Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem

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Abstract Monitoring of ecological restoration treatments often focuses on changes in community structure and function. We suggest that long-term changes in community composition also need to be explicitly considered when evaluating the success of restoration treatments. In 1992, we initiated an experiment in a ponderosa pine-bunchgrass ecosystem to evaluate responses to restoration treatments: (a) thinning the overstory vegetation ('thinning'), (b) thinning plus forest floor manipulation with periodic prescribed burning ('composite'), and (c) untreated 'control.' Treatments were further stratified by forest patch type: presettlement tree clumps (trees that established prior to the onset of fire exclusion in 1876), patches of retained postsettlement trees, patches where all postsettlement trees were removed, and remnant grass openings. Species richness did not differ among treatments for 10 years, but was highest in the composite treatment in 11th and 12th year after initial treatment. Community composition diverged among treatments 5 years after initial treatment, and compositional changes were greatest in the composite treatment. Species richness and composition differed among patch types prior to treatment. Remnant grass patches were the most diverse and presettlement patches were the least diverse. Following treatment, species richness in the postsettlement removed and retained patches, gradually approached levels found in remnant grass patches. Compositional differences among patch types changed a little by 2005. Species richness at the 2 m^2 scale increased only where the overstory was thinned and the understory was burned. However, these changes may not be detectable for many years, and can vary temporally in response to events such as severe droughts. Nonnative species establishment may be reduced by scheduling longer burn intervals or by refraining from burning where fuel loads are not hazardous, though these options may hinder goals of increasing diversity. Restoring species diversity and community composition continues to be more difficult than restoring ecosystem structure and function.

Key-words Long-term studies · Permutational MANOVA · *Pinus ponderosa* · Prescribed fire · Species richness · Thinning · Understory

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Introduction

Evaluations of management or ecological restoration treatments should consider changes in community structure, function, and composition, but these community attributes are not given equal weight in most assessments. Structural components such as tree density are the simplest to measure and interpret (e.g., Covington et al. 1997). Functional attributes such as net primary productivity are more difficult to measure, and therefore, correlated variables, such as peak herbaceous standing crop, are used instead (e.g., Tilman et al. 2002; Moore et al. 2006). Compositional metrics can be difficult to interpret given their multidimensional nature (Legendre and Legendre 1998; McCune and Grace 2002) and are rarely considered in the context of ecological restoration, in part because long-term data are necessary to detect compositional trends (Lindborg and Eriksson 2004). However, we suggest that composition should be explicitly considered because having restored ecosystem structure and functioning does not necessarily mean that composition has also been restored (Lockwood and Pimm 1999), and often there is not a direct relationship between species diversity, composition, and ecosystem functioning (Schwartz et al. 2000; Cortina et al. 2006). For example, an area with the desired plant cover and standing crop could be dominated by nonnative species, and therefore, be a failure with respect to plant community composition (e.g., Christian and Wilson 1999). Given that a community's composition is the net effect of births, deaths, immigrations, and emigrations of individuals of many species, composition is likely to respond more slowly than many structural and functional attributes. However, we often do not know the temporal or spatial scales, at which species richness and composition change given the differences in lifespan and dispersal capabilities among species.

Montane ponderosa pine forests in the southwestern United States have been fundamentally altered during the past century through the synergistic effects of livestock overgrazing, fire exclusion, overstory harvesting, and climatic events (Allen et al. 2002). Together, these have resulted in dramatic increase in the density of ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.), which in turn have led to reduced diversity and altered assemblages of herbaceous plants (Covington and Moore 1994;

Bakker and Moore 2007). Diversity theories predict that species richness will increase when a dominant species is removed from a community (Grime 1979; Tilman 1982; Keddy 2005). Thus, thinning dense stands of ponderosa pine should allow for the colonization and establishment of herbaceous understory species, leading to greater diversity in the understory. However, removing a dominant plant does not always lead to increased diversity (e.g., MacDougall and Turkington 2005; Keddy et al. 2006).

In 1992, a long-term restoration project was implemented in a ponderosa pine-bunchgrass ecosystem in northern Arizona. The project involved thinning the ponderosa pine overstory, and conducting repeated prescribed burns. The original goals of this project were to restore the pre-Euroamerican settlement forest structure (tree density, age and spatial structure; Mast et al. 1999) and to increase herbaceous understory standing crop. These original goals were successfully met (Covington et al. 1997; Moore et al. 2006), though restoration success was highly dependent on local microenvironment; that is, herbaceous standing crop beneath patches of trees was generally unresponsive to treatments, even though areas were burned periodically (Laughlin et al. 2006).

