Common and Uncommon Understory Species Differentially Respond to Restoration Treatments in Ponderosa Pine/Douglas-Fir Forests, Montana

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Abstract

Restoration treatments have been widely advocated to address declining conditions in *Pinus ponderosa* forests throughout the western United States. However, few studies have examined treatment effects on individual plant species or whether responses differ for common species and uncommon species (those with low abundance in the community)—information that may be critical in managing for long-term biodiversity. We investigated understory species responses to restoration treatments in ponderosa pine/Douglas-fir forests using a randomized block experimental design with three blocks and four treatments (control, burn-only, thin-only, and thin-burn). Understory vegetation was sampled before treatment and for three consecutive years after treatment. We used richness and an index of uniqueness to compare responses of common and uncommon native understory species among treatments, and indicator species analysis to identify individual species that responded to each treatment. Treatments that included thinning had significantly more unique species assemblages than the control. The thin-only treatment increased common native species richness, whereas all active treatments significantly increased uncommon native species richness over the control, especially the thin-burn. Generally, life-forms did not explain the responses of individual species, though in the final sampling year several graminoids were exclusively indicative of treatments that included thinning. Very few species had reduced abundance in the thinning and burning treatments by the final sample year, whereas many uncommon and short-lived species benefited from active treatments, especially the combined thin-burn treatment. Active restoration treatments in these forests may foster plant diversity by minimally impacting common species while significantly benefiting disturbance-dependent native species.

Key words: **diversity, fuel reduction, indicator species, locally rare species, prescribed burning, thinning.**

Introduction

Maintaining or increasing biodiversity has become an important consideration in forest management and an essential component of forest restoration (Fiedler et al. 1992; Halpern & Spies 1995; Covington et al. 1997; Thysell & Carey 2001; Lindenmayer & Franklin 2002; Decocq et al. 2004). Disturbances play a critical role in maintaining diversity in many ecosystems, reducing the abundance of dominant species and allowing establishment of early-successional species (Connell 1978; Sousa 1984; Wohlgemuth et al. 2002). Over long time periods, species evolve adaptations to their associated natural disturbance regime (Denslow 1980; Sousa 1984; Lawrence et al. 2005). When the disturbance regime is altered, as with fire exclusion in fire-prone ecosystems, numerous species adapted to that disturbance may be lost from the community (Leach & Givnish 1996; Quintana-Ascencio & Menges 2000; Wohlgemuth et al. 2002; Lyons et al. 2005).

Frequent surface fires historically shaped forests dominated by ponderosa pine (*Pinus ponderosa*) in many areas of the American West (e.g., Cooper 1960; Arno et al. 1995; Everett et al. 2000; Fulé et al. 2003; Hessburg & Agee 2003), though not all pine forests were characterized by frequent low-intensity fire (Shinneman & Baker 1997; Veblen 2003). Burning in pine forests within the frequent-fire regime created receptive seedbeds, facilitated nutrient cycling, and discriminated against shade-tolerant species (Covington & Moore 1994; Arno et al. 1995; Hessburg & Agee 2003). Since Euro-American settlement in the late 1800s, anthropogenic activities in these forests (including fire exclusion) have fundamentally altered forest density, structure, and overstory species composition (Covington et al. 1997; Keane et al. 2002; MacKenzie et al. 2004); changed understory vegetation dynamics (Gruell et al. 1982; Newland & DeLuca 2000; Gildar et al. 2004); and reduced understory richness and productivity (Covington & Moore 1994; Fulé et al. 1997; Laughlin et al. 2004; Wienk et al. 2004). Forest restoration efforts utilizing silvicultural thinning and prescribed burning treatments have been widely proposed for frequent-fire forests to reduce

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tree density, restore ecosystem structure and process, and increase resilience to natural disturbances such as wildfire (Moore et al. 1999; Fiedler et al. 2001; Allen et al. 2002; Hessburg & Agee 2003; Brown et al. 2004).

Little is known about the response of many understory species to treatment-related disturbances, despite the increasingly broadscale application of restoration treatments in forests of the American West. There are few quantitative standards of understory communities from the pre-Euro-American settlement period against which to compare (Gildar et al. 2004; Laughlin et al. 2004), but documenting understory species responses can provide local information to guide management decisions and minimize negative treatment impacts on uncommon and declining species (Allen et al. 2002). Restoration treatments may benefit species by emulating disturbances and conditions that were critical parts of their evolutionary history (Fiedler et al. 1992; Ayers et al. 1999; Brown et al. 2004). However, life-form, physiological tolerances, and reproductive strategies determine different species responses to disturbance (Riegel et al. 1995; Decocq et al. 2004). Species richness may increase following management treatments due to establishment of native and exotic ruderal species (Halpern & Spies 1995; Wienk et al. 2004; Fulé et al. 2005), although native species adapted to undisturbed forest conditions may simultaneously decline or be eliminated (Halpern & Spies 1995; Meier et al. 1995; Wohlgemuth et al. 2002; Halpern et al. 2005).

Ecosystem function is altered by a gain or loss of species (Hooper et al. 2005). Uncommon species (species with low abundance) constitute much of the floral diversity in many ecosystems (Halpern & Spies 1995; Stohlgren et al. 1998, 2005; Lyons et al. 2005) and may be the most susceptible to local extirpation following disturbances (Robinson & Quinn 1988; Halpern et al. 2005). Some ecosystem functions may depend on uncommon species despite their low contributions to overall biomass (Lyons & Schwartz 2001; Zavaleta & Hulvey 2004; Lyons et al. 2005). However, the responses of these species to restoration treatments have seldom been investigated partly because sampling them requires large spatial scales (Stohlgren et al. 1998) and partly because restoration is a relatively recent phenomenon (Arno & Fiedler 2005).

The overall objective of this study was to evaluate restoration treatment effects on individual, common, and uncommon understory species in a *P. ponderosa*/Douglas-fir (*Pseudotsuga menziesii*) forest in Montana. We hypothesized that both disturbance-dependent native species that may have declined with fire exclusion and exotic species would be favored by active restoration treatments, but later-successional species would be favored by no action (control) given the current altered fire regime. The combined thin-burn treatment was expected to have some of the same effects as the thin-only and burn-only treatments as well as unique effects due to the possible additive or synergistic effects of these two treatments. Specifically, we address the following questions: (1) Do restoration treatments differentially affect common or uncommon native species as groups? (2) What individual species are favored or harmed by particular restoration treatments? (3) Do individual understory plant species responses to restoration treatments follow their functional group membership (i.e., life-form [graminoids, forbs, shrubs, trees], origin [native, exotic], and longevity [annual, biennial, perennial])?

