Forest Ecology and Management 260 (2010) 1702–1707

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Dry coniferous forest restoration and understory plant diversity: The importance of community heterogeneity and the scale of observation

Erich K. Dodson*, David W. Peterson

U.S. Forest Service, Pacific Northwest Research Station, 1133 N. Western Avenue, Wenatchee, WA 98801, United States

ARTICLE INFO

Article history:
Received 26 April 2010
Received in revised form 3 July 2010
Accepted 11 August 2010

Keywords:
Beta diversity
Burning
Colonization
Ponderosa pine
Spatial scale
Thinning

ABSTRACT

Maintaining understory plant species diversity is an important management goal as forest restoration and fuel reduction treatments are applied extensively to dry coniferous forests of western North America. However, understory diversity is a function of both local species richness (number of species in a sample unit) and community heterogeneity (beta diversity) at multiple spatial scales, while studies of restoration treatment effects often only examine local species richness at one or two spatial scales. We studied experimental thinning and prescribed fire treatment effects on understory plant species richness and community heterogeneity at three spatial scales using additive diversity partitioning. We also evaluated treatment effects on understory plant species colonization and extirpation at two spatial scales. There was no evidence that active restoration treatments reduced species richness or increased local extirpation of species. Restoration treatments significantly increased herbaceous species richness at the treatment-unit level primarily by increasing community heterogeneity among sampling points within the units. The combination of thinning and burning produced the greatest increase in community heterogeneity, and increased colonization by species that were not sampled prior to treatment. These results suggest that restoration treatments designed primarily to reduce fire hazard and promote sustainable conditions in these fire-adapted ecosystems can also increase community heterogeneity and facilitate colonization by new understory species without significant local extirpation of extant species.

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1. Introduction

Increasing native understory species abundance and diversity is an important objective in dry forest restoration, with implications for watershed functioning, fire behavior, wildlife habitat and overall ecosystem biodiversity (Covington et al., 1997; Allen et al., 2002). In western North America, dry coniferous forest ecosystems with a substantial component of ponderosa pine have been degraded by the combined effects of human activities such as livestock grazing, logging, and fire exclusion (Covington and Moore, 1994; Hessburg and Agee, 2003). Restoration treatments utilizing thinning and/or prescribed burning have been widely advocated to reverse these impacts and increase the resiliency of these forests to natural disturbances, including wildfire and insect outbreaks (Brown et al., 2004; Agee and Skinner, 2005). However, restoration treatment prescriptions often focus on modifying fuels and stand structure with less regard to other ecological impacts (Lehmkuhl et al., 2007). A better understanding of how plant communities and individual species respond to management treatments at multiple scales is needed to help land managers understand the diversity conservation implications of various management strategies.

Implicit within the concept of restoration is that native species will benefit from re-establishment of conditions under which they evolved (Fiedler et al., 1992; Kerns et al., 2006). However, restoring dry coniferous forest diversity has proven more difficult than restoring forest structure (Laughlin et al., 2008), with a recent meta-analysis finding no consistent pattern of understory responses to restoration treatments (Schwilk et al., 2009). Differences in the spatial scale at which the understory vegetation is sampled may contribute to this lack of a consistent response (Dodson and Fiedler, 2006; Metlen and Fiedler, 2006).

Restoration treatments are typically applied at scales of tens of hectares, while treatment effects are monitored at much smaller scales (e.g., 1–1000 m^2). Such fine-scale diversity is but one component of total landscape diversity (Whittaker, 1972; Veech et al., 2002). Conditions or management actions that promote diversity at one spatial scale may be neutral or even negative at other scales (Crawley and Harral, 2001; Clough et al., 2007). Recent studies in other ecosystems that have partitioned diversity into additive hierarchical components have revealed that much of the floral or faunal diversity is due to differentiation in species composition among plots or sites (beta diversity; Chandy et al., 2006; Clough et al., 2007). With the widespread application of dry forest restoration

* Corresponding author. Tel.: +1 509 664 1731; fax: +1 509 665 8362.
E-mail address: edodson@fs.fed.us (E.K. Dodson).

