Monitoring an Arizona Ponderosa Pine Restoration: Sampling Efficiency and Multivariate Analysis of Understory Vegetation

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Abstract

As monitoring plans for the restoration of *Pinus ponderosa* forests in the southwestern United States evolve toward examining multifactor ecosystem responses to ecological restoration, designing efficient sampling procedures for understory vegetation will become increasingly important. The objective of this study was to compare understory composition and diversity among thin/burn and control treatments in a *P. ponderosa* restoration, while simultaneously examining the effects of sampling design and multivariate analyses on which conclusions were based. Using multi-response permutation procedures (MRPP), we tested the null hypothesis of no difference in understory species composition among treatments using different data matrices (e.g., frequency and cover) for two different sampling methods. Treatment differences were subtle and were detected by an intensive 50, 1-m^2 subplot sampling method for all data matrices but were not detected by a less intensive point-intercept sampling method for any matrix. Sampling methods examined in this study controlled results of multivariate analyses more than the data matrices used to summarize data generated by a sampling method. We partitioned data into plant life form and native/exotic species categories for MRPP, and this partitioning isolated plant groups most responsible for treatment differences. We also examined the effects of number of 1-m^2 subplots sampled on mean-species-richness/m^2 estimates and found that estimates based on 10 subplots and based on 50 subplots were highly correlated ($r = 0.99$). Species–area curves indicated that the 50, 1-m^2 subplot sampling method detected the common species of sites but failed to detect the majority of rare species. Additional sampling-design studies are needed to develop single sampling designs that produce multifactor data on plant composition, diversity, and spatial patterns amenable to multivariate analyses as part of monitoring plans of vegetation responses to ecological restoration.

Key words: **diversity, forest, ground flora, indicator species analysis, multi-response permutation procedures, species richness, species–area curves.**

Introduction

Millions of hectares of contemporary *Pinus ponderosa* (ponderosa pine) forests in the southwestern United States exhibit higher tree densities, greater susceptibility to unnatural stand-replacing wildfires, and less understory cover than pre-settlement forests (Covington & Moore 1994*b*; Covington et al. 1994). These undesirable changes were facilitated by past overgrazing and disruptions of historic fire regimes through the 1900s (Weaver 1951; Cooper 1960; Covington & Moore 1994*a*). Restoring these degraded forests entails thinning post-settlement origin trees (age <120 years) and reinstating frequent, low-intensity fires historically characteristic of *P. ponderosa* forests (Covington et al. 1997; Allen et al. 2002). Numerous studies in *P. ponderosa* forests have examined relationships between forage production and overstory characteristics, thinning treatments, and prescribed fire (Moir 1966; McConnell & Smith 1970; Harris & Covington 1983; Oswald & Covington 1984; Tapia et al. 1990; Moore & Deiter 1992). These studies have reported declines in forage production with increasing overstory density and increases in forage production following thinning or burning.

With few exceptions, however, studies in *P. ponderosa* forests have not examined overall understory composition (species and relative abundance) and diversity changes following treatments. Armour et al. (1984) applied univariate statistics on a species-by-species basis to assess understory responses to burning, while Griffis et al. (2001) compared understory species richness among thin and burn treatments but did not include compositional data. Vose and White (1991) examined biomass responses of four species following prescribed burning, and White et al. (1991) studied the responses of four grass species to fire.

Clearly, more research is needed on understory compositional responses to restoration treatments in *P. ponderosa* forests, but there is little specific guidance available for designing efficient sampling plans for monitoring understory

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vegetation in ecological restoration experiments. A common conclusion of sampling-design studies is that sampling designs for ecological studies depend on the objectives of the study (Gauch 1982; Kenkel et al. 1989). However, single-vegetation sampling designs also are needed that have flexibility for meeting multifactor study objectives, including examining plant composition, diversity, and spatial patterns and maximizing the number of species detected. Obtaining these multifactor data simultaneously will become increasingly important as monitoring plans for ecological restoration evolve toward examining multifactor ecosystem characteristics (Covington et al. 1997).

The overall goal of this study was to examine the ecology of understory differences among treatments in a *P. ponderosa* restoration experiment, while simultaneously assessing the sampling design and the statistical methods on which conclusions are based. Specific objectives of this study were to (1) compare understory species composition among treatments in a *P. ponderosa* forest restoration and to examine the relative abilities of a high- and a low-intensity sampling method for detecting differences, (2) determine the effects of using different data matrices (e.g., frequency and cover) in compositional multivariate analyses, and (3) assess sampling adequacy for detecting species and for attaining sample compositional homogeneity.

Methods

Study Area

This study was carried out in a 1,200-ha section of the 2,003-ha Fort Valley Experimental Forest (35°16′ N, 111°43′ W) within the Coconino National Forest, 15 km north of the city of Flagstaff in northern Arizona. Annual precipitation averages 57 cm, with 50% falling as snow (Fulé et al. 2001). Elevation of the study area is 2,300 m, with rolling topography and slope gradients less than 25%. Soils are of volcanic origin and consist of a complex of fine, montmorillonitic, frigid Typic Argiborolls and Mollic Eutroboralfs (Fulé et al. 2001). General pre-settlement vegetation consisted of widely spaced groups of *Pinus ponderosa* averaging about 60 trees/ha (Mast et al. 1999). The study area is part of a 3.4 million–ha complex of *P. ponderosa*-dominated forests occupying portions of New Mexico and north-central Arizona (Brown 1994). Pre-settlement understory composition was dominated by grasses, commonly *Festuca arizonica* (Arizona fescue), *Muhlenbergia montana* (mountain muhly), *Poa fendleriana* (muttongrass), and *Elymus elymoides* (squirreltail), and a variety of forbs (Pearson 1942; Cooper 1960). European settlement of the area beginning in the 1870s resulted in the logging of large trees, overgrazing, and fire suppression, facilitating increases in *P. ponderosa* densities of several hundred trees/ha or more (Cooper 1960). These changes were manifested in rapid declines of grass cover and understory diversity, culminating today in dense stands susceptible to unnatural stand-replacing wildfires (Covington & Moore 1994*a*).

