Can Forest Management Reduce Fuels and Still Promote Biodiversity in Forests with a Mixed Severity Fire Regime?

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6/2020

Abstract

The Klamath Mountains mixed evergreen forest is adapted to frequent, low to moderate severity fires. Today, the Karuk Tribe, US Forest Service, and local community organizations have formed the Western Klamath Restoration Partnership to restore this fire regime, altered by a century of fire suppression. The WKRP seeks to reduce fuel loads around communities while addressing concerns about the impacts to biodiversity of high severity fire on one hand, and of the exclusion of fire on the other. First, I investigate how communities of plants, birds, lichens and insects differ between long-unburnt stands, low severity burns and high severity burns. Next I evaluate the response of diversity to two management options used to mitigate the riskof high severity fire by reducing fuels and canopy cover: multiple burns (wildland fire use) and thinning and burning. Based on 110 plots across the WKRP project area, low severity burns and unburnt areas did not differ in species composition. Plant, bird and insect diversity (alpha, beta and gamma) were as high or higher in high severity burns as in low severity/unburnt stands. Lichens were negatively impacted by high severity fire, beginning to recover only after 16 years. Multiple burns and thinned/burnt stands had the highest diversity, because they provided habitat for both species preferring high severity burns and those preferring low severity/unburnt stands. This suggests that management, whether passive (allowing fires to burn and overlap) or active (thinning and burning) can help maintain biodiversity in this fire-dependent landscape.

Summary

- No detectable difference in species composition between long-unburnt stands and low severity burns. This suggests that in fire-suppressed stands, fires that lead to a reduction in canopy cover of less than 25% do not cause a strong biodiversity response. Active management may need to reduce canopy cover much more (to 30-60%) where appropriate if conserving and restoring understory species is important.
- Plant and bird diversity in high severity burns is as high or higher than in low severity/unburnt plots. Almost all measures of diversity are highest in multiple burns and/or thinned and burnt plots.
  - **Alpha**: High severity burns have higher plant species richness than low severity/unburnt stands, but bird species richness is similar and lichen species richness lower. Several taxa of insect pollinators and herbivores are significantly more abundant in high severity plots than in low severity/unburnt plots.
  - **Beta**: High severity burns are more heterogeneous than low severity/unburnt plots.
  - **Gamma**: The total species pool is lowest in low severity/unburnt stands (except for lichens).
  - **Multiple burns** and **prescribed burns** have the highest bird diversity (alpha, beta and gamma), and similar to higher plant diversity.
- A majority of species with a strong preference for either high severity burns or low severity/unburnt stands also favor multiple burn and prescribed burnt plots, suggesting that such stands can provide suitable habitat for both groups of species.

Introduction

After a century of fire suppression, concerns are mounting over the effect of changing fire regimes on biodiversity in Western North American forests adapted to frequent, low to moderate severity fires (Haugo et al., 2019; Hessburg et al., 2005; Steel et al., 2015). These changes have resulted in two contrasting impacts: increasing extent of high severity fire on one hand, and the exclusion of fire on the other. The former threatens species and ecosystem services associated with mature forests (Miller et al., 2018; Miller and Safford, 2019), while the latter threatens early seral habitats and open forests (Knapp et al., 2013; Odion et al., 2014; Swanson et al., 2014). Despite a broad concensus that the exclusion of fire has been detrimental to biodiversity, disagreement remains over how to balance the ecological need to allow more fire in fire-dependent ecosystems and the need to mitigate the risk of high severity fires to old growth-associated species, communities, and ecosystem services.

Managers may turn to two approaches to achieve this balance and move away from total fire suppression. The active approach is to thin and burn stands to enhance populations of species negatively impacted by fire exclusion and minimize the likelihood of high severity fires in places where there is a concern over the vulnerability of resources and rural communities (Abella and Springer, 2015; Kalies and Yocom Kent, 2016; Wayman and North, 2007; Webster and Halpern, 2010). However, thinning and burning has been criticized on the grounds that reducing the extent of high severity fire could reduce the availability of ecologically-important early seral habitats, while at the same time disturbing mature forest habitats and threatening associated species (Baker, 2015; Odion et al., 2014). The second approach is to let fires burn when appropriate; this passive approach could lead to more frequent fires, thus reducing fuel loading and canopy homogeneity (North et al., 2012). Understanding the impacts of both active and passive forms of management is important to build a consensus over how to meet both fire management and biodiversity targets.

Such concensus is particularly needed in the context of collaborative landscape management agreements that are becoming increasingly common, particularly on national forests. In the Klamath Mountains of northern California, the Karuk Tribe, United States Forest Service and community and environmental organizations have formed the Western Klamath Restoration Partnership (WKRP) in order to restore the historically low to mixed severity fire regime that prevailed prior to the disruption of Indigenous fire management (Crawford et al., 2015; Fry and Stephens, 2006; Taylor et al., 2016). Extensive planning discussions have taken place to identify zones of agreement among all partners, such as limiting damage to communities from high severity fires and enhancing biodiversity (including both late-seral species and fire-dependent, early-seral species) (Harling and Tripp, 2014). But can management achieve both of these objectives, or are will there necessarily be trade-offs?

Studies from related forest types such as inland dry forests suggest that treatments that reduce canopy cover promote biodiversity (Bartuszevige and Kennedy, 2009), but such results are inconsistent (Willms et al., 2017) and their applicability to mixed-severity forests is questionable (Hessburg et al., 2016). In this study, I surveyed biodiversity (birds, plants, lichens and insects) in long-unburnt stands and low severity and high severity single burns. I identified species associated with high severity burns and long unburnt stands as early- and late-seral species respectively. I also surveyed thinned and burnt stands and multiple burns with intermediate canopy cover representative of forest restoration goals aimed at minimizing the risk of high severity burns. To determine whether this type of management is also compatible with biodiversity conservation objectives, I then ask: do areas with intermediate canopies (actively or passively managed) provide habitat for early-seral species, late-seral species, both, or neither?

Methods

Study area

Located in the Klamath-Siskiyou mountains of northern California, the WKRP is a 1.2 million-acre collaborative landscape restoration effort between the Karuk Tribe, US Forest Service and local NGOs (Harling and Tripp, 2014) (Figure 1). The area's main vegetation class is mixed evergreen forest (Steel et al., 2015). The prevalence Douglas-fir (*Pseudotsuga menziesii*) and diverse hardwoods such as tanoak (*Notholithocarpus densiflorus*), black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*), and madrone (*Arbutus menziesii*) distinguish the Klamath-Siskiyou mixed evergreen forests from those of the Cascade Mountains and Sierra Nevada (Barbour and Billings, 2000; Whittaker, 1961). These forests were historically managed by the Karuk tribe using frequent (~12.5 year interval), low-intensity prescribed burning (Crawford et al., 2015; Taylor and Skinner, 2003, 1998). As a result, the historic fire regime was one of more frequent and generally lower severity fires than most other mixed severity fire regime forests or wetter conifer forests to the north (Taylor and Skinner, 1998). One of the main goals of the WKRP is to restore the fire regimes within the Karuk tribe's aboriginal territory in a way that promotes the resilience of these ecosystems to high severity fire and climate change (Harling and Tripp, 2014).

Data collection

I conducted surveys at 110 sites varying in time-since-fire and burn severity (48 sites surveyed in 2018 and 62 in 2019). Sampling sites were in lower elevation (mean 759m, range 241-1500m) mixed evergreen forest, with some in transition areas into dry or moist mixed conifer (classification based on FRID data, Safford and Van de Water (2014)). The median historic fire return interval in these forests is 13 years (Van de Water and Safford, 2011).

Sampling sites were placed in low severity and high severity burns, defined respectively as <25% canopy mortality and >75% canopy mortality (Miller et al., 2009), in long-unburnt stands (>80 years since last fire), in sites affected by multiple burns, and sites that were thinned and burnt. At all burnt sites, time-since-fire varied from 2 to 32 years. Multiple burns and thinned and burnt sites were placed in areas with intermediate canopy cover (30-75% cover). While this eliminates high severity reburns and multiple burns or restoration treatments that retain high levels of canopy cover, I was only interested in "treatments" (active or passive) that reduce canopy cover significantly. Such canopy reduction corresponds to the level recommended for understory restoration (Abella and Springer, 2015) and for mitigating the risk of crown fires (Moghaddas et al., 2010). As a result of this approach, the habitats studied follow a gradient of canopy cover (Figure 2). Burn severity was evaluated a priori based on the relative difference normalized burn ratio (Miller and Thode, 2007) and verified in situ by visually estimating the magnitude of canopy cover reduction. Since the habitats differ mostly by the severity of fire's impact, I will henceforth refer to different "severity categories" for simplicity, even though this is an imperfect description of multiple burn and thinned and burnt sites.

