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Post-fire management affects species composition but not Douglas-fir regeneration in the Klamath Mountains

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ABSTRACT

Ensuring adequate conifer regeneration after high severity wildfires is a common objective for ecologists and forest managers. In the Klamath region of Oregon and California, a global hotspot of botanical biodiversity, concerns over regeneration have led to post-fire management on many sites, which involves salvage logging followed by site preparation, conifer planting, and manual shrub release. To quantify the impacts of post-fire management, we sampled 62 field sites that burned at high severity nearly 20 years ago in the Klamath-Siskiyou Mountain bioregion, stratifying by management and aspect. We measured cover of shrubs and trees and density and frequency of trees and used Nonmetric Multidimensional Scaling to compare community composition, plant community assemblage based on regenerative traits, and density of tree species between aspect and management. On average, shrub cover exceeded the cover of conifers, hardwoods or grasses, regardless of management history or aspect. The average number of species was lower and resprouting species were less abundant on south aspect sites; seed banking species were most abundant on north aspects. Post-fire management was associated with greater cover of seed banking and nitrogen-fixing species but it did not affect diversity. Management had no impact on Douglas-fir regeneration, the main species of concern in the region. Regeneration of ponderosa pine was higher on sites with post-fire management, but only on south slopes. The frequency of Douglas-fir was associated with aspect, while the frequency of ponderosa pine was associated with management. Overall, our study demonstrates the important role that aspect plays in determining the effectiveness of management after high severity wildfires. Indeed, the effect of aspect on site conditions often overwhelmed the ability of management to influence community composition (including different regenerative strategies), species diversity, and regeneration. Managed sites differed from unmanaged sites in several diverse ways with varied implications for longer-term forest development. Managed sites had taller dominant conifers, which suggests that post-fire management could hasten the period needed to achieve fire resistance. Managed sites were similar in plant community composition but had more homogeneous structure–e.g., managed sites had fewer snags, which are an important habitat feature for several bird species in the region. Finally, management was not associated with conifer regeneration success on north slopes, suggesting that interventions may not be needed uniformly across post-fire landscape. New policies of ecosystem-based management in the Klamath region should consider the important interactions between aspect and post-fire management, and tailor management practices based on specific objectives and landscape context.

1. Introduction

Vegetation dynamics during the first few decades after stand replacing wildfires are of fundamental interest to ecologists because these patterns will determine composition, structure and function for decades to centuries (Agee, 1993). It is also a long-standing topic of interest for forest managers who want to ensure that there is adequate conifer regeneration after large wildfires (Donato et al., 2009). Recent and

projected changes to the climate system are widely expected to reduce the success of conifer regeneration (Serra-Diaz et al., 2018; Stevens-Rumann et al., 2017, Harvey et al., 2016) as the occurrence of large wildfires increases (Stevens-Rumann et al., 2017). This is generating uncertainty about post-fire recovery (Tepley et al., 2017; Anderson-Teixeira et al., 2013) with potential implications for ecosystem resilience (Stevens-Rumann, 2017; Harvey et al., 2016).

Concerns about conifer regeneration have a long history in the Klamath region of northern California and southern Oregon. This region is a global hotspot of botanical conifer diversity and has been shaped by recurrent fires of mixed severity (Taylor and Skinner, 1998, 2003, Skinner et al., 2006, Thompson and Spies, 2010). Widespread regeneration failures in conifer plantations in the 1970s and 1980s led to concerns about conifer resilience (Hobbs, 1992). These concerns are exacerbated by the increased susceptibility to higher severity fire events due to climate change and fire suppression (Agee and Skinner, 2005). Severe fires often convert mixed-conifer cover to early-seral vegetation dominated by broadleaf trees and shrubs, since these establish very quickly following wildfire through sprouting and germination from the seed bank. Initially, these hardwoods and shrubs suppress conifer regeneration, through intense competition for light and near-surface soil moisture content (Conard and Radosevich, 1982, Sessions et al., 2004). Such concerns notwithstanding, several authors have documented successful natural establishment at densities more than sufficient to permit forest recovery (Shatford et al., 2007; Donato et al., 2009), with conifers gradually growing to overtop hardwoods and shrubs after about 20 years post-fire (Tepley et al., 2017). Furthermore, there is evidence that shrubs, such as *Ceanothus* spp. and *Arctostaphylos* spp. (Keeley, 1987) may aid conifer seedling survival by reducing soil temperature or enriching available soil nitrogen through N fixation (Conard and Radosevich, 1982, Oakley et al., 2003, 2006), primarily on sites with low productivity (Yelenik et al., 2013).

Due to concerns over regeneration, salvage logging followed by site preparation, conifer planting, and manual shrub release was the de facto management response for the latter half of the twentieth century in the Klamath region (Holder, 1990; McIver and Starr, 2001; Beschta et al., 2004). However, in recent decades there has been a controversy regarding whether salvage logging and planting is necessary for conifer forest recovery (Sessions et al., 2004; Donato et al., 2009). The cost of post-fire management activities such as planting and salvage logging are significant, and their effectiveness in maintaining adequate conifer regeneration is uncertain over the long term (Thompson et al., 2007).

In the Klamath region, there are stark differences between north and south aspects in terms of solar radiation, air temperature, humidity, heat load, soil moisture (Rosenberg et al., 1983) and plant community composition (Small and McCarthy, 2002; Keeley et al., 2005). Post-fire recovery differs dramatically between aspect in the Klamath (Irvine et al., 2009), which is not surprising given that climatic conditions and conifer regeneration success are tightly coupled (Stevens-Rumann et al., 2017; Anderson-Teixeira et al., 2013). On south aspects, Douglas-fir (*Pseudotsuga menziesii*) shares dominance with hardwoods such as black oak (*Quercus kelloggii*), white oak (*Quercus garryana*) and canyon live oak (*Quercus chrysolepis*). As soil moisture increases on more northerly aspects, the dominant hardwoods shift from oaks to Pacific madrone (*Arbutus menziesii*) with tanoak (*Notholithocarpus densiflorus*) on the more mesic sites. On more mesic sites, true firs (Abies spp.) dominate especially at higher elevation. Pine species, ponderosa pine (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*), contribute to pure and mixed conifer stands on southerly aspects. Aspect also affects fire frequency with higherfrequency on south slopes (Taylor and Skinner, 1998, 2003). While the effects of shrubs and hardwoods on conifer establishment and growth are likely variable across space and time, detailed information about the density and frequency of conifer regeneration after large, intense forest fires on sites with and without post-fire management is critical in this region.

Here we fill an important knowledge gap by addressing the following questions: (1) How does post-fire management affect species composition, stand structure (i.e. tree height, snags) and the success of species' reproductive strategies? (2) Does post-fire management increase the abundance and frequency of conifer regeneration? We hypothesized that management would lower overall shrub and hardwood cover, increase the abundance of species that rely on off-site seed sources, increase conifer height through competition reduction, and decrease snags by salvage logging. We also predicted that management would increase the density and frequency of conifer regeneration, with significant differences by aspect. To address our questions, we sampled vegetation twenty years after a high severity fire, comparing sites with and without management in contrasting microclimates in the Klamath Mountains.

2. Methods

2.1. Study area

The Klamath region of northwestern California and southwestern Oregon covers an area of approximately 22,500 km^2 (Skinner et al., 2006). It extends from the Cascade Range in the east to the Coast Range in the west, and is 390 km north to south (Hobbs, 1992, Strittholt et al., 1999). The terrain is rugged and deeply incised (Palazzi et al., 1992). The climate is Mediterranean, with mild wet winters and dry summers. The duration of the wet and dry seasons, as well as the total annual precipitation, is spatially variable due to a strong west-to-east moisture and temperature gradient caused by proximity to the Pacific Ocean (Whittaker, 1960, Skinner et al., 2006).

This study focuses on the Douglas-fir vegetation series, which ranges in elevation from 200 to 2000 m. Slopes range from zero to 120 percent (Atzet and Wheeler, 1982). Precipitation ranges from about 1100 mm to 2000 mm, 90% of which falls between October and May. The average July temperature in the center of the study area (330 m in elevation) is 25.7 °C. Mixed-severity fire is a common disturbance in the study area (Halofsky et al., 2011) with a median historic fire return interval (FRI) of 12–19 years in the central part of the study area (Taylor and Skinner, 1998). This return interval pre-dates fire suppression efforts that began in the middle of the 20th century, which have been very successful at preventing fire in the region. Despite the effectiveness of fire suppression, large fires still occur in the region, such as occurred in 1987 and 2002.