Restoration Treatments

Thinning and burning restoration treatments began in the study area in 1998 with the goals of reestablishing historic forest structure and increasing native plant diversity. The experiment included 12, 14-ha treatment (thin + burn) and control areas, with three areas for each of four treatments (Fulé et al. 2001). All thinning treatments were burned after thinning using strip headfires. Thinning treatments were based on site-specific replacement ratios of pre-settlement tree densities where different numbers of trees of post-settlement origin were retained to replace old trees that had previously died or had been logged (Fulé et al. 2001). Treatments retained all live trees of pre-settlement origin (age >120 years). In order of intensity, thinning treatments included a 3–6 tree replacement (low intensity), a 2–4 tree replacement (medium intensity), and a 1.5–3 tree replacement (high intensity). For example, the 1.5–3 treatment means that on average 1.5 post-settlement trees greater than 40 cm in diameter at 1.4 m were retained on a site for every dead old-growth tree and three post-settlement trees less than 40 cm in diameter were retained if sufficient larger trees did not occur within 20 m of a dead old-growth tree location. The high-intensity treatment reduced density and basal area most closely to pre-settlement levels. Pre- and post-treatment mean densities (trees/ha) (all *P. ponderosa*) of the four treatments (Fulé et al. 2001), respectively, were as follows: 1,188 and 1,188 (control); 1,044 and 243 (low intensity); 1,492 and 170 (medium intensity); 956 and 140 (high intensity). Pre- and post-treatment mean basal areas (m^2/ha), respectively, were as follows: 38 and 38 (control); 34 and 22 (low intensity); 38 and 18 (medium intensity); 35 and 16 (high intensity).

Plot Sampling

Twenty plots were established before treatment in 1998 on a 60-m grid in each of the 12 treatment or control areas, and trees were sampled on a 0.04-ha circular plot (Fulé et al. 2001). Understory and substrate characteristics were sampled on a 50-m transect centered at the plot center using a point-intercept sampling method (Fulé et al. 2001). At points (166 total points per transect) every 30 cm along the transect, the understory species present (if any) and substrate (soil, rock, litter, or coarse woody debris) were recorded. The point-intercept sampling method has been widely used for understory sampling in ecological restoration studies in this region and also is commonly used for sampling rangeland vegetation (Stohlgren et al. 1998).

For the present study, two or three of the 20 plots of each of the 12 treatment areas were randomly selected for sampling, for eight plots for each of the four treatments.

Selected plots were required to be separated by at least 120 m from another selected plot to reduce spatial autocorrelation (Hurlbert 1984). We used distance segregation rather than sampling and averaging two or more close plots because averaging would cause difficulty for some of the statistical analyses, such as spatial statistics, that we wished to apply to this dataset (Dale 1999). A mantel test (Mantel 1967) of Sørensen plot distances (based on relative species frequencies) and geographic plot distances (meters) found that community composition was not significantly correlated with geographic distance ($r = 0.097$, $p = 0.1064$, 9,999 permutations).

On each plot, a 1×50–m subplot transect, consisting of 50 contiguous 1-m^2 subplots, was centered at the plot center and orientated north–south. The percent cover of each species rooted in each subplot was visually classified. Cover classification was standardized by dividing subplots into quarters or eighths and estimating cover to the nearest 1% up to 10% cover and then at 5% intervals. Along the same transect, understory vegetation and substrate also were sampled using the point-intercept method. The subplot method is a more intensive and time-consuming sampling method than the point-intercept method, with the subplot method averaging 75 minutes to complete per plot and the point-intercept method averaging 15 minutes. Plants not readily identified in the field were collected and identified to species when possible. Sampling occurred between 20 September 2002 and 28 October 2002. Nomenclature and classification of species as native or exotic follows that of USDA-NRCS (2002).

Statistical Analyses

Indicator species analysis (Dufrene & Legendre 1997) in the software PC-ORD (McCune & Mefford 1999) was used to ascertain species that may have changed in abundance after treatments and, thus, distinguished treatments. This analysis integrates the proportional abundance and constancy of a species in each treatment into an indicator value that ranges from 0 (no indication) to 100 (perfect indication). Significance of indicator values was assessed using a Monte-Carlo randomization test based on 1,000 permutations (McCune & Mefford 1999).

To test the null hypothesis of no difference in understory species composition among treatments, we ran separate multi-response permutation procedure (MRPP) analyses using different plot × species data matrices (e.g., presence/absence and relative percent cover) derived from subplot and point-intercept sampling methods. Multi-response permutation procedures are multivariate, nonparametric tests that evaluate the null hypothesis of no difference, such as in species composition, between groups (Zimmerman et al. 1985; McCune & Grace 2002). Our purpose in these analyses was to compare relative abilities of different sampling methods and data summary techniques to detect differences among treatments. A priori, we chose to use results from the subplot sampling method and species importance values (average of relative frequency and relative percent cover) and relative frequency (sums to 100 for all species on a plot) for assessing actual treatment differences other than for methodological comparative purposes. The subplot method was chosen because it is the more intensive sampling design; importance values were chosen because theoretically they are the most quantitative measure by integrating both relative percent cover and frequency; and relative frequency was chosen because it equalizes species of different growth forms and should be the most reproducible measure because it does not involve visual cover estimates. Using relative frequency data from the subplot sampling method, we also partitioned the data into plant life form (e.g., forbs only) and native/exotic species categories to determine the plant groups most responsible for compositional treatment differences. If an overall MRPP test among treatments was significant, pairwise tests were used for multiple comparisons (McCune & Mefford 1999).