In this article, we evaluated herbaceous understory species richness and community composition in areas subject to no treatment ('control'), a one-time selective tree thinning in 1993 ('thinning'), and selective tree thinning followed by prescribed fires every 4 years ('composite'). We predicted that species richness would increase and community composition would diverge within treated areas relative to control areas. We also examined whether differences in richness and composition among patch types (i.e., forest patches ranging from full canopy to no canopy) persist following restoration, and whether response to restoration treatment differs among patch types. Remnant grass patches are productive and species rich, and provide the best example of reference conditions with respect to the understory vegetation in this system (Laughlin et al. 2006). We, therefore, used these patches as the reference to assess restoration success. We predicted that herbaceous vegetation in patches where small-diameter trees were removed, would become more similar to the remnant grass patches. The long-term duration of

this project (1992–2005) permitted us to evaluate the temporal dynamics of richness and composition. Finally, we tested whether individual plant species could be identified as indicators of restoration treatments or patch types.

Methods

Study system

This study was conducted at the Gus Pearson Natural Area (GPNA), located ~10 km northwest of Flagstaff, Arizona in the Fort Valley Experimental Forest in the Coconino National Forest. The ~4.3 ha study site ranges from 2,195 to 2,255 m in elevation, and has a flat to gently rolling topography. Soils are derived from Tertiary basalt flows and cinders, and are classified as a Brolliar stony clay loam and a complex of fine, smectitic Typic Argiborolls and Mollic Eutroboralfs (Kerns et al. 2003). The average annual temperature is 7.5°C. Average annual precipitation is ~570 mm, and follows a bimodal pattern with approximately half of the precipitation occurring as rain in July and August, and half as snow in the winter (NOAA 2005). Drought was common during this study. A severe drought occurred in 2002, when precipitation was 77% below normal at the study area (Moore et al. 2006).

The study area has been ungrazed by livestock for more than 50 years (Olberding 2000). A few trees were removed from GPNA in 1894, but it did not receive commercial harvest after that time (Avery et al. 1976). Although timber harvest was minimal, tree density in 1992 (prior to treatment) was >3,000 trees ha^{-1} (Covington et al. 1997). These high densities existed due to favorable climatic events for regeneration and the exclusion of fire from the study area since 1876 (Dietrich 1980).

Ponderosa pine is the only tree species on the study site. The understory is dominated by native perennial graminoid species, including *Festuca arizonica* Vasey (Arizona fescue), *Elymus elymoides* (Raf.) Swezey ssp. *elymoides* (bottlebrush squirrel-tail), *Muhlenbergia montana* (Nutt.) A. S. Hitchc. (mountain muhly), *Poa fendleriana* (Steud.) Vasey (muttongrass), and *Carex geophila* Mackenzie (White Mountain sedge). Dominant native perennial forb species include *Vicia spp.* (combination of

V. americana Muhl. Ex. Willd. and *V. pulchella* Kunth), *Astragalus rusbyi* Greene (Rusby's milk-vetch), *Lupinus argenteus* Pursh (silvery lupine), *Achillea millefolium* L. var. *occidentalis* DC. (western yarrow), and *Cirsium wheeleri* (Gray) Petrak (Wheeler's thistle). Six exotic species were recorded at the site during this study, with the two most common being the biennial forb *Verbascum thapsus* L. (common mullein) and the perennial graminoid *Poa pratensis* L. (Kentucky bluegrass).

Experimental design

Fifteen treatment plots, each 0.2–0.3 ha, were established in 1992. Each treatment plot was assigned to one of the three treatments (control, thinning, or composite) to yield five replicates per treatment. The five control plots were located nonrandomly on one side of the study site, while the thinning and composite treatment plots were assigned randomly. This design was necessary so that the fuel break created by the treated plots would protect the historical buildings of the adjacent Fort Valley Experimental Station. The control plots are located at the same elevation, and have similar slopes, aspects, and soil types as the treatment plots. Moreover, total herbaceous standing crop was the same in control and treatment plots prior to treatment (Moore et al. 2006). Therefore, we believe that all plots possessed the same environmental potential at the beginning of the experiment. Detailed accounts of the experimental design, thinning and prescribed burn characteristics, treatment protocol, and effects on other ecosystem components are available in Covington et al. (1997) and subsequent articles (Feeney et al. 1998; Kolb et al. 1998; Kaye and Hart 1998; Mast et al. 1999; Skov et al. 2004; Boyle et al. 2005; Moore et al. 2006). Here, we briefly summarize the key aspects relevant to this study.