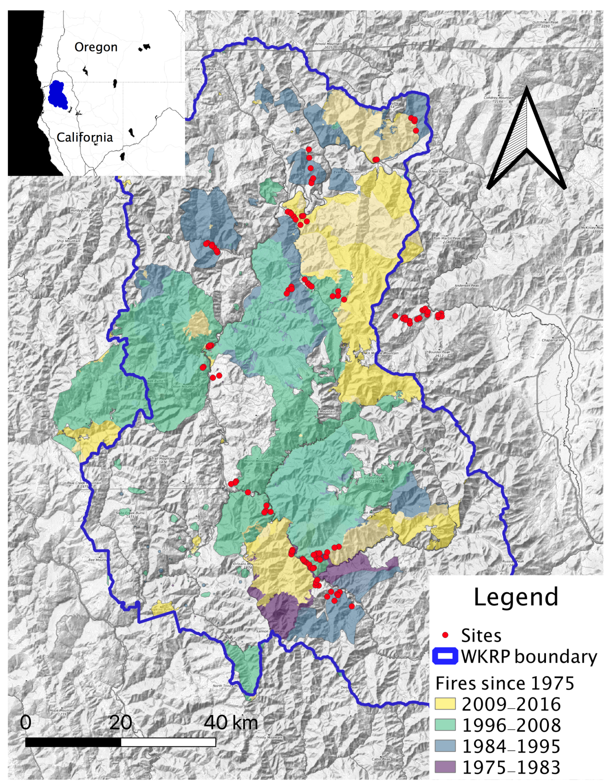


Figure 1: Map of WKRP project area and sampling sites

Several tests were used to ensure that the differences observed between site categories were not the product of a climatic or topographic pattern rather than fire and management history. To test for climate differences, I compared the climatic water deficit (CWD, the difference between potential and actual evapotranspiration). Using the Basin Characterization Model 30-

year average for 1981-2010 (Flint et al., 2013), I found no difference between the severity categories (ANOVA, F = 1.41, p = 0.237). Heat load, which accounts for the effect of slope, aspect and lattitude on insolation and temperature (McCune and Keon, 2002), was not different among categories except that it was slightly lower for high severity sites (although this might seem counterintuitive, it is explained by the fact that high severity sites were steeper on average, and heat load decreases with slope gradient on north-facing aspects). However, due to the limited availability of thinned and burnt areas, I had to make some concessions in study design. While there were numerous sites available for the other severity categories, the only prescribed burn sites that met my criteria for minimum size, canopy reduction, and absence of other disturbance factors were located in two project areas. These were higher in elevation on average than the other severity categories (mean = 1101m, 95% CL = 965-1237m) and more clustered (average distance among sites <10km compared to 28-36km for the other severity categories). While these factors limit the generalizability of the patterns observed at these sites, this is a common challenge for studies of prescribed fires. Therefore I still include the thinned and bunrt sites in the study in the hope that my findings can be used in designing more robust future investigations.

At each site, I recorded aspect, slope, elevation, and canopy cover (trees over 5m in height, by visual estimation). For all sites, I surveyed plants, epiphytic lichens, and birds. Presence of all plants and lichen species was determined in an 11.3m-radius plot following the Common Stand Exam protocol (USFS, 2008). Plants were identified using the Jepson manual (Baldwin et al., 2012) and lichens were identified using Mccune and Geiser's Macrolichens of the Pacific Northwest (McCune and Geiser, 2009). Only native plant species are included in the analysis, although exotic species were generally few. Species of some plant genera were pooled if they shared similar ecological requirements (eg. *Arctostaphylos*, *Cryptantha*, *Pyrola*). Species of the lichen genera *Usnea* and *Bryoria* were also pooled because of he difficulty in differentiating them. I also conducted two 10-minute bird point counts at each site on separate, non-consecutive days. All bird detections within a 100m radius were recorded. The two hummingbird species (Anna's and Rufous Hummingbird) were pooled, as were Black-throated Gray Warblers and Hermit Warblers (*Setophaga* sp.), because it was not always possible to differentiate these species by ear. Lastly, for high severity, low severity and unburnt sites, I set up a custom-built flight-intercept trap for flying insects that was left out for two days (Russo et al., 2011). Insects were identified to the order or suborder level.

Analysis

Species composition

I conducted a non-parametric multivariate permutational analysis of variance (PERMANOVA) to test the significance of dissimilarity between the different severity categories (McArdle and Anderson, 2001) using the adonis2() function from the vegan package v.2.5.6 in R (Oksanen et al., 2007), with 999 permutations. PERMANOVA uses calculates a pseudo-F value similar to the F-statistic in ANOVA models, and obtains p-values based on permutation procedures (9999 permutations in this case) (Anderson, 2017). Then I conducted PERMANOVA pairwise comparisons between each severity category. To minimize the risk of making a type-1 error from carrying out multiple pairwise tests on a single data set, I adjusted the p-values using the Bonferroni correction method (Rice, 1989).

To visualize the difference in species composition in each severity category, I used non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity matrices using the metaMDS() function of the vegan package in R (Oksanen et al., 2007).

Diversity patterns

Next, I analyzed patterns of alpha, beta and gamma diversity for plants, birds, and lichens. Alpha diversity is equivalent to species richness per plot. I tested for the significance of the difference in richness between severity categories with anovas and post-hoc Tukey tests using the R package "emmeans" (Lenth et al., 2020). To further evaluate the influence of canopy cover on species richness, I performed anovas with plant and bird richness as the response variable and percent tree cover as the predictor for the lower canopy cover habitat (high severity burns), intermediate canopy habitats (multiple and thinned and burnt stands), and higher canopy cover habitats (low severity and unburnt). This tiered approach was chosen to isolate the effect of treatment and of canopy cover, since the treatments themselves are the principal driver of canopy cover differences.

I calculated beta diversity, or the amount of variation in species composition and richness between sites within each severity category, using the R package vegetarian v1.2 (Charney and Record, 2009). I used the Jaccard index (Jost, 2007) to represent the extent to which species are shared in each pair of samples. I compared results between treatments using standard errors from bootstrapping given by the package vegetarian.

Because the number of samples in each severity category was unequal, simply comparing the total number of species found in each severity category was not an adequate way to evaluate gamma diversity, the size of the species pool for each habitat. Instead, I generated sample-based rarefaction curves (Colwell et al., 2012) using package iNEXT v. 2.0.20 (Chao et al., 2014; Hsieh et al., 2016). This method uses Hill numbers, or effective species numbers based on species richness. Estimates were interpolated from site-based incidence data to account for unequal sample sizes (Colwell et al., 2012) and then extrapolated to twice the size of the smallest sample (Chao et al., 2014). I compared results between treatments using 95% confidence intervals from bootstrapping.

Indicator species analysis

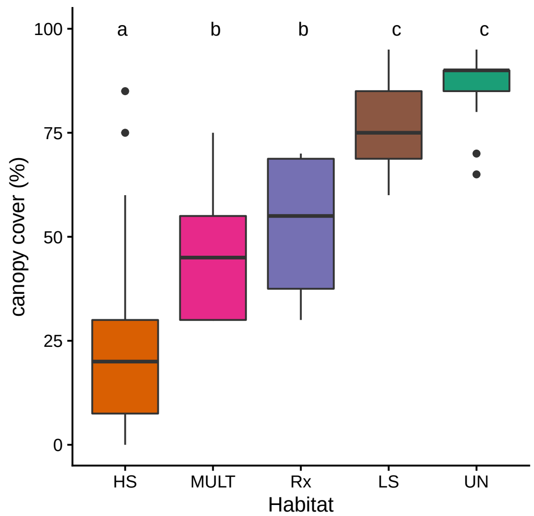
Insects were not sampled in the multiple burns and thinned and burnt sites, but I include them nevertheless to compare species communities in the unburnt, low severity and high severity burns. Comparisons of alpha, beta and gamma diversity were not as meangingful for insects, because of the small number of taxa (at the order or suborder level). Instead, I used an indicator species analysis using the function multipatt() in the package indicspecies v1.7.8 (De Cáceres and Legendre, 2009) to determine which taxa showed a preference for high severity or low severity and unburnt stands (the latter were pooled because the PERMANOVA suggested their community composition did not differ). I used the same procedure to identify indicator species for birds and plants in the high severity and low severity/unburnt categories.

