Season and severity of prescribed burn in ponderosa pine forests: Implications for understory native and exotic plants. Ecoscience 13:44–55.

Key, C. H., and N. C. Benson. 2006. Landscape assessment (LA): Sampling and analysis methods. USDA Forest Service General Technical Report RMS-GTR-164-CD. Ogden, UT, USA.

Kolden, C. A., J. A. Lutz, C. H. Key, J. T. Kane, and J. W. van Wagtendonk. 2012. Mapped versus actual burned area within wildfire perimeters: Characterizing the unburned. Forest Ecology and Management 286:38–47.

Kolden, C., T. Bleeker, A. Smith, H. Poulos, and A. Camp. 2017. Fire effects on historical wildfire refugia in contemporary wildfires. Forests 8:400.

Krawchuk, M. A., S. L. Haire, J. D. Coop, M.-A. Parisien, E. Whitman, G. W. Chong, and C. Miller. 2016. Topographic and fire weather controls of fire refugia in forested ecosystems of northwestern North America. Ecosphere 7(12).

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: The current and future distribution of wildfire. PLoS ONE 4.

Landesmann, J. B., J. H. Gowda, L. A. Garibaldi, and T. Kitzberger. 2015. Survival, growth and vulnerability to drought in fire refuges: Implications for the persistence of a fire-sensitive conifer in northern Patagonia. Oecologia 179:1111–1122.

Landesmann, J. B., and J. M. Morales. 2018. The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia. Plant Ecology 219:455–466.

Lentile, L. B., F. W. Smith, and W. D. Shepperd. 2005. Patch structure, fire-scar formation, and tree regeneration in a large mixed-severity fire in the South Dakota Black Hills, USA. Canadian Journal of Forest Research 35:2875–2885.

Leonard, S. W. J., A. F. Bennett, and M. F. Clarke. 2014. Determinants of the occurrence of unburnt forest patches: Potential biotic refuges within a large, intense wildfire in south-eastern Australia. Forest Ecology and Management 314:85–93.

Loarie, S. R., B. E. Carter, K. Hayhoe, S. McMahon, R. Moe, C. A. Knight, and D. D. Ackerly. 2008. Climate change and the future of California’s endemic flora. PLoS ONE 3.

Mackey, B., S. Berry, S. Hugh, S. Ferrier, T. D. Harwood, and K. J. Williams. 2012. Ecosystem greenspots: Identifying potential drought, fire, and climate-change micro-refuges. Ecological Applications 22:1852–1864.

Magoulick, D. D., and R. M. Kobza. 2003. The role of refugia for fishes during drought: A review and synthesis. Freshwater Biology 48:1186–1198.

Mason, G. 2001. Guide to plants of the Wallowa Mountains of northeastern Oregon. University of Oregon Press, Eugene, OR, USA.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR, USA.

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. 2011. PC-ORD. Multivariate analysis of ecological data. Version 6. MjM Software, Gleneden Beach, Oregon, USA.

Mclaughlin, B. C., D. D. Ackerly, P. Z. Klos, and J. Natali. 2017. Hydrologic refugia, plants, and climate change:1–21.

Meddens, A. J. H., C. A. Kolden, and J. A. Lutz. 2016. Detecting unburned areas within wildfire perimeters using Landsat and ancillary data across the northwestern United States. Remote Sensing of Environment 186:275–285.

Meddens, A. J. H., C. A. Kolden, J. A. Lutz, A. M. S. Smith, C. A. Cansler, J. T. Abatzoglou, G. W. Meigs, W. M. Downing, and M. A. Krawchuk. 2018. Fire refugia: What are they and why do they matter for global change? Manuscript submitted for publication.

Meigs, G. W., and M. A. Krawchuk. 2018. Composition and structure of forest fire refugia: What are the ecosystem legacies across burned landscapes? forests 9.

Merschel, A. G., T. A. Spies, and E. K. Heyerdahl. 2014. Mixed-conifer forests of central Oregon: Effects of logging and fire exclusion vary with environment. Ecological Applications 24:1670–1688.

Mielke, P. W., K. J. Berry, and G. W. Brier. 1981. Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. Monthly Weather Review 109:120–126.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance. Science 349:823–826.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forest of the future: Managing in the face of uncertanity. Ecological Applications 17:2145–2151.

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.

Morelli, T. L., C. Daly, S. Z. Dobrowski, D. M. Dulen, J. L. Ebersole, S. T. Jackson, J. D. Lundquist, C. I. Millar, S. P. Maher, W. B. Monahan, K. R. Nydick, K. T. Redmond, S.

C. Sawyer, S. Stock, and S. R. Beissinger. 2016. Managing climate change refugia for climate adaptation. PLoS ONE 11:1–17.

Mosgrove, J. L. 1980. The Malheur National Forest: An Ethnographic History. USDA, Forest Service, Region 6, Malheur National Forest, Portland, OR.

Murtaugh, P. A. 2014. In defense of P values. Ecology 95:611–617.

Mutch, R. W., S. F. Arno, J. K. Brown, C. E. Carlson, R. D. Ottmar, and J. L. Peterson. 1993. Forest health in the Blue Mountains: A management strategy for fire-adapted ecosystems. USDA Forest Service, General Technical Report, PNW-GTR-310. Pacific Northwest Research Station, Portland, Oregon, USA.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, H. Wagner, and M. J. Oksanen. 2017. Vegan: community ecology package. R Package Version 2. 4-6.

Ott, T. M., E. K. Strand, and C. L. Anderson. 2015. Niche divergence of Abies grandis-Abies concolor hybrids. Plant Ecology 216:479–490.

Ouarmim, S., L. Paradis, H. Asselin, Y. Bergeron, A. Ali, and C. Hély. 2016. Burning potential of fire refuges in the boreal mixedwood forest. Forests 7:246.

Owen, S. M., C. H. Sieg, A. J. Sánchez Meador, P. Z. Fulé, J. M. Iniguez, L. S. Baggett, P. J. Fornwalt, and M. A. Battaglia. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. Forest Ecology and Management 405:134–149.

Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. Forest Ecology and Management 262:703–717.

Powell, D. 1994. Effects of the 1980s western spruce budworm outbreak on the Malheur National Forest in northeastern Oregon. USDA Forest Service Technical Report R6-FI&D-TP-12-94. Pacific Northwest Region Forest Insects and Disease Group, Portland, OR, USA.

PRISM. 2018. PRISM Climate Group, Oregon State University. http://www.prism.oregonstate.edu.

Pyne, S. J. 1982. Fire in America: A Cultural History of Wildland and Rural Fire. Princeton University Press, Princeton, New Jersey, USA.

R Core Team. 2017. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. www.R-project.org. https://www.r-project.org/.

Rau, B. M., J. C. Chambers, R. R. Blank, and D. W. Johnson. 2008. Prescribed fire, soil, and plants: Burn effects and interactions in the central Great Basin. Rangeland Ecology and Management 61:169–181.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985-2010). Ecosphere 8.

Robbins, R. G., and D. W. Wolf. 1994. Landscape and the intermontane Northwest: An environmental history. USDA Forest Service, General Technical Report, PNW-GTR-319. Pacific Northwest Research Station, Portland, Oregon, USA.

Robinson, N. M., S. W. J. Leonard, E. G. Ritchie, M. Bassett, E. K. Chia, S. Buckingham, H. Gibb, A. F. Bennett, and M. F. Clarke. 2013. Refuges for fauna in fire-prone landscapes: Their ecological function and importance. Journal of Applied Ecology 50.

Rogers, B. M., R. P. Neilson, R. Drapek, J. M. Lenihan, J. R. Wells, D. Bachelet, and B. E. Law. 2011. Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. Journal of Geophysical Research: Biogeosciences 116:1–13.

Román-Cuesta, R. M., M. Gracia, and J. Retana. 2009. Factors influencing the formation of unburned forest islands within the perimeter of a large forest fire. Forest Ecology and Management 258:71–80.

Rother, M. T., T. T. Veblen, and L. G. Furman. 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Canadian Journal of Forest Research 45:1607–1616.

Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135–154 in R. W. Wein and D. A. MacLean, editors. The Role of Fire in Northern Circumpolar Ecosystems. Wiley, New York.

Safford, H. D. 2013. Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the bioregional assessment area, including the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests. Unpublished report. USDA Forest Service, Pacific Southwest Region, Vallejo, CA.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35:967–977.

Sedell, J., G. H. Reeves, R. F. Hauer, J. A. Standford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems.

Shatford, J. P. A., D. E. Hibbs, and K. J. Puettmann. 2007. Conifer regeneration after forest fire in the Klamath-Siskiyous: How much, how soon? Journal of Forestry 105:139–146.

Sheil, D., and D. F. R. P. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: A response to Fox. Trends in Ecology and Evolution 28:571–572.

Shepperd, W. D., C. B. Edminster, and S. A. Mata. 2006. Long-term seedfall, establishment, survival, and growth of natural and planted ponderosa pine in the Colorado Front Range. Western Journal of Applied Forestry 21:19–26.

Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. Conservation Biology 20:351–362.

Stephens, S. L., J. K. Agee, P. Z. Fule, M. P. North, W. H. Romme, T. W. Swetnam, and M. G. Turner. 2013. Managing forests and fire in a changing climate. Science 342:41–42.

Stephens, S. L., B. M. Collins, C. J. Fettig, M. A. Finney, C. M. Hoffman, E. E. Knapp, M. P. North, H. D. Safford, and R. B. Wayman. 2017. Drought, Tree Mortality and Wildfire in Forests Adapted to Frequent Fire. BioScience XX:1–38.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. Ecology Letters 21:243–252.

Stewart, J. R., A. M. Lister, I. Barnes, and L. Dalén. 2010. Refugia revisited: Individualistic responses of species in space and time. Proceedings of the Royal Society B: Biological Sciences 277:661–71.

Stickney, P. F. 1990. Early development of vegetation following holocaustic fire in northern Rocky Mountain forests. Northwest Science 64:243–246.

Stine, P., P. Hessburg, T. Spies, M. Kramer, C. J. Fettig, A. Hansen, J. Lehmkuhl, K. O'Hara, K. Polivka, P. Singleton, S. Charnley, A. Merschel, and R. White. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. USDA Forest Service, General Technical Report, PNW-GTR-897. Pacific Northwest Research Station, Portland, Oregon, USA.

Swan, M., C. Galindez-Silva, F. Christie, A. York, and J. Di Stefano. 2016. Contrasting responses of small mammals to fire and topographic refugia. Austral Ecology 41:443–451.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117–125.

Taylor, A. H., and C. N. Skinner. 1998. Fire history and landscape dynamics in a late-sucessional reserve, Klamath Mountians, Califorina, USA. Forest Ecology and Management 44:1–17.

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.

Tepley, A. J., and T. T. Veblen. 2015. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. Ecological Monographs 85:583–603.

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

Turner, M. G., W. H. Romme, R. H. Gardner, and W. W. Hargrove. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park 67:411–433.

Vanbianchi, C. M., M. A. Murphy, and K. E. Hodges. 2017. Canada lynx use of burned areas: Conservation implications of changing fire regimes. Ecology and Evolution:2382–2394.

Wahlenberg, W. G. 1930. Effect of ceanothus brush on western yellow pine plantations in the northern Rocky Mountains. Journal of Agricultural Research 41:601–612.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (Pinus) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34.

Wallace, J. M., P. L. S. Pavek, and T. S. Prather. 2015. Ecological characteristics of Ventenata dubia in the intermountain Pacific Northwest. Invasive Plant Science and Management 8:57–71.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. Locally downscaled and spatially customizable climate data for historical and future periods for North America. PLoS ONE 11:1–17.

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.

Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philosophical Transactions of the Royal Society of London B: Biological Sciences 371:717–728.

Whittaker, A. R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Wickman, B. E. 1992. Forest health in the Blue Mountains : The influence of insects and disease. USDA Forest Service, General Technical Report, PNW-GTR-295. Pacific Northwest Research Station, Portland, Oregon, USA.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81–120.

Wilkin, K. M., D. D. Ackerly, and S. L. Stephens. 2016. Climate change refugia, fire ecology and management. Forests 7.

Wood, S. W., B. P. Murphy, and D. M. J. S. Bowman. 2011. Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the Tasmanian Wilderness World Heritage Area. Journal of Biogeography 38:1807–1820.

Wright, C. S., and J. K. Agee. 2004. Fire and Vegetation History in the Eastern Cascade Mountains, Washington 14:443–459.

Yocom-Kent, L. L., P. Z. Fulé, W. A. Bunn, and E. G. Gdula. 2015. Historical high-severity fire patches in mixed-conifer forests. Canadian Journal of Forestry Research 45:1587–1596.

Young, J. A., and R. A. Evans. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34:501–506.

Youngblood, A., K. L. Metlen, and K. Coe. 2006. Changes in stand structure and composition after restoration treatments in low elevation dry forests of northeastern Oregon. Forest Ecology and Management 234:143–163.

Youngblood, A., C. S. Wright, R. D. Ottmar, and J. D. McIver. 2008. Changes in fuelbed characteristics and resulting fire potentials after fuel reduction treatments in dry forests of the Blue Mountains, northeastern Oregon. Forest Ecology and Management 255:3151–3169.

Zavitkovski, J., and M. Newton. 1968. Ecological Importance of Snowbrush Ceanothus Velutinus in the Oregon Cascades. Ecology 49:1134–1145.

Zavitkovski, J., M. Newton, and B. El-Hassan. 1969. Effects of snowbrush on growth of some conifers. Journal of Forestry 67:242–246.

APPENDICES

Appendix 1: Seedling regeneration data and results from GLMMs

Table A.1.1. Parameter estimates and p-values for models fit with linear terms for elevation and climatic moisture deficit (CMD). With the exception of a positive association with CMD and ponderosa pine seedling abundance, elevation and CMD were not linearly associated with seedling densities in our models. The Δ AIC for each parameter represents the difference in AIC between a reduced model (a model without the parameter) and a full model (all parameters included). Large Δ AIC values and small p-values indicate important drivers of post-fire seedling densities in our models. Statistically significant (p-value < 0.05) parameters are in bold. For simplicity, parameter estimates, p-values, and Δ AIC were not reported for the other variables in the models.

