Title

Post-wildfire forest recovery and land management in the Sierra Nevada, CA, USA

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Publication Date

2022

Peer reviewed|Thesis/dissertation

Post-wildfire forest recovery and land management in the Sierra Nevada, CA, USA

By

TARA LISA URSELL

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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Committee in Charge

2022

Acknowledgements

I am so grateful to the many people who helped me complete this dissertation and succeed as a graduate student at UC Davis.

First, Hugh Safford and Jim Sanchirico were instrumental as my PhD advisors. Hugh's vast knowledge about forest management in California has shaped my thinking and helped me ask questions that are important for both science and practice. Jim has always been willing to talk technical details with me, and I have learned so much from him about the research process, including how to analyze data systematically. I especially appreciate his total willingness to talk forest ecology with me!

Mark Schwartz was very generous with his time as a qualifying exam and dissertation committee member. I really appreciate his critical thinking about my studies, and his comments helped me to vastly improve my study design (Ch 1) and writing (esp. Ch 2 and 3).

Jenny Gremer also went above and beyond in helping me with my dissertation proposal. Emilio Laca very gamely agreed to help out with my QE committee and I'm so grateful for that. I also enjoyed working with Susan Harrison for my qualifying exam, but more than that I enjoyed working with her as a TA for ESP 100. I learned something new even on the 4th year of watching her lectures!

Lab meetings certainly made research more fun. Thanks so much to the Safford lab for the good times and for all of the advice (and commiseration) on field work and data analysis. I also learned a ton from attending NatuRE Policy meetings, so I thank that group for indulging me as a GGE interloper. Last, thank you so much to the members of SeverityFest – the least official but perhaps most useful study group of my time at UC Davis. I appreciate the camaraderie but also the focus and dedication that we all brought to our discussions.

Special thanks to the SLG for keeping me sane over the years. Many thanks to all of my friends and family who provided support, joy, and love during this time. I am grateful to my parents for supporting me, both emotionally and with homecooked meals and baked goods. Sonya has provided

much-needed comic relief over the years, and some of my best writing was also done in her and Abhishek's cozy sunroom. Last and definitely not least, I am so grateful to my husband, Derek, for his help, support, and friendship. As a brilliant forest ecologist, he could have done everything I did, but better. Having his insights and second opinion helped me feel more confident with my work. I'm so grateful to him and for everyone else who's given me the encouragement and courage to do this.

Abstract

Forests in California face numerous anthropogenic disturbances, several of which are contributing to changes in wildfire regimes. Climate change is leading to hotter and drier conditions, and fire suppression has led to the densificiation of forests and associated increases in flammable biomass. Both factors have been changing the weather and fuel conditions driving wildfires. In yellow pine and mixed conifer forests, contemporary wildfires are leading to much larger areas of very high tree mortality than the conditions to which those forests are adapted. This has comprised regeneration processes in this system, as conifer recruitment depends on the dispersal of seeds from nearby live trees. To address these challenges, land managers can accelerate forest recovery through practices like reforestation.

I investigated three facets of forest management in yellow pine and mixed conifer forests of California. First, I performed an observational study investigating whether planting small forest stands has spatially and temporally broader effects on tree recruitment. Second, I investigated whether shrub removal accelerates forest recovery through a field study as well as through longer-term simulations. Last, I investigated the longevity of standing dead trees and whether their availability over time meets land management objectives. Collectively, this dissertation addresses several facets of post-wildfire management that are ultimately centered on how land management affects ecological processes and forest recovery.

Contents

Introduction

Fire-adapted forests in California (and the western United States more broadly) face numerous anthropogenic disturbances. Climate change is leading to hotter, drier seasons with longer snow-free periods (Abatzoglou and Williams 2016; Westerling 2016). Land managers and fire-fighting agencies have prioritized fire suppression management practices, which has led to the "densification" of forests (McIntyre et al. 2015). These factors have changed the weather and "fuel" (flammable biomass) conditions driving wildfire patterns: fires under modern conditions are burning over larger areas and at higher severities, both compared with pre- Euro-American settlement conditions and increasingly in the past few decades (Mallek et al. 2013; Steel et al. 2018; Parks and Abatzoglou 2020). Thus, many fire-adapted forest and shrublands are currently experiencing wildfire regimes that are of different frequencies and severities than those to which they are adapted (Mallek et al. 2013).

These changes are likely to influence long-term vegetation dynamics. Low- to mid-elevation pine-dominated and mixed conifer forests in California are adapted to frequent, low-to-moderate fire severities (a metric that refers to vegetation change – often the amount of overstory tree mortality; Morgan et al. 2014), which translates to reproductive trees being relatively available across the landscape to act as seed sources for regeneration. This is essential for conifer species in these ecosystems, which do not resprout or have a seed bank and therefore recruit from live trees each year (Safford and Stevens 2017). The increasing "core areas" of high tree mortality after wildfires (Steel et al. 2018) compromise these processes and may lead to wildfire-driven type conversion if trees are unable to disperse into and grow in previously forested areas (Coop et al. 2020).

In addition to the indirect anthropogenic drivers of forest change mentioned above (climate change, fire suppression), land managers can also directly influence ecological processes. For example, they can mimic natural ecological processes (e.g., forest thinning or prescribed burning), remove stressors (e.g., invasive species control), and remove barriers to establishment (e.g., fertilizing, seeding or planting). In the context of post-wildfire conditions, tree planting can enable establishment in seed-limited

systems and may be appropriate where seed limitation is due to large-scale, high-severity fires. In USDA Forest Service lands this management goal is consistent with their broad mandate to maintain forested lands "in appropriate forest cover" (National Forest Management Act 1976). The mandate specifies that management plans direct reforestation toward areas that have been "cut-over or otherwise denuded or deforested" (National Forest Management Act 1976)–historically focusing on harvested areas but now potentially applying to regions affected by wildfire (Dumroese et al. 2019). From 2010-2020, over 3400 hectares of Forest Service lands in California were planted (USDA Forest Service 2022, Ursell 2022).

Planting is often done in combination with other types of forest management: a typical sequence is salvage logging (to clear hazards and large fuels); site preparation (to clear smaller dead fuels and other vegetation); the control of competing vegetation (hereafter "CCV") by either manual, mechanical, or chemical means; and additional thinning and pruning treatments, such as pre-commercial and commercial thins (Tappeiner et al. 2007). On wildfires that burned from 2010 to 2020, 62 percent of areas planted were salvage-logged beforehand, 62 had some form of site preparation activities, and 54 percent had post-planting control of competing vegetation (Ursell 2022). Given the scale of post-wildfire planting needs, there is increased interest in refining management practices to meet this need (see e.g., North et al. 2019; Stevens et al. 2021).

This dissertation was inspired by efforts to rethink land management practices in new ecological contexts. In Chapter 1, I performed an observational study of planted forest stands to investigate whether they can serve as "nuclei" that enable additional tree recruitment and forest expansion away from the planted sites. This has been proposed to accelerate forest recovery, particularly in areas that are difficult to plant directly. In Chapter 2, I investigated the ecological outcomes of treatments to remove competing vegetation: first, I investigated effects of these treatments on forest structure in the short term, as apparent through an observational field study. I then used a simulation approach to model the longer-term outcomes of these field plots. Chapter 3 addresses standing dead trees ("snags") on the landscape. Removing snags is often done for cost recovery, but it is also often a pre-condition for planting due to

worker safety. Yet snags are also valuable habitat for many wildlife species and serve many other important ecological roles. This last chapter assesses the longevity of snags as well as their availability in the post-wildfire landscape. Collectively, this dissertation addresses several facets of post-wildfire management that are ultimately centered on how land management affects ecological processes and forest recovery.

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Chapter 1: Nucleation sites and forest recovery under high shrub competition

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A version of this chapter is published in Ecological Applications (https://doi.org/10.1002/eap.2711)

Abstract

Forests currently face numerous stressors, raising questions about processes of forest recovery as well as the role of humans to stimulate recovery through planting trees that might not otherwise regenerate. Theoretically, planted trees can also provide a seed source for further recruitment once the planted trees become reproductive, acting as "nucleation" sites; however, it is unclear whether changing site conditions over time (e.g., through the growth of competitors like woody shrubs) influences establishment in the long term, even if seed availability increases. We tested the nucleation concept in a system where shrub competition is known to influence tree establishment and growth, performing an observational study of sites within and close to newly reproductive planted stands in yellow-pine and mixed-conifer ecosystems in the Sierra Nevada, CA. We surveyed and then modeled both seedling occurrence and density as a function of distance to seed sources, competing woody vegetation, and other environmental characteristics. We found that proximity to a planted stand is associated with an increase in the probability of yellow pine (YP) seedlings (species more likely to originate from the planted stand) from 0.33 at 35 meters from the planted stand to 0.56 directly adjacent to the stand and 0.65 within the stand. However, we did not find a significant effect of proximity on YP seedling density. This proximity effect suggests that seed availability continues to be a driver of recruitment several decades post-wildfire, though other processes may influence the expected density of recruits. Proxies for competitive pressure (shrub volume and shrub cover) were not significant, suggesting that competing vegetation did not have a major influence on recruitment. While seedling presence and density appeared to be independent of shrub

impacts, we did find that shrubs were significantly taller than seedlings. Therefore, we suggest that shrubs may not limit seedling establishment, but they may negatively affect seedlings' ability to grow and serve as a seed source for further recruitment and forest expansion. Altogether, we find that planting may provide a statistically significant but small role in driving recruitment outside of the planted site.

Introduction

Understanding patterns and drivers of forest recovery has become increasingly pressing as forests face mounting threats from deforestation, pests and disease, wildfires, and climate change broadly (Curtis et al. 2018, Kautz et al. 2018, Wees et al. 2021, Seidl et al. 2017). Given the array of ecosystem services that forests provide, reforestation and forest restoration have become key priorities in public, private, and social sectors (see initiatives cited in Holl and Brancalion 2020 and Di Sacco et al. 2021). This enthusiasm for large-scale forest planting and management raises questions about scalability, potential scope, and long-term outcomes of these forest management interventions (see e.g., Holl and Brancalion 2020). We investigated some of these questions in the context of reforestation in the Western United States, focusing primarily on post-wildfire systems that may prompt this kind of active forest management.

In semi-arid pine-dominated and mixed conifer systems of the Western U.S., successful conifer regeneration is influenced by interactions between seed production (masting), dispersal, precipitation patterns, and the availability of suitable substrates (Donato et al. 2009, Keyes and Manso González 2015, Haffey et al. 2018, Stevens-Rumann and Morgan 2019). Before fire exclusion beginning in the late 19th Century, low and moderate severity burning was frequent and pervasive, and pine regeneration was promoted by the widespread availability of bare mineral soil and high light incidence at the soil surface (Safford and Stevens 2017, van Wagtendonk et al. 2018). Recently, however, stand densification and fuel accumulation driven by a century of fire exclusion as well as anthropogenic climate change have led to major changes in wildfire behavior, with fires growing larger and more "severe" (characterized as having a greater amount of change in vegetation and/or soils; see Morgan et al. 2014) on average (Parks and

Abatzoglou 2020). Large, contiguous areas of very high, fire-associated tree mortality have become common in much of the Western United States (see e.g., Steel et al. 2018); such high-severity patches are inimical to regeneration of non-serotinous conifers as they contain very few – if any – surviving trees and unburned areas that might serve as seed sources for future generations. Accordingly, it is unclear whether tree regeneration in these landscapes will be sufficient to maintain forest cover in the future (Coop et al. 2020).

Planting trees effectively removes dispersal limitation and can enable tree establishment in the absence of nearby surviving or unburned reproductive trees ("seed trees"). However, this strategy is difficult to implement at broad scales: appropriate genetic stock must be collected and grown in a nursery, sites must be accessible and safe for planting crews (e.g., close to roads, walkable terrain, clear of hazards – potentially including standing dead trees), and funding and staff must be available for all of these steps (Tappeiner et al. 2007, Fargione et al. 2021). In Region 5 of the Forest Service (principally California), for example, conifer planting over recent decades has rarely exceeded 12,000 ha (R. Rojas, USDA Forest Service, pers. comm.), but the area of burned forest warranting planting intervention in recent years has often been 5-10 times greater. Given the scale of the need as well as the hurdles involved in widespread planting, one proposed alternative is to plant small "founder stands" to grow and eventually serve as seed sources for the surrounding region (North et al. 2019).

The idea of strategic planting to achieve broader landscape restoration is closely associated with concepts of "applied nucleation" that have been investigated in other ecological contexts. "Nucleation" describes the process by which early-arriving individuals establish and serve as a focal point for other species to coalesce, eventually creating patches that expand and contract in size as successional processes proceed (Yarranton and Morrison 1974). In an applied context, planting these "nuclei" can accelerate the establishment of a more heterogeneous forest or woodland ecosystem by attracting animal dispersers, serving as an aggregation point for wind-dispersed vegetation, or otherwise creating appropriate conditions for a more diverse set of tree species (Rey Benayas et al. 2008, Corbin and Holl 2012). While

there has been empirical support for the use of planted nuclei to accelerate the creation of later-successional forest structure, it is less clear whether nuclei lead to a substantial expansion from the original site. Existing studies in tropical forest sites have found some recruitment in areas immediately surrounding a planted stand (1 meter: Zahawi and Augspurger 2006; 6 meters: Holl et al. 2020). In other studies that assessed recruitment farther from planted stands, recruitment extended fairly equally over a wider space – likely reflecting dispersal syndromes that promote travel outside of the immediate vicinity of the planted individual (e.g., lightweight, wind-dispersed seeds; Corbin et al. 2016) as well heavier seeds dispersed by highly mobile animal dispersers (Rey Benayas et al. 2015, Corbin et al. 2016). Such cases may not apply to systems where distance is a strong predictor of regeneration success, such as in yellow pine and mixed conifer forests (collectively, "YPMC"). We are not aware of any applied nucleation studies in this system.

In YPMC forests, distance to seed trees is a key predictor of regeneration success. This has been shown in several post-fire studies, with conifer regeneration decreasing as distance to surviving seed trees increases in landscapes sampled within a few years post-wildfire (Welch et al. 2016, Shive et al. 2018, Stevens-Rumann and Morgan 2019). Dispersal kernels also have been evaluated in post-harvest landscapes, where gap studies show that seed availability is correlated with proximity to forest edges (McDonald 1980).

In addition to seed availability, changes in vegetation that occur in the years following disturbance have relevant associations with future regeneration and should be considered in nucleation or founder stand reforestation strategies. Depending on the environmental context and species mix, co-occurring shrubs can have facilitative or competitive impacts on seedlings. Facilitative relationships particularly have been found in lower-elevation, sun-exposed, and drier sites or years compared with higher-elevation, shaded, and wetter conditions (Gómez-Aparicio et al. 2004)—a finding that is consistent with theory that predicts more positive interspecific interactions under stressful abiotic conditions (Bertness and Callaway 1994).

In YPMC forests, competition is the dominant paradigm used to explain seedling interactions, with the quick regeneration and recruitment of shrub species (such as Arctostaphylos spp. and Ceanothus spp.) after wildfires potentially inhibiting forest recovery (North et al. 2019). Shrub competition can reduce the growth and survival of trees, particularly among shade-intolerant pine species (McDonald and Fiddler 2010, Tubbesing et al. 2020, Airey Lauvaux et al. 2016). When shrubs are among the first to establish, the effects can be long-lasting: trees establishing later in chaparral patches can have persistent slow growth rates for 30 or more years until they emerge from the shrub canopy (Nagel and Taylor 2005, Airey Lauvaux et al. 2016). Therefore, many silviculturists choose to plant trees only immediately after disturbances and then only in conjunction with the removal of competing vegetation (Tappeiner et al. 2007).

Given the important role of proximity to seed sources as well as the role of shrub competition, we investigated the relative importance of these factors in the context of applied nucleation or founder stand reforestation. We performed an observational study of sites that had been planted 25-27 years prior and where we could evaluate regeneration patterns associated with the stand. We focused on two hypotheses:

- Dispersal limitation hypothesis: If seedling establishment is limited by seed availability, then we expected to observe greater densities of seedlings close to planted stands compared with areas outside of the planted stand's seed shadow.
- Competitive impacts hypothesis: If seedling establishment is limited by competing vegetation, then we expected to observe negative correlations between seedling density and shrub cover. While under some conditions non-tree woody vegetation can have a facilitative effect, we felt that existing empirical work in similar ecosystems favored a hypothesis that included negative interactions between the plant forms.

These hypotheses evaluate both seed availability and one important axis of site suitability (interactions with other woody plant forms) as potential drivers of plant regeneration. In testing these, we aimed to evaluate a specific proposed land management practice, the application of nucleation concepts

through the planting of “founder stands”, as well as develop insight into the relative role of these constraints in a period relatively late in the post-disturbance trajectory.

Methods

Study design

To address our hypotheses, we characterized tree regeneration in plots that varied in distance to planted stands as well as in shrub competition. We surveyed plots in planted stands that were 25-30 years old – old enough to have been reproductive for several years to account for intra-annual variation in seed production, but young enough to ensure that the focal seedlings (those originating from planted trees) could be aged by counting bud scars (Hankin et al. 2018). We also sampled in areas that had a well-defined boundary between planted and unplanted areas, with planted areas visually identifiable due to containing a single-aged cohort in a grid configuration. We sampled in areas that did not have an observable difference in substrate that explained the planting perimeter: in one location (SNF), planting boundaries had been established for an unrelated research purpose rather than due to reforestation needs; the second location (ENF) spanned an ownership boundary, with early reforestation on one side and no management on the other side; and for a third location (TNF), we determined through site visits that there was likely no difference between planted and unplanted areas. Two of the sites were planted post-fire (SNF, ENF), and we included the TNF site because 1.) there was a clear and seemingly arbitrary planting boundary that was suitable for testing nucleation processes, and 2.) we believed based on the presence of coarse woody debris and forest designations on available land cover map products (U.S. Forest Service 2019) that the region historically supported trees. We also restricted sampling to locations that had a minimal number of nearby large trees, as our aim was to characterize regeneration associated with planted trees specifically; we later confirmed through an RdNBR-based severity analysis that all ENF plot areas and 94% of the SNF plot areas burned at high severity (Miller and Thode 2007) and largely burned at high severity within 100 meters of the plots. Table 1.1 and Figure 1.1 provide detail on the location,

climate, management history, and fire history of these sites. We analyzed 87 plots within these three locations.

Location and Coordinates	Elevation	Vegetation+	Site History	# of Transects
Eldorado National Forest (ENF) 38.7872, −120.4308	1409-1437 m	Ponderosa Pine (PPN), Montane Chaparral (MCP)	Burned in Cleveland Fire (1992) Within plot area: - 100% High Severity++ Within 100m of plots: -94% High Severity -6 % Moderate Severity	6
Sierra National Forest (SNF) 37.2150, −119.2572	1593-2301 m	Jeffrey Pine (JPN), Ponderosa Pine (PPN), Sierran Mixed Conifer (SMC), Montane Chaparral (MCP), White Fir (WFR)	Burned in Big Creek Fire (1994) Within plot area: -94% High Severity -6 % Moderate Severity Within 100m of plots: -89% High Severity -11 % Moderate Severity	11
Tahoe National Forest (TNF) 39.4028, −120.0661	1930-1960 m	Eastside Pine (EPN), Sierran Mixed Conifer (SMC), Montane Chaparral (MCP)	Unknown; no fire apparent. Likely planted ca. 1990.+++	6

Table 1.1 Locations for data collection, along with site, vegetation, and management characteristics.
+ Dominant vegetation is characterized using the California Wildlife Habitat Relationship (WHR) classification scheme as reported in the USDA Forest Service's EVeg map product (U.S. Forest Service 2019)
++ Fire severity is characterized according to methods published in Miller and Thode (2007) and with severity map products published by the U.S. Forest Service (2018).
+++ Trees in this area were almost exclusively Pinus jeffreyi and followed a grid pattern typical of planted stands. Management records indicate that the area received a "release" treatment typical of early plantations in 1991 ("Forest Service Activity Tracking System (FACTS)" 2018)

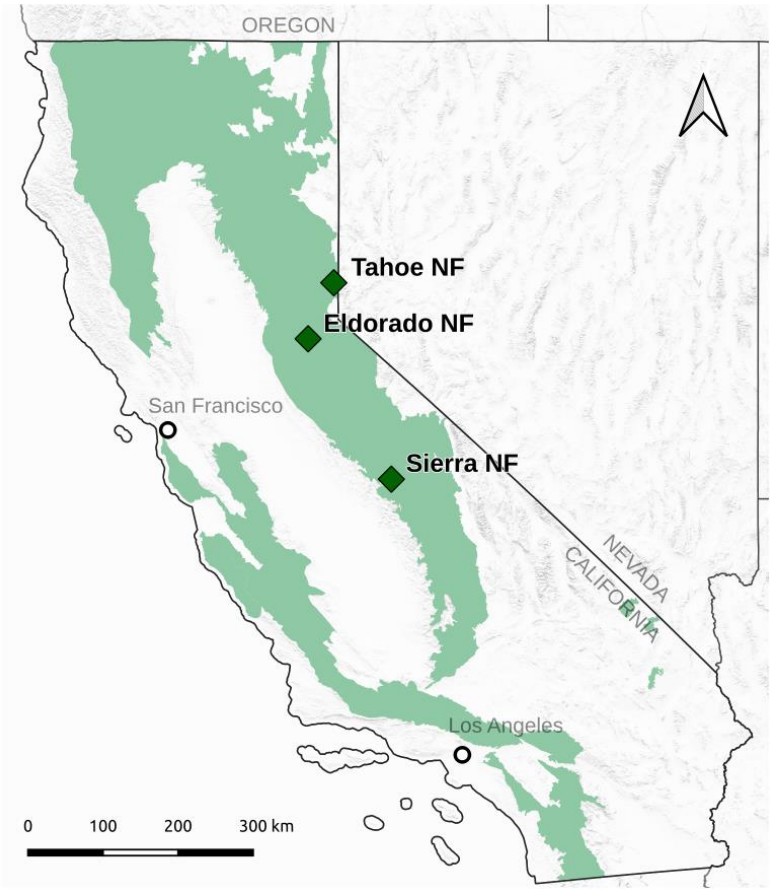

Figure 1.1. Locations for data collection, produced using a USGS shaded relief base map (U. S. Geological Survey - National Geospatial Program 2020) and overlaid with a vegetation range map that includes California Wildlife Habitat Relationship (WHR) classes found at the study sites and as reported in the USDA Forest Service's EVeg map product (U.S. Forest Service 2019a, 2019b). Montane chaparral (MCP) has been excluded because it extends to much lower-elevation sites and likely is not representative of the potential range of our focal conifer species.

Data Collection

We sampled plots along transects that bisected the boundary between planted and unplanted areas: one plot center was located 15m into a planted stand, the second plot center was 10m outside of the planted stand, and each subsequent plot center was 25 m further out. We used a variable plot size, defaulting to sampling within a 10m-radius circular plot but shrinking the sampling area to 8-, 6-, 4-, or 2-meter radius plots if regeneration was dense; we aimed to sample about 10 seedlings per species per plot.

We sub-sampled on a species-by-species basis, and in most cases, we sampled the full 10-meter radius plot. For all plots, we later multiplied counts by a multiplicative factor to express them per 10-m radius plot and per hectare for comparison with other studies.

