

CONTROLS ON VEGETATION STRUCTURE IN SOUTHWESTERN PONDEROSA PINE FORESTS, 1941 AND 2004

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Abstract. Long-term studies can broaden our ecological understanding and are particularly important when examining contingent effects that involve changes to dominance by long-lived species. Such a change occurred during the last century in Southwestern (USA) ponderosa pine (*Pinus ponderosa*) forests. We used five livestock grazing exclosures established in 1912 to quantify vegetation structure in 1941 and 2004. Our objectives were to (1) assess the effects of historical livestock grazing on overstory structure and age distribution, (2) assess the effects of recent livestock grazing and overstory on understory vegetation, and (3) quantify and explain changes in understory vegetation between 1941 and 2004. In 1941, canopy cover of tree regeneration was significantly higher inside exclosures. In 2004, total tree canopy cover was twice as high, density was three times higher, trees were smaller, and total basal area was 40% higher inside exclosures. Understory species density, herbaceous plant density, and herbaceous cover were negatively correlated with overstory vegetation in both years. Most understory variables did not differ between grazing treatments in 1941 but were lower inside exclosures in 2004. Differences between grazing treatments disappeared once overstory effects were accounted for, indicating that they were due to the differential overstory response to historical livestock grazing practices. Between 1941 and 2004, species density declined by 34%, herbaceous plant density by 37%, shrub cover by 69%, total herbaceous cover by 59%, graminoid cover by 39%, and forb cover by 82%. However, these variables did not differ between grazing treatments or years once overstory effects were accounted for, indicating that the declines were driven by the increased dominance of the overstory during this period. Our results demonstrate that historical livestock grazing practices are an aspect of land-use history that can affect ecosystem development. Grazing history must be considered when extrapolating results from one site to another. In addition, the understory vegetation was more strongly controlled by the ponderosa pine overstory than by recent livestock grazing or by temporal dynamics, indicating that overstory effects must be accounted for when examining understory responses in this ecosystem.

Key words: Coconino National Forest, Arizona (USA); Hill plots; land-use history; long-term studies; meta-analysis; overstory–understory relationships; *Pinus ponderosa*; stand structure.

INTRODUCTION

Long-term studies can broaden our understanding of reference conditions (Moore et al. 1999), invasion by exotic species (Strayer et al. 2006), vegetation dynamics, and successional theory (Bakker et al. 2002, Rango et al. 2005). Remeasurements of long-term permanent plots have demonstrated large changes in species composition (Crawley et al. 2005) and forest structure (Moore et al. 2004). Long-term studies are also necessary to detect responses that are contingent upon site differences, interannual variability, or other factors (Bakker et al. 2003, Yeo 2005).

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Contingent effects may be particularly important when they involve changes in life form dominance (House et al. 2003), particularly to dominance by long-lived species. This type of transition occurred in the ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forests of the southwestern United States in the early 1900s. Lines of evidence pointing to increased tree densities include repeat photography (Gordon et al. 1992; see Fig. 1, Plate 1), written accounts of early explorers (Cooper 1960), stand reconstruction modeling (Fulé et al. 1997), and remeasurements of historical permanent plots (Moore et al. 2004). Fire exclusion was an important factor contributing to increased tree densities in these forests (Weaver 1951, Cooper 1960, Covington and Moore 1994, Fulé et al. 1997), but it likely was not the only factor. For example, woody plant encroachment often coincides with intense livestock grazing (Archer 1994) and tree densities are often higher in grazed areas than in relict areas, where topographic features prevent access by

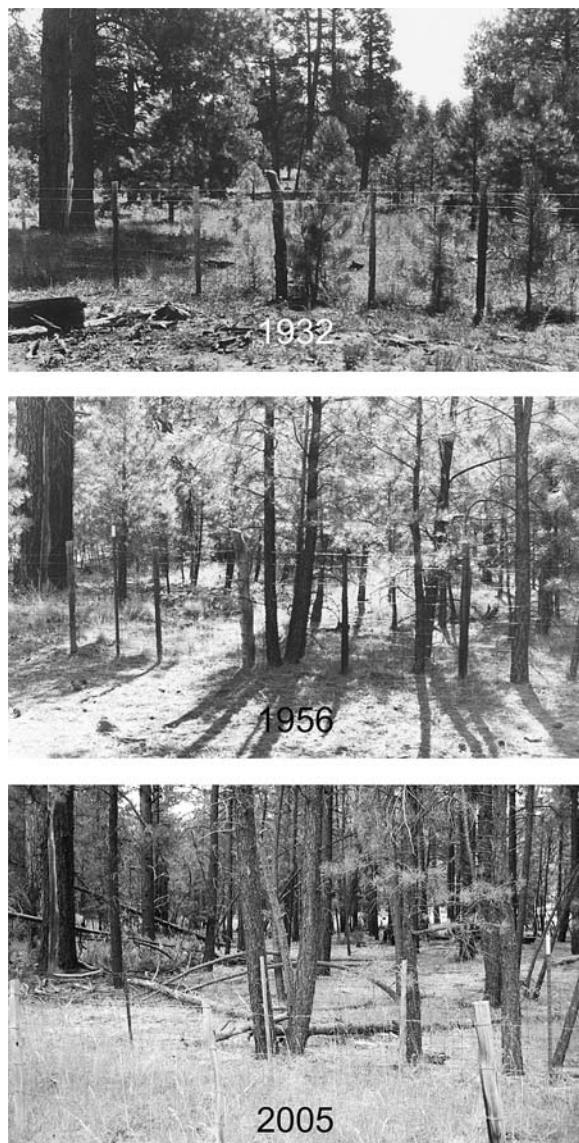


FIG. 1. Photographs of the livestock enclosure at Rogers Lake, Arizona, USA, in 1932 (top), 1956 (middle), and 2005 (bottom). In each photo, the fence separates areas outside and inside the enclosure (foreground and background, respectively). The 1932 photo was taken by J. D. Jones (USDA Forest Service photo 269997), the 1956 photo by T. M. Smith (USDA Forest Service photo 485803), and the 2005 photo by J. D. Bakker. For reference, note the large scarred tree on the left side of all photos.

livestock (Rummell 1951, Schmutz et al. 1967, Madany and West 1983; cf. Harris et al. 2003, Guenther et al. 2004).

A growing body of evidence demonstrates that land-use history can constrain subsequent vegetation development (Dupouey et al. 2002, Foster et al. 2003, Briggs et al. 2006, Fraterrigo et al. 2006). Historical livestock grazing practices may have had similar effects, particularly at very unsustainable intensities as occurred in the

Southwest in the late 1800s (Haskett 1936, Abruzzi 1995, Fredrickson et al. 1998). Woody plants are most sensitive to grazing when young (Archer 1994), but effects could remain evident due to their long life spans. Grazing is thought to have promoted the establishment of ponderosa pine seedlings in the Southwest by reducing the competitive dominance of the herbaceous understory vegetation (Pearson 1942, Elliott and White 1987).

Of course, livestock also directly impact the shrub and herbaceous species on which they graze. Models suggest that