0378-1127/$ – see front matter. Published by Elsevier B.V.
doi:10.1016/j.foreco.2010.08.012

and fuel reduction treatments and their potential implications for diversity conservation, we need to understand the scales at which treatments influence diversity so that biodiversity effects can be monitored at appropriate levels.

Species respond to land management activities individually based on adaptations to disturbance and tolerances for altered environmental conditions (Halpern and Spies, 1995; Riegel et al., 1995). If constitutive species exhibit trade-offs between traits such as colonization ability and competitive ability (e.g., Kneitel and Chase, 2004; Cadotte, 2007), then active management may increase the frequency and abundance of some species while reducing the frequency and abundance of others. For example, management practices may increase the frequency of seral species with good dispersal and establishment traits while reducing the frequency of species well adapted to undisturbed forest conditions (e.g., Halpern and Spies, 1995; Battles et al., 2001). Alternatively, land management can also promote species co-existence by increasing environmental heterogeneity (Gundale et al., 2006; Wayman and North, 2007). Clumpy tree distributions created by thinning and variable burn severities may create patches with different environmental conditions, each of which favors a group of species, with variability among patches allowing co-existence of many species at broader spatial scales.

In this study, we examined restoration treatment effects on understory richness at multiple scales using an additive partitioning approach (Lande, 1996; Veech et al., 2002) and on local understory plant species colonization and extirpation. We addressed the following research questions: (1) what are the relative contributions of sample richness (alpha diversity) and compositional heterogeneity among samples (beta diversity) to total pretreatment richness? (2) do restoration treatments (thinning and prescribed burning) alter richness or community heterogeneity at any spatial scale? (3) do restoration treatments favor disturbance-adapted species over extant forest species? We hypothesized that the primary effect of prescribed fire would be to increase turnover of understory plant species (local extirpation and colonization). Thinning was designed to leave a clumpy distribution of overstory trees; therefore, we hypothesized that thinning would increase environmental heterogeneity leading to increased understory compositional heterogeneity (beta diversity).

2. Methods

2.1. Study site

The Mission Creek study site is located on the Okanogan–Wenatchee National Forest of Washington State in the eastern Cascade Mountains at approximately 47°25′N latitude and 120°32′W longitude. Forests within the study area are dominated by ponderosa pine (*Pinus ponderosa* C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Climate is typical of the Eastern Cascades, with warm dry summers and cool wet winters (Dodson et al., 2008). Like many dry forest sites in the region, the area was heavily grazed and logged in the late 1800s to early 1900s. Similar forests within the Okanogan–Wenatchee National Forest burned frequently prior to Euro-American settlement, but the fire-free interval has greatly increased during the past century (Wright and Agee, 2004). More detailed site information is provided by Dodson et al. (2008) and Harrod et al. (2009).

2.1.1. Treatments

Four thinning and burning treatments were replicated among twelve 10-ha treatment units using a completely randomized design. The original study plan called for three replicates of each treatment: (1) mechanical thinning (thin-only), (2) prescribed fire (burn-only), (3) thinning followed by prescribed fire (thin/burn) and (4) no treatment (control). However, two prescribed fires were not completed due to weather and personnel constraints, so the result was an unbalanced design of four thin-only, four control, two burn-only, and two thin/burn stands.

The mechanical cutting treatment (thinning hereafter) was designed to reduce residual basal area of the stands to 10–14 m^2/ha. The thinning prescription called for retaining large, vigorous trees free of disease or insect infestations and for increasing spatial aggregation of residual trees, consistent with historical reconstructions of presettlement stand structure in the area (Harrod et al., 1999). Logging slash was lopped and scattered. Thinning treatments were completed in the spring of 2003.

Prescribed fire treatments were applied in the spring of 2004 (late April to early May). Each of the four burned units (two burn-only and two thin/burn) was treated separately. Prescribed fires were ignited by hand or helicopter, and flame lengths ranged from 0.2 to 1 m. Some understory species were actively growing when prescribed fire treatments were applied, resulting in patchy burn coverage (Agee and Lolley, 2006).