In 1992, a 2.4 m tall electrified fence was constructed to exclude ungulates from the experiment to control for grazing effects. Fuhlendorf and Engle (2004) demonstrated that grazing and fire interact in grassland systems, but, since our system did not evolve in an environment of intense grazing (Milchunas 2006), we focused on the possible interactions between fire and overstory thinning. We acknowledge that epizoochory (seed dispersal via animals)

may be hampered due to this design. The thinning and composite treatments were thinned from below (i.e., small trees from lower crown classes were removed; Smith et al. 1997) in the fall of 1993, retaining all presettlement trees (defined as trees established prior to 1876 and/or trees >37.5 cm diameter at breast height (dbh); Fulé et al. 1997) and three postsettlement trees to replace each dead presettlement tree or stump (Fulé et al. 1997; Mast et al. 1999). Thinning resulted in the removal of ∼2,200 trees ha^{-1} per hectare of the >3,000 trees per hectare that were present before the study began in 1992 (Covington et al. 1997), including most of the postsettlement trees. All slash was removed by hand, while all extant presettlement coarse woody debris were retained (Covington et al. 1997).

In the composite treatment, the forest floor was manipulated by raking the litter layer aside, removing accumulated forest floor duff, and returning the current (∼3 years) litter layer to the site. To simulate the presettlement condition of a grass-dominated understory, which carried frequent fire, approximately 670 kg ha^{-1} of herbaceous vegetation from Hart Prairie (4.8 km to the north) was harvested in late September 1994, and scattered across the plots (Covington et al. 1997); this supplementation occurred only once. The composite treatment received an initial prescribed burn in 1994, and additional prescribed burns in 1998 and 2002. All burns were conducted in October, after data collection was completed for that year.

The area within each treatment plot was stratified into four patch types: 'presettlement,' 'postsettlement removed,' 'postsettlement retained,' and 'remnant grass' (Laughlin et al. 2006). Presettlement patches consisted of groups of two or more large presettlement trees (mostly > 30 cm at dbh). Postsettlement retained patches consisted of groups of small-diameter (<30 cm dbh) postsettlement trees, thereby representing dense forest habitat. Postsettlement removed patches consisted of areas where all postsettlement trees were thinned and removed from the site, thereby creating openings in the canopy. Remnant grass patches were small open areas consisting of native grasses and forbs. Since the remnant grass patches represent diverse and productive stands of native herbaceous vegetation (Laughlin et al. 2006), they served as the reference community against which changes in other patch types were assessed.

A 2.5 m radius circular subplot was established within each patch type in each treatment plot. In total, 55 subplots were established (four per treatment plot in the thinning treatment ($n = 20$) and composite treatment ($n = 20$), and three per treatment plot in the control ($n = 15$, because controls did not contain postsettlement removed patches)). Subplots represent the range of conditions (i.e., open to full canopy) sampled within treatment plots. For this study, vegetation data were examined at the treatment-level ($n = 15$ plots) and at the patch-level within treated areas ($n = 40$ subplots).

Complete species lists were collected in two 1 m^2 (0.5 × 2 m) quadrats per circular subplot. For each subplot, therefore, species were noted as being present on 0, 1, or 2 quadrats. Quadrats were arranged in a wagon-wheel configuration around the circular subplot center, and were rotated each year to avoid harvesting vegetation repeatedly from the same area for another study (Moore et al. 2006). Data were collected in September for the following years: 1992 (pretreatment), 1994 (after thinning, but before the first burn), 1995, 1996, 1998, 1999, 2002, 2004, and 2005.

Statistical analyses

Separate analyses were conducted for treatment- and patch-level effects. Treatment-level effects were analyzed with plots nested within treatments as the error term. Patch-level effects were analyzed with a model that included treatment, plot nested within treatment, patch, and treatment × patch terms; the residuals formed the error term for tests of patch and treatment × patch effects. For each type of analysis, data from 1992 were analyzed to identify pretreatment differences, and data from 1994–2005 were analyzed using a repeated measures analysis to identify overall differences after treatment. Significant posttreatment differences were followed by analyses of individual years to identify particular years when effects differed. All tests were conducted with α = 0.05.

The analyses included four components: species richness (total and native), community composition, net change in composition from 1992 to 2005, and Indicator Species Analysis. Total species richness per subplot was calculated as the total number of species

in the 2 m^2 quadrats. Native species richness was calculated as the number of species native to North America, as defined by USDA NRCS (2006), per 2 m^2 quadrats. Analyses of treatment and patch effects on species richness were conducted using repeated measures MANOVA with SAS JMP-IN software (version 5.1.2; SAS 2004).

