

Restoration treatment effects on the understory of ponderosa pine/Douglas-fir forests in western Montana, USA

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Abstract

Fire exclusion and high-grade logging have altered the structure and function of ponderosa pine (*Pinus ponderosa*) forests across the American West. Restoration treatments are increasingly being used in these forests to move stand density, structure, and species composition toward more historically sustainable conditions. Yet little research has focused on how restoration treatments influence the associated understory plant communities, particularly in the northern Rocky Mountains of the USA. To this end, we implemented a replicated ($N = 3$), randomized block experiment in a second-growth western Montana ponderosa pine/Douglas-fir (*Pseudotsuga menziesii*) forest that initiated after harvest in the early 1900s and has not burned since. We evaluated the effects of no action (control), silvicultural cutting (thin-only), spring burning (burn-only), and silvicultural cutting followed by spring burning (thin-burn) on the understory community. Treatments were implemented at an operational scale (9 ha). Data were collected before treatment and in three subsequent years, at two spatial scales: plot (1000 m²) and quadrat (1 m²). Richness, Simpson's evenness index, and cover were calculated for the total vascular plant community. Species origin and lifeform were used to further investigate richness and cover responses to treatment. Treatments differentially impacted the understory community, with the most dramatic changes in the thin-burn. The burn-only treatment initially reduced richness and cover of the understory, but by year three all active treatments increased plot-scale understory richness relative to pre-treatment and the control. Simpson's evenness increased the first growing season after burning, but was not influenced by treatment in subsequent years. Forbs, both native and exotic, were the most responsive lifeform and increased in richness and cover after thinning, with the greatest response in the thin-burn. Increased native richness was not detected at the quadrat-scale in any treatment, but was significant at the plot-scale in numerous combinations of treatments and years. A short-term reduction in shrub richness and abundance after burning was detected at the quadrat-scale. Sapling density was reduced in all active treatments. Although active treatments create more open overstories and increase understory diversity at the stand level, a mix of treated and untreated areas will likely maximize heterogeneity and diversity at the landscape scale.

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1. Introduction

Structure and function of millions of hectares of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.)/Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco var. *glauca* (Beissn.) Franco) forests have been altered over the last century. A number of factors, including effective fire suppression, live-stock grazing, and high-grade logging, have encouraged stand densification, development of ladder fuels, and increased composition of shade-tolerant species—all stand structural changes that favor intense crown fires and alter ecosystem

function (Gruell et al., 1982; Arno and Brown, 1989; Mutch et al., 1993; Brown et al., 1994; Covington and Moore, 1994; Stephens, 1998; Hessburg and Agee, 2003; Wienk et al., 2004). Stand replacement fires are a natural and healthy part of some forest ecosystems, but they can have debilitating impacts in drier ponderosa pine and pine/fir forests adapted to low- and mixed-intensity fire regimes (Mutch et al., 1993; Brown et al., 1994; Arno et al., 1995a; Friederici, 2003). These blazes can decimate native understory species not adapted to intense fire while facilitating the invasion of exotic forbs (Crawford et al., 2001; Griffis et al., 2001). Proximate ponderosa pine seed sources can also be killed, leading to localized deforestation of this dispersal limited species (Fiedler et al., 2001). Densification of coniferous regeneration through encroachment into open areas and a species shift toward more shade-tolerant

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species have also resulted in less diverse and vigorous understory communities (Hall, 1977; Gruell et al., 1982; Gruell, 1983; Arno and Gruell, 1986; Mutch et al., 1993; Covington and Moore, 1994; Hessburg and Agee, 2003).

Reference conditions representing the range of natural or historical variability of ecosystem structures and processes have been proposed as a reasonable restoration goal (Arno et al., 1995a; Fulé et al., 1997; Moore et al., 1999; Fiedler et al., 2001; Friederici, 2003; Hessburg and Agee, 2003). Regionally, ponderosa pine/Douglas-fir forests were historically shaped by frequent, low-intensity fire—a disturbance regime that sustained open, large-tree dominated structures with vigorous understory communities (Hall, 1977; Arno, 1980; Everett et al., 2000; Hessburg and Agee, 2003). Restoration treatments that approximate these structures and increase understory richness and abundance also increase understory resilience to fire and exotic invasion (Covington et al., 1997; Swetnam et al., 1999; Harrod, 2001). Techniques to restore forest structure and function include manipulation of the overstory component with silvicultural cutting, prescribed burning, or both (Arno et al., 1995a; Moore et al., 1999; Fiedler et al., 2001; Friederici, 2003; Hessburg and Agee, 2003).

The efficacy of treatments aimed at developing a more fire-resistant forest structure has been both modeled and observed (Wagle and Eakle, 1979; Stephens, 1998; Pollet and Omi, 2002; Fulé et al., 2001; Fiedler et al., 2003; Agee and Skinner, 2005); however, effects on the understory can be highly variable. In the Blue Mountains of eastern Oregon, thinning and burning treatments had relatively little short-term impact on the understory, reflecting adaptation of this system to low intensity disturbance (Metlen et al., 2004). Silvicultural cutting to reduce overstory density has repeatedly been shown to increase understory productivity, particularly when pre-treatment stands are dense (McConnell and Smith, 1970; Bedunah et al., 1988; Moore and Deiter, 1992; Thysell and Carey, 2001). Similarly, burning alone can result in increased forb abundance (Wienk et al., 2004), graminoid abundance, and understory species richness (Busse et al., 2000; Laughlin et al., 2004). Cutting and burning treatments applied individually to ponderosa pine stands in South Dakota had similar understory effects (Wienk et al., 2004).

Understory response is driven by changes in the availability of limiting resources—primarily nitrogen and water—in dry, relatively infertile pine forests (Riegel et al., 1992, 1995; Kolb and Robberecht, 1996; Coomes and Grubb, 2000). For example, both silvicultural cutting and cutting plus burning increased N availability in forests of northern Arizona (Kaye and Hart, 1998). Regionally, however, prescribed burning following silvicultural cutting has been shown to stimulate nutrient cycling and provide resources not available after cutting alone (DeLuca and Zouhar, 2000; Wienk et al., 2004; Gundale et al., 2005). When compared to thin-only or burn-only treatments, combined thin-burn treatments typically result in greater understory richness and abundance, particularly of forbs (Wienk et al., 2004) and graminoids (Griffis et al., 2001), although these more intense treatments may reduce the abundance of shrubs important for browse (Ayers et al.,

1999). Regionally replicated experiments involving operational-scale treatments are necessary to better understand the implications of treatment and improve management decisions that will set forests on a more healthy and sustainable trajectory (Michener, 1997; Friederici, 2003; Hessburg and Agee, 2003).

The Fire/Fire Surrogates (FFS) Project (Weatherspoon, 2000) is a national network of 13 sites designed to evaluate the effects of thinning and burning treatments on vegetation, fuels, wildfire hazard, and ecosystem structure and process in short-interval fire adapted forests. To allow comparisons among and between sites, the FFS sites were implemented with a randomized and replicated study design and a common set of response variables. Primary treatment objectives include altering potential wildfire behavior (Arno and Brown, 1989; Stephens, 1998; Fulé et al., 2001; Fiedler et al., 2003) and returning historical forest structure and function (Covington et al., 1997; Arno et al., 1995a; Weatherspoon, 2000; Hessburg and Agee, 2003). Increasing overstory vigor (Biondi, 1996; Kolb et al., 1998), returning a more historical understory community (Covington et al., 1997; Arno et al., 1995a), inducing regeneration of ponderosa pine (Fiedler et al., 2001), and increasing understory diversity (Wienk et al., 2004) and resistance to exotic invasion (Busse et al., 2000; Harrod, 2001) are additional hypothesized treatment benefits. This paper analyzes results from the FFS study site in ponderosa pine/Douglas-fir forests at the University of Montana's Lubrecht Experimental Forest.

Here, we assess the understory vegetation community before treatment, and one (2002), two (2003), and three (2004) seasons after treatment. This fully replicated experiment was designed to test the effects of four operational restoration treatments: no action (control), silvicultural cutting (thin-only), spring burning (burn-only), and silvicultural cutting followed by spring burning (thin-burn). Changes in the overall understory community were described in an ordination context. Richness, Simpson's evenness, and cover of all species together were used to describe broad patterns of change in the understory community following treatment. Richness and cover of widely accepted functional groups (exotics, natives, graminoids, forbs, and shrubs) were used to identify those that might be harmed or benefited by treatments. Two scales (1000 m² (plot) and 1 m² (quadrat)) were used to detect richness patterns that vary spatially and may not be accurately described using only one scale (Schwilk et al., 1997; Stohlgren et al., 1998; Keeley et al., 2003).

The primary objective of this study was to experimentally evaluate the extent to which restoration treatments designed to restore an approximation of historical structure and function in ponderosa pine/Douglas-fir forests differentially impact understory richness and abundance. An untreated control was used for comparison with active (thinning and burning) treatments. We hypothesized that active (non-control) treatments would reduce excessive sapling density and increase richness and abundance of understory vegetation. A fundamental difference was expected between treatments that included burning (burn-only and thin-burn) and those that did not (thin-only and control). Burning was expected to more

effectively eliminate conifer saplings and stimulate nutrient cycling, while treatments that included thinning were expected to better reduce competition from the overstory. Consequently, we hypothesized that the thin-burn treatment would elicit the greatest increases in native understory richness and cover compared to pre-treatment conditions and the control, with intermediate levels of response in the thin-only and burn-only treatments. Exotic species were also expected to increase following treatment-related disturbance. Richness and cover of graminoids and forbs were expected to increase with active treatments, while burning was anticipated to reduce shrub cover. Treatments were intended to move the understory community toward conditions within the natural range of variability and were therefore interpreted in a historical context.

2. Methods

2.1. Study site

The study site is located at the University of Montana's Lubrecht Experimental Forest in the Blackfoot Valley of western Montana, at 47° north latitude and 113° west longitude (Fig. 1). Mean yearly temperature is 7 °C, and mean annual precipitation is 55 cm—nearly half falling as snow (Nimlos, 1986).