We used Sørensen distances and PC-ORD default group weightings for all MRPP analyses (McCune & Grace 2002). Multi-response permutation procedures also provide an A-statistic, the chance-corrected within-group agreement, which provides an estimate of the effect size that is independent of the sample size. A is maximized at 1 when all plots within groups are identical, but in community ecology, A is commonly below 0.1 (McCune & Grace 2002). Species occurring in only one plot were removed from the dataset before MRPP analyses; these rare species increase the number of zeros and contribute little to analyses (Gauch 1982).

Mean richness of native and exotic species at 1-m^2 and 50-m^2 scales from the subplot sampling method was compared among treatments in separate analyses using one-way analysis of variance (df model = 3, df error = 28) and Fisher's least significant difference (SAS Institute 1999). Raw data approximated homogeneity of variance (Levene test) and normality (Shapiro–Wilk test) assumptions. To examine whether sampling intensity influenced conclusions, analysis of variance was used to compare mean species richness per m^2 among treatments with means based on 10, 1-m^2 subplots (located every 5 m) and on all 50, 1-m^2 subplots per plot.

Species–Area and Compositional Curve Development

Species–area curves have long been used in many applications in vegetation ecology (Cain 1938; Connor & McCoy 1979; Palmer & White 1994). We used species–area and compositional curves for assessing the adequacy of subsampling in detecting species and in attaining compositional homogeneity relative to a full sample. Minimum sample area on species–area curves is indicated where the curve generally levels off, and compositional homogeneity is indicated by a multivariate distance less than 10% from a full sample (Dietvorst et al. 1982).

To evaluate the adequacy of the 50, 1-m^2 subplot sampling method for detecting species at a site, we constructed species–area curves as a function of the number of subplots sampled using PC-ORD (McCune & Mefford 1999). This analysis calculates the mean number of species for different combinations of subplot sample sizes, where sample size is the number of subplots (McCune & Mefford 1999). Compositional curves, using percent cover and Sørensen distance, were simultaneously constructed following a procedure of centroid calculation for the full plot and subplot combinations documented in McCune and Mefford (1999). Species–area and compositional curves were calculated for all 32 plots individually and then averaged into composite curves. Standard errors are reported as a measure of how the mean curve is likely to vary. We evaluated the adequacy of the number of plots sampled for detecting species and attaining compositional homogeneity in the geographic area of the experiment by constructing curves on a plot basis. This procedure resulted in the construction of one species–area and one compositional curve, and standard deviations are reported as a measure of the variability of the data used for curve construction.

Results

Treatments were graminoid and forb dominated, with all treatments except for the high-intensity restoration treatment exhibiting greater cumulative frequencies of graminoids than forbs despite higher species richness of forbs (Table 1). *Elymus elymoides*, *Carex geophila* (White Mountain sedge), *Muhlenbergia montana*, *Cirsium wheeleri* (Wheeler thistle), and *Poa fendleriana* were the most common species among treatments. Three exotic species exhibited 1-m^2 frequencies greater than 5%, with *Verbascum thapsus* (common mullein) and *Linaria dalmatica* (dalmatian toadflax) being the most frequent. Only 3 (*E. elymoides*, *C. wheeleri*, and *Pinus ponderosa* seedlings) of the 90 species recorded in this study exhibited significant ($p < 0.05$) indicator values for a treatment in indicator species analysis. These species were more common in restoration plots than in control plots, although indicator values were low (<52).

Using data from the 50, 1-m^2 subplot sampling method, MRPP indicated that overall understory composition differed significantly among treatments regardless of the

Table 1. Mean percent frequency at 1-m^2 and 50-m^2 scales for understory species with 5% or greater frequency at 1-m^2 scales for four restoration treatments, Fort Valley Experimental Forest, northern Arizona (values are mean 1-m^2 frequency ± SD [50-m^2 frequency]).