	Ponderosa pine			***Douglas-fir***			***Grand fir***			***All species***		
Parameter	*Coef.*	*Δ AIC*	*p-value*	*Coef.*	*Δ AIC*	*p-value*	*Coef.*	*Δ AIC*	*p-value*	*Coef.*	*Δ AIC*	*p-value*
dist. to seed source	-	-	-	-	-	-	-	-	-	-	-	-
fire refugia density	-	-	-	-	-	-	-	-	-	-	-	-
burn severity	-	-	-	-	-	-	-	-	-	-	-	-
elevation	-0.314	0	0.172	-0.001	1	0.33	0.001	2	0.50	0.005	0	0.15
moisture deficit	**0.008**	**10**	**<0.001**	0.0004	2	0.92	-0.0001	2	0.99	0.019	0	0.11
heat load	-	-	-	-	-	-	-	-	-	-	-	-
basal area	-	-	-	-	-	-	-	-	-	-	-	-
shrub cover	-	-	-	-	-	-	-	-	-	-	-	-

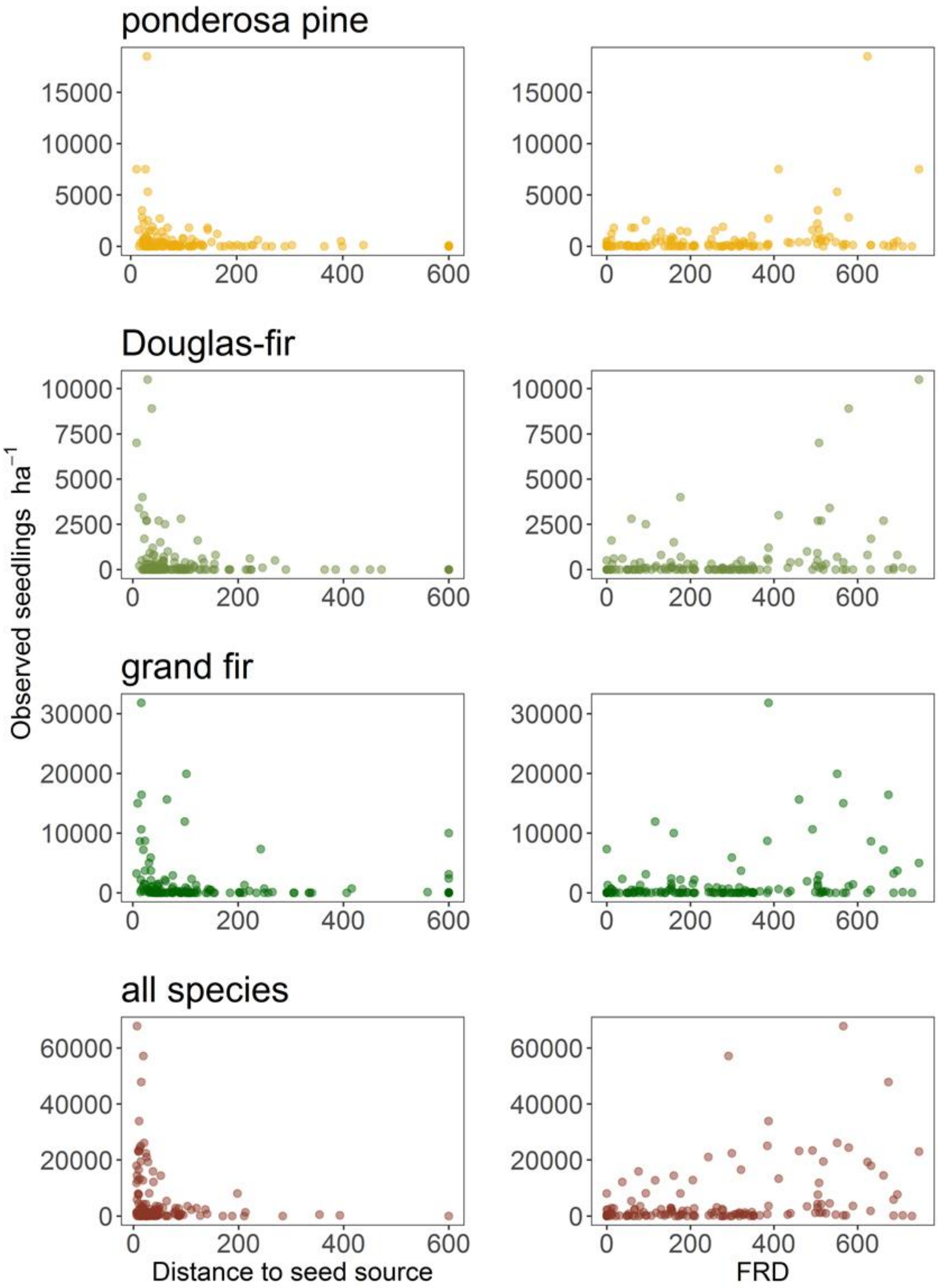


Figure A.1.1. Observed seedling densities for ponderosa pine, Douglas-fir, grand fir, and all species combined along gradients of distance to seed source and landscape fire refugia density (FRD). Note y-axis scales are different between plots due to significant variation in observed seedling densities for different species.

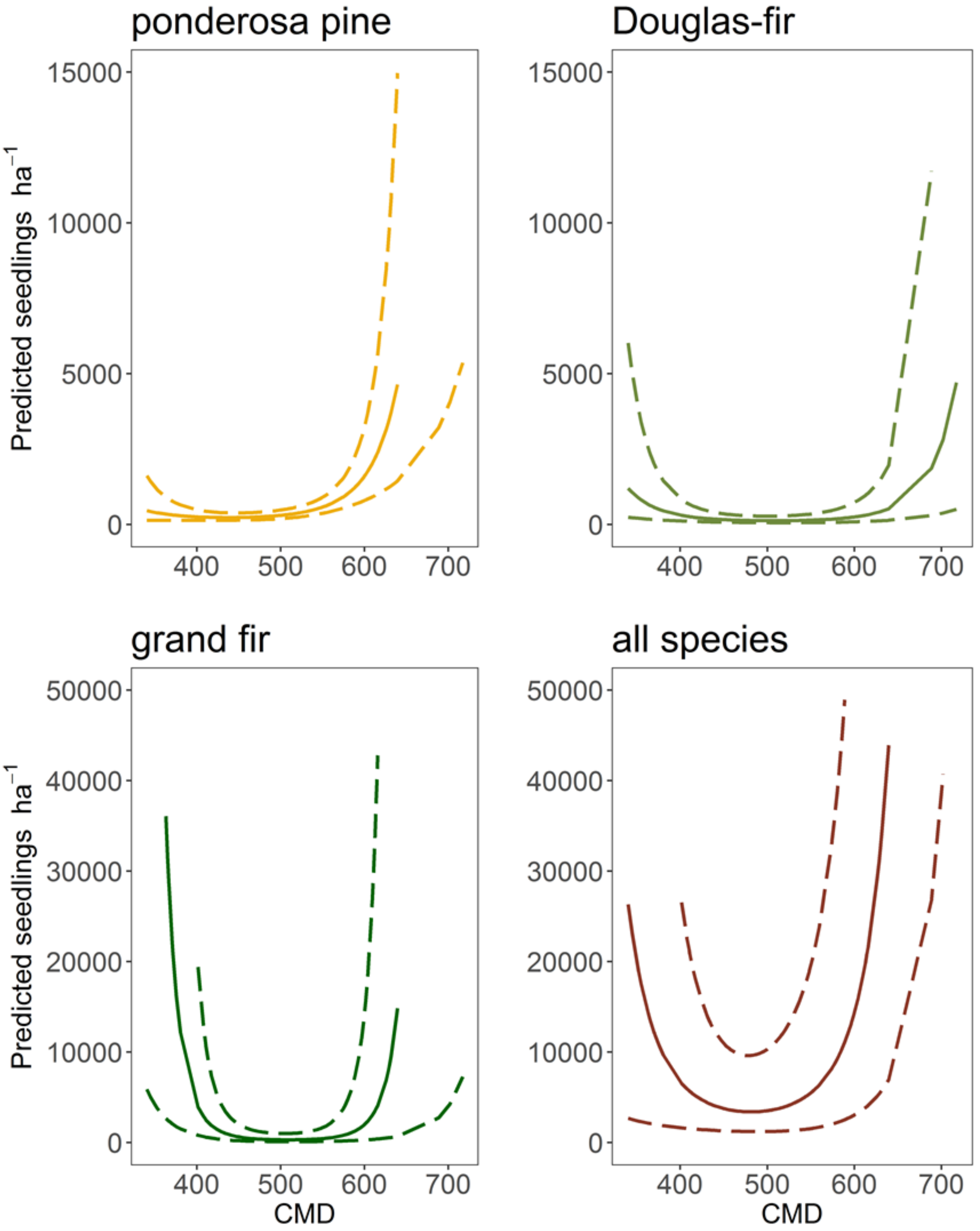


Figure A.1.2. Added variable plots of climatic moisture deficit and predicted seedling densities, with all other variables held constant at median values. Predicted seedling densities responded non-linearly along a gradient of climate moisture deficit (CMD). Dotted lines represent 95% confidence intervals. Note y-axis scales are different between plots due to significant variation in predicted seedling densities for different species. The y-scale is limited in all plots to highlight the form of the non-linear relationship between predicted seedling densities and CMD. Lines representing predicted values and confidence intervals are truncated as a result.

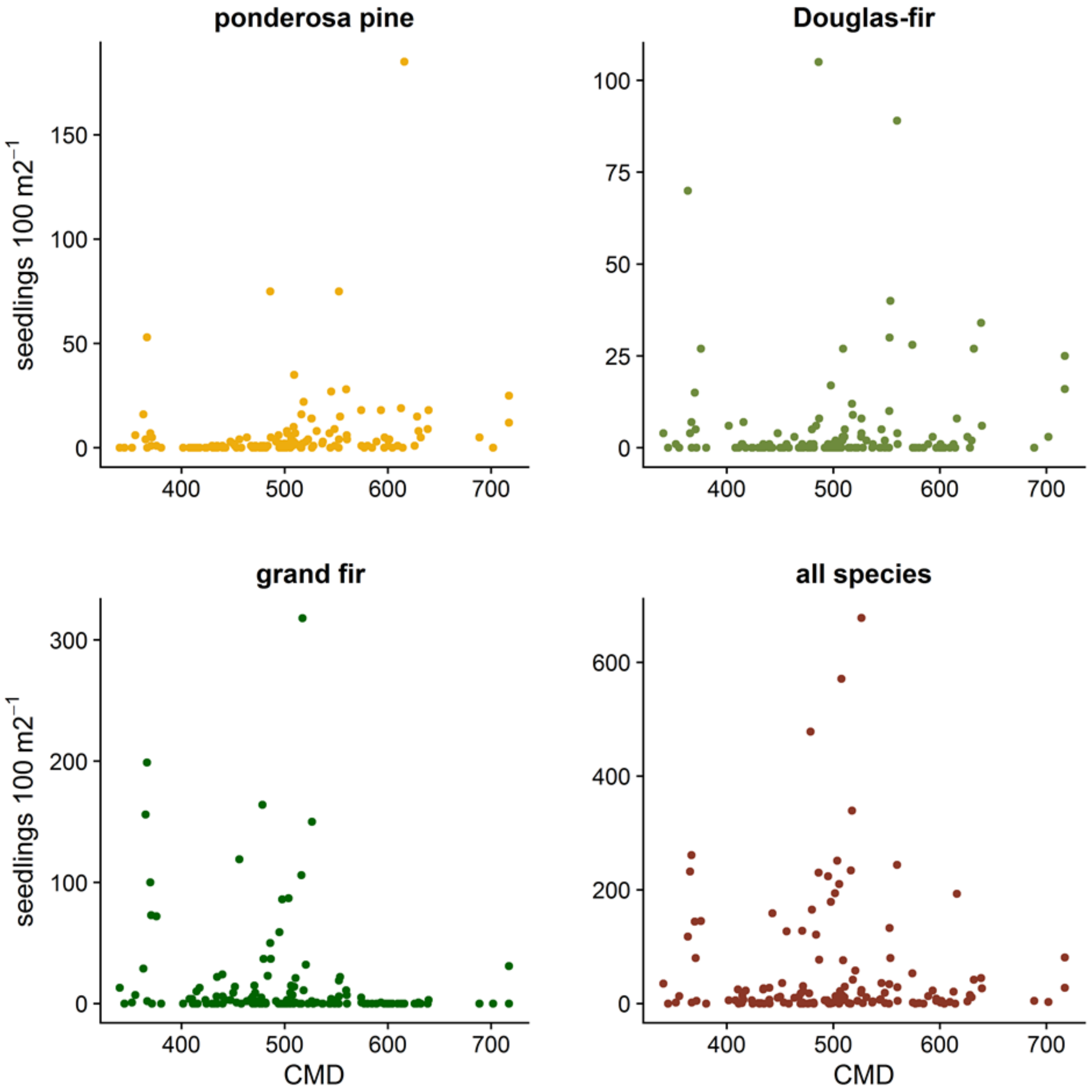


Figure A.1.3. Observed seedling densities for ponderosa pine, Douglas-fir, grand fir, and all species combined along the climatic moisture deficit (CMD) gradient. Densities are quantified at the plot scale (seedlings 100 m2^{-1}) rather than as seedlings per hectare.