The research stands are primarily ponderosa pine and Douglas-fir in composition, with scattered western larch (*Larix occidentalis* Nutt.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.). These second-growth stands regenerated following heavy harvesting in the early 1900s, in which nearly all well-formed trees larger than 30 cm in diameter were removed (Goetz, personal communication, 2005). Most trees are 80–90 years old, with scattered clumps of regeneration and occasional trees up to 200 years old. Typical of ponderosa forests in the region, the study area has been subject to moderate grazing over the last 100 years. To better isolate response of the understory community to overstory manipulations and burning, the research blocks were fenced to exclude livestock. Frequent, low-intensity fire characterized the historical fire regime (Arno, 1980; Brown et al., 1994). However, no burning has occurred in the study area since the late 1800s.

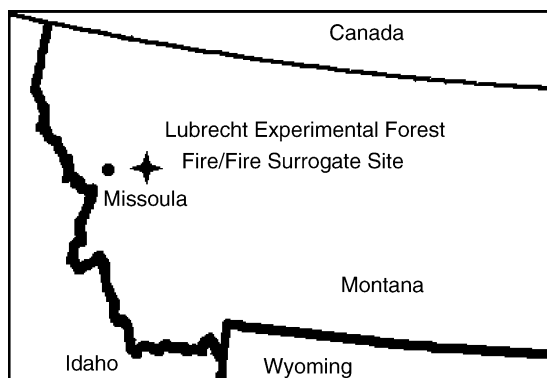


Fig. 1. The Lubrecht Experimental Forest Fire/Fire Surrogate study site is located 55 km east of Missoula, Montana.

Over the 5-year span of the study, 219 species of vascular plants were identified: 38 graminoids, 153 forbs, 23 shrubs, and 5 trees. The five most frequently occurring graminoids were: *Calamagrostis rubescens* Buckl., *Carex geyeri* Boott, *Carex concinnoides* Mackenzie, *Carex rossii* Boott, and *Festuca idahoensis* Elmer. The five most frequently occurring forbs were: *Achillea millefolium* L., *Antennaria* spp. (*An. microphylla* Rydb., *An. umbrinella* Rydb., *An. parvifolia* Nutt., and *An. rosea* Greene), *Arnica* spp. (*Ar. cordifolia* Hook. and *Ar. latifolia* Bong.), *Collinsia parviflora* Lindl., and *Fragaria virginiana* Duchesne. The five most frequently occurring shrubs were: *Symphoricarpos albus* (L.) Blake, *Arctostaphylos uva-ursi* (L.) Spreng., *Mahonia repens* (Lindl.) G. Don, *Spiraea betulifolia* Pallas, and *Amelanchier alnifolia* (Nutt.) Nutt. In the final sampling year, 25 exotic species were identified. The five most frequently occurring species were: *Taraxacum officinale* G.H. Weber ex Wiggers, *Poa pratensis* L., *Potentilla recta* L., *Cirsium vulgare* (Savi) Ten., and *Trifolium* spp. (*T. repens* L., *T. pratense* L., and *T. hybridum* L.).

2.2. Restoration treatments

Treatments were designed to move treated stands toward a desired range of conditions. At Lubrecht Forest, this target was defined as uneven-aged stands comprised of $\geq 90\%$ seral species (ponderosa pine, western larch, lodgepole pine), with $\leq 10\%$ of the relatively shade-tolerant Douglas-fir. Desired stand conditions would be relatively open (basal area 10–18 m²/ha), and dominated by larger trees with random to clumpy spatial distribution. In accordance with the national FFS network, an additional requirement was that “... each non-control treatment shall be designed to achieve stand and fuel conditions such that, if impacted by a head fire under 80th percentile weather conditions, at least 80% of the basal area of overstory (dominant and codominant) trees will survive” (Weatherspoon, 2000). Thirty-six years (1966–2002) of weather data (July 15 to September 15) from the Missoula Mountain Remote Access Weather Station (RAWS) were analyzed with Fire Family Plus (Main et al., 1990) to determine 80th percentile weather conditions of 30 °C and 26% relative humidity.

Cutting treatments were designed to reestablish ponderosa pine as the dominant component of existing stands, and to create conditions suitable for regeneration of shade-intolerant seral species, especially ponderosa pine. Leave tree marking reserved a target basal area of 11 m²/ha (Fig. 2). Marking favored larger diameter trees of seral species, but healthy medium-sized and smaller trees of seral species were also retained, if available. Low thinning and improvement/selection cutting were completed January through March of 2001 on snow-covered soil. A single-grip harvester was used to cut, limb, and buck timber into logs. Non-merchantable material was left in place and trampled by the harvest machinery. Logs were decked by product in the woods, and then moved to the landing area by a self-loading forwarder.

Prescribed burning was conducted in May and June of 2002 using a strip headfire technique. Relative humidity ranged from

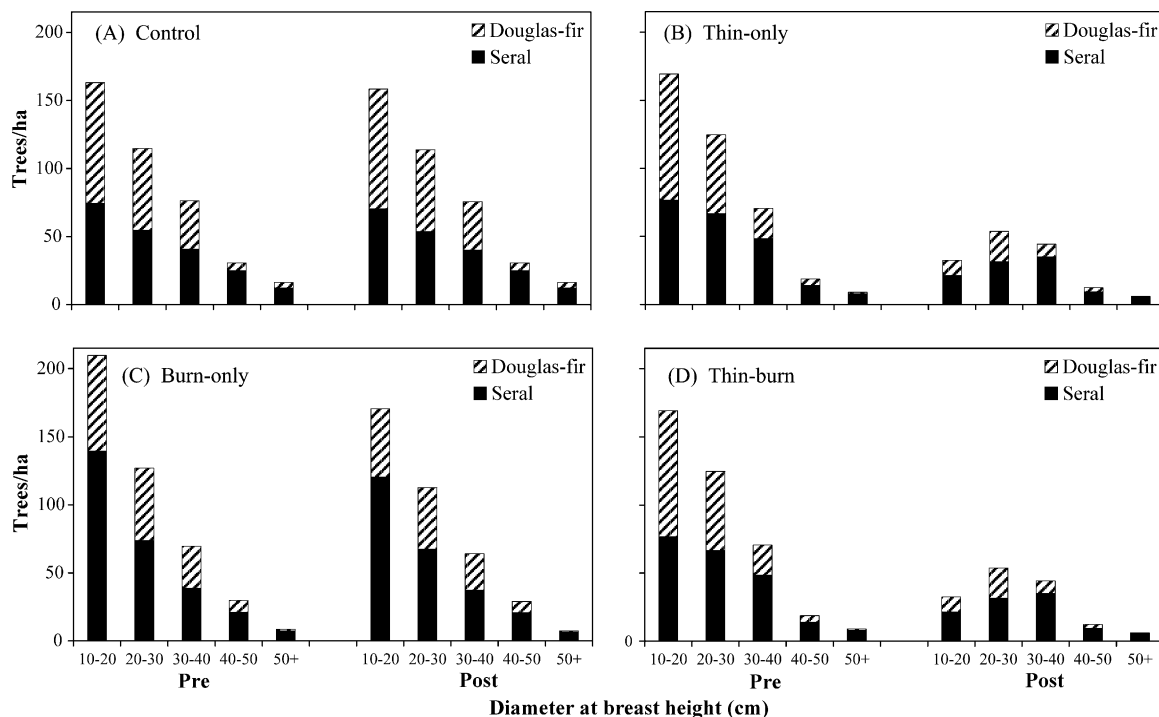


Fig. 2. Douglas-fir and seral (ponderosa pine, western larch, lodgepole pine) trees per ha by 10 cm diameter classes (pre- and post-treatment), for four restoration treatments: (A) control, (B) thin-only, (C) burn-only, and (D) thin-burn.

20–48%, and averaged around 34%. Ambient temperature ranged from 9–29 °C, and averaged around 18 °C. Winds during burn operations were fairly calm, ranging from 2–13 km/h, with gusts during one burn up to 21 km/h. Flame lengths varied from 0.2 to 1.2 m in the burn-only treatment, and from 0.2 to 2.7 m in the thin-burn. Prescribed burning reduced mean pre-burn duff depths of 2.0 cm in the burn-only and 2.3 cm in the thin-burn by 0.6 and 0.5 cm, respectively.

2.3. Field methods

This experiment employed a randomized block design with nested sampling, a design shown to maximize statistical rigor

(Legendre et al., 2004). As recommended by Wienk et al. (2004), the use of a strong experimental design coupled with pre-treatment data allowed a statistically rigorous evaluation of the restoration treatments used in this study. Controls allowed us to account for interannual variability and more clearly isolate the effects of treatment.

Three 36-ha blocks were delineated in moderately dense ponderosa pine/Douglas-fir forests on gentle to moderate slopes. Each block was divided into four square treatment units of 9 ha each, with one replicate of each treatment in each block. Treatment units were similar in habitat type (Pfister et al., 1977), and elevation (Table 1). Existing firebreaks predetermined the assignment of one burn treatment in two blocks; all

Table 1
Physical characteristics of the Lubrecht FFS study by block and treatment

Treatment	Block	Mean elevation (m)	Mean aspect (°)	Mean slope (°)	Habitat type	Dominant soil series
Control	1	1319	125	13	PSME/VACA	Winkler
Control	2	1265	75	5	PSME/VACA	Tevis-Mitten
Control	3	1253	59	5	PSME/VACA	Bignell
Thin-only	1	1306	138	9	PSME/VACA	Winkler
Thin-only	2	1271	3	8	PSME/VACA	Tevis-Mitten
Thin-only	3	1262	98	8	PSME/VACA	Bignell
Burn-only	1	1350	127	10	PSME/VACA	Winkler
Burn-only	2	1289	336	5	PSME/VACA	Tevis-Mitten
Burn-only	3	1268	303	5	PSME/VACA	Bignell
Thin-burn	1	1363	123	10	PSME/SPBE	Winkler
Thin-burn	2	1307	11	8	PSME/VACA	Tevis-Mitten
Thin-burn	3	1249	263	7	PSME/VACA	Bignell

PSME = *Pseudotsuga menziesii*, SPBE = *Spiraea betulifolia*, VACA = *Vaccinium caespitosum*; treatment-units are 9 ha and encompass a range of topographic features and habitat types. All data were taken from 10 sample plots in each treatment unit. Habitat type from Pfister et al. (1977).