	Restoration Treatment Intensity[a]			
	Control	*Low*	*Medium*	*High*
Graminoids				
Carex geophila	35 ± 14 (100)	34 ± 23 (100)	45 ± 26 (100)	33 ± 19 (100)
Elymus elymoides	28 ± 24 (100)	30 ± 16 (100)	54 ± 34 (100)	61 ± 28 (100)
Festuca arizonica	8 ± 12 (50)	8 ± 12 (50)	5 ± 4 (75)	13 ± 17 (63)
Koeleria macrantha	5 ± 8 (38)	—	<1 ± 1 (13)	4 ± 6 (38)
Muhlenbergia montana	26 ± 19 (100)	29 ± 27 (88)	9 ± 11 (75)	39 ± 21 (100)
Poa fendleriana	12 ± 10 (75)	8 ± 9 (75)	6 ± 5 (88)	20 ± 20 (100)
Shrubs				
Ceanothus fendleri	<1 ± 1 (13)	5 ± 5 (63)	4 ± 3 (88)	3 ± 2 (75)
Rosa woodsii	17 ± 31 (38)	<1 ± 1 (38)	<1 ± 1 (25)	6 ± 7 (50)
Seedling				
Pinus ponderosa	1 ± 1 (50)	7 ± 6 (75)	5 ± 6 (75)	2 ± 3 (38)
Forbs				
Achillea millefolium	6 ± 17 (25)	<1 ± 1 (25)	1 ± 2 (38)	9 ± 18 (50)
Artemisia carruthii	1 ± 2 (25)	2 ± 5 (38)	1 ± 1 (50)	5 ± 7 (50)
Astragalus humistratus	<1 ± 2 (13)	3 ± 3 (50)	2 ± 4 (38)	6 ± 8 (63)
Chenopodium graveolens	<1 ± 1 (13)	2 ± 2 (50)	7 ± 8 (63)	4 ± 9 (25)
Cirsium vulgare[b]	—	—	<1 ± 1 (38)	5 ± 8 (38)
Cirsium wheeleri	7 ± 11 (63)	10 ± 16 (63)	12 ± 12 (88)	38 ± 20 (100)
Geranium caespitosum	6 ± 9 (50)	3 ± 6 (50)	<1 ± 1 (25)	4 ± 5 (38)
Laennecia schiedeana	—	3 ± 4 (50)	13 ± 18 (50)	21 ± 29 (50)
Linaria dalmatica[b]	—	4 ± 11 (13)	4 ± 6 (38)	5 ± 11 (25)
Lotus wrightii	4 ± 7 (50)	5 ± 6 (63)	4 ± 7 (75)	13 ± 12 (88)
Packera multilobata	1 ± 3 (13)	4 ± 3 (88)	3 ± 4 (75)	5 ± 8 (88)
Penstemon barbatus	—	<1 ± 1 (25)	—	6 ± 17 (13)
Potentilla subviscosa	2 ± 3 (50)	3 ± 5 (25)	2 ± 6 (13)	7 ± 12 (38)
Pseudocymopterus montanus	5 ± 13 (13)	<1 ± 1 (13)	4 ± 4 (63)	2 ± 6 (25)
Solidago velutina	8 ± 8 (63)	14 ± 25 (63)	9 ± 14 (63)	7 ± 10 (50)
Verbascum thapsus[b]	—	<1 ± 1 (13)	12 ± 17 (38)	14 ± 30 (50)
Vicia americana	5 ± 7 (50)	4 ± 11 (25)	<1 ± 2 (13)	10 ± 10 (63)

[a] Treatment intensity indicates increasing degrees of thinning (high-intensity treatment reduced tree densities most closely to pre-settlement densities).
[b] Exotic species, following USDA-NRCS (2002).

data matrix (e.g., mean cover and relative frequency) used to summarize species abundances (Table 2). Results of multiple comparisons, however, varied depending on the data matrix. The a priori selected matrices of relative frequency and importance values were the most sensitive and approximately equally sensitive to treatment differences in multiple comparisons. No MRPP test for any data matrix was significant using community data from the point-intercept sampling method. Matrix partitioning to determine the plant categories most responsible for differences among treatments detected using the subplot method indicated that grass species composition differed among treatments in overall MRPP tests, whereas forb composition did not (Table 3).

Mean richness of native and exotic species per 50 m^2 did not differ among treatments (Fig. 1). At the 1-m^2 scale, however, the high-intensity restoration treatment exhibited significantly higher native species richness than did the other treatments. Species-richness/m^2 estimates from the subplot sampling method based on 10, 1-m^2 subplots (located every 5 m along a 50-m subplot transect) and based on all 50 subplots per plot were highly correlated (Pearson $r = 0.99$). Separate analyses of variance of species richness/m^2 among treatments using 10 subplots and using 50 subplots per plot provided nearly identical results (Table 4).

A species–area curve comparing the number of species detected as a function of increasing numbers of 1-m^2 subplots sampled per plot averaged for all plots showed little

Table 2. Comparison of multi-response permutation procedure tests of the null hypothesis of no difference in understory species composition among restoration treatments for two sampling methods and different data matrices, Fort Valley Experimental Forest, northern Arizona.

	Restoration Treatment Intensity[a]						
Data Matrix	*Control*	*Low*	*Medium*	*High*	*A*[c]	*t*	*p*
		Sørensen Dissimilarity Distances (%)					
Subplot sampling method							
Presence/absence	53 a	49 ab	43 b	44 b	0.036	−2.21	0.0239
Ranked species IV	19 a	20 ab	18 b	21 b	0.042	−2.91	0.0070
Mean percentage cover	63 a	65 a	62 a	60 b	0.057	−3.42	0.0036
Mean percentage frequency	59 a	60 a	55 a	57 b	0.044	−2.91	0.0090
Relative percentage cover	56 a	53 a	51 b	53 a	0.054	−2.92	0.0092
Relative percentage frequency	55 a	53 abc	47 b	52 c	0.046	−3.19	0.0046
IV	55 a	52 ab	49 c	50 b	0.053	−3.23	0.0049
IV ranked distance	52 a	45 a	41 b	41 a	0.102	−2.97	0.0076
Point-intercept sampling method							
Presence/absence	76	70	53	59	0.011	−0.41	0.3097
Percent cover	85	79	67	73	0.028	−1.31	0.1033
Relative percentage cover	81	76	62	66	0.035	−1.34	0.0990
Percent cover ranked distance	59	53	36	42	0.040	−1.15	0.1270

For significant overall tests, treatments within a row without shared letters differ at $p < 0.05$. IV, importance value (average of relative frequency and relative percentage cover).