Methods

Study Area

The study site was established in a second-growth *Pinus ponderosa*/*Pseudotsuga menziesii* forest at the University of Montana's Lubrecht Experimental Forest in west-central Montana, U.S.A. It is situated in gentle mountainous terrain, characterized by 10–20% slopes. The site is located at lat 47° N and long 113° W, and ranges in elevation from 1263 to 1388 m. Mean annual air temperature is 7°C and mean annual precipitation is 50 cm (Nimlos 1986). During the course of this study, annual precipitation for the nearest official weather station in Missoula, Montana (about 50 km west of the study site) was 9% below normal in 2000, 3% below normal in 2001, 26% below normal in 2002, 10% above normal in 2003, and 11% above normal in 2004. April to July precipitation was 39% below normal in 2000, 22% above normal in 2001, 1% above normal in 2002, less than 1% above normal in 2003, and 19% above normal in 2004 (Western Regional Climate Center, http://www.wrcc.dri.edu/).

The current forest largely regenerated after heavy harvesting in the early 1900s. No formal fire history study has been conducted in the study area; however, the multicentury age range of old-growth relicts and patches within the study area provide strong anecdotal evidence of a frequent surface fire regime. *Pinus ponderosa* and *Ps. menziesii* comprise the majority of the overstory, with scattered *Pinus contorta* and *Larix occidentalis*. Regeneration of shade-tolerant *Ps. menziesii* is abundant in the understory, whereas the most abundant undergrowth species (in order of abundance) include *Arnica* spp., *Spiraea betulifolia*, *Symphoricarpos albus*, *Calamagrostis rubescens*, and *Carex geyeri*. Like many ponderosa pine forests in the region, the study area has been subject to moderate livestock grazing during the past century. For this reason, research blocks were fenced to exclude livestock and better isolate treatment effects on understory vegetation.

Experimental Design

This study is part of the Fire and Fire Surrogates (FFS) national study network (http://www.fs.fed.us/ffs/), which includes 13 research sites utilizing similar experimental designs and sampling protocols. The FFS study is a multiyear interdisciplinary study investigating the effectiveness of thinning and burning treatments for reducing wildfire hazard. It is also examining treatment effects on vegetation, soils, insects, and birds and small mammals.

Prior to treatment, three 36-ha blocks were established about 2 km apart in the 900-ha study area. Each block was subdivided into four square treatment units of 9 ha. Each of the four treatments—prescribed spring burning (burn only), cutting (thin only), cutting followed by prescribed spring burning (thin-burn), and no treatment (control)—was assigned once in each of the three blocks. All treatments were randomly assigned, with the exception of two burn treatment units that were located because of proximity to roads and fire breaks. A six-by-six grid of 36 points was systematically established in each treatment unit, with 50 m between points. Using a stratified random design to ensure dispersion, 10 points were selected within each treatment unit to serve as plot centers for 20 $\times$ 50–m (1,000 m^2) modified Whittaker plots. Locations were assigned such that each row and column in the grid had at least one plot but no more than two. Twelve 1-m^2 quadrats (1 $\times$ 1 m) were then dispersed within each 1,000-m^2 plot using a stratified random design (Metlen & Fiedler 2006).

Restoration Treatments

The cutting treatment (hereafter referred to as "thinning") consisted of an improvement/selection cutting and a low thinning. Large trees of seral species (*P. ponderosa*, *L. occidentalis*, and *P. contorta*) were favored to be left on site. The prescription was designed to reduce basal area density by about half, to 11 m^2/ha, a sufficiently low density to induce regeneration of shade-intolerant seral species (Fiedler et al. 1988). A cut-to-length system was used to cut, top, and delimb trees, and a forwarder transported the logs to a landing outside the block. Slash was left on site and driven over by the harvesting equipment to condense fuel accumulations. Harvesting was conducted in the winter of 2001 over a snowpack, resulting in no detectable soil compaction (Gundale et al. 2005).

Prescribed broadcast burns were conducted separately for each of the six burn treatment units during May and June of 2002. Relative humidity during burning ranged from 20 to 48%, and averaged about 34%. Burn-day temperatures ranged from 9 to 29°C, and averaged around 18°C. Winds were fairly calm, ranging from 2 to 13 km/hr, although one burn had gusts up to 21 km/hr. For a more detailed description of the study site, experimental design, and treatments, see Metlen and Fiedler (2006).

Vegetation Sampling

All plant species present on plots (1,000 m^2) and associated quadrats (1 m^2) were identified. Cover was visually estimated to the nearest percent at the 1-m^2 scale for each species, including tree species less than 1 m in height. Pre-treatment data were collected in June and July of 2000 (thin-only and thin-burn) and 2001 (burn-only and control). Post-treatment data were collected on all treatments during June and July of 2002, 2003, and 2004. Plants that could not consistently be identified to species were identified to genus. Nomenclature follows that in the USDA PLANTS database (USDA-NRCS 2005). The PLANTS database was also used to determine plant origin (native or exotic to North America), typical longevity (annual, biennial, or perennial), and life-form (graminoid, forb, shrub, or tree).

Statistical Analysis

Plant species may be classified as rare due to limited geographical range, habitat specificity, or low local population density (Rabinowitz 1981). We utilized this last criterion to define uncommon and common species at our study site based on their frequency as in Meier et al. (1995) and McIntyre and Lavorel (1994). Using pre-treatment data, uncommon species were defined as those that occurred on less than 10% of the 1,000-m^2 plots (this included all species that were only found following treatments), occasional species occurred on 10–33% of the plots, and common species on more than 33%. None of the species classified as uncommon had an estimated cover of greater than 0.02% prior to treatment, a threshold as low or lower than those used to define locally rare species in other studies (e.g., Murray & Lepschi 2004; Lyons et al. 2005).