2.2. Site selection

Field sites were selected from patches within the fire matrix that burned at high severity in the 1987 fires and had supported older, unmanaged Douglas-fir prior to 1987 (Fig. 1). Sites occurred within the boundary of 11 fires on the Klamath National Forest. Candidate sites were divided into sites with no post-fire management and managed sites that were logged and planted after the fire (Lopez Ortiz, 2007). Sampling in each group was stratified by aspect. Only north or south aspect sites (± 45° from north or south) were considered. GIS layers of topography, fire severity within a fire boundary, and cutting activities since 1970 were overlaid to discriminate unmanaged from managed sites and to determine aspect and elevation. Aerial photographs from 1987 were assessed to confirm that the overstory was removed by the fire (i.e. that they were high severity burns). For managed sites, stand records were used to identify post-fire management activities; management was further confirmed by site inspection. We selected managed sites that presented the most common combination of post-fire management activities: salvage logging, fuel reduction, tree planting, and a one-time shrub cutting around selected conifer seedlings. No additional treatments (e.g. herbicide application) were recorded. According to stand records, sites were salvage logged within the first three years after the fire. Seedlings were planted 2–4 years after fire, most often with a mixture of 60% Douglas-fir and 40% ponderosa pine (*Pinus*
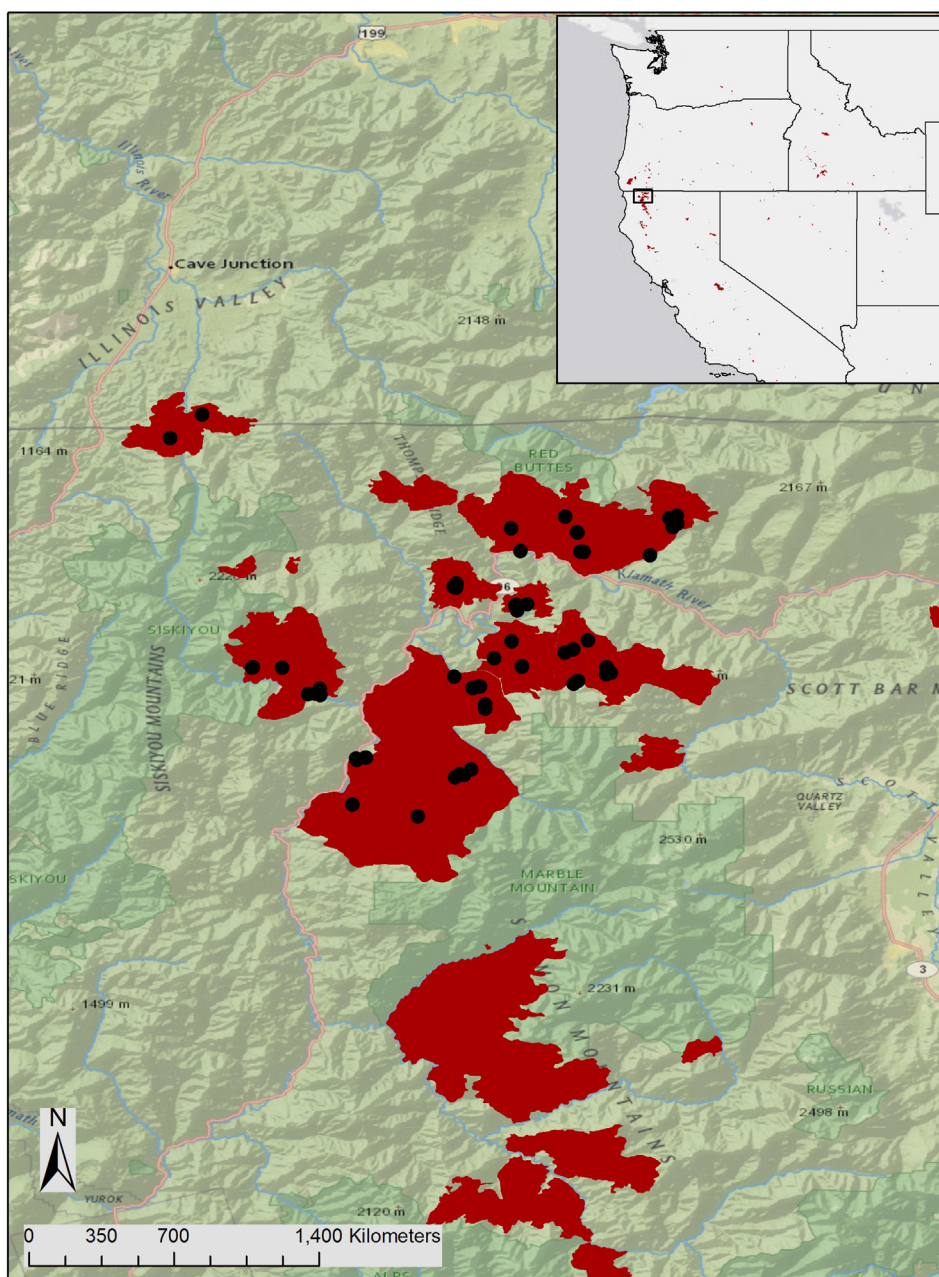
Fig. 1. Study site location. Black dots indicate study sites. Red polygons indicate wildfires from the year 1987.

ponderosa) at a ~3 × 3 m spacing. Shrub release, the cutting of shrubs within a 2 m radius around a conifer seedling, was performed two years after seedlings were planted.

2.3. Sampling

Vegetation was sampled from mid-June through September in 2005 and 2006, eighteen to nineteen years after the fires. A total of 62 sites (25 unmanaged (16 north aspect, 9 south aspect) and 37 managed (23 north, 14 south)) were sampled. Sixty sites were located in the U.S. Forest Service Happy Camp Ranger District. Two managed sites (1 north aspect and 1 south aspect) were located in the U.S.F.S. Cave Junction Ranger District. Elevation of the sites ranged from 374 to 1506 m. Average slope for the sites was 60% with a range from 20% to 100% (Table 1).

The sample unit (plot) was situated randomly within openings created by a high severity fire. We used a 12 × 40 m plot divided into

Table 1

Summary of site characteristics. Mean values and range (where appropriate) are presented.

	Unmanaged	Managed
Total number of plots	25	37
North aspect	16	23
South aspect	9	14
Slope (%)	58 (18–100)	60 (28–80)
Elevation (m)	993 (374–1506)	913 (431–1496)

30 cells of 4 × 4 m to ensure a thorough search for tree seedlings. Plot level measurements included elevation, slope, aspect and geographic location (GPS coordinates, ± 20 m). Trees included all conifer and hardwood species capable of reaching a mature height of more than five meters. We tallied all conifers by height/DBH class (0–2, 2.1–4.0, 4.1–6.0 cm, etc. DBH) and measured the diameter at breast height

(DBH), total height, and percentage of live crown of the biggest conifer in each cell. For hardwood trees, species and size class data were collected on all managed sites and on 18 of the 25 unmanaged sites. Hardwoods were grouped in size classes with 0.5 m height intervals up to 1.5 m; seedling or hardwoods clumps taller than 1.5 m were grouped in DBH classes with 2 cm intervals. For multi-stemmed hardwoods (clumps), only the biggest stem was measured and assigned to a DBH class. The DBH of all snags was also recorded.

To estimate vegetation cover, we divided the plot into thirds. In each third (12 × 12 m), we visually estimated percent cover of trees and shrubs by species and averaged the three values for an overall estimate. To reduce individual bias, two people worked together and comparison charts were used to aid in assessing percent cover. Grasses, forbs, and ferns were each treated as a taxonomic group.

2.4. Cover of life form groups

We described the plant community structure of unmanaged and managed sites using the average percent cover of the main species of each life form group: conifers, hardwoods, shrubs, and forbs/grasses/ferns. We used two sample t-tests (S-plus V.7) to compare cover of the main life form groups (conifers, hardwoods, shrubs, forbs, grasses, and ferns) between unmanaged and managed sites. Bonferroni's correction was used to balance individual and family-wise confidence intervals.