We analyzed compositional differences with a distance-based permutational multivariate analysis of variance (DISTLM; Anderson 2001; McArdle and Anderson 2001). This technique is a straightforward extension of MANOVA that is applicable to multivariate response data; the test statistic is a pseudo-F statistic. We used Bray-Curtis dissimilarity as our distance measure (Faith et al. 1987), and 9,999 permutations to calculate the significance of the pseudo-F statistic. The net change in composition from 1992 to 2005 was assessed by calculating the Bray-Curtis distance measure for each subplot based on its composition in these years. This distance ranges from 0 (completely identical) to 1 (completely dissimilar). As recommended by McCune and Grace (2002), analyses of community composition were restricted to species that occurred on at least 5% of subplots (out of all 495 subplot-year combinations).

Indicator Species Analysis (ISA; Dufrêne and Legendre 1997) was used to identify species associated with the observed differences among treatments and patches. Since we were trying to explain these differences, we only conducted ISAs for years, in which composition differed among treatments (1998–2005; see *Results*, below). Further, since the results of an ISA depend on how data are grouped (Dufrêne and Legendre 1997), we used the results of the compositional analysis (see *Results*, below) to identify the comparisons of interest. Two biologically motivated comparisons were made among treatments: (1) control versus treated (a combination of composite and thinning treatments) to examine species responses to thinning, and (2) composite versus unburned (a combination of control and thinning treatments) to examine species responses to burning. Patch effects were compared between presettlement, postsettlement (a combination of retained and removed), and remnant grass patches. If a species was an indicator in both comparisons for treatment effect, it was identified as an indicator of the group in which its Indicator Value (IV) was greatest. However, a given species could be an indicator of treatment and of patch effects, as these

effects are not hierarchical. An IV was calculated independently for each species as the product of its relative abundance and frequency, and the significance of the calculated IV was assessed using 999 Monte Carlo randomizations. ISAs were conducted using code written for R (v. 2.2.1; code available from J.D. Bakker). A separate ISA was conducted for each year, and results were combined using meta-analytical techniques (Bakker 2005). For a given species in a given group, the IVs from every year, that it occurred, were averaged to yield a mean IV, and the associated P-values were combined using a weighted Z-transform (Whitlock 2005). Combining results from multiple years reduces the likelihood of spurious results (Bakker 2005). We required that significant indicators have a mean IV ≥25 and combined P-value < 0.05 (Dufrêne and Legendre 1997).

Results

Eighty-nine species were detected in the study area from 1992 to 2005. Thirty-nine species occurred on at least 5% of the subplot-year combinations, and were included in analyses of community composition.

Treatment effects

Total species richness (per 2 m^2) was similar among treatments in 1992 before treatment ($F_{2,12} = 1.00$, $P = 0.394$), but not after treatment (repeated measures analysis of 1994–2005 data: $F_{2,12} = 5.19$, $P = 0.024$). Richness remained similar among treatments until 11 and 12 years after treatment (2004, 2005), when more species occurred in the composite than in control or thinning treatments (Fig. 1). Similar results were obtained when native species richness was analyzed separately (data not shown).

Species richness was temporally variable (Fig. 1). Mean species richness within plots was not correlated with interannual precipitation ($P > 0.05$). However, the severe drought of 2002 coincided with a noticeable reduction in species richness across all treatments (Fig. 1).

Plant community composition was similar among treatments in 1992 before treatment, but not after treatment (Table 1). Composition first diverged among treatments in 1998, 5 years after the overstory
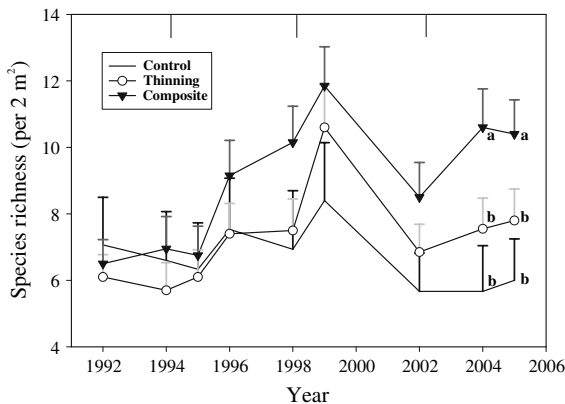
Fig. 1 Total species richness (+1 standard error) at the 2 m² subplot scale ($n = 55$) remained similar among treatments until 11 and 12 years after treatment (2004, 2005). Within each year, treatments that differ from one another are indicated with different lowercase letters; letters are not shown if treatments did not differ. Analyses of native species richness yielded similar results. Overstory thinning occurred in 1993, and prescribed fires (denoted by vertical lines at top) occurred after sampling in 1994, 1998, and 2002

was thinned, but were not consistent through time. In 1998, 1999, 2004, and 2005, composition differed between the composite and control treatments, but composition in the composite treatment was similar to the control during the severe drought of 2002. In 1999 and 2002, composition differed among the thinning and control treatments, while composition differed among the thinning and composite treatments in 2002 and 2004.