We calculated richness for uncommon and common native species at 1- and 1,000-m^2 spatial scales prior to treatment and 3 years post-treatment (2004). We also used a uniqueness index (Stohlgren et al. 2005) to determine how treatments affected the average rarity of plant species on a plot (1,000 m^2). The uniqueness index reflects the relative rarity of species on a plot after correcting for plot-level richness and was calculated according to the following equation:

$$\text{Uniqueness} = 1 - \frac{\sum \text{species proportional frequencies on a plot}}{\text{species richness on a plot}} \quad (1)$$

The proportional frequency for each species was the number of plots on which the species occurred divided by the total number of plots on which it could occur (120 total plots). Both proportional frequencies and species richness for a plot were calculated prior to treatment and in 2004. The uniqueness index ranges from 0 to 1. Plots with only ubiquitous species have low uniqueness scores, whereas those with numerous uncommon species present would have higher scores.

Differences in common native species richness, uncommon native species richness, and plot uniqueness were tested among treatments using analysis of variance in SPSS (v. 12.0; SPSS, Inc., Chicago, IL, U.S.A.). Post hoc least significant difference tests were used for pair-wise comparisons between treatments when the overall test was significant ($p \leq 0.05$). Pre-treatment and 2004 data were tested separately, with square root and natural log transformations used when necessary to meet parametric assumptions. Pearson correlations were then calculated between plot uniqueness values and native and exotic species richness for both years.

Species and groups of species that may be responding to particular treatments were identified with indicator species analysis (ISA; Dufrêne & Legendre 1997) in PC-ORD version 4 (McCune & Mefford 1999), using plot-level means ($n = 30$). This technique produces an indicator value (IV) for every species that ranges from 0 to 100—with 100 being a perfect indicator, present in only one treatment and in all plots of that treatment. Separate analyses were performed for each year using 1-m^2 cover (mean cover of 12 quadrats in a plot) and 1,000 m^2 presence/absence (presence anywhere in the entire plot).

Because different treatments may have similar effects on a given species, each active treatment (burn-only, thin-only, and thin-burn) was compared pair-wise with the control—both before treatment and in all post-treatment years. Thus, we identified not only those species similarly affected by multiple treatments, but also those uniquely impacted by specific treatments. There were few indicator species before treatment, and these were not reported to focus the analysis on responsive understory species rather than on differences in understory composition due to site-specific differences. Indicators of the control are reported because they represent species that declined in treated units. We did not use a cutoff value for the IVs if they were found significant ($p \leq 0.05$), thereby maximizing the potential to detect treatment effects on less common species. To reduce the chances of a type I error given the potentially large number of tests, we focused our interpretation of individual species responses within functional groups (origin, longevity, and life-form).

Implementation and sampling costs associated with replicating restoration treatments at an operational scale (9-ha treatment units) limited replication in this study. These analyses were conducted using multiple plots nested within treatment units ($n = 30$ plots per treatment), limiting the scope of inference to our study site. However, several characteristics of this study, including a randomized block design, pre- and post-treatment data collection, experimental controls, operational scale of treatment application, and multiscale sampling provide a strong framework for furthering our understanding of restoration treatment effects on understory species.

Results

Prior to treatment (2000 and 2001), there were no differences in common or uncommon native species richness among treatments at either spatial scale (1 m^2 or 1,000 m^2; all p values > 0.2). After treatment, common native species richness differed among treatments at the 1-m^2 ($F_{[3,116]} = 4.4$, $p = 0.006$) and 1,000-m^2 ($F_{[3,116]} = 8.8$, $p < 0.001$) scales. At both scales, common native species richness was significantly higher in the thin only than all other treatments, whereas the control was also significantly higher than the thin-burn at the 1,000-m^2 scale (Fig. 1). Uncommon native species richness also differed among treatments at the 1-m^2 ($F_{[3,116]} = 8.1$, $p < 0.001$) and 1,000-m^2 ($F_{[3,116]} = 8.4$, $p < 0.001$) scales in 2004. In contrast to common species richness, uncommon native species richness was significantly higher in the thin-burn than in all the other treatments at both scales (Fig. 1). All active treatments had significantly higher uncommon native species richness than the control at the 1,000-m^2 scale.

Prior to treatment application, there were no differences among treatments in plot uniqueness ($F_{[3,116]} = 0.7$, $p = 0.600$), but there were differences in 2004, three years after treatment ($F_{[3,116]} = 9.1$, $p < 0.001$). The thin-burn plots were significantly more unique than plots in all other treatments, whereas the thin-only plots were significantly more unique than those in the control. Both exotic and native species richness were strongly correlated with plot uniqueness in all years (all Pearson correlations >0.7; all p values < 0.001).

Differential responses among treatments were corroborated by ISA. Of the 219 species identified in the study, 78 were significant indicators of at least one treatment in at least one post-treatment sample year. Combining the results from both scales (1 and 1,000 m^2), 15 unique species were indicators of the burn only, 23 of the thin only, and 42 of the thin-burn when each treatment was compared with the control. Conversely, the control had 21, 3, and 13 unique indicator species when compared with the burn-only, thin-only, and thin-burn, respectively.

Burn-Only versus Control Indicators

ISA contrasting the burn-only and control treatments revealed only one species as indicative of the burn-only in 2002, the first year following treatment. However, the number of indicator species increased with each subsequent year to a total of 13 in 2004 (Tables 1 & 2). By 2004, the majority of indicator species in the burn-only consisted of uncommon and occasional species. Several native forbs (*Chamerion angustifolium*, *Epilobium brachycarpum*, *E. glaberrimum*, and *Claytonia perfoliata*) were indicative of the burn-only by 2004. Four short-lived exotic forbs (*Cirsium vulgare*, *Verbascum thapsus*, *Logfia arvensis*, and *Lactuca serriola*) were burn-only indicators in 2003 and 2004.