At each plot, we characterized regeneration by identifying each conifer tree to species, measuring its current height and prior year's height (seedlings, saplings), measuring its diameter at breast height ("dbh"; only for trees), and counting terminal bud scars to estimate age (all). We categorized trees as individuals > 3 cm dbh, saplings as individuals < 3 cm dbh but taller than 1.4 m, and seedlings as individuals < 1.4 m height. Several of our plots had a fairly broad range of seedling ages due to natural regeneration from existing large trees (e.g., trees that survived the wildfire). Though we attempted to sample in areas that had few large seed trees (e.g., high-severity areas in post-fire regions; see Table 1.1 for fire severity summaries), such trees were still present in the broader landscape and potentially contributed seed rain to all plots. Hereafter, we refer to them as "Large Tree Seed Sources" (LTSS).We focused our analysis on trees that were 10 years old or younger in light of the potential influence of natural regeneration, thereby evaluating the establishment patterns of seedlings that plausibly could have come from the planted stand (based on expected ages of reproductive maturity). Hereafter and particularly for the statistical analysis and results, we refer to these as "seedlings" and the older individuals as "Other Natural Regeneration". We were unable to assess prior year's height or bud scar-age for Calocedrus decurrens due to its morphology; however, we did not observe this species in any of the planted stands and therefore did not consider it to be a focal species for our research question.

To evaluate the role of seed dispersal, we estimated proximity to seed sources from the center of the plot. First, the distance to planted trees was accounted for in the plot placement. Based on the dispersal patterns of the tree species common to YPMC–and particularly Pinus ponderosa and Pinus jeffreyi (hereafter aggregated as "Yellow Pine" or "YP"), which accounted for most of the planted trees – we expected seed rain to occur in the plot within the planted stand and just adjacent to the planted stand. This expectation was informed by the height of the planted trees (average height of YP: 9 m; data not

shown) and prior work showing that most seed falls within 1.5 times the height of the average dominant tree (in this case, within 13.5 m) (McDonald 1980). However, we continued to sample farther from this expected range to account for potential longer-distance dispersal. Second, we accounted for the distance to LTSS. From each plot, we used a laser rangefinder to measure the distance to the nearest three individuals or clumps of trees for each species, up to a distance of 500 meters (corresponding to the technical limits of our rangefinder). We then aggregated these by multiplying the inverse of the distance by the number of individuals at that distance, and then we summed across the three individuals or clumps; this index represents the potential seed rain by species in that higher values indicate more seed potentially arriving to the site, and it accounts for the potential of seed rain from multiple sources. Last, we accounted for natural regeneration that was functionally similar to planted trees (hereafter "Natural Regeneration Seed Source (NRSS)"). These trees were of similar size and age to planted trees but were inconsistent with the regular grid and/or planting boundary that characterized the planted stand; we assume that they likely germinated as natural regeneration from nearby large trees. We used the same index method to account for the potential seed contribution of these trees.

We also characterized competing vegetation and other site characteristics at the plot scale. For shrub competition, we assessed the percent cover and modal height of all woody, non-tree species, and we generated species-level estimates for the three most abundant species and any species with > 10 percent cover. In our analysis, we tested the effect of shrub percent cover as well as an index of shrub volume, which we computed by summing the percent cover multiplied by height across shrub species meeting our threshold ("Shrub Volume"). To account for tree competition, we assessed the percent cover and height of overstory trees within the plot. In our analysis, we also accounted for intra- seedling/sapling competition by controlling for the density of individuals older than 10 years in each plot ("Other Natural Regeneration"). We accounted for the availability of suitable substrate by estimating percent cover for the following ground cover categories: large rocks and bedrock (>0.5 m in shortest dimension); cobbles and

stones (75-500 mm); litter, bare soil, and small rocks (<75 mm); basal vegetation; and woody debris. We also collected data on elevation, slope, and aspect at the plot scale.

Statistical Analyses

We fit a binomial generalized linear mixed model to predict whether seedlings would occur in a given plot, and we used a negative binomial generalized linear mixed model to predict the densities at each plot. We analyzed these data in R 3.6.3 using the glmmTMB (Brooks et al. 2017) and lme4 packages (Bates et al. 2015). We fit a minimum model that included hypothesized mechanisms driving seedling establishment (seed rain from planted and surviving trees, as well as shrub competition) and a random intercept to account for the nested plot structure within transects. We added other explanatory factors (ground cover, overstory cover, abiotic site characteristics) if they improved the model fit based on an AICc comparison.

We focused our analysis on the yellow pines (*Pinus ponderosa* and *Pinus jeffreyi*) because the vast majority of trees planted were of these species. While we observed single planted individuals of other species (e.g., *Pinus lambertiana*, *Pseudotsuga menziesii*) within some of the planted stands, there were not enough individuals – and not close enough to the planted edge – for us to assess seed rain from those particular species. However, we also analyzed regeneration of all species aggregated together in order to evaluate whether proximity to planted stands engenders a broader edge effect in terms of enabling recruitment from large surviving trees.

Results

We analyzed the presence and density of conifer seedlings as associated with proximity to seed sources – stratified across distances to nearby, reproductive planted stands – and as associated with other potential drivers of regeneration success such as shrub competition, competition from other seedlings and saplings, and environmental characteristics (Table 1.2). Seedling counts were very low in most plots, with

median counts of 0 or 1 in all three locations but with counts as high as 375 at our highest-density plot. Table 1.3 provides summary statistics for seedling counts, shrubs, and LTSS.

	Presence (YP)		Density (YP)	
Predictors	Log-Odds	p	Log-Mean	p
(Intercept)	0.64 (-0.30 – 1.57)	0.183	0.48 (-0.26 – 1.21)	0.201
Distance from planted stand (m)	-0.04 (-0.07 – -0.01)	0.011	-0.01 (-0.03 – 0.01)	0.383
Shrub Volume	-0.29 (-1.03 – 0.46)	0.452	-0.63 (-1.31 – 0.04)	0.067
Other natural regen (density)	0.93 (-0.22 – 2.09)	0.113	0.86 (0.25 – 1.47)	0.006
Large trees seed source (index)	0.53 (-0.23 – 1.28)	0.172	0.35 (-0.18 – 0.89)	0.199
Nat. Regen seed source (index)	-0.10 (-0.69 – 0.49)	0.748	-0.08 (-0.55 – 0.38)	0.721
Random Effects				
σ2	3.29		1.35	
τ00	1.01 transect		0.65 transect	
ICC	0.24		0.32	
N	23 transect		23 transect	
Observations	87		87	
Marginal R2 / Conditional R2	0.361 / 0.511		0.479 / 0.648	

Table 1.2. Model results for probability of observing ("presence" columns) and density of yellow pine seedlings.

Loc and dist. to planted stand	YP Seedlings (Count)		All Seedlings (Count)		Shrub % Cover	Shrub Volume	YP Prefire Trees (Index)	Prefire Trees (Index)
	Mean (SD)	Med	Mean (SD)	Med	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
ENF								
0	2.2 (2.4)	2	3.3 (3.4)	3	44.7 (34.4)	313.7 (316.7)	0.008 (0.002)	0.008 (0.002)
10	0.5 (1.2)	0	1.2 (1.6)	0.5	95 (8.4)	1199.5 (598.5)	0.009 (0.002)	0.009 (0.002)
35	0.6 (0.9)	0	1.2 (2.2)	0	100 (0)	1200.4 (483.2)	0.011 (0.002)	0.011 (0.002)
60	0.2 (0.4)	0	0.2 (0.4)	0	99 (2.2)	1202.8 (394.6)	0.013 (0.003)	0.013 (0.003)
SNF								
0	4.8 (4.7)	3.9	22.6 (54.6)	6	15.7 (16.3)	67 (72.4)	0.094 (0.077)	0.166 (0.172)
10	23.5 (42.7)	1.9	96 (129.5)	28.6	35.8 (32.8)	169.2 (213.4)	0.029 (0.052)	0.088 (0.14)
30-35	9.5 (23.8)	0	45.5 (63.3)	1	54.7 (31.9)	283.3 (232.9)	0.039 (0.049)	0.125 (0.159)
50-70	9.2 (16.8)	0	19.3 (25.7)	5.7	58.7 (33)	303.7 (219)	0.051 (0.057)	0.131 (0.164)
TNF								
0	1.2 (1.2)	1	1.2 (1.2)	1	50 (7.1)	149 (47.7)	0.159 (0.087)	0.192 (0.101)
10	1.2 (1.2)	1	1.3 (1)	1	65.8 (9.2)	171.5 (64.2)	0.113 (0.051)	0.172 (0.067)
35	0 (0)	0	0 (0)	0	59 (23)	159.4 (82.3)	0.102 (0.018)	0.183 (0.103)
60	0 (0)	0	0 (0)	0	58.3 (16.1)	181 (96.6)	0.133 (0.064)	0.165 (0.084)

Table 1.3. Summary statistics of field data, grouped by location and distance to the planted stand.

Distance effects

We found that the probability of observing a YP seedling in a plot was negatively correlated with distance from the planted edge, with the mean model-predicted probability going from 0.65 within the plantation to 0.56 just adjacent to the plantation to 0.33 at a distance of 35 m from the planted stand edge (Figure 1.2). We did not observe a significant effect of distance on the density of YP seedlings. YP density (but not probability of occurrence) was also positively correlated with the density of other (larger) natural regeneration, likely reflecting plots that had a generally high amount of seed rain from large, surviving trees.

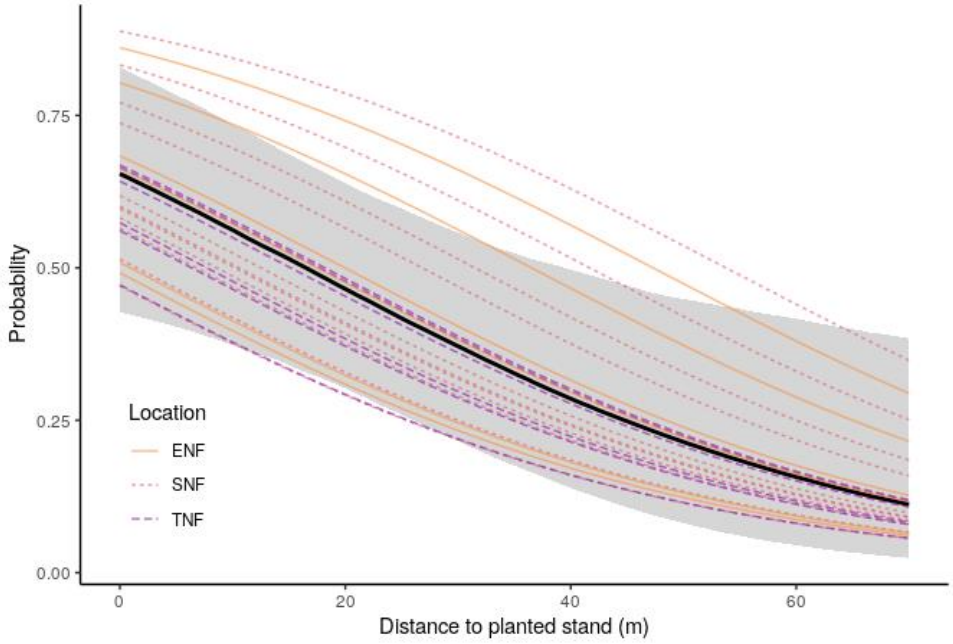

Figure 1.2. Predicted probability of YP seedling presence, based on distance to the planted stand and with all other variables held constant at their mean observed value. Relatively high seedling probabilities at relatively large distances from the planted stands (> 40m) likely reflect either long-distance dispersal from the planted stand or dispersal from alternate seed sources (LTSS and NRSS). Predicted probability is in black with a 95% confidence interval in gray. Transect-level predictions are included in color and varying linetypes to demonstrate variation between locations.

Shrub effects

We did not observe a significant effect of shrub percent cover or shrub volume in either of our models, though we did find that higher shrub volume was marginally associated with a decline in seedling density. For all models, we tested the effect of shrub percent cover as well as shrub volume. We found that they had very comparable effects in the models (data not shown), and therefore we retained the shrub volume estimate because it accounted for shrub height as well as horizontal spread.

Non-focal seedlings

We also analyzed the presence and density of seedlings of all conifer species (except *Calocedrus decurrens*; see above) in addition to our YP-only analysis. The purpose of the all-conifer analysis was to assess whether the presence of a planted stand could influence recruitment aside from being a seed source (e.g., provide edge effects like shelter or shading, or serve as habitat for seed dispersers or seed predators). We found largely similar effects compared with the YP-only model (Table 1.4). First, both probability and density of seedlings were correlated with proximity to the planted stand, with the probability going from 0.97 within the plantation to 0.93 just adjacent to the plantation to 0.62 at a distance of 35 m from the planted stand edge (Figure 1.3). Both presence and density of seedlings were correlated with the density of older natural regeneration. Shrub competition, as indicated by the percent cover or the volume of shrub species in the plot, was not significant in these models. Including the percent ground cover of litter also improved our density model, reflecting a positive correlation between available substrate and seedling establishment.

	Presence (all species)		Density (all species)	
Predictors	Log-Odds	p	Log-Mean	p
(Intercept)	3.35 (0.96 – 5.74)	0.006	0.98 (0.07 – 1.89)	0.034
Distance from planted stand (m)	-0.08 (-0.14 – -0.03)	0.003	-0.02 (-0.03 – -0.00)	0.021
Shrub Volume	0.15 (-0.81 – 1.11)	0.760	-0.43 (-0.95 – 0.08)	0.101
Other natural regen (density)	4.46 (-0.23 – 9.16)	0.063	0.65 (0.27 – 1.02)	0.001
Large trees seed source (index)	0.93 (-0.49 – 2.34)	0.199	0.22 (-0.33 – 0.77)	0.429
Nat. Regen seed source (index)	0.58 (-0.49 – 1.65)	0.288	0.10 (-0.25 – 0.46)	0.569
Ground cover: litter (pct)			0.37 (0.05 – 0.68)	0.022
Random Effects				
σ2	3.29		0.88	
τ00	4.01 transect		3.48 transect	
ICC	0.55		0.80	
N	23 transect		23 transect	
Observations	87		87	
Marginal R2 / Conditional R2	0.761 / 0.893		0.223 / 0.844	

Table 1.4. Models results for probability of observing ("presence" columns) and density of all conifer seedlings (except Calocedrus decurrens).

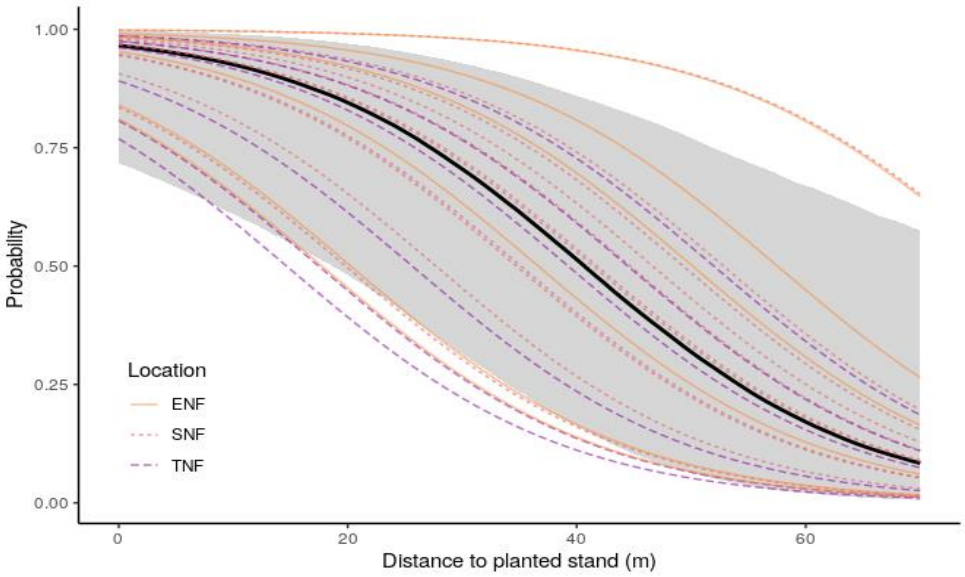

Figure 1.3. Predicted probability of seedlings (except C. decurrens), based on distance to the planted stand and with all other variables held constant at their mean observed value. Predicted probability is in black with a 95% confidence interval in gray. Transect-level predictions are included in color and varying linetypes to demonstrate variation between locations.

Disturbance history

We performed all analyses on all data as well as without TNF plots, as the latter were not postfire and therefore had a different disturbance history. All significant variables had coefficients within 20% and with the same slope direction in both datasets; the only exceptions were the non-focal-seedling intercepts, which was expected given our random intercept model structure, and ground cover in our non-focal density model. Model comparisons are included in Appendix 1.1.

Discussion

We surveyed conifer recruitment in the context of newly reproductive planted stands in order to evaluate the role of dispersal limitation and shrub competition in controlling seedling establishment. Our data provide some support for the dispersal limitation hypothesis: YP seedlings were largely found within the immediate vicinity of planted stands and dropped off substantially as distance from the stand

increased, suggesting that planted trees can serve as a seed source for future generations within a certain radius of the planted area. We observed this pattern in models of seedling presence but not density. It is possible that density is correlated with factors outside the scope of this study, such as the availability of microsites or the presence of animal dispersers, and thus was too variable to detect a significant relationship with proximity to a planted stand (Stevens-Rumann and Morgan 2019). While we focused on species that are known to be primarily wind- and gravity- dispersed, secondary dispersal may also play a role in this system, particularly for *Pinus Jeffreyi* (Vander Wall 2008). When we included other conifer species in our model (*Abies* spp., *Pinus lambertiana, Pseudotsuga menzesii*), we found that both presence and density were positively correlated with proximity. We interpret these findings to suggest that planted stands can not only serve as a seed source but also may increase the site suitability for seedlings of other species. Existing literature suggests that sites closer to forest edges may have more moderate microclimates (see e.g., Baker et al. 2014), which may especially be important for shade-tolerant species like *A. concolor* and *C. decurrens*. Applied nucleation theory would also suggest that animal dispersers may be attracted to forest patches, thereby providing a mechanism for dispersing species not common in the planted stand; however, this is unlikely given that the species found are primarily gravity- and wind-dispersed.

We also found that the density of older natural regeneration was positively correlated with YP seedling density, highlighting the importance of large trees, such as those that survive wildfires or are present at wildfire edges—or other remnant trees from much older cohorts in non-wildfire context. Large trees generated seed rain for decades prior (the older natural regeneration) and likely continued to enable the establishment of seedlings within the focal age range. While we attempted to control for seed availability from large trees by measuring distances to these trees, our model did not capture a significant relationship with this term. One limitation of our study was that we could only measure distances to standing trees, whereas seed sources for older natural regeneration could have fallen in the interim. This is especially possible given the high amount of drought- and beetle- driven pine and fir mortality in this

region in the five years prior to our field surveys (Young et al. 2017, Restaino et al. 2019). Given this or simply due to the high context-dependency of dispersal and establishment processes, it may be that the density of other natural regeneration provided a more direct estimate of seed rain from these trees – or microsite suitability – and was therefore a better explanatory variable.

We did not find a significant relationship between shrub competition and seedling establishment; therefore, our competitive impacts hypothesis was not supported based on these data. One potential explanation is that our sample size was too low. In fact, we did find that shrub volume had a marginally significant negative effect on seedling density for both YP-only and all-seedling models. This is suggestive of a true effect, though it would require additional data collection for statistical confirmation. Another potential explanation is that shrub cover may affect a different part of the life cycle than the one we were observing. We focused on germination and early establishment and therefore modeled seedling presence and density; however, it may be that seedling and sapling growth will continue to be impacted by shrub competition (Werner et al. 2019) and slow the transition to forest cover.

It is also possible that we observed a net neutral observed effect because both facilitative and competitive processes were operating in this system. Observational studies have suggested that shrubs can be positively correlated with tree regeneration (see e.g., Shatford et al. 2007, Collins and Roller 2013, Downing et al. 2019), though this pattern is hard to disentangle from a scenario where productivity—rather than facilitation—drives increases in both plant forms. Experimental studies generally have shown negative or neutral shrub effects: one study demonstrating generally facilitative interactions among planted shrub-tree pairs in Spanish ecosystems facing similar climatic patterns (e.g., heat stress and lack of water availability during the growing season) also found that this effect was not significant among higher-elevation pines – the species mix most resembling our focal species (Gómez-Aparicio et al. 2004). Other empirical work in YPMC systems suggests that depending on environmental conditions, shrubs may play a competitive or facilitative role with regard to the survival of young pine seedlings (Legras et al. 2010, Werner et al. 2019), but they consistently have negative effects on growth (Werner et al. 2019).

Further, the negative effect of shrubs on seedling growth rates may contribute to higher YP mortality (Tubbesing et al. 2020). Thus, it might be reasonable to expect that 1.) environmental heterogeneity led to a variety of interactions across plots, obscuring a directional pattern, or 2.) negative interactions might be increasingly influential once seedlings are established.

The potentially contingent nature of tree-shrub interactions highlights a major limitation of our study: a single-year snapshot observation of tree regeneration is unable to capture the nuances between seedling life stages. We observed only seedlings that survived long enough to be observed and as a result are not able to disentangle germination rates from survival – and whether facilitation and competition might operate at either or both of these stages. Thus, our inferences come from a relatively narrow band in tree life stages: seedlings that have initially survived but whose long-term growth and viability may be impacted by shrubs.

In fact, shrub heights vastly exceeded seedling heights in most of our plots (Figure 1.4), calling into question how quickly these seedlings will be able to grow under these circumstances. It is likely that these seedlings will grow much slower and may even have reduced survival under these conditions (Tubbesing et al. 2020, Airey Lauvaux et al. 2016, Werner et al. 2019), and it may take several decades before they are able to overtop shrubs and capture the resources needed for more rapid growth (Airey Lauvaux et al. 2016). If this is the case, then the second cohort of trees in the zone surrounding the planted stand may be delayed in contributing seed for further expansion, and early expansion may be limited to longer-distance dispersal from the original planted cohort or other seed sources distributed in the landscape. This could limit the potential for planting to accelerate a shift from montane chaparral landscapes to forest cover across a broad landscape.

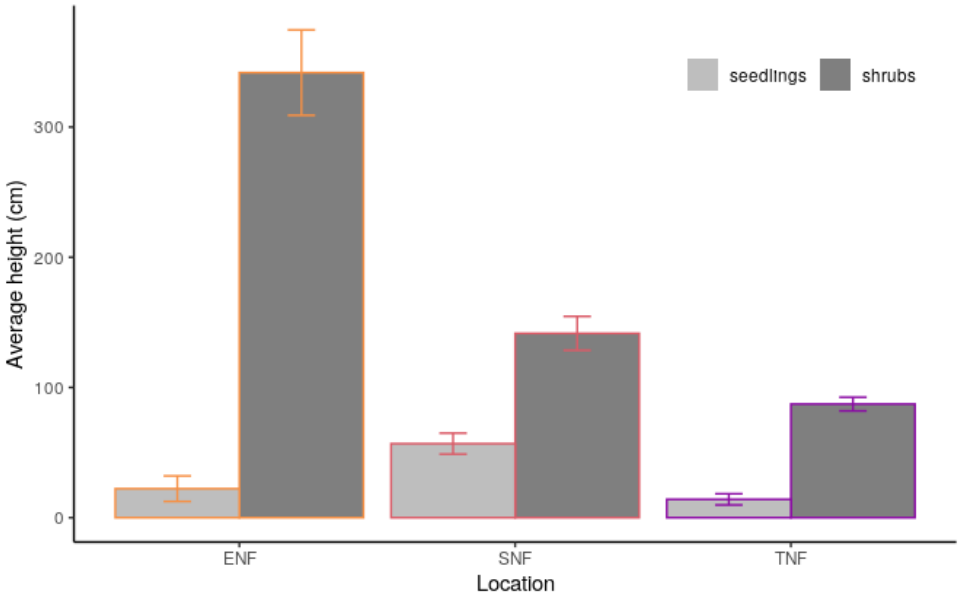

Figure 1.4. Mean and standard error of shrub and seedling heights, summarized for all plots across the three study locations.