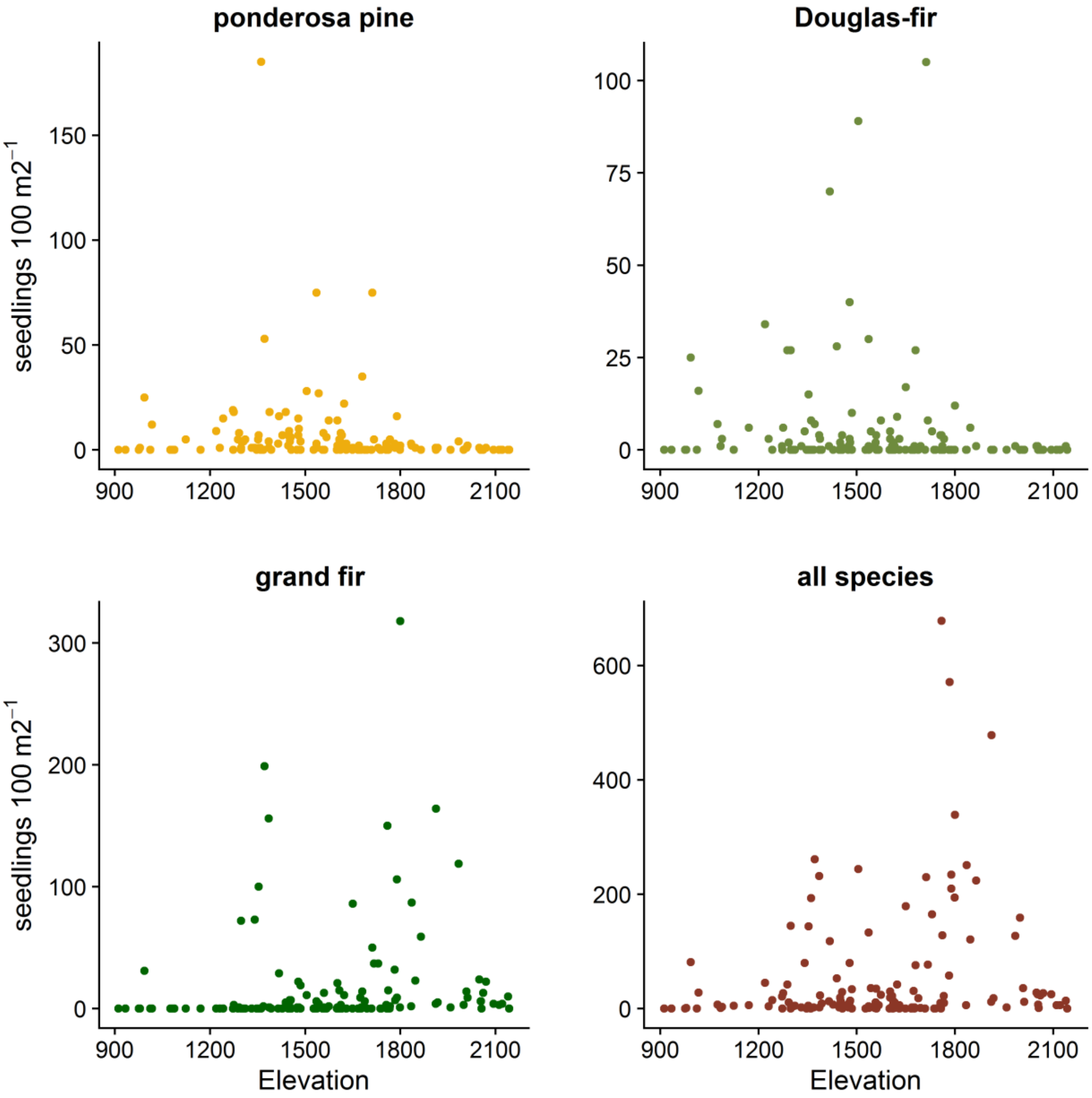


Figure A.1.4. Observed seedling densities for ponderosa pine, Douglas-fir, grand fir, and all species combined along the elevation gradient. Strong linear relationships are not apparent. Densities are quantified at the plot scale (seedlings 100 m2^{-1}) rather than as seedlings per hectare.

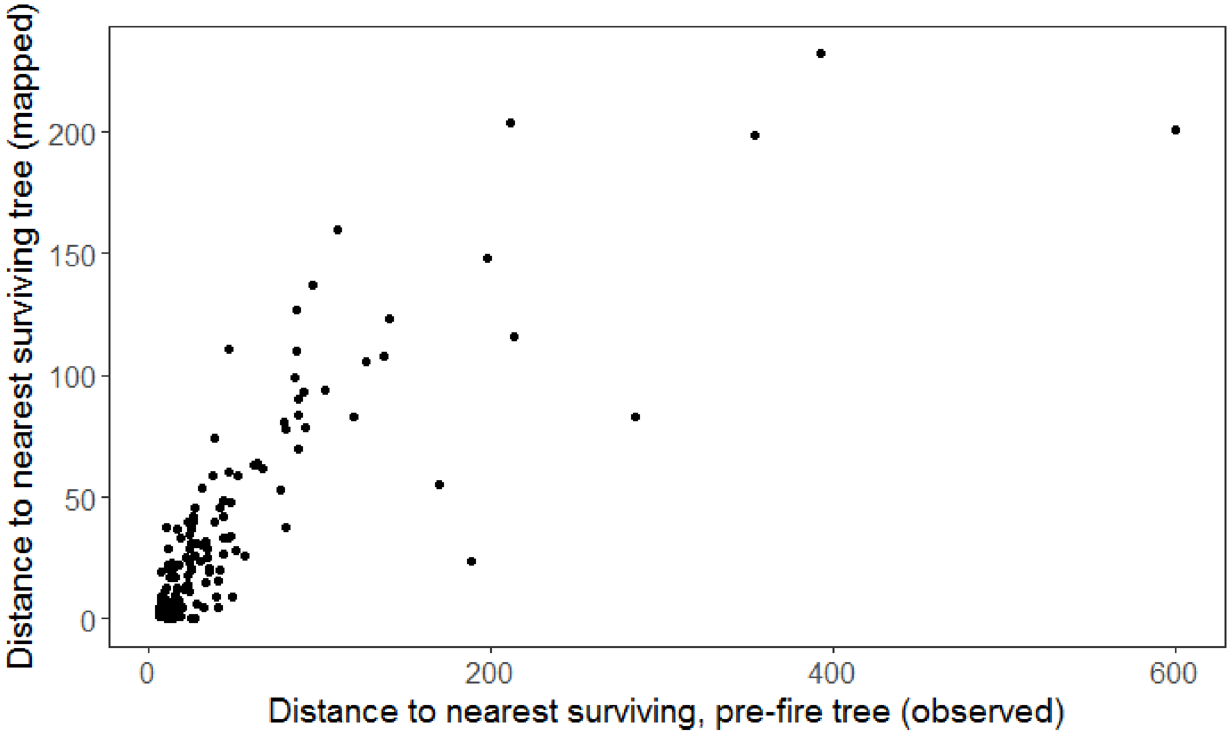


Figure A.1.5. Relationship between field-based measurements of distance to nearest surviving, pre-fire tree and distance estimates from fire refugia maps created with 1 meter aerial imagery. Field-based measurements of distance to nearest surviving, pre-fire tree are well correlated ($R^2 = 0.66$) with estimates from fire refugia maps.

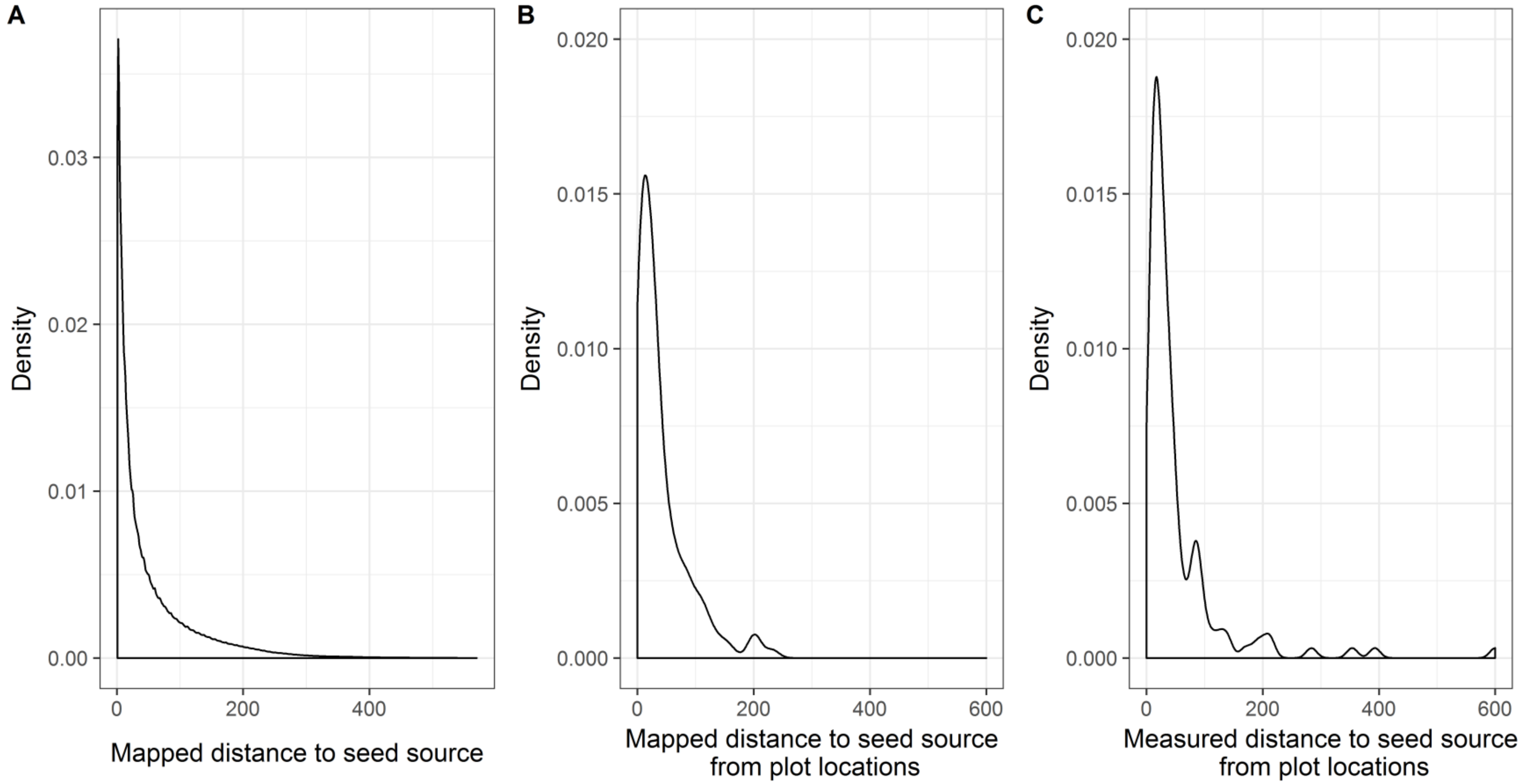


Figure A.1.6. Density plots comparing the distribution of distance to nearest seed source in our study fires and distance to nearest seed source for our sample plots. (A) Mapped distances to nearest seed source for all pixels outside of fire refugia calculated from the NAIP-based fire refugia maps. (B) Mapped distances to nearest seed source calculated from the NAIP-based fire refugia maps for our 135 plot locations. (C) Distances to nearest seed source for our 135 plot locations measured using a laser rangefinder in the field.

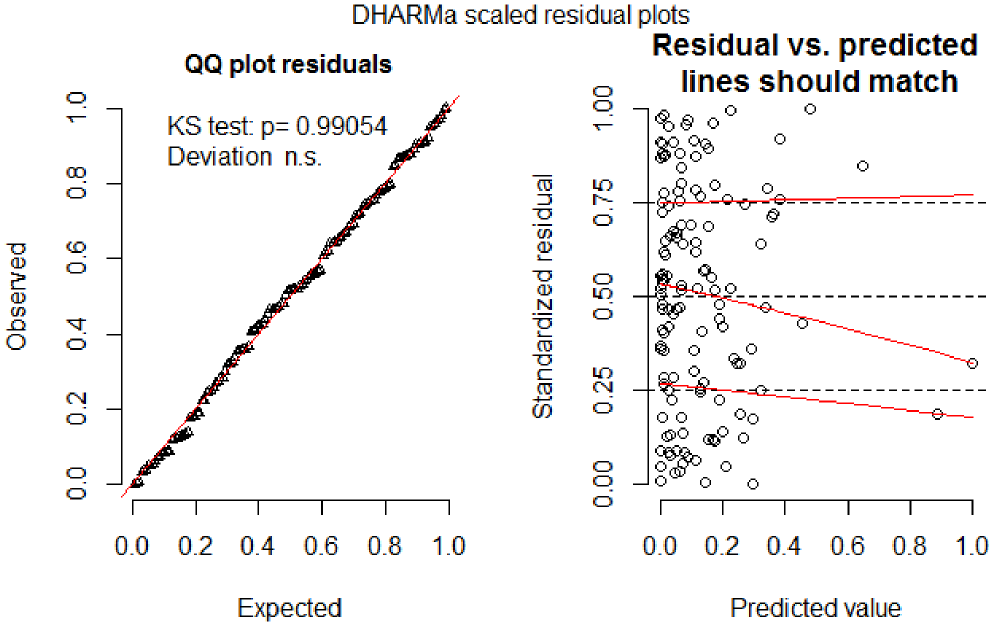


Figure A.1.7. Residual plots for ponderosa pine model. Model parameters were scaled by standard deviation. A one-sample Kologorov-Smirnov test (KS test) tests for overall uniformity of residuals.

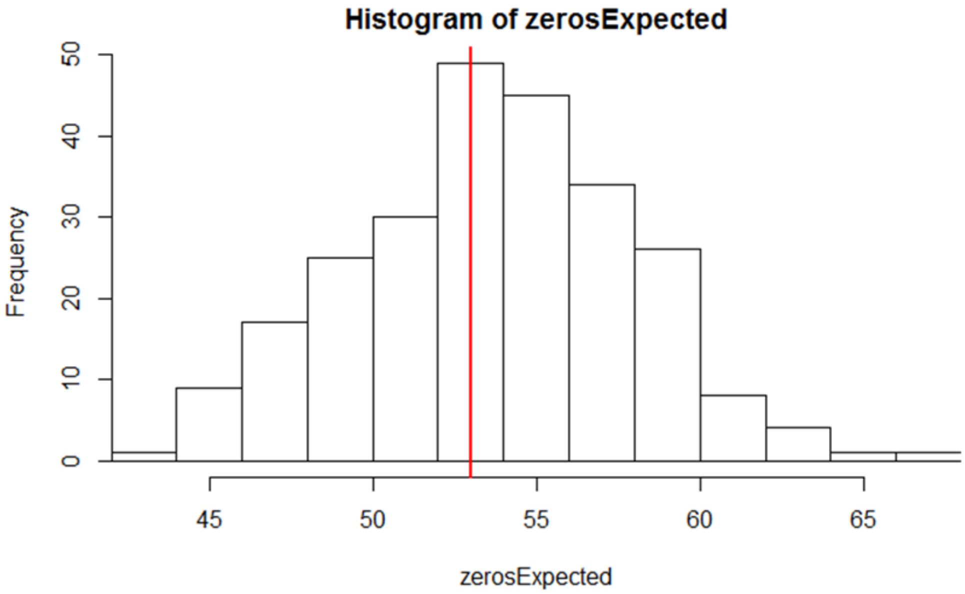


Figure A.1.8. Histogram comparing the distribution of expected zeros in the data based on the negative binomial model for ponderosa pine, and observed zeros). Vertical red line represents the observed number of zeros in the data. The negative binomial model is accounting for the overdispersion in the data and there is no evidence of zero-inflation.