Early and late seral species in actively and passively managed stands

Lastly, I wanted to determine if the multiple burns and thinned and burnt stands tended to contain species affiliated with high severity burns and/or those associated with low severity and unburnt stands. Four hypotheses were envisioned: 1) Species associated with high severity burns are associated with the actively or passively managed stands; 2) Species associated with unburnt stands and low severity burns are associated with the actively or passively managed stands; 3) Both of these species cohorts are found in the actively or passively managed stands, presumably because they are intermediate in environmental characteristics such as canopy cover; 4) Neither cohort is found in the actively or passively managed stands, presumably because the intermediate canopy cover creates inhospitable conditions for both and favors a completely different species assemblage. The third hypothesis would mean that reducing canopy cover for fire management would be compatible with biodiversity objectives, while the fourth would be the worst case scenario. To determine which of these four hypotheses was correct, I identified species that prefer high severity burns and species that prefer unburnt stands and low severity burns by using a simple criterion: if a species was found twice as frequently in one habitat than the other, I considered that it exhibited a preference for that habitat. Only species that occurred in more than five sites (18% of the total number of sites) were included. For each cohort (early-seral species, found twice as frequently in the high severity burns, and late-seral species, found twice as frequently in the low severity burns and unburnt stands), I then determined if it was also found twice as frequently in the multiple burns and/or thinned and burnt stands. To determine which of the four hypotheses above was correct, I evaluated the frequency with which species preferring high severity burns or low severity burns and unburnt stands also favored the multiple burns and/or thinned and burnt stands.

Results

Fig.2: Canopy cover in each severity category



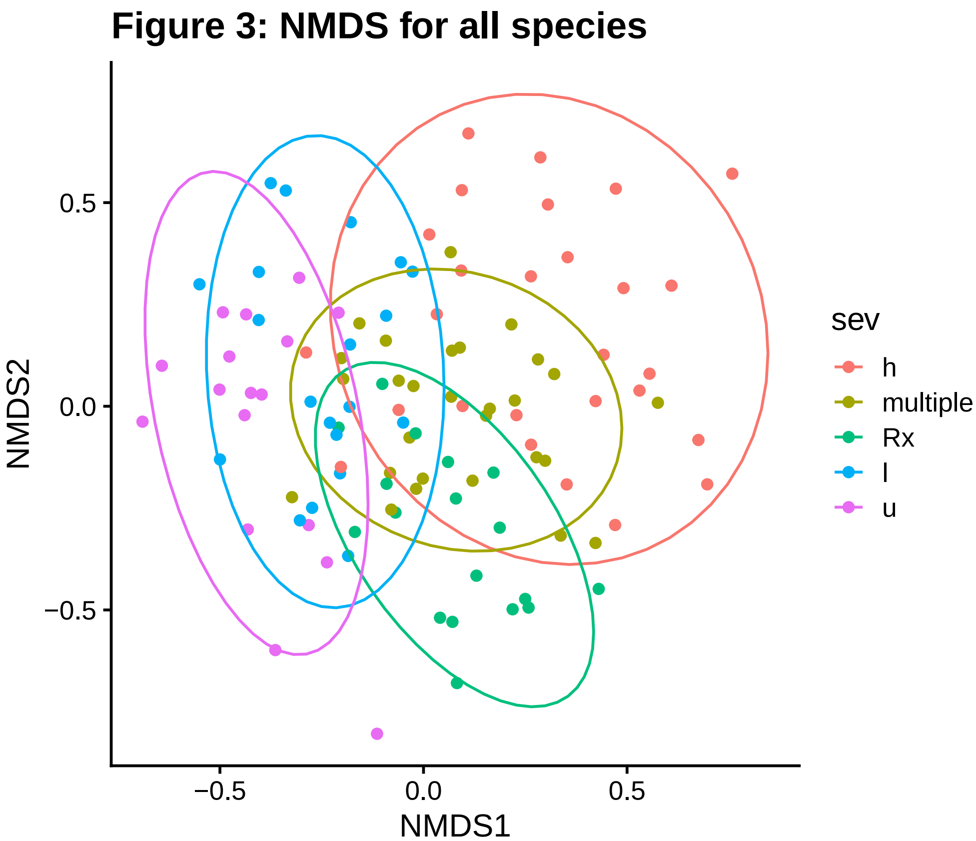
Variation in community composition across habitats

Effect of fire history on species composition

The main PERMANOVA revealed that species composition varies for all taxa in response to the severity category ($p < 0.001$). Using pairwise PERMANOVAs to compare the habitats, there is no detectable difference between plant, bird or lichen communities of low severity and unburnt stands (Table 1) (plants: pseudo-$F_{(1,35)} = 2$ and $p = 0.21$; birds: pseudo-$F_{(1,35)} = 2.68$ and $p = 0.13$; lichens: pseudo-$F_{(1,35)} = 1.04$ and $p = 0.427$). In addition, bird communities of high severity burns and multiple burns are not detectably different (pseudo-$F_{(1,53)} = 1.72$ and $p = 0.84$). For lichens, the only habitat that stands out is the HS habitat ($p < 0.02$), although it is not statistically different from the MULT habitat ($p = 1$).

Table 1: Pairwise PERMANOVA results

	plants		birds		lichens	
Pair	F_model	p_adj	F_model	p_adj	F_model	p_adj
HS vs LS	7.321	0.01	6.45	0.01	16.34	0.01
HS vs MULT	3.200	0.01	1.72	0.84	25.11	0.01
HS vs Rx	7.432	0.01	8.11	0.01	18.11	0.01
HS vs UN	9.946	0.01	12.06	0.01	16.46	0.01
LS vs MULT	5.986	0.01	4.52	0.01	3.41	0.01
LS vs Rx	6.849	0.01	6.53	0.01	6.63	0.01
LS vs UN	1.996	0.21	2.68	0.13	1.04	1.00
MULT vs Rx	4.152	0.01	5.90	0.01	6.41	0.01
MULT vs UN	6.984	0.01	8.79	0.01	3.72	0.01
UN vs RX	5.680	0.01	8.73	0.01	7.48	0.01



Species assemblage ordination

The NMDS confirms a considerable overlap in species communities of long-unburnt and low severity burn stands. High severity stands have distinct species communities, while the communities in thinned and burnt stands and multiple burn stands appear to be intermediate between the high severity stands and long-unburnt/low severity stands. Figure 3 shows the first two dimensions of a 3-dimensional ordination that found convergent solutions with a stress of 0.176.

Alpha, Beta, Gamma diversity patterns

Alpha diversity

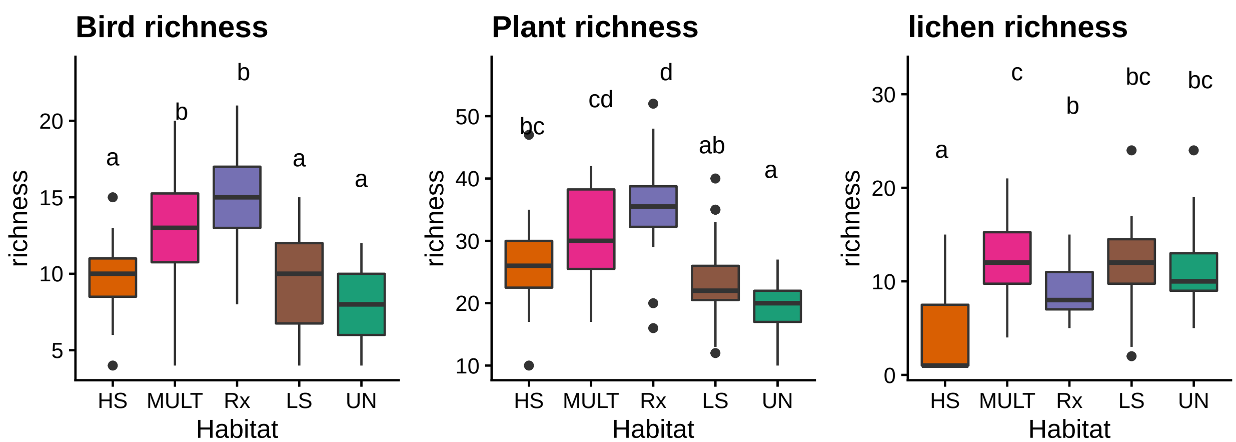


Fig.4: Bird, plant and lichen species richness

Bird and plant species richness were highest in the multiple burns and thinned and burnt stands (for plants the difference between high severity burns and multiple burns was not significant) (Figure 4). Bird and plant richness in low severity burns and unburnt plots was slightly lower than in high severity burns, but the difference was overall not significant. Lichens were predictably less diverse in the high severity stands, but richness in the other severity categories was similar.