Applications

Though we found that planted trees can serve as seed sources for further establishment, there are some limitations to the extent to which this finding can be applied for landscape restoration as implied by the nucleation and founder stand frameworks. Notably, we found that there was only a 65% probability of observing YP seedlings directly within the planted stand, with this probability dropping substantially moving away from the stand. In areas directly adjacent to the planted stand, we observed average YP seedling densities commensurate with 46 (18) trees per hectare (acre). This amount is within the range of historical densities of adult trees (Collins et al. 2015, Stephens et al. 2015), but it may not reflect a suitable density for seedlings. USDA Forest Service silvicultural guidelines specify a target stocking rate of about 500-740 trees per hectare in these forest types, indicating that the observed levels may not be considered sufficient by forest managers. Even outside the context of agency-specific guidelines, typical seedling densities in unburned areas may be closer to 750 individuals per hectare (Welch et al. 2016).

The low probability-of-occurrence and density of seedlings within and adjacent to seed sources may indicate that site suitability continues to be a key factor limiting establishment, though we were

unable to attribute it to any one specific biotic or abiotic driver. We can infer based on comparing shrub and seedling heights that competitive dynamics may limit seedling growth. Under these ecological conditions, forest managers wanting to accelerate the transition from shrub cover to forest cover often may consider it worthwhile to remove competing vegetation (McDonald and Fiddler 2010) or otherwise prepare sites for recruitment near planted sites (North et al. 2019); however, this may not be feasible in the remote circumstances that necessitate the nucleation or founder stand strategy in the first place. However, planting founder stands may be a realistic option in cases where management is limited for other reasons – e.g., to limit soil disturbance (such as near archaeological sites) or where other management goals conflict with reforestation objectives. In these cases, planted founder stands may provide a critical source of seed rain to areas unable to be replanted directly, though land managers should not expect seedling density or vigor to be comparable to actively replanted areas.

Site productivity, the disturbance context, and land use histories are also likely to be important considerations when using nucleation strategies. While we did not find that the inclusion of unburned sites with post-fire sites substantially changed our model results, we did observe that regeneration at TNF was quite low (Table 1.3), potentially due to being a higher-elevation, lower-productivity region. We interpret this as a signal that the overall effect of planted nuclei may be similar among locations, but the landscape-level impact in terms of tree densities may differ based on local conditions. Given the pace of climate and other global change, it will be important to consider whether site conditions are able to support both the pace of planted tree growth as well as associated seedling growth in order to meet density targets.

Forest managers may wish to consider modifying the species composition of planted stands to favor shade-tolerant species and/or species with a long dispersal range. While planting practices often prioritize species that are shade-intolerant or have a short dispersal range in order to achieve establishment that may not otherwise occur – as well as to steer forest composition towards a fire-adapted species mix that reflects pre-fire suppression conditions, planting for nucleation purposes may benefit

from a more diverse species mix. In YPMC forests, for example, Abies concolor seedlings are able to survive and grow slowly even when over-topped by shrubs (Oakley et al. 2006), particularly in comparison with co-occurring pine species (Tubbesing et al. 2020). Abies concolor also has small seeds relative to co-occurring pines, corresponding to a larger dispersal range (Safford and Stevens 2017). Including A. concolor and species with similar traits in the planting mix could be a "bet hedging" strategy that increases the likelihood and range of forest expansion in the long term.

Our models also captured the importance of older natural regeneration in predicting younger seedling establishment, indirectly pointing to the role of surviving LTSSes in driving recruitment. This pattern suggests that large trees could play a significant role relative to planted trees, especially given that propagule pressure scales with tree size (Greene and Johnson 1994; Clark et al. 1999). This would be consistent with findings across many ecosystems that large remnant or "scattered" trees can have a dramatic impact on the surrounding land, including serving as seed sources for regeneration (Manning et al. 2006). Our surveys did not stratify across distances to LTSSes (and in fact tried to minimize the influence of these trees), but we suggest that a rigorous investigation of the relative contributions of remnant trees versus planted trees to multi-generational recruitment would be an fruitful avenue for further research. Depending on these relative contributions, land managers may find it worthwhile to invest significantly more in management practices that protect tree stands from mortality ("green forest management") to obviate the major expenses—and higher uncertainty—associated with active post-mortality planting – and particularly if planting is focused on spatially expanding the forest stand. The efficacy of nucleation treatments will also likely depend on dispersal syndromes and management objectives. Our study focuses on species that are primarily wind- or gravity- dispersed; however, many nucleation applications pertain to zoochorous plants and the important role of planted nuclei in terms of attracting dispersers and therefore increasing biodiversity across multiple trophic levels (see Guevara et al. 1986, as well as Holl et al. 2020 for a more complete review). Our study takes a limited approach in terms of only considering the impact of nuclei on additional regeneration, and this may ignore some of the

other ecological impacts of planted nuclei. Even within the context of stimulating regeneration, the role of shrubs may differ based on ecological context: for example, shrubs may facilitate regeneration if they attract animal dispersers or favorably modify abiotic conditions, but this positive interaction may change over different life stages and may not apply to wind-dispersed seeds (Holl 2002). Given these nuances, land managers will need to consider the specific dispersal strategies and shrub interactions of their ecosystem as they decide whether nucleation is likely to succeed.

Conclusion

The scale of high-severity wildfire in the Western U.S. has raised concern about the ability for forest recovery to occur over broad regions that now experience limited dispersal from surviving or unburned trees (e.g., North et al. 2019) – a concern that echoes questions globally about whether forests will recover after land conversion, pest outbreaks, and other stressors that can lead to widespread mortality of seed trees (Peñuelas et al. 2017, Safford and Vallejo 2019). These questions have prompted a reckoning over the role of reforestation and other management to accelerate forest recovery (and linked ecosystem service and conservation goals; Kemppinen et al. 2020, Staples et al. 2020). However, it remains unclear whether planting can have predictable and continued effects outside of the immediate planting zone and therefore at the landscape scale. We find that planting mostly wind- and gravity-dispersed trees can lead to subsequent regeneration outside of the planted stand, but that this regeneration is limited in scale (low probability, potentially low density) and may have limited vigor and/or long-term survival; thus, the continued outward expansion from planted stands may occur over a much longer time horizon than desired by forest managers or permitted by the current (or future) fire regime. In systems with increasing fire frequency and the potential for short-interval reburns, and where shrub-dominated vegetation may decrease seedling growth and increase future fire severity (Coppoletta et al. 2016), forest recovery will depend on whether regeneration and tree growth can keep pace with mortality from wildfire events. This scenario characterizes the contemporary YPMC ecosystem in much of the western U.S. Our empirical study provides estimates of expected recruitment that can aid in projecting the likelihood of

forest recovery in YPMC-type forests, particularly over the mid- to long- term following disturbance. These estimates may differ from other ecosystems, but they suggest that expectations for recruitment and forest recovery should generally reflect not only seed availability but also whether site conditions enable tree growth rates that can keep pace with disturbance trends.

Acknowledgements

We thank Arianna Stokes and Miroslava Munguia-Ramos for assistance in the field. Thanks to Eldorado National Forest, Sierra National Forest, and Tahoe National Forest staff for help with site access and understanding management history. James Sanchirico and Derek Young provided valuable advice on study design and analysis, and Malcolm North provided comments that helped improve this manuscript. We would also like to thank our editor and two anonymous reviewers, whose comments and suggestions greatly improved this manuscript.

This study was funded by the California Department of Forestry and Fire Protection as part of the California Climate Investments Program.

Appendix 1.1: Model comparisons

The following tables contain model results from the full dataset (Table 1.3, Table 1.4) as well as a subset of the data that does not include TNF plots. Coefficients of significant variables do not substantially change between the datasets. We performed this test on TNF specifically because it had a categorically different management history compared with ENF and SNF: planted sites were not established post-fire. We interpret these comparisons as confirmation that model results (and therefore our inferences) are not sensitive to this study location.

Presence models

	Presence (all spp.)		**Presence w/o TNF (all spp.)**	
Predictors	Log-Odds	p	Log-Odds	p
(Intercept)	**3.351 (0.960 – 5.741)**	**0.006**	**5.785 (1.820 – 9.750)**	**0.004**
Distance from planted stand (m)	**-0.082 (-0.136 – -0.028)**	**0.003**	**-0.081 (-0.148 – -0.014)**	**0.018**
Shrub Volume	0.15 (-0.810 – 1.111)	0.759	0.191 (-0.866 – 1.247)	0.724
Other natural regen (density)	4.461 (-0.235 – 9.157)	0.063	1.165 (-0.416 – 2.746)	0.149
Large trees seed source (index)	0.926 (-0.486 – 2.339)	0.199	5.997 (1.489 – 10.504)	0.009
Nat. Regen seed source (index)	0.579 (-0.490 – 1.649)	0.288	1.453 (-0.397 – 3.302)	0.124
Ground cover: litter (pct)				
Random Effects				
σ2	3.29		3.29	
τ00	4.01 transect		2.54 transect	
ICC	0.55		0.44	
N	23 transect		17 transect	
Observations	87		67	
Marginal R2 / Conditional R2	0.762 / 0.893		0.901 / 0.944	

Density models

	Density (all spp.)		**Density w/o TNF (all spp.)**	
Predictors	Log-Mean	p	Log-Mean	p
	0.981		**1.608**	
(Intercept)	**(0.074 – 1.889)**	**0.034**	**(0.615 – 2.601)**	**0.002**
Distance from planted	**-0.019**		**-0.016**	
stand (m)	**(-0.034 – -0.003)**	**0.021**	**(-0.034 – 0.002)**	**0.088**
	-0.431		-0.598	
Shrub Volume	(-0.946 – 0.085)	0.101	(-1.151 – -0.044)	**0.034**
Other natural regen	**0.646**		**0.682**	
(density)	**(0.272 – 1.021)**	**0.001**	**(0.264 – 1.100)**	**0.001**
Large trees seed source	0.221		0.483	
(index)	(-0.326 – 0.767)	0.428	(-0.342 – 1.307)	0.252
Nat. Regen seed source	0.104		0.258	
(index)	(-0.254 – 0.463)	0.569	(-0.221 – 0.736)	0.291
Ground cover: litter	**0.367**		**0.238**	
(pct)	**(0.053 – 0.682)**	**0.022**	**(-0.138 – 0.614)**	**0.215**
Random Effects				
σ2	0.88		0.89	
τ00	3.48 transect		2.19 transect	
ICC	0.8		0.71	
N	23 transect		17 transect	
Observations	87		67	
Marginal R2 / Conditional R2	0.223 / 0.844		0.430 / 0.835	

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Chapter 2. Efficacy of shrub removal for meeting restoration targets in reforested areas

Abstract

Wildfire-adapted forests in the Western United States are burning under novel conditions driven by climate change and fire suppression policies, resulting in a substantial increase in the amount of land burning under conditions that result in high fire severities. This has raised questions about the potential for fire-driven type conversion in the yellow pine and mixed conifer ecosystems of the Sierra Nevada, California, where recruitment depends on the availability of nearby live seed trees. Forest managers in this system may opt to plant trees to ensure regeneration, and they may opt to remove competing vegetation (e.g., shrubs) to accelerate tree growth. We investigated the ecological outcomes from these types of plantings in five national forests in the Sierra Nevada. First, we performed an observational study of paired planted stands with and without the removal of competing vegetation. We found that shrub removal marginally increased the probability of tree emergence over the shrub canopy. We also investigated the long-term outcomes of these stands using the Forest Vegetation Simulator, simulating stand dynamics in the plots under four wildfire scenarios and analyzing outcomes under four metrics of ecological recovery. We found that the effect of CCV was highly variable: it was associated with faster ecological recovery in specific environmental conditions and wildfire scenarios (e.g., wetter sites with higher-intensity simulated wildfires) but not all, and our statistical model suggested that shrub removal was negatively associated with the likelihood of recovery for one of our metrics. Collectively, our results suggest that shrub removal may be associated with forest recovery in the short term, but it does not produce consistent results under long term simulations. We caution that our study is derived from observational data where treatments may have been applied opportunistically, and therefore we suggest that more experimental work be performed to further test these findings. Nevertheless, these results may guide land managers seeking to target planting and the management of planted stands to areas in which it has the greatest effect on forest recovery.

Introduction

Wildfire-adapted forests in the Western United States are burning under novel conditions driven by climate change and pervasive fire suppression management policies. Climate change is producing hotter, drier, and longer fire seasons with longer snow-free periods (Abatzoglou and Williams 2016; Westerling 2016), and the continued practice of fire suppression among federal and state fire management agencies has led to the build-up of flammable biomass that has greatly increased live and dead fuel loading and continuity (McIntyre et al. 2015; van Wagtendonk et al. 2018). In combination, these factors are leading to a rapid rise in wildfire size, producing annual burned areas that are progressively closer to pre-fire suppression values but burning under conditions that result in higher fire severities and vastly greater amounts of tree mortality (Steel et al. 2018; Safford et al. 2022).

The extent of high-severity fire has raised questions about the potential for fire-driven type conversion of forested ecosystems (Coop et al. 2020). Conifer species in the mid-elevation, yellow pine-dominated and mixed-conifer ("YPMC") forests of California's Sierra Nevada (USA) are adapted to low- to moderate- severity fire, which translates to relatively low tree mortality and therefore reproductive trees being relatively available across the landscape to act as seed sources for regeneration. A living seed source is crucial for conifer species of this ecosystem, which do not resprout, do not have a seed bank, and are not serotinous (Safford and Stevens 2017). Moreover, these seed sources must be relatively nearby, as seed tree proximity is a strong predictor of post-wildfire seedling recruitment (Welch et al. 2016; Shive et al. 2018). This process of natural recruitment is therefore compromised under contemporary wildfire conditions that produce large patches of high-severity burned areas with few seed trees.

Increasingly, land managers are turning to reforestation to restore forests where fire-driven type conversion is possible (Dumroese et al. 2019). On National Forests, reforestation was historically done either in logged areas or in areas impacted by disturbances like wildfires, which previously tended to be much smaller and therefore able to be financed through timber management programs (Dumroese et al.

2019). Under atimber management paradigm, reforestation is often management-intensive: best practices include salvage logging (to clear hazards and large fuels); site preparation (to clear smaller dead fuels and other vegetation); the control of competing vegetation (hereafter "CCV") by either manual, mechanical, or chemical means; and additional thinning and pruning treatments, such as pre-commercial and commercial thins (Tappeiner et al. 2007).

The removal of fuels and vegetation through site preparation and CCV is particularly relevant in California YPMC forests. This is not only to reduce the likelihood of high-severity fire but also because shrubs often resprout or reseed aggressively after wildfires (Knapp et al. 2012; Collins and Roller 2013), competing with tree seedlings and potentially delaying the emergence of a tree overstory (Nagel and Taylor 2005; Airey Lauvaux et al. 2016). This practice has been the focus of numerous USDA Forest Service field trials, from which the findings generally emphasize the importance of removing competing vegetation (see trials summarized in McDonald and Fiddler 2010), Zhang et al. 2013)). However, the field trials also demonstrate that only the highest-intensity treatments (e.g., cut & chemical vs. cut-only, or whole-plot shrub removal vs. a smaller radius surrounding each tree) have a significant impact on tree growth (see Tables 8 and 9, McDonald and Fiddler 2010).

Many lessons from production-oriented field trials can be readily applied to forest restoration, but they do not completely overlap. Whereas the emphasis of timber production tends to be growth and maximization of tree volume, the emphasis of forest restoration can be quite different. On Forest Service lands, the 2012 Planning Rule (36 CFR Part 219) identifies ecological integrity, characterized as when the "dominant ecological characteristics…occur within the natural range of variation…" as a main management objective. In YPMC forests of the Sierra Nevada, the natural range of variation has been defined for numerous ecological traits, including stand-level density of trees (60-328 trees per ha) and basal area (21-54 m^2 ha^{-1}) (Safford and Stevens 2017). Slightly further north in the YPMC of the North Coast Range, Southern Cascades, and Southern Oregon, density estimates are 14-314 trees per ha (Bohlman et al. 2021). These ranges are based on reconstructions from historic timber inventories and

other surveys, including modern reference sites (Lydersen et al. 2013; Collins et al. 2015; Stephens et al. 2015). More informally, many forest managers report that their management goal is to ensure that the stand can survive the next wildfire.

Our aim was to evaluate the relevance of treatments for the control of competing vegetation (CCV) in the forest restoration paradigm. We build on similar work that aims to increase the efficiency of reforestation strategies given the increased scale of high-severity wildfire as well as the lack of funding for intensive management (see e.g., North et al. 2019; Shive et al. 2018; Stewart et al. 2021). First, we used observational, field-collected data to ask whether CCV treatments are associated with significant differences in forest stand structure. We then used these data to parameterize forest growth simulation models. With the latter, we evaluated whether CCV treatments influenced whether and when a stand reached a "restored" state – here defined as within natural range of variation densities (Safford and Stevens 2017; Bohlman et al. 2021; Meyer et al. 2021) as well as whether CCV promoted stands that exceeded the 10 percent canopy cover threshold typically used to identify "forests" in this region (CALFIRE Fire and Resource Assessment Program 2018).

Does CCV lead to significant differences in stand structure?

Methods

We collected data on forest structure from plots that had been planted after a wildfire, selecting plots that met the following criteria:

- Within the Sierra Nevada (California, USA)
- Burned 5-30 years prior to sampling. We assessed burn area using the California Department of Forestry and Fire Protection fire perimeters database, which includes all observed fires > 10 acres in forested areas (California Department of Forestry and Fire Protection 2018)
- Contained areas that had post-planting control of competing vegetation (CCV) treatments as well as areas from the same planting year that did not have CCV, with both types no more than 1 km

in distance from each other. We assessed these using the Forest Service Activity Tracking System ("FACTS"), a spatial database of all management activities (USDA Forest Service 2018).

In Summer 2018, we surveyed vegetation in plots within the identified polygons (Figure 2.1). Sampling plots were chosen by gridding points across planted areas (100-meter spacing) and choosing paired plots (CCV and no-CCV) that had similar topography (aspect and slope) based on a digital elevation model processed using the "raster" package in R (U.S. Geological Survey 2017; Hijmans 2020; R Core Team 2020). For example, if we sampled a north-facing CCV plot, we preferentially sampled at a grid point that was north-facing in the non-CCV polygon. We made all plot selections prior to visiting them in person; however, if the plot center ended up in an unforested, riparian, or other unrepresentative cover type, we relocated the plot center 30 meters away in the direction that most directly escaped the undesirable feature.

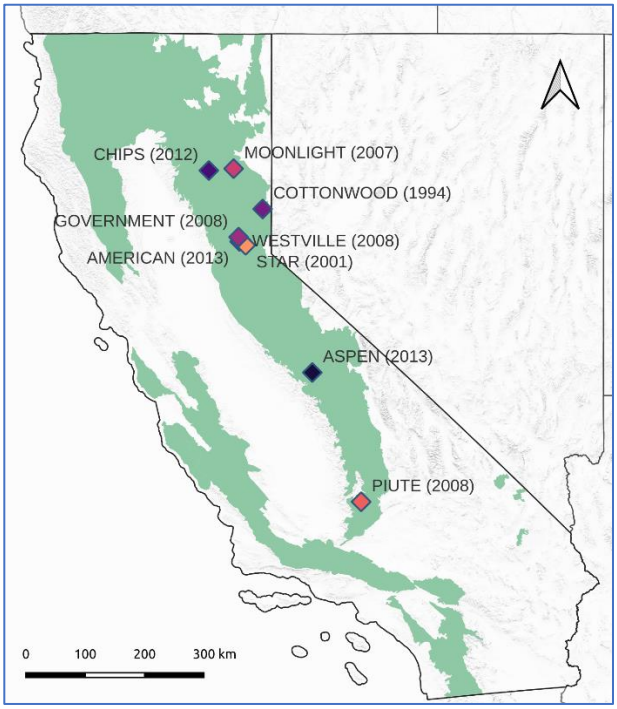

Figure 2.1. Map of plot locations, identified by the name and year of the last wildfire. Green shading indicates areas with forest cover similar to that found within or close to the sampled plots, according to California Wildlife Habitat Relationship (WHR) classes.

We sampled trees greater than 25 cm in height within 400 m^2 (1/10-acre) circular plots, subsampling natural regeneration as necessary to reduce labor. Specifically, we subsampled if a quick visual assessment indicated that there were more than 20 qualifying trees (i.e., > 25cm height) within the plot. Subsamples consisted of 2-meter belt transects extending from transect tapes that delineated North, South, East, and West from plot center, but these subsamples were aggregated to the plot level through a multiplicative factor for analysis. The subsampling protocol applied only to suspected natural regeneration; we collected data on all trees that we suspected to be planted based on size, configuration (planting grid spacing), and obvious signs of vegetation management (e.g., grubbing).

For each tree, we recorded the species, diameter at breast height (dbh) if > 1 cm, total height, the previous year's height (ground to the current year's bud), and the previous year's growth (current year's bud to the most recent bud scar prior). We included the two latter measurements in order to have a standardized measure across plots, as total height was likely influenced by sampling date. We also characterized the proximate vegetation for each tree: first, we roughly categorized whether the tree was taller than, shorter than, or about the same height as its immediate neighbors, and we also estimated the percent cover and modal height of the three highest-cover shrubs within 1 meter of the tree.

At each plot, we also collected data to characterize environmental conditions and potential competitive pressures. First, we used a laser rangefinder to measure the distance to the nearest tree of each species that survived the previous wildfire – i.e., potential seed trees for natural regeneration–up to a maximum distance of 500 meters. We estimated the percent of the plot area covered by large rocks and bedrock (>0.5 m in shortest dimension); cobbles and stones (75-500 mm); litter, bare soil, and small rocks (<75 mm); basal vegetation; and woody debris (collectively "ground cover"). We also estimated the plot-wide canopy cover and height of trees and shrubs, and we coarsely characterized whether shrubs appeared low-, moderate-, or high- density based on our experience in the YPMC ecosystem. Our post-hoc analyses indicated substantial overlap in the distributions of these environmental and biological covariates between

CCV and non-CCV plots (Appendix 2.1), which increased our confidence in comparing these two treatment types in our observational data.

To assess effects on forest structure, we compared levels of tree emergence from the shrub canopy. Prior literature suggests that seedlings grow much slower and may have reduced survival under a shrub canopy, and overtopping by shrubs can lead to decades-long delays in tree emergence into the overstory (Airey Lauvaux et al. 2016; Werner et al. 2019; Tubbesing et al. 2020). Therefore, our tree emergence metric captures the trees most likely to become the forest canopy in the near to mid term. To account for other potential drivers of tree emergence, we also performed a binomial regression to assess the probability that a plot would contain at least one emerged tree. We also tested the probability that a plot had at least three emerged trees, as this was the minimum number within our plot size that would be consistent with the natural range of variation for tree densities. For model selection, we included our hypothesized driver (CCV treatment status) and stand age in the minimum model, and we included other variables if they improved the model based on comparing AICc values. We used the "lmer" and "MuMIn" libraries (Bates et al. 2015; Bartoń 2022) for all statistical analyses, and we used "merTools", "sjPlot", and numerous packages in the "tidyverse" for supplemental analyses and visualization (Wickham et al. 2019; Knowles et al. 2020; Lüdecke 2021). All were performed using R 3.6.3 (R Core Team 2020).