2.2. Understory vegetation sampling

Six 1000-m^2 (20-m × 50-m) modified Whittaker plots were randomly established in each 10-ha treatment unit. Twenty 1-m^2 sampling quadrats were dispersed randomly throughout each plot to sample herbaceous vegetation. Ten 50-m^2 quadrats were systematically placed within each plot to sample shrubs. Species lists were produced for each quadrat by identifying and recording all herbaceous (1-m^2 quadrats) or shrub (50-m^2 quadrats) species. Difficulties in identification led to some species being grouped at the genera level. Species that could not be identified to genus (a total of eight) were assigned a unique identifier. Pretreatment data were collected in 2000 and 2001. Post-treatment data were collected for all sites in 2005, the second growing season after burning and third growing season after thinning. All of the unique species sampled within quadrats on a plot were used to derive plot-level richness. Similarly, unit-level richness was derived from all the unique species present from sub-samples within the unit.

2.3. Statistical analyses

Additive partitioning of diversity methods (Lande, 1996; Veech et al., 2002) were used to quantify variability in plant species richness across a hierarchical gradient of spatial scales (quadrat, plot, and unit) within the study site and to evaluate treatment effects on plant species richness across spatial scales. Additive partitioning separates total diversity at one level into alpha diversity (the mean number of species that occur within a sampling unit at the next lower level) and beta diversity (compositional differences among sampling units at the lower level). For example, the total species sampled on a plot is equal to the average number of species in a quadrat (alpha diversity) plus the compositional differences (beta diversity) among quadrats within a plot. These partitions can be repeated for multiple hierarchical spatial scales (Veech et al., 2002).

Changes in species richness were calculated at the quadrat, plot, and unit levels, while changes in community heterogeneity were assessed among quadrats and plots only. Change was used to focus the analyses on treatment effects without the potential influence of pre-existing differences.

For each diversity response variable, we evaluated the effects of thinning, burning and their interaction with analysis of variance (ANOVA). We used a 2 × 2 factorial design with thinning and burning treated as fixed effects with two levels (yes or no) in a generalized linear model (PROC GLM, SAS Institute, 2008, version

9.2). All statistical tests of treatment effects were performed at the treatment-unit level ($n = 12$ units). Prior to analyses a Type I error rate of 5% ($P < 0.05$) was chosen as the significance threshold for evaluating treatment effects.

Separate ANOVA models were developed for each combination of species group (herbaceous or shrub) and for species richness and community heterogeneity at each level. Where significant effects were found, post hoc tests were performed to compare effects among individual treatments. Due to the low degree of replication in this management study (two to four replicates of each treatment) we did not adjust post hoc tests for multiple comparisons. All ANOVA models were evaluated for adherence to assumptions of independence, normality and equal variance.

Treatment effects on species dynamics were examined at the plot and unit levels by categorizing species into three groups (Reilly et al., 2006): survivors (found before and after treatment), colonizers (found only after treatment) and evaders (found only before treatment). Data from shrub and herbaceous quadrats were combined to produce species lists for each of the 72 plots before and after treatment. Plot lists were then combined to create species lists for each of the 12 units. The total number of survivor, colonizer, and evader species was then calculated at each scale for each of the 12 treatment units. Plot-level data were averaged to the treatment-unit level prior to statistical analyses. Unknown species and tree seedlings were excluded from these analyses. Where significant effects were found, post hoc tests were performed to compare individual treatments.

3. Results

Species richness increased across all treatments over the course of this study. We sampled a total of 123 understory plant species prior to treatment and 176 species after treatment. Species richness on control units (herbaceous species and shrubs) averaged 51 species before treatment but increased to 59 species following treatment. To account for these background changes, we first describe the pretreatment contribution of various scales (including heterogeneity among samples) to total species richness and then assess treatment effects on changes in species richness at multiple scales compared to background changes in the control.