Within the multiple burns and thinned and burnt stands, canopy cover was negatively correlated with plant richness ($F_{(1,44)} = 8.99$, $p = 0.004$) and bird richness ($F_{(1,44)} = 8.99$, $p = 0.004$). In the low severity and long-unburnt stands, canopy cover was negatively correlated bird richness ($F_{(1,35)} = 10.482$, $p = 0.003$), but only weakly correlated with plant richness ($F_{(1,35)} = 3.133$, $p = 0.085$). In the high severity stands, canopy cover was not correlated with either plant or bird richness ($F_{(1,25)} = 2.538$, $p = 0.124$ and $F_{(1,25)} = 1.806$, $p = 0.191$ respectively).

Beta Diversity

Beta diversity was highest in the high severity burns and multiple burns for birds and plants, and lowest for the thinned and burnt stands, possibly because they were spatially clustered rather than because of an effect of treatment (figure 5). For lichens, high severity burns had the highest beta diversity, likely not because of a high level of species turnover between sites, but rather because of the variation in species richness between plots with no surviving trees and those that had surviving trees, and therefore lichens.

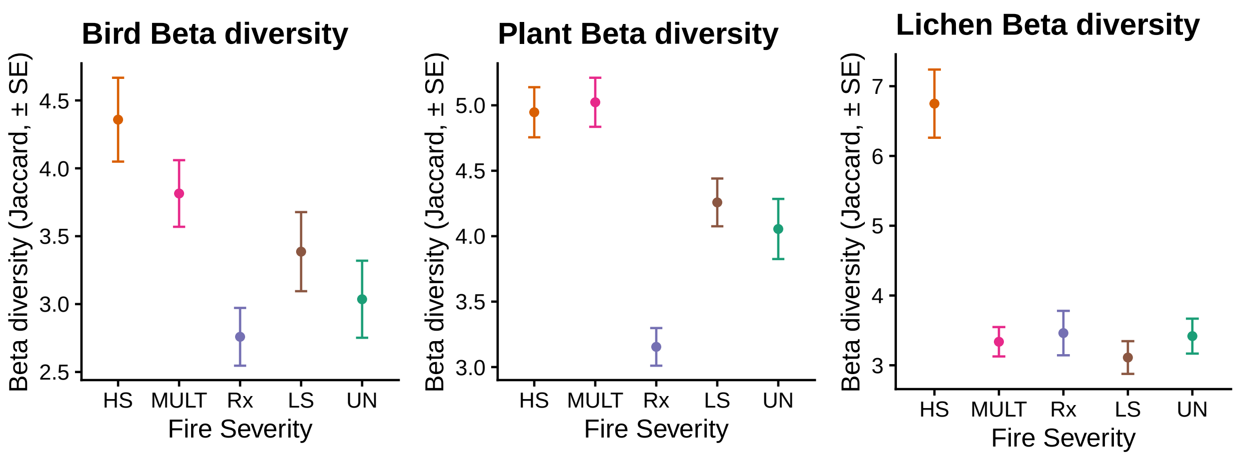


Fig.5: Bird, plant and lichen beta diversity (Jaccard)

Gamma diversity

Based on the extrapolated species richness, the total pool of species for birds appears to be largest in the multiple burns and thinned and burnt stands, intermediate in the high severity burns, and lowest in the low severity and long-unburnt stands (Fig. 5). For plants, the pattern is the same except that species pool from the thinned and burnt stands appears smaller than the high severity burns, and more similar to the low severity stands instead. High severity fire eliminates lichens and most of their substrate (Miller et al., 2018), and their species pool is smaller in the high severity stands than in the other severity categories, which are similar.

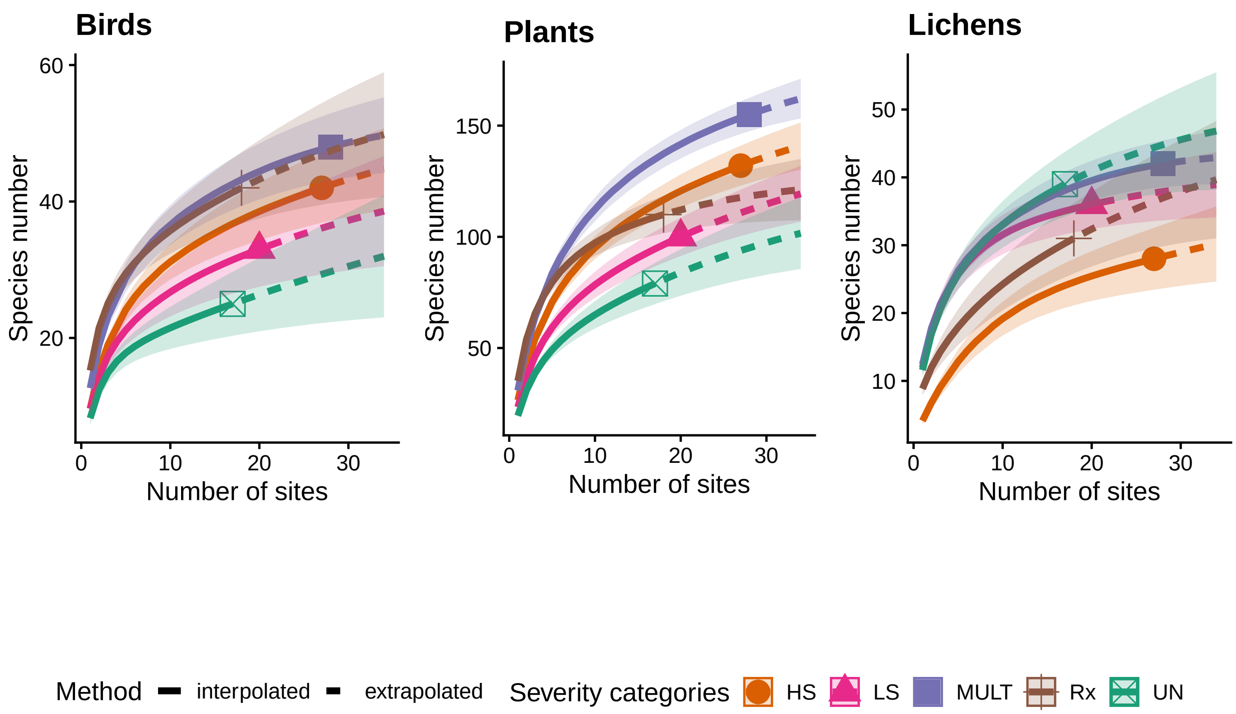


Figure 6: Gamma diversity, extrapolated based on species richness.
Shaded area represents 95% confidence intervals.

Insect Indicator Species Analysis

Six insect taxa (order or suborder) were indicators of the high severity habitats (table 2). These were mainly pollinators (Aculeata (bees/stinging wasps), Brachyceran flies, Coleoptera) and herbivores (Homoptera, Heteroptera, Orthoptera), which probably reflects the higher abundance of flowers and broadleaf shrubs/trees in high severity burns.

Table 2: Table 2: Insect indicators of early seral habitat

	IndVal	P-value
Homoptera	0.91	0.002
Coleoptera	0.87	0.001
Aculeata	0.86	0.009
Brachycera	0.82	0.014
Orthoptera	0.67	0.052
Heteroptera	0.64	0.015

Table 3: Indicator species for high severity burns and low severity/unburnt stands. Species highlighted in gray also favored multiple burns and/or thinned and burnt stands. Species in bold have a highly significant *p*-value (<0.01).