Results

We did not observe a difference between CCV and non-CCV plots in our direct comparisons of tree emergence over shrubs, whether in comparing treatments binned by age class (Figure 2.2a) or overall ($p = 0.337$). We observed that emergence generally dropped between the youngest (< 5 years) and next-youngest (5-10 years) plots before increasing substantially in older plots, though tree heights generally increased in absolute terms (Figure 2.2b). Tree heights were not significantly associated with CCV status, but we did observe generally higher mean and median heights for plots that had CCV.

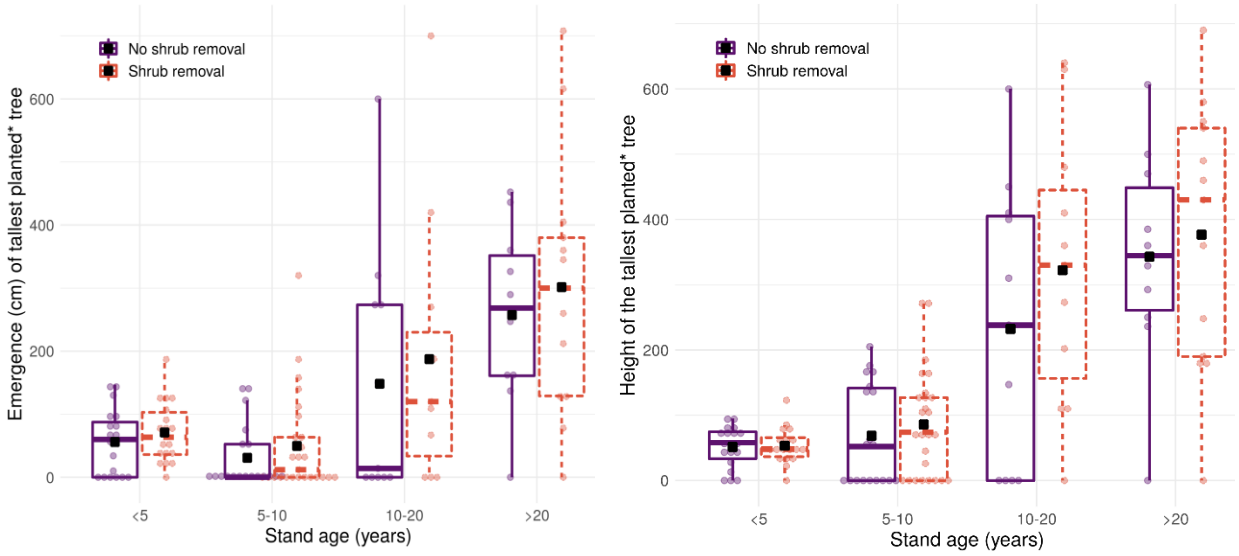

Figure 2.2: Summary statistics for the height emergence (left) and absolute height (right) of the tallest tree identified in the field as planted or likely planted over proximate shrubs reveal no significant difference between stands that had CCV (orange dashed lines) and stands that did not (purple solid lines). Summaries are shown for binned age classes, and they include boxplots as well as mean values marked with black squares. Plot data are included as faded points to demonstrate the distribution.

Several plots did not have any emerged trees at all, even though they were planted and therefore should have had several trees with a head start over shrubs and other neighboring vegetation. Our regression analysis identified the probability that a plot would have at least one emerged tree (Figure 2.3), and we found that having had CCV treatment had a marginally significant but relatively substantial effect: the probability increased from 61 percent in plots without CCV to 77 percent in plots with CCV. Shallower slopes and lower elevations also increased the probability of emergence. Similarly, in our tests of the probability that a plot would have at least three emerged trees, we found that CCV was marginally significant but would raise the probability from 62 to 76 percent. In the latter model, shrub cover significantly reduced the probability of emergence, but only in plots without CCV treatment.

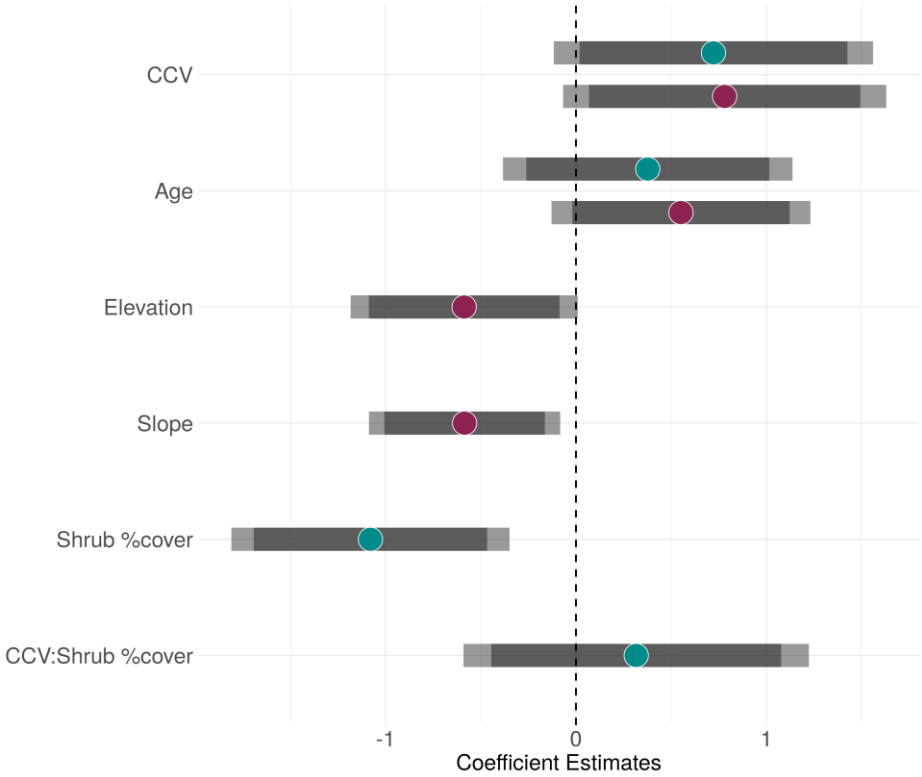

Figure 2.3: Coefficient estimates from best-fit models of the probability of a plot containing at least one emerged tree (purple) or at least three emerged trees (teal). CCV = previous treatment for the control of competing vegetation. 95th percentile ranges are displayed in light gray, and 90th percentile ranges are displayed in dark gray.

While the height and emergence of planted trees trended upward for plots with CCV, especially in older plots, patterns in densities were more mixed. Among trees identified as likely planted, we found no significant differences between treatment types. Densities were highest in the youngest plots, fell in the next-youngest plots, and remained fairly stable in the older age bins (Figure 2.4a). When we included all trees (including those likely to be natural regeneration), we also found no significant difference between treatment types although plots with CCV were generally lower-density than those without CCV (Figure 2.4b).

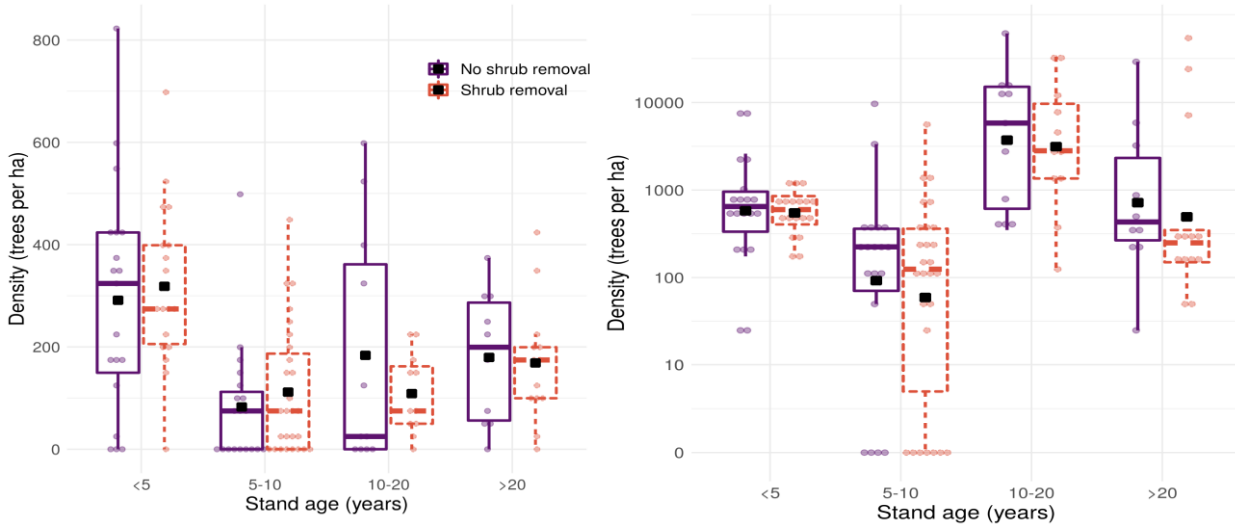

Figure 4: The densities of planted trees (left) and all trees (right; note the log scale), categorized by stand age.

Discussion

We found that planted stands with control of competing vegetation (CCV) treatments did not have significantly higher emergence heights, absolute heights, or densities than planted stands that did not have post-planting CCV treatments. However, our dataset spanned a wide range of wildfire and planting years, and therefore we were able to investigate patterns in stand growth using a space-for-time substitution. While we also did not observe significant changes within binned ages (planted <5, 5-10, 10-20, and 20+ years prior to field surveys), we did observe some general trends that were consistent with our expectations of this ecosystem. First, absolute heights as well as the emergence heights (difference between tree and shrub heights) were generally higher in CCV compared with non-CCV plots. This pattern is consistent with the general rationale for CCV treatments in this system – namely, that CCV promotes tree establishment and growth particularly in areas with shrub competition. It is possible that we simply did not have sufficient power to detect a significant difference given our small sample size. It is also possible that our results demonstrate a realistically broad range of CCV effects. Prior CCV trials in these systems have demonstrated consistently large effects of CCV when that treatment is repeated,

intense, or both, but the effects of CCV on growth is reduced and often statistically insignificant for less-intense treatments (e.g., single versus multiple passes with herbicide or manual removal within a short radius of the planted tree versus the whole stand; see McDonald and Fiddler 2010). Among our 69 CCV plots, only 2 had chemical removal and 4 had more than one treatment, suggesting that treatments implemented by practitioners on these lands are less intense than those identified in field trials to be most efficacious.

The observational nature of our field study also might have obscured CCV effects. While we attempted to sample in paired plots that were spatially close and had similar environmental and productivity conditions, it is possible – even likely– that land managers preferentially implemented CCV treatments in areas known or anticipated to have strong shrub growth based on biological or environmental conditions (R. Mustatia, US Forest Service, *pers. comm.*). This is a common practice in land management and a pitfall for making inferences about treatment effects (Simler-Williamson and Germino 2022). For this reason, we also performed a regression analysis to assess CCV effects while controlling for other site factors. With this approach, we found that CCV was marginally associated with increases in the probability of observing at least one emerged tree (hereafter "1ET") as well as the probability of enough emerged trees to be within the historical range of variation (three emerged trees, hereafter "3ET"). The apparent effect of shrub removal on emergence was bolstered in the 3ET model, as increasing shrub cover was negatively associated with the probability of emergence. Interestingly, we only found this pattern in plots that did not receive CCV treatment, implying that CCV may reduce the competitive effects of shrubs over time. We also found shrub cover effects in the 3ET model but not in the 1ET model. By contrast, we found that environmental factors such as higher elevations and steeper slopes significantly affected the probability of 1ET. It is somewhat surprising that the 1ET and 3ET should have differing significant factors. Based on these data, we suggest that there may be different types of ecological filtering: topographic and productivity characteristics may determine whether sites are capable of supporting an emergent tree (1ET), whereas shrub cover more directly predicts whether the site

is more widely suitable (3ET). The potential for filtering to drive forest recovery outcomes is an interesting avenue for further research.

In addition to our emergence metrics, we initially investigated the effect of CCV status and stand age on tree densities. In the absence of natural regeneration, planted trees should have been equivalent between CCV and no-CCV plots and relatively low in density; indeed, we found that densities of planted trees were largely within the natural range of variation. However, we found substantial natural regeneration in the plots, with 50% of plots exceeding 375 trees and mean densities exceeding 3000 trees. The challenge of inferring forest health from densities is that too few trees lead to insufficient forest recovery and potential type conversion, but too many trees increase fuels, especially "ladder fuels" that carry wildfires into tree canopies. This potentially leads to higher severity wildfire and compromised post-wildfire recovery. Our field study was able to address the question of whether recovery was occurring in the short run, but it was unable to address whether there was "too much" growth of small-diameter trees that could compromise the long-term viability of the forest stand. With this challenge, we turned to simulation models to investigate the long-term potential outcomes of our field plots.

Does CCV improve long-term forest restoration outcomes?

Methods

We used the Forest Vegetation Simulator with Fire and Fuels Extension (FVS-FFE) to model the long-term outcomes of our sampled plots (Rebain 2015; Dixon 2018). FVS-FFE is a growth-and-yield model developed by the USDA Forest Service, and it includes regional variants with parameters embedded for the locally relevant species. We used the Western Sierra variant. FVS does not explicitly model tree-shrub interactions, but the simulation of forest stand development with different initial conditions (CCV, non-CCV) was sufficient to address our research question.

We evaluated several restoration targets, focusing on whether plots met estimates of forest density based on reconstructions of historical forest structure prior to fire suppression (60-328 trees per

ha; Safford and Stevens 2017) and whether canopy cover exceeded 10 percent per forest typology guidelines established by the the USDA Forest Service's Forest Inventory and Analysis program and the California Department of Forestry and Fire Protection (USDA Forest Service, n.d.; California Department of Forestry and Fire Protection 2018). We evaluated our hypothesis by assessing whether CCV status had a significant influence on the likelihood of a plot meeting the restoration target.

We describe each of these steps and components below.

Plot and tree inputs

We used data from the surveyed plots (see "Field-collected data") as inputs for the FVS simulations. Per FVS requirements, we converted all data to United States customary units and, in cases where a tree was shorter than breast height, input the nominal value of 0.1 as the diameter at breast height (dbh). We ran each plot independently and for a time period of 150 years. We tested alternate end dates (100 years, 200 years) but found that our results were not sensitive to the end date.

Wildfire

We modeled a wildfire within the simulation period in order to assess resilience to disturbance. Our interest was two-fold: first, we were interested in whether a disturbance would influence the likelihood of reaching the ecological target, and second, we were interested in the ecological recovery time *after* a simulated disturbance. The latter investigation was inspired by conversations with several foresters and other land managers, who often describe their management objective as ensuring that the focal stand or region is able to withstand the next wildfire.

We modeled two fire time periods as well as two fire intensities in order to evaluate CCV effects under various scenarios. In the FVS programming environment, we simulated a fire either in 2030 or in 2050. The former approximates an interval that is within the natural range of variation for Euro-American fire suppression forest management: in YPMC forests, wildfires have a natural fire return interval of about 11 years on average, ranging from 5-50 years (Van de Water and Hugh D. Safford 2011a). Wildfires under the current fire suppression management regime burn much less frequently (Mallek et al.

2013: Steel et al. 2015), and we included the 2050 fire simulations to capture a longer time horizon. We evaluated two different fire intensities by varying weather scenarios. FVS-FFE models fire using methods from Rothermel (1972), Albini (1976), Van Wagner (1977), Andrews (1986), and Scott and Burgan (2005) to estimate fire intensity and fire crowning from fuel and weather conditions (Rebain 2015). We modeled "fire season" weather conditions, which included the lowest possible fuel moisture levels, and weather conditions derived from local weather stations. Specifically, we downloaded hourly temperature and windspeed data from the two Remote Automated Weather Stations (RAWS) stations closest to each sampled wildfire and for the years 2014-17. For each station, we focused only on data from June through October to isolate the most likely "fire season", and we generated medians and 95th percentiles from these data. Our high-intensity and moderate-intensity fire scenarios then used 95th percentile and median temperatures and windspeeds as inputs, respectively.

Regeneration

We evaluated outcomes based solely on the field-collected forest inventory data as well as under scenarios that included tree regeneration. To model regeneration, we simulated the addition of seedlings by estimating the seed shadow following methods described in Clark et al. (1999). To estimate seed rain we used our field-observed distances between the plot and the nearest potential seed tree, and we estimated fecundity assuming a 100 cm dbh - sized tree and other parameters from Clark et al. (1999). We did not have parameter estimates for several species, so we applied model parameters for *Pinus ponderosa* to *P. Jeffreyii*, and we used average parameter values based on the available species for *Pseudotsuga menzesii*, *Calocedrus decurrens*, and *Juniperus occidentalis*.

Analysis

We used approaches from survival analysis to assess the effect of CCV treatments on the likelihood of a plot reaching a given ecological target. We focused on this approach because our framework generated right-censored data – plots that did not ever reach their ecological target (e.g., those with very low field-observed densities or those with very high mortality from the simulated fire). Our

approach, a mixed-effects Cox proportionate hazards model fit, estimates a likelihood function of reaching the ecological target rather than a specific target date, and therefore it could incorporate all of our data regardless of final status. This model assumes that covariates influence the hazard rate through a multiplicative factor, resulting in proportional difference in hazard rates between groups associated with different covariates. The final model took the form

$$h(t) = h_0(t) * exp(\alpha_j + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

where:

- h_0 refers to a baseline "hazard" rate (analogous to a baseline rate of ecological recovery in this context),
- α is a random intercept that captures variation at the fire level (similar region and timeframe of fire effects and management),
- β_1 is an indicator variable for plots receiving CCV, and
- β_2-β_x are other measured plot-level or fire-level characteristics that may influence the recovery rate.

In our model selection process, we fit a minimum model that included the CCV indicator and the plot "age" (years between planting and observation), and we added other variables if they improved the model fit based on an AICc comparison. We tested several interactions based on theory and prior knowledge of the system, such as whether CCV effects are conditional on the amount of shrub cover or interactions between slope and the distance to large seed trees. We performed model selection simultaneously for all four scenarios, and in rare cases where the addition of a variable improved the model fit for at least two scenarios and reduced it for the others, we retained the model with more variables to reduce bias in our estimates.

In addition to investigating the drivers of restoration outcomes with the survival analysis, we also investigated the prevalence and timing of the restoration outcomes. Specifically, we calculated the

number of years for each plot to reach the restoration target based on treatment status and age as well as other environmental characteristics found to be significant in the survival analysis. For the latter, we binned sites based on whether they were in the lowest quadrant, highest quadrant, or middle half of values based on all planted sites within the wildfire perimeter and evaluated outcomes within these bins; we expanded beyond planting units we sampled so that our binned predictor variable represented a fuller range of planted sites. By necessity we restricted the timing analysis only to plots that eventually reached the restoration target, so we also calculated the fraction of plots that reached the restoration target within 50 years, corresponding to the maximum observed fire return interval in this system and well above the mean fire return interval (Van de Water and Safford 2011).

We evaluated simulation outcomes in the context of several different hypotheses. First, we evaluated whether the simulated outcome revealed differences between CCV and non-CCV plots that were not apparent in the field-collected data simply due to the extended length of observation time. Under this hypothesis, we expected significant differences in the number of years and fraction of plots reaching density and canopy cover targets. Second, we evaluated whether significant differences were apparent after the simulated wildfires; this hypothesis was based on our theory that the payoff of competitive release treatments is associated with fuel reduction and mitigation of future wildfire severity. With this hypothesis, we expected a shorter number of years for CCV plots to reach the post-fire restoration targets, everything else being equal.

Results

We evaluated the effect of treatments for CCV on metrics of forest recovery that included the length of time before tree densities fell within the natural range of variation for this ecosystem, the length of time before the stand reached 10 percent canopy cover, and the length of time after a simulated wildfire for these two outcomes to occur (Figure 2.5). CCV was not significantly associated with the ability for stands to reach the target density, and it was negatively associated with the stands reaching the target

canopy cover. However, target densities were less likely to be reached in areas with higher shrub cover, implying a potential relationship between shrub cover and tree establishment.

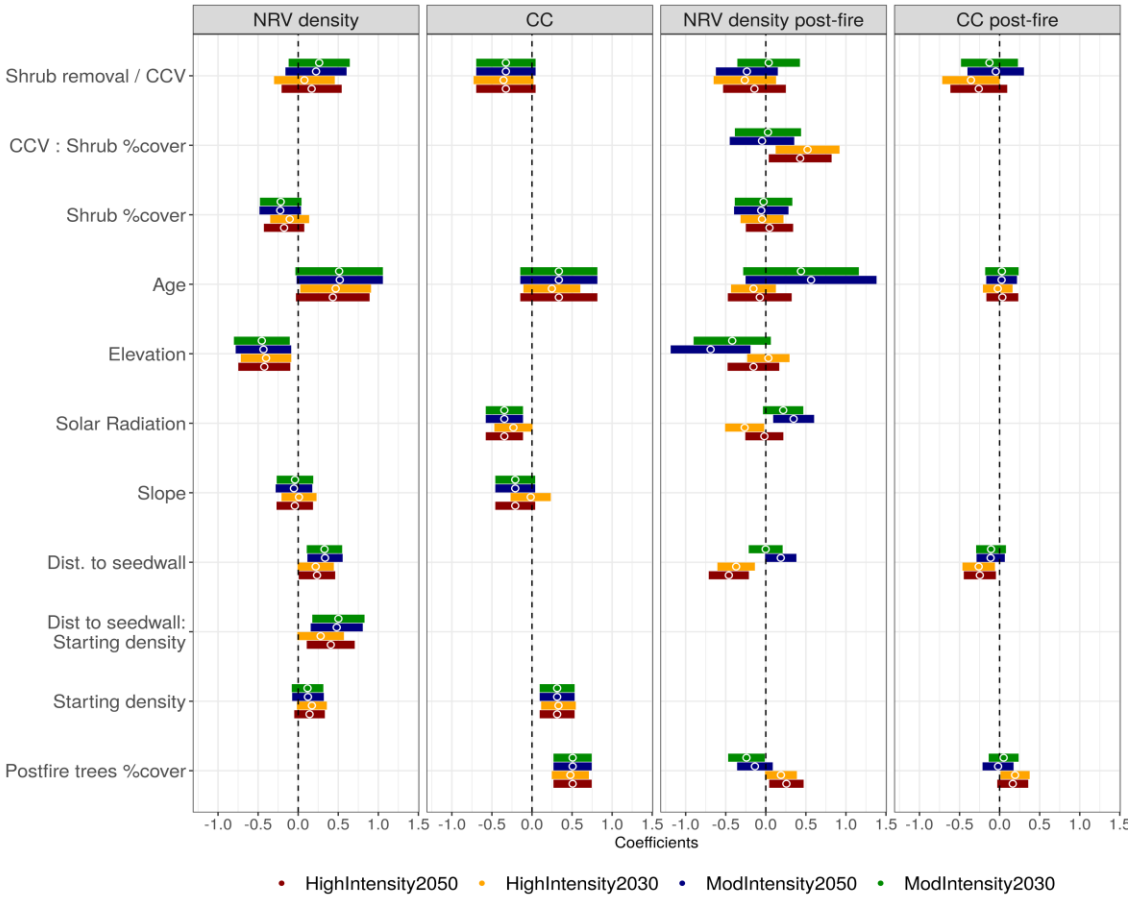

Figure 2.5: Coefficient estimates for the best-fit models for the likelihood of forest recovery based on (far-left) tree densities falling within the Natural Range of Variation (NRV; Safford and Stevens (2017), (mid-left) canopy cover exceeding 10 percent, (mid-right) densities falling within NRV after a simulated wildfire, and (far-right) canopy cover exceeding 10 percent after a simulated wildfire. Colors refer to different wildfire simulations, including the intensity (high or moderate) based on weather factors as well as the year (2050 or 2030). Coefficient ranges are displayed for the confidence interval at 95%, and mean values are indicated with a white circle.