Three measures of species diversity were used: average number of species, Simpson's diversity index (Simpson, 1949), and the Shannon-Wiener diversity index (MacArthur and MacArthur, 1961). Simpson's diversity index was calculated as $D = 1 - \sum_i^S p_{i^2}$ where pi is the proportion of individuals belonging to species i and S is the total number of species. This measure emphasizes common species and is little affected by addition or loss of rare species (McCune and Grace, 2002). The Shannon-Wiener index was calculated as: $H^{'} = -\sum_i^S p_i ln p_i$ where pi is the proportion of individuals belonging to species i. This measure is intermediate between average number of species and Simpson's index in its sensitivity to rare species (McCune and Grace, 2002). We also reported Whittaker's beta diversity (Whittaker, 1972), calculated as $\beta_w = \frac{S}{\alpha}$ where S is the total number of species and α is the average number of species.

2.5. Community composition

We compared community composition between unmanaged and managed sites using Nonmetric Multidimensional Scaling (NMS, Kruskal, 1964, Mather, 1976). NMS uses an iterative search for an ordination with low stress, as measured by the relationship between ranked distances in the original multidimensional space and the ranked distance in the reduced dimensions of the ordination (McCune and Grace, 2002). Ordination of community data with NMS requires no assumptions of multivariate normality or linearity, and is robust with large numbers of zero values.

To reduce noise from rare species, those occurring in less than five percent of the plots were deleted from the data set prior to analysis. The resulting matrix included 62 plots and 44 species. Analyses were run using Autopilot in the slow and thorough mode of NMS in PC-ORD version 5 (McCune and Mefford, 1999), which used 250 runs with real data and 250 runs with randomized data for a Monte Carlo test of significance. Each NMS ordination used Sørensen's distance, and each began with a different random configuration. The best solution was assessed based on the final minimum stress and the Monte Carlo test. The data were not relativized, allowing differences in the total abundance of species to be expressed in the analysis. The NMS Autopilot in PC-ORD chose a 3-dimensional solution as providing a considerable and statistically significant reduction in stress as compared with randomized data (final stress = 15.0; p = 0.004 for all axes).

Environmental and treatment variables were related to ordination results using overlay and joint plots. Environmental variables included:

elevation, aspect (folded around the north-south line), slope (%), and heat load index. The heat load index represents the amount of heat a site potentially receives and is derived from models based on latitude, slope, and aspect (McCune and Keon, 2002). Unmanaged and managed were considered as treatments variables. For visual clarity, the ordination was rotated to align treatments with the horizontal axis.

2.6. Vertical structure

Average height of the most abundant species in each group was used to describe the vertical structure of unmanaged and managed sites. The height of dominant conifers was not recorded in 32% of the cases (401 out of 1235); we estimated the missing heights using equations that predict height as a function of DBH. Parameter estimates used in the height equation were obtained from a larger data set for this region (Shatford unpublished data; Hann unpublished data). At each candidate site, we evaluated presence and diameter of snags (for unmanaged sites), and stumps (for managed sites), soils (non-ultramafic), and aspect (north or south).

2.7. Regeneration traits

To examine plant community assemblage from a trait perspective, the abundance of plant species based on traits was ordinated using a similar NMS approach as described above. The abundance of traits was obtained by multiplying the species abundance matrix by a binary matrix of traits. Each element of the resulting matrix multiplication represents the abundance of a specific trait on a given plot. Traits were derived from the life form data base of the USDA Forest Service (http://www.fs.fed.us/database/feis/plants) and from the literature. The binary matrix included three regeneration strategies (seed banking, resprouting, and obligate seeding) and the ability to fix atmospheric nitrogen. When more than one type of regeneration was used by a species, we assigned the type according to the most common response to high severity fire mentioned in the literature. Seed banking species were defined as those species killed by the fire and whose persistence relies on seeds stored in the canopy or in soil banks. Species from the genera *Ceanothus* and *Arctostaphylos* as well as knobcone pine (*Pinus attenuata)* were included under this category. Resprouting species included hardwood and shrub species which are mentioned in the literature as able to resprout after fires. Obligate seeding, included all species that, after high severity fires, rely on off-site seed sources. This category included conifer species (except knobcone pine) and common whipplea (*Whipplea modesta*) (for responses to high severity burn for this species, see Halpern, 1989). Species from the genus *Ceanothus* were also coded as a nitrogen fixing species.

To compare regeneration traits, we used a 3-dimensional NMS solution as providing a considerable and statistically significant reduction in stress as compared with randomized data to compare composition (final stress = 15.42; p = 0.004 for all axes). A two-dimension ordination was chosen as the best solution, representing 95% of the community variation.

Grouping the species by their regeneration responses normalized the data and facilitated parametric analyses. We used simple linear regression to test for linear relationships between environmental variables and the abundance of species with a specific regenerative trait (S-plus v.7). The abundance of seed bank and resprouting species were used as the response variable and heat load as the independent variable. Two-way ANOVA (S-plus v.7) was used to determine if management, aspect, or the interaction of management and aspect significantly affected the cover of each trait.

2.8. Density and frequency of tree regeneration

We used NMS ordination to examine the effects of aspect, elevation and management on the density of all tree species. We also tested for

differences in the density and spatial distribution of conifers between unmanaged and managed sites. The total number of conifers per plot was used as a measure of density, while the frequency of cells in a plot with conifers establishment was used to describe how the conifers were distributed spatially. Frequency was calculated as the proportion of the total number of cells that were occupied by conifers (e.g. 30 cells occupied represented a frequency of 100%).

We tested for differences in density and frequency of conifers using a two-way analysis of variance (ANOVA) with management and aspect as explanatory variables. Interactions between management and aspect were tested at each level. To better meet assumptions of normality and equal variance, transformations were performed before conducting the ANOVA; density was log-transformed, and frequency was arc-sine transformed.

3. Results

3.1. Community composition

Twenty years after high severity wildfire, shrubs had the highest percentage of cover (~35%) regardless of management or aspect, while hardwoods had the second largest percentage (~15%, Fig. 2). Conifers only comprised ~10%, with ferns, forbs, and grasses making up the smallest percentage (~5%). Total cover for any life-form groups (conifers, hardwoods, shrubs, and forbs/grasses/ferns) was not significantly different between managed and unmanaged sites on either the north or south aspect. A 3-dimensional NMS ordination (final stress = 15.0; p = 0.004 for all axes) explained 76% of the variation in life form with aspect and heat load accounting for 32% of the variation (Fig. 3). Management (axis 1) accounted for 25% of the variation.

Even though cover of physiognomic groups was fairly consistent, the cover of individual species varied with both management and microclimate (e.g. elevation, aspect). Thimbleberry (*Rubus parviflorus*), Douglas-fir, red-flower currant *(Ribes sanguineum)*, and dwarf rose *(Rosa gymnocarpa)* were positively associated with north aspects (Fig. 4). In contrast, deerbrush (*Ceanothus integerrimus*), California black oak *(Quercus kelloggii)*, Pacific poison oak *(Toxicodendron diversilobum)*, and canyon live oak showed the strongest positive association with south aspects, especially *Ceanothus* spp. On north aspects, dominance was more equally shared among species and life form groups. About half of the unmanaged sites were similar in composition to managed sites. California lilac *(Ceanothus americanus)*, beaked hazel (*Corylus cornuta*), California snowberry (*Symphoricarpos mollis*), and ponderosa pine *(Pinus ponderosa)* were most strongly associated with managed areas, while whiteleaf manzanita *(Arctostaphylos viscida)*, huckleberry oak *(Quercus vacciniifolia)*, and tanoak showed the strongest association with unmanaged sites (Fig. 4).

The average number of species and species diversity showed a greater difference between north and south aspect slopes (between 5 and 18% depending on the metric) than between managed and unmanaged (< 4%, Table 2).

The diameter distributions of conifers on unmanaged and managed sites showed similar distribution patterns; both had a large number of individuals in the lower diameter classes (Appendix A). The average height of dominant conifers was significantly higher on managed sites than on unmanaged sites 3.6 m (SE = 0.30 m) and 2.5 m (SE = 0.34 m) respectively (*p* < 0.05, n = 62), though the number of individuals was similar.

Snags constituted an important structural element on unmanaged sites but there were no snags on managed sites. The mean density of snags was 125 snags/ha (21–229 snags/ha) and their size varied widely (10–115 cm) with a mean DBH of 45 cm.