Species	IndVal	*p*-value	Species	IndVal	*p*-value
Plants			**Birds**		
Indicators of high severity burns					
Ceanothus integerrimus	**82**	**0.001**	**Spotted Towhee**	**79**	**0.001**
***Madia* spp.**	**73**	**0.001**	**Lazuli Bunting**	**69**	**0.001**
Ribes spp.	65	0.01	Nashville Warbler	62	0.012
Melica harfordii	62	0.046	**Western Wood-Pewee**	**61**	**0.001**
Elymus glaucus	**61**	**0.003**	Northern Flicker	57	0.01
Festuca microstachys	**59**	**0.001**	**MacGillivray's Warbler**	**54**	**0.008**
Rubus leucodermis	59	0.02	**Wrentit**	**54**	**0.001**
Asyneuma prenanthoides	**58**	**0.001**	House Wren	48	0.011
Solanum parishii	**56**	**0.002**	Hummingbird sp.	48	0.01
Rubus ursinus	54	0.012	Acorn Woodpecker	44	0.085
Collomia heterophylla	53	0.06	Purple Finch	44	0.082
Rubus parviflorus	51	0.08	Lesser Goldfinch	38	0.021
Agoseris spp.	48	0.012	Bewick's Wren	33	0.076
Calystegia occidentalis	48	0.011	Bushtit	33	0.067
Chamerion angustifolium	**48**	**0.005**			
Silene spp.	45	0.034			
Arctostaphylos spp.	44	0.081			
Quercus garryana	44	0.078			
Bromus carinatus	43	0.01			
Daucus pusillus	**43**	**0.005**			
Eriophyllum lanatum	**43**	**0.007**			
Achillea millefollium	40	0.072			
Dichelostemma spp.	38	0.026			
Hossackia crassicaulis	38	0.032			
Fragaria vesca	33	0.075			
Sambucus nigra	33	0.067			
Indicators of low severity/unburnt stands					
Pseudotsuga menziesii	**74**	**0.008**	Black-throated Gray/ Hermit Warbler	68	0.031
Anisocarpus madioides	**65**	**0.005**	Cassin's Vireo	66	0.033
Iris spp.	63	0.039	**Red-breasted Nuthatch**	**63**	**0.001**
Adenocaulon bicolor	**59**	**0.004**	**Chestnut-backed Chickadee**	**61**	**0.006**
Pinus lambertiana	57	0.036	**Hutton's Vireo**	**61**	**0.008**
***Pyrola* spp.**	**56**	**0.009**	**Brown Creeper**	**59**	**0.009**
Osmorrhiza berteroi	52	0.043	Hermit Thrush	40	0.025
Chimaphila umbellata	**49**	**0.004**			
Viola lobata	49	0.015			
Abies concolor	43	0.074			
Goodyera oblongifolia	43	0.04			

Early and late seral species in actively and passively managed stands

The indicator analysis for birds and plants of high severity and low severity/unburnt stands suggests distinct communities in each habitat (Table 2). Plants preferring such stands were predictably shade-tolerant species (e.g. *Goodyera oblongifolia*, *Pyrola spp.*, *Adenocaulon bicolor*, *Anisocarpus madioides*), whereas these stands were favored by bark-gleaning (Red-breasted Nuthatch and Brown Creeper) and canopy-dwelling birds (Chestnut-backed Chickadee, Black-throated Gray/Hermit Warbler, Cassin's Vireo). In contrast, species that preferred early seral conditions created by high severity fire included shrubs (e.g. *Ceanothus integerrimus*, *Rubus spp.*, *Arctostaphylos spp.*, *Solanum parishii*), grasses (e.g. *Melica harfordii*, *Elymus glaucus*, *Bromus carinatus*), annual forbs (e.g. *Madia spp.*, *Collomia heterophylla*, *Cryptantha spp.*, *Epilobium spp.*) and perennial forbs (e.g. *Asyneuma prenanthoides*, *Eriophyllum lanatum*, *Dichelostemma spp.*, *Chamerion angustifolium*, *Hossackia crassicaulis*). Birds that favored these stands tended to be species associated with shrubs and deciduous tree cover (e.g. Spotted Towhee, Wrentit, Nashville Warbler, MacGillivray's Warbler, Anna's/Rufous Hummingbirds, Black-headed Grosbeak), open habitat species (Lesser Goldfinch, Lazuli Bunting), and cavity nesters (Acorn Woodpeckers, House Wren, Northern Flicker).

I identified 61 species (birds, plants and lichens combined) that seemed to favor high severity burns (species found twice as frequently in that habitat compared to low severity and unburnt stands), and 45 species that favored low severity and unburnt stands (species found twice as frequently in that habitat compared to high severity burns). Additionally, most species that have a preference for either of these habitats exhibited the same affinity for multiple burns and thinned and burnt sites: 34 species (76%) preferring low severity and unburnt stands also favor multiple burns, while 31 (69%) also favor thinned and burnt sites. Conversely, 49 species (80%) that prefer high severity burns also favor multiple burns, and 41 (67%) also favor thinned and burnt sites. Figure 7 displays graphically the proportion of plants and birds that prefer high severity burns or unburnt and low severity stands that also favor multiple burns and thinned and burnt sites.

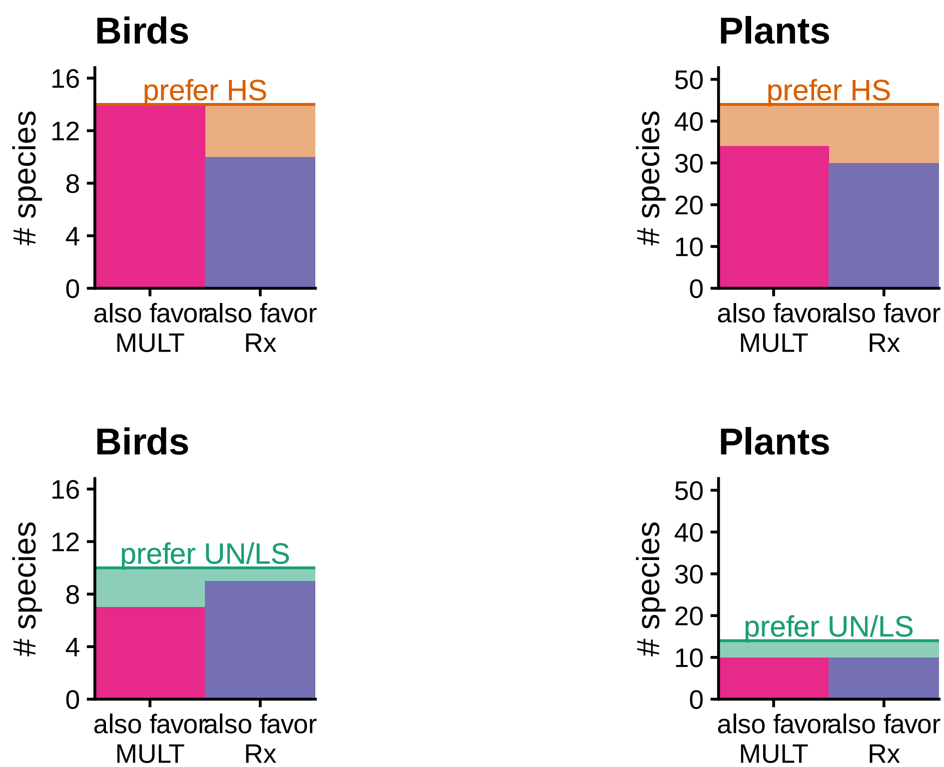


Fig. 7: Most species that prefer HS or UNLS also favor MULT and Rx

Discussion

The management and restoration of mixed-severity forests is challenged by the scale of the problem, the relative lack of studies (compared with forests with a low-severity fire regime), and the difficulties in navigating different management trade-offs (Hessburg et al., 2016; Perry et al., 2011). In this study however, management options that mitigate the risk of high severity fires by reducing canopy cover and continuity were also found to be favorable to enhanced biodiversity outcomes for birds, plants, and lichens. Diversity for all three taxa was as high or higher in multiple burns and thin+burn plots, which provided habitat for species associated with both high severity burns and dense, long-unburnt or low severity burn stands. Low severity burns were not linked to a detectable change in species composition compared with long-unburnt stands. These stands had similar to lower diversity in birds, plants, lichens and insects compared with high severity burn patches. Management that aims to mitigate the risk of high severity fire by reducing canopy cover to 30-60% can also meet biodiversity objectives by accommodating both early- and late-seral associated species.