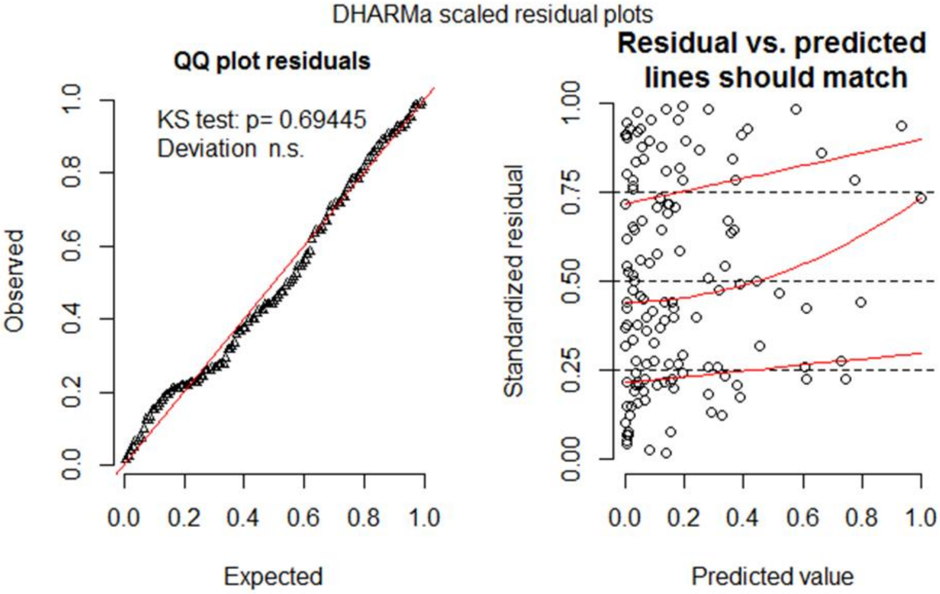


Figure A.1.9. Residual plots for Douglas-fir model. Model parameters were scaled by standard deviation. A one-sample Kologorov-Smirnov test (KS test) tests for overall uniformity of residuals.

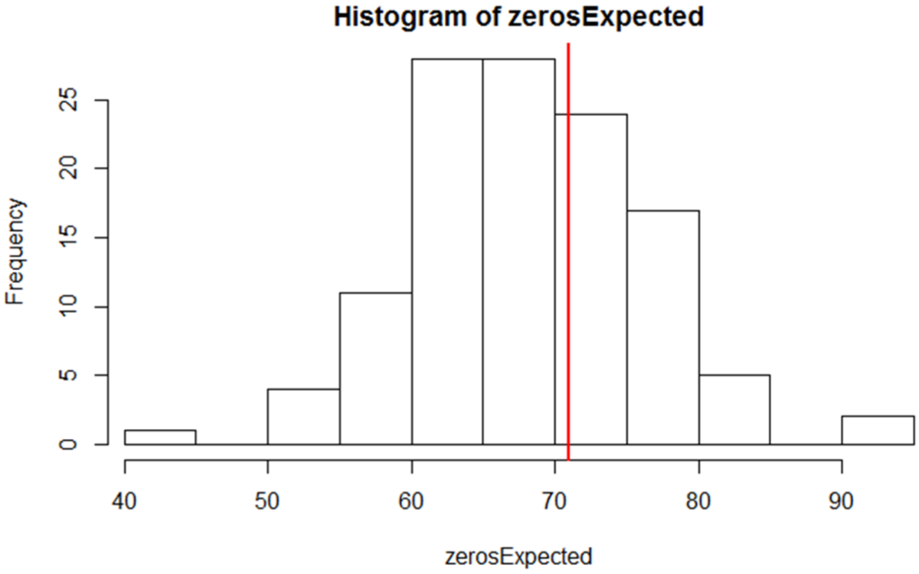


Figure A.1.10. Histogram comparing the distribution of expected zeros in the data based on the negative binomial model for Douglas-fir, and observed zeros. Vertical red line represents the observed number of zeros in the data. The negative binomial model is accounting for the overdispersion in the data and there is no evidence of zero-inflation.

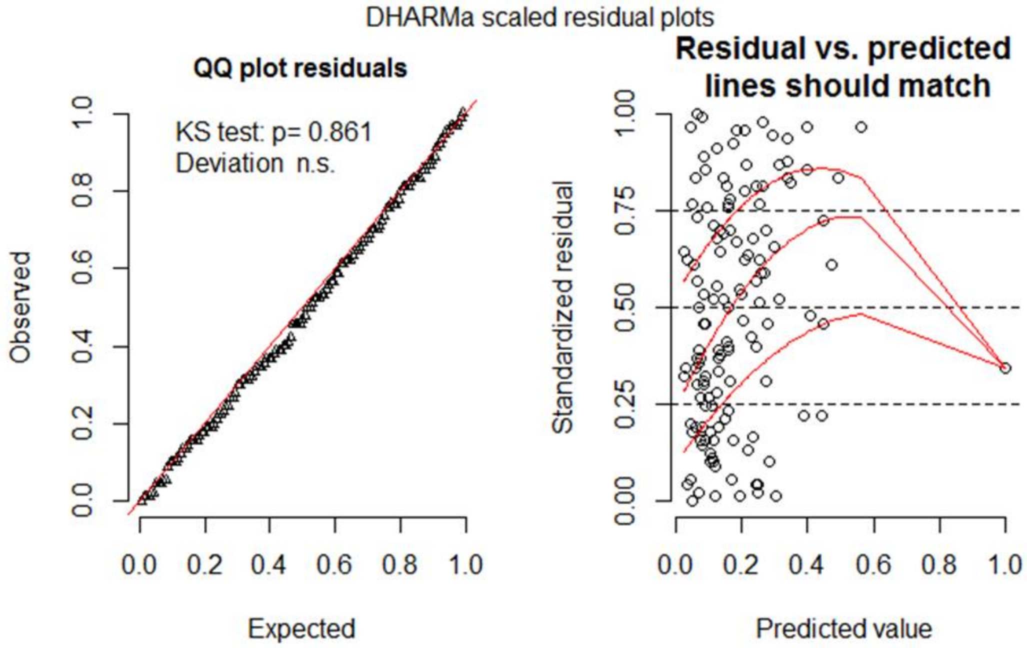


Figure A.1.11. Residual plots for grand fir model. Model parameters were scaled by standard deviation. A one-sample Kologorov-Smirnov test (KS test) tests for overall uniformity of residuals.

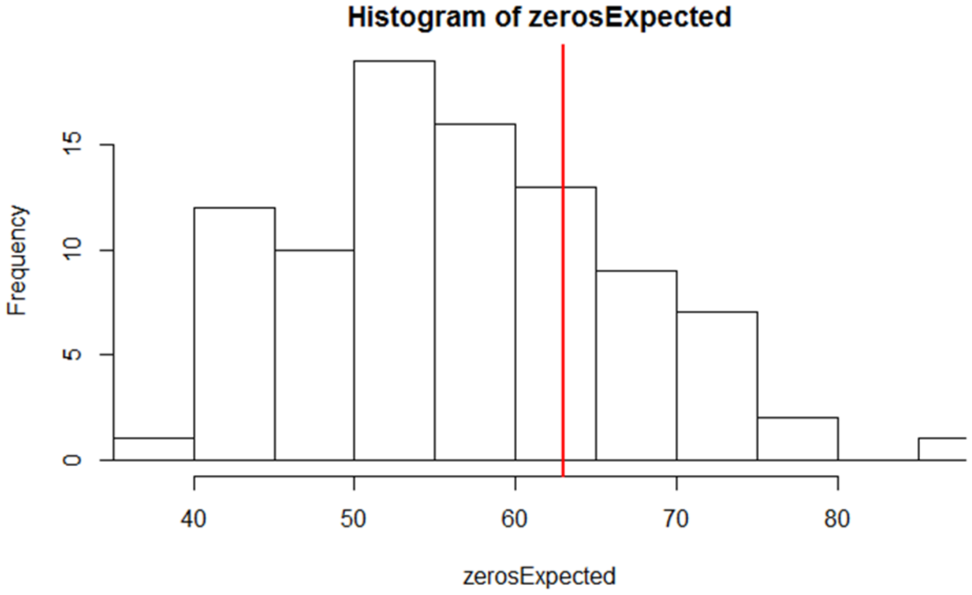


Figure A.1.12. Histogram comparing the distribution of expected zeros in the data based on the negative binomial model for grand fir, and observed zeros. Vertical red line represents the observed number of zeros in the data. The negative binomial model is accounting for the overdispersion in the data and there is no evidence of zero-inflation.

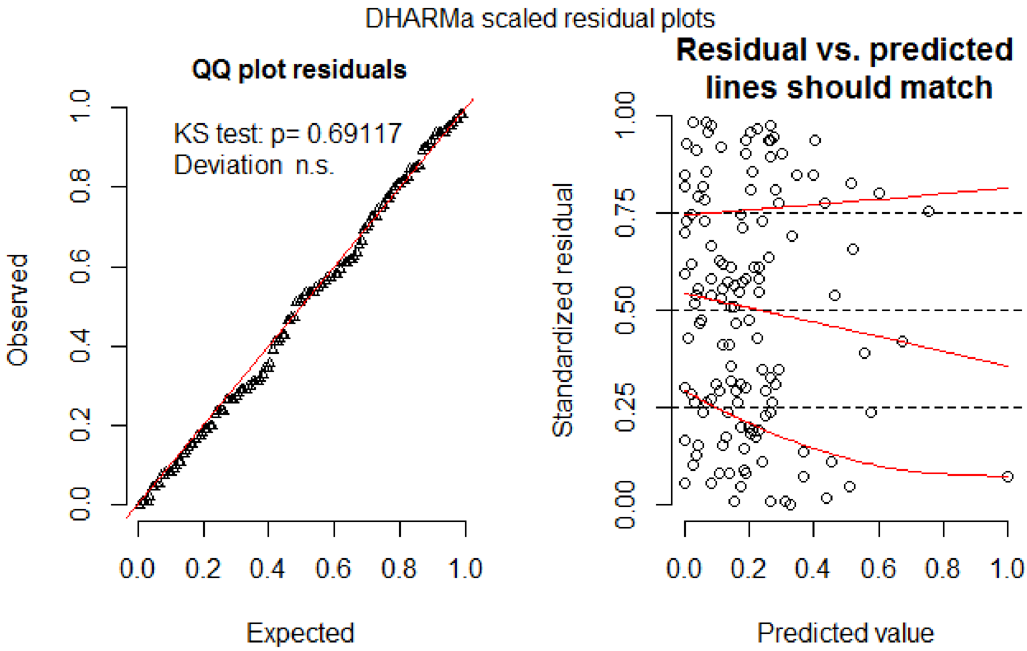


Figure A.1.13. Residual plots for all species model. Model parameters were scaled by standard deviation. A one-sample Kologorov-Smirnov test (KS test) tests for overall uniformity of residuals.

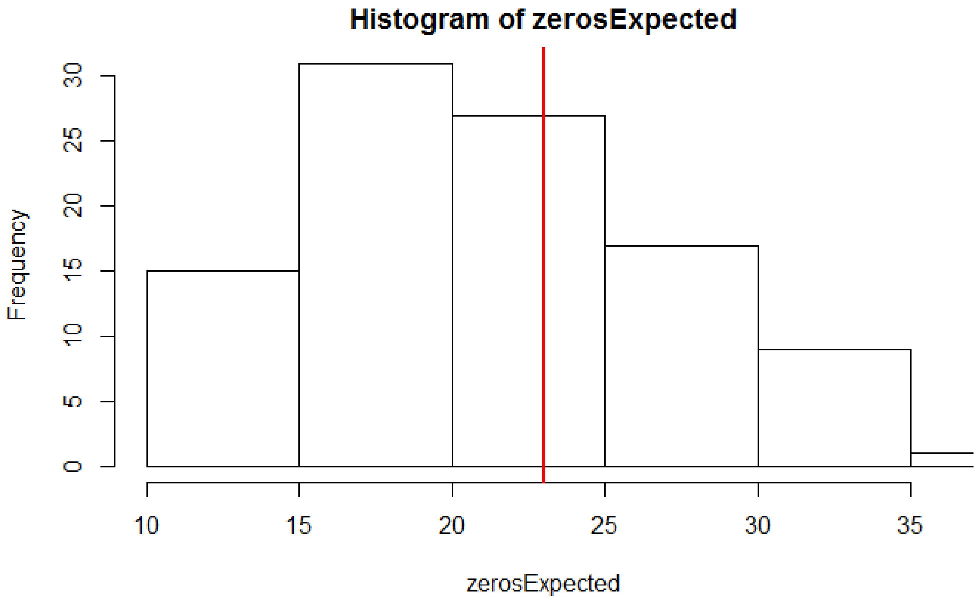


Figure A.1.14. Histogram comparing the distribution of expected zeros in the data based on the negative binomial model for all species, and observed zeros. Vertical red line represents the observed number of zeros in the data. The negative binomial model is accounting for the overdispersion in the data and there is no evidence of zero-inflation.