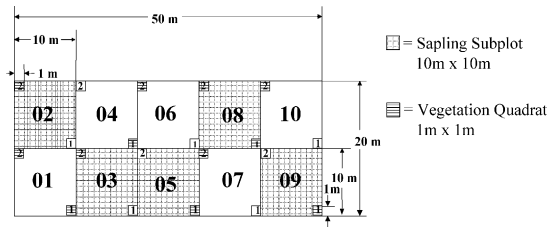


Fig. 3. Schematic of a modified Whittaker plot used to sample vegetation at the FFS site at Lubrecht Forest. Understory species richness was sampled on the entire plot. Understory richness and cover were sampled on twelve 1 m × 1 m quadrats dispersed throughout the plot. Saplings were tallied on five subplots.

other treatments were assigned randomly. A 6 × 6 grid of reference points (36 total) at 50 m intervals was permanently established in each treatment unit.

Vegetation was sampled on modified Whittaker plots (Schwilk et al., 1997) randomly located at 10 of the 36 reference points. Each 20 m × 50 m (1000 m²) Whittaker plot was subdivided into ten 10 m × 10 m (100 m²) subplots with two 1 m × 1 m (1 m²) quadrats in opposite corners of each subplot (Fig. 3). Twelve of the 20 quadrats in each plot were randomly selected to sample understory vegetation. Species accumulation curves, generated using PC-ORD 4.28 (McCune and Mefford, 1999), were constructed for each treatment unit using plot- and quadrat-level data. Results showed that understory richness was adequately sampled in all units (data not shown). We tallied saplings (trees taller than 1.37 m and smaller than 10 cm DBH) by size class and species in five randomly selected subplots within each plot. All sampling areas (plots, subplots, and quadrats) were selected in a stratified random fashion to ensure dispersion (Hurlbert, 1984). Distances were slope corrected to ensure the same vertical projection in every plot. Reference points, Whittaker plots, and quadrats were permanently marked with metal stakes driven flush with the litter to ensure exact relocation for sampling in subsequent years.

Pre-treatment vegetation data were collected during 2000 in the thin-only and thin-burn treatment units, and 2001 in the control and burn-only units. Post-treatment data were collected in 2002, 2003, and 2004 for all treatments. Sampling occurred at nearly the same period of the growing season every year. Saplings were counted prior to treatment and in 2003. Vascular plant species richness was sampled at two scales: 1000 m² (plot), and 1 m² (quadrat). Trees <1 m in height were included as part of the understory vegetation. Plants were identified to species using the terminology and common names of the PLANTS database (USDA, 2004). Some species were too similar to distinguish in the field under all morphological conditions; therefore, species richness was slightly underestimated due to occasional grouping of species by genus.

Abundance (percent cover) of every species in the 1 m² quadrats was ocularly estimated. Before treatment, cover codes were used: 0 = 0%, 1 = <1%, 2 = 1–10%, 3 = 11–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%. These codes were then converted to estimated actual covers by assigning the mid-point of the cover class. After treatment, percent cover was estimated to the nearest 1%.

2.4. Analytical methods

Before analysis, *P*-values <0.05 were chosen as significant and *P*-values <0.1 as marginally significant. These values were appropriate because the variability inherent in natural systems can mask otherwise significant relationships. Greater replication could overcome this variability, but the cost of implementing treatments at a management scale made this prohibitive (*N* = 3). Consequently, all *P*-values <0.1 were reported to allow the reader some latitude in interpreting the data.

Multi-response permutation procedures (MRPP; Mielke, 1984; Zimmerman et al., 1985) were used for all tests between and among treatments. Non-parametric tests were chosen because many of the understory variables were not normally distributed and were heteroscedastic, as determined from scatterplots and Levene's test for homogeneity of variance. Because appropriate transformations were not possible for all variables, non-parametric statistics were used throughout. All permutation procedures were conducted using PC-ORD 4.28 (McCune and Mefford, 1999). As a non-parametric equivalent to multivariate ANOVA, MRPP measures whether one or more response variables are more alike within groups than would be predicted by chance based on random data reshufflings. Chance-corrected within group agreement (*A*) gets closer to 1 as groups become more distinct from each other. Conversely, an *A* of 0 indicates that results are random and values closer to –1 are indicative of greater similarities among than within groups. While *A* gives the practical significance (effect size) of a test, the associated *P*-value provides the statistical significance of that effect, much like the *P*-value in ANOVA (McCune and Grace, 2002). In all instances, Euclidean distance was used to accommodate negative values in some response variables.

Overall community composition and abundance changes were described using Nonmetric Multidimensional Scaling (NMS; Mather, 1976; Kruskal, 1964), a non-parametric ordination technique. The ordination was run with quadrat-scale (1 m²) species cover data averaged to the plot level (*N* = 30) using PC-ORD 4.28 (McCune and Mefford, 1999). Species cover values were adjusted by subtracting the block median cover for each species to minimize block effects before analysis (McCune, personal communication, 2004). Euclidean distance was used, and a Monte Carlo test with 50 random iterations was employed to determine the probability of obtaining an equally good solution by chance. One solution was derived for the dataset containing pre- and post-treatment data for all treatments. This provided locations in ordination space before and after treatment for each plot. Within each year, differences among treatments in ordination space for all NMS axes were tested using MRPP. When significant (*P* < 0.05) differences were detected among treatments, differences between treatments were tested using pairwise MRPP.

Richness and cover of understory vegetation were divided into three classifications: total, natives versus exotics, and lifeform (graminoids, forbs, or shrubs). Native and exotic classifications were based on Hitchcock and Cronquist (1973) and the PLANTS database (USDA, 2004). Exotic species included all non-native species and were not necessarily

invasive. Graminoids were defined as species of the families *Gramineae*, *Poaceae*, *Cyperaceae*, or *Juncaceae*. Forbs were defined as non-woody, broadleaf plants not in the above families. Woody species <10 m in height at maturity were defined as shrubs. Trees, defined as woody species >10 m in height at maturity, were split into three categories: seedlings (<1.7 m in height), saplings (>1.7 m in height and <10 cm DBH), and trees (>10 cm DBH).

Quadrat-scale richness, Simpson's evenness, and percent cover were calculated at the 1-m² level and averaged to the plot. Simpson's evenness was calculated in accordance with Smith and Wilson (1996). It was chosen as an additional diversity measure because it has attributes desirable in a diversity index, including insensitivity to species richness (Smith and Wilson, 1996). Sapling density (stems/ha) was calculated for every plot. Inherent differences among treatment units were tested using pre-treatment data (2000 or 2001). In subsequent years (2002, 2003, and 2004), pre-existing differences in richness and cover were accounted for by subtracting pre-treatment from post-treatment values and conducting statistical tests on these change variables.

Differences in understory species richness and cover, Simpson's evenness, and sapling density were tested among treatments with blocked multi-response permutation procedures (BMRPP; Mielke, 1984; Zimmerman et al., 1985), using median alignment within blocks and unit-level means ($N = 3$). Median alignment subtracted the median value for a block from the original data for that block, focusing the analysis on the effect of treatment within a block. When significant ($P < 0.05$) differences were observed among treatments, pairwise MRPP's between treatments were conducted with data averaged to the plot level ($N = 30$) within a treatment. Plot-level replication had to be used for pairwise comparisons because six observations are not sufficient to conduct meaningful MRPP (McCune and Grace, 2002). Significance of these pairwise tests was evaluated with a Bonferroni adjusted P -value of 0.0083.

3. Results

3.1. Community response

Understory plant communities were sensitive to treatments and interannual variability (Fig. 4). A final NMS solution with three axes, a stress of 11.7, a final instability of 0.00045, and a Monte Carlo P -value of 0.020 accounted for most of the variability in this community ($r^2 = 0.93$). Before treatment, there were no significant differences among treatments in ordination space. In 2002, differences among treatments became highly significant ($P = 0.001$); the thin-only and control treatments were significantly different from the burn-only and thin-burn treatments ($P < 0.003$). Treatment differences were marginally significant in 2003 ($P = 0.059$), but became significant again in 2004 ($P = 0.048$). Pairwise testing showed no significant differences between active treatments in 2004; however, the thin-only was marginally different from the control ($P = 0.074$), and the burn-only and the thin-burn

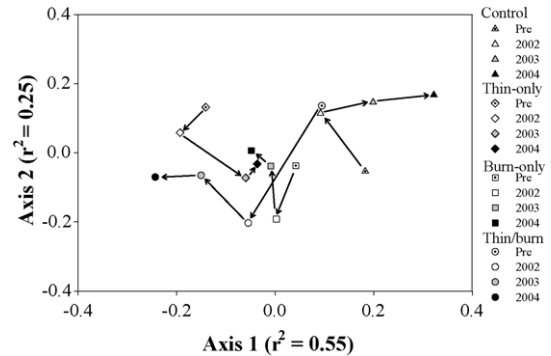


Fig. 4. NMS ordination of the understory plant community at the Lubrecht Forest FFS site before treatment and in the three subsequent years. Individual species covers were aligned to the block median cover (for each species) before analysis.

were significantly different from the control ($P = 0.037$ and $P = 0.045$, respectively).

3.2. Richness (plot-scale)

Species richness at the plot-scale did not differ significantly between any treatments for any lifeform before treatment (Table 2). Plot-scale differences among treatments for graminoid richness were detected with BMRPP, but these differences were not evident using pairwise comparisons with MRPP. In post-treatment years, total, native, exotic, and forb species richness at the plot-scale demonstrated significant differences among and between treatments (Table 2).

Total richness at the plot-scale was affected by all treatments, though relative relationships among treatments changed yearly (Table 2). In 2002 (the season immediately following burning), total richness at the plot-scale increased most in the thin-only ($P < 0.001$) and least in the burn-only treatment ($P < 0.006$). By 2003, the thin-only and thin-burn exhibited greater increases in richness per plot than the burn-only and control ($P < 0.001$). In 2004, the thin-only and thin-burn treatments had increased plot-scale richness compared to the control ($P < 0.001$), resulting in the most species in the thin-burn, followed by the thin-only, burn-only, and control. Similar differences were observed for native species richness among treatments, but with the thin-burn and thin-only exhibiting statistically equivalent increases in richness by 2004. Plot-scale richness of exotics responded to thinning treatments, with significantly ($P < 0.001$) greater increases in exotic richness (three species) in the thin-only and thin-burn treatments than in the control (one species) in 2002. In 2003 and 2004, increases in the number of exotic species in the thin-burn treatment significantly exceeded those in the thin-only and burn-only treatments ($P < 0.001$), which in turn had increased plot-scale exotic species richness ($P < 0.001$) compared to the control (Table 2).