The control had 17 indicator species in 2002 when compared with the burn-only treatment, but the number of indicators decreased with each subsequent year to a low of seven species in 2004 (Tables 1 & 2). The majority of indicator species in the control were common or occasional. Only one uncommon species (*Astragalus miser*) remained indicative of the control in 2004. All the indicator species in the control were native and perennial, with the exception of the exotic annual graminoid *Bromus tectorum*, in 2003. Seedlings (<1 m) of the two most common tree species (*Pinus ponderosa* and *Pseudotsuga menziesii*) were indicative of the control with 1-m^2 cover (Table 1). In contrast, tree regeneration was not indicative of either the burn-only or control using 1,000-m^2 frequency (Table 2). Numerous shrub species were indicative of the control in 2002 (*Arctostaphylos uva-ursi*, *Mahonia*

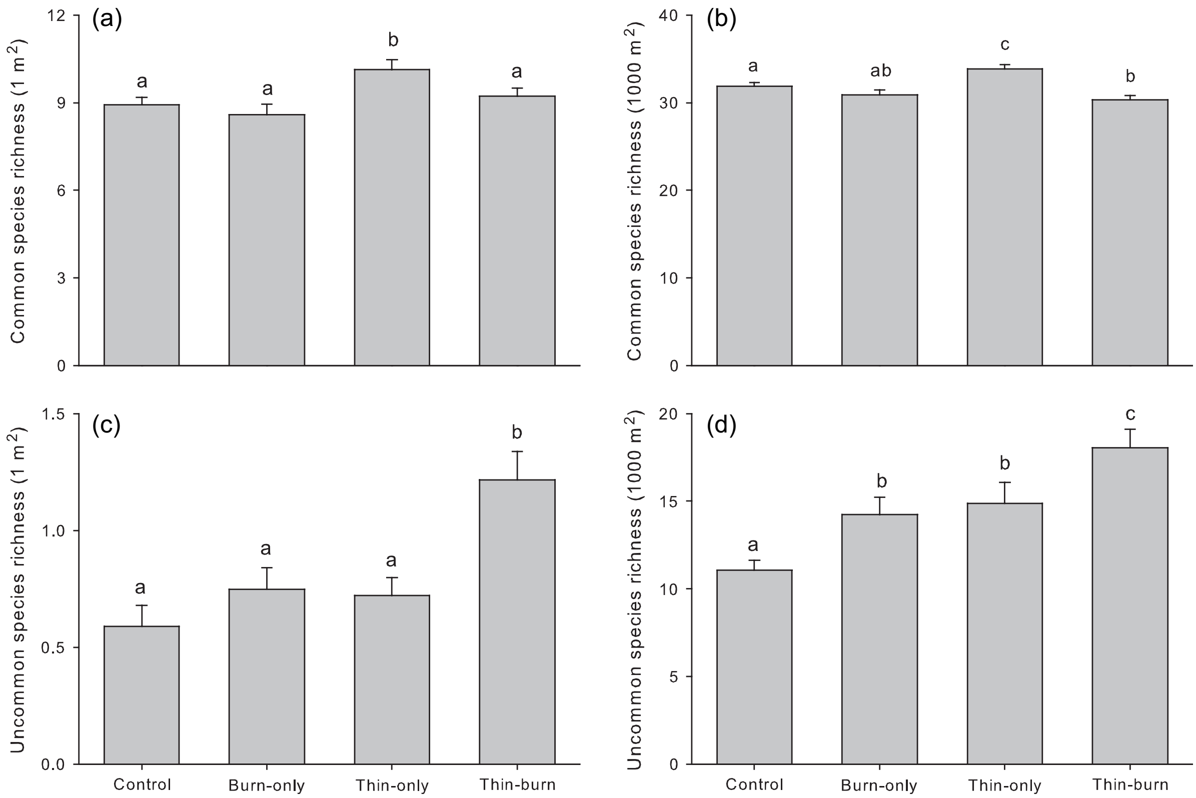

Figure 1. Treatment means (+SE) in 2004 for (a) common native species richness at the 1-m^2 scale, (b) common native species richness at the 1,000-m^2 scale, (c) uncommon native species richness at the 1-m^2 scale, and (d) uncommon native species richness at the 1,000-m^2 scale. Analysis of variance was used to test for differences among treatments. When significant differences ($p < 0.05$) were found, post hoc least significant difference tests were used to compare between treatments. Different letters above bars indicate significant differences.

repens, *Symphoricarpos albus*, *Ceanothus velutinus*, and *Juniperus scopulorum*), but few graminoid or shrub species were indicative of either the burn-only or the control by 2004.

Thin-Only versus Control Indicators

The number of species that ISA identified as indicative of the thin-only treatment as compared to the control increased from 7 in 2002 to 16 by 2004 (Tables 3 & 4), a pattern similar to that observed in the burn-only. Many common species were favored by the thin-only using 1-m^2 cover, whereas many uncommon species were representative of this treatment using 1,000-m^2 frequency. By 2004, two graminoid species were indicators of the thin-only, *Agrostis scabra* and *Calamagrostis rubescens*, as were two shrub species, *Vaccinium caespitosum* and *A. uva-ursi*. Several native perennial forbs (*Achillea millefolium*, *C. angustifolium*, *Solidago missouriensis*) and a few short-lived native forbs (*Cl. perfoliata* and *Gentianella amarella*) were indicative of the thin-only by 2004. Three exotic biennial forbs (*Ci. vulgare*, *Cynoglossum officinale*, and *V. thapsus*) were also representative of this treatment by 2004.

The control had few indicators in any year when compared with the thin-only (Tables 3 & 4). Only the native perennial forbs *Goodyera oblongifolia* and *Galium boreale* persisted as indicators of the control beyond 2002.