Appendix 2: Species-area curves, dominance curves, and plant species lists

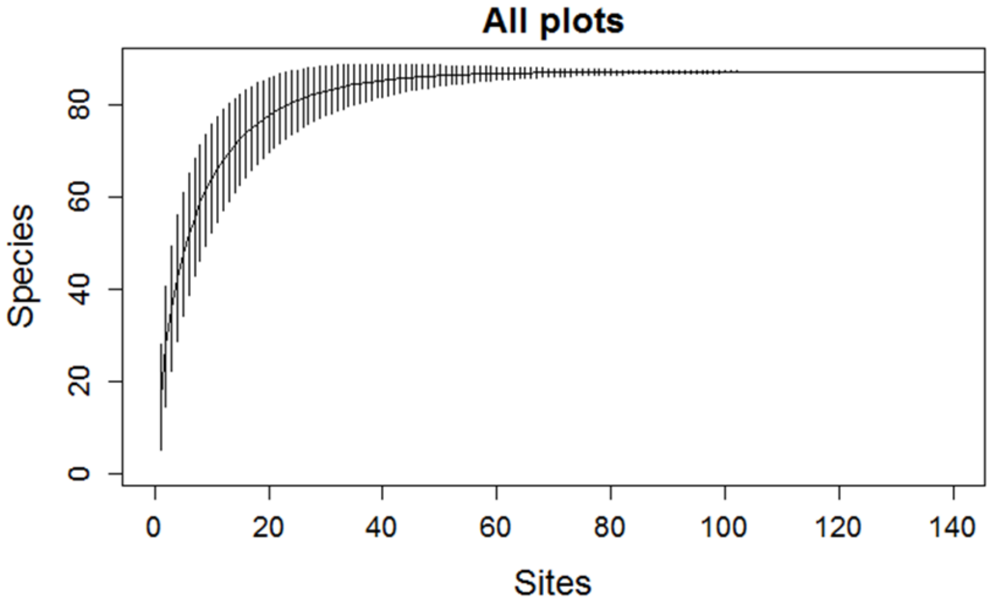


Figure A.2.1. Species-area curve for all plots after removing rare species. We accumulated the majority of species included in multivariate analyses with approximately 40 sample plots.

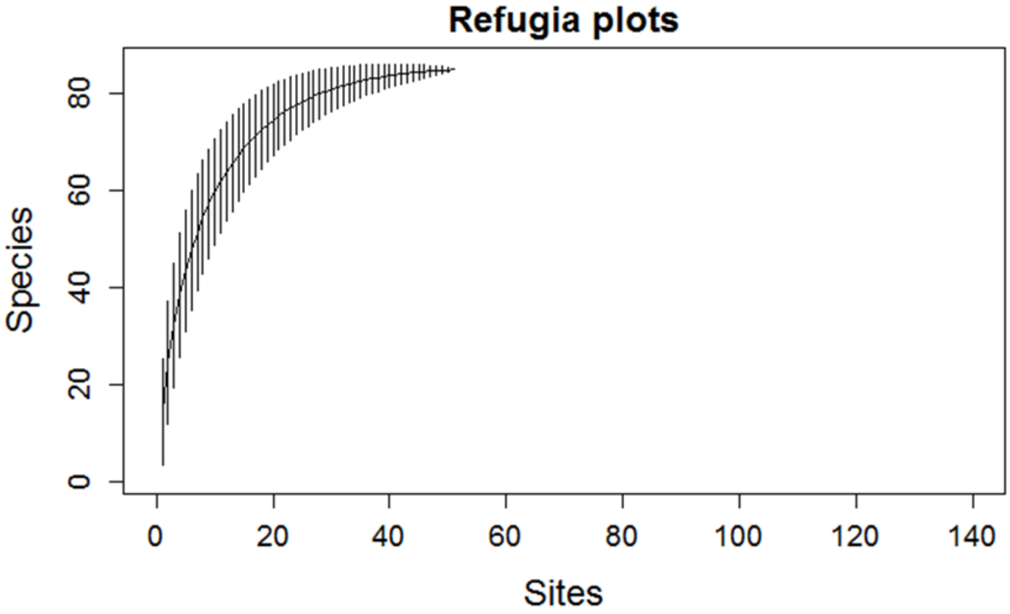


Figure A.2.2. Species-area curve for fire refugia plots after removing rare species. All species included in multivariate analyses occurred in fire refugia plots.

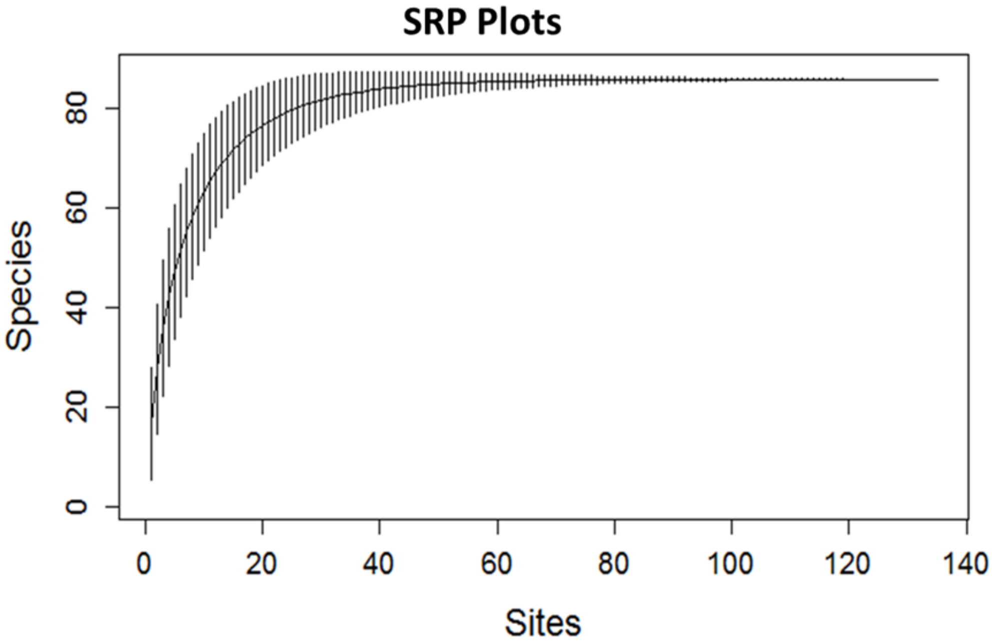


Figure A.2.3. Species-area curve for stand-replacement patch (SRP) plots after removing rare species.

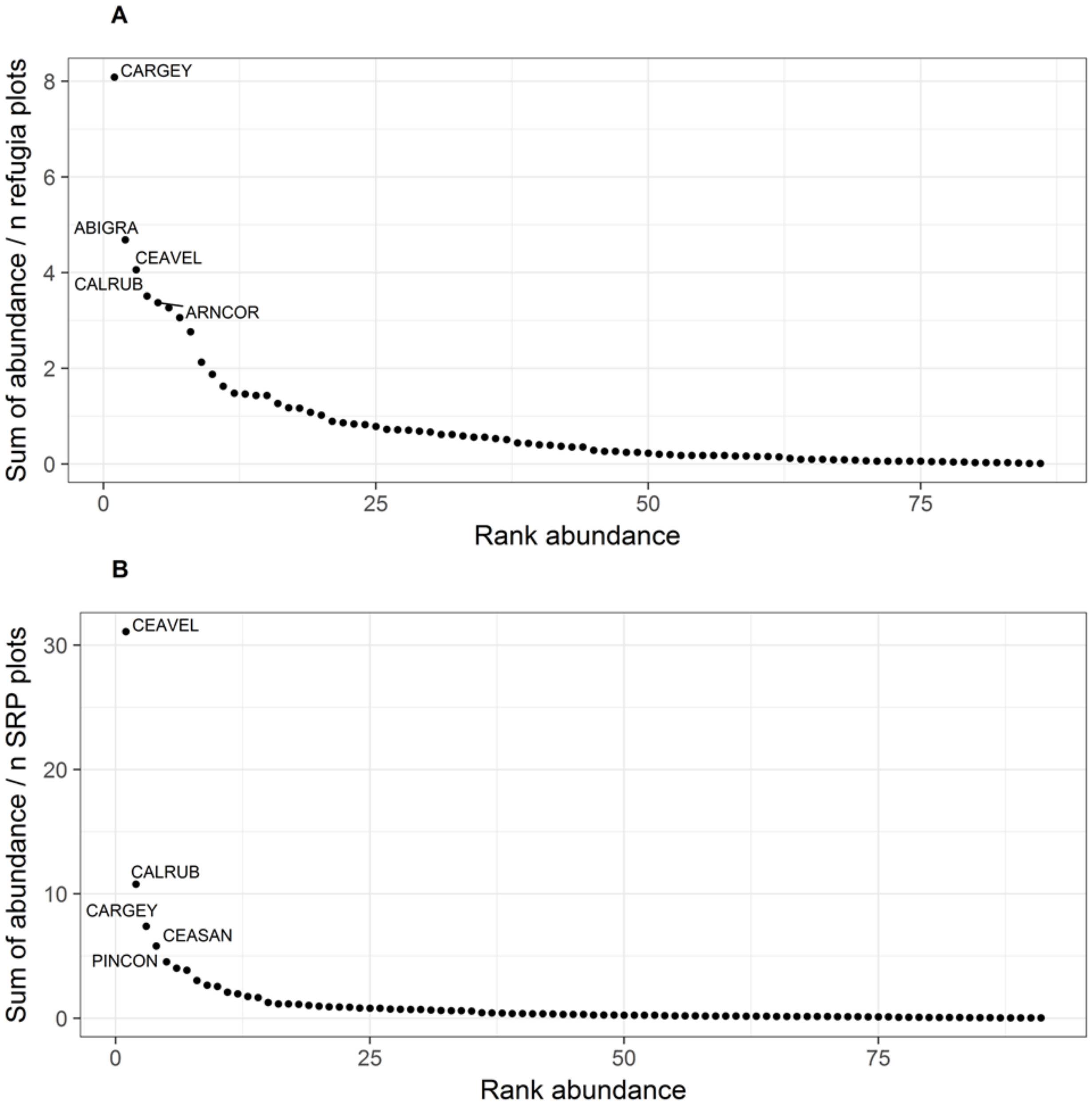


Figure A.2.4. Dominance curves for fire refugia and stand-replacement patch plots after removing rare species. Several hyper-dominant species were present in both fire refugia and stand-replacement patch plot types. The sum of abundance for each species is relativized by the number of refugia plots (n = 52) in dominance curve for fire refugia plots (A). The sum of abundance is relativized by the number of stand-replacement plots (n = 135) in dominance curve for stand-replacement plots.

Table A.2.1. List of common plant species present in >5% of sample plots. Maximum and mean cover, rank abundance, and rank frequency reported for each species in fire refugia and stand-replacement patch plots.

Species	**ID**	**Fire refugia plots**				**Stand-replacement patch plots**			
		max.	mean	Rank Abun.	Rank Freq.	max.	mean	Rank Abun.	Rank Freq.
Abies grandis	ABIGRA	59.5	4.6	2	5	25.0	2.1	11	12
Acer glabrum	ACEGLA	29.0	1.0	20	43	29.0	0.3	44	60
Achillea millefolium ssp. lanulosa	ACHMILLAN	7.5	1.1	18	2	7.5	1.3	15	1
Amelanchier alnifolia	AMEALN	2.5	0.2	58	44	7.5	0.3	50	41
Anaphalis margaritaceae	ANAMAR	17.5	0.3	44	76	29.0	0.4	40	42
Antennaria microphylla	ANTMIC	29.0	0.7	30	35	7.5	0.1	67	49
Arctostaphylos nevadensis	ARCNEV	2.5	0.2	52	63	7.5	0.1	72	80
Arctostaphylos patula	ARCPAT	0.5	0.0	85	85	41.5	0.8	25	31
Arnica cordifolia	ARNCOR	62.5	3.3	5	7	62.5	1.7	14	11
Balsamorhiza sagittata	BALSAG	7.5	0.5	35	33	17.5	0.1	70	85
Bromus briziflormis	BROBRI	7.5	0.2	61	75	17.5	0.4	43	61
Bromus carinatus	BROCAR	29.0	1.8	10	6	62.5	3.0	8	6
Bromus squarrosus	BROSQU	7.5	0.2	59	68	29.0	0.4	38	70
Bromus tectorum	BROTEC	29.0	1.6	11	26	17.5	0.8	26	23
Calamagrostis rubescens	CALRUB	62.5	3.4	4	17	87.5	10.8	2	5
Carex geyeri	CARGEY	62.5	7.9	1	1	62.5	7.4	3	3
Carex rossii	CARROS	41.5	1.5	12	28	7.5	0.7	29	28
Ceanothus sanguineus	CEASAN	17.5	0.6	31	32	87.5	5.8	4	38
Ceanothus velutinus	CEAVEL	62.5	4.0	3	8	87.5	31.1	1	2
Claytonia perfoliata	CLAPER	0.5	0.0	76	49	2.5	0.1	82	59
Clarkia rhomboidea	CLARHO	0.5	0.0	79	58	0.5	0.0	84	66
Collomia grandiflora	COLGRA	2.5	0.2	56	20	2.5	0.3	48	14

Species	ID	Fire refugia plots				Stand-replacement patch plots			
		max.	mean	Rank Abun.	Rank Freq.	max.	mean	Rank Abun.	Rank Freq.
Collinsia parviflora	COLPAR	7.5	0.4	41	3	17.5	0.7	31	13
Elymus elymoides	ELYELY	7.5	0.3	45	34	7.5	0.2	54	39
Elymus glaucus	ELYGLA	2.5	0.1	66	79	41.5	0.7	30	65
Epilobium angustifolium	EPIANG	7.5	0.4	38	11	62.5	2.5	10	4
Epilobium paniculatum	EPIPAN	2.5	0.3	47	12	29.0	0.7	28	7
Erigeron inornatus	ERIINO	0.5	0.0	83	70	0.5	0.0	85	67
Ericameria nauseosa	ERINAU	0.5	0.0	77	53	7.5	0.2	63	37
Eurybia conspicua	EURCON	2.5	0.1	65	74	7.5	0.2	58	53
Eurybia radulina	EURRAD	2.5	0.1	75	81	7.5	0.1	66	77
Festuca idahoensis	FESIDA	62.5	2.7	8	21	41.5	1.0	20	25
Fragaria vesca	FRAVES	29.0	1.4	14	15	17.5	1.2	16	10
Fragaria virginiana	FRAVIR	41.5	0.9	21	46	29.0	0.6	32	48
Galium aparine	GALAPA	7.5	0.2	48	25	2.5	0.4	42	15
Hieracium albertinum	HIEALB	7.5	0.5	36	13	2.5	0.1	71	29
Hieracium scouleri	HIESCO	2.5	0.2	53	19	2.5	0.2	61	27
Holodiscus discolor	HOLDIS	17.5	1.2	17	38	17.5	0.9	23	40
Juniper occidentalis	JUNOCC	2.5	0.2	54	39	0.5	0.0	87	86
Larix occidentalis	LAROCC	7.5	0.6	33	40	95.0	3.5	7	21
Lathyrus lanszwertii	LATLAN	7.5	0.2	60	71	7.5	0.2	64	75
Lupinus caudatus	LUPCAU	7.5	0.3	46	51	7.5	0.1	65	76
Lupinus polyphyllus	LUPPOL	62.5	1.4	15	56	17.5	0.3	49	68
Lupinus spp.	LUPSP.	2.5	0.2	51	30	2.5	0.1	73	36
Madia gracilis	MADGRA	7.5	0.2	55	59	62.5	1.0	19	33
Mahonia repens	MAHREP	7.5	0.7	29	4	7.5	0.6	35	19
Mitella trifida	MITTRI	2.5	0.1	63	60	2.5	0.1	74	63