3.1. Pretreatment diversity partitioning

Very few of the total number of species sampled prior to treatment were sampled on the average quadrat (Fig. 1). The average quadrat sampled 4.2 herbaceous species and 3.4 shrub species, which was less than 12% of the total number of pretreatment species sampled for each group (Fig. 1). Similarly, less than 30% of total pretreatment species richness was captured on the 20 herbaceous quadrats and 10 shrub quadrats on the average modified Whittaker plot. Shrub plot-level richness was about equally split between quadrat richness and heterogeneity among quadrats while herbaceous species plot-level richness was largely due to heterogeneity in species composition among quadrats (beta diversity; Fig. 1). The total number of species on a treatment unit was about equally split between the average plot-level richness and plot-level compositional heterogeneity. More than 50% of the total pretreatment species richness for both herbaceous species and shrubs was from compositional differences among the 12 treatment units.

3.2. Treatment effects

Treatment effects on herbaceous species richness varied by level of observation. Treatments did not significantly affect herbaceous species richness at the quadrat level (Table 1). However, thinning increased compositional differences among quadrats within a plot, plot-level species richness, compositional differences among plots within a unit, and total unit-level species richness (Table 1; Fig. 2a). Burning (thin/burn and burn-only) also significantly increased unit-level species richness (Table 1), adding about 6 species compared to unburned units (control and thin-only treatments). Thinning and burning effects on species richness were additive at all levels, with no significant interactive effects (Table 1).

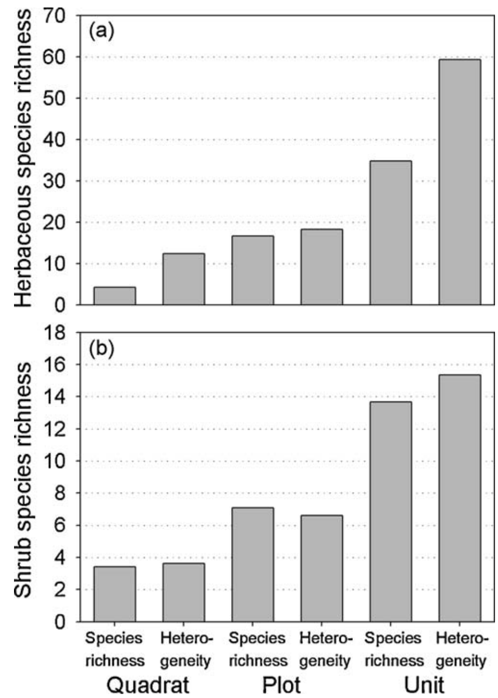

Fig. 1. Hierarchical additive partitioning of pretreatment species richness at Mission Creek for (a) herbaceous species and (b) shrub species at three levels of organization. The richness at a given level is equal to the richness of the average sample unit at the next lower level plus the compositional differences among sample units at the lower level (heterogeneity).

The combined thin/burn treatment had the greatest effect on herbaceous species, significantly increasing both species richness and community heterogeneity at the plot and treatment-unit levels relative to the burn-only and control treatments (Fig. 2a). The thin-only treatment significantly increased community heterogeneity among plots within units and unit-level species richness compared to the control treatment, while the burn-only treatment had no significant effect (Fig. 2a).

Thinning modified the effects of prescribed fire on shrub species richness at the quadrat, plot, and treatment-unit levels (Table 1). At the quadrat and plot levels, the thin/burn treatment increased species richness significantly more than any other treatment (Fig. 2b). At the unit level, the thin/burn treatment increased species richness significantly more than the burn-only and control treatments, but was not significantly different from the thin-only treatment. At each level, the slight increase in shrub species richness produced by the thin-only treatment was significantly different than the decline in species richness produced by the burn-only treatment (Fig. 2b), though neither effect was significantly different than that observed for the control treatment.

3.3. Species dynamics

Restoration treatments did not significantly alter rates of species persistence or local extirpation at either the plot or unit levels (Table 2). However, the thin/burn treatment increased colonization significantly more than all the other treatments (Fig. 3). The control, burn-only and thin-only treatments each gained an aver-

Table 1
Type III tests of treatment effects on species richness at multiple scales. Significant effects are bolded. Heterogeneity refers to compositional differences among sample units (beta diversity).