[a] Treatment intensity indicates increasing degrees of thinning (high-intensity treatment reduced tree densities most closely to pre-settlement densities).

[b] Higher distances indicate greater compositional heterogeneity within a treatment.

[c] *A*-statistic (chance-corrected within-group agreement).

Table 3. Multi-response permutation procedure tests of the null hypothesis of no difference in understory species composition among four restoration treatments for different plant life form and native/exotic species categories, Fort Valley Experimental Forest, northern Arizona.

	Restoration Treatment Intensity[a]						
	Control	*Low*	*Medium*	*High*	*A*[c]	*t*	*p*
		Sørensen Dissimilarity Distances (%)					
Grasses only	45 ab	37 a	34 b	35 a	0.059	−2.67	0.0129
Shrubs only	59 a	80 ab	62 b	79 b	0.093	−2.69	0.0158
Seedlings only	67	74	63	59	0.019	−0.39	0.2857
Forbs only	84	78	71	67	0.019	−1.55	0.0727
Grasses + shrubs	49 a	40 a	35 b	38 a	0.065	−3.26	0.0044
Grasses + forbs	53 a	51 abc	47 b	51 c	0.040	−2.64	0.0128
Native species only	55 a	52 abc	45 b	50 c	0.048	−3.37	0.0032
Exotic species only	25	64	57	72	0.003	−0.08	0.3853

Data were derived from a subplot sampling method using 50, 1-m^2 subplots. For significant overall tests, treatments within a row without shared letters differ at $p < 0.05$.

[a] Treatment intensity indicates increasing degrees of thinning (high-intensity treatment reduced tree densities most closely to pre-settlement densities).

[b] Higher distances indicate greater compositional heterogeneity within a treatment.

[c] *A*-statistic (chance-corrected within-group agreement).

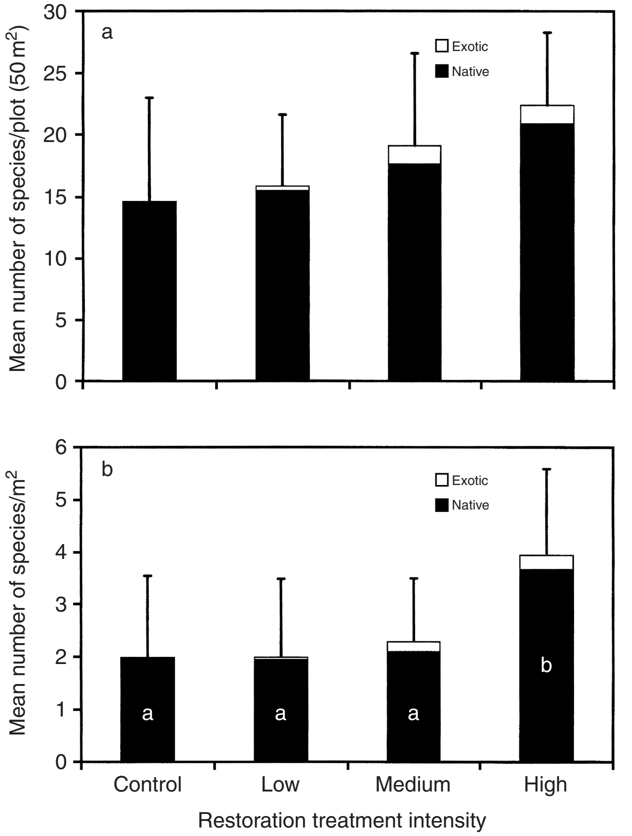

Figure 1. Mean species richness per 50 m^2 (a) and per 1 m^2 (b) for four restoration treatments, Fort Valley Experimental Forest, northern Arizona. Error bars are 1 standard deviation for total mean species richness. Means without shared letters for native species richness indicate significant differences among treatments (exotic species richness did not differ among treatments at either scale).

indication of leveling off (Fig. 2). When species that occurred in only one subplot of a plot were removed, however, on average, 93% of the total number of species occurring on a 50-m^2 plot had been detected after 25 subplots were sampled on a plot. Mean Sørensen distance declined below 10% after about 30 subplots were sampled on a plot, indicating that community compositional estimates were relatively stable.

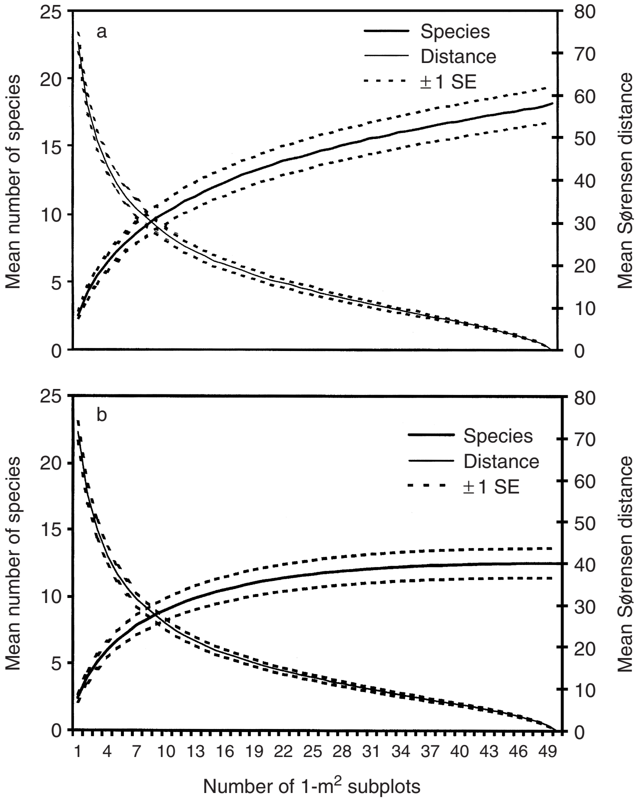

Figure 2. Subplot species–area and compositional curves for all species (a) and with species occurring in only one subplot per plot removed (b) for a *Pinus ponderosa* forest restoration, northern Arizona.