Species	ID	Fire refugia plots				Stand-replacement patch plots			
		max.	mean	Rank Abun.	Rank Freq.	max.	mean	Rank Abun.	Rank Freq.
Moehringia macrophylla	MOEMAC	7.5	0.6	32	9	7.5	0.4	37	17
Osmorhiza chilensis	OSMCHI	17.5	0.8	25	16	7.5	0.2	52	26
Patchistima myrsinits	PATMYR	2.5	0.1	69	61	2.5	0.2	53	30
Phacelia hastata	PHAHAS	0.5	0.0	84	72	2.5	0.1	81	73
Phacelia heterophylla	PHAHET	0.5	0.0	81	69	1.0	0.1	79	45
Physocarpus malvaceus	PHYMAL	7.5	0.4	40	52	29.0	1.2	17	56
Picea engelmannii	PICENG	2.5	0.1	71	77	12.5	0.3	47	72
Pinus contorta	PINCON	10.0	0.5	37	36	72.5	4.1	5	22
Pinus ponderosa	PINPON	17.5	0.8	24	18	51.5	1.9	12	8
Poa pratensis	POAPRA	7.5	0.2	49	67	17.5	0.3	45	46
Poa secunda	POASEC	41.5	3.0	7	37	41.5	0.5	36	87
Poa spp.	POASP.	7.5	0.7	28	27	7.5	0.2	56	50
Polemonium pulcherrimum	POLPUL	7.5	0.2	57	57	0.5	0.0	86	74
Potentilla glandulosa	POTGLA	0.5	0.1	67	31	7.5	0.3	46	24
Prunus emarginata	PRUEMA	29.0	0.7	26	54	17.5	0.4	39	47
Pseudotsuga menziesii	PSEMEN	18.0	1.4	13	14	31.5	0.9	22	20
Pseudoroegneria spicata	PSESPI	29.0	3.2	6	22	62.5	1.7	13	44
Ribes cereum	RIBCER	2.5	0.1	70	65	7.5	0.2	51	52
Ribes lacustre	RIBLAC	7.5	0.2	50	45	2.5	0.1	75	71
Ribes viscosissimum	RIBVIS	17.5	0.5	34	48	7.5	0.4	41	34
Rosa gymnocarpa	ROSGYM	7.5	0.7	27	24	17.5	1.1	18	18
Rubus parviflorus	RUBPAR	17.5	0.3	43	80	62.5	0.8	24	57
Rumex acetosella	RUMACE	0.5	0.0	82	66	7.5	0.1	69	58
Salix spp.	SALSP.	41.5	1.1	19	42	62.5	3.9	6	9
Sambucus nigra cerulea	SAMNIG	2.5	0.1	72	83	17.5	0.7	27	32

Species	ID	Fire refugia plots				Stand-replacement patch plots			
		max.	mean	Rank Abun.	Rank Freq.	max.	mean	Rank Abun.	Rank Freq.
Sedum stenopetalum	SEDSTE	7.5	0.4	39	23	17.5	0.2	55	64
Senecio serra	SENSER	2.5	0.1	73	82	7.5	0.1	77	84
Silene menziesii	SILMEN	2.5	0.1	68	47	7.5	0.2	59	43
Smilacina stellata	SMISTE	17.5	0.4	42	62	2.5	0.1	83	78
Spiraea betulifolia	SPIBET	17.5	0.8	23	29	29.0	0.9	21	35
Symphoricarpos albus	SYMALB	29.0	2.1	9	10	41.5	2.7	9	16
Symphorycarpus spp.	SYMSP.	2.5	0.1	74	73	7.5	0.1	76	83
Tragopogon dubius	TRADUB	0.5	0.0	78	55	2.5	0.1	78	51
Unknown forb	UNKFOR	0.5	0.0	80	64	8.0	0.2	60	82
Unknown Poaceae	UNKPOA	29.0	0.8	22	50	17.5	0.2	62	79
Vaccinium membranaceum	VACMEM	2.5	0.1	64	78	17.5	0.2	57	81
Vaccinium scoparium	VACSCO	7.5	0.1	62	86	29.0	0.6	33	69
Ventenata dubia	VENDUB	29.0	1.2	16	41	29.0	0.6	34	55
Verbascum thapsus	VERTHA	0.5	0.0	86	84	7.5	0.1	68	62

Table A.2.2. List of rare plant species present in <5% of sample plots. Maximum and mean cover reported for each species in fire refugia (Refugia) and stand-replacement patch (SRP). Rank abundance and frequency are not reported because these values were all low for rare species.

Species	ID	Refugia plots		SRP plots	
		max.	mean	max.	mean
Abies lasiocarpa	ABILAS	2.5	0.1	0.5	0.0
Achnatherum nelsonii	ACHNEL	17.5	0.3	7.5	0.1
Achnatherum occidentale	ACHOCC	7.5	0.1	7.5	0.2
Actaea rubra	ACTRUB	0.0	0.0	7.5	0.1
Adenocaulon bicolor	ADEBIC	7.5	0.2	0.5	0.0
Agastache urticifolia	AGAURT	2.5	0.0	2.5	0.1
Agoseris aurantiaca	AGOAUR	0.5	0.0	0.5	0.0
Agoseris glauca	AGOGLA	0.0	0.0	0.5	0.0
Agoseris grandiflora	AGOGRA	0.5	0.0	0.5	0.0
Agoseris heterophylla	AGOHET	0.5	0.0	0.5	0.0
Agoseris retrorsa	AGORET	0.5	0.0	0.5	0.0
Agrostis stolonifera	AGRSTO	0.0	0.0	2.5	0.0
Allium acuminatum	ALLACU	0.5	0.0	0.5	0.0
Alnus viridis ssp. sinuata	ALNVIRSIN	0.0	0.0	17.5	0.1
Alopercurus pratensis	ALOPRA	2.5	0.1	0.5	0.0
Alyssum alyssoides	ALYALY	0.0	0.0	0.5	0.0
Antennaria racemosa	ANTRAC	2.5	0.0	0.0	0.0
Apocynum androsaemifolium	APOAND	0.5	0.0	0.5	0.0
Aquilegia formosa	AQUFOR	0.5	0.0	0.5	0.0
Arabis drummondii	ARADRU	0.0	0.0	0.5	0.0
Arabis hirsuta	ARAHIR	0.0	0.0	0.5	0.0
Arenaria congesta	ARECON	7.5	0.1	0.0	0.0
Arenaria serpyllifolia	ARESER	0.5	0.0	0.5	0.0
Arnica mollis	ARNMOL	0.0	0.0	2.5	0.0
Aspidotis densa	ASPDEN	0.5	0.0	0.0	0.0
Astragalus filipes	ASTFIL	7.5	0.1	0.0	0.0
Astragalus reventus	ASTREV	0.0	0.0	0.5	0.0
Bromus spp.	BROSP.	7.5	0.2	2.5	0.0
Carex disperma	CARDIS	0.0	0.0	41.5	0.3
Carex multicostata	CARMUL	2.5	0.0	2.5	0.0
Castilleja glandulifera	CASGLA	0.5	0.0	2.5	0.0
Castilleja hispida	CASHIS	0.0	0.0	0.5	0.0

Species	**ID**	**Refugia plots**		**SRP plots**	
		max.	mean	max.	mean
Castilleja linariifolia	CASLIN	0.5	0.0	0.5	0.0
Castilleja miniata	CASMIN	0.5	0.0	17.5	0.1
Castilleja spp.	CASSP.	0.0	0.0	0.5	0.0
Cerastium fontanum	CERFON	0.0	0.0	0.5	0.0
Cercocarpus ledifolius	CERLED	0.5	0.0	0.5	0.0
Chimaohila umbellata	CHIUMB	2.5	0.1	0.5	0.0
Chrysothamnus viscidiflorus	CHRVIS	0.0	0.0	0.5	0.0
Circaea alpina	CIRALP	0.0	0.0	2.5	0.0
Cirsium arvense	CIRARV	0.0	0.0	7.5	0.1
Cirsium brevifolium	CIRBRE	2.5	0.0	0.5	0.0
Cirsium spp.	CIRSP.	0.5	0.0	0.5	0.0
Cirsium vulgare	CIRVUL	0.5	0.0	0.5	0.0
Cistanthe umbellata	CISUMB	0.0	0.0	0.5	0.0
Clintonia uniflora	CLIUNI	0.5	0.0	0.5	0.0
Coalochortus macrocarpus	COAMAC	0.5	0.0	0.5	0.0
Collomia linearis	COLLIN	0.0	0.0	7.5	0.1
Collomia spp.	COLSP.	0.5	0.0	0.5	0.0
Cornus nuttallii	CORNUT	7.5	0.1	0.0	0.0
Crepis acuminata	CREACU	0.5	0.0	0.0	0.0
Crepis atribarba	CREATR	0.5	0.0	0.0	0.0
Crepis occidentalis	CREOCC	0.5	0.0	0.0	0.0
Crepis spp.	CRESP.	0.5	0.0	0.5	0.0
Cryptantha affinis	CRYAFF	0.5	0.0	0.0	0.0
Cryptantha simulans	CRYSIM	0.0	0.0	0.5	0.0
Cryptantha spp.	CRYSP.	0.5	0.0	2.5	0.0
Cynoglossum officinale	CYNOFF	0.0	0.0	7.5	0.1
Cystopteris fragilis	CYSFRA	2.5	0.1	2.5	0.0
Dactylis glomerata	DACGLO	2.5	0.1	0.0	0.0
Danthonia intermedia	DANINT	29.0	0.8	0.5	0.0
Delphinium nuttallianum	DELNUT	0.5	0.0	0.0	0.0
Delphinium occidentale	DELOCC	0.0	0.0	7.5	0.1
Deschampsia elongata	DESELO	0.0	0.0	2.5	0.0
Draba verna	DRAVER	0.5	0.0	0.5	0.0
Elymus lanceolatus ssp. lanceolatus	ELYLANLAN	0.0	0.0	17.5	0.2
Epilobium cilliatum	EPICIL	0.5	0.0	0.5	0.0

Species	ID	Refugia plots		SRP plots	
		max.	mean	max.	mean
Epilobium minutum	EPIMIN	0.0	0.0	0.5	0.0
Erigeron corymbosus	ERICOR	0.0	0.0	0.5	0.0
Eriogonum elatum	ERIELA	0.5	0.0	0.5	0.0
Eriogonum heracleoides	ERIHER	0.0	0.0	2.5	0.0
Eriophyllum lanatum	ERILAN	0.0	0.0	0.5	0.0
Eriogonum spp.	ERIOSP.	0.0	0.0	0.5	0.0
Erigeron speciosus	ERISPE	0.5	0.0	7.5	0.1
Festuca occidentalis	FESOCC	2.5	0.1	17.5	0.2
Festuca spp.	FESSP.	0.0	0.0	2.5	0.0
Fritillaria pudica	FRIPUD	0.5	0.0	0.0	0.0
Galium boreale	GALBOR	0.0	0.0	0.5	0.0
Galium spp.	GALSP.	0.5	0.0	0.5	0.0
Galium triflorum	GALTRI	0.5	0.0	0.0	0.0
Geranium viscosissimum var. nervosum	GERVISNER	0.5	0.0	0.0	0.0
Geum macrophyllum	GEUMAC	0.0	0.0	17.5	0.1
Geum triflorum	GEUTRI	0.5	0.0	2.5	0.0
Glyceria spp.	GLYSP.	0.0	0.0	7.5	0.1
Goodyera oblongifolia	GOOOBL	0.5	0.0	0.0	0.0
Hackelia micrantha	HACMIC	0.0	0.0	17.5	0.2
Helianthella uniflora	HELUNI	0.5	0.0	0.5	0.0
Heracleum lanatum	HERLAN	17.5	0.3	0.0	0.0
Heuchera cylindrica	HEUCYL	0.0	0.0	0.5	0.0
Heuchera micrantha	HEUMIC	0.0	0.0	7.5	0.1
Hieracium albertinum	HIEALBT	0.5	0.0	0.0	0.0
Hieracium spp.	HIESP.	0.0	0.0	0.5	0.0
Holosteum umbellatum	HOLUMB	0.5	0.0	2.5	0.0
Hydrophyllum capitatum	HYDCAP	2.5	0.0	0.0	0.0
Hypericum perforatum	HYPPER	0.0	0.0	0.5	0.0
Iliamna rivularis	ILIRIV	0.5	0.0	2.5	0.1
Juncus confusus	JUNCON	0.5	0.0	0.0	0.0
Juncus ensifolius	JUNENS	0.0	0.0	7.5	0.1
Lactuca seriola	LACSER	0.5	0.0	0.5	0.0
Leptosiphon harknessii	LEPHAR	0.5	0.0	0.0	0.0
Leucanthemum vulgare	LEUVUL	0.0	0.0	7.5	0.1
Linnaea borealis	LINBOR	7.5	0.1	2.5	0.0