Graminoid and shrub richness were not responsive to treatment at the plot-scale, whereas forb richness responded similarly to total, native, and exotic richness (Table 2). Plot-scale forb richness increased significantly more in the thin-only

Table 2

Mean plot-scale richness for all species (total), native species, exotic species, graminoids, forbs, and shrubs by treatment and year, with standard errors in parentheses

Plot-scale richness	Year	Control	Thin-only	Burn-only	Thin-burn	A	P
Total	Pre	36.3 (1.3)	37.3 (2.3)	34.5 (3.9)	36.1 (3.1)	−0.067	0.606
	2002	46.8 (1.9) a	52.4 (4.2) b	39.4 (4.0) c	44.9 (2.4) a	0.543	0.005*
	2003	53.7 (1.6) a	61.2 (3.9) b	53.8 (5.0) a	63.8 (5.5) b	0.670	0.003*
	2004	57.3 (2.7) a	66.2 (4.1) bc	59.7 (7.1) ab	68.6 (7.7) c	0.301	0.024*
Native	Pre	34.1 (0.6)	34.8 (1.7)	32.9 (3.2)	33.5 (2.0)	−0.078	0.632
	2002	43.7 (1.0) a	47.6 (3.1) b	37.0 (3.1) c	39.8 (1.4) c	0.558	0.005*
	2003	49.9 (0.7) a	54.8 (2.7) b	48.9 (4.0) a	54.4 (3.6) b	0.599	0.007*
	2004	52.8 (1.8) a	59.3 (3.0) b	53.7 (5.2) ab	58.4 (5.1) b	0.328	0.036*
Exotic	Pre	2.2 (0.7)	2.3 (0.7)	1.6 (0.8)	2.6 (1.1)	0.007	0.440
	2002	3.0 (1.0) a	4.8 (1.1) b	2.4 (0.9) a	5.1 (1.4) b	0.552	0.018*
	2003	3.7 (0.8) a	6.2 (1.2) b	4.8 (1.2) b	9.4 (1.9) c	0.704	0.002*
	2004	4.4 (0.9) a	6.9 (1.1) b	5.9 (2.0) b	10.2 (2.7) c	0.224	0.040*
Graminoid	Pre	6.1 (0.2)	6.8 (0.5)	5.4 (0.4)	6.9 (0.5)	0.449	0.013*
	2002	9.5 (1.3)	10.8 (0.9)	7.7 (1.3)	10.1 (1.1)	0.121	0.237
	2003	11.5 (1.5)	12.8 (1.0)	9.8 (1.7)	13.9 (1.7)	0.288	0.090
	2004	12.5 (1.6)	14.0 (1.1)	11.6 (2.1)	14.1 (2.0)	0.119	0.211
Forb	Pre	20.7 (1.2)	19.5 (1.5)	20.2 (2.6)	18.8 (2.3)	−0.026	0.510
	2002	26.8 (0.8) a	30.1 (2.4) b	23.1 (2.4) c	25.3 (1.7) a	0.461	0.010*
	2003	31.3 (0.5) a	36.1 (1.9) b	34.2 (2.9) b	39.3 (4.0) c	0.614	0.002*
	2004	33.9 (1.5) a	39.6 (1.9) b	38.1 (4.3) b	43.7 (5.8) c	0.295	0.021*
Shrub	Pre	7.5 (0.6)	8.7 (1.1)	6.8 (1.0)	8.1 (1.1)	0.200	0.060
	2002	8.4 (0.9)	9.3 (1.0)	6.5 (0.8)	7.7 (1.4)	0.303	0.061
	2003	8.7 (1.0)	9.9 (1.2)	7.7 (0.7)	8.4 (1.4)	0.041	0.376
	2004	8.8 (0.9)	10.2 (1.3)	7.9 (0.8)	8.5 (1.5)	0.159	0.162

Overall tests are BMRPP on untransformed data. Post-treatment tests are on the difference between pre- and post-treatment unit means ($N = 3$) among treatments, within years. Letters represent significant differences between treatments, within years, as tested with pairwise MRPP tests, using plot-scale means ($N = 30$). Pairwise tests were Bonferroni corrected.

* $P \leq 0.05$.

in 2002 (11 species) than in any other treatment ($P < 0.001$). Conversely, the burn-only gained significantly fewer forb species (3) than any other treatment ($P < 0.002$). In 2003 and 2004, the thin-burn gained the most species (21 and 25, respectively), significantly more than all other treatments ($P < 0.005$). Forb richness in this time period increased least in the control ($P < 0.003$); in 2004 there were 10 fewer forb species in the control than the thin-burn, and 6 and 4 fewer species than in the thin-only and burn-only, respectively (Table 2).

3.3. Richness (quadrat-scale)

Initially, all treatments had statistically equivalent quadrat-scale species richness, ranging from 7.7 to 8.6 species/m² (Table 3). Treatments that involved burning reduced quadrat-scale species richness in 2002. In the burn-only treatment, this reduction was significant relative to richness changes in all other treatments ($P < 0.001$). In 2003, quadrat-scale species richness increased less in the burn-only, relative to pre-treatment, than in any other treatment ($P < 0.001$). In 2004, the thin-burn had the most species at the quadrat-scale (12.9), a significantly greater increase than that observed for the burn-only and control treatments ($P < 0.001$).

Quadrat-scale native species richness in 2002 was lowest in the burn-only and thin-burn treatments. Changes from the pre-

treatment condition differed significantly from those observed in the thin-only and control ($P < 0.001$). The burn-only treatment increased native species richness less than all other treatments in 2003 and 2004 ($P < 0.002$). In 2002, quadrat-scale exotic richness increased more in the thin-burn than in any other treatment ($P < 0.001$), a relationship that continued in 2003 and 2004 (Table 3).

Quadrat-scale graminoid richness was not significantly influenced by treatments (Table 3). Forb richness in 2002 increased most in the thin-only and control treatments, followed by the thin-burn ($P < 0.001$), but decreased in the burn-only ($P < 0.001$). In 2003, forb richness increases were greatest in the thin-only and thin-burn and least in the control ($P < 0.003$) and burn-only ($P < 0.001$). By 2004, forb richness was lowest in the control, with significantly greater increases in the thin-only ($P = 0.003$) and thin-burn ($P < 0.001$). Changes in quadrat-scale shrub richness never differed except for significant ($P < 0.001$) reductions in the burn treatments in 2002, the first year of response after spring burning (Table 3).

3.4. Evenness (quadrat-scale)

Simpson's evenness index for the full understory community did not differ among treatments prior to treatment (Table 4). A short-term increase in evenness was observed in 2002, the growing season after burning ($P = 0.009$). These changes were

Table 3
Mean quadrat-scale richness for all species (total), native species, exotic species, graminoids, forbs, and shrubs by treatment and year, with standard errors in parentheses

Quadrat-scale richness	Year	Control	Thin-only	Burn-only	Thin-burn	A	P
Total	Pre	7.7 (0.2)	8.6 (0.5)	8.3 (1.4)	8.4 (1.0)	−0.139	0.745
	2002	9.7 (0.2) a	10.4 (0.6) a	7.4 (1.0) c	8.6 (0.7) b	0.505	0.007*
	2003	10.3 (0.2) a	11.4 (0.6) a	9.8 (1.2) b	11.4 (0.8) a	0.313	0.033*
	2004	10.8 (0.4) ac	12.2 (0.7) ab	10.5 (1.4) c	12.9 (1.5) b	0.469	0.009*
Native	Pre	7.6 (0.2)	8.4 (0.4)	8.1 (1.2)	8.1 (0.9)	−0.134	0.748
	2002	9.5 (0.2) a	10.2 (0.5) a	7.2 (0.8) b	8.1 (0.6) b	0.520	0.006*
	2003	10.1 (0.2) a	11.1 (0.5) a	9.6 (1.0) b	10.7 (0.6) a	0.289	0.037*
	2004	10.5 (0.3) a	11.8 (0.5) a	10.1 (1.2) b	11.6 (1.0) a	0.467	0.016*
Exotic	Pre	0.2 (0.1)	0.2 (0.1)	0.2 (0.1)	0.3 (0.2)	−0.186	0.900
	2002	0.2 (0.1) a	0.3 (0.1) a	0.2 (0.1) a	0.4 (0.2) b	0.334	0.023*
	2003	0.2 (0.1) a	0.3 (0.1) a	0.3 (0.2) a	0.7 (0.3) b	0.489	0.016*
	2004	0.3 (0.1) a	0.4 (0.2) a	0.5 (0.2) a	1.3 (0.6) b	0.340	0.023*
Graminoid	Pre	1.5 (0.0)	1.5 (0.1)	1.5 (0.1)	1.5 (0.1)	0.002	0.425
	2002	2.0 (0.1)	2.0 (0.1)	1.7 (0.1)	2.0 (0.0)	0.151	0.154
	2003	2.3 (0.1)	2.2 (0.1)	2.0 (0.1)	2.6 (0.2)	0.051	0.275
	2004	2.4 (0.2)	2.4 (0.1)	2.0 (0.1)	2.8 (0.2)	0.086	0.232
Forb	Pre	3.8 (0.1)	4.0 (0.3)	4.3 (1.3)	4.0 (0.7)	−0.184	0.939
	2002	4.8 (0.2) a	5.2 (0.3) a	3.7 (0.9) c	4.3 (0.3) b	0.451	0.010*
	2003	5.2 (0.2) a	5.8 (0.4) b	5.5 (1.1) a	6.1 (0.5) b	0.424	0.027*
	2004	5.5 (0.3) a	6.4 (0.4) b	6.2 (1.3) ab	7.4 (1.1) c	0.513	0.008*
Shrub	Pre	2.0 (0.1)	2.6 (0.2)	2.0 (0.3)	2.4 (0.5)	0.234	0.089
	2002	2.3 (0.1) a	2.8 (0.3) a	1.7 (0.1) b	2.2 (0.5) b	0.313	0.024*
	2003	2.4 (0.1)	2.9 (0.3)	2.1 (0.2)	2.6 (0.6)	0.002	0.444
	2004	2.4 (0.2)	2.9 (0.3)	2.1 (0.3)	2.5 (0.7)	0.263	0.059

Overall tests are BMRPP on untransformed data. Post-treatment tests are on the difference between pre- and post-treatment unit means ($N = 3$) among treatments, within years. Letters represent significant differences between treatments, within years, as tested with pairwise MRPP tests, using plot-level means ($N = 30$). Pairwise tests were Bonferroni corrected.