Older stands had a greater likelihood of reaching the target density but were not significant in the canopy cover model. Environmental variables were also mixed: higher-elevation plots were less likely to

reach the target density but were not included in our best-fit model for canopy cover, and higher solar radiation sites were less likely to reach target canopy covers but did not enter our best-fit model for density. Both the starting density of trees in the plots as well as the percent cover of these trees were significantly associated with reaching the target canopy cover. In the density model, the starting density only significantly influenced the target density in plots that were far from the nearest seed wall. Likewise, this interaction indicates that proximity to the seedwall only influenced the likelihood of reaching the target density when starting tree densities were low. In general, however, greater distances (lower proximity) increased the likelihood of reaching the target density – particularly in scenarios where the simulated fire weather was more moderate.

Many of these variables had less pronounced effects on the recovery of density and canopy cover after the simulated wildfire. We included age in all models due to our expectation that the starting forest structure would impact recovery rates, but the effect of age dissipated following the simulated wildfire. Similarly, the starting density of trees in the plots was no longer influential to recovery after the wildfire, including when we tested interactions with distance to the nearest seed wall. Greater distances decreased the likelihood of recovery according to both density and canopy cover metrics, but only following wildfires simulated to be high-intensity. Interestingly, we also found that CCV treatments increased recovery to the target density in high-shrub-cover conditions, but only in the high-intensity wildfire scenarios. Otherwise, shrub cover and shrub removal (CCV) did not significantly impact the likelihood of recovery.

In our analysis of the timing and percentages of plots that reached the restoration target, we found that over 75 percent of both CCV and non-CCV plots reached all restoration targets within 50 years (Appendix 2.1, Figure 2.A1a), and the average recovery time was even shorter (19-25 years to reach the target density and 14-26 years to reach the target canopy cover, depending on the simulation; Appendix 2.1 Figure 2.A1b). The only plots that did not reach the canopy cover target were observed to have zero trees during the field data collection.

CCV plots did not consistently outperform non-CCV plots. When we evaluated the timing of restoration across age classes, we found that CCV plots in the youngest and oldest age classes tended to reach the target density before non-CCV plots, but the opposite was true for 5-20-year-old plots in most simulated wildfire scenarios (Figure 2.6). Both CCV and non-CCV plots reached the canopy target on similar timescales or with non-CCV plots reaching the target canopy cover more quickly (as in the 5-10-year age class). Collectively, these provided mixed support for our first hypothesis that the beneficial effects of CCV might be apparent on our simulation timescale if not in the observational study.

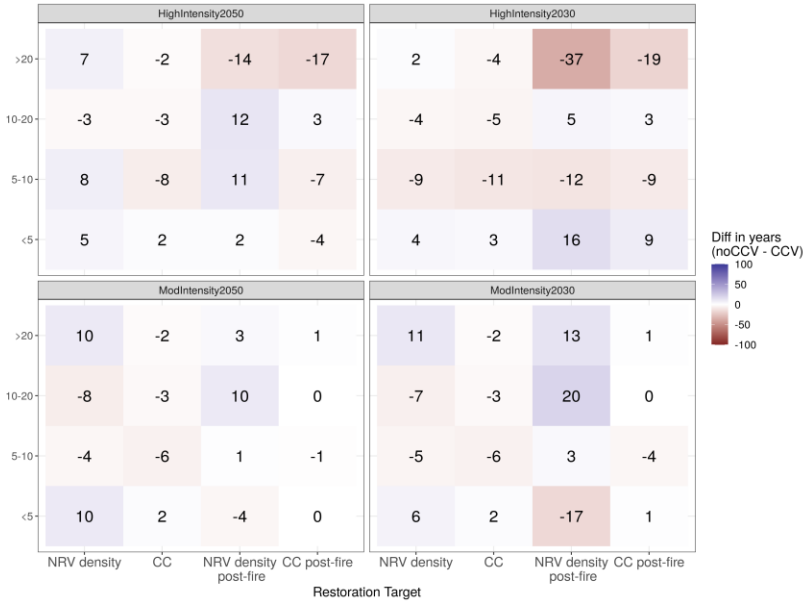

Figure 2.6: Difference in the average number of years that CCV versus non-CCV plots take to achieve the restoration target. The horizontal axis indicates different restoration targets, the vertical axis indicates different age classes of planted stands, and each grid pertains to a different wildfire simulation.

Similarly, we found mixed support for our hypothesis that the benefits of CCV might be apparent after a simulated wildfire and reflect impacts on wildfire resilience: several age classes reached the target density more quickly in CCV compared with non-CCV plots, but other age classes had the opposite effect. When simulated wildfires were moderate-intensity, the highest and lowest elevation plots demonstrated our hypothesized pattern: CCV plots met post-fire target densities more quickly, even

where the overall target density indicated neutral or slightly negative effects of CCV (Figure 2.7). The strongest support for CCV was apparent in low-solar-radiation sites experiencing high-intensity wildfire; these plots also tended to reach density, canopy cover, and post-fire canopy cover targets very quickly. (Figure 2.8). In moderate-intensity wildfire scenarios, however, low-solar-radiation plots also were less likely be resilient to the simulated wildfire in terms of the target density; a relatively low percentage of these plots reached the post-fire density target within 50 years, and it ultimately took 58-74 years for those that ultimately reached this restoration target.

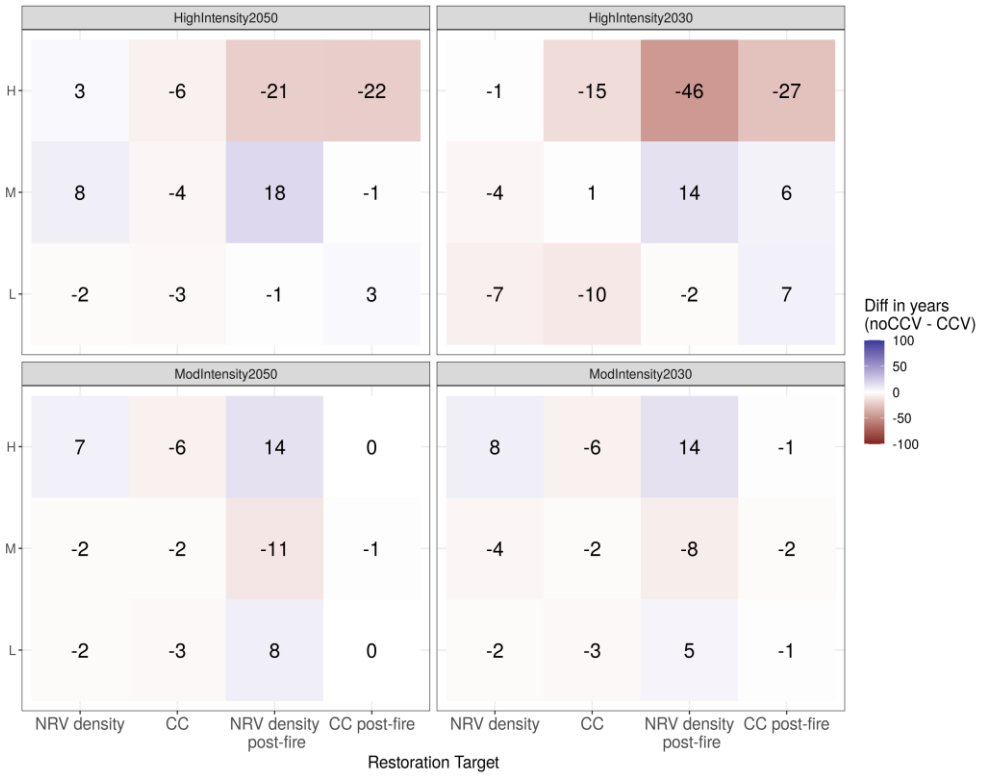

Figure 2.7: Difference in the average number of years that CCV versus non-CCV plots take to achieve the restoration target. The horizontal axis indicates different restoration targets, the vertical axis indicates different elevation classes of planted stands, and each grid pertains to a different wildfire simulation. L refers to "low" elevation sites (those within the lowest quartile of planted areas within the sampled wildfire perimeters), H refers to "high" elevation sites (upper quartile) and M refers to all others.

Figure 2.8: Average number of years before each plot type reached the restoration target (left), and percentage of plots that reached the restoration target within each bin (right). The horizontal axis indicates different restoration targets, the vertical axis indicates different solar radiation classes and treatment statuses of planted stands (e.g., CCV L refers to low-solar-radiation plots that had CCV treatments), and each grid pertains to a different wildfire simulation.

Discussion

We found mixed effects of CCV treatments on the likelihood of stands reaching their restoration targets. We did not find that CCV was associated with reaching the target stand density, and it was negatively associated with the stand reaching the target canopy cover. This was surprising, as we expected that any negative physical effect of CCV on canopy cover (e.g., removing naturally regenerating tree competitors in addition to shrubs) would negatively impact density estimates as well. That CCV would have a negative effect on reaching the target canopy cover was also surprising but may reflect the potential facilitative rather than competitive interactions between trees and shrubs (see e.g., Gomez-Aparicio et al. 2004; Werner et al. 2019). Specifically, it is possible that plots with CCV have less robust tree seedlings due to shrub removal and associated shade loss and increase in microsite aridity; this scenario would generate negative effects on canopy cover (which is more closely related to tree growth) but would be less influential on tree density (which is more closely related to dispersal and establishment). While we did find that several measures of tree health appeared greater for CCV in our field study (Part I: emergence, absolute height), we were also limited in our ability to summarize tree

health through observations at the plot level. By contrast, the simulation study enabled a more holistic view of whether the quantity and condition of trees within the entire plot was sufficient to meet restoration criteria.

Many of the covariates in our statistical models were consistent with our expectations based on ecological theory, which increased our confidence in the simulation model. For example, the starting density and canopy cover increased the likelihood of reaching the canopy cover target. It was less associated with the density target; this may be because the NRV target had an upper density limit that was exceeded even in the starting time period for several plots. The interaction between starting density and seedwall distances similarly highlights the important role of natural regeneration: at high starting densities, the likelihood of reaching the target increases as seedwall distance increases (i.e., less natural regeneration). At low starting densities, the likelihood increases only if seedwall is close (distance is low). This is consistent with our expectation that density targets can be reached either by the trees present from the initial conditions or through natural regeneration enabled by nearby trees. However, the seedwall distance coefficient also highlights that distance can be beneficial: particularly in moderate-intensity fires, the likelihood of reaching the target increased with seedwall distance. This is likely due to the higher survival of trees within the stand; any influx from nearby trees potentially pushes the density above the NRV target.

In addition to investigating the drivers of restoration success, we also calculated the fraction of plots that actually reached the restoration targets and the time it took to reach those targets. Recovery rates were fairly high, particularly for reaching the canopy cover targets (Appendix 2.1, Figure 2.A1). Fewer plots met density targets, but with the exception of near-term high-intensity fires they tended to be met within 1-2 decades of our chosen cutoff (50 years). As expected, near-term high-intensity fires resulted in a much longer ecological recovery period.

Few plots demonstrated our hypothesized patterns – first, that CCV effects may be apparent from initial recovery patterns (“NRV density”, “CC”), and second, that they may especially be apparent from

recovery after simulated wildfires (“NRV density post-fire”, “CC post-fire”). Wetter sites (low solar radiation; e.g., north-facing slopes) demonstrated these patterns, but only under simulations that included high-intensity wildfires. Given the increasing prevalence of these types of wildfires (Steel et al. 2018; Safford et al. 2022 Apr), this may be the most realistic scenario. Regardless, this pattern elucidated an important trend in our data: the continued relevance of high tree density. Wetter sites recovered relatively quickly under high-intensity wildfires but reached their post-wildfire density target relatively infrequently and over longer periods of time after moderate-severity wildfires (Figure 2.8). We found that many of the non-recovered and slowest-recovered plots in fact had too high of a density to meet the threshold – a pattern also apparent from the fact that post-fire canopy cover thresholds were much more quickly met. In this case, the moderate-intensity simulated fire failed to thin the trees sufficiently, whereas the high-intensity wildfire facilitated the recovery of a stand density within the natural range of variation. While we were aware from the observational study that several stands started off with a density of trees that exceeded ecological targets, this pattern demonstrated the persistence of these trends from both in situ survival and likely from simulated regeneration as well.

Broader significance

Our field and simulation studies suggest that CCV potentially has near-term positive effects on the emergence of planted trees above the shrub canopy – and therefore the growth rate and recovery of the forest stand – but its long-term benefits are less certain. Our plot summaries revealed that fewer plots with CCV met their restoration targets, and our regression analysis indicated that CCV did not significantly influence the likelihood of reaching restoration targets and may even have decreased the likelihood of reaching 10 % canopy cover.

The benefit and challenge of our field-collected data is that they came from planted stands established on National Forest lands for purposes other than research. There could have been an element of randomness in which plots did nor did not have CCV (e.g., if it was planned but not executed for logistical or financial reasons), but it is also possible that CCV was planned for areas that were expected

to have compromised tree growth from shrub competition. This could have obscured some of the impact of CCV in our analysis (Simler-Williamson and Germino 2022). On the other hand, the benefit of our study design is realism: we observed CCV at levels actually implemented by land managers.

Our study also used a simulation approach to understand potential long-term outcomes from stands with and without CCV. A significant downside to our framework was that the modeling software we used was unable to directly model tree-shrub interactions; we are unaware of alternate options that have a comparable level of biological detail for tree growth. However, the framework allowed us to explore how initial forest structure – including with and without CCV – impacted long-term forest structure. More importantly, it allowed us to simulate wildfire disturbances, which are pervasive in YPMC ecosystems. Prior studies evaluating CCV as well as shrub effects more generally have been able to detect near-term and direct effects (McDonald and Fiddler 2010; Zhang et al. 2013), but they do not address whether CCV is relevant in terms of resilience to wildfire. Given that land management agencies are increasingly transitioning from planting in a post-harvest context to planting as a forest restoration mechanism (Dumroese et al. 2019), it is important to evaluate the long term effects for forest recovery.

With the scale of post-wildfire restoration need, it is not only important to identify the ecological impact of land management practices but also the cost-effectiveness. On average, CCV costs $281 per acre (Appendix 2.2). Planting is somewhat less expensive, averaging $192 per acre (but note that our data pertain only to outplanting costs). While our study identified a potential, marginally significant effect of CCV in the observational study, the simulation study suggested that CCV may not be a worthwhile investment. In fact, both planted stands with and without CCV had relatively high rates of ecological recovery. This would suggest that landscape-level forest recovery may be accelerated more through investments in planting than investments in CCV.

We recognize that this finding departs from standard reforestation practices in the YPMC ecosystem,. While we suggest that this may be due to our selected metrics for forest restoration (i.e., density metrics consistent with the natural range of variation rather than a yield-based approach), we

cannot rule out the possibility of confounding effects in our observational study. We therefore propose a next generation of forest growth studies: field trials with randomized CCV treatments, but in densities commensurate with ecological targets. We also identified several conditions in which CCV may be most likely to accelerate recovery and resilience to subsequent fires; this may guide plot placement for the proposed research, and more importantly it suggests areas where CCV treatments may be more successfully deployed by practitioners. For example, it may be more beneficial to implement CCV in wetter sites, particularly where high-intensity fires are expected. Similarly, our study suggests that CCV may be more effective in promoting fire resilience in low- and high-elevation sites where moderate intensity fires are expected. While future wildfire intensity cannot be predicted, practitioners may consider implementing this strategy in areas with other wildfire-mitigation practices in place.

Contemporary forests will increasingly be shaped by the frequency, intensity, and spatial arrangement of wildfires – initially due to effects on existing trees and subsequently due to effects on regeneration (see e.g., Coop et al. 2020). Climate change is likely to impact multiple facets of this process, from the timing and behavior of the wildfires themselves (Abatzoglu and Williams 2016) as well as the survival and growth of regeneration – both natural and planted (Dobrowski et al. 2015). In this context, it will be necessary to adapt and fine-tune land management practices to accommodate the changing ecological drivers as well as shifting land management goals. Our study provides a modest step towards rethinking the application of vegetation management treatments in an ecological context. We anticipate that reassessing these types of land management practices will aid in forest managers' efforts to restore large landscapes after wildfires.

Acknowledgements

We thank Adam Fuentes for help collecting field data and numerous Forest Service staff for their advice and help in accessing plots. This study was funded by the USDA Forest Service's Western Wildland Environmental Threat Assessment Center.

Appendix 2.1: Supplemental data and results

Field observations

Figure 2.A1 and the summary statistics in Table 2.A1 include environmental and relevant ecological characteristics for regeneration and tree growth. We selected plots within CCV and no-CCV treatment polygons according to their rough comparability in aspect (see *Methods*) but no other plot-level characteristics. Therefore, we performed a post-hoc analysis of the dataset to confirm that the treatment types were balanced in terms of their site conditions.

Figure 2.A1

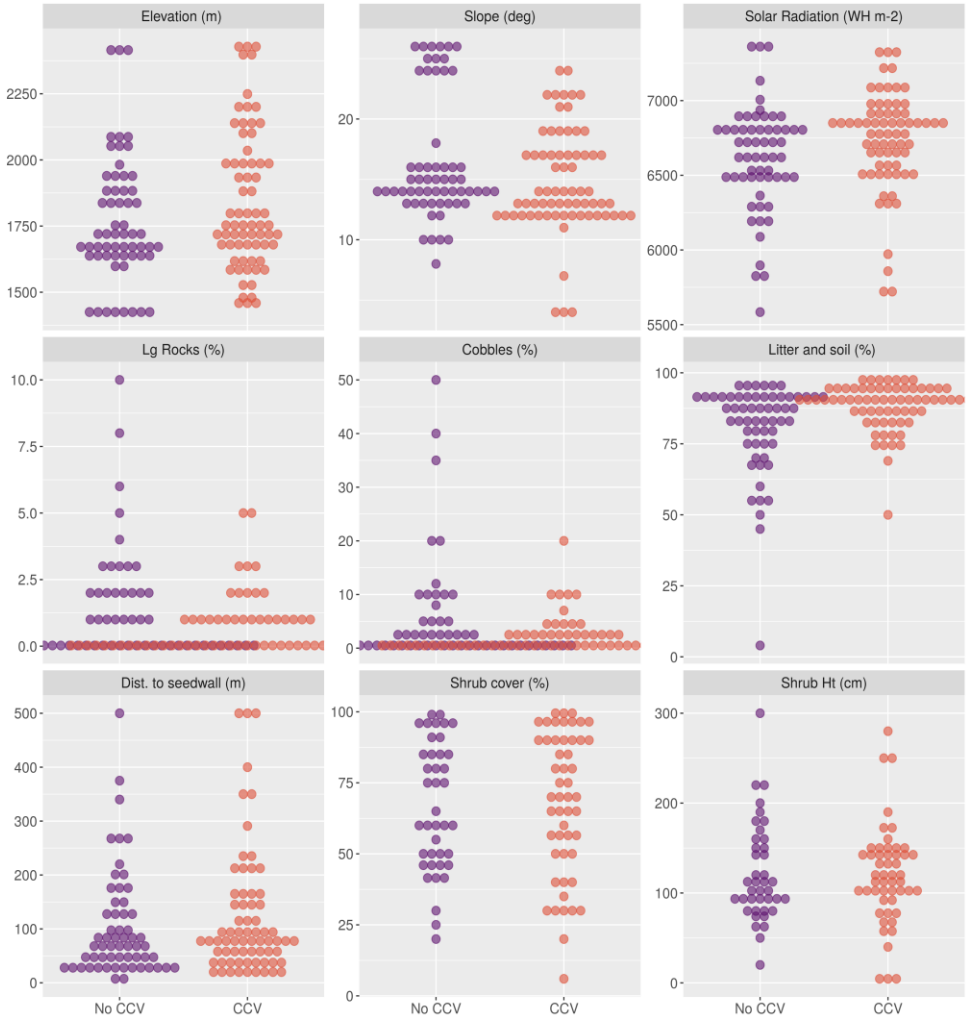

Table 2.A1

CCV	Elev	SolarRad	Slope	LgRocks	Cobbles	LitterSoil	ShrubPct	ShrubHt	SeedwallDist
N	1771 (237)	6618 (355)	16.5 (5.1)	1.2 (2)	4.9 (9.8)	81.1 (16)	66.5 (22.6)	121.8 (55)	102 (98.7)
Y	1841 (262)	6736 (332)	14.8 (4.3)	0.7 (1.1)	2 (3.4)	88.2 (8)	68.1 (25.3)	118.8 (54.8)	121 (117)

Simulation model summaries

Figure 2.A1.1

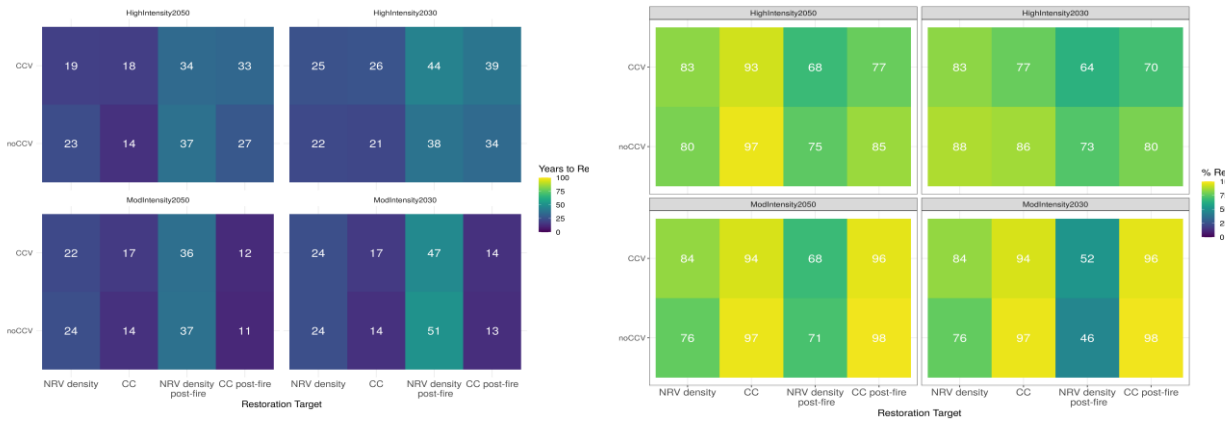

Figure 2.A1.1: Average number of years before each treatment type reached the restoration target (left), and percentage of plots in each treatment type that reached the restoration target (right). The horizontal axis indicates different restoration targets, the vertical axis indicates treatment statuses of planted stands, and each grid pertains to a different wildfire simulation.

Appendix 2.2: Estimating costs of planting and the control of competing vegetation treatments in planted stands.