The net change in composition from 1992 to 2005 was significantly greater ($F_{2,12} = 3.89$, $P = 0.047$) for

the composite treatment (mean Bray-Curtis distance = 0.59) than the control treatment (mean Bray-Curtis distance = 0.36). The thinning treatment had a mean Bray-Curtis distance of 0.44, which did not differ from either the composite treatment or the control.

No species were indicators of the control treatment (Table 2). Two C_3 grasses (*Elymus elymoides*, *Festuca arizonica*) and two legumes (*Astragalus rusbyi*, *Vicia* spp.) were indicators of treated plots (combination of composite and thinned treatments). *Lupinus argenteus*, a legume, and *Verbascum thapsus*, a nonnative forb, were indicators of the burned composite treatment. One C_4 grass, *Muhlenbergia montana*, was an indicator of unburned plots (combination of control and thinning treatments).

Patch effects

Before treatment, total species richness (per 2 m²) was greatest in remnant grass patches and lowest in presettlement patches ($F_{3,24} = 121.50$, $P < 0.001$; Fig. 2). Following treatment, richness continued to differ among patch types (repeated measures analysis of 1994–2005 data: $F_{3,24} = 33.70$, $P < 0.001$) but the treatment × patch interaction was not significant ($F_{3,24} = 0.36$, $P = 0.785$), indicating that patch types in the composite and thinning treatments responded similarly. Presettlement patches always had the lowest richness, and remnant grass patches generally had the highest richness, though richness increased in

	Year	Pseudo-$F_{2,12}$	P	Differences among treatments		
				Control	Thinning	Composite
Table 1 Restoration treatments did not affect community composition until 5 years after initial treatment	Pre-treatment					
	1992	0.72	0.720			
	Posttreatment					
	1994–2005*	1.73	0.049			
	1994	1.09	0.396			
Within each year, treatments that differed from one another are indicated with different lowercase letters; letters are not shown if treatments did not differ	1995	1.44	0.141			
	1996	1.42	0.147			
	1998	1.83	0.025	a	ab	b
	1999	2.34	0.009	a	b	b
	2002	1.84	0.008	a	b	a
	2004	2.46	0.001	a	a	b
*Repeated measures analysis	2005	1.90	0.026	a	ab	b

Table 2 Indicator species associated with treatments from 1998 to 2005

Treatment	Species	Mean IV	Combined P	Life form	Postfire regeneration strategy[c]	Nativity
Comparison 1: control versus treated						
Control	No indicator species	–	–			
Treated[a]	Astragalus rusbyi	25.0	<0.001	Herbaceous legume	Sprouter	Native[d]
	Elymus elymoides	54.1	<0.001	C_3 grass	Sprouter, seeder	Native
	Festuca arizonica	31.3	0.041	C_3 bunchgrass	Sprouter	Native
	Vicia spp.	26.7	0.001	Herbaceous legume	Sprouter	Native
Comparison 2: composite (burned) versus unburned						
Composite	Lupinus argenteus	30.3	<0.001	Herbaceous legume	Sprouter, seeder	Native
	Verbascum thapsus	25.2	<0.001	Biennial forb	Seeder	Nonnative
Unburned[b]	Muhlenbergia montana	34.0	0.007	C_4 bunchgrass	Sprouter	Native

A separate Indicator Species Analysis was conducted for each year using all subplots ($n = 55$), and results were combined using meta-analytic techniques

[a] Combination of composite and thinning treatments

[b] Combination of control and thinning treatments

[c] Species are classified as either a sprouter, a seeder, or both (Whelan 1995), based on published and unpublished sources of information summarized in the U.S. Department of Agriculture Forest Service's Fire Effects Information System (http://www.fs.fed.us/database/feis/)