3.2. Regeneration traits of trees and shrubs

Regeneration traits varied along the microclimate N-S gradient.
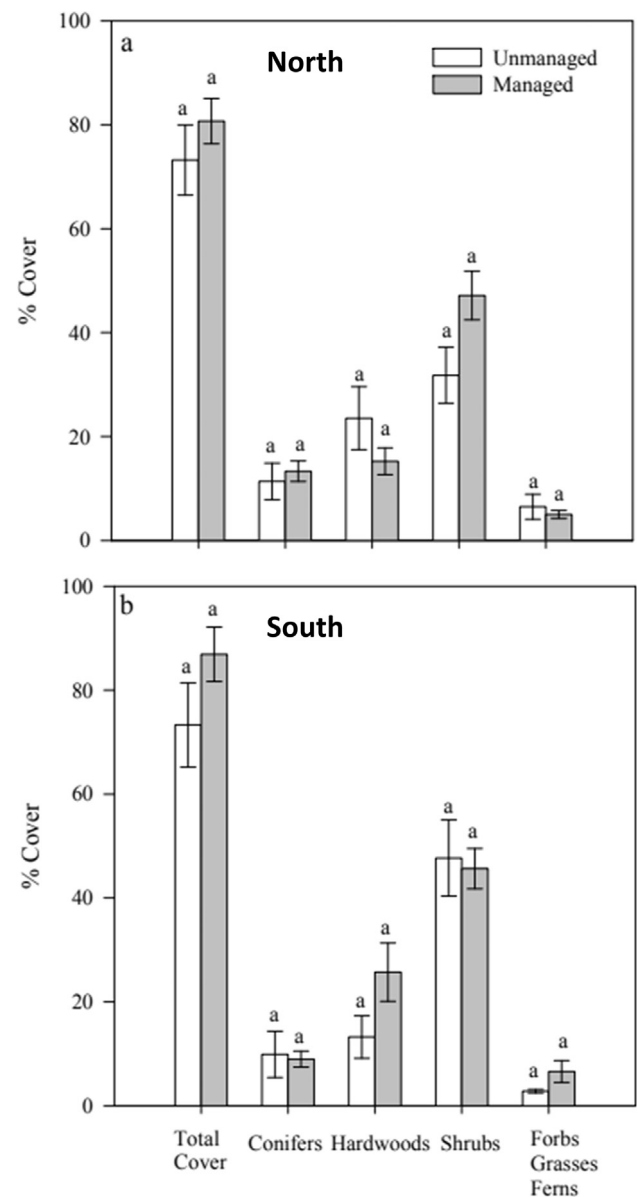

Fig. 2. Contribution of life form groups to the average total % cover on northerly (a), and southerly aspects (b). Bars represent mean and error bars are standard errors. For a given life form group: means with the same letter are not significantly different (p > 0.05) using the Bonferroni correction.

Most of the variation in regeneration traits (56%) was associated with aspect and heat load according to our NMS ordination (axis 2, Fig. 5). Correlation analysis supported this result; seed bank species abundance was strongly associated with south aspects (r = 0.931), while sprouting species abundance was associated with north aspects (r = −0.438). Regeneration traits also varied along the management gradient (axis 1), which explained 25% of the variation. California lilac, beaked hazel, California snowberry, and ponderosa pine were most strongly associated with managed areas, while whiteleaf manzanita, huckleberry oak, whipplea, and tanoak were most strongly associated with unmanaged sites. The third axis of the ordination, representing 19% of the variation, was related to elevation.

Seedbanking species had higher cover on south aspects and on managed sites (Fig. 6), likely due to planting, but obligate seeders were unaffected by aspect or management. Sprouters were favored on north aspects, but were unaffected by management. There was evidence that the interaction between management and aspect significantly affected
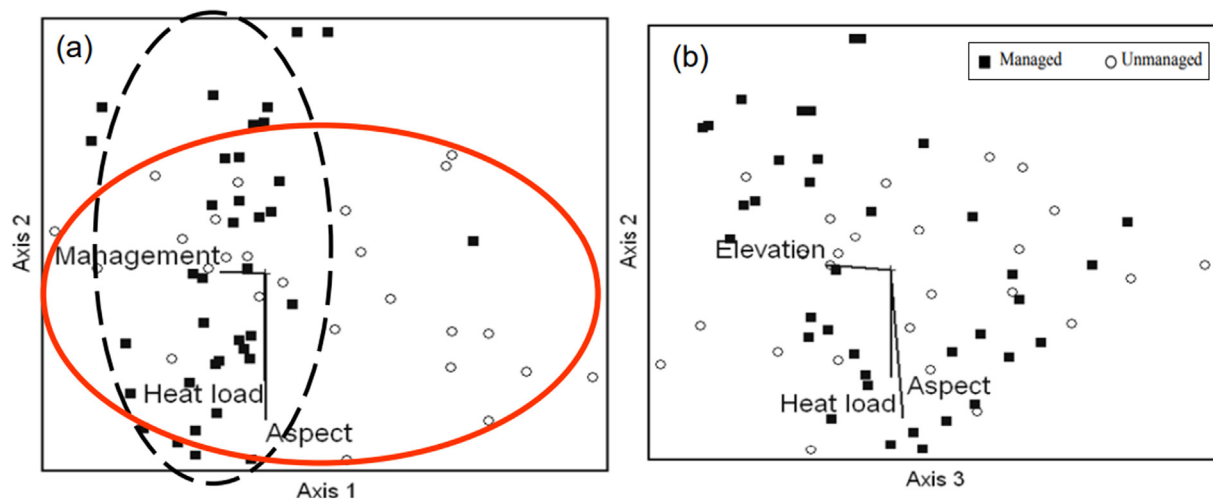
Fig. 3. NMS ordination of life form % cover using 44 species that occur in more than 5% of the sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with r2 > 0.200. Red ovals shows spread of unmanaged sites while dashed black oval shows aggregation of managed sites.

the cover of N-fixing species (*Ceanothus* spp., Fig. 6, $p = 0.030$). Also the high cover of N-fixing species on south slopes corresponded with a greater average height of dominant conifers on managed sites.

3.3. Density and frequency of tree regeneration

In our ordination, the density of all hardwood and conifer species was associated with aspect and elevation, but not with post-fire management (Fig. 7). Axis 2 was aligned with aspect ($r = -0.444$) and represented most of the variation (32%). Douglas-fir, bigleaf maple *(Acer macrophyllum)*, and white fir *(Abies concolor)* were associated with north aspects, while California black oak, canyon live oak, and knobcone pine were associated with south aspects. Elevation (represented by axis 1, $r = 0.642$) explained 24% of the variation. Seedlings of ponderosa pine and sugar pine were positively associated with elevation, while canyon live oak, madrone, and tanoak were negatively associated with elevation. No variable was associated with axis 3 (18% of the variation); management did not associate with any of the axes.

In our analysis of variance, aspect affected density of Douglas-fir, while management and aspect interacted to affect ponderosa pine density. Density of Douglas-fir was higher on north than south aspects, as expected (Fig. 8), but was unaffected by management, even though this involved planting. Management increased the density of ponderosa pine *on* south aspects ($p < 0.05$, *t*-test), but had no impact on north aspects. No significant differences were found in the density of hardwoods between unmanaged and managed sites or between north and south aspects (data not shown). Overall, density of hardwoods was 325 trees/ha (range 0–1187) on unmanaged sites and 268 trees/ha (range 0–979) on managed sites. This was much lower than the density of conifers, which was 4425 seedlings/ha (range 20–22062) on unmanaged sites and 3543 seedlings/ha (range 187–14416) on managed sites.

We found strong evidence that differences in the frequency of conifers (conifer presence in 4 m × 4 m cells within a plot) were associated with aspect ($p = 0.004$) and management ($p = 0.001$). Average conifer frequency was 58% for unmanaged sites (3–100%) and 75% (23–100%) for managed sites (Fig. 9). The average frequency of Douglas-fir and ponderosa pine together was 49% (0–100%) for unmanaged sites and 70% (7–100%) for managed sites. Differences in conifer frequency were also associated with aspect. Post-fire management had a greater effect on the frequency of ponderosa pine ($p = 0.004$) than Douglas-fir ($p = 0.083$). The effect of aspect was significant for both species with higher frequency on N aspects.