* $P \leq 0.05$.

short-lived; in 2003 and 2004 changes from the pre-treatment condition were equivalent in all treatments (Table 4).

3.5. Cover (quadrat-scale)

Total and native species cover exhibited similar treatment responses (Table 5). Prior to treatment, there was significantly greater cover in the thin-only and thin-burn treatments than in the burn-only ($P < 0.001$) and control ($P < 0.001$). In 2002, the thin-burn treatment lost more total ($P < 0.006$) and native ($P < 0.004$) cover than any other treatment. In subsequent years, however, this treatment effect disappeared. By 2004, the only significant treatment response ($P < 0.001$) was an increase

in exotic cover in the thin-burn compared to the other treatments, an effect observed in every post-treatment sampling year ($P < 0.001$; Table 5).

There were no significant treatment effects on graminoid cover, but forb cover was significantly reduced ($P < 0.006$) in 2002 in all three active treatments compared to the control. Forb cover responses were indistinguishable among treatments in subsequent years (Table 5). Before treatment, there were no significant pairwise differences between treatments for shrub cover. Shrub cover was reduced relative to pre-treatment levels in all treatments in 2002, with the greatest reductions in the thin-burn ($P < 0.001$), and burn-only ($P < 0.001$) relative to the control. In 2003, shrub cover in the control increased

Table 4
Mean Simpson's evenness for all species by treatment and year, with standard errors in parentheses

Year	Control	Thin-only	Burn-only	Thin-burn	A	P
Pre	0.46 (0.01)	0.48 (0.01)	0.48 (0.05)	0.48 (0.02)	−0.130	0.770
2002	0.58 (0.04) a	0.58 (0.03) a	0.80 (0.05) b	0.75 (0.07) b	0.397	0.009*
2003	0.53 (0.04)	0.51 (0.01)	0.57 (0.04)	0.52 (0.04)	−0.087	0.645
2004	0.51 (0.04)	0.49 (0.01)	0.53 (0.02)	0.50 (0.02)	0.001	0.483

Overall tests are BMRPP on untransformed data. Post-treatment tests are on the difference between pre- and post-treatment unit means ($N = 3$) among treatments, within years. Letters represent significant differences between treatments, within years, as tested with pairwise MRPP tests, using plot-level means ($N = 30$). Pairwise tests were Bonferroni corrected.

* $P \leq 0.05$.

Table 5

Mean quadrat-scale percent cover for all species (total), native species, exotic species, graminoids, forbs, and shrubs by treatment and year, with standard errors in parentheses

Quadrat-scale cover	Year	Control	Thin-only	Burn-only	Thin-burn	A	P
Total	Pre	22.4 (1.4) a	28.9 (3.5) b	20.7 (1.2) a	28.8 (2.9) b	0.301	0.018*
	2002	21.1 (2.1) a	22.7 (1.4) ab	11.2 (1.1) b	14.5 (2.0) c	0.580	0.010*
	2003	26.4 (2.7)	27.7 (0.7)	22.0 (1.7)	27.5 (2.2)	0.155	0.090
	2004	27.9 (2.8)	31.8 (1.3)	25.9 (1.7)	30.8 (3.1)	−0.164	0.925
Native	Pre	22.3 (1.4) a	28.4 (3.5) b	20.5 (1.1) a	28.6 (3.0) b	0.279	0.025*
	2002	20.9 (2.1) a	22.4 (1.5) ab	11.0 (1.1) b	14.0 (2.2) c	0.572	0.011*
	2003	26.2 (2.7)	27.3 (0.7)	21.7 (1.5)	25.5 (3.3)	0.130	0.118
	2004	27.6 (2.8)	31.2 (1.2)	25.3 (1.5)	28.3 (3.2)	−0.164	0.925
Exotic	Pre	0.1 (0.1)	0.6 (0.3)	0.1 (0.1)	0.2 (0.2)	−0.015	0.485
	2002	0.2 (0.1) a	0.4 (0.2) a	0.2 (0.2) a	0.6 (0.3) b	0.214	0.040*
	2003	0.2 (0.1) a	0.4 (0.2) a	0.3 (0.2) a	2.0 (1.1) b	0.257	0.016*
	2004	0.3 (0.1) a	0.6 (0.3) a	0.6 (0.3) a	2.4 (1.3) b	0.206	0.045*
Graminoid	Pre	3.2 (0.8)	3.2 (1.1)	2.2 (0.2)	3.0 (0.6)	−0.175	0.802
	2002	2.6 (0.3)	2.5 (0.2)	1.8 (0.1)	2.2 (0.1)	−0.229	0.898
	2003	2.8 (0.3)	2.9 (0.2)	2.2 (0.2)	3.4 (0.1)	−0.147	0.782
	2004	2.9 (0.3)	3.6 (0.4)	2.4 (0.0)	4.1 (0.4)	−0.102	0.730
Forb	Pre	7.3 (0.3)	10.3 (1.0)	6.6 (0.8)	9.9 (1.5)	0.224	0.099
	2002	8.8 (1.4) a	9.3 (0.1) b	5.0 (1.0) b	7.2 (1.3) b	0.405	0.014*
	2003	10.8 (1.8)	11.4 (0.5)	9.4 (1.1)	12.8 (1.0)	−0.094	0.696
	2004	12.2 (2.4)	13.2 (0.6)	11.4 (1.0)	14.0 (0.6)	−0.241	0.944
Shrub	Pre	9.9 (0.3)	13.5 (0.9)	9.7 (0.1)	13.8 (1.9)	0.333	0.028*
	2002	8.5 (1.1) a	10.0 (1.6) ab	3.9 (0.6) bc	4.9 (1.3) c	0.673	0.005*
	2003	11.6 (1.3) a	12.3 (0.6) b	9.8 (0.7) ab	11.0 (2.6) b	0.211	0.032*
	2004	11.4 (0.9)	13.8 (0.5)	11.5 (0.6)	12.3 (3.2)	0.081	0.261

Overall tests are BMRPP on untransformed data. Post-treatment tests are on the difference between pre- and post-treatment unit means ($N = 3$) among treatments, within years. Letters represent significant differences between treatments, within years, as tested with pairwise MRPP tests, using plot-level means ($N = 30$). Pairwise tests were Bonferroni corrected.

* $P \leq 0.05$.

significantly more than in the thin-only and thin-burn ($P < 0.004$), which remained reduced relative to pre-treatment. No differences in shrub cover response were observed in 2004 (Table 5).

3.6. Sapling density

Prior to treatment, there were no differences in sapling density among the four treatments. All active treatments

reduced sapling density significantly compared to the control ($P < 0.000$); however, all active treatments were not equal. The thin-burn treatment reduced sapling density significantly more than the thin-only ($P < 0.000$). The number of saplings per ha actually increased in the control from pre-treatment to 2003 (Fig. 5).

4. Discussion

4.1. Community response

Active treatments resulted in post-treatment understory communities with significantly increased richness compared to the untreated control—despite no differences before treatment. Richness increased annually in nearly all treatment units in every sampling year, however, our experimental design allowed detection of significant treatment effects despite high inter-annual variability. Evenness increased immediately after burning, but changes were transitory, suggesting that treatments did not strongly influence this aspect of diversity. Abundance of understory vegetation (as measured by cover) was little influenced by our treatments. The thin-burn treatment resulted in the greatest understory community change from pre-treatment and control conditions, followed by the thin-only, with the least change in the burn-only treatment. These outcomes are consistent with studies contrasting cutting and

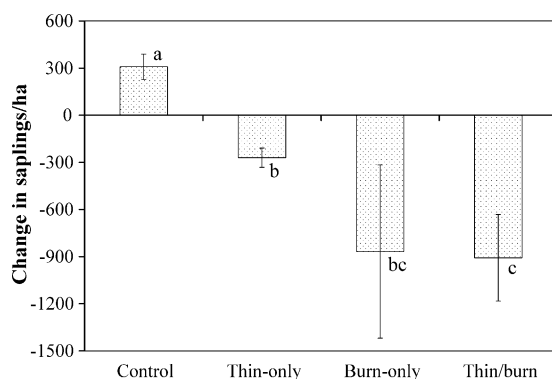


Fig. 5. Change in saplings per ha from pre-treatment to 2003 after restoration treatments ($\pm$ S.E.). Letters represent significant differences, as tested with pairwise MRPP tests, using plot-level means ($N = 30$). Pairwise tests were Bonferroni corrected.

burning treatments in ponderosa pine forests in other regions (Griffis et al., 2001; Wienk et al., 2004).

In 2002, the thin-only treatment elicited a plot-scale increase in total, native, exotic, and forb richness, and an increase in total and forb richness at the quadrat-scale. Similar harvest treatments have resulted in reduced richness in the first year of response in eastern Oregon (Metlen et al., 2004) and in pine forests of South Dakota (Wienk et al., 2004), but Wienk et al. (2004) found an additional year of response brought about increased richness. Thysell and Carey (2001) also observed increased total richness after cutting treatments to increase structural heterogeneity in Douglas-fir forests of western Washington.

Understory cover initially decreased in the thinning-related treatments at our site, a response similar to that observed by Thysell and Carey (2001) and Metlen et al. (2004). This reduction in cover was likely due to physical obstruction to growth resulting from the tree tops and limbs generated by the cut-to-length harvest system used in our study—a system that leaves slash in the woods where trees are cut, topped, and limbed. We documented no significant differences in understory cover in the thin-only treatment in 2004, suggesting that reduced understory abundance was short-lived. More commonly, understory productivity increases after reductions in overstory density (McConnell and Smith, 1970; Bedunah et al., 1988; Moore and Deiter, 1992; Wienk et al., 2004).