Methods

Statistical model

We modeled forest management costs as a function of task characteristics, environmental and biological conditions, and logistical difficulty, and we developed separate models for planting and the control of competing vegetation (CCV). We included a random intercept for the last fire that burned prior to the management activity, thereby capturing regional and temporal variation not already accounted for in the statistical model. Our model took the form:

$$y_{ij}^{Pl,CCV} = \alpha_j + \beta_i X_{ij} + \epsilon_{ij}$$

where y_{ij} refers to the per-acre costs of planting ("Pl") or the removal of competing vegetation like shrubs ("CCV"), adjusted to 2020 dollars for comparability across years. Our model accounts for outplanting costs, but it does not account for the seed collection nor nursery costs, which can substantially increase the total cost (see estimates in Fargione et al. 2021).

Data

Our primary dataset was the Forest Activity Tracking System ("FACTS"), a spatial database of the USDA Forest Service's (USFS) management activities (USDA Forest Service 2022). This dataset contains a separate entry for each instance of a management activity at a particular location (delineated as a polygon); we focused on management categorized as "Planting" and "Tree Release and Weed" (CCV), but we also incorporated relevant information about other post-fire management that occurred on-site ("Site preparation" and "Salvage logging", as described below). With the FACTS dataset, we extracted information on each activity's cost, the method used for the activity (e.g., manual vs. chemical removal of competing vegetation), and the equipment used (e.g., hoedads vs. augers for planting and hand tools vs. power tools for CCV). Ultimately, we also decided to aggregate polygons that had the same management treatment, equipment, cost, and award date, and which were located within 1 km of each

other. This decision was based on a preliminary review of several planting contracts and conversations with USFS silviculture staff. Through these efforts, it became apparent that a single per-acre contract price could apply to several different plots, implying that the level of cost aggregation could be different than units as entered into the database. Our aggregation process was an attempt to evaluate costs at a scale that represented the actual contract system, and our aggregation procedure is described more fully in Supplement 1.

We used other data sources to estimate values within the spatial polygons described in FACTS. We summarize key variables below and include further detail in Supplement 1.

To represent the productivity and biomass at the site, we used environmental and biological variables that included solar radiation (a proxy for site aridity) as well as the number of years between the last fire and the management date (a proxy for the amount of vegetation that regrew post-fire). We estimated solar radiation using the Area Solar Radiation tool in ArcGIS, specifically drawing estimates from the summer solstice. We also included site elevation (U.S. Geological Survey 2017) as a coarse estimate of productivity.

We used several metrics to capture the difficulty of working at a particular site:

Steepness. To represent steepness, we calculated slope from the digital elevation model (U.S. Geological Survey 2017).

Distance between the site and the closest major road (US Census Bureau 2019). We used the Cost Distance function implemented in ArcGIS and assumed a tenfold difficulty (cost) increase when the travel path switched from roads to walking.

Management history. We assessed what fraction of a particular management unit had a site preparation treatment ("Site Prep") or salvage logging ("Salvage") prior to planting or release; this variable was intended to capture whether the site was more accessible due to the cutting and/or removal of shrubs, standing dead trees, and coarse woody debris. For release treatments, we also computed

whether there had been previous release treatments at the site ("Prev Release"). All of these calculations were performed by computing the area overlap of the prior management treatment (site prep, salvage logging, release) and the focal management unit (planting, release), considering only treatments that occurred between the last fire and the post-fire planting.

For all raster-based maps (solar radiation, elevation, slope, cost distance), we computed area-weighted estimates using the "sf" and "terra" packages in R v3.6.3 (Pebesma 2018; R Core Team 2020; Hijmans 2022).

Last, we included several fixed effects:

- Year. This variable is intended to capture intertemporal variation in costs; for example, costs may be higher in one year if many units require treatment
- National Forest. This variable is intended to capture jurisdictional differences; for example, if one NF tends to negotiate lower prices.
- Zone. This variable is intended to capture differences between broad regions. If crews tend to be based on one part of the state, then prices may be set more locally than the full dataset.

We generated predicted costs based on mean variables of environmental conditions and for multiple fixed effects (all years, two representative National Forests in the Sierra Nevada, and all zones).

Results

Table 2.A2.1 Cost of treatment in 2020$

Type	Median	Mean	SD
CCV	255	281	151
Planting	167	192	102

Table 2.A2.2

	Planting			**CCV**		
Predictors	Estimates	CI	p	Estimates	CI	p
(Intercept)	142.5	52.93 – 232.07	**0.002**	204.58	117.59 – 291.57	**<0.001**
Slope (mean)	10.26	-9.94 – 30.46	0.32	-11.04	-34.01 – 11.93	0.346
Area (m2)	**-10.13**	**-16.88 – -3.38**	**0.003**	-3.3	-12.29 – 5.70	0.473
Low Acreage (0/1)	**154.4**	**4.22 – 304.58**	**0.044**	-115.23	-291.59 – 61.14	0.2
Area*LowAcreage01	273.97	-63.67 – 611.60	0.112	-209.11	-554.77 – 136.55	0.236
Years since fire	0.84	-1.37 – 3.04	0.457	-1.62	-3.73 – 0.48	0.13
Solar Radiation	12.31	-14.97 – 39.58	0.376	-17.62	-52.10 – 16.86	0.317
Site Prep (%)	-27.92	-62.73 – 6.89	0.116	6.28	-34.49 – 47.06	0.763
Salvage Logged (%)	13.87	-8.58 – 36.31	0.226	5.6	-26.68 – 37.88	0.734
Distance to primary road	-0.02	-0.05 – 0.01	0.129	**0.04**	**0.01 – 0.07**	**0.016**
Elevation	-7.51	-27.59 – 12.58	0.464	0.78	-27.49 – 29.05	0.957
Equip:Auger	11.15	-16.69 – 38.99	0.433			
Equip: Hand(misc)	**-77.17**	**-148.10 – -6.23**	**0.033**			
Equip: Shovel(class)	30.74	-24.07 – 85.55	0.272			
Equip:NA	-13.24	-60.37 – 33.90	0.582	-2.44	-46.51 – 41.64	0.914
Equip: Chip/Shred(class)				**192.25**	**137.59 – 246.90**	**<0.001**
Equip: Hand(class)				**47.28**	**15.67 – 78.88**	**0.003**
Equip: HeavyEquip(class)				-49.8	-222.49 – 122.89	0.572
Equip: Mechanical(class)				**36.47**	**0.79 – 72.15**	**0.045**
Equip: Sprayer(class)				-13.1	-59.62 – 33.42	0.581
Zone: Great Basin	-2.63	-150.32 – 145.05	0.972	-111.83	-327.64 – 103.98	0.31
Zone: North Coast	-24.68	-88.06 – 38.70	0.445	-59.09	-129.89 – 11.71	0.102
Zone: Northern Sierra	-21.93	-83.46 – 39.61	0.485	32.15	-36.37 – 100.67	0.358
Zone: Southern CA	**80.34**	**11.44 – 149.25**	**0.022**	**-104.78**	**-201.45 – -8.12**	**0.034**
Angeles NF	-40.48	-113.87 – 32.92	0.28	44.61	-58.78 – 148.00	0.398
Cleveland NF	**483.1**	**344.78 – 621.41**	**<0.001**	33.74	-144.61 – 212.09	0.711
Klamath NF	17.74	-25.28 – 60.76	0.419	**-104.38**	**-154.66 – -54.11**	**<0.001**
Lassen NF	38.21	-14.80 – 91.22	0.158	-58.68	-125.06 – 7.70	0.083
Los Padres NF	-51.4	-228.28 – 125.49	0.569	-147.06	-344.07 – 49.94	0.143
Modoc NF	12.42	-44.37 – 69.21	0.668	-10.16	-82.58 – 62.27	0.783

Plumas NF	28.72	-17.65 – 75.08	0.225	-39.57	-108.07 – 28.92	0.257
Sequoia NF	-1.33	-98.61 – 95.94	0.979	-48.06	-177.40 – 81.28	0.466
Sierra NF	**133.41**	**32.85 – 233.96**	**0.009**	-55.75	-159.08 – 47.59	0.29
Stanislaus NF	-19.46	-92.00 – 53.09	0.599	-44.19	-135.69 – 47.30	0.344
Year: 2001	-29.38	-108.09 – 49.33	0.464	50.96	-24.60 – 126.51	0.186
Year: 2002	-3.58	-80.46 – 73.29	0.927	47.82	-33.90 – 129.55	0.251
Year: 2003	-36.71	-135.65 – 62.24	0.467	**146.37**	**75.10 – 217.64**	**<0.001**
Year: 2004	-27.55	-109.09 – 53.98	0.508	**96.08**	**23.25 – 168.91**	**0.01**
Year: 2005	12.53	-66.13 – 91.18	0.755	-11.6	-92.33 – 69.12	0.778
Year: 2006	-6.76	-88.28 – 74.76	0.871	35.88	-36.29 – 108.05	0.33
Year: 2007	32.68	-45.02 – 110.39	0.41	47.57	-26.30 – 121.43	0.207
Year: 2008	-26.19	-103.11 – 50.73	0.505	50.79	-35.40 – 136.97	0.248
Year: 2009	25.86	-52.56 – 104.27	0.518	**155.04**	**77.87 – 232.21**	**<0.001**
Year: 2010	-29.27	-104.32 – 45.77	0.445	**100.23**	**24.56 – 175.90**	**0.009**
Year: 2011	-3.63	-79.13 – 71.86	0.925	**125.34**	**55.34 – 195.35**	**<0.001**
Year: 2012	-47.54	-127.23 – 32.15	0.242	**80.36**	**9.89 – 150.82**	**0.025**
Year: 2013	27.78	-55.16 – 110.73	0.511	**153.28**	**73.03 – 233.53**	**<0.001**
Year: 2014	10.48	-70.01 – 90.97	0.799	**101.96**	**24.85 – 179.06**	**0.01**
Year: 2015	23.57	-54.85 – 102.00	0.556	**111.11**	**33.29 – 188.92**	**0.005**
Year: 2016	27.09	-49.89 – 104.08	0.49	**174.25**	**98.91 – 249.58**	**<0.001**
Year: 2017	-1.66	-78.82 – 75.51	0.966	**187.6**	**113.45 – 261.75**	**<0.001**
Year: 2018	-23.6	-103.47 – 56.26	0.562	**129.73**	**53.53 – 205.93**	**0.001**
Year: 2019	-13.28	-92.64 – 66.08	0.743	**110.34**	**32.60 – 188.09**	**0.005**
Year: 2020	-5.29	-86.43 – 75.84	0.898	41.87	-35.99 – 119.74	0.292
Year: 2021	1.9	-80.01 – 83.80	0.964	**90.68**	**15.87 – 165.49**	**0.018**
Random Effects						
σ2		5186.28			11573.81	
τ00		3252.13 Fire			4484.49 Fire	
ICC		0.39			0.28	
N		164 Fire			150 Fire	
Observations		587			726	
Marginal R2 / Conditional R2		0.244 / 0.535			0.287 / 0.486	

Table 2.A2.2. Model coefficients predicting the cost of planting (left columns) and control of competing vegetation (right columns) using data from the Forest Service Activity Tracking System (USDA Forest Service 2022)

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Chapter 3. Snag persistence and structure under contrasting fire severities

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Abstract

The prevalence of wildfire in the Western United States and the increasingly high-severity component of burned areas has increased the salience of standing dead trees ("snags") in the post-wildfire landscape. Snags provide habitat for many wildlife species but may be particularly important to avian species that use them as nesting or foraging substrates. In yellow pine and mixed-conifer regions of the Sierra Nevada, species such as the black-backed woodpecker preferentially use small-diameter, densely packed snags, whereas species such as the white-headed woodpecker and great gray owl preferentially use larger-diameter snags. We investigated the availability and persistence of these snag types following a wildfire in the Sierra Nevada (CA, USA). First, we investigated drivers of snag fall, including tree-level characteristics (e.g., size, fire injury) as well as the environmental context (e.g., fire severity). We then investigated differences in snag availability on the landscape and compared our empirical results with management targets and habitat requirements for the aforementioned avian species.

The probability that a given snag would fall was driven by species identity and size but not any of our measures of tree injury. However, we did find that the presence of pouch fungus was correlated with increased likelihood of snag fall. We found that a higher initial density of snags–rather than our fire severity variable – was correlated with a higher likelihood of snag fall.

As expected, areas characterized as moderate-to-high severity versus low severity also had a greater density of snags. The density of these snags met the post-fire management targets of the federal jurisdiction in both severity classes. However, the densities we observed were quite low compared with the potential habitat requirements for avian species we investigated.

Our findings of tree-level snag persistence are largely consistent with other work, though our results also suggest that wildfire severity, a commonly used metric of post-fire condition, is not a useful predictor of persistence. By focusing on the significant predictors of persistence, forest managers may be more strategic at retaining snags likely to remain standing for wildlife habitat. We also found that low- and moderate-to-high- severity plots provided a diversity of snag types, though the latter contained a greater number of these snags. These results support the increased use of fire to increase and improve habitat availability, especially if controlled through a prescribed burn or managed wildfire.

Introduction

Wildfires are increasing in size throughout the Western United States, both in terms of area burned as well as the amount of land burning at high severity (Parks and Abatzoglou 2020). In yellow pine-dominated and mixed-conifer regions of the Sierra Nevada (CA, USA), areas burning at high severity may even be increasing disproportionately to the overall increase in area burned (Mallek et al. 2014, Steel, Koontz, and Safford 2018, Safford et al. 2022). These trends have increased the salience of standing dead trees ("snags") in the post-wildfire landscape (Safford and Stevens 2017).

Snags have always been important features in forest ecosystems, mediating nutrient flows in the ecosystem and providing habitat for plants, animals, and fungi (reviewed in Harmon et al. 1986). Much of the literature on snag function pertains to its role as wildlife habitat, such as by providing nesting and foraging sites (see e.g., Saab, Russell, and Dudley 2009; White et al. 2016). However, there are also several incentives to remove snags following a disturbance event like a wildfire. If harvested through "salvage logging", snags can provide an immediate financial return through the timber sale as well as a

potential longer-term benefit if salvage logging is a precondition or a funding mechanism for reforestation. When left on-site, snags can contribute "fuels" to the ecosystem—initially as standing ladder fuels that are at risk for lightning strikes, torching, or which present a hazard for management or fire personnel, and later as fallen surface fuels that can substantially increase the fuel load on the landscape (Hood et al. 2021). While fire models tend to focus on the contribution of smaller fuels to fire spread, larger woody debris like fallen dead trees may provide a flammable substrate for embers to catch, retain fire that would otherwise pass more quickly through the landscape and potentially result in mass fire behavior as weather conditions change, and increase the hazards and response effort of fire managers (Brown, Reinhardt, and Kramer 2003; Stephens et al. 2022). The conflicting benefits of snag retention for wildlife management objectives and snag removal for economic and fire management objectives has produced an array of recommendations for how to achieve multiple objectives on a landscape (Ganey 2016; Hutto 2006). For example, snag density targets and size targets based on wildlife-related criteria can help land managers focus removal efforts on snags that do not provide these services. Other examples include snag retention strategies that group snags, scatter snags or a mix of scattering and grouping snags.

In the yellow pine and mixed-conifer (YPMC) regions of the Sierra Nevada, nearly a third of avian and mammal species use snags for nesting, denning, foraging, communication, and cover (Raphael and White 1978, 1984; Farris and Zack 2005). Species vary in their use of particular snags, primarily driven by tree-level parameters of size (height and diameter) and soundness, and stand-level parameters of density, distance to unburned forest edge, burn severity, and vegetation type (Fontaine and Kennedy 2012; Saab et al. 2002; White et al. 2016). The requirements of each species or group depend on several life history factors, including nesting or denning substrate, diet or foraging strategy, and excavation ability. Wildlife species of particular interest include those that are strongly associated with burned forest, such as the black-backed woodpecker (*Picoides articus*; Bond, Siegel, and Craig 2012), those that depend on snags for survival or reproduction, such as cavity-nesting birds and small mammals (Raphael and White 1978), and those that are of management and conservation interest, such as the California spotted

owl (*Strix occidentalis*), great gray owl (*S. nebulosa*), and various bat species (Chiropterans; USDA Forest Service 2007). Woodpeckers are considered a keystone species in these systems because they create cavities that would be otherwise limited in the YPMC zone but are used by many other species ("secondary cavity users", Tarbill, Manley, and White 2015; Trzcinski et al. 2022). Therefore, managing snag requirements of woodpeckers may provide habitat for more than thirty vertebrate species in the Sierra Nevada, from mountain bluebirds (*Sialia currucoides*) to Northern flying squirrels (*Glaucomys sabrinus*). Black-backed woodpeckers are often considered burn specialists: their strong excavation ability allows them to create cavities in recently killed trees of relatively small diameter, and they tend to prefer areas with high densities of snags (~200 stems per ha; Stillman et al. 2019; Tarbill, White, and Manley 2018). In contrast, white-headed woodpeckers (*Dryobates albolarvatus*) are weak excavators that tend to select large-diameter (>50 cm diameter at breast height, "DBH"), highly decayed snags in stands with low canopy cover (Tarbill, Manley, and White 2015; Wightman et al. 2010). Snags are also important to nocturnal raptors that use them as both hunting perches and nest substrates. California spotted owl, while largely associated with late seral stages, may also nest and forage in burned forest, and they tend to use stands with medium to large snags (>25 cm DBH, Kramer et al. 2021; >50 cm DBH, Call, Gutiérrez, and Verner 1992). Great gray owls also use large snags (> 100 cm DBH and > 18 m height) as hunting perches near meadows and recently burned or logged forests (Duncan 1997; Siegel et al. 2019; Wu et al. 2015). Thirteen Chiropteran species in the Sierra Nevada roost in snags, with most species using large (>100 cm DBH and >40 m height) and sound (low-decay) snags in open stands (Blakey et al. 2019; Mirts et al. 2021; Ormsbee and McComb 1998). These and other wildlife preferences have contributed to the recommendations for multi-use management mentioned previously as well as in guidelines for specific land jurisdictions. For example, the relevant planning document in our study area includes a snag density target of 2-40 snags per 4 hectares (USDA Forest Service 2019).

Given the importance of snags to these and other wildlife species, many studies have been conducted to characterize both snag requirements of focal species as well as to characterize snags in a

variety of landscapes. Two important facets of snag dynamics as reported in the literature are the amount of time the snag remains standing (or, inversely, the fall rate) and the recruitment rate (the rate at which live trees die and become snags). In post-wildfire conditions, several studies indicate that the highest fall rates occur in the first decade after a wildfire; for example, Raphael and Morrison (1987) found that most fire-killed trees fell within 10 years of a fire, regardless of species or size, and Passovoy and Fule (2006) found that fall rates generally increased from about 10-20% four years post-fire to 50-60% eight years post-fire. However, there is also some evidence of snag longevity past the first decade: Everett et al. (1999) estimated that for large Douglas-fir (*Pseudotsuga menziesii*), 40% will remain standing after 80 years post-fire.

Species identity and snag size likely play a role in determining post-fire snag longevity. Pines (*Pinus* spp.) are likely to fall more quickly than true fir (*Abies* spp.), incense cedar (*Calocedrus decurrens*), and Douglas-fir (see e.g., Grayson, Cluck, and Hood 2019; Morrison and Raphael 1993; Russell et al. 2006); and smaller-diameter trees are likely to fall more quickly than larger-diameter trees (see e.g., Morrison and Raphael 1993; Grayson, Cluck, and Hood 2019). Possible explanations for these differential rates include different structural material between species (e.g., heartwood-to-sapwood ratios or rooting structures) and different volumes of structural support (heartwood) present in small versus large snags. In the case of fire-killed trees, fire-caused injury would seemingly influence tree structure and therefore fall rates. Grayson et al. (2019) found that crown injury is associated with decreased longevity among large white fir (*Abies concolor*) and ponderosa pine (*Pinus ponderosa*) but increased longevity among smaller-diameter trees; however, tree injury remains an understudied aspect of snag dynamics.

We aimed to build on the literature investigating wildfire as a snag-generating process, focusing on whether patterns of fire severity are manifested in terms of snag availability. Fire severity is a common metric of fire effects, often referring either to the percentage of mortality in trees or to the amount of deviation in vegetation cover pre- and post- fire (Morgan et al. 2014), and accordingly it is often used to

plan post-wildfire management. Therefore, we were interested in evaluating snags across a severity gradient due to its putative utility for land managers (sensu Ganey 2016). Additionally, we hypothesized that severity may correlate with snag fall by capturing important patterns related to wildfire as a mortality agent. Fire severity is related both to the intensity of the wildfire as it burns as well as the residence time of the wildfire (National Wildfire Coordinating Group n.d.), and both factors impact the structural integrity of the tree. For this reason, we investigated whether severity sufficiently captured patterns of snag fall and snag availability on the landscape.

We used a unique dataset tracking snags in large plots for 10 years after a wildfire and aimed to answer the following questions:

- What factors influence whether and when a snag will fall?
- How does snag component of forest structure change over time and across a fire severity gradient?
- Is fire severity associated with habitat availability for snag-dependent avian species?

Methods

Data Collection

Plot identification and surveys

Our dataset is composed of snag surveys from the Sierra National Forest in the central-southern Sierra Nevada in California, USA. The surveys occurred in elevations ranging from 1528-2337 meters. This study area has a largely Mediterranean climate, with an average January minimum temperature of -1 ^{o}C, average July maximum temperature of 28 ^{o}C, and 970 mm precipitation annually but with a substantial amount of precipitation falling as snow in the winter (PRISM Climate Group 2017; USDA Forest Service 2019). In 1994, a wildfire ("Big Creek") burned approximately 2300 ha (5700 acres), and plots were established soon after to study post-wildfire successional processes in the absence of active management like logging and planting. The latter actions were widely implemented, including surrounding the study plots. Plots were initially identified by randomly selecting 5-acre polygons on a

grid spanning the fire area (centered at -119.27, 37.21), ensuring that these areas were within forested land cover and within 30 minutes hike of the nearest road, and classifying them based on topography, vegetation type, and fire effects. The final 40 plots were selected to meet stratification conditions within a factorial design that included two severity strata (areas experiencing low fire severity and areas experiencing moderate- to high- severity), two vegetation types (ponderosa pine- dominated or mixed conifer (> 10 % fir)), and two slope positions (lower than or higher than halfway between a ridge and a creek drainage). As a result, there were 5 replicates of each combination of severity, vegetation type, and slope position. Figure 3.1 displays the distribution of plots across the landscape.