4. Discussion

4.1. Post-fire management and aspect affect species composition and stand structure

Fires are an important factor shaping the structure of western forests (Agee, 1993, Turner et al., 1997), but most studies examining forest regeneration focus on the first decade after a high severity fire (Welch et al., 2016, Donato et al., 2009, Turner et al., 1997). We examined vegetation twenty years after a stand-replacing fire, expecting management to suppress shrub and hardwood cover. Management in this region was guided by the Northwest Forest Plan, though the adaptive management aspects were not fully realized (Spies et al., 2018). Specific treatments in this area included site preparation and planting of Douglas-fir and ponderosa pine, along with shrub removal, in order to facilitate conifer regeneration. Instead we found that management treatments did not affect cover among physiognomic groups (conifers, hardwoods, shrubs). Shrubs were always the dominant cover type in our study area. Previous studies have shown that shrubs rapidly establish after a high severity fire, since they sprout from surviving root crowns or germinate from seed banks (Helms and Tappeiner, 1996; Russell et al., 1998). Seeds from shrubs can remain viable in the soil for decades and their germination is often stimulated by fire (Talley and Griffin, 1980).

Our study also found that understanding the effect of post-fire management on plant community composition requires consideration of aspect. Management on south slopes promoted cover of deerbrush, thimbleberry, madrone, and ponderosa pine at the expense of manzanita and California bay laurel (*Umbellularia californica*). On north slopes, management promoted thimbleberry, bigleaf maple, canyon live oak, and Douglas-fir, while snowberry, tanoak and white fir declined. These shifts in species composition have large implications for wildlife, especially the increases in deerbrush and thimbleberry. Deerbrush provides high-quality and palatable forage for wildlife, especially deer (Talley and Griffin, 1980), and can significantly enrich soil nitrogen (Binkley and Husted, 1983, Oakley et al., 2003). The fruits of thimbleberry are consumed by many animals including bears, rabbits, and birds (Van Dersal, 1938, Oleskevich et al., 1996).

North aspect sites had higher species diversity and community heterogeneity than south aspect sites. This is expected because south aspects typically experience higher temperatures, greater light intensity and lower soil moisture than north-facing slopes (Small and McCarthy, 2002), which may limit establishment of some species. Aspect appeared
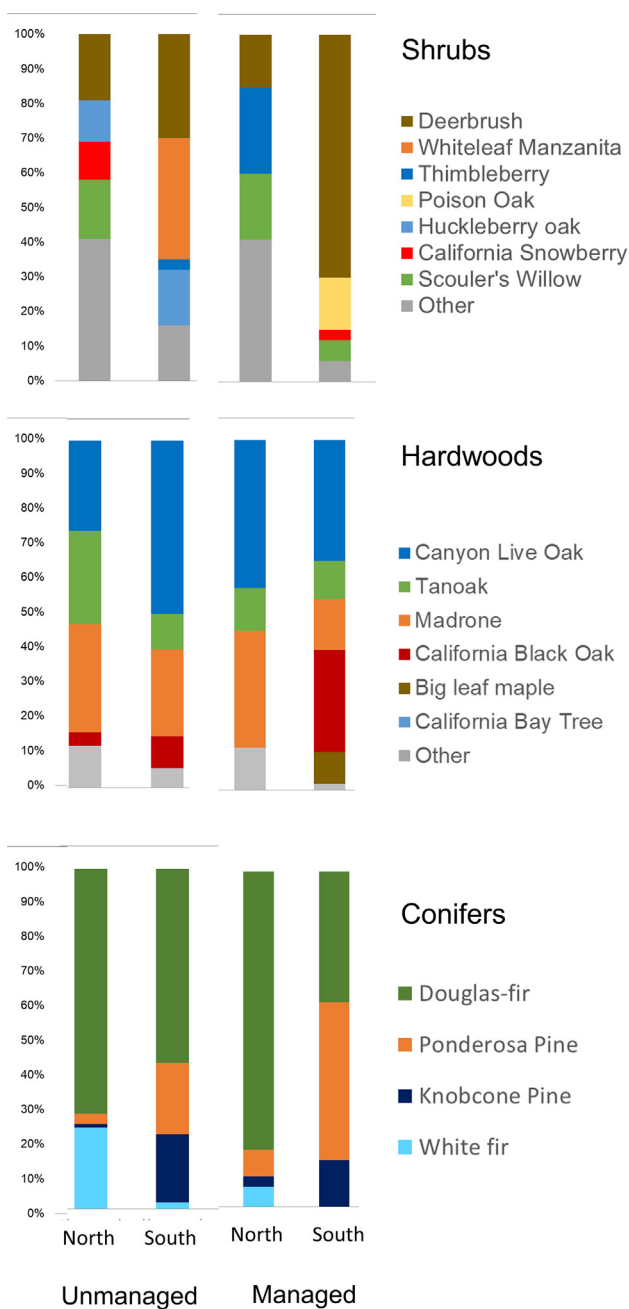
Fig. 4. Contribution of individual species to total percentage of cover of each group (conifers, hardwoods, shrubs), separated by aspect and management.

Table 2

Species diversity on unmanaged and managed sites, broken down by aspect. Diversity was calculated using several metrics: Average number of species, Beta diversity (β_w, the total number of species divided by the average number of species), Simpson's index (D), and Shannon-Wiener index (H′).

Group (sample size)	Average number of species (S.D.)	β_w	D	H′
Unmanaged North (16)	18 (0.4)	3.1	0.76	1.92
Managed North (23)	18 (0.5)	2.8	0.76	1.92
Unmanaged South (9)	13 (0.4)	3.3	0.66	1.54
Managed South (14)	12 (0.4)	2.9	0.72	1.61
Unmanaged (25)	16 (0.4)	3.8	0.72	1.78
Managed (37)	16 (0.4)	3.3	0.75	1.81

to have a stronger control on overall species richness than management. Forest management practices in this post-wildfire setting did not result in a reduction of woody plant diversity, but it did have important consequences for stand structure. Managed sites had taller dominant conifers, which suggests that post-fire management could be effective in helping conifers to survive subsequent fires. However, management eliminated snags that are critical nesting habitat for a variety of bird species in the region, including the northern spotted owl (North et al., 1999).

During forest planning, managers have to find a balance among economic, social and environmental factors. Over the last fifteen years, for instance, management objectives on federal lands have changed from a species-based approach to an ecosystem management approach, a strategy in which the full array of forest values and functions is maintained at the landscape level (Kline et al., 2013, Turner et al., 1995). One of the major challenges to implementation of ecosystem management is the uncertainty not only about ecosystem responses to natural disturbance but also to management. The combination of natural disturbances and management compound the uncertainty and our study provides evidence that management should be stratified by aspect following high severity fires.

4.2. Post-fire management and aspect affects species' reproductive strategies

Management actions (which included planting of conifers) promoted seed banking species, an action which may be critical as the climate warms. Recent studies indicate that the recovery of these species may be curtailed under a fire regime of increasing frequency and severity with distance to seed source becoming a significant limiting factor (Tepley et al., 2017, Harvey et al., 2016). Other authors have reported positive responses of resprouters to logging and fires in the region (Strothmann and Roy, 1984, Tappeiner et al., 1992). In our study, resprouters were the dominant functional group after fire, particularly on north aspects. However, they were not affected by management, suggesting that these hardwoods are resilient regardless of treatment (Tappeiner et al., 1992, Fites-Kaufman et al., 2006).

Microclimate also played an important role in driving regeneration strategies. Seed banking species had higher cover on southerly aspects, indicative of the association between the abundance of seed bank species and drier conditions. A similar association between seed bank species and hot, dry conditions has been reported for other ecosystems with Mediterranean climate, such as California chaparral (Dell et al., 1986, Meentemeyer et al., 2001). The difference in regenerational strategies between north and south aspects in the Klamath Mountains has also been associated with differences in fire frequency. Fire burned less frequently on north slopes than on south slopes (Taylor and Skinner, 1998, 2003). Germination of the seed banking species is fire dependent; thus fire might have acted as a sorting factor over time, favoring the abundance of seed bank species on sites with higher fire frequency. These can in turn replenish the seedbank with fire-dependent species, causing a positive feedback. Elevation also played an important role in influencing conifer regeneration, similar to previous studies (Shatford et al., 2007). In contrast, the abundance of resprouting species was associated with decreasing levels of heat load and more northerly aspects, consistent with Keeley (1986) and Meentemeyer et al. (2001), who found more resprouters on north facing slopes in California chaparral.