	Model r^2	Thin		Burn		Thin × burn	
		F	*P*	*F*	*P*	*F*	*P*
Herbaceous species							
Quadrat richness	0.43	3.4	0.102	2.6	0.148	0.1	0.748
Quadrat heterogeneity	0.67	15.6	**0.004**	0.7	0.440	2.7	0.142
Plot richness	0.66	11.8	**0.009**	1.5	0.261	1.9	0.209
Plot heterogeneity	0.70	13.6	**0.006**	5.2	0.052	0.8	0.399
Unit richness	0.80	25.4	**0.001**	6.6	**0.033**	2.1	0.184
Shrub species							
Quadrat richness	0.69	12.2	**0.008**	0.0	0.843	11.2	**0.010**
Quadrat heterogeneity	0.42	5.5	**0.047**	0.2	0.666	0.6	0.476
Plot richness	0.79	27.4	**0.001**	0.6	0.470	8.1	**0.021**
Plot heterogeneity	0.16	1.2	0.309	0.1	0.769	0.8	0.403
Unit richness	0.65	13.4	**0.006**	0.0	1.000	5.4	**0.048**

age of 19–23 species per unit during the study period, while the thin/burn treatment gained 38 new species per unit (Fig. 3a). Similarly the thin/burn treatment added about 14 new species per plot, on average, while the other treatments averaged about nine new species per plot (Fig. 3b).

Numerous unique species colonized the combined thin/burn treatment. A total of 56 unique species colonized at least one of the two thin/burn units and 90 unique species colonized at least one of the 12 thin/burn plots. Colonizing species were from all life-forms (shrubs, graminoids and forbs) and both annual and perennial species were well represented. The large majority of colonizing species were native as there were only five exotic colonizers at each level. Some of the most frequent colonizers at the plot-level (colonizing at least eight of the 12 thin/burn plots) were native forbs often considered to be disturbance-adapted species, such as *Chamerion angustifolium* (L.) Holub and *Claytonia perfoliata* Donn ex Willd.

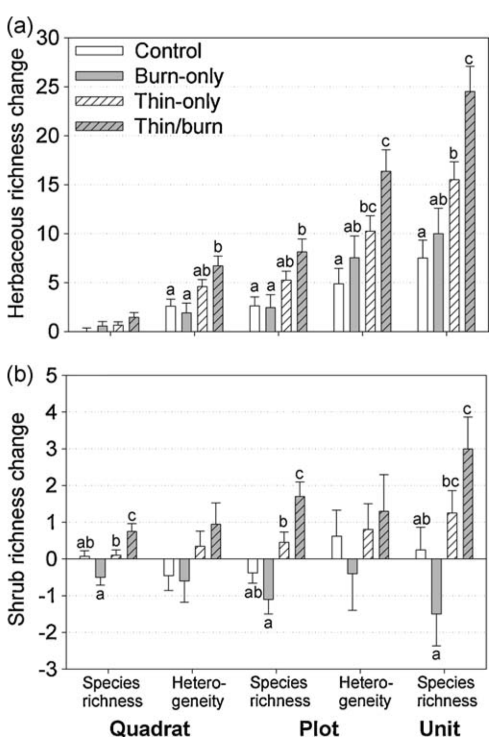

Fig. 2. Least square means (plus one standard error) for change in a) herbaceous and b) shrub species richness at three hierarchical levels (quadrat, plot and unit) using an additive partitioning approach. Different letters indicate significant differences among treatments in post hoc tests. The richness at a given level is equal to the richness of the average sample unit at the next lower level plus the compositional differences among sample units at the lower level (heterogeneity).