Species	ID	Refugia plots		SRP plots	
		max.	mean	max.	mean
Linaria dalmatica	LINDAL	0.0	0.0	2.5	0.0
Lithophragma glabrum	LITGLA	17.5	0.3	0.0	0.0
Lithospermum ruderale	LITRUD	0.5	0.1	0.5	0.0
Lomatium ambiguum	LOMAMB	0.5	0.0	0.0	0.0
Lomatium dissectum	LOMDIS	0.5	0.0	0.0	0.0
Lomatium grayi	LOMGRA	2.5	0.0	2.5	0.0
Lomatium nudicaule	LOMNUD	2.5	0.1	2.5	0.0
Lomatium spp.	LOMSP.	0.5	0.0	0.0	0.0
Lomatium triternatum	LOMTRI	7.5	0.2	0.5	0.0
Lonicera utahensis	LONUTA	2.5	0.0	0.5	0.0
Lupinus argenteus ssp. argenteus var. laxiflorus	LUPARGARG	2.5	0.1	2.5	0.0
Lupinus leucophyllus	LUPLEU	0.0	0.0	7.5	0.1
Lupinus sericeus	LUPSER	0.0	0.0	17.5	0.2
Luzula comosa	LUZCOM	2.5	0.0	0.5	0.0
Machaeranthera canescens ssp. canescens	MACCANCAN	0.0	0.0	0.5	0.0
Madia spp.	MADSP.	0.5	0.0	2.5	0.0
Mahonia nervosa	MAHNER	0.0	0.0	0.5	0.0
Melica subulata	MELSUB	2.5	0.1	2.5	0.0
Mertensia oblongifolia	MEROBL	7.5	0.1	0.0	0.0
Microsteris gracilis	MICGRA	0.0	0.0	2.5	0.0
Mimulus lewisii	MIMLEW	0.0	0.0	2.5	0.0
Mimulus moschatus	MIMMOS	0.0	0.0	0.5	0.0
Mitella pentandra	MITPEN	0.0	0.0	29.0	0.2
Montia linearis	MONLIN	17.5	0.3	0.0	0.0
Navarretia divaricata	NAVDIV	0.0	0.0	2.5	0.0
Nemophila parviflorum	NEMPAR	0.0	0.0	0.5	0.0
Noccaea fendleri	NOCFEN	2.5	0.0	0.0	0.0
Orobanche uniflora	OROUNI	0.0	0.0	2.5	0.0
Osmorhiza occidentalis	OSMOCC	0.5	0.0	0.5	0.0
Pedicularis racemosa	PEDRAC	2.5	0.1	0.0	0.0
Penstemon attenuatus	PENATT	0.0	0.0	0.5	0.0
Penstemon fruticosus	PENFRU	0.5	0.0	17.5	0.2
Penstemon rydbergii	PENRYD	0.5	0.0	2.5	0.0
Penstemon venustus	PENVEN	0.0	0.0	0.5	0.0

Species	ID	Refugia plots		SRP plots	
		max.	mean	max.	mean
Philadelphus lewisii	PHILEW	29.0	1.0	7.5	0.1
Phlox austromontana	PHLAUS	17.5	0.3	0.5	0.0
Phlox caespitosa	PHLCAE	0.5	0.0	0.0	0.0
Phlox hoodii	PHLHOO	0.0	0.0	0.5	0.0
Pinus albicaulis	PINALB	0.0	0.0	0.5	0.0
Pinus monicola	PINMON	0.5	0.0	0.0	0.0
Platanthera dilatata	PLADIL	0.5	0.0	2.5	0.0
Plectritis macrocera	PLEMAC	0.0	0.0	0.5	0.0
Poa bulbosa	POABUL	2.5	0.1	0.5	0.0
Poa nervosa var. wheeleri	POANERWHE	0.0	0.0	2.5	0.0
Polygonum bistortoides	POLBIS	41.5	0.8	0.0	0.0
Polystichum munitum	POLMUN	7.5	0.2	0.5	0.0
Populus tremuloides	POPTRE	0.0	0.0	0.5	0.0
Populus trichocarpa	POPTRI	0.0	0.0	0.5	0.0
Potentilla gracilis	POTGRA	29.0	0.6	0.0	0.0
Prosartes hookeri	PROHOO	0.5	0.0	0.5	0.0
Prunus virginiana	PRUVIR	2.5	0.0	29.0	0.2
Pteridium aquilinum	PTEAQU	0.0	0.0	7.5	0.1
Purshia tridentata	PURTRI	2.5	0.0	0.0	0.0
Pyrola picta	PYRPIC	0.5	0.0	0.0	0.0
Pyrola secunda	PYRSEC	0.5	0.0	2.5	0.0
Ranunculus uncinatus	RANUNC	0.0	0.0	0.5	0.0
Rosa nutkana	ROSNUT	7.5	0.2	0.5	0.0
Rubus leucodermis	RUBLEU	0.0	0.0	0.5	0.0
Rubus ursinus	RUBURS	0.0	0.0	2.5	0.0
Rudbeckia occidentalis	RUDOCC	0.0	0.0	2.5	0.0
Sambucus racemosa	SAMRAC	0.0	0.0	7.5	0.1
Sanicula graveolens	SANGRA	0.0	0.0	2.5	0.0
Saxifraga integrifolia	SAXINT	0.5	0.0	0.0	0.0
Scrophylaria lanceolata	SCRLAN	0.0	0.0	0.5	0.0
Senecio intergerrimus	SENINT	7.5	0.1	0.0	0.0
Senecio triangularis	SENTRI	0.0	0.0	29.0	0.2
Shepherdia canadensis	SHECAN	0.0	0.0	0.5	0.0
Sidalcea oregana	SIDORE	2.5	0.1	7.5	0.1
Silene douglasii	SILDOU	0.5	0.0	0.5	0.0

Species	ID	Refugia plots		SRP plots	
		max.	mean	max.	mean
Silene oregana	SILORE	0.5	0.0	0.5	0.0
Silene spp.	SILSP.	0.5	0.0	2.5	0.0
Unknown Silene	SILSP.	0.5	0.0	2.5	0.0
Sisyrinchium idahoense	SISIDA	0.5	0.0	0.0	0.0
Smilacina racemosa	SMIRAC	0.5	0.0	0.5	0.0
Smilacina spp.	SMISP.	0.5	0.0	0.5	0.0
Solidago multiradiata	SOLMUL	2.5	0.0	7.5	0.1
Sorbus scopulina	SORSCO	0.0	0.0	7.5	0.1
Spiranthes romanzoffiana	SPIROM	2.5	0.0	0.0	0.0
Symphoricarpos oreophilus	SYMORE	0.0	0.0	7.5	0.1
Synthyris missurica	SYNMIS	62.5	1.2	0.0	0.0
Taraxacum officinale	TAROFF	0.5	0.0	0.5	0.0
Thalictrum fendleri	THAFEN	2.5	0.1	7.5	0.1
Thalictrum occidentale	THAOCC	0.5	0.0	0.5	0.0
Thalictrum spp.	THASP.	0.5	0.0	0.5	0.0
Thalictrum venulosum	THAVEN	0.0	0.0	0.5	0.0
Tiarella unifoliata	TIAUNI	0.0	0.0	0.5	0.0
Trisetum canescens	TRICAN	0.5	0.0	7.5	0.1
Triteleia grandiflora	TRIGRA	0.0	0.0	0.5	0.0
Trifolium longipes	TRILON	41.5	0.8	0.5	0.0
Trifolium macrocephalum	TRIMAC	17.5	0.3	0.0	0.0
Unknown Brassicaceae	UNKBRA	0.5	0.0	0.0	0.0
Unknown Fabaceae	UNKFAB	7.5	0.2	0.0	0.0
Unknown Ranunculaceae	UNKRAN	0.0	0.0	0.5	0.0
Valeriana sitchensis	VALSIT	7.5	0.2	0.0	0.0
Veronica arvensis	VERARV	0.5	0.0	0.0	0.0
Veronica serpyllifolia	VERSER	0.5	0.0	0.0	0.0
Vicia americana	VICAME	0.5	0.0	7.5	0.1
Viola adunca	VIOADU	0.0	0.0	1.5	0.0
Viola glabella	VIOGLA	7.5	0.2	0.5	0.0
Viola palustris	VIOPAL	0.5	0.0	0.0	0.0
Viola purpurea	VIOPUR	0.5	0.0	2.5	0.0
Viola spp.	VIOSP.	0.0	0.0	0.5	0.0
Vulpia microstachys	VULMIC	2.5	0.0	0.0	0.0
Vulpia myuros	VULMYU	0.5	0.0	0.0	0.0

Species	**ID**	**Refugia plots**		**SRP plots**	
		max.	mean	max.	mean
Zigadenus venenosus	ZIGVEN	0.5	0.0	0.5	0.0

Appendix 3: Implications of data relativization and inclusion of strata totals in the community matrix for multivariate analysis

The methods used to prepare and analyze community data have significant implications for the eventual biological interpretation. The methods we used here are just one of many possible approaches. Coop et al. (2016) performed a similar analysis with unrelativized species cover data and strata totals (shrub, herbaceous, tree) in the community matrix. We compared the results of our approach with the approach used by Coop et al. (2016). We found that including strata totals and not relativizing community data effectively ignores more than 95% of the community data, which inflates compositional differences between fire refugia and stand-replacement patch plots in nonmetric multidimensional scaling (NMS) and multi-response permutation procedures (MRPP) analyses.

Transformations and relativizations are common tools used in community to analysis to decrease the influence of hyper-dominant species on the interpretation of the structure of the community dataset, and to emphasize differences in species composition (McCune and Grace 2002). Strata totals (i.e., total shrub, herbaceous, and tree cover) are a useful way to characterize vegetation structure in sample plots. The interpretation of community ordinations can be enhanced when strata totals are included in the environmental matrix and used to symbolize plots in species space (Figure A.3.1 – 3.3). However, it is problematic to include strata totals in the community matrix (Bruce McCune, personal communication). Specifically, strata totals in the community matrix present a double-counting problem because each species in the community matrix contributes cover values to the strata totals. Additionally, strata totals will always be as large or larger than any cover values for an individual species in a particular plot. This is a particularly serious problem when community data are not relativized or transformed because any differences identified between plots in NMS and MRPP analyses will primarily reflect differences in the abundance of hyper-dominant species (e.g., largest column totals). In the case of an unrelativized community dataset that includes strata totals, the most dominant "species" will always be the strata totals themselves.

By definition, there are strong and unequivocal differences in physical structure between fire refugia and stand-replacement areas. These differences are reflected in the overwhelming influence of strata totals and a small number of hyper-dominant species, which is evident from a visual comparison of Figure A.3.1 and Figure A.3.2. Both are ordinations of unrelativized community data including three strata totals. The community matrix used to create Figure A.3.1 contained 293 species. The community matrix used to create Figure A.3.2 contained the five most common species (species that occurred in >50% of plots). The two ordinations are virtually indistinguishable. The 288 species excluded from the ordination in Figure A.3.2 do not substantially influence the ordination in Figure A.3.1. This comparison demonstrates that an analysis including strata totals is insensitive to the vast majority of community data. Such analyses do not appear to constitute a direct comparison of community composition.

At the same time, the ordinations in Figure A.3.1 and A.3.2 do appear to represent relatively strong compositional differences between refugia and stand-replacement patch plots. High shrub cover in stand-replacement patch plots compared to fire refugia plots was a defining feature of the physical structure in the sampled post-fire landscapes, and symbolizing plots by percent shrub cover enhances the visual impression of strong differences between plot types. Despite the visually compelling differences apparent in Figures A.3.1 and A.3.2, strong compositional differences between fire refugia and stand-replacement patches do not exist when following best practices for community analysis. Specifically, the differences represented in Figure A.3.1 and A.3.2 are primarily a function of including strata totals in the community matrix. When strata are removed from the community matrix, the differences between plot types are significantly reduced (Figure A.3.3, Table A.3.1). In the final analysis, we chose to remove rare species (species occurring in <5% of plots, Figure A.3.4). Removing rare species dilutes the noise in community datasets and enhances the ability to detect relationships between community composition and environmental gradients (McCune and Grace 2002), while preserving the relationship between plot types (Figure A.3.3 and A.3.4).

Our assessment indicates that including strata totals in the community matrix distorts NMS ordinations and potential interpretations of MRPP results. The chance corrected within-group homogeneity (A statistic), a measure of effect size generated by MRPP, differed by a factor of six between different approaches (Table A.3.1). Although including strata totals underscores the structural differences between fire refugia and stand-replacement patch plots, strata totals confound these statistical approaches and preclude specific research questions about differences in community composition. As such, including strata enhances the inherent structural differences between plot types in our dataset, differences that our sample design explicitly addresses and assessed with other descriptive metrics and analyses. As shown here, including strata totals and not relativizing by species could lead to the spurious inference that fire refugia support understory plant communities that are substantially different from those in stand-replacement patches (Table A.3.1).

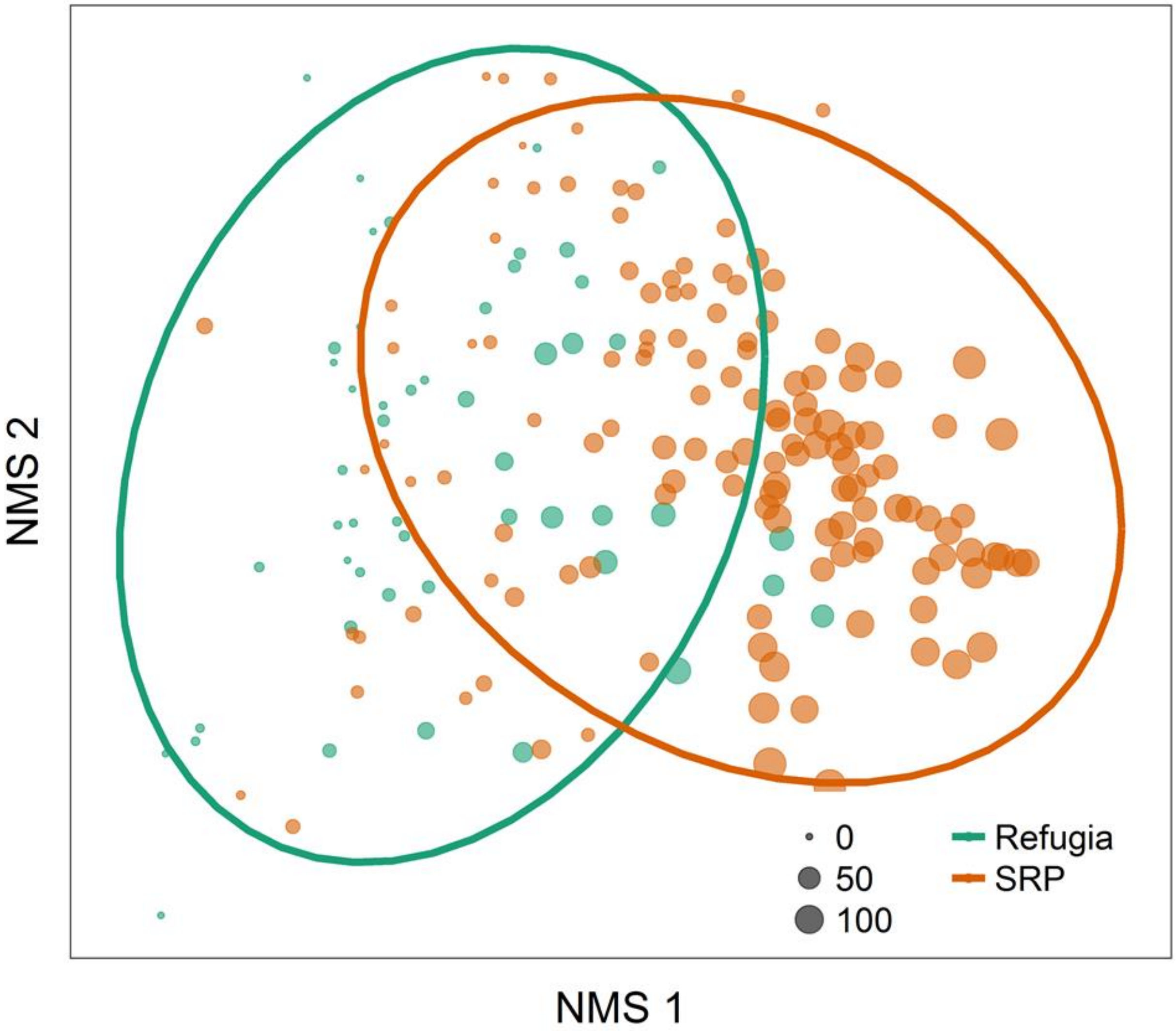


Figure A.3.1. Fire refugia (Refugia) and stand-replacement patch (SRP) plots ordinated in species space. The community matrix included all species and three strata (186 plots x 293 species + strata totals). The size of points represents the percent cover of shrubs in each plot. The difference between plot types appears relatively strong.