4.3. Management promotes ponderosa pine but not Douglas-fir regeneration twenty years after fire

The issue of post-fire management is contentious in the Klamath region, as elsewhere (e.g. Sessions et al., 2004). One study showed that salvage logging, the most common post-fire management treatment, causes many detrimental effects that include changing the structural complexity of forest stands and the composition of the forest
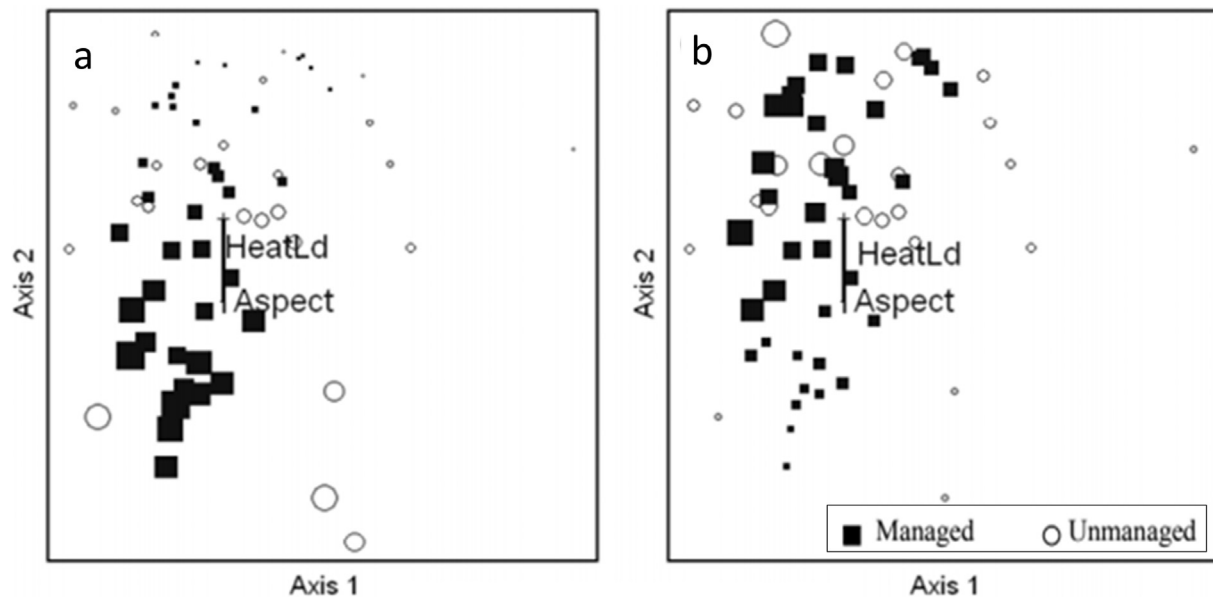
Fig. 5. NMS ordination of % cover of (a) seed banking species and (b) resprouting species in plots in trait space based on 44 species that occur in more than 5% of the sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with $r^2 > 0.10$. Symbol size reflects relative cover of a trait group in a plot.
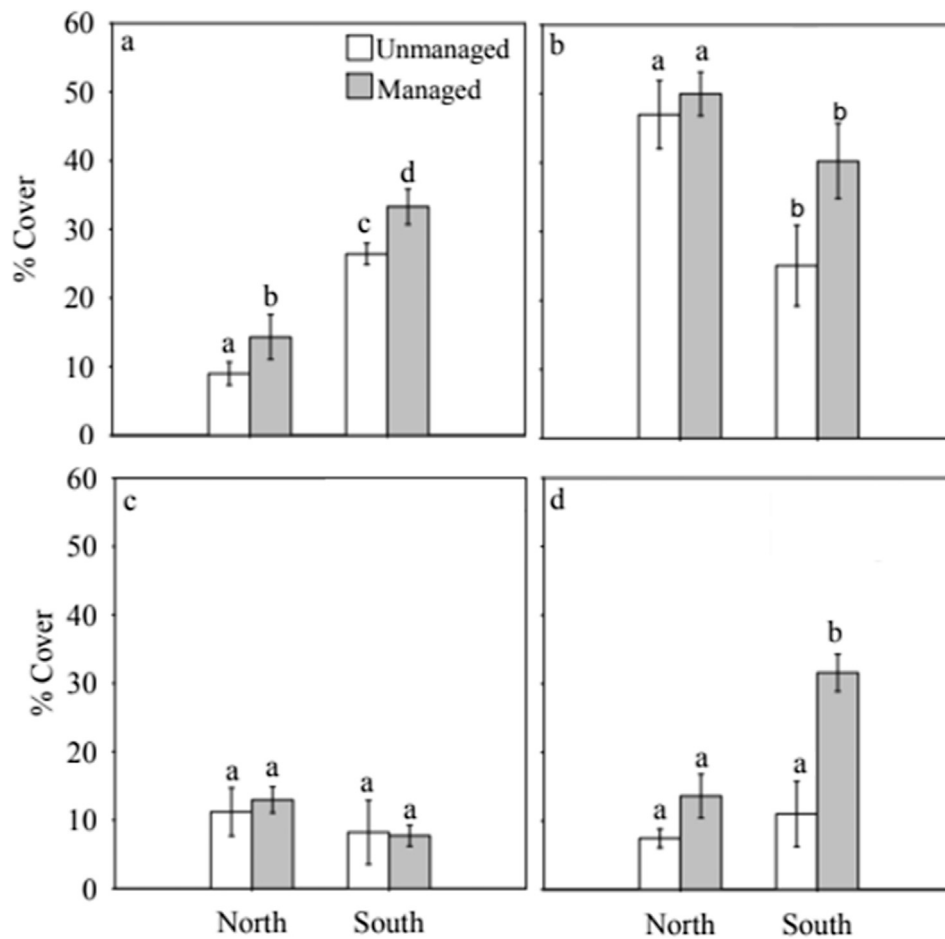

Fig. 6. Distribution of % cover of (a) seed banking species, (b) resprouting species, (c) obligate seeding species, (d) N-fixing species; broken down by aspect and management. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different (p > 0.05).
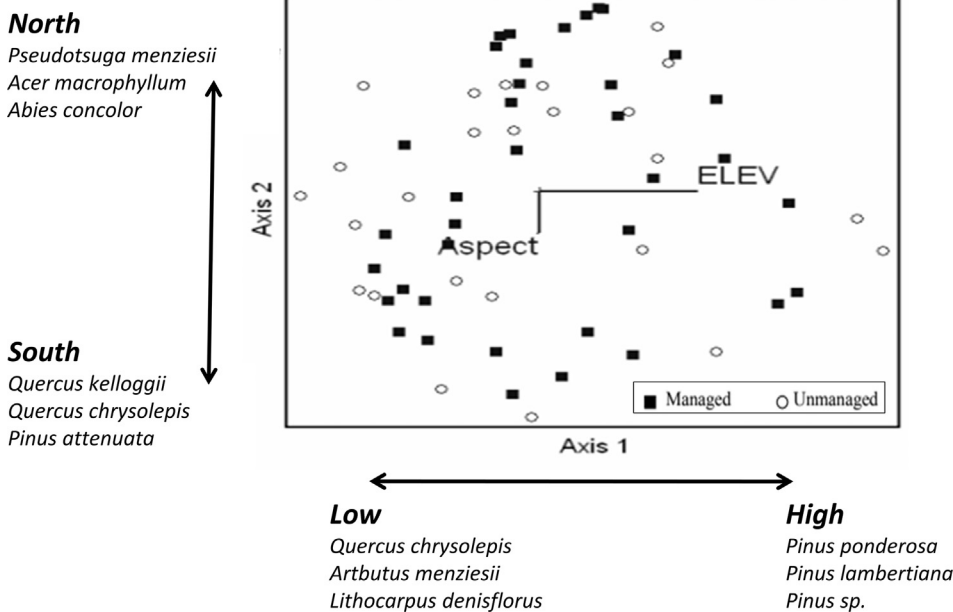
Fig. 7. NMS ordination of density of hardwood and conifers species space based on 15 species that occur in more than 5% of sample units. For joint plots, the length of the correlation vector represents the strength of the correlation; correlation vectors are given only for variables with $r^2 > 0.100$. Ordination was rotated 26 degrees to align aspect with axis 2.
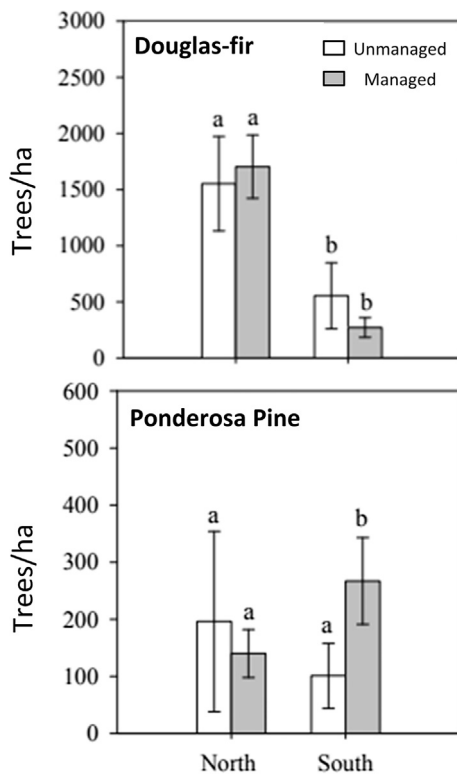