Thin-Burn versus Control Indicators

When we used ISA to contrast the thin-burn and the control, the number of indicator species in the thin-burn increased each year from 7 in 2002 to a maximum of 33 in 2004 (Tables 5 & 6). The preponderance of indicators of the thin-burn were uncommon species. Numerous short-lived native forbs were indicative of the thin-burn by 2004 (*Arabis holboellii*, *Cl. perfoliata*, *Collinsia parviflora*, *Montia linearis*, *Cryptantha affinis*, *Descurainia incana*, and *Gayophytum decipiens*). However, several short-lived exotic forbs were also indicative of the thin-burn treatment (*Carduus nutans*, *Ci. vulgare*, *Cy. officinale*, *Lo. arvensis*, *La. serriola*, and *V. thapsus*), including all the exotic species indicative of the thin-only and burn-only. Several native perennial graminoids (*Ag. scabra*, *Ca. rubescens*, *Carex rossii*, and *Koeleria macrantha*) were indicative of the thin-burn treatment by 2004, including both species that were indicative of the thin-only. Many native perennial forbs were significant representatives of the thin-burn, including *Ac. millefolium*, *C. angustifolium*, *E. glaberrimum*, *E. brachycarpum*, and *Prunella vulgaris*. At the 1,000-m^2 scale,

Table 1. ISA at the quadrat level (1 m^2) for the burn-only versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002 IV	2002 p	2003 IV	2003 p	2004 IV	2004 p
Burn-only							
Ceanothus velutinus	ONPS	—	NS	27	0.015*	—	NS
Chamerion angustifolium	UNPF	—	NS	63	0.001**	43	0.001**
Collinsia parviflora	CNAF	—	NS	70	0.001**	61	0.005**
Dodecatheon pulchellum	ONPF	—	NS	—	NS	32	0.036*
Logfia arvensis	UEAF	—	NS	23	0.005**	33	0.002**
Microseris nutans	ONPF	—	NS	—	NS	39	0.050*
Control							
Arctostaphylos uva-ursi	CNPS	67	0.003**	63	0.009**	—	NS
Arnica spp.	CNPF	72	0.005**	—	NS	—	NS
Calochortus spp.	CNPF	36	0.004**	—	NS	—	NS
Geranium viscosissimum	ONPF	29	0.006**	29	0.006**	28	0.011*
Luzula campestris	UNPG	—	NS	21	0.047*	—	NS
Mahonia repens	CNPS	54	0.041*	—	NS	—	NS
Pinus ponderosa	CNPT	57	0.013*	—	NS	57	0.005**
Poa secunda	UNPG	17	0.047*	—	NS	—	NS
Pseudotsuga menziesii	CNPT	64	0.007**	63	0.010*	64	0.009**
Silene menziesii	ONPF	29	0.025*	—	NS	—	NS
Symphoricarpos albus	CNPS	72	0.001**	—	NS	—	NS
Viola adunca	ONPF	21	0.042*	24	0.027*	27	0.010*

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. *P* values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$), *$p \leq 0.05$, **$p < 0.01$.

the seral tree species *Larix occidentalis* also became an indicator of the thin-burn in 2004 (Table 6).

All indicators of the control when compared to the thin-burn were native and perennial, and most were common species (Tables 5 & 6). *Pinus ponderosa* and *Ps. menziesii* were strong indicators of the control relative to the thin-burn at the 1-m^2 scale (Table 5). The number of indicators in the control declined with each year for 1-m^2 cover, but not for 1,000-m^2 frequency. Similar to the comparison with the thin only, *G. oblongifolia* was an indicator of the control in 2003 and 2004 when compared to the thin-burn at the 1,000-m^2 scale.

Discussion

Common and Uncommon Understory Species

Understory plant species responded differently to the restoration treatments evaluated in this study. Differences among treatments were generally similar at both spatial scales of analysis (1 and 1,000 m^2), so results are not discussed further relative to scale. Common species showed only modest responses to treatment, slightly increasing richness in the thin only and slightly decreasing richness in the thin-burn, relative to the control. Few common species were indicative of any treatment by the third post-treatment sampling year. The majority of species observed at our site were uncommon ("locally rare" species as in Murray & Lepschi 2004 and Lyons et al. 2005), a pattern previously reported for several other ecosystems (Halpern & Spies 1995; Stohlgren et al. 1998, 2005; Zavaleta & Hulvey 2004; Lyons et al. 2005). Although a few uncommon species were reduced by active treatments in our study, significant increases in uniqueness, uncommon native species richness, and numbers of uncommon indicators in treated areas suggest that restoration treatments (especially the thin-burn) benefited many uncommon native species.

Disturbances can increase species richness by maintaining competitively subordinate species in the community (Connell 1978; Sousa 1984). Many of the uncommon species that responded positively to active treatments in this study were short lived (annual or biennial). Positive responses by short-lived species to thinning (McConnell & Smith 1965), burning (Merrill et al. 1980; Laughlin et al. 2004), and combined thinning and burning treatments (Fulé et al. 2005) have been reported in other ponderosa pine forests. To establish, short-lived species may require disturbances such as fire that expose mineral soil and increase light availability (Steele & Geier-Hayes 1987). Short-lived species are largely absent from fire-excluded pine forests but present in forests that have burned frequently and therefore may represent more historical conditions (Laughlin et al. 2004; see Fulé et al. 2003 for fire histories).

Studies of uncommon plants indicate that these species may be more susceptible to disturbance than common species (Robinson & Quinn 1988; McIntyre & Lavorel 1994; Halpern et al. 2005) or, conversely, that they may depend on disturbance to remain in the community (Leach & Givnish 1996; Lesica & Cooper 1999; Quintana-Ascencio & Menges 2000). This inconsistency demonstrates the

Table 2. ISA at the plot level (1,000 m^2) for the burn-only versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002		2003		2004	
		IV	p	IV	p	IV	p
Burn-only							
Chamerion angustifolium	UNPF	—	NS	67	0.001**	69	0.001**
Cirsium vulgare	UEBF	—	NS	—	NS	32	0.026*
Claytonia perfoliata	UNAF	—	NS	20	0.020*	34	0.003**
Epilobium brachycarpum	UNAF	—	NS	42	0.002**	37	0.002**
Epilobium glaberrimum	UNPF	—	NS	40	0.001**	54	0.001**
Festuca idahoensis	CNPG	50	0.044*	—	NS	—	NS
Lactuca serriola	UEAF	—	NS	43	0.001**	40	0.001**
Logfia arvensis	UEAF	—	NS	64	0.001**	50	0.001**
Pseudognaphalium canescens	UNBF	—	NS	—	NS	20	0.026*
Solidago multiradiata	UNPF	—	NS	—	NS	39	0.028*
Verbascum thapsus	UEBF	—	NS	23	0.012*	33	0.002**
Control							
Achnatherum richardsonii	CNPG	50	0.010*	—	NS	—	NS
Antennaria racemosa	CNPF	—	NS	51	0.042*	—	NS
Astragalus miser	UNPF	17	0.044*	17	0.047*	17	0.042*
Bromus tectorum	UEAG	—	NS	20	0.050*	—	NS
Ceanothus velutinus	ONPS	27	0.009**	—	NS	—	NS
Juniperus scopulorum	ONPS	30	0.006**	35	0.008**	—	NS
Luzula campestris	UNPG	30	0.007**	45	0.011*	—	NS
Poa secunda	UNPG	20	0.049*	—	NS	—	NS
Shepherdia canadensis	CNPS	36	0.022*	—	NS	—	NS
Thalictrum occidentale	CNPF	—	NS	—	NS	43	0.024*
Valeriana dioica	ONPF	28	0.016*	31	0.050*	33	0.024*
Viola adunca	ONPF	—	NS	34	0.003**	34	0.003**