This finding is encouraging given the focus on increasing the pace and scale of forest restoration across the West (Charnley et al., 2016). Recent policy priorities have emphasized the expansion of forest restoration, while collaborative landscape restoration partnerships such as the WKRP have been building grassroots momentum and multi-stakeholder consensus for such projects (Harling and Tripp, 2014). In addition to the goal of reducing the risk of high severity fires, such treatments aim to address the threat to biodiversity from fire suppression, which has reduced successional diversity and areas of open forest. These were once much more widespread due to historically frequent, low severity fires, particularly in areas with a high level of ignitions from Native Americans (Crawford et al., 2015; Metlen et al., 2018; Taylor et al., 2016). Restoring a more open forest structure is expected to increase diversity in understory plants (Wayman and North, 2007; Webster and Halpern, 2010) and birds (Gaines et al., 2010, 2007; Kalies and Rosenstock, 2013). Many studies have documented an increase in diversity at intermediate disturbance and canopy levels (Richter et al., 2019), although it is unclear whether this tends to benefit early-seral or late-seral associated species. In contrast, some researchers have noted the benefits of high severity fire for many species and suggested that forest restoration could damage habitat used by late-seral associates while creating conditions that are unsuitable for species associated with post-fire early-seral habitats (Odion et al., 2014). This study demonstrates that actively or passively restored stands are more diverse precisely because they accommodate both species associated with denser forests, and those associated with high severity patches.

Despite a recent increase in the size and prevalence of high severity burn patches (Stevens et al., 2017; Taylor and Skinner, 1998), fire frequency remains significantly below historic levels across much of the landscape in the Klamath Mountains (Fry and Stephens, 2006; Steel et al., 2015; Taylor and Skinner, 1998). In other ecoregions with forests with low and mixed severity fire regimes, fire suppression has caused sharp increases in canopy cover. Mixed conifer forests of the Sierra Nevada had a canopy cover of ~25% in early 20th century (S. L. Stephens et al., 2015), and similar figures have been given based on reference conditions, historical data and modelling (Fornwalt et al., 1998; Stephens et al., 2007). While precise estimates of historical canopy cover are lacking for the Klamath Mountains, it is clear that open forests have been lost across the region due to fire suppression, leading to a more homogenous, denser forest (Taylor and Skinner, 2003).

In this study, stands where fire had been excluded had the lowest plant species richness and the smallest pool of species for both birds and plants. Only select groups of species appear to prefer these conditions, including shade-tolerant plants and bark-gleaning and canopy-dwelling bird species. Fire-sensitive species, including all lichens and a small number of plants (eg. *Goodyera oblongifolia*) were also associated with these stands and absent from high severity burns (lichens began to recolonize as early as 16 years after a high severity burn). Meanwhile, the latter were home to a variety of shade-intolerant grasses, shrubs and forbs, and open area, shrub-nesting and cavity-nesting bird species that were found rarely, if ever, in unburnt stands. Several taxa of insect pollinators and herbivores were also strongly associated with high severity burns. Arthropods are an important part of the diet of many bird species, and their increase after fires may favor insectivorous birds (Seavy and Alexander, 2014). While the species of denser, fire-suppressed stands and those of post-fire early seral habitats are largely segregated in today's forested landscape, this pattern may not be representative of historical conditions in which finer-scale heterogeneity was prevalent (Hanberry et al., 2020; Taylor and Skinner, 2003). This is why I chose to investigate how low severity and multiple burns and thin+burn treatments might allow for these two species cohorts to coexist within stands.

However, the sharp distinction between the species communities of denser forests and high severity patches was not significantly altered by the occurrence of low severity fire. While it might have been expected that surface fires would play a restorative role in fire-suppressed stands (leading to an increase in shade-intolerant species for example), the small magnitude of the reduction in canopy cover after a low severity burn was insufficient to achieve this result. Other studies in mixed conifer forest have suggested that a considerable reduction in canopy cover (to 30-50%) is necessary before understory richness can be expected to increase (Abella and Springer, 2015). Douglas-firs (and white firs at higher elevations) are unlikely to be thinned by surface fires, particularly once they have reached 30cm dbh (Becker and Lutz, 2016; Collins et al., 2011; Knapp et al., 2013). Trees that have grown since fire-suppression began have reached this fire-resistant size in the productive forests of the Klamath Mountains. Since low severity fires are not significantly changing forest structure and species composition, management options that restore a lower canopy cover need to be considered.

The multiple burns and thin+burn stands in this study had a canopy cover of 30-75% (mean = 48%, sd = 15%), and were associated with the highest levels of species richness for birds and plants. Lichen species richness was also similar to that of the low severity and unburnt stands. I also found that canopy cover was negatively associated with bird and plant species richness within these habitats. Canopy cover is recognized as a key driver of species diversity (Stephens et al., 2007; Stevens et al., 2019), and my findings echo the suggestion by Abella and Springer tha ta reduction in canopy cover to 30-50% is needed to achieve significant increases in species diversity (Abella and Springer, 2015). When management results in this level of canopy cover, species typically restricted to high severity burns and those that occur in denser mature forests can coexist in a single stand.

Managing wildfires for resource benefit is a strategy that is recommended for its outcomes for bird diversity (Fontaine et al., 2009; J. L. Stephens et al., 2015), plant diversity (Laughlin et al., 2004), and ecosystem resilience (Barros et al., 2018; Boisramé et al., 2017; Nesmith et al., 2011). While there has been a focus on the capacity of high severity reburns to perpetuate "non-forest" vegetation conditions (Odion et al., 2010; Tepley et al., 2017; Thompson and Spies, 2010), low to moderate severity multiple burns can also increase fine-scale heterogeneity by creating multi-layered stands with canopy cover levels intermediate between unburnt (and low severity) stands and high severity burns. I found that such areas represent biodiversity hotspots on the landscape because the structure of these stands accommodated both fire-sensitive species (e.g. lichens) and fire-dependent species (eg. shade-intolerant herbaceous plants and shrub-nesting birds).

Thinned and burnt stands achieved the same result, particularly when there had been a significant reduction in canopy cover. As was the case for the multiple burns, I focused my sampling on stands with a canopy cover of 30-70%. This represents a important reduction in canopy cover and may not represent standard practices. But this study joins others in highlighting the ecological benefits of higher severity burns, or at least treatments that include patches of high severity (Fulé et al., 2004; Stephens et al., 2012). Just like low severity burns in this study, treatments that maintain a high canopy cover are unlikely to stimulate a response of understory diversity. Despite the potential benefits of treating stands to reverse the effects of fire exclusion, such treatments remain very scarce in the study region. This led to some sacrifices in sampling rigor (eg. sites were more spatially clustered), and as a result caution is needed in interpreting some of the results (eg. lower beta diversity in the thin+burn stands). More importantly, while the results are encouraging, the vanishingly small footprint of active forest restoration brings into question the ability for agencies to deploy such treatments on the scale that is needed. The footprint of wildfires, including reburns, exceeds active management by a considerable margin. Much more widespread restoration efforts will be needed, for example through collaborative approaches such as the WKRP, and wildland fire use should also be embraced as an alternative when conditions allow. In the meantime, umplanned ignitions, including high severity burn patches, are critical to the maintenance of biodiversity in the fire suppressed forests of the Klamath Mountains.

This study had other weaknesses aside from the difficulty in finding acceptable actively restored stands. The number of samples and variation associated with complex topographic and environmental factors did not allow for an in-depth analysis of the role of time-since-fire, which may have masked the response of some species (Smucker et al., 2005). Scale-related challenges are common in ecological research, and this study was no exception, taking into account only stand-level variables but leaving out potentially important landscape patterns (Betts et al., 2010). Lastly, it would be useful to more thoroughly investigate the full range of outcomes from multiple burns and thin+burn treatments, including quantifying their spatial extent. This study joins others in showing that positive biodiversity outcomes are possible under some conditions, but to what extent these are realized remains to be determined.

Management implications

Fire suppressed stands have similar or lower plant and bird diversity (alpha, beta, gamma diversity) than high severity burn burns, and low severity burns do not appear to change this pattern. While high severity burns are important for biodiversity when compared with unburnt/low severity stands, species that are associated with both of these habitats also favor multiple burns and prescribed burns. As a result, such stands are more diverse than either high severity burns or (especially) unburnt/low severity burn stands. This suggests that both active (thin+burn) and passive (wildland fire use) management can achieve biodiversity conservation goals while also achieving fuels reduction and forest and community resilience objectives. Fuels reduction treatments can be conducted in a way that benefits biodiversity (Dodson and Peterson, 2010; Dodson et al., 2008; Wayman and North, 2007). However, canopy cover and small to medium tree density must be significantly reduced to achieve such benefits (Abella and Springer, 2015; Kalies and Rosenstock, 2013), and repeated treatments are necessary (Goodwin et al., 2018). Multiple burns can achieve similar results, suggesting that wildland fire use should be used to promote diverse forests at a scale much larger than current active restoration treatments allow. In the absence of passive or active restoration, mosaics of different fire severiies, including high severity patches, are important to the maintenance of biodiversity in the fire suppressed forests of the Klamath Mountains.