Fig. 8. Mean density of Douglas-fir and ponderosa pine, broken down by aspect and management. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different ($p > 0.05$).

community (Lindenmayer, 2004). Another study suggested that areas that were salvage-logged and planted burn more severely fifteen years later than comparable unmanaged areas (Thompson et al., 2007, 2010). Changes in fuel profile likely increased the average burn severity in managed areas. Even though post-fire management is expected to have a negative influence on the abundance of conifer regeneration shortly after salvage logging (Sexton, 1998, Donato et al., 2006), it is also expected to increase the abundance of conifers by planting activities (Sessions et al., 2004; Weatherspoon and Skinner, 1995). Thus, we

might presume that one management activity may have counteracted the other. This situation, along with the abundant natural regeneration observed in the region, likely caused the similarities between unmanaged and managed sites in terms of overall seedling density and composition, with the exception of ponderosa pine, which was promoted on south aspect sites with management. In fact, the high density of conifers on both naturally regenerated sites and managed sites suggest that these forests are quite resilient with respect to intense natural disturbances. Abundant conifer regeneration has been reported to occur shortly after stand replacing fires (Donato et al., 2006) and continues to occur nineteen years after stand replacing fires in the Klamath region (Shatford et al., 2007). The dense conifer regeneration reported here in both unmanaged and managed sites, as well as the diameter frequency distributions, support the idea that conifer regeneration occurs naturally without human intervention (Gray and Franklin, 1997; Nathan and Muller-Landau, 2000; Shatford et al., 2007). Similar density of conifers between unmanaged and post-fire managed sites was also reported two years after management in southern Oregon (Sexton, 1998) and fifteen years after management in northeast California (Bock et al., 1978). Our study, as does others, raises the question of whether the costs of post-fire management strategies are justifiable if the density of conifers is not strongly affected by planting. The increased abundance of ponderosa pine on south aspect sites may point towards management being more effective if tailored to drought-tolerant ponderosa pine on south aspects, particularly under a climate warming scenario.

In our study, changes in density and frequency associated with post-fire management were more evident for ponderosa pine than for Douglas-fir. This is not a surprising result considering that Douglas-fir is the most abundant conifer species in unburned forests (Rice and Chaney, 1989; Holder, 1990), which may also imply more available seed sources. Shatford et al. (2007), for instance, reported that within the Douglas-fir series, 51% of the seedlings were Douglas-fir, while only 14% of the seedlings were ponderosa pine. Hence, planting would be expected to have a stronger effect on the abundance of ponderosa pine than on Douglas-fir.

Overall, conifer regeneration was strongly influenced by aspect, which is consistent with previous studies (Whittaker, 1960, Atzet and Wheeler, 1982, Ohmann and Spies, 1998). Drought stress and soil surface temperature are generally higher on south aspects (Rosenberg et al., 1983), which reduced regeneration, particularly for Douglas-fir. This is consistent with reports that found soil surface temperature to
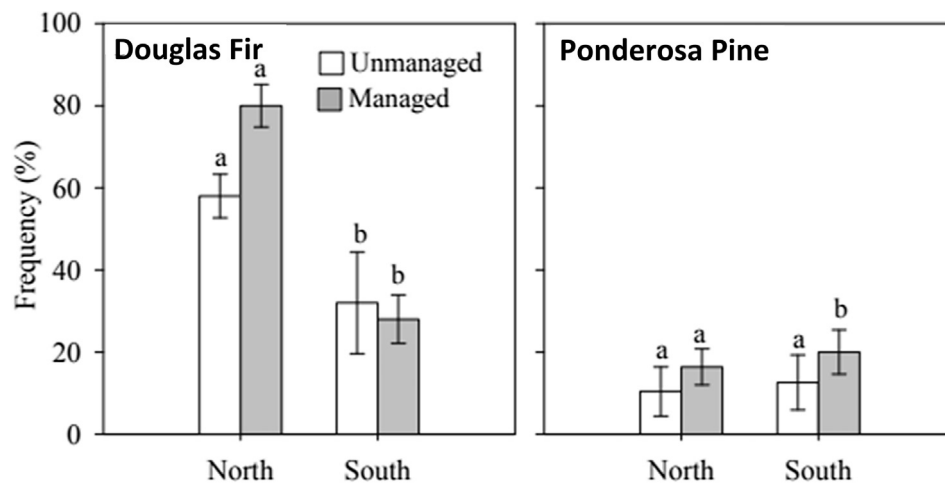
Fig. 9. Frequency of Douglas-fir and ponderosa pine. Bars represent mean and error bars are standard errors. For a given aspect, means with the same letter are not significantly different (p > 0.05).

exceed temperatures lethal to Douglas-fir seedlings on south facing clear-cuts almost twice as frequently as on north facing clear-cuts (Silen, 1960). In contrast, ponderosa pine can survive in xeric environments by maintaining high water use efficiencies and deep root systems (Kolb and Robberecht, 1996). In general, management interventions might be more successful on south aspects with more gentle slopes.

Over the last twenty years, large wildfires have affected hundreds of thousands of acres in the western United States and climate change will likely lead to an increase in the area burned and wildfire severity in this region (Torn et al., 1998, Westerling, 2006). Whether an increase in wildfire activity will create enough early seral communities to allow managers to meet conifer stocking rates is unclear. Also, post-fire planting may become increasingly important as the climate warms and regeneration is limited (Welch et al., 2016). Twenty years after high severity fires provides an opportunity to measure the resilience of these forests to disturbance but is likely too short a time to fully answer the questions mentioned above.

The interactions detected between post-fire management and aspect remind us of the challenges to implementing ecosystem management in complex and diverse ecosystems such as the Klamath region. There are many gaps in our present understanding of the importance of early seral communities to ecosystem processes and its changes in response to post-fire management. Observational studies such as this one are just the first step in developing such understanding. Long term monitoring and research in this area is needed to support informed adaptive management decisions in this region. Further, understanding the role and dynamics of early seral communities, their composition, and structure will inform management in fire prone ecosystems.

Acknowledgements

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2018.10.030.

References

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

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96.

Anderson-Teixeira, K.J., Miller, A.D., Mohan, J.E., Hudiburg, T.W., Duval, B.D., DeLucia, E.H., 2013. Altered dynamics of forest recovery under a changing climate. Glob. Change Biol. 19 (7), 2001–2021.

Atzet, T., Wheeler, D.L., 1982. Historical and Ecological Perspectives on Fire Activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire management on forested public lands of the western United States. Conserv. Biol. 18, 957–967.

Binkley, D., Husted, L., 1983. Nitrogen accretion, soil fertility, and Douglas-fir nutrition in association with redstem *Ceanothus*. Can. J. For. Res. 33, 2274–2279.

Bock, J.H., Raphael, M., Bock, C.E., 1978. A comparison of planting and natural succession after a forest fire in the northern Sierra Nevada. J. Appl. Ecol. 15, 597–602.

Conard, S.G., Radosevich, S.R., 1982. Growth responses of white fir to decreased shading and root competition by montane chaparral shrubs. For. Sci. 28, 309–320.

Dell, B., Hopkins, A.J.M., Lamont, B.B., 1986. Resilience in Mediterranean Type Ecosystems. Kluwer Academic Publishers, Dordrecht; Boston Norwell, MA.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post-wildfire logging hinders regeneration and increases fire risk. Science 311, 352.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Can. J. For. Res. 39 (4), 823–838.

Fites-Kaufman, J., Bradley, A.F., Merrill, A.G., 2006. Fire and plant interactions. In: Fire in California's ecosystems. University of California, Berkeley, pp. 94–117.

Gray, A.N., Franklin, J.F., 1997. Effects of multiple fires on the structure of southwestern Washington forest. Northwest Sci. 71, 174–185.