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. *p* values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$), *$p \leq 0.05$, **$p < 0.01$.

importance of evaluating the type of disturbance within the evolutionary environment of the ecosystem. Historically, many ponderosa pine forests were maintained in open conditions by surface fires occurring every 7–24 years (Arno et al. 1995; Everett et al. 2000; Fulé et al 2003; Hessburg & Agee 2003; Brown et al. 2004). Fire exclusion has been found to reduce understory richness and productivity in frequent-fire pine forests (Covington & Moore 1994; Fulé et al. 1997; Laughlin et al. 2004; Wienk et al. 2004) and, in other ecosystems, to reduce abundance of uncommon native species that are adapted to fire (Lesica 1999; Lesica & Cooper 1999; Quintana-Ascencio &

Table 3. ISA at the quadrat level (1 m^2) for the thin-only versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002		2003		2004	
		IV	p	IV	p	IV	p
Thin-only							
Achillea millefolium	CNPF	—	NS	—		56	0.048*
Arctostaphylos uva-ursi	CNPS	—	NS	62	0.026*	62	0.015*
Calamagrostis rubescens	CNPG	—	NS	57	0.039*	63	0.001**
Calochortus spp.	CNPF	—	NS	46	0.036*	—	NS
Dodecatheon pulchellum	ONPF	—	NS	29	0.025*	39	0.015*
Gentianella amarella	UNAF	—	NS	—	NS	23	0.010*
Poa pratensis	OEPG	—	NS	31	0.026*	—	NS
Solidago multiradiata	UNPF	—	NS	—	NS	21	0.032*
Control							
Danthonia unispicata	ONPG	18	0.017*	—	NS	—	NS
Galium boreale	ONPF	26	0.022*	26	0.023*	27	0.018*

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. *p* values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$)L, *$p \leq 0.05$, **$p < 0.01$.

Table 4. ISA at the plot level (1,000 m^2) for the thin-only versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002 IV	2002 p	2003 IV	2003 p	2004 IV	2004 p
Thin-only							
Agrostis scabra	UNPG	—	NS	42	0.002**	41	0.002**
Chamerion angustifolium	UNPF	—	NS	—	NS	41	0.004**
Cirsium vulgare	UEBF	20	0.025*	37	0.001**	38	0.005**
Claytonia perfoliata	UNAF	—	NS	—	NS	24	0.021*
Crataegus douglasii	UNPS	—	NS	17	0.046*	—	NS
Cynoglossum officinale	UEBF	37	0.001**	43	0.001**	43	0.001**
Epilobium brachycarpum	UNAF	—	NS	—	NS	38	0.003**
Festuca idahoensis	CNPG	55	0.011*	—	NS	—	NS
Gentianella amarella	UNAF	27	0.003**	—	NS	27	0.016*
Logfia arvensis	UEAF	—	NS	—	NS	23	0.010*
Poa pratensis	OEPG	45	0.027*	51	0.009**	—	NS
Potentilla glandulosa	ONPF	—	NS	31	0.041*	—	NS
Solidago missouriensis	UNPF	20	0.034*	24	0.024*	30	0.002**
Solidago multiradiata	UNPF	—	NS	33	0.022*	—	NS
Spiraea betulifolia	CNPS	55	0.045*	—	NS	—	NS
Tragopogon dubius	OEBF	—	NS	—	NS	33	0.047*
Vaccinium caespitosum	CNPS	—	NS	52	0.018*	52	0.026*
Verbascum thapsus	UEBF	—	NS	43	0.001**	50	0.001**
Control							
Goodyera oblongifolia	UNPF	17	0.049*	23	0.010*	33	0.002**

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. p values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$), *$p \leq 0.05$, **$p < 0.01$.

Menges 2000). Therefore, many uncommon native species in this study may have benefited from restoration treatments that reestablished conditions and processes that were critical components of their evolutionary history (Fiedler et al. 1992; White & Jentsch 2001).

Identifying species that are susceptible to damage or displacement is an important component of preserving understory diversity through restoration treatments (Allen et al. 2002). Some species, such as *Arctostaphylos uva-ursi*, responded differently to thinning versus burning treatments. Our technique of using pair-wise comparisons of active treatments with the control allowed us to identify both positive and negative treatment effects on individual species. Nearly all indicators of the control were native perennial species. However, the number of indicator species in the control tended to decline with each subsequent post-treatment year, suggesting that native perennial species quickly return to pre-treatment levels in the treatment areas. Also, no single species was consistently indicative of the control when compared to all three active treatments. Other investigators have also found that understory vegetation in ponderosa pine forests is highly resilient to disturbances associated with restoration treatments (Busse et al. 2000; Metlen et al. 2004; Fulé et al. 2005). Collectively, these results suggest that few understory species—common or uncommon—will be negatively impacted by restoration treatments in pine forests, especially if treated and untreated areas are intermixed across the landscape. Conversely and equally importantly, they also suggest that restoration treatments or similar disturbances may be necessary to retain many uncommon native species in the understory community, thus maximizing diversity. Increased understory diversity may provide greater resilience to future disturbances, as well as more diverse forage and habitat for associated biota.