[d] Astragalus rusbyi has been listed as a sensitive species on the Coconino National Forest due to its limited range
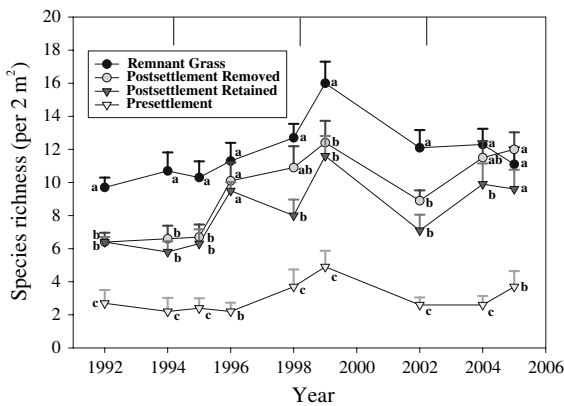

Fig. 2 Total species richness (+1 standard error) at the 2 m^2 subplot scale ($n = 40$) differed among patch types within treated areas at the beginning of the study, but richness in postsettlement removed and postsettlement retained patches increased to similar levels detected in the remnant grass patches over time. Within each year, different letters indicate differences among patch types. Analyses of native species richness yielded similar results. Overstory thinning occurred in 1993, and prescribed fires (denoted by vertical lines at top) occurred after sampling in 1994, 1998, and 2002

both types of postsettlement patches. In particular, richness was similar between remnant grass and postsettlement removed patches in 1996, 1998, 2004, and 2005, and between remnant grass and postsettlement retained patches in 1996 and 2005. Similar results were obtained when we analyzed native species richness exclusively (data not shown).

Community composition differed among patch types prior to treatment. Remnant grass and presettlement patches were distinct from one another and from both types of postsettlement patches (Table 3). These inter-patch differences persisted after treatment, and did not differ among thinning and composite treatments. Interannual differences were minimal, though the composition of the postsettlement removed and postsettlement retained patches diverged in 2002 and 2005.

The net change in composition from 1992 to 2005 differed among patch types ($F_{3,24} = 5.96$, $P = 0.004$). The magnitude of change was greatest for presettlement patches (mean Bray-Curtis distance = 0.73) and lowest for remnant grass patches (mean Bray-Curtis distance = 0.32). Postsettlement removed and postsettlement retained patches had intermediate mean Bray-Curtis distances (removed: 0.56; retained: 0.44), and did not differ from other patch types. The treatment × patch interaction was not significant ($F_{3,24} = 0.36$, $P = 0.780$).

Table 3 Community composition remained distinct among patch types throughout the experiment

Within each year, treatments that differed from one another are indicated with different lowercase letters. The treatment × patch interaction was not significant (repeated measures analysis of 1994–2005 data: pseudo-$F_{3,24} = 0.63$, $P = 0.917$)

*Repeated measures analysis

Year	Pseudo-$F_{3,24}$	P	Differences among patch types			
			Presettlement	Postsettlement retained	Postsettlement removed	Remnant grass
Pretreatment						
1992	5.91	<0.001	a	b	b	c
Posttreatment						
1994–2005*	6.17	<0.001	a	b	b	c
1994	5.66	<0.001	a	b	b	c
1995	4.37	<0.001	a	b	b	c
1996	4.19	<0.001	a	b	b	c
1998	3.85	<0.001	a	b	b	c
1999	4.38	<0.001	a	b	b	c
2002	3.56	<0.001	a	b	c	d
2004	3.47	<0.001	a	bc	b	c
2005	4.24	<0.001	a	b	c	d

No species were indicators of the presettlement patch type, and *Elymus elymoides* was the only indicator of postsettlement (combination of postsettlement retained and postsettlement removed) patch types (Table 4). Nine species were indicators of remnant grass patches, including three C_3 graminoids (*Carex geophila*, *Festuca arizonica*, *Poa fendleriana*), one C_4 graminoid (*Muhlenbergia montana*), three legumes (*Astragalus rusbyi*, *Lupinus argenteus*, *Vicia* spp.), and two non-leguminous perennial forbs (*Achillea millefolium*, *Cirsium wheeleri*).

Discussion

Treatment effects

Increased pine densities and cessation of a frequent-fire regime are thought to have reduced species richness and altered the composition of understory plant communities in ponderosa pine forests (Covington and Moore 1994; Allen et al. 2002). This study supports these assumptions, since reducing pine densities and applying prescribed fire increased native species richness and altered community

Table 4 Indicator species associated with patch types from 1992 to 2005

A separate Indicator Species Analysis was conducted for each year using subplots from the thinning and composite treatments ($n = 40$), and results were combined using meta-analytic techniques. All species in this table are native

[a] Combination of postsettlement retained and postsettlement removed patch types