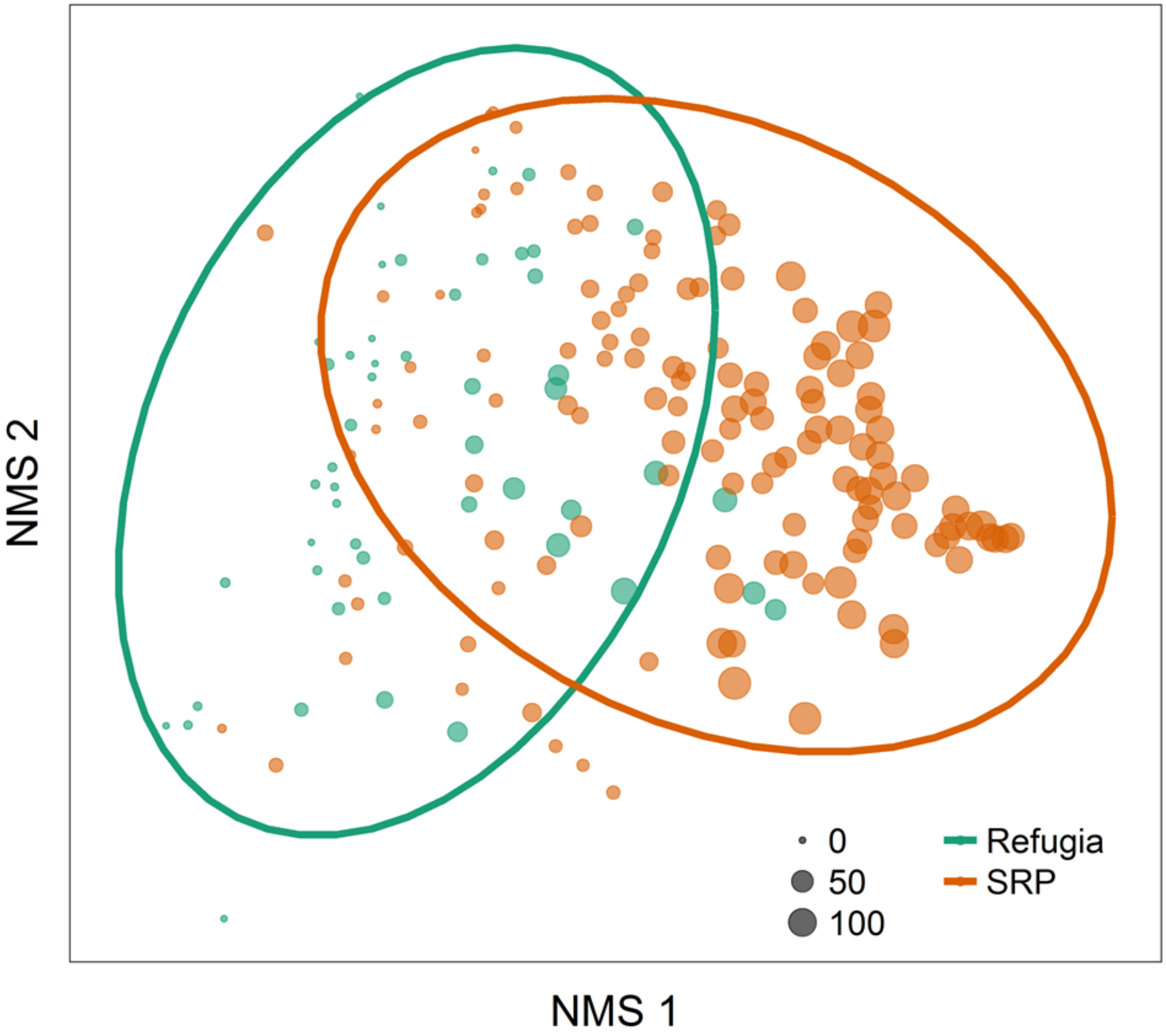


Figure A.3.2. Fire refugia (Refugia) and stand-replacement patch (SRP) plots ordinated in species space. Species occurring in fewer than 50% of plots (<90) were removed and strata were included in the community matrix. Little apparent difference between ordination results in Figure A.3.1 after removing 288 species from the analysis. Removing species that occurred in fewer than 50% of plots (<90) left 5 species, approximately 2.5% of the original 293 species. The species retained in the community matrix were *Ceanothus velutinus*, *Achillea millefolium*, *Epilobium angustifolium*, *Calamagrostis rubescens*, and *Carex geyeri*, along with the three strata totals (186 x 8). The size of points represents the percent cover of shrubs in each plot. The difference between plot types appears strong. Ordination results are virtually indistinguishable from Figure A.3.1 in which all species were included.

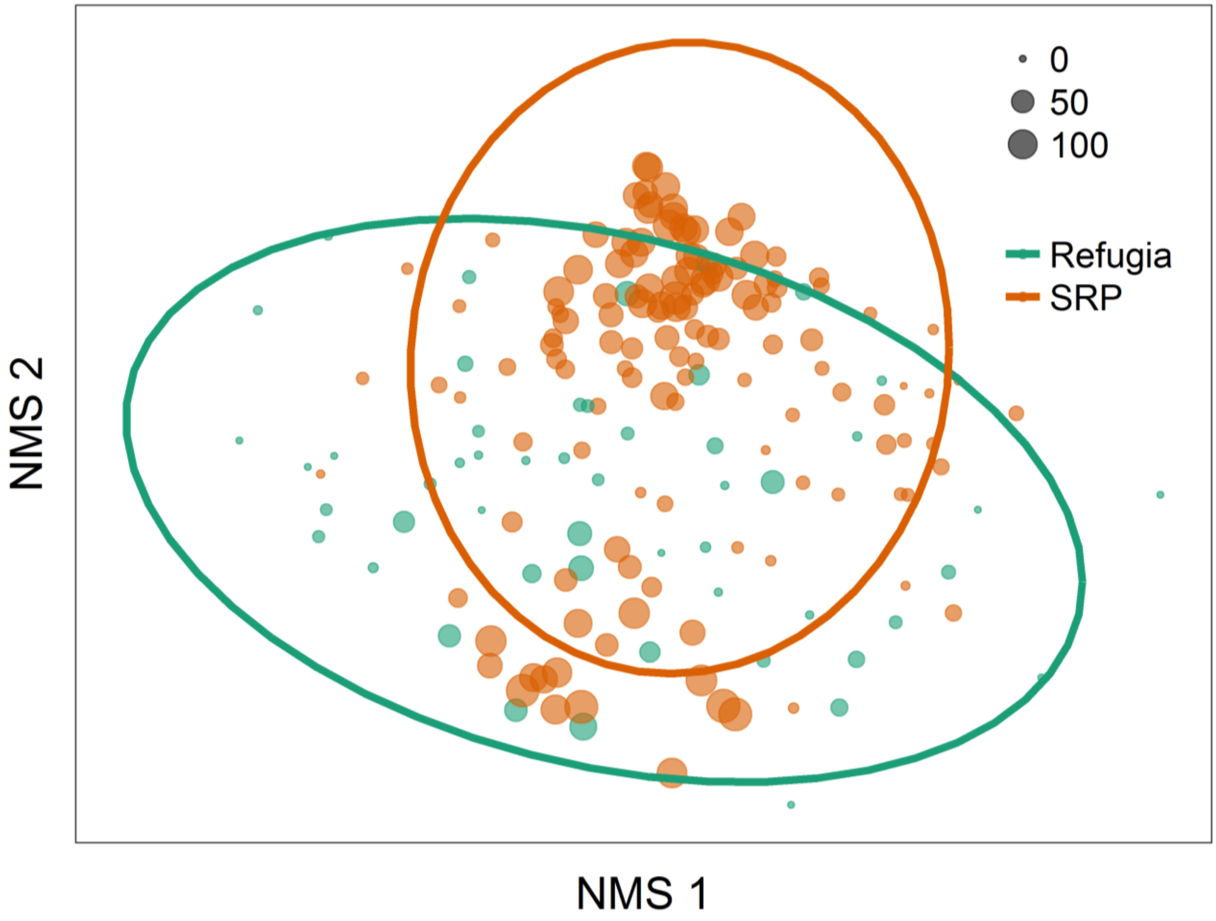


Figure A.3.3. Fire refugia (Refugia) and stand-replacement patch (SRP) plots ordinated in species space. The community matrix contains unrelativized cover data for all species (186 x 293). Strata are not included in the community matrix. Ordination results are substantially different from Figure A.3.1 and A.3.2 after removing strata from the community matrix. The size of points represents the percent cover of shrubs in each plot. The difference between plot types is considerably weaker than it appears in Figures A.3.1 and A.3.2.

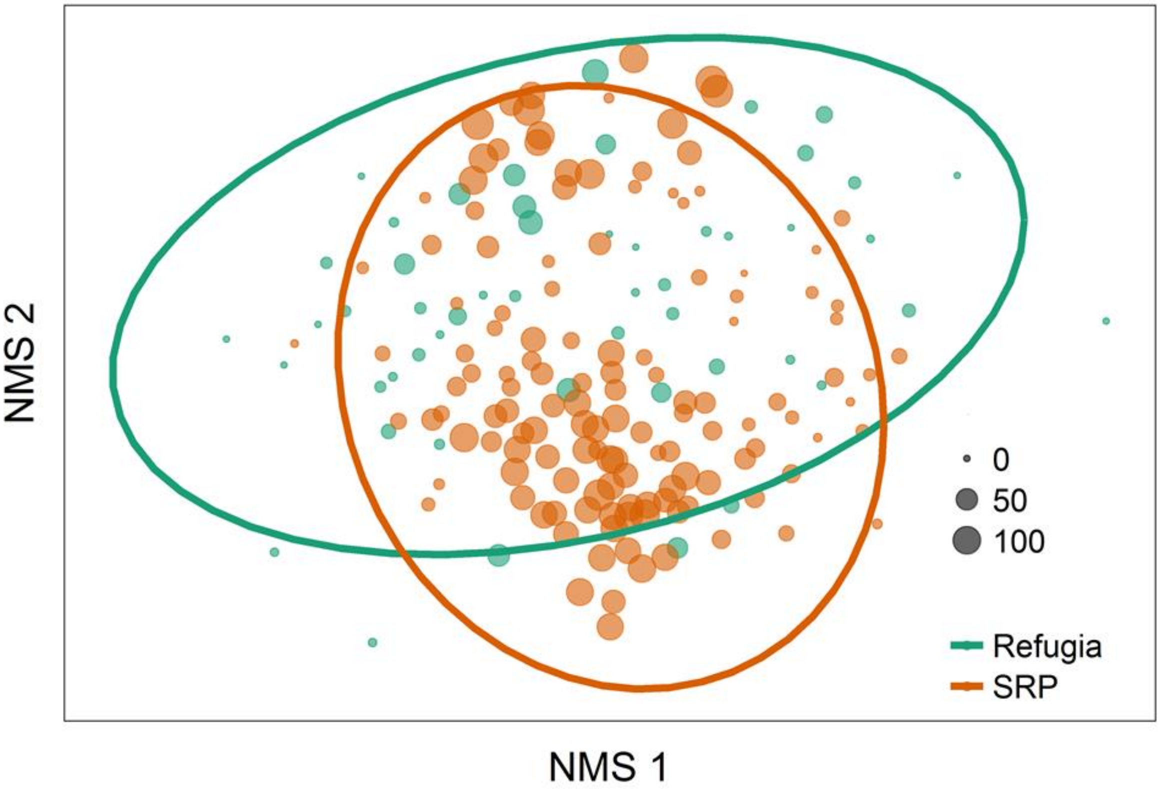


Figure A.3.4. Fire refugia (Refugia) and stand-replacement patch (SRP) plots ordinated in species space. The community matrix contains cover data relativized by species maximum, and rares have been removed (186 x 84). Strata are not included in the community matrix. The size of points represents the percent cover of shrubs in each plot. This ordination was used in the final analysis and interpretation, prior to rotation.

Table A.3.1. Comparison of MRPP results with different approaches to preparing the community matrix. Including strata in the community matrix increases the difference between plot types (higher A statistic) by as much as a factor of six (0.013 - 0.081). The A statistic represents the "effect size" of the difference between plot types (refugia, stand-replacement patches). In community ecology, statistically significant A values are commonly below 0.1, and an A > 0.3 is considered fairly large (McCune and Grace 2002).

Community Matrix	**Figure**	**p value**	***A***
Unrelativized (186 plots x 293 species + strata totals)	A.3.1	0.001	0.056
Unrelativized (186 plots x 5 species + strata totals)	A.3.2	0.001	0.081
Relativized (186 x 293)	A.3.3	0.001	0.025
Relativized (186 x 84)	A.3.4	0.001	0.013