On a 50-m^2 plot basis for all species, the species–area curve increased sharply, indicating that the sampling design did not adequately detect species across broader scales in the geographic area of the experiment after 32 plots had been sampled (Fig. 3). Excluding species occurring in only one plot, also similar to results for the subplots (Fig. 2), resulted in the leveling off of the species–area curve. Of the 90 total species recorded on plots in this study, only 47 species occurred in more than one plot. There was no apparent trend for higher or lower numbers of rare species with treatment intensity, with all treatments supporting between about 25 and 35% of species occurring in only one plot.

Table 4. Comparison of one-way analysis of variance results for mean species richness/m^2 among four restoration treatments for a subset of 10, 1-m^2 subplots and all 50, 1-m^2 subplots per plot, Fort Valley Experimental Forest, northern Arizona.

	Restoration Treatment Intensity[a]						
	Control	*Low*	*Medium*	*High*	*F*	*p*	*LSD*
Ten subplots	1.96 ± 1.65 a	1.93 ± 1.51 a	2.26 ± 1.24 a	3.95 ± 1.81 b	3.02	0.0463	1.60
Fifty subplots	1.99 ± 1.56 a	1.98 ± 1.50 a	2.28 ± 1.21 a	3.94 ± 1.65 b	3.16	0.0403	1.53

Values are mean ± SD. Means within a row without shared letters differ at $p < 0.05$. LSD, least significant difference.

[a] Treatment intensity indicates increasing degrees of thinning (high-intensity treatment reduced tree densities most closely to pre-settlement densities).

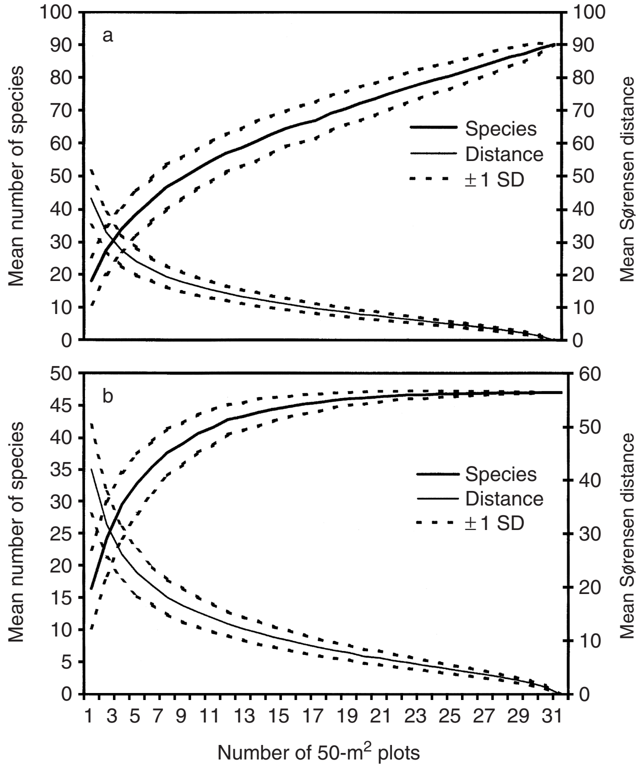

Figure 3. Plot species–area and compositional curves for all species (a) and with species occurring in only one plot removed (b) for a *Pinus ponderosa* forest restoration, northern Arizona.

Discussion

Species Composition

Exotic species *Verbascum thapsus* and *Linaria dalmatica* were absent from control plots and increased in frequency with increasing treatment intensity (Table 1). *Verbascum thapsus* in the treatment areas probably originated from the seed bank and germinated after soil disturbances and open canopies were created by treatment application (Gross & Werner 1978; Pratt et al. 1984). In pole-sized *Pinus ponderosa* forests 130 km north of the study area, for example, Springer (1999) reported that there were 917 viable seeds/m^2 in the seed bank for *V. thapsus*, 12 times more seeds than the next most common species. *Verbascum thapsus* is a biennial, and although its seed may be ubiquitous, this species typically does not persist for more than a few years following disturbance in the presence of competing vegetation (Gross & Werner 1978). It is unlikely therefore that *V. thapsus* will remain an important aboveground vegetation component in the restoration communities. *Linaria dalmatica*, in contrast, is a long-lived perennial, prolifically produces seed, and aggressively spreads vegetatively by root expansion (Vujnovic & Wein 1997). Although not currently frequent in the restoration communities, the persistence and competitive ability of *L. dalmatica* for soil moisture (Vujnovic & Wein 1997) suggest that this species is the exotic species of greatest concern in the restoration treatments.

Rosa woodsii, a native species, was more frequent in the control than in the treated areas (Table 1). However, 1-m^2 frequency of this species in the control was variable, and 50-m^2 frequencies were not appreciably different among treatments. Vose and White (1987, 1991) concluded that a prescribed burn did not significantly decrease *R. woodsii* but noted a lack of other published research on the response of this species to disturbance. *Elymus elymoides* increased with treatment intensity, consistent with previous research (Young & Miller 1985; Vose & White 1991; White et al. 1991). Detecting longer-term trends (>5 years) in both native and exotic species dynamics in the restoration communities requires repeated temporal monitoring and is a research need for southwestern *P. ponderosa* forest restoration.