4. Discussion

We found that restoration treatment effects on species richness varied with spatial scale, a result that is consistent with previous reports (Abella and Covington, 2004; Metlen and Fiedler, 2006). We found no significant treatment effects on herbaceous understory plant species richness at the quadrat-level and no evidence that treatments affected species that were present prior to treatment (evaders and survivors). This corresponds with many previous studies of dry forest restoration where treatments have not strongly affected understory vegetation (Abella and Covington, 2004; Metlen and Fiedler, 2006; Nelson et al., 2008). However, we found significant increases in species richness when treatments, especially the thin/burn, were evaluated for their effects on community heterogeneity and unit-level species richness. This suggests that evaluating restoration treatments effects on understory species can benefit from an approach that looks at multiple scales, including community heterogeneity. It also suggests that restoration treatments have "hidden benefits" (Clough et al., 2007)

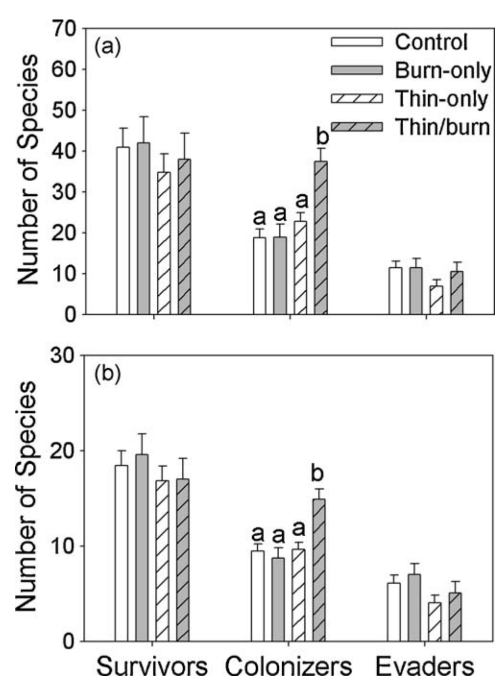

Fig. 3. Least square means (plus one standard error) for richness by treatment at a) the treatment-unit level and b) the plot-level for survivors (found before and after treatment), colonizers (found only after treatment) and evaders (found only before treatment). Different letters denote significant treatment effects.

Table 2
Type III tests of treatment effects on species dynamics. Significant effects are bolded.

	Model r^2	Thin		Burn		Thin × burn	
		F	*P*	*F*	*P*	*F*	*P*
Unit							
Survivors	0.14	0.9	0.385	0.2	0.713	0.0	0.845
Evaders	0.38	2.0	0.193	0.8	0.393	0.8	0.393
Colonizers	0.77	17.3	**0.003**	7.7	**0.024**	7.2	**0.028**
Plot							
Survivors	0.14	1.2	0.305	0.1	0.751	0.1	0.799
Evaders	0.40	3.9	0.085	0.9	0.375	0.0	0.937
Colonizers	0.74	11.9	**0.009**	6.1	**0.039**	10.4	**0.012**

as treatments increased community heterogeneity and unit-level species richness more than they increased species richness at the typically monitored levels or scales (quadrat, plot).

The increase in community heterogeneity found with treatments in this study may be largely due to increased variability in environmental conditions. The thinning treatment prescribed increasing spatial aggregation of residual trees, and thinning removed from 16 to 80% of the basal area on individual Whittaker plots. This likely increased heterogeneity in understory shading and light availability, which can promote a diverse understory as individual species have different optimal light levels (Naumburg and DeWald, 1999). Thinning may also have resulted in patchy soil disturbance that could have further added to environmental heterogeneity. Similarly, the prescribed fires burned with variable intensity across the treatment units, including leaving unburned areas (Agee and Lolley, 2006). Therefore, treatments likely produced a mosaic of patches of varying burn severity, each of which may have favored different species assemblages. Fuel augmentation by the thinning treatment (Agee and Lolley, 2006) may have further increased intensity and variability in burn intensity on the thin/burn units, producing a stronger understory response. Thinning followed by prescribed fire likely increased heterogeneity in both overstory canopy cover and surface burn severity, thereby maximizing understory environmental heterogeneity, opportunities for plant species colonization, and potential plant community heterogeneity.