The strongest understory responses were first year post-burn reductions in richness and cover of the total understory community and associated increases in equitability. All species were reduced to very low cover values in the burned units. Thus, even though richness and abundance were reduced, no species accounted for disproportionate areal cover, possibly driving the trend of increased evenness. At the quadrat-scale, natives, forbs, and shrubs were significantly reduced in the burn-only and thin-burn treatments. A similar trend was observed at the plot-scale, though only reductions in the total community and natives were significant. The initial reductions in richness and cover rapidly reversed in subsequent years, especially in the thin-burn treatment. These changes suggest that reductions in cover associated with treatment may be short-lived and could demonstrate the resilience of these forest understory communities to burning and thinning. Similar patterns of response were reported by Antos et al. (1983) and Metlen et al. (2004). Authors working in ecosystems with comparable understory composition (Schoennagel et al., 2004; MacKenzie et al., 2004) found that shrub cover gradually increases with time since fire, but that resprouting shrub species (such as those found at our site) respond rapidly to burning. The dominant shrub species in our region (i.e., Scouler's willow (*Salix scouleriana* Barratt ex Hook.), white spirea (*Spiraea betulifolia*), snowberry (*Symphoricarpos albus*), and huckleberry (*Vaccinium* species)), rapidly respond to burning by regrowth and, in many cases, rhizomatous colonization (Lyon and Stickney, 1976; Stickney and Campbell, 2000). This rapid shrub recovery partially explains why differences in the understory community became less significant—but more varied—with time since treatment. Differences observed in 2003 and 2004 were likely due to colonization by native and exotic forbs.

In contrast to the immediate and short-term negative effects of burning on shrubs, the forb component in our study responded most strongly the second and third year after treatment. Busse et al. (2000) also found increased herbaceous richness in thinned ponderosa pine forests of central Oregon two years after spring burning, though changes in abundance were not detected. Cutting and spring burning also resulted in increased forb abundance in a ponderosa pine forest in South Dakota (Wienk et al., 2004). However, the pre-treatment understory of this Black Hills forest was extremely depauperate after 125 years of fire exclusion. As with our study, Wienk et al. (2004) reported similar post-treatment understory communities following burn-only and thin-only treatments. At the Lubrecht site, increased native and exotic forb richness and abundance were observed in both thinning-related treatments, but were greatest in the thin-burn.

Differential treatment impacts on limiting resources, particularly underground resources, could explain the variable understory response to treatment. In a review of the ecological literature, Coomes and Grubb (2000) found that light was the primary limiting resource in areas of high moisture and nutrient availability, while underground resources were more often limiting in drier forests. Moisture and available *N* are the resources typically limiting in these regionally dry, relatively infertile forest systems (Riegel et al., 1992; Riegel et al., 1995; Kolb and Robberecht, 1996). For example, Kolb and Robberecht (1996) found that root exclusion dramatically reduced seedling mortality in ponderosa pine forests of northern Idaho. Cover of understory lifeforms was little influenced by canopy reduction in pine forests of eastern Oregon, while root trenching increased density and cover of all lifeforms two years after treatment (Riegel et al., 1995). While some individual species in this Oregon study responded to a >100% increase in photosynthetically active radiation, the majority of understory species responded to root trenching. Similarly, trenching to eliminate underground competition from the overstory also resulted in greater increases in total understory biomass than overstory density reduction alone (Riegel et al., 1992).

Overstory removal in our harvested units increased light availability and reduced underground competition from the overstory, possible explanations for the strong response observed in the thin-only treatment. However, as Arno et al. (1995a) suggest, restoration treatments that do not include burning are incomplete because thinning alone is not sufficient to remove small trees and promote nutrient cycling. Thinning to presettlement forest densities, as well as thinning followed by prescribed burning, resulted in increased moisture and *N* availability in northern Arizona pine forests (Kaye and Hart, 1998). Regionally, burning in conjunction with silvicultural cutting serves to stimulate nutrient cycling and decomposition (DeLuca and Zouhar, 2000; Gundale et al., 2005), resulting in greater resource availability belowground in the thin-burn treatment than the thin-only. An underlying theme from these studies is that directly reducing overstory competition (cutting), in conjunction with returning historical nutrient cycling mechanisms (burning), should yield the greatest increases in understory richness and abundance.

Short interval, fire-adapted ponderosa pine forests are generally able to capitalize on sudden increases in available resources. Fire exclusion and subsequent conifer encroachment can reduce nutrient cycling (MacKenzie et al., 2004; Wienk et al., 2004), which likely reduces the abundance of shorter-lived species on the landscape (Hall, 1977; Laughlin et al., 2004) and leads to decreased understory richness and cover. Seed banking, seed dispersal over long distances, and rapid resprouting of native species are mechanisms that allow native shade-intolerant species to respond to increased resource availability, reversing this trend (Riegel et al., 1992; Wienk et al., 2004). Collectively, these factors should translate into increased richness and abundance of native species; however, many native species are adapted to low resource levels and reach peak metabolic rates at lower resource levels than many exotics (Chapin, 1980). Consequently, not all natives can compete effectively in higher nutrient environments.

Restoration treatments may increase abundance of exotic species along with early successional natives. Alternatively, untreated forest conditions are likely to be susceptible to intense wildfire and subsequently more aggressive exotic invasion than that observed after our treatments. In the event that wildfire should occur, a number of authors have documented the efficacy of fuel reduction treatments for reducing wildfire intensity (Wagle and Eakle, 1979; Pollet and Omi, 2002; Agee and Skinner, 2005). Choromanska and DeLuca (2001) found that prescribed burning significantly ameliorated the negative impacts on soil nutrient availability and microbial biomass that resulted from wildfire subsequently burning over the same location. Griffis et al. (2001) investigated the effects of thinning, prescribed burning, and wildfire of increasing intensity on understory vegetation in northern Arizona. They found increasing native graminoid abundance, but little evidence for increasing exotic invasion, with increased prescribed burning intensity. Conversely, intense wildfire increased exotic invasion while severely curtailing native graminoids. Many exotic species are relatively short-lived and are likely to be out-competed as resources gradually become more limiting, favoring more resource efficient native species as in Antos et al. (1983) and Thysell and Carey (2001). An increase in exotics may be an unavoidable short-term consequence in the process of reducing hazard and developing vigorous native plant communities that are more resilient to exotic invasion should wildfire occur.

Intense burning associated with slash piles led to increased invasion of exotics in Arizona (Haskins and Gehring, 2004). Burn-pile sites had lower richness than other areas, exotics were four times as abundant, and biomass was 19% greater than in unburned areas. De Deyn et al. (2004) demonstrated that soil sterilization (a potential effect of intense wildfire) favored early- and mid-successional species, though this response was dependent on soil biota present. Seeding with native species and mycorrhizae could reverse this trend by increasing native competition with exotic species (Korb et al., 2004). Carefully designed treatments can help avoid these effects. For example, we found increased native richness associated with the thin-burn and thin-only treatments in our study, particularly at the

larger spatial scale. Gundale et al. (2005) investigated pre-treatment and immediate post-treatment soil nutrient and microbial responses to the restoration treatments at our site. They found little treatment effect on the microbial community (based on phospholipid fatty acid profiles), but significant among-treatment differences in nitrogen availability (Gundale et al., 2005). Harvesting over a snowpack, broadcast versus pile burning, differential propagule pressure, and an existing, relatively vigorous native plant community are factors that may explain the significant increase in native richness and cover at our site with gains in exotics that, in the short-term, are not overwhelming.

4.2. Scale

Characteristics of understory vegetation vary in the spatial and temporal scales at which they are detectable. Sampling at multiple spatial scales is therefore necessary to fully describe the vegetation of a site (Schwilk et al., 1997; Stohlgren et al., 1998; Keeley et al., 2003). At the Lubrecht site, sampling at the quadrat-scale adequately captured differences in abundance of common species. The quadrat-scale was less sensitive to changes in rare species, however, as demonstrated by the lag in detecting increased total richness in the thin-only and increased exotic richness in the thin-burn compared to the plot-scale. In the burn-only treatment, total richness decreased at the quadrat-scale in all years, but only in 2002 at the plot-scale. Increased native richness was not detected at the quadrat-scale in any treatment, but was significant at the plot-scale in numerous combinations of active treatments and years. Alternatively, the plot-scale did not detect short-term reductions in shrub cover and richness, suggesting that the quadrat-scale is necessary to detect decreasing abundance of common species as a result of treatment.

We found more statistically significant differences among treatments at the plot- than the quadrat-scale, and with increasing time since treatment. Abella and Covington (2004) observed the opposite phenomenon in ponderosa pine forests of northern Arizona, where increases in species richness in restoration treatments of greater intensity were significantly different at 1 m², but not at 50 m². Keeley et al. (2003) and Schwilk et al. (1997) also found stronger trends at 1 m² than at larger spatial scales. The need to sample at multiple spatial scales, particularly early in a study before treatment responses and spatial patterns of the local understory community are understood, is highlighted by these differences.

4.3. Historical context

Many authors have proposed restoration as a process by which the structure and function of native communities are returned to a range of conditions compatible with their historical range of variability (Arno et al., 1995a; Covington et al., 1997; Fiedler, 2002; Harrod et al., 1999; Moore et al., 1999; Swetnam et al., 1999; Everett et al., 2000; Friederici, 2003). Restoration, then, is based on the best knowledge of what conditions were like previous to some degradation process

or event (such as fire exclusion). This knowledge is used to direct management actions, which are modified as needed to accommodate shifting long-term management goals, environmental conditions, exotic species, and economics (Arno et al., 1995a; Covington et al., 1997; Harrod et al., 1999; Moore et al., 1999; Swetnam et al., 1999; Everett et al., 2000; Friederici, 2003; Hessburg and Agee, 2003).

Direct comparisons of the current understory with historical conditions previous to Euro-American settlement are not possible. Regional anecdotal accounts, historical photographs, investigations of community change with increasing time since fire, and study of the response of these systems to contemporary disturbances, are all contrasting lines of evidence from which we can infer a probable range of historical conditions (Fiedler et al., 1996; Moore et al., 1999; Friederici, 2003; Hessburg and Agee, 2003).