Halofsky, J.E., Donato, D.C., Hibbs, D.E., Campbell, J.L., Cannon, M.D., Fontaine, J.B., Spies, T.A., 2011. Mixed-severity fire regimes: lessons and hypotheses from the Klamath-Siskiyou Ecoregion. Ecosphere 2 (4).

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

Harvey, B.J., Donato, D.C., Turner, M.G., 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. Glob. Ecol. Biogeogr. 25 (6), 655–669.

Helms, J.A., Tappeiner, J.C., 1996. Silviculture in the Sierras. Sierra Nevada Ecosystem Project final report to Congress: Status of the Sierra Nevada, Sierra Nevada Ecosystem Project Science Team, vol. 2, Ch. 15, 530.

Hobbs, S.D., 1992. Seedling and site interactions. In: Reforestation practices in Southwestern Oregon and Northern California. Forest Research Laboratory Oregon State University, Corvallis, OR, pp. 114–134.

Holder, B., 1990. King-Titus fire recovery project. Klamath National Forest. Final environmental impact statement. Pages 671 in U. S. D. A. F. Service, editor.

Keeley, J.E., 1986. Resilience of mediterranean shrub communities to fire. In: Dell, B., Hopkins, A.J.M., Lamont, B.B. (Eds.), Resilience in Mediterranean-type Ecosystems.

Keeley, J.E., 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68, 434–443.

Keeley, J.E., Fotheringham, C.J., Baer-Keeley, M., 2005. Factors affecting plant diversity during post-fire recovery and succession of mediterranean climate shrublands in California, USA. Divers. Distrib. 11, 525–537.

Kline, J.D., Mazzotta, M.J., Spies, T.A., Harmon, M.E., 2013. Applying the ecosystem services concept to public land management. Agric. Resour. Econ. Rev. 42 (01), 139–158.

Kolb, P.F., Robberecht, R., 1996. *Pinus ponderosa* seedling establishment and the influence of competition with the bunchgrass *Agropyron spicatum*. Int. J. Plant Sci. 157, 509–515.

Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29, 115–119.

Lindenmayer, D.B., 2004. ECOLOGY: enhanced: salvage harvesting policies after natural disturbance. Science 303 (5662) 1303–1303.

Lopez Ortiz, M.J., 2007. Plant Community Recovery after High Severity Wildfire and Post-fire Management in the Klamath Region. Thesis M S. Oregon State University.

MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42, 594–598.

Mather, P.M., 1976. Computational Methods of Multivariate Analysis in Physical Geography, London.

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

McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13, 603–606.

McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach.

McIver, J.D., Starr, L., 2001. A literature review on the environmental effects of postfire logging. West. J. Appl. For. 16, 159–168.

Meentemeyer, R.K., Moody, A., Franklin, J., 2001. Landscape-scale patterns of shrub-species abundance in California chaparral – the role of topographically mediated resource gradients. Plant Ecol. 156, 19–41.

Nathan, R., Muller-Landau, H.C., 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15, 278–285.

North, M., Franklin, J., Carey, A., Forsman, E., Hamer, T., 1999. Forest Stand Structure of the Northern Spotted Owl's Foraging Habitat. For. Sci. 45 (4), 520–527.

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

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

Ohmann, J.L., Spies, T.A., 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecol. Monogr. 68, 151–182.

Oleskevich, C., Punja, Z.K., Shamoun, S.F., 1996. The biology of Canadian weeds. 105. *Rubus strigosus* Michx., Rubus parviflorus Nutt., and *Rubus spectabilis* Pursh. Can. J. Plant Sci. 76 (1), 187–201.

Palazzi, L.M., Powers, R.F., McNabb, D.H., 1992. Ecology and soils. In: Hobbs, S.D., Tesch, S.D., Owston, P.W., Stewart, R.E., Tappeiner, G.E. (Eds.), Reforestation practices in southwestern Oregon and northern California, pp. 48–72.

Rice, R.L., Chaney, M.S. 1989. Final Environmental Impact Statement. In: U.S.D.A.F. Service (Ed.), Grider Fire Recovery Project, Klamath National Forest, pp. 434.

Rosenberg, N.J., Blad, B.L., Verma, S.B., 1983. Microclimate: The Biological Environment, second ed. Wiley, New York.

Russell, W.H., McBride, J., Rowntree, R., 1998. Revegetation after four stand-replacing fires in the lake Tahoe basin. Madrono 45 (1), 40–46.

Serra-Diaz, J.M., Maxwell, C., Lucash, M.S., Scheller, R.M., Laflower, D.M., Miller, A.D., Tepley, A.J., Epstein, H.E., Anderson-Teixeira, K.J., Thompson, J.R., 2018. Disequilibrium of fire-prone forests sets the stage for a rapid decline in conifer dominance during the 21st century. Sci. Rep. 8, 6749.

Sessions, J., Bettinger, P., Buckman, R., Newton, M., Hamann, J., 2004. Hastening the return of complex forests following fire: the consequences of delay. J. For. 102, 38–45.

Sexton, T.O., 1998. Ecological Effect of Post-Wildfire Management Activities (Salvage-Logging and Grass-Seeding) on Vegetation Composition, Diversity, Biomass, and Growth and Survival of Pinus Ponderosa and Purshia Tridentata. Thesis M S. Oregon State University.

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

Silen, R.R., 1960. Lethal Surface Temperatures and their Interpretation for Douglas-fir. Thesis Ph D. Oregon State College.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Skinner, C.N., Taylor, A.H., Agee, J.K., 2006. Klamath Mountain Bioregion. In: Sugihara, N.G., Van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.). Fire in California's Ecosystems, Los Angeles.

Small, C.J., McCarthy, B.C., 2002. Spatial and temporal variation in the response of understory vegetation to disturbance in a central Appalachian oak forest. J. Torrey Bot. Soc. 129, 136–153.

Spies, T.A., Stine, P.A., Gravenmier, R., Long, J.W., Reilly, M.J., 2018. Gen. Tech. Rep. PNW-GTR-966. Synthesis of Science to Inform Land Management within the Northwest Forest Plan Area, vol. 3, 1020.

Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P., Veblen, T.T., 2017. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21 (2), 243–252.

Strittholt, J.R., Frost, P.A., Carroll, C., 1999. A Science-Based Conservation Assessment for the Klamath-Siskiyou Ecoregion.

Strothmann, R.O., Roy, D.F., 1984. Regeneration of Douglas-fir in the Klamath Mountains region, California and Oregon. U.S. Dept. of Agriculture Forest Service Pacific Southwest Forest and Range Experiment Station, Berkeley, Calif.

Talley, S.N., Griffin, J.R., 1980. Fire ecology of a montane pine forest, Junipero Serra Peak, California. Madrono 27, 49–60.

Tappeiner, I.J.C., Newton, M., McDonald, P.M., Harrington, T.B., 1992. Ecology of hardwoods, shrubs, and herbaceous vegetation: effects on conifer regeneration. In: F.R.L.O.S. University (Ed.), Reforestation Practices in Southwestern Oregon and Northern California, Corvallis, OR, pp. 136–164.

Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. For. Ecol. Manage. 111, 285–301.

Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. Ecol. Appl. 13, 703–719.

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. Glob. Change Biol. 23 (10), 4117–4132.

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 Ecol. 25 (5), 775–789.

Thompson, J.R., Spies, T.A., Ganio, L.M., 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. PNAS 104, 10743–10748.

Torn, M.S., Mills, E., Fried, J., 1998. Will Climate Change Spark More Wildfire Damage? Lawrence Berkeley National Laboratory, Berkeley.

Turner, M.G., Gardner, R.H., O'Neill, R.V., 1995. Ecological dynamics at broad scales. Bioscience 45, S29–S35.

Turner, M.G., Dale, V.H., Everham, E.H., 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. Bioscience 47, 758–768.

Van Dersal, W.R., 1938. Native Woody Plants of the United States, Their Erosion Control and Wildlife Values. Washington, DC.

Weatherspoon, C.P., Skinner, C.N., 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in northern California. For. Sci. 41, 430–451.

Welch, K.R., Safford, H.D., Young, T.P., 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7 (12), e01609.

Westerling, A.L., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313 (5789), 940–943.

Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30, 279–338.

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

Yelenik, S., Perakis, S., Hibbs, D., 2013. Regional constraints to biological nitrogen fixation in post-fire forest communities. Ecology 94, 739–750.