Relationships to Broad Species Groupings

Many forb species were indicative of the active treatments, especially the thin-burn. Forbs comprised the majority of indicator species; they were also the most responsive life-form to restoration treatments in a companion study at our site (Metlen & Fiedler 2006). However, multiple individual species were indicative of every treatment, demonstrating that the response of individual species is more complex than suggested by examining the life-form as a group (Antos et al. 1983; Riegel et al. 1995). Graminoid richness, for example, can be promoted by disturbance (Griffis et al. 2001; Fynn et al. 2004) and variable overstory structures that provide an array of light conditions (Naumburg & DeWald 1999). Even though overall richness and cover of graminoids were not significantly different among treatments at our site (Metlen & Fiedler 2006), a few individual graminoid species (*Agrostis scabra*, *Calamagrostis rubescens*, *Carex rossii*, and *Koeleria macrantha*) showed persistent positive responses exclusively to thinning-related treatments, especially the thin-burn. Shrub abundance in ponderosa pine forests, in

Table 5. ISA at the quadrat level (1 m^2) for the thin-burn versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002 IV	2002 p	2003 IV	2003 p	2004 IV	2004 p
Thin-burn							
Achillea millefolium	CNPF	—	NS	59	0.022*	65	0.001**
Agrostis scabra	UNPG	—	NS	41	0.001**	36	0.005**
Arabis holboellii	UNBF	—	NS	—	NS	31	0.013*
Calamagrostis rubescens	CNPG	—	NS	—	NS	64	0.001**
Carex rossii	CNPG	—	NS	51	0.012*	67	0.001**
Ceanothus velutinus	ONPS	—	NS	31	0.005**	—	NS
Chamerion angustifolium	UNPF	—	NS	47	0.001**	47	0.001**
Cirsium vulgare	UEBF	—	NS	20	0.013*	72	0.001**
Claytonia perfoliata	UNAF	—	NS	—	NS	20	0.026*
Collinsia parviflora	CNAF	—	NS	65	0.001**	55	0.038*
Epilobium brachycarpum	UNAF	—	NS	—	NS	32	0.014*
Koeleria macrantha	ONPG	—	NS	40	0.010*	41	0.013*
Lactuca serriola	UEAF	—	NS	—	NS	17	0.050*
Logfia arvensis	UEAF	—	NS	27	0.006**	47	0.001**
Montia linearis	UNAF	—	NS	—	NS	22	0.034*
Myosotis stricta	UEAF	—	NS	17	0.050*	—	NS
Poa pratensis	OEPG	—	NS	43	0.002**	—	NS
Polygonum douglasii	UNAF	—	NS	38	0.006**	—	NS
Potentilla glandulosa	ONPF	—	NS	20	0.015*	—	NS
Pseudoroegneria spicata	UNPG	27	0.006**	—	NS	—	NS
Solidago multiradiata	UNPF	—	NS	—	NS	21	0.042*
Taraxacum officinale	CEPF	47	0.025*	50	0.017*	54	0.006**
Trifolium spp.	OEPF	—	NS	40	0.014*	39	0.006**
Verbascum thapsus	UEBF	27	0.007**	53	0.001**	47	0.001**
Control							
Antennaria racemosa	CNPF	42	0.029*	—	NS	—	NS
Arnica spp.	CNPF	63	0.033*	—	NS	—	NS
Balsamorhiza sagittata	ONPF	—	NS	22	0.032*	22	0.045*
Erythronium grandiflorum	CNPF	64	0.001**	—	NS	—	NS
Hieracium cynoglossoides	CNPF	42	0.046*	—	NS	42	0.037*
Pinus ponderosa	CNPT	76	0.001**	70	0.001**	69	0.001**
Pseudotsuga menziesii	CNPT	79	0.001**	74	0.001**	72	0.002**
Sedum stenopetalum	CNPF	42	0.025*	45	0.022*	—	NS
Symphoricarpos albus	CNPS	72	0.001**	—	NS	—	NS

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. *p* values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$), *$p \leq 0.05$, **$p < 0.01$.

contrast, has been shown to decline, at least initially, following fire due to burning of the aboveground vegetation (Ayers et al. 1999; Busse et al. 2000; MacKenzie et al. 2004). Several shrub species in our study were initially indicators of the control treatment when compared to the burn treatments; however, by 2004 the only evident shrub response was an increase of *A. uva-ursi* and *Vaccinium caespitosum* in the thin-only treatment.

Tree recruitment into the overstory was relatively uncommon in pine forests historically (Cooper 1960). However, tree regeneration has become an increasingly large part of the understory during the period of fire exclusion, with an apparent species shift toward *Pseudotsuga menziesii* in our region (Gruell et al. 1982; Arno et al. 1995; MacKenzie et al. 2004). The results of this study suggest that burning, probably due to its inherently variable nature, can reduce the cover of dominant tree regeneration without eliminating it. *Larix occidentalis*, a seral tree species that requires mineral soil or burned seedbeds to regenerate (Fiedler & Lloyd 1995), responded positively to the thin-burn treatment. This suggests that restoration treatments may promote subsequent regeneration of seral species, a critical objective of our restoration prescription. Long-term monitoring will be necessary to determine if this increase in seedlings leads to recruitment into larger size classes and if other seral tree species respond similarly.

Several studies have recently documented increasing numbers of exotic species following restoration treatments or other stand manipulations in ponderosa pine forests (e.g., Griffis et al. 2001; Wienk et al. 2004; Fulé et al. 2005). Metlen and Fiedler (2006) and Dodson and Fiedler (2006) have described similar trends at our study site as well. Exotic species were uncommon in this study prior to treatment application (total cover of 0.3%), and the

Table 6. ISA at the plot level (1,000 m^2) for the thin-burn versus the control in 2002, 2003, and 2004.[a]