Previous studies have found mechanical cutting and burning can increase disturbance-adapted species while simultaneously reducing or locally extirpating late successional species in more mesic forests (Roberts and Gilliam, 1995; Halpern and Spies, 1995; Battles et al., 2001). However, in these frequent-fire adapted forests (Wright and Agee, 2004) we found thinning followed by prescribed fire increased colonization without increased local extirpation. A similar pattern was found for dry forest restoration treatments in Montana (Dodson et al., 2007). In historically open forests there may be very few species dependent on undisturbed forest conditions, and species found under a dense canopy may be a shade tolerant subset of species found in openings (Spyreas and Matthews, 2006). In fact, in ecosystems where disturbances were historically frequent, disturbance can be essential for preventing species losses due to competitive exclusion (Denslow, 1980; Cadotte, 2007). Many of the colonizers in this study were likely disturbance adapted species that declined in the absence of fire and increasing canopy closure. The environmental heterogeneity created by treatments likely provided favorable microsites for disturbance-adapted species establishment while also providing microsites that are favorable for currently extant species, thereby increasing species co-existence at the treatment-unit level.

The colonizing species in the thin/burn treatment could have come from many sources, including the soil seed bank, areas of less dense forest, or increased frequency of uncommon species. Although we did not survey the soil seed bank, previous studies have found it to be of minor importance in dry coniferous forests (Vose and White, 1987; Wienk et al., 2004). Also, few of the colonizing species in the thin/burn treatment were sampled in open meadow patches within the treatment units (Dodson, unpublished data). This suggests that much of the colonization may have come from an increase in the frequency of species that were present on the treatment units before treatment, but were too infrequent to be sampled. Dodson et al. (2007), working in dry coniferous forests in Montana, found that many species with low abundance prior to treatment tended to increase cover and frequency with treatments, especially the combination of thinning followed by burning.

5. Conclusions

Reducing fire hazard in dry coniferous forests through fuels modification may require trade-offs with ecological management objectives such as protection of biodiversity and species habitats (Lehmkuhl et al., 2007). However, we found no evidence that any of the active restoration treatments reduced species richness at any scale, including community heterogeneity. In contrast, the thin/burn treatment increased community heterogeneity and colonization by new species without increasing local species extirpation. Collectively, these results suggest that few species in these frequent-fire adapted forests are negatively impacted by restoration treatments. They also suggest that many native species in these forests can quickly re-establish when thinning and burning treatments re-create historical patterns and processes. The thin/burn treatment was the most effective for enhancing biodiversity in this study, and is also the most effective treatment for reducing surface fuels and restoring fire resilient overstory canopy structures in degraded fire-prone forest ecosystems (Schwilk et al., 2009). Therefore, reducing fire hazard and restoring diverse understory plant communities may be complementary management goals, at least in this forest type.

Recently there has been a movement toward planning and applying restoration treatments at a landscape scale, creating a mosaic of patches across the landscape, including untreated areas (Lehmkuhl et al., 2007). This landscape level planning may allow the integration of fuel reduction objectives with biological conservation objectives (Noss et al., 2006; Lehmkuhl et al., 2007). Landscape level planning also provides the opportunity to promote environmental heterogeneity, which is correlated with plant diversity (Ricklefs, 1977; Gundale et al., 2006). Therefore, many restoration treatment objectives, including increasing understory plant diversity, may be maximized by planning for heterogeneity within treatment units and a mosaic of treatments across the landscape, both spatially and temporally.

Acknowledgements

This work was funded by the U.S. National Fire Plan through the U.S. Forest Service Pacific Northwest Research Stations and by the U.S. Joint Fire Science Program through the National Fire and Fire Surrogates (FFS) project. This is Contribution Number 210 of the

National Fire and Fire Surrogate Project (FFS), funded by the U.S. Joint Fire Science Program. We greatly appreciate the hard work of the numerous field crew members. We thank Pat Cunningham for a statistical review of the manuscript. Richy Harrod provided the pretreatment data and oversaw much of the treatment implementation and data collection portions of the project. The comments of two anonymous reviewers and Kerry L. Metlen improved this manuscript.

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