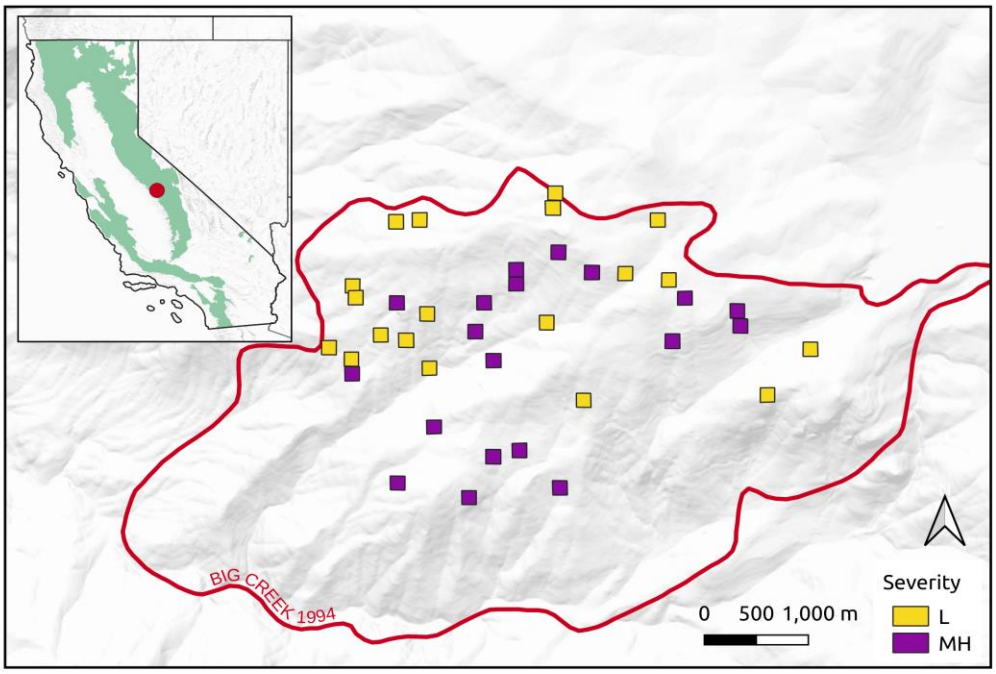

Figure 3.1: Study region, with the red perimeter showing the fire extent and square polygons indicating the snag plot locations. Low-severity (L) plots are shaded in yellow, and moderate-to-high-severity (MH) plots are shaded in purple. Green shading in the inset indicates areas with similar forest cover: California Wildlife Habitat Relationship (WHR) types for Jeffrey pine (JPN), ponderosa pine (PPN), Sierran mixed conifer (SMC), and white fir (WFR) as reported in the USDA Forest Service's EVeg map product (U.S. Forest Service 2019)

All snags were censused and resurveyed according to the following schedule:

- 1994: Big Creek fire
- 1995: Plot scouting and set-up (described above)
- 1996: Snags tagged, initial measurements collected, and condition assessed with respect to physical injury and biotic signs of decomposition (see Snag characteristics and Supplement 1)
- 1997, 1998, 2000, 2002, 2004: Snags resurveyed and measurements collected on height and condition according to customized condition codes.

Snag characteristics

In the initial survey, each snag was identified to species and measured for diameter at breast height, overall height, and the highest point of scorch ("scorch height"). Snags were also characterized in terms of their position in the stand (Dominant, Co-dominant, Intermediate, Suppressed), the percent of bark remaining, and the percent of the bole with limbs remaining. The survey also included descriptions of characteristics through "condition codes"; these conditions were assessed during each subsequent survey. Condition codes included estimates of needle consumption, whether the tree had a dead or missing top, whether the tree had a "cat face" (scar at the tree base), whether it had evidence of Polyporus volvatus ("pouch fungus") or other fungal fruiting bodies, and whether it seemed to have died due to stress rather than wildfire. During analysis, we added the variable "Scorch percent height", calculated as the ratio of scorch height to total height; the purpose of this variable was to serve as an estimate of how much of the tree was potentially injured by the fire.

Plot-level variables

We used publicly available datasets and map products to extract plot-level data for relevant topographic and other variables. Specifically, we used a 10-meter digital elevation model (U.S. Geological Survey 2017) and the "terra" and "sf" packages in R (R Core Team 2020; Pebesma 2018; Hijmans 2022) to calculate average elevation and slope within the plot area. We used the Geographic Resources Analysis Support System ("GRASS") in QGIS (GRASS Development Team, n.d.; QGIS

Development Team 2020) to calculate total irradiation at the summer and winter solstices as a metric of dryness; this method takes into account topographic shading and day length in addition to aspect when determining the heat load. We selected these particular dates under the assumption that the summer solstice might capture patterns related to photodegradation or other decomposition driven by heat and dryness whereas the winter solstice might capture patterns related to snow accumulation and decomposition driven by cool and wet conditions. Table 1 displays summary statistics for each of the plot-level variables. Mean elevation, slope, and solar radiation do not differ between low and moderate-to-high (hereafter also referred to as "higher") severity plots, suggesting that the severity stratification was relatively balanced with regard to other potentially important drivers.

We used an RdNBR-based fire severity map product (Miller and Thode 2007, U.S. Forest Service 2018) to identify whether plots burned at high, medium, or low severity. While fire severity was assessed on the ground during the plot selection process, this information was lost in intervening years and we resorted to an alternate source of this information during analysis. Based on the RdNBR method, 21 plots were classified as low-severity and 19 were classified as moderate- or high- severity. This suggests that originally one of the low-severity plots was considered to be moderate-to-high severity, but we proceeded with the analysis because the severity stratification was still quite balanced.

Last, we generated an estimate of snag density in each plot by simply summing the number of individual snags in each plot. As expected, low-severity plots had significantly lower densities of snags compared with the higher severity plots (Table 3.1)

Severity	Elevation (m)	Slope (deg.)	Solar radiation (June)	Solar radiation (Dec)	Initial density of snags
Low	1910 (273)	22 (6)	8626 (479)	705 (99)	42 (25)
Moderate-High	1888 (253)	24 (7)	8454 (686)	710 (107)	72 (11)

Table 3.1: Mean and standard deviation (in parentheses) of plot-level characteristics, summarized by fire severity class. The elevation, slope, and solar radiation (direct and diffuse in watt hours per m2) in June and December were not significantly different between severity types, suggesting that the sites are comparable. The initial density of snags was much higher in Moderate-High-severity plots, as expected by definition.

Analysis of snag fall

We used a Cox proportionate hazard model to evaluate factors associated with snag-fall. This form of regression accommodates "censored" data – in this case, snags for which there was no fall observed within the study period. In most cases, this was due to the snag remaining standing in the final survey; however, in a small number of cases (30 out of 2261), the snag fall year was not recorded so we identified that observation as censored after the last completed survey. This regression approach allowed us to include these censored observations without making assumptions about whether and when the snags fell.

Our model selection process involved testing plot-level and tree-level variables. We included species identity and diameter at breast height in the minimum model, and we included other variables if they improved the model fit after comparing AIC values. We tested interactions between species identity, diameter, and height, and we included a random intercept for each plot to account for variation not captured by our plot-level covariates.

Our final model estimated the hazard function (likelihood of fall at a particular timestep, given survival until that timestep) and took the form:

$$h(t) = h_0(t) \times exp(\alpha_j + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_p x_p)$$

where h_0 refers to a baseline hazard rate, α is a random intercept that captures plot-level variation, and the β coefficients refer to tree-level and plot-level covariates.

In addition to modeling fall rates for all species together, we tested each of the four most common species separately in order to assess whether there were species-specific drivers of fall rates.

Analysis of forest structure

We aggregated snags across plots to estimate densities, stratifying by severity to evaluate easily observable post-fire conditions and stratifying by size class to evaluate snags that may be more meaningful as wildlife habitat. First, we evaluated the densities of snags greater than 50 cm (20 inches), the size class targeted in the draft Sierra National Forest Management Plan (USDA Forest Service 2019). We also investigated this size class because it is preferred by the white-headed woodpecker (Wightman et al. 2010) and is more likely to support the California spotted owl (Call, Gutiérrez, and Verner 1992; Kramer et al. 2021), great gray owl (Wu et al. 2015), and several bat species (Blakey et al. 2019). We then specifically evaluated the densities of snags that met the conditions listed in Table 3.3, assuming that a snag was suitable if it was within the mean plus or mean minus one standard deviation. For example, for our black-backed woodpecker analysis, we tallied snags that were 25-43 cm dbh and 10-22 m tall. We chose this approach to capture the majority of suitable snags without broadening the range to include those that were only marginally suitable. We focused on height estimates from the initial survey period, and we also analyzed the data with only a minimum height cutoff to account for the fact that snags lose height through breakage over time and may become suitable after the initial survey period. In the black-backed woodpecker example, this amounts to tallying snags 25-43cm dbh and >= 10 m tall.

Focal wildlife species	DBH in centimeters	Height in meters	Source
Black-backed woodpecker	34 (9)	16 (6)	(Tarbill, Manley, and White 2015)
White-headed woodpecker	preferred: > 50 cm; potential: > 20 cm	-	(Milne and Hejl 1989; Tarbill, Manley, and White 2015)
Great gray owl	100.5 (30.3)	18.7 (8.1)	(Wu et al. 2015)

Table 3.3: Summary of habitat requirements for three bird species in the YPMC, including the diameter at breast height (dbh) and height associated with nesting sites.

Results

What factors influence whether and when a snag will fall?

We found that species, size (as measured by diameter at breast height), and the presence of pouch fungus (*Cryptoporus volvatus*) strongly influenced the likelihood of snag fall (Table 3.4). Relative to the base level estimates for white fir, ponderosa pine was about twice as likely to fall and incense cedar was about 70 percent less likely to fall. Larger-diameter snags were less likely to fall than small-diameter snags, and we found size interactions with several species: larger-diameter ponderosa pine were less likely to fall than smaller ponderosa pine, and larger-diameter California black oak (*Quercus kelloggii*) were more likely to fall than smaller-diameter individuals of that species.

None of the tree injury variables were significantly correlated with snag fall in our all-species model.

In terms of plot-level variables, we found that lower elevations were associated with higher likelihood of snag fall. The initial density of snags was positively correlated with snag fall; however, severity was not a significant predictor of snag fall.

	Full Model			**Best Fit Model**		
Predictors	Estimates	CI	p	Estimates	CI	p
Sp: ABMA	1.35	0.802 – 2.274	0.259	1.332	0.789 – 2.250	0.283
Sp: CADE	0.321	0.220 – 0.468	**<0.001**	0.336	0.231 – 0.489	**<0.001**
Sp: PIJE	1.302	0.412 – 4.115	0.654	1.274	0.402 – 4.041	0.681
Sp: PILA	1.199	0.847 – 1.698	0.306	1.24	0.877 – 1.754	0.224
Sp: PIPO	1.982	1.525 – 2.577	**<0.001**	2.024	1.560 – 2.625	**<0.001**
Sp: QUCH	1.687	0.020 – 142.895	0.817	1.716	0.020 – 146.113	0.812
Sp: QUKE	0.082	0.035 – 0.189	**<0.001**	0.081	0.035 – 0.186	**<0.001**
DBH (cm)	0.993	0.987 – 1.000	**0.045**	0.991	0.985 – 0.996	**<0.001**
Height (m)	0.991	0.980 – 1.003	0.141			
Inj: catface	0.94	0.602 – 1.469	0.786			
Inj: scorch (% of height)	1	0.997 – 1.003	0.801			
Inj: scorch	0.787	0.580 – 1.069	0.126			
P. volvatus	1.236	1.028 – 1.486	**0.024**	1.216	1.016 – 1.456	**0.033**
Inj: needles present	1.056	0.932 – 1.198	0.391			
Inj: % bole w limbs remaining	1.001	0.999 – 1.003	0.363			
Stress	1.062	0.826 – 1.365	0.64			
Elevation (m)	0.999	0.998 – 1.000	**0.001**	0.999	0.998 – 1.000	**<0.001**
Slope (scaled)	0.933	0.709 – 1.228	0.621			
Solar Radiation (Jun)	0.865	0.620 – 1.206	0.391			
Solar Radiation (Dec)	1.057	0.857 – 1.303	0.607			
Severity: MH	0.844	0.617 – 1.154	0.288			
SDT density	1.007	1.000 – 1.015	0.06	1.006	1.000 – 1.012	0.052
Sp: ABMA * DBH (cm)	1.001	0.991 – 1.012	0.83	1.001	0.991 – 1.012	0.845
Sp: CADE * DBH (cm)	0.995	0.986 – 1.005	0.353	0.996	0.986 – 1.006	0.395
Sp: PIJE * DBH (cm)	1.02	0.983 – 1.058	0.299	1.02	0.983 – 1.059	0.284
Sp: PILA * DBH (cm)	0.997	0.989 – 1.006	0.506	0.997	0.988 – 1.005	0.415
Sp: PIPO * DBH (cm)	0.994	0.988 – 1.001	0.074	0.994	0.987 – 1.000	0.053
Sp: QUCH * DBH (cm)	0.941	0.842 – 1.050	0.275	0.941	0.843 – 1.051	0.284
Sp: QUKE * DBH (cm)	1.034	1.016 – 1.054	**<0.001**	1.036	1.017 – 1.054	**<0.001**
Inj: scorch (ignore)	1.001	0.996 – 1.006	0.626			
N	40 plot_id			40 plot_id		
Observations	2202			2202		
AIC	22597.38			22591.218		

Table 3.2: Model results from the best-fit model as well as results that include all variables we tested; the latter is included for additional reference as well as because the estimates and AIC values do not differ dramatically from the best-fit model.

The differential fall rates between species in our tree-level analysis also suggests that the species composition of snags varies substantially over time; this was borne out in our comparison of aggregate snags 2 years versus 10 years post-fire (Figure 3.2). While ponderosa pine was highly represented in our

initial dataset, comprising 36% of snags immediately post-fire, that fraction dropped to 19% standing after 10 years. Likewise, incense cedar was relatively over-represented in the snags after 10 years compared with immediately post-fire. These patterns were also reflected in our estimated short-term fall rates: ponderosa pine fell at a rate of 11.4 percent per year whereas white fir fell at 9 percent and incense cedar much lower at 4.9 percent.

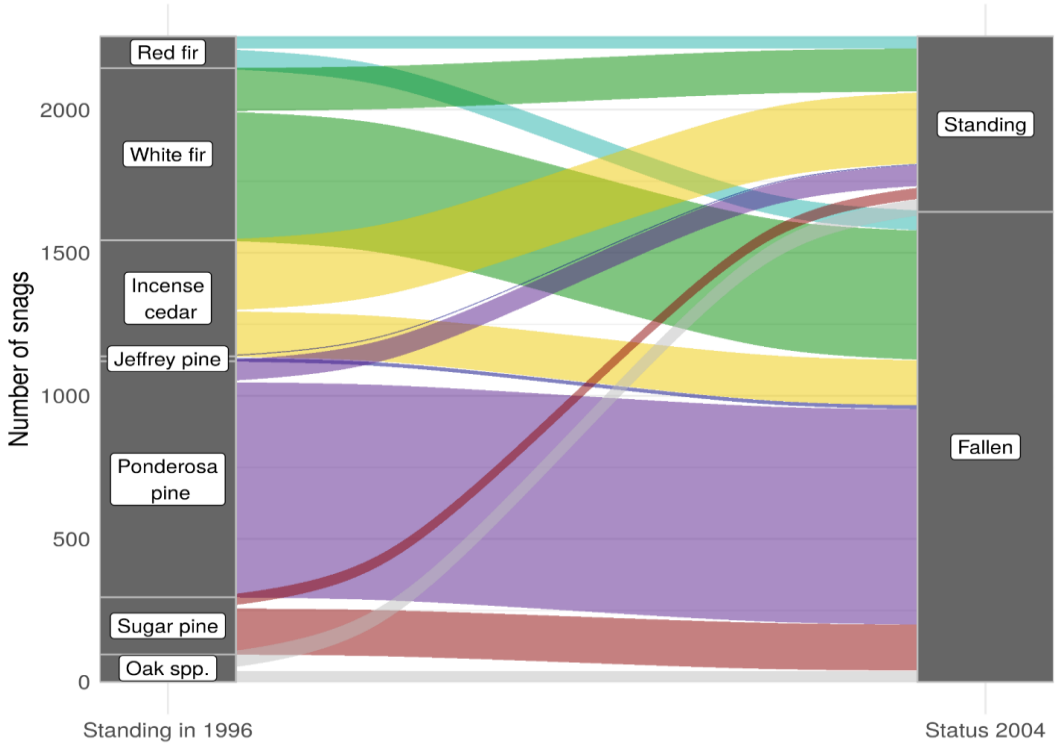

Figure 3.2: Species composition of snags in the initial sampling period (left) and the final sampling period (right). Colors and labels on the left-hand side indicate different species. Labels on the right-hand side indicate whether the snag was fallen or standing in the final sampling period.

Does the snag component of forest structure differ based on fire severity?

Plots burning at moderate- to high- severity contained a greater density of snags compared with plots burning at low severity; this pattern held at both the beginning and end of the sampling period as well as among multiple size classes (Figure 3.3).

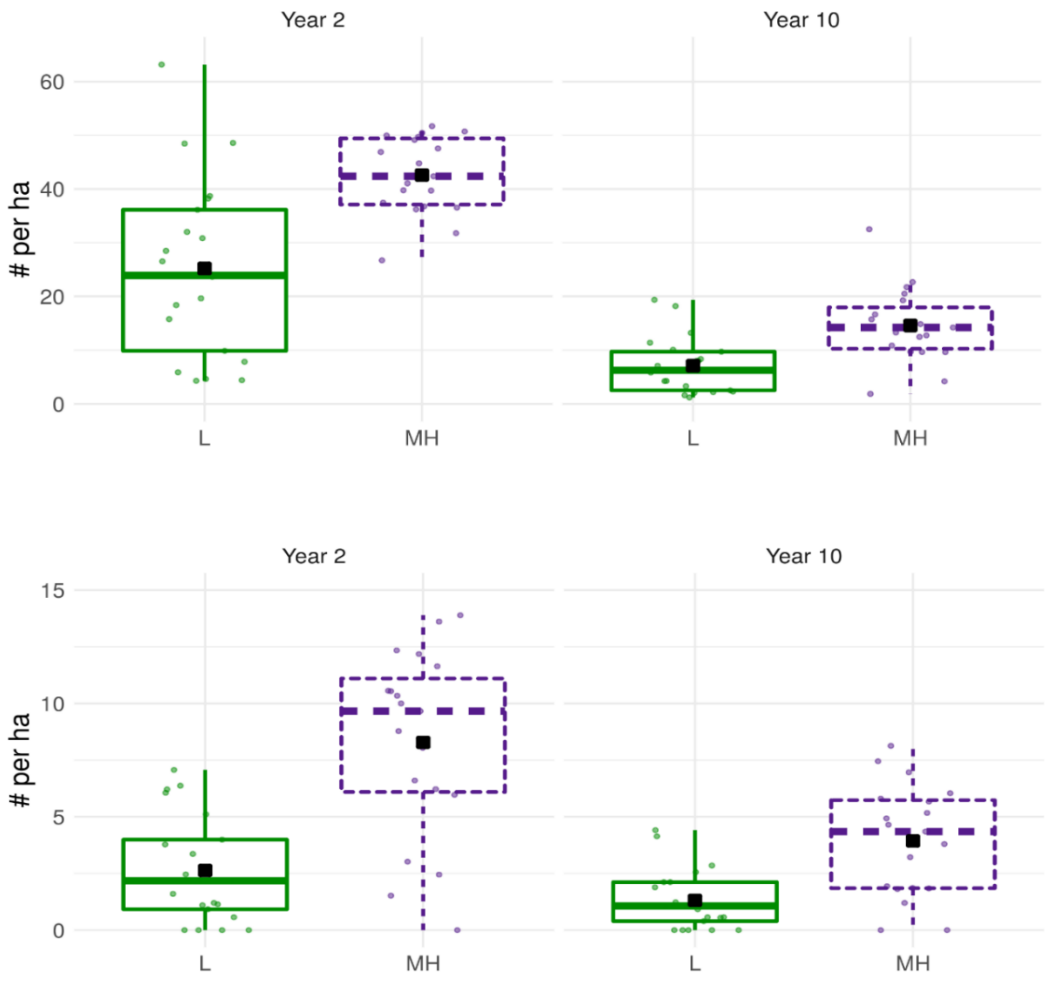

Figure 3.3: Densities among all snags (top row) and larger size classes (bottom row) in the initial sampling period (left column) and those remaining at the final sampling period (right column). The left-hand, green boxplot in each sub-figure captures summary statistics for low-severity plots (L), and the righthand, purple boxplot captures summary statistics for moderate- to high- severity (MH) plots. The black squares in each boxplot are at the mean value for their respective groups, and the dots are individual plot densities that have been jittered for display.

While the number of snags in lower versus higher plots differed between size classes and among canopy position ($p < 0.001$), the fraction of snags in each size class did not significant differ based on severity ($p = 0.592$ with all classes aggregated; $p > 0.1$ for each class separately; Figure 3.4).

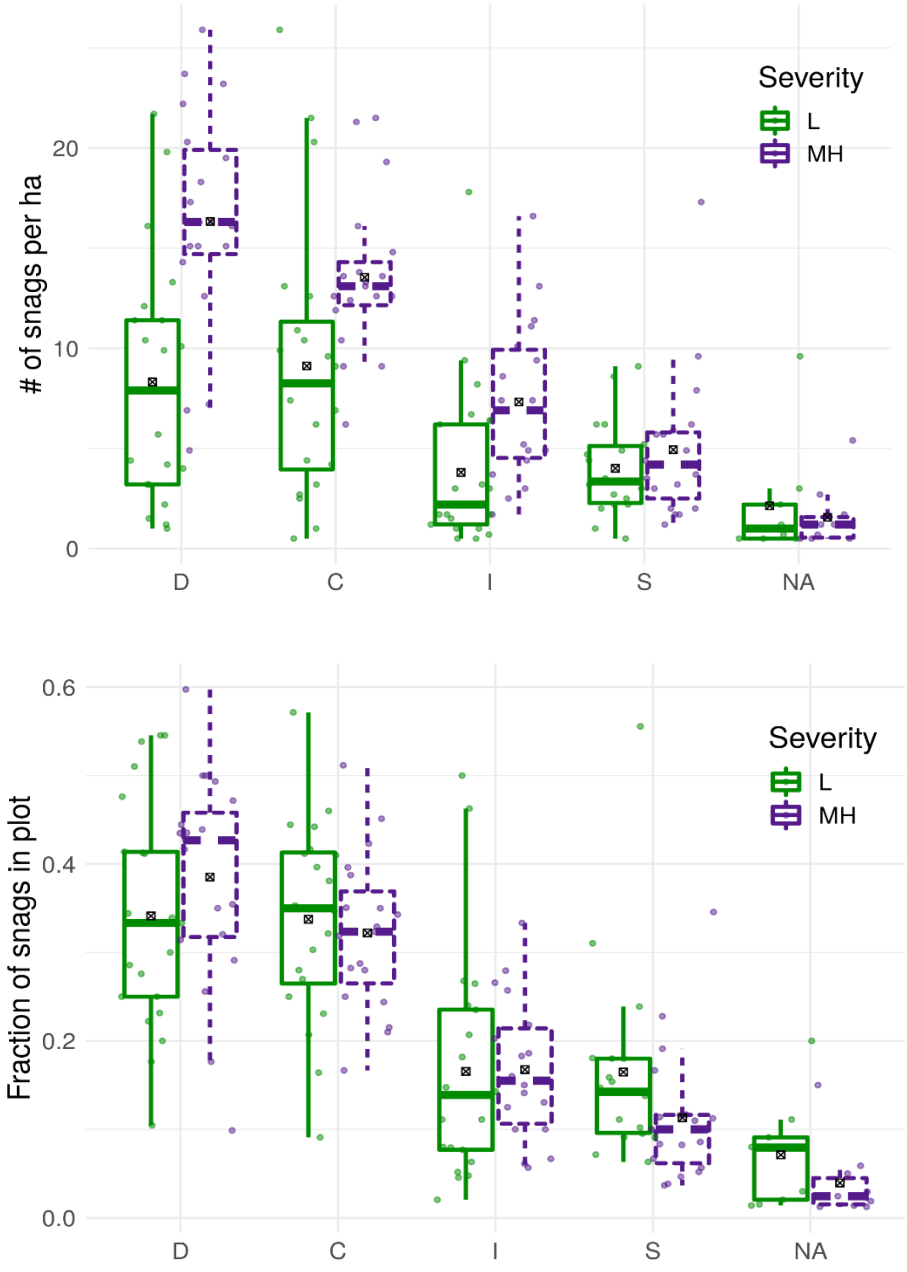

Figure 3.4: Distribution of snags in different canopy positions, comparing low and higher-severity plots. The top figure displays densities, and the bottom figure displays canopy position as a fraction of the total number of snags in that particular plot. The left-hand, green boxplot in each sub-figure captures summary statistics for low-severity plots, and the righthand, purple boxplot captures summary statistics for moderate- to high-severity plots. The black squares in each boxplot are at the mean value for their respective groups, and the dots are individual plot densities that have been jittered for display. D = dominant, C = co-dominant, I = intermediate, S = suppressed, NA = not available (canopy position not identified).