Acknowledgements

I would like to extend my deepest gratitude to the Karuk Tribe and tribal members and fire practitioners including Frank Lake, Bill Tripp, Renée Stauffer, and members of the Karuk Research Approval Board for their guidance. I am also grateful to the staff of the Six Rivers and Klamath National forests for their support, and to my academic mentors at UC Davis, including Beth Rose Middleton, Hugh Safford, and Dan Potter. Several brave interns helped me gather the data and process insect specimens: Jacob Wilson, Diana Cuevas, Shaden Cortez, Vincent Ho, and Sierra Schluep. Funding was provided by the the Henry A. Jastro Research Fellowship, California Lichen Society, Northern California Botanists, and California Native Plant Society.

References

Abella, S.R., Springer, J.D., 2015. Effects of tree cutting and fire on understory vegetation in mixed conifer forests. Forest Ecology and Management 335, 281–299. https://doi.org/10.1016/j.foreco.2014.09.009

Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA), in: Wiley StatsRef: Statistics Reference Online. American Cancer Society, pp. 1–15. https://doi.org/10.1002/9781118445112.stat07841

Baker, W.L., 2015. Are High-Severity Fires Burning at Much Higher Rates Recently than Historically in Dry-Forest Landscapes of the Western USA? PLoS ONE 10. https://doi.org/10.1371/journal.pone.0136147

Baldwin, B.G., Goldman, D.H., Keil, D.J., Patterson, R., Rosatti, T.J., Vorobik, L.A., 2012. The Jepson manual: Vascular plants of California. Univ of California Press.

Barbour, M.G., Billings, W.D., 2000. North American terrestrial vegetation. Cambridge University Press.

Barros, A.M.G., Alan A., A., Day, M.A., Krawchuk, M.A., Spies, T.A., 2018. Wildfires managed for restoration enhance ecological resilience. Ecosphere 9, e02161. https://doi.org/10.1002/ecs2.2161

Bartuszevige, A.M., Kennedy, P.L., 2009. Synthesis of knowledge on the effects of fire and thinning treatments on understory vegetation in US dry forests.

Becker, K.M., Lutz, J.A., 2016. Can low-severity fire reverse compositional change in montane forests of the Sierra Nevada, California, USA? Ecosphere 7.

Betts, M.G., Hagar, J.C., Rivers, J.W., Alexander, J.D., McGarigal, K., McComb, B.C., 2010. Thresholds in forest bird occurrence as a function of the amount of early-seral broadleaf forest at landscape scales. Ecological Applications 20, 2116–2130.

Boisramé, G.F.S., Thompson, S.E., Kelly, M., Cavalli, J., Wilkin, K.M., Stephens, S.L., 2017. Vegetation change during 40years of repeated managed wildfires in the Sierra Nevada, California. Forest Ecology and Management 402, 241–252. https://doi.org/10.1016/j.foreco.2017.07.034

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecological Monographs 84, 45–67. https://doi.org/10.1890/13-0133.1

Charnley, S., Kelly, E.C., Wendel, K.L., 2016. All lands approaches to fire management in the Pacific West: A typology. Journal of Forestry 115, 16–25.

Collins, B.M., Everett, R.G., Stephens, S.L.;., 2011. Impacts of fire exclusion and recent managed fire on forest structure in old growth Sierra Nevada mixed-conifer forests. Ecosphere 2, 1–14.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L., Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5, 3–21. https://doi.org/10.1093/jpe/rtr044

Crawford, J.N., Mensing, S.A., Lake, F.K., Zimmerman, S.R., 2015. Late Holocene fire and vegetation reconstruction from the western Klamath Mountains, California, USA: A multi-disciplinary approach for examining potential human land-use impacts. The Holocene 25, 1341–1357. https://doi.org/10.1177/0959683615584205

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

Dodson, E.K., Peterson, D.W., 2010. Dry coniferous forest restoration and understory plant diversity: The importance of community heterogeneity and the scale of observation. Forest Ecology and Management 260, 1702–1707. https://doi.org/10.1016/j.foreco.2010.08.012

Dodson, E.K., Peterson, D.W., Harrod, R.J., 2008. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. Forest Ecology and Management. 255: 3130-3140.

Flint, L.E., Flint, A.L., Thorne, J.H., Boynton, R., 2013. Fine-scale hydrologic modeling for regional landscape applications: The California Basin Characterization Model development and performance. Ecological Processes 2, 25. https://doi.org/10.1186/2192-1709-2-25

Fontaine, J.B., Donato, D.C., Robinson, W.D., Law, B.E., Kauffman, J.B., 2009. Bird communities following high-severity fire: Response to single and repeat fires in a mixed-evergreen forest, Oregon, USA. Forest Ecology and Management 257, 1496–1504. https://doi.org/10.1016/j.foreco.2008.12.030

Fornwalt, P.J., Kaufmann, M.R., Huckaby, L.S., Stoker, J.M., 1998. Using the Forest Vegetation Simulator to reconstruct historical stand conditions in the Colorado Front Range. Proceedings RMRS. 108.

Fry, D.L., Stephens, S.L., 2006. Influence of humans and climate on the fire history of a ponderosa pine-mixed conifer forest in the southeastern Klamath Mountains, California. Forest Ecology and Management 223, 428–438. https://doi.org/10.1016/j.foreco.2005.12.021

Fulé, P.Z., Cocke, A.E., Heinlein, T.A., Covington, W.W., 2004. Effects of an Intense Prescribed Forest Fire: Is It Ecological Restoration? Restoration Ecology 12, 220–230. https://doi.org/10.1111/j.1061-2971.2004.00283.x

Gaines, W., Haggard, M., Begley, J., Lehmkuhl, J., Lyons, A., 2010. Short-Term Effects of Thinning and Burning Restoration Treatments on Avian Community Composition, Density, and Nest Survival in the Eastern Cascades Dry Forests, Washington. Forest Science 56, 88–99. https://doi.org/10.1093/forestscience/56.1.88

Gaines, W.L., Haggard, M., Lehmkuhl, J.F., Lyons, A.L., Harrod, R.J., 2007. Short-Term Response of Land Birds to Ponderosa Pine Restoration. Restoration Ecology 15, 670–678. https://doi.org/10.1111/j.1526-100X.2007.00279.x

Goodwin, M.J., North, M.P., Zald, H.S.J., Hurteau, M.D., 2018. The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. Forest Ecology and Management 429, 617–624. https://doi.org/10.1016/j.foreco.2018.07.058

Hanberry, B.B., Bragg, D.C., Alexander, H.D., 2020. Open forest ecosystems: An excluded state. Forest Ecology and Management 472, 118256. https://doi.org/10.1016/j.foreco.2020.118256

Harling, W., Tripp, B., 2014. Western Klamath Restoration Partnership: A Plan for Restoring Fire Adapted Landscapes.

Haugo, R.D., Kellogg, B.S., Cansler, C.A., Kolden, C.A., Kemp, K.B., Robertson, J.C., Metlen, K.L., Vaillant, N.M., Restaino, C.M., 2019. The missing fire: Quantifying human exclusion of wildfire in Pacific Northwest forests, USA. Ecosphere 10, e02702. https://doi.org/10.1002/ecs2.2702

Hessburg, P.F., Agee, J.K., Franklin, J.F., 2005. Dry forests and wildland fires of the inland Northwest USA: Contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management, Relative Risk Assessments for Decision Making Related To Uncharacteristic Wildfire 211, 117–139. https://doi.org/10.1016/j.foreco.2005.02.016

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

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613

Jost, L., 2007. Partitioning Diversity into Independent Alpha and Beta Components. Ecology 88, 2427–2439. https://doi.org/10.1890/06-1736.1

Kalies, E.L., Rosenstock, S.S., 2013. Stand structure and breeding birds: Implications for restoring ponderosa pine forests. The Journal of Wildlife Management 77, 1157–1165. https://doi.org/10.1002/jwmg.577

Kalies, E.L., Yocom Kent, L.L., 2016. Tamm Review: Are fuel treatments effective at achieving ecological and social objectives? A systematic review. Forest Ecology and Management 375, 84–95. https://doi.org/10.1016/j.foreco.2016.05.021

Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 310, 903–914. https://doi.org/10.1016/j.foreco.2013.09.041

Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Springer, J.D., Gildar, C.N., Green, A.M., Covington, W.W., 2004. Toward reference conditions: Wildfire effects on flora in an old-growth ponderosa pine forest. Forest Ecology and Management 199, 137–152. https://doi.org/10.1016/j.foreco.2004.05.034

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2020. Emmeans: Estimated Marginal Means, aka Least-Squares Means (Version 1.4. 7).