Patch type	Species	Mean IV	Combined P	Life form
Presettlement	No indicator species	–	–	
Postsettlement[a]	*Elymus elymoides*	40.9	<0.001	C_3 grass
Remnant Grass	*Achillea millefolium*	36.0	<0.001	Perennial forb
	Astragalus rusbyi	26.8	0.013	Herbaceous legume
	Carex geophila	48.0	<0.001	C_3 sedge
	Cirsium wheeleri	29.7	<0.001	Perennial forb
	Festuca arizonica	66.0	<0.001	C_3 bunchgrass
	Lupinus argenteus	64.5	<0.001	Herbaceous legume
	Muhlenbergia montana	63.8	<0.001	C_4 bunchgrass
	Poa fendleriana	33.7	<0.001	C_3 bunchgrass
	Vicia spp.	63.7	<0.001	Herbaceous legume

composition. However, these changes may occur slowly, and may not be detectable for many years. Thus, long-term monitoring is essential when evaluating the success of restoration treatments.

We expected to observe increases in species richness in both thinning and composite treatments. Pine trees intercept light (Naumburg and DeWald 1999) and precipitation (McLaughlin 1978), produce abundant needle-fall, and compete for soil nutrients near the soil surface. All these mechanisms can impact herbaceous productivity and species composition due to interspecific differences in response to resource availability (Riegel et al. 1995). In this experiment, thinning alone did not increase species richness, whereas thinning plus repeated burning increased species richness 11 years after initial treatment (Fig. 1). Repeated disturbances, such as prescribed fire, likely reduced competitive interactions among dominant species (Huston 1979), and created sites for seedling establishment (Grime 1977), thereby promoting species coexistence at small spatial scales.

While restoration treatments did not result in increased richness until more than a decade after initial treatment, herbaceous standing crop increased rapidly (Moore et al. 2006). Species richness exhibits a quadratic relationship with total standing crop within a given year (D.C. Laughlin and M.M. Moore, unpublished data), such that species richness is maximal at approximately 100 g m^{-2}. The 'hump-shaped' relationship between richness and standing crop suggests that richness is regulated at the higher levels of herbaceous production due to competitive exclusion and recruitment limitation (Grime 1979; Keddy 2005). This suggests that management goals of increasing productivity and diversity at relatively small scales cannot be achieved simultaneously if herbaceous productivity levels are too high.

We did not directly study colonizing mechanisms that might have led to increased species richness. However, 15 species that were present in 2004 and 2005 were not present at the beginning of the study, suggesting that they colonized from the soil seed bank or from off-site population sources. Observed increases in species richness were not entirely due to new colonists, but were likely also caused by dispersal from adjacent remnant grass patches. Approximately half of these new colonists were annuals, which is consistent with research suggesting

that reintroducing fire into these systems increases the richness and abundance of native annuals (Laughlin et al. 2004, 2005, 2006; Fulé et al. 2005; Moore et al. 2006). The exclusion of ungulates from the study area may have hampered dispersal of off-site species dependent on epizoochory.

Long-term experiments allow for comparisons of treatments among climatically variable years (Tilman 1989). The severe drought of 2002 (77% below normal precipitation) coincided with reduced species richness among all treatments. Water is a major limiting resource in semi-arid systems (e.g., Breshears et al. 2005), and the lack of water in 2002 likely contributed to the temporary loss of species in the community. However, richness began to increase again after the severe drought. Interestingly, the severe drought apparently nullified the compositional differences between the composite and control treatments, yet the thinning treatment remained distinct. This further demonstrates the need for long-term evaluations of treatment effects in order to understand the background variation caused by interannual climatic variability.

The treatments significantly altered community composition after 5 years. Two native cool-season grasses, *Festuca arizonica* and *Elymus elymoides*, were indicators of treated rather than control areas, suggesting that thinning the overstory canopy promoted their establishment (Naumburg and DeWald 1999; Naumburg et al. 2001). However, a dominant warm-season native bunchgrass, *Muhlenbergia montana*, was negatively affected by repeated prescribed fires that occurred in the fall, which is consistent with published reports for *M. montana* (Gaines et al. 1958), but counter to the recent hypothesis that increased fire frequency is linked to the expansion of C_4 graminoids (Keeley and Rundel 2005). This effect may relate to the season of burn; *M. montana* would likely be favored by burns that occur before it starts investing energy in vegetative growth. Vose and White (1991) concluded that the net effect of a prescribed fire on *M. montana* was negative due to high mortality and low seedling recruitment. Fire-induced mortality might be directly due to the buildup of dry flammable material at the base of *M. montana* plants (Vose and White 1991). Two native leguminous forbs, *Vicia* spp. and the endemic *Astragalus rusbyi*, were also more frequent and abundant in both treatments. These species can

increase the rate of nitrogen fixation, a critical ecosystem function in this nitrogen-limited ecosystem. Notably, *A. rusbyi* has been listed as a sensitive species by the U.S. Forest Service due to its limited range, and its positive response to restoration treatments is encouraging.