The preferred snags for white-headed woodpecker matched those specified as targets in the draft Sierra National Forest Management Plan (> 20 inches or 50 cm; Figure 3.3). Initially these occurred at a plot-level density of 3 snags per ha in the lower-severity plots and 8 snags per ha in the higher-severity plots and then dropping after the 10th year to 1 and 4 per ha, respectively. When we broadened our criteria for the white-headed woodpecker to include smaller-diameter trees (those likely to be potential but not preferred habitat for nesting birds), we found a substantially higher density of qualifying snags in the initial survey period (Year 2: 16 snags per ha in lower severity, 31 snags per ha in higher severity), but these densities also dropped by the 10 year post-fire period (Figure 3.5).

The density of snags suitable for the black-backed woodpecker ranged from 0 - 17 per ha, with an average of 7 per ha in low-severity plots and 11 per ha in higher-severity plots. After 10 years, these severity types contained an average of 2 and 3 suitable snags per hectare, respectively. While higher plots had more snags on average and in median values, there was a broad range of densities particularly in the low severity plots. In fact, the highest density of snags suitable for black-backed woodpecker was found in low severity. We found very similar values for all statistical summaries even when removing the maximum height restriction (Appendix 3.1).

Very few snags were suitable for great gray owls. An average of 0.2 snags per ha (more intuitively, 1 snag per 5 ha) were available in lower-severity plots, and 1.5 per ha were available in higher-severity plots. These numbers were halved by the 10th year (0.1 and 0.8 per ha, respectively). When we removed our maximum height restriction, we estimated substantially more suitable snags (Year 2: 1 snag per ha in low severity, 3.8 per ha in higher severity), but these densities were also halved by the 10th year (0.5 and 1.8 snags per ha, respectively).

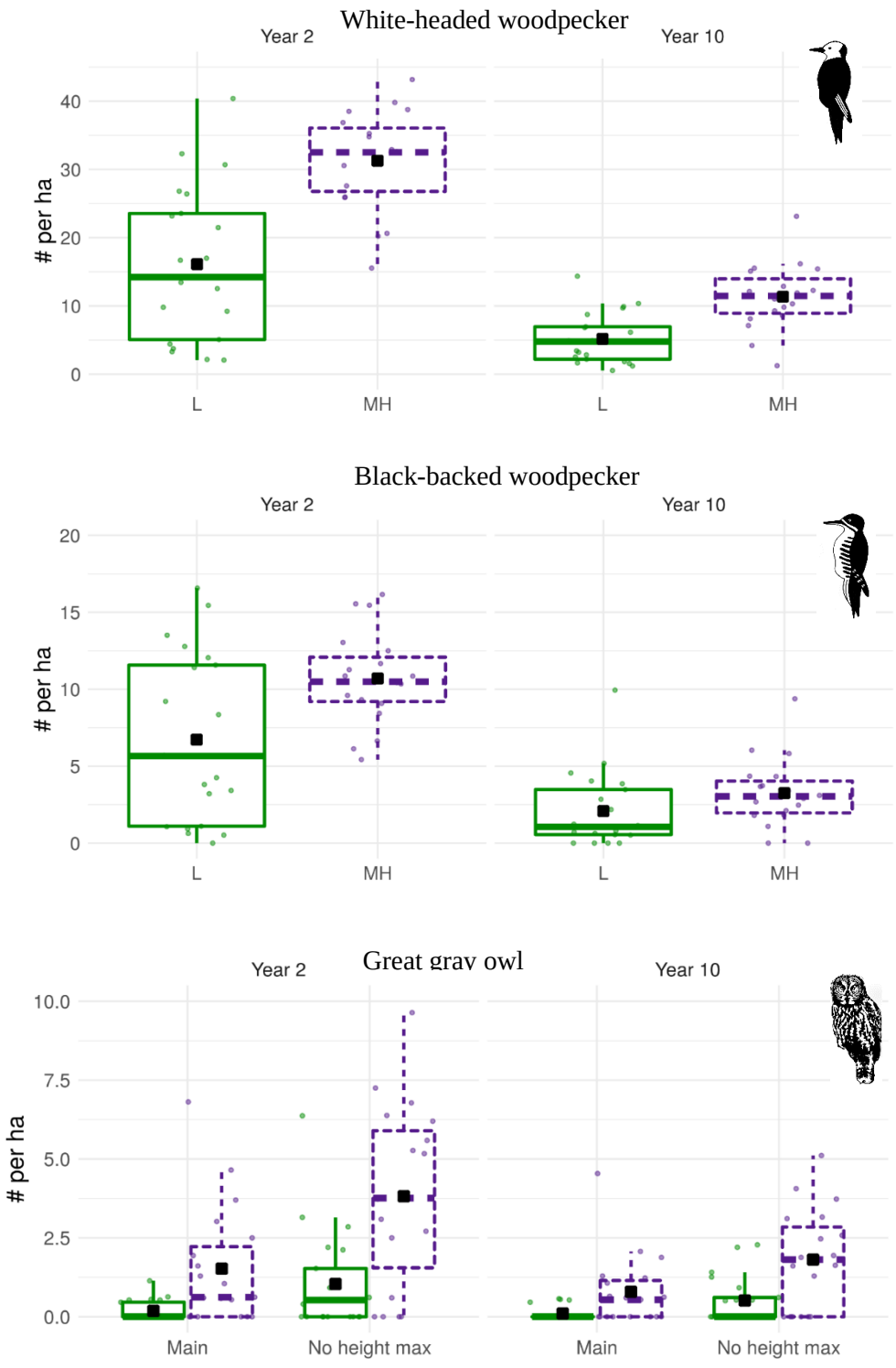

Figure 3.5: Summary statistics for the availability of snags that met habitat criteria (see Table SnagCriteria) for the white-headed woodpecker, black-backed woodpecker, and great gray owl. The left-hand, green boxplot in each sub-figure captures summary

statistics for low-severity plots, and the righthand, purple boxplot captures summary statistics for moderate- to high- severity plots. The black squares in each boxplot are at the mean value for their respective groups, and the dots are individual plot densities that have been jittered for display. For the great gray owl, we show estimates of snag density including height restrictions ("Main") as well as estimates that allow snags to be taller than reported as ideal in other studies ("No height max")

Discussion

Our study of snag dynamics following the Big Creek fire involves questions at the tree scale as well as the landscape scale. Surveying numerous tree- and plot- level attributes allowed us to investigate multiple potential drivers of snag fall, and censusing all snags within 40 large plots improved our understanding of how these snags are distributed in the post-wildfire landscape.

Our snag fall analysis highlighted the importance of both tree-level and plot-level attributes. At the tree level, we found that ponderosa pine was significantly more likely to fall in any particular timestep, relative to white fir, and that incense cedar was significantly less likely to fall. Similar patterns have been found by Ritchie et al. (2013) in the Southern Cascade region of California and Grayson et al. (2019) at sites spanning the California Sierra Nevada: both observed that most ponderosa pine snags fell within 10 years, compared with 40-50 % of red fir and very few incense cedar. Our results also show increasing fall rates for smaller snags, consistent with work in conifer systems throughout the Western U.S. (Chambers and Mast 2005; Grayson, Cluck, and Hood 2019; Lutz et al. 2020; Ritchie, Knapp, and Skinner 2013).

At the plot level, we found that snag fall was correlated with elevation. That trees in higher-elevation sites are less likely to fall may be due to the effect of temperature on decomposition processes; we expect slower decomposition in cooler temperatures and therefore infer that snag structural integrity may last longer at higher elevations. However, we did not find that solar radiation was a strong predictor of fall likelihood – a surprising result as we tested summer and winter solar radiation as potentially better proxies for decomposition-associated processes. An alternate explanation is that lower elevations tended

to contain more pine whereas higher elevations contained more true fir, suggesting that elevation may be capturing some of the species-level variation.

Our model also showed that tree fall was more likely in plots with a greater number of snags. Despite appearances, this was not an obvious result because our analysis pertained to tree-level likelihoods. While we cannot make a specific mechanistic claim for this pattern, we suggest two potential explanations. First, it is possible that snag density simply captured severity patterns better than our severity variable. If this is the case, then our theory that severity might act as a coarse proxy for tree injury might apply to the density finding. Potentially more likely is that higher-density plots increased the likelihood of any one snag falling, as falling snags may physically knock over or additionally injure neighboring snags. Likewise, fungi or other organisms associated with decomposition may spread more easily where snags are dense. In our species-level analysis (S1), we found that snag density was included in the best-fit models for ponderosa pine and sugar pine but not for white fir nor incense cedar; potentially this could reflect species-level traits related to structural integrity, or it could reflect site-level abiotic conditions that are correlated with species composition (e.g., soil type). Our estimated short-term fall rates are somewhat comparable with drought- and beetle- associated snag fall rates elsewhere in the Sierra National Forest (Hood et al. 2021), but they do diverge for some species. We estimated annual fall rates of 4.9 percent for incense cedar, which is on par with Hood et al. (2021)'s estimate of 4.3 percent. However, we estimate significantly higher white fir and ponderosa pine fall rates (9.4 percent and 11.4 percent in our study compared with 0.5 and 6.5 percent). This range might be attributable to the differing disturbance agents, which may have had different impacts on the structural integrity of the snags. Understanding these drivers and rates can have implications both to the short-term management of disturbance-impacted forests (e.g., hazard tree removal or other management) as well as to models that may use these short-term estimates for longer-term projections (e.g., the Forest Vegetation Simulator; Rebain et al. 2015).

Snag availability to meet landscape targets

To better understand snag availability on the landscape, we evaluated snag densities in the initial survey period (2 years post-fire) and those that remained at the last survey period (10 years post-fire); the former represents the time at which active post-fire management (e.g., salvage logging) is likely to take place or be planned, and the latter represents longer-lasting fire effects or areas managed for snag retention. We focused particularly on snags greater than 20 inches in diameter at breast height as they are specifically called for in the draft Land Management Plan (LMP) for the Sierra National Forest, the federal land management document pertinent to the study area. This document describes a desired post-fire condition of patchily distributed snags greater than 20 inches in diameter, with 2-40 snags per 10 acres (4 ha) at the landscape scale (USDA Forest Service 2019) – a range that we simplified to 0.5-10 snags per ha for ease of comparison.

Our study plots generally met these guidelines, with an average of 2.6 snags per ha in low-severity plots and 8.3 snags per ha in higher severity plots. After 10 years, this density dropped to an average of 1.3 and 3.9 snags per ha, respectively. Thus, both fire severity classes continued to have an adequate density to meet the LMP guidelines. Importantly, there were plots that individually did not meet the management plan criteria: 5 plots had zero eligible snags, and 6 plots had greater than 10. Given that the LMP criteria is specified for a landscape scale, it is not very concerning that several randomly selected plots are slightly outside of the range. Nonetheless, we do note that 4 out of 5 of the zero-snag plots were in lower-severity fire and all 6 of the excess-snag plots were in higher-severity fire – indicating that lower-severity fire is less likely to produce a sufficient number of snags and higher-severity fire is more likely to overshoot. In light of individual snag fall probabilities (species, snag size, presence of fungus) and snag density found in different severity classes, land managers may wish to retain individual snags with lower probability of falling (e.g., larger trees, white fir or incense cedar) scattered across low severity burn areas. This would be particularly true at lower elevations. That is, meeting LMP snag guidelines in low severity stands may require the retention of persistent snags that are more widely

scattered. LMP criteria are more easily met in higher severity areas; the relatively higher snag numbers with the desired snag diameters in these areas provide greater flexibility in meeting LMP snag criteria. Snags could be retained in groups similar the 5-acre plots in this study; our findings would indicate that this type of grouped snag retention strategy would meet the short and long term LMP snag guidelines. Where salvage logging is also a management goal, smaller snag groups or a smaller proportion of a landscape retaining snags may be needed to meet the same standard. For example, Eklund et al. (2009) examined a range of retention strategies to meet the needs of cavity nesting birds and economic recovery post fire and found the most favorable habitat for the two cavity-nesting birds in that study retained all snags standing in large un-salvaged groups farthest away from the logging operations. Thus, land managers may need to scale the size of groups based upon the landscape snag desired conditions and the structure of the post-wildfire higher-severity forest.

Snag availability for avian species

White-headed woodpeckers tend to nest in large diameter, highly decayed snags, likely due to their limited excavation abilities (Lorenz et al. 2015). The same snag types identified for the Sierra National Forest LMP are preferred by white-headed woodpeckers, suggesting that nest sites are likely to be retained. When we considered the density of snags in our study, we found them to be lower than what has been described for white-headed woodpecker nests. Following the 2007 Angora Fire near Lake Tahoe, California, Tarbill et al. (2015) found that white-headed woodpeckers nested in sites with an average (SD) of 95 (76) stems per ha in small snags and 17 (24) stems per ha in large snags. While the substantial variation implies that some low-density plots may be suitable for white-headed woodpecker, they are nonetheless substantially higher than in our study (ranging from 0 to 13.9, with means of 2.6 in low-severity plots and 8.3 in higher-severity plots). When we expanded our criteria to include snags greater than 20 cm – a size class roughly comparable to the “small” snags in Tarbill et al. (2015) – we found densities ranging from 4.3 to 26.7 snags per ha. However, density of snags around the nest tree may also be a secondary consideration for white-headed woodpeckers; other studies found that the availability

of an appropriate nest tree and a mix of fire severity proximate to the nest tree were more important components of nest site selection (Tarbill 2010, Wightman et al. 2010). One possible explanation for this discrepancy is the spatial scale of sampling: Tarbill et al. (2015) examined 0.04 ha plots surrounding a nesting tree, whereas our estimates come from plots that were 50 times larger. Our plots likely encompassed greater forest stand heterogeneity and might have contained smaller clusters of denser snags; we anticipate investigating these hypothesized spatial patterns in future work.

Snag density around the nest tree tends to be the most important factor determining nest site selection for black-backed woodpeckers (Seavy and Burnett 2012), with nests located in dense patches of small- to medium- sized snags (White et al. 2016, Tarbill et al. 2018). However, we found that the small-diameter snags most suitable for black-backed woodpeckers were present at a density of 7-11 snags per ha, compared with their preferred density of 100 snags per ha (White et al. 2016, Tarbill et al. 2018). Even the plots with the highest density of snags did not have a sufficiently high density for this bird species. Black-backed woodpeckers may prefer nesting in higher elevation forests (e.g. lodgepole forest) in the Sierra Nevada (Saracco et al. 2011, White et al 2019) due to the dense patches of smaller diameter trees that offer ample foraging and nesting resources for a species with some degree of site fidelity (Siegel et al. 2016). Our study occurred at lower elevations which may partially explain why snag densities were lower. Again, we offer that our sampling design may not have captured locally dense patches. Regardless, we found that the densities of suitable trees dropped off dramatically over time to 2-3 snags per ha in both severity classes. This finding is consistent with our finding that smaller-diameter trees (those preferred by the black-backed woodpecker) had a higher likelihood of falling (see tree-level analysis in Part 1), and it highlights that any density benefit found in higher-severity areas may be short-lived in terms of providing suitable habitat. By contrast, snags suitable for the great gray owl were very infrequent, with most plots containing zero candidates, but those that were available tended to persist to later years. Again, this pattern is likely due to the rarity of large-diameter snags on the landscape as well

as their tendency to remain standing. Snags with a broken top (a particularly desirable feature for this species) were exceedingly rare, occurring at a density of 1 snag per 10 ha in both severity types.

The fraction of snags in Dominant, Codominant, Intermediate, and Suppressed stand positions was relatively similar between severity types, which was counter to our expectation. We anticipated that low-severity fires would disproportionately indicate mortality in the Suppressed category and relatively fewer dead trees in the Dominant category. While these general patterns appear in our data, they are far less pronounced than expected and are not statistically significant. This would imply that lower and higher-severity burns have relatively similar proportional impacts on stand structure. As potential nest sites, perches, and for other wildlife uses, therefore, our data suggests that low- and high- severity fires can produce the types of tree structures required by certain species. However, given the overall higher abundance of snags in higher-severity fires, there is a correspondingly higher abundance of habitat trees in those patches as well.

Caveats

Several important factors must be considered when interpreting this dataset. First, the dataset tracks only snags that were present in the initial survey year (1996) and therefore does not assess snag "recruitment" from tree mortality that occurred within the survey period. This could potentially include fire-killed trees with delayed mortality exceeding 2 years. Other studies suggest that delayed mortality in excess of 2 years post-fire is possible but uncommon (Hood, Smith, and Cluck 2010). Therefore, we believe that densities from our surveys capture the dominant snag dynamics, though they represent the low end of possible snag densities on the landscape. Second, we do not have estimates of live-tree density and therefore do not have specific estimates of how the densities and composition of snags compare with live trees. Live-tree density may play an important role in snag dynamics, as they may act as a wind-break for smaller snags (Chambers and Mast 2005, Grayson et al. 2019).

Summary and Conclusions

In spite of these limitations, our analysis is relevant to several facets of fire management. First, our analysis of characteristics driving snag fall can help land managers develop more precise expectations for the quantity and quality of snags on in a post-fire landscape. We performed such an analysis by estimating the density and structure of snags, stratified by fire severity because it is a common post-fire landscape classification approach. With these findings, land managers may be able to better target snag retention efforts based on severity, such as by retaining long-lasting snags in low-severity zones and focusing group retention in high-severity zones. The severity stratification can also help apply our findings to contemporary landscapes: contemporary wildfires increasingly have high-severity fire effects (Parks and Abatzoglou 2020, Safford et al. 2022), and our higher-severity findings therefore may apply to this fraction of the burn area. Similarly, proactive fire management like prescribed fire and managed wildfire is often designed to have low-severity fire effects, so our findings may help improve forecasts of post-management forest structure. We do find that low-severity fires do provide a diverse mix of snags, though in lower abundance than in higher-severity fires. Based on these inferences, our research supports the use of prescribed and managed wildfire to increase snag structures on the landscape. Ultimately, however, all severity types can be managed to ensure adequate snag retention after wildfires.

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Appendix 3.1: Supplemental data and results

Plot area

The study was designed to assess snags within a five-acre plot. However, initial data collection predated the widespread availability of Global Positioning System (GPS) handheld units, and as a result the plot boundaries were delineated based on best-guesses in the field. Given the high topographic variation within plots, this was a challenging task and raises questions in the current day about whether the plots truly spanned five acres. Our main analysis presents the data based on boundaries delineated in a Geographic Information System (GIS) by one of the initial surveyors (R. Rojas). However, we also investigated two alternate estimates that span lower and higher ends of the potential range:

- "Five acre" – this estimate assumes that all sampled plots were five acres in area. This is likely an overestimate of area and therefore leads to an underestimate of density.
- "Hull" – this estimate uses area produced from a convex hull based on tree locations. By construction this method leads to an underestimate of area and therefore an overestimate of density.

Severity

Plots were classified on-site as having burned low-, moderate-, or high- severity fire effects. "Low" corresponded to less than 36 % basal area mortality, "moderate" corresponded to 36-68 %, and "high" to greater than 68 %. These categories were subsequently lumped to produce two groups: a low-severity group ("L") and a moderate-to-high severity group ("MH").

Species-level analysis

When we analyzed each species individually, we found that size (DBH) was an important predictor of fall probability for all species, with smaller-diameter trees associated with increases in fall probability. The importance of plot-level variables and tree injury variables differed by species. For the most commonly found species, ponderosa pine, the probability of fall increased for those with a catface

injury. The best-fit model also included snag density, although the it was not a significant predictor. Sugar pine (*Pinus lambertiana; PILA)* and white fir *(Abies concolor; ABCO)* fall probabilities decreased with elevation and were higher for trees with *Polyporus volvatus.* Similar to ponderosa pine, the best-fit model for sugar pine included plot-level snag density as a non-significant predictor. For incense cedar (*Calocedrus decurrens; CADE)*, fall probabilities decreased significantly with DBH and with elevation.

	PIPO			PILA			ABCO			CADE		
Predictors	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p	Estimates	CI	p
DBH (cm)	**0.986**	**0.982 – 0.990**	**<0.001**	**0.986**	**0.978 – 0.993**	**<0.001**	**0.989**	**0.984 – 0.995**	**<0.001**	**0.99**	**0.981 – 0.998**	**0.018**
SDT density	1.005	0.998 – 1.011	0.136	1.013	0.997 – 1.030	0.112						
Inj: catface	**1.634**	**0.920 – 2.903**	**0.094**							0.306	0.041 – 2.265	0.246
Elevation (m)				**0.998**	**0.996 – 0.999**	**0.003**	**0.999**	**0.997 – 1.000**	**0.048**	**0.998**	**0.996 – 0.999**	**0.004**
P. volvatus				**1.661**	**1.008 – 2.737**	**0.046**	**1.617**	**1.008 – 2.594**	**0.046**			
N plots		33			26			26			26	
Observations		801			199			594			389	

Table 3.S.1. Model results for the best-fit model, fit for each tree species individually.

Wildlife parameters (sensitivity)

We did not find that our estimates of black-backed woodpecker densities changed substantially based on our height criteria.

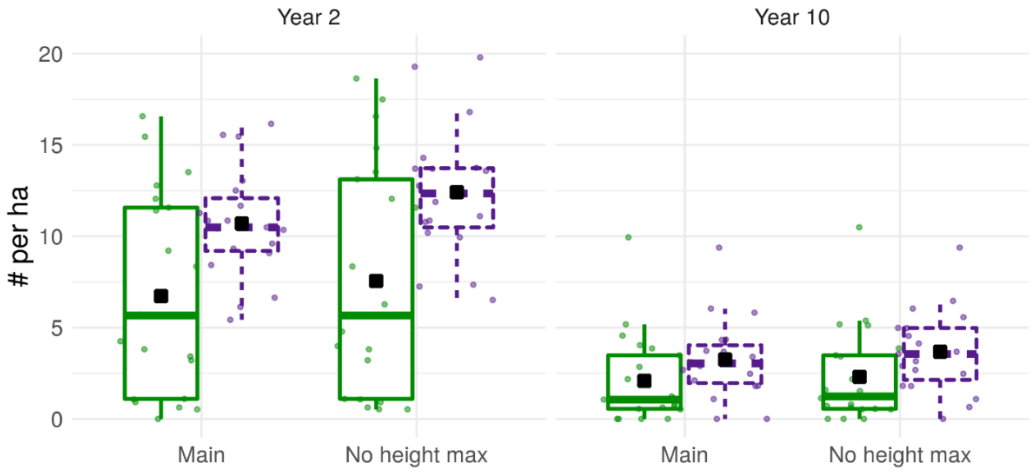

Figure 3.S.1. Density of trees suitable for black-backed woodpeckers under two suitability assumptions.