Historically, many ponderosa pine/Douglas-fir forests experienced low- to mixed-severity wildfires at mean fire intervals ranging from 7 to 24 years (Hall, 1977; Arno, 1980; Everett et al., 2000; Hessburg and Agee, 2003). Work conducted regionally and based on forest habitat types (Pfister et al., 1977) suggests that our study area would have burned at approximately 20-year intervals (Arno, 1980). Such a disturbance regime would create conditions favoring perennial species capable of resprouting from underground parts, or short-lived species capable of residing in the seed bank or dispersing long distances. A frequent fire regime would also make conifer recruitment into the overstory difficult (Weaver, 1951; White, 1985), resulting in uneven-aged stand structures such as that observed in old-growth ponderosa pine forests (White, 1985; Arno et al., 1995b; Kaufmann et al., 2000; Morgan et al., 2002; Youngblood et al., 2004), and open understories such as described regionally by Hall (1977), Gruell et al. (1982), and Gruell (1983). Effective fire suppression, grazing, landscape fragmentation, and changes in traditional land use practices (Arno and Brown, 1989; Mutch et al., 1993; Hessburg and Agee, 2003) have resulted in delaying this fire return interval for nearly a century. Fire exclusion results in densification of coniferous regeneration and associated decreases in understory vigor and richness, a well-documented trend in ponderosa pine dominated forests in Montana (Gruell et al., 1982; Gruell, 1983; Arno and Gruell, 1986; MacKenzie et al., 2004), eastern Oregon (Hall, 1977; Mutch et al., 1993), northern Arizona (Covington and Moore, 1994), and South Dakota (Wienk et al., 2004).

Our treatments have initiated the process of restoring historical overstory structure and ecosystem processes, as suggested by Arno et al. (1995a), Fiedler et al. (1998), Harrod et al. (1999), and Moore et al. (1999). Restoration treatments should facilitate the return of a more historical understory community as well (Friederici, 2003; Hessburg and Agee, 2003; Arno and Fiedler, 2005). Prior to Euro-American settlement, stands were reportedly open, with abundant forage. Gruell et al. (1982) provide more specific understory descriptions, based on forests habitat types (Pfister et al., 1977). Our research stands are predominantly classified within the Douglas-fir/dwarf huckleberry (*Vaccinium caespitosum*

Michx.) habitat type (Table 1), but with inclusions of drier (Douglas-fir/pinegrass (*Calamagrostis rubescens*) and Douglas-fir/snowberry (*Symphoricarpos albus*) habitat types. The observations of Gruell et al. (1982) suggest that sod-forming native graminoids (e.g., pinegrass and elk sedge (*Carex geyeri*)) and low shrubs (e.g., huckleberry, snowberry, and white spirea) would have dominated the more mesic sites, while bunchgrasses and forbs would have historically dominated drier sites. Hall (1977) indicated that frequent underburning maintained similar conditions in eastern Oregon pine forests—understories dominated by pinegrass, elk sedge, and resprouting shrubs. In both regions, a gradual conversion to understories dominated by large shrubs and then by coniferous regeneration was observed with the exclusion of fire.

Results from numerous independent studies and anecdotal accounts are corroborated by a recent study contrasting old-growth ponderosa pine stands with and without fire exclusion (Gildar et al., 2004). Working in northern Arizona, Gildar et al. (2004) found that decreases in understory richness and cover were related to significantly greater tree densities and duff depths at fire-excluded sites. Forest floor depths have been reported to increase with time since fire in western Montana pine/fir forests as well (MacKenzie et al. 2004). In a meta-analysis of 35 independently published studies, Xiong and Nilsson (1999) found that plant litter significantly reduced understory richness and aboveground biomass, lending further credence to litter depth as a possible mechanism in the reduced diversity associated with fire exclusion.

The return of wildfire to the stands studied by Gildar et al. (2004), after 76-years of fire exclusion, led to decreased duff and total forest floor depth and increased understory richness and cover, and greater similarity to reference conditions (Laughlin et al., 2004). Comparison (reference) sites were old-growth ponderosa pine stands that had experienced occasional large and small fires throughout the 76-year period, the same period in which the study stands had fire excluded. As with our study, an increase in mostly native short-lived forbs was a major component of the change from fire-excluded conditions. Laughlin et al. (2004) suggest that annual and biennial forbs may have comprised an important component of historical ponderosa pine stands in northern Arizona, a component greatly reduced in fire-excluded forests.

Active restoration treatments in our study made substantial progress toward a more historical understory community. General treatment objectives included a reduction in density of conifer regeneration and larger shrubs, with an increase in understory diversity—particularly graminoids and forbs. Increased abundance and vigor of native forbs and graminoids were also objectives. All active treatments successfully reduced conifer sapling densities, with the most dramatic changes in the thin-burn. Significantly increased native richness (particularly of forbs) in all active treatments indicates some success in returning understory species to the landscape. Given the increased richness of native species in all active treatments, a parallel increase in native abundance might also be expected. Cover data varied widely, however, so trends of increasing cover in the treated units were not statistically significant.

The thin-burn treatment resulted in conditions most similar to those described historically, with significantly reduced conifer regeneration, and increased native richness and abundance. This treatment was also associated with the most negative aspect of restoration—exotic species invasion. The thin-only treatment also increased understory diversity, and is a reasonable tool for restoration when burning is not practical (Arno et al., 1995a; Arno and Fiedler, 2005). Both the thin-only and burn-only treatments resulted in similar understory communities at the plot-scale, but a greater richness response was observed in the thin-only treatment. Multiple burn entries, or single entry burns in which more overstory trees are scorched or killed, may increase the efficacy of the burn-only treatment.

This study provides evidence that alternative restoration treatments have differential impacts on understory plant communities. Taken collectively, results from our study suggest that all active treatments promote a more open overstory and diverse understory community—characteristics commonly associated with historically sustainable conditions. However, a mosaic of treatments (including untreated areas) would likely be needed to increase landscape-scale heterogeneity and improve longer-term sustainability of this ponderosa pine ecosystem.

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References

- Abella, S.R., Covington, W.W., 2004. Monitoring an Arizona ponderosa pine restoration: sampling efficiency and multivariate analysis of understory vegetation. *Restor. Ecol.* 12, 359–367.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. *Forest. Ecol. Manage.* 211, 83–96.
- Antos, J.A., McCune, B., Bara, C., 1983. The effect of fire on an ungrazed western Montana grassland. *Am. Midl. Nat.* 110, 354–364.
- Arno, S.F., 1980. Forest fire history in the northern Rockies. *J. Forest.* 78, 460–465.
- Arno, S.F., Gruell, G.E., 1986. Douglas-fir encroachment into mountain grasslands in southwestern Montana. *J. Range Manage.* 39, 272–276.
- Arno, S.F., Brown, J.K., 1989. Managing fire in our forests – time for a new initiative. *J. Forest.* 87, 44–46.
- Arno, S.F., Harrington, M.G., Fiedler, C.E., Carlson, C.E., 1995a. Restoring fire-dependent ponderosa pine forests in western Montana. *Restor. Manage. Notes* 13, 32–36.
- Arno, S.F., Scott, J.H., Hartwell, M.G., 1995b. Age-class structure of old growth ponderosa pine/Douglas-fir stands and its relation to fire history. USDA For. Serv. Res. Paper INT-481. Rocky Mountain Research Station, Fort Collins, CO.
- Arno, S.F., Fiedler, C.E., 2005. Mimicking Nature's Fire: Restoring Fire-Prone Forests in the West. Island Press, Washington, DC.
- Ayers, D.M., Bedunah, D.J., Harrington, M.G., 1999. Antelope bitterbrush and Scouler's willow response to a shelterwood harvest and prescribed burn in western Montana. *West. J. Appl. Forest.* 14, 137–143.
- Bedunah, D., Pfingsten, W., Kennett, G., Willard, E., 1988. Influence of stand canopy density to forage production. In: Schmidt, W.C. (Ed.), *Proceedings of the Future Forests of the Mountain West: A Stand Culture Symposium*. USDA For. Serv. Gen. Tech. Re INT-243. Intermountain Research Station, Ogden, UT, 99–107.
- Biondi, F., 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: evidence for inverse (a)symmetric competition. *Can. J. Forest. Res.* 26, 1397–1406.
- Brown, J.K., Arno, S.F., Barrett, S.W., Menakis, J.P., 1994. Comparing the prescribed natural fire program with presettlement fires in the Selway-Bitterroot Wilderness. *Int. J. Wildland Fire* 4, 157–168.
- Busse, M.D., Simon, S.A., Riegel, G.M., 2000. Tree-growth and understory response to low-severity prescribed burning in thinned ponderosa pine forests of central Oregon. *Forest. Sci.* 46, 258–268.
- Chapin III, F.C., 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11, 223–260.
- Choromanska, U., DeLuca, T.H., 2001. Prescribed fire alters the impact of wildfire on soil biochemical properties in a ponderosa pine forest. *Soil Sci. Soc. Am. J.* 65, 232–238.
- Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* 70, 171–207.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. Forest.* 92, 39–47.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.W., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in *Pinus ponderosa* forests of the Southwest. *J. Forest.* 95, 23–29.
- Crawford, J.A., Wahren, C.-H.A., Kyle, S., Moir, W.H., 2001. Response of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *J. Veg. Sci.* 12, 261–268.
- De Deyn, G.B., Raaijmakers, C.E., van der Putten, W.H., 2004. Plant community development is affected by nutrients and soil biota. *J. Ecol.* 92, 824–834.
- DeLuca, T.H., Zouhar, K.L., 2000. Effects of selection harvest and prescribed fire on the soil nitrogen status of ponderosa pine forests. *Forest. Ecol. Manage.* 138, 263–271.
- Everett, R.L., Schellhaas, R., Keenum, D., Spurbeck, D., Ohlson, P., 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *Forest. Ecol. Manage.* 129, 207–225.
- Fiedler, C.E., Arno, S.F., Harrington, M.G., 1996. Flexible silvicultural and prescribed burning approaches for improving health of ponderosa pine forests. USDA For. Serv. Gen. Tech. Re RMRS-278. Rocky Mountain Research Station, Ft. Collins, CO, 69–74.
- Fiedler, C.E., Arno, S.F., Harrington, M.G., 1998. Reintroducing fire in ponderosa pine-fir forests after a century of fire exclusion. In: Pruden, T.L., Brennan, L.A. (Eds.), *Proceedings of the Tall Timbers Fire Ecology Conference*, Tall Timbers Research Station, Tallahassee, FL, 20, pp. 245–249.
- Fiedler, C.E., Arno, S.F., Keegan, C.E., Blatner, K.A., 2001. Overcoming America's wood deficit: an overlooked option. *BioScience* 51, 53–58.
- Fiedler, C.E., 2002. Natural process-based management of fire-adapted western forests. In: Baumgartner, D.M., Johnson, L.R., DePuit, E.J. (Eds.), *Proceedings of Small Diameter Timber: Resource Management, Manufacturing, and Markets*, Washington State University Cooperative Extension, Corvallis, OR, pp. 147–151.
- Fiedler, C.E., Keegan, C.E., Morgan, T.A., Woodall, C.W., 2003. Fire hazard and potential treatment effectiveness: a statewide assessment in Montana. *J. Forest.* 101, 7.
- Friederici, P. (Ed.), 2003. *Ecological Restoration of Southwestern Ponderosa Pine Forests*. Island Press, Washington, DC.
- Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.* 7, 895–908.