Multi-Response Permutation Procedures

A more intensive subplot sampling method tested in this study detected differences in community composition among restoration treatments in overall MRPP tests for any data matrix, whereas a less intensive point-intercept sampling method did not detect differences among treatments for any matrix. Sampling methods examined in this study constrained community compositional results and conclusions more than the data matrices used to summarize data derived from a sampling method. A matrix of relative species frequencies from the subplot sampling method, however, detected more differences among treatments than did matrices of mean or relative percent cover. Relative frequency also performed similar to an importance value matrix (average of relative frequency and relative cover), suggesting that obtaining plant cover estimates during sampling was not necessary for detecting differences in community composition among treatments in this study.

Although the subplot method was more effective for detecting treatment differences than the point-intercept sampling method, the subplot method averaged 75 minutes of sampling time per plot compared with 15 minutes for the point-intercept method. To standardize sampling time at 15 minutes between methods, we conducted MRPP tests using a subset of 10 (located every 5 m) of the 50, 1-m^2 subplots per plot with species data summarized by a relative frequency matrix. An overall MRPP test among treatments also was significant ($A = 0.044$, $t = -3.20$, $p = 0.0045$) and comparable to results using all 50 subplots ($A = 0.046$, $t = -3.19$, $p = 0.0046$). This finding suggests that if rapid assessments of species composition are needed, then a sampling design employing a dispersed arrangement of small subplots is more effective for detecting treatment differences than is point-intercept sampling.

Results of MRPP analyses are partly explained by within-group Sørensen distances, where Sørensen distances for matrices derived from the point-intercept sampling method were higher than for the subplot method. Higher within-group distances indicate greater compositional variability within a treatment, making it more difficult to detect treatment differences. These higher distances associated with the point-intercept method were a sampling phenomenon where this method quantified community composition less effectively than the subplot method. Ranked species importance values from the subplot method resulted in the lowest within-group Sørensen distances, but this ranking results in the questionable procedure of assigning quantitative values to species when they are absent (McCune & Grace 2002). Ranking the distance matrix (importance value ranked distance matrix) resulted in lower within-group distances and a higher *A*-statistic, consistent with previous reports (McCune & Grace 2002). This ranking procedure, however, caused decreased sensitivity to treatment differences compared to the unranked importance value matrix.

Species Richness and Area Curves

Differences in species richness among treatments were scale specific, with a high-intensity restoration treatment exhibiting significantly greater mean native species richness than other treatments at a 1-m^2 scale but not at a 50-m^2 scale. Native species richness/m^2 did not increase significantly until the high-intensity restoration treatment, suggestive at least in the short term of a treatment-intensity threshold that needed to be passed before native richness increased. However, exotic richness also increased with treatment intensity, due to greater frequencies of species such as *Cirsium vulgare* (bull thistle) and *L. dalmatica* in the medium- and high-intensity restoration treatments.

Mean-species-richness/m^2 estimates based on a subset of 10, 1-m^2 subplots per plot differed by only 0.05 species or less from estimates based on all 50 subplots per plot for all treatments. This similarity is consistent with results of MRPP compositional analyses, where results of an overall test were nearly identical between relative frequency matrices from 10 and 50 subplots. Although sampling a small area per plot such as 10 m^2 may be inadequate for many community sampling objectives like detecting rare species, the ability of 10 dispersed subplots per plot to effectively quantify community characteristics such as species richness at fine scales suggests that such sampling designs show promise for rapidly monitoring restoration effectiveness. However, species–area curves indicated that incorporating larger plots into the sampling design would be necessary to increase species detection at the site scale and in the geographic area in which the restoration experiment is conducted. Maximizing species detection during sampling is important in many restoration contexts, such as for the early detection of exotic species before infestations occur (Stohlgren et al. 1998).

Conclusion

An advantage of contiguous subplot sampling methods such as the one employed in this study is that they facilitate the application of spatial statistics for examining patterns of species and species-richness distributions (Dale 1999). Unless plants are mapped, sampling methods such as modified 0.1-ha Whittaker sampling plots do not generate the type of data needed for spatial statistics applications at plot scales (Stohlgren et al. 1995). It is unlikely, however, that the intensive subplot method tested in this study could achieve a community sampling goal of maximizing species detection because it is difficult to cover large areas during sampling. Future research could examine ways to extend contiguous subplot methods to sample larger areas, by increasing the size of subplots (greater than the 1 m^2 used in this study), to possibly improve species detection while facilitating spatial pattern analyses.

Short-term (3 years) species compositional differences among treatments in this experiment were subtle, indicated by low MRPP *t*-statistics in multivariate analyses (McCune & Grace 2002). Univariate indicator species analysis (Dufrene & Legendre 1997) returned significant indicator values for only 3% of the species recorded in this study, suggesting that few individual species were substantially more abundant in specific treatments. Indicator species analysis was not successful in this study because differences among treatments resulted from cumulative differences in individual species expressed on a community basis; therefore, multivariate methods such as MRPP could detect treatment differences, whereas the univariate indicator species analysis could not. Studies such as this one that examine the community ecology and sampling efficiency of understory vegetation with a goal of including species composition, diversity, and pattern in a multifactor sampling approach tractable for multivariate analyses will be increasingly needed to design efficient monitoring strategies for ecological restoration experiments.