Compositional changes may not be desirable if they involve increases in nonnative species. Relatively few nonnative species were present in our study area, however, likely because the site has been little disturbed for nearly a century (Korb et al. 2005). *Verbascum thapsus*, a nonnative biennial, was an indicator of the composite treatment, consistent with the findings of Korb et al. (2005). Disturbance-adapted nonnative species can increase after wildfires (Crawford et al. 2001; Griffis et al. 2001), and prescribed fires (Wolfson 2005) in southwestern ponderosa pine forests and in other regions (Dodson and Fiedler 2006; Keeley 2006). No nonnative species were indicators of the thinning treatment. Therefore, scheduling longer burn intervals (see also Keeley (2006) and Fulé and Laughlin (2007)), or refraining from burning in thinned forests, especially where fuel loads are not considered hazardous, may reduce nonnative species establishment. However, this option must be weighed against the potential loss of frequent fire-dependent species.

These results illustrate the importance of long-term monitoring, but care should be taken when extrapolating beyond the scale of this study. The treatments implemented in 1993 are not operationally feasible at landscape scales due to logistical constraints, though traditional thinning and burning techniques are occurring at landscape scales. Furthermore, this experiment was conducted at a site with uniform soils, and response variables were analyzed at a single spatial scale. More research is needed to assess the generality of these results on other soil types and at other spatial scales.

Patch effects

Response to restoration treatments differed among forest patch types. The remnant grass patches are viewed as being the most similar to pre-Euroamerican settlement reference conditions (Laughlin et al. 2006), and therefore, served as the target against which changes in other patch types were compared.

Species richness in postsettlement removed and postsettlement retained patches increased to levels found in remnant grass patches toward the end of the study (Fig. 2). Species richness did not increase in presettlement tree patches where large trees suppress understory vegetation. These results highlight the importance of creating sufficiently large gaps in the canopy within treatments because a few retained trees can have a disproportionately large effect on understory responses (Moore and Deiter 1992).

Postsettlement removed and postsettlement retained patches were disturbed by harvesting activities and by prescribed fires in the composite treatment. Composition of these patches remained distinct from that of the remnant grass patches (Table 3), suggesting that removing some or all of the small diameter trees, and applying prescribed fire, were not enough to restore community composition in this time frame. *Elymus elymoides*, the only indicator of postsettlement patches, colonizes disturbed sites rapidly (Jones 1998), likely due to its highly mobile wind-dispersed caryopses, and high germination rates. *E. elymoides* may be an important facilitator of postfire vegetation dynamics.

While most indicators of remnant grass patches (Table 4) were already abundant in these patches in 1992 and maintained their abundance through 2005, two species (*Astragalus rusbyi* and *Poa fendleriana*) increased in frequency and abundance from 1992 to 2005. However, no indicators of remnant grass patches have become very abundant in the postsettlement removed and postsettlement retained patches. Further research is needed to determine whether these species are dispersal or microsite limited, and the degree to which competition with neighboring vegetation affects their spread. Diversity and composition of postsettlement removed and retained patches might be enhanced by outplanting nursery-grown plugs or by seeding native species (Springer and Laughlin 2004), though seeding in semi-arid forests is often not very successful.

Conclusion

Restoring the composition of a plant community is a difficult task compared to restoring ecological structure or function (Lockwood and Pimm 1999). The results from this study suggest that restoration

treatments can significantly increase species richness, and alter understory plant community composition in a pine-bunchgrass ecosystem. However, these changes may not be detectable for many years, and can vary temporally in response to events such as severe droughts. Thus, the value of long-term studies increases with each year of monitoring. Though diversity increased in patches where small trees were removed, composition continued to differ among remnant grass patches and other patch types, suggesting that composition changes slowly in this system. While nonnative species were minimal in the study area, one such species was abundant where prescribed fires occurred. Scheduling longer intervals between prescribed burns or refraining from burning in thinned forests, especially where fuel loads are not hazardous, may reduce invasion by nonnative species, but may hinder goals of increasing diversity. In the ponderosa pine-bunchgrass ecosystems of the southwestern United States, land managers may expect rapid responses in herbaceous understory production following treatment, but should not expect rapid responses in diversity and composition.

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