- Fulé, P.Z., Waltz, A.E.M., Covington, W.W., Heinlein, T.A., 2001. Measuring forest restoration effectiveness in reducing hazardous fuels. *J. Forest.* 99, 24–29.
- Gildar, C.N., Fulé, P.Z., Covington, W.W., 2004. Plant community variability in ponderosa pine forest has implications for reference conditions. *Nat. Area. J.* 24, 101–111.
- Gruell, G.E., Schmidt, W.C., Arno, S.F., Reich, W.J., 1982. Seventy-years of vegetative change in a managed ponderosa pine forest in western Montana: implications for resource management. USDA For. Serv. Gen. Tech. Re INT-130. Intermountain Forest and Range Experiment Station, Ogden, UT.
- Griffis, K.L., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. *Forest. Ecol. Manage.* 146, 239–245.
- Gruell, G.E., 1983. Fire and vegetative trends in the northern Rockies: interpretations from 1871–1982 photographs. USDA For. Serv. Gen. Tech. Re INT-158. Intermountain Forest and Range Experiment Station, Ogden, UT.
- Gundale, M.J., DeLuca, T.H., Fiedler, C.E., Ramsey, P.W., Harrington, M.G., Gannon, J.E., 2005. Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical, and biological properties. *Forest. Ecol. Manage.* 213, 25–38.
- Hall, F.C., 1977. Ecology of natural underburning in the Blue Mountains of Oregon. USDA For. Serv. R6-ECOL-79-001. Pacific Northwest Research Station, Portland, OR.
- Harrod, R.J., 2001. The effect of invasive and noxious plants on land management in eastern Oregon and Washington. *Northwest Sci.* 75, 85–89.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *Forest. Ecol. Manage.* 114, 433–446.
- Haskins, K.E., Gehring, C.A., 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. *J. Appl. Ecol.* 41, 379–388.
- Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. *Forest. Ecol. Manage.* 178, 23–59.
- Hitchcock, C.L., Cronquist, A., 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- Kaufmann, M.R., Regan, C.M., Brown, P.M., 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Can. J. Forest. Res.* 30, 698–711.
- Kaye, J.P., Hart, S.C., 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine-bunchgrass ecosystem. *Ecol. Appl.* 8, 1052–1060.
- Keeley, J.E., Lubin, D., Fotheringham, C.J., 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecol. Appl.* 13, 1355–1374.
- 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.
- Kolb, T.E., Holmberg, K.M., Wagner, M.R., Stone, J.E., 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. *Tree Physiol.* 18, 375–381.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2004. Slash pile effects on soil biotic and chemical properties and plant establishment: recommendations for amelioration. *Restor. Ecol.* 12, 52–62.
- Kruskal, J.B., 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29, 115–129.
- Laughlin, D.C., Bakker, J.D., Stoddard, M.T., Daniels, M.L., Daniels, M.L., Springer, J.D., Gilder, C.M., Green, A.M., Covington, W.W., 2004. Toward reference conditions: wildfire effects on flora in an old-growth ponderosa pine forest. *Forest. Ecol. Manage.* 199, 137–152.
- Legendre, P., Dale, M.R.T., Fortin, M.J., Casgrain, P., Gurevitch, J., 2004. Effects of spatial structures on the results of field experiments. *Ecology* 85, 3202–3214.
- Lyon, L.J., Stickney, P.F., 1976. Early vegetal succession following large northern Rocky Mountain wildfires. In: Komarek, Sr., E.V. (Ed.), *Proceedings of the Tall Timbers Fire Ecol. Conference*, 14. pp. 355–373.
- MacKenzie, M.D., DeLuca, T.H., Sala, A., 2004. Forest structure and organic horizon analysis along a fire chronosequence in the low elevation forests of western Montana. *Forest. Ecol. Manage.* 203, 331–343.
- Main, W.A., Paananen, D.M., Burgan, R.E., 1990. *Fire Family Plus*. USDA For. Serv. Gen. Tech. Re NC-138. North Central Forest Experiment Station, St. Paul, MN.
- Mather, P.M., 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. John Wiley and Sons, London.
- McConnell, B.R., Smith, J.G., 1970. Response of understory vegetation to *Pinus ponderosa* thinning in eastern Washington. *J. Range Manage.* 23, 208–212.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.
- McCune, B., Mefford, M.J., 1999. *PC-ORD: Multivariate Analysis of Ecological Data*, version 4.27. MjM Software Design, Gleneden Beach, OR.
- Metlen, K.L., Fiedler, C.E., Youngblood, A., 2004. Understory response to fuel reduction treatments in the Blue Mountains of northeastern Oregon. *Northwest Sci.* 78, 175–185.
- Michener, W.K., 1997. Quantitatively evaluating restoration “experiments”: research design, statistical analysis, and data management considerations. *Restor. Ecol.* 5, 324.
- Mielke Jr., P.W., 1984. Meteorological applications of permutation techniques based on distance functions. In: Krishnaiah, P.R., Sen, P.K. (Eds.), *Handbook of Statistics*, vol. 4. Elsevier Science Publishers, pp. 813–830.
- Moore, M.M., Deiter, D.A., 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. *J. Range Manage.* 45, 267–271.
- Moore, M.M., Covington, W.W., Fulé, P.Z., 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol. Appl.* 9, 1266–1277.
- Morgan, T.A., Fiedler, C.E., Woodall, C.W., 2002. Characteristics of dry site old-growth ponderosa pine in the Bull Mountains of Montana, USA. *Nat. Area. J.* 22, 11–19.
- Mutch, R.W., Arno, S.F., Brown, J.K., Carlson, C.E., Ottmar, R.D., Peterson, J.L., 1993. Forest health in the Blue Mountains: a management strategy for fire-adapted ecosystems. USDA For. Serv. Gen. Tech. Re PNW-310. Pacific Northwest Research Station, Portland, OR.
- Nimlos, T.J., 1986. *Soils of Lubrecht Experimental Forest*. Miscellaneous Publication No. 44. Montana Forest and Conservation Experiment Station, Missoula, MT.
- Pfister, R.D., Kovalchik, B.L., Arno, S.F., Presby, R.C., 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Re INT-34. Intermountain Research Station, Ogden, UT.
- Pollet, J., Omi, P.N., 2002. Effect of thinning and prescribed burning on crown fire severity in ponderosa pine forests. *Int. J. Wildland Fire* 11, 1–10.
- Riegel, G.M., Miller, R.F., Krueger, W.C., 1992. Competition for resources between understory vegetation and overstory ponderosa pine. *Ecol. Appl.* 2, 71–85.
- Riegel, G.M., Miller, R.F., Krueger, W.C., 1995. The effects of aboveground and belowground competition on understory species composition in a *Pinus ponderosa* forest. *Forest. Sci.* 41, 864–889.
- Schoennagel, T., Waller, D.M., Turner, M.G., Romme, W.H., 2004. The effect of fire interval on post-fire understory communities in Yellowstone National Park. *J. Veg. Sci.* 15, 797–806.
- Schwilk, D.W., Keeley, J.E., Bond, W.J., 1997. The intermediate disturbance hypothesis does not explain fire and diversity pattern in fynbos. *Plant Ecol.* 132, 77–84.
- Smith, B., Wilson, J.B., 1996. A consumer’s guide to evenness indices. *Oikos* 76, 70–82.
- Stephens, S.L., 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behavior in Sierra Nevada mixed-conifer forests. *Forest. Ecol. Manage.* 105, 21–35.
- Stickney, P.F., Campbell Jr., R.B., 2000. Data base for early postfire succession in northern Rocky Mountain forests. USDA For. Serv. Gen. Tech. Re RMRS-61CD. Rocky Mountain Research Station, Ogden, UT.
- Stohlgren, T.J., Bull, K.A., Otsuki, Y., 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *J. Range Manage.* 51, 164–172.

- Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* 9, 1189–1206.
- Thysell, D.R., Carey, A.B., 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. *Can. J. Forest. Res.* 31, 1513–1525.
- US Department of Agriculture Natural Resource Conservation Service, 2004. The PLANTS Database, version 3.5 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA.
- Wagle, R.F., Eakle, T.W., 1979. A controlled burn reduces the impact of a subsequent wildfire in a ponderosa pine vegetation type. *Forest. Sci.* 25, 123–129.
- Weatherspoon, C.P., 2000. A proposed long-term national study of the consequences of fire and fire surrogate treatments. In: Neuenschwander, L.F., Ryan, K.C., Goldberg, G.E. (Eds.), *Proceedings of the Joint Fire Science Conference and Workshop*, University of Idaho, Moscow, ID, pp. 117–126.
- Weaver, H., 1951. Fire as an ecological factor in the southwestern ponderosa pine forests. *J. Forest.* 49, 93–98.
- White, A.S., 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66, 589–594.
- Wienk, C.L., Sieg, C.H., McPherson, G.R., 2004. Evaluating the role of cutting treatments, fire and soil seed banks in an experimental framework in ponderosa pine forests of the Black Hills, South Dakota. *Forest. Ecol. Manage.* 192, 375–393.
- Xiong, S., Nilsson, C., 1999. The effects of plant litter on vegetation: a meta-analysis. *J. Ecol.* 87, 984–994.
- Youngblood, A., Max, T., Coe, K., 2004. Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California. *Forest. Ecol. Manage.* 199, 191–217.
- Zimmerman, G.M., Goetz, H., Mielke, P.Q., 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology* 66, 606–611.