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: A comment on distance-based redundancy analysis. Ecology 82, 290–297.

McCune, B., Geiser, L., 2009. Macrolichens of the Pacific Northwest, 2nd edition. ed. Oregon State University Press.

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13, 603–606. https://doi.org/10.1111/j.1654-1103.2002.tb02087.x

Metlen, K.L., Skinner, C.N., Olson, D.R., Nichols, C., Borgias, D., 2018. Regional and local controls on historical fire regimes of dry forests and woodlands in the Rogue River Basin, Oregon, USA. Forest Ecology and Management 430, 43–58. https://doi.org/10.1016/j.foreco.2018.07.010

Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative Evidence for Increasing Forest Fire Severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. Ecosystems 12, 16–32. https://doi.org/10.1007/s10021-008-9201-9

Miller, J.D., Thode, A.E., 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109, 66–80. https://doi.org/10.1016/j.rse.2006.12.006

Miller, J.E.D., Root, H.T., Safford, H.D., 2018. Altered fire regimes cause long-term lichen diversity losses. Global Change Biology 1–10. https://doi.org/10.1111/gcb.14393

Miller, J.E.D., Safford, H., 2019. Plant community responses to wildfire may be contingent upon historical disturbance regimes. https://doi.org/10.32942/osf.io/8sxfh

Moghaddas, J.J., Collins, B.M., Menning, K., Moghaddas, E.E., Stephens, S.L., 2010. Fuel treatment effects on modeled landscape-level fire behavior in the northern Sierra Nevada. Canadian Journal of Forest Research 40, 1751–1765.

Nesmith, J.C., Caprio, A.C., Pfaff, A.H., McGinnis, T.W., Keeley, J.E., 2011. A comparison of effects from prescribed fires and wildfires managed for resource objectives in Sequoia and Kings Canyon National Parks. Forest Ecology and Management 261, 1275–1282.

North, M., Collins, B.M., Stephens, S., 2012. Using Fire to Increase the Scale, Benefits, and Future Maintenance of Fuels Treatments. Journal of Forestry 110, 392–401. https://doi.org/10.5849/jof.12-021

Odion, D.C., Hanson, C.T., Arsenault, A., Baker, W.L., DellaSala, D.A., Hutto, R.L., Klenner, W., Moritz, M.A., Sherriff, R.L., Veblen, T.T., Williams, M.A., 2014. Examining Historical and Current Mixed-Severity Fire Regimes in Ponderosa Pine and Mixed-Conifer Forests of Western North America. PLOS ONE 9, e87852. https://doi.org/10.1371/journal.pone.0087852

Odion, D.C., Moritz, M.A., DellaSala, D.A., 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. Journal of Ecology 98, 96–105. https://doi.org/10.1111/j.1365-2745.2009.01597.x

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M.H.H., Oksanen, M.J., Suggests, M., 2007. The vegan package. Community ecology package 10, 631–637.

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

Rice, W.R., 1989. Analyzing tables of statistical tests. Evolution 43, 223–225.

Richter, C., Rejmánek, M., Miller, J.E.D., Welch, K.R., Weeks, J., Safford, H., 2019. The species diversity x fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. Ecosphere 10, e02882. https://doi.org/10.1002/ecs2.2882

Russo, L., Stehouwer, R., Heberling, J.M., Shea, K., 2011. The Composite Insect Trap: An Innovative Combination Trap for Biologically Diverse Sampling. PLOS ONE 6, e21079. https://doi.org/10.1371/journal.pone.0021079

Safford, H.D., Van de Water, K.M., 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on national forest lands in California (No. PSW-RP-266).

U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA. https://doi.org/10.2737/PSW-RP-266

Seavy, N.E., Alexander, J.D., 2014. Songbird response to wildfire in mixed-conifer forest in south-western Oregon. International Journal of Wildland Fire 23, 246–258. https://doi.org/10.1071/WF12081

Smucker, K.M., Hutto, R.L., Steele, B.M., 2005. Changes in bird abundance after wildfire: Importance of fire severity and time since fire. Ecological Applications 15, 1535–1549.

Steel, Z.L., Safford, H.D., Viers, J.H., 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6, art8. https://doi.org/10.1890/ES14-00224.1

Stephens, J.L., Ausprey, I.J., Seavy, N.E., Alexander, J.D., 2015. Fire severity affects mixed broadleafConifer forest bird communities: Results for 9 years following fire. The Condor 117, 430–446. https://doi.org/10.1650/CONDOR-14-58.1

Stephens, S.L., Fry, D.L., Franco-Vizcaíno, E., Collins, B.M., Moghaddas, J.M., 2007. Coarse woody debris and canopy cover in an old-growth Jeffrey pine-mixed conifer forest from the Sierra San Pedro Martir, Mexico. Forest Ecology and Management 240, 87–95. https://doi.org/10.1016/j.foreco.2006.12.012

Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., Meyer, M.D., 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6, 1–63. https://doi.org/10.1890/ES14-00379.1

Stephens, S.L., McIver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., Schwilk, D.W., 2012. The Effects of Forest Fuel-Reduction Treatments in the United States. BioScience 62, 549–560. https://doi.org/10.1525/bio.2012.62.6.6

Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. Forest Ecology and Management 406, 28–36. https://doi.org/10.1016/j.foreco.2017.08.051

Stevens, J.T., Miller, J.E.D., Fornwalt, P.J., 2019. Fire severity and changing composition of forest understory plant communities. Journal of Vegetation Science 30, 1099–1109. https://doi.org/10.1111/jvs.12796

Swanson, M.E., Studevant, N.M., Campbell, J.L., Donato, D.C., 2014. Biological associates of early-seral pre-forest in the Pacific Northwest. Forest ecology and management 324, 160–171.

Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains.

Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. Forest Ecology and Management 111, 285–301. https://doi.org/10.1016/S0378-1127(98)00342-9

Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S., 2016. Socioecological transitions trigger fire regime shifts and modulate fire-climate interactions in the Sierra Nevada, USA, 16002015 CE. Proceedings of the National Academy of Sciences 201609775. https://doi.org/10.1073/pnas.1609775113

Tepley, A.J., Thompson, J.R., Epstein, H.E., Anderson-Teixeira, K.J., 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. Global Change Biology 23, 4117–4132. https://doi.org/10.1111/gcb.13704

Thompson, J.R., Spies, T.A., 2010. Factors associated with crown damage following recurring mixed-severity wildfires and post-fire management in southwestern Oregon. Landscape Ecology 25, 775–789. https://doi.org/10.1007/s10980-010-9456-3

USFS, 2008. Common stand exam user's guide. USDA Forest Service, Albany, California, USA.

Van de Water, K.M., Safford, H.D., 2011. A Summary of Fire Frequency Estimates for California Vegetation before Euro-American Settlement. Fire Ecology 7, 26–58. https://doi.org/10.4996/fireecology.0703026

Wayman, R.B., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. Forest Ecology and Management 239, 32–44. https://doi.org/10.1016/j.foreco.2006.11.011

Webster, K.M., Halpern, C.B., 2010. Long-term vegetation responses to reintroduction and repeated use of fire in mixed-conifer forests of the Sierra Nevada. Ecosphere 1, 1–27. https://doi.org/10.1890/ES10-00018.1

Whittaker, R.H., 1961. VEGETATION HISTORY OF THE PACIFIC COAST STATES AND THE "CENTRAL" SIGNIFICANCE OF THE KLAMATH REGION. Madroño 16, 5–23.

Willms, J., Bartuszevige, A., Schwilk, D.W., Kennedy, P.L., 2017. The effects of thinning and burning on understory vegetation in North America: A meta-analysis. Forest Ecology and Management 392, 184–194. https://doi.org/10.1016/j.foreco.2017.03.010