	Functional Group[b]	2002 IV	2002 p	2003 IV	2003 p	2004 IV	2004 p
Thin-burn							
Agoseris glauca	ONPF	—	NS	34	0.022*	—	NS
Agrostis scabra	UNPG	—	NS	51	0.001**	61	0.001**
Carduus nutans	UEBF	20	0.025*	53	0.001**	57	0.001**
Chamerion angustifolium	UNPF	—	NS	68	0.001**	79	0.001**
Chenopodium capitatum	UNAF	—	NS	20	0.027*	—	NS
Cirsium arvense	UEPF	—	NS	30	0.004**	34	0.002**
Cirsium vulgare	UEBF	53	0.001**	70	0.001**	84	0.001**
Claytonia perfoliata	UNAF	—	NS	43	0.001**	54	0.001**
Cryptantha affinis	UNAF	—	NS	40	0.046*	49	0.005**
Cynoglossum officinale	UEBF	—	NS	23	0.005**	33	0.002**
Descurainia incana	UNAF	—	NS	—	NS	17	0.049*
Epilobium brachycarpum	UNAF	—	NS	55	0.001**	81	0.001**
Epilobium glaberrimum	UNPF	—	NS	47	0.001**	40	0.001**
Erigeron divergens	UNBF	—	NS	—	NS	30	0.005**
Gayophytum decipiens	UNAF	—	NS	—	NS	44	0.019*
Gentianella amarella	UNAF	23	0.012*	—	NS	34	0.003**
Lactuca serriola	UEAF	—	NS	27	0.011*	40	0.002**
Larix occidentalis	UNPT	—	NS	—		20	0.049*
Logfia arvensis	UEAF	—	NS	77	0.001**	73	0.001**
Poa palustris	UNPG	33	0.030*	—	NS	—	NS
Poa pratensis	OEPG	—	NS	53	0.006**	—	NS
Polygonum aviculare	UEAF	—	NS	17	0.045*	17	0.046*
Polygonum douglasii	UNAF	—	NS	43	0.017*	—	NS
Prunella vulgaris	UNPF	—	NS	20	0.023*	30	0.002**
Pseudognaphalium canescens	UNBF	—	NS	33	0.002**	43	0.001**
Rumex acetosella	UEPF	—	NS	20	0.048*	33	0.002**
Tragopogon dubius	OEBF	—	NS	—	NS	39	0.025*
Verbascum thapsus	UEBF	44	0.001**	73	0.001**	80	0.001**
Control							
Amelanchier alnifolia	CNPS	—	NS	55	0.043*	—	NS
Cypripedium montanum	UNPF	—	NS	25	0.031*	—	NS
Erythronium grandiflorum	CNPF	66	0.001**	—	NS	—	NS
Goodyera oblongifolia	UNPF	—	NS	23	0.008**	33	0.002**
Juniperus scopulorum	ONPS	—	NS	38	0.003**	31	0.013*
Pinus ponderosa	CNPT	58	0.003**	—	NS	—	NS
Sedum stenopetalum	CNPF	53	0.005**	51.2	0.051	55	0.006**

[a] IV range from 0 to 100, with 100 being a perfect indicator of a treatment. p values represent the probability of obtaining an IV as large or larger by chance, based on a Monte Carlo test with 1,000 randomizations.
[b] Functional groups are labeled as follows: C = common, O = occasional, or U = uncommon (see text); N = native or E = exotic; A = annual, B = biennial, or P = perennial; and G = graminoid, F = forb, S = shrub, or T = tree. NS = not a significant indicator ($p > 0.05$), *$p \leq 0.05$, **$p < 0.01$.

response of exotic species largely paralleled the response of uncommon native species. Both as groups and as individual species, exotic and uncommon native plants responded positively to all active treatments but especially strongly to the thin-burn. Interestingly, exotic indicator species of the thin-burn included all the exotic indicators of the thin-only and burn-only treatments. Disturbances may be essential for maintaining native biodiversity, while also facilitating invasion by exotic species (Hobbs & Huenneke 1992). Conversely, increasing native richness and functional group diversity may provide increased resistance to exotic invasion (Zavaleta & Hulvey 2004; Pokorny et al. 2005), although exotic richness and native richness are often positively correlated at larger spatial scales (Stohlgren et al. 1999). However, Fulé et al. (2005) found exotic cover to be higher 5 years following restoration treatments in Southwestern pine forests than it was in either the first or the second post-treatment year. Continued monitoring will be required at our site to determine longer-term successional trends and possible negative impacts of exotic invasion.

Conclusions

The majority of understory species at our site were resilient to restoration treatments, especially when given several growing seasons to respond. Conversely, many native species that were uncommon prior to treatment benefited from active restoration treatments, especially the thin-burn. The key to preserving or restoring biodiversity may be preventing dominance by a few species, either native or exotic (Connell 1978; Houlahan & Findlay 2004). Restoration treatments that included burning initially reduced the abundance of several common species at our site, thereby increasing evenness (Metlen & Fiedler 2006). This temporary decrease in competition, combined with resources made available by the restoration treatments, may have allowed additional species (uncommon natives and exotics) the opportunity to increase in abundance. However, exotic species may require specific management strategies to limit their establishment and spread following treatments.

Although some species were common indicators for multiple treatments, the magnitude of response differed among treatments, and each treatment had at least a few unique indicator species. This suggests that the maximum number of species and greatest biodiversity may be achieved by establishing a mosaic of treatments across the landscape. Such varied conditions may create the multiplicity of structures (Oliver et al. 1998; Naumburg & DeWald 1999; Allen et al. 2002) and heterogeneity of resources (Ricklefs 1977; Gundale et al. 2006) necessary for many different species to survive. Further monitoring will be necessary to determine long-term community trends at our site and whether patterns of understory response are similar in ponderosa pine forests elsewhere. However, restoration treatments show promise for favoring disturbance-dependent native species, particularly uncommon and short-lived species that may have declined in pine forests during a century of fire exclusion.

Implications for Practice

- Active restoration treatments (thin-only, thin-burn, and burn-only) have the potential to increase understory diversity by benefiting uncommon native species while having little effect on common species.
- Native and exotic species were similarly favored by restoration treatments, suggesting that specific management actions may be required to control exotics.
- Short-lived (annual and biennial) species were favored by treatments that included burning.
- Two native grasses (*Calamagrostis rubescens* and *Agrostis scabra*) were favored by treatments that included thinning.

Acknowledgments

We thank field crewmembers Seth Kahn, Matt Judd, Tucker Bishop, Robert Nelson, Holly Miller, Doug Bushey, Amber Harrison, and Shelly Saras. The manuscript benefited from review by James Riser, Marc Weber, and Amber Harrison. Vegetation specimens were verified by P. Lesica, Affiliated Faculty, Division of Biological Sciences, University of Montana. This research is contribution 119 of the National Fire Surrogates Project (FFS), funded by the U.S. Joint Fire Science Program.

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