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LITERATURE CITED

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Shulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications **12:**1418–1433.

Armour, C. D., S. C. Bunting, and L. F. Neuenschwander. 1984. Fire intensity effects on the understory in ponderosa pine forests. Journal of Range Management **37:**44–49.

Brown, D. E., editor. 1994. Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City.

Cain, S. A. 1938. The species–area curve. American Midland Naturalist **19:**573–581.

Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species–area relationship. American Naturalist **113:**791–833.

Cooper, C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecological Monographs **30:**129–164.

Covington, W. W., R. L. Everett, R. Steele, L. L. Irwin, T. A. Daer, and A. N. D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. Journal of Sustainable Forestry **2:**13–63.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. Journal of Forestry **95:**23–29.

Covington, W. W., and M. M. Moore. 1994*a*. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. Journal of Sustainable Forestry **2:**153–181.

Covington, W. W., and M. M. Moore. 1994*b*. Southwestern ponderosa forest structure: changes since Euro-American settlement. Journal of Forestry **92:**39–47.

Dale, M. R. T. 1999. Spatial pattern analysis in plant ecology. Cambridge University Press, New York.

Dietvorst, P., E. van der Maarel, and H. van der Putten. 1982. A new approach to the minimal area of a plant community. Vegetatio **50:**77–91.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67:**345–366.

Fulé, P. Z., C. McHugh, T. A. Heinlein, and W. W. Covington. 2001. Potential fire behavior is reduced following forest restoration treatments. Pages 28–35 in R. K. Vance, C. B. Edminster, W. W. Covington, and J. A. Blake, editors. Ponderosa pine ecosystems restoration and conservation: steps toward stewardship. Proceedings RMRS-P-22. U.S. Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Griffis, K. L., J. A. Crawford, M. R. Wagner, and W. H. Moir. 2001. Understory response to management treatments in northern Arizona ponderosa pine forests. Forest Ecology and Management **146:** 239–245.

Gross, K. L., and P. A. Werner. 1978. The biology of Canadian weeds. 28. *Verbascum thapsus* L. and *V. blattaria* L. Canadian Journal of Plant Science **58:**401–413.

Harris, G. R., and W. W. Covington. 1983. The effect of a prescribed fire on nutrient concentration and standing crop of understory vegetation in ponderosa pine. Canadian Journal of Forest Research **13:**501–507.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54:**187–211.

Kenkel, N. C., P. Juhasz-Nagy, and J. Podani. 1989. On sampling procedures in population and community ecology. Vegetatio **83:**195–207.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research **27:**209–220.

Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. Ecological Applications **9:**228–239.

McConnell, B. R., and J. G. Smith. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. Journal of Range Management **23:**208–212.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Mefford. 1999. PC-ORD: multivariate analysis of ecological data. Version 4. User's guide. MjM Software Design, Gleneden Beach, Oregon.

Moir, W. H. 1966. Influence of ponderosa pine on herbaceous vegetation. Ecology **47:**1045–1048.

Moore, M. M., and D. A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona ponderosa pine forests. Journal of Range Management **45:**267–271.

Oswald, B. P., and W. W. Covington. 1984. Effect of a prescribed fire on herbage production in southwestern ponderosa pine on sedimentary soils. Forest Science **30:**22–25.

Palmer, M. W., and P. S. White. 1994. Scale dependence and the species–area relationship. American Naturalist **144:**717–740.

Pearson, G. A. 1942. Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the Southwest. Ecological Monographs **12:**315–338.

Pratt, D. W., R. A. Black, and B. A. Zamora. 1984. Buried viable seed in a ponderosa pine community. Canadian Journal of Botany **62:** 44–52.

SAS Institute. 1999. SAS/STAT user's guide. Version 8. SAS Institute, Incorporated, Cary, North Carolina.

Springer, J. D. 1999. Soil seed bank in southwestern ponderosa pine: implications for ecological restoration. M.S. thesis. School of Forestry, Northern Arizona University, Flagstaff, Arizona.

Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998. Comparison of rangeland vegetation sampling techniques in the central grasslands. Journal of Range Management **51:**164–172.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117:**113–121.

Tapia, L. A. B., P. F. Ffolliott, and D. P. Guertin. 1990. Herbage production–forest overstory relationships in two Arizona ponderosa pine forests. Journal of Range Management **43:**25–28.

USDA-NRCS (U.S. Department of Agriculture, Natural Resources Conservation Service). 2002. The PLANTS Database, Version 3.5. National Plant Data Center, Baton Rouge, Louisiana.

Vose, J. M., and A. S. White. 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. Canadian Journal of Botany **65:**2280–2290.

Vose, J. M., and A. S. White. 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. Forest Ecology and Management **40:**175–187.

Vujnovic, K., and R. W. Wein. 1997. The biology of Canadian weeds. 106. *Linaria dalmatica* (L.) Mill. Canadian Journal of Plant Science **77:**483–491.

Weaver, H. 1951. Observed effects of prescribed burning on perennial grasses in the ponderosa pine forests. Journal of Forestry **49:** 267–271.

White, A. S., J. E. Cook, and J. M. Vose. 1991. Effects of fire and stand structure on grass phenology in a ponderosa pine forest. American Midland Naturalist **126:**269–278.

Young, R. P., and R. F. Miller. 1985. Response of *Sitanion hystrix* (Nutt.). J.G. to prescribed burning. American Midland Naturalist **113:** 182–187.

Zimmerman, G. M., H. Goetz, and P. W. Mielke. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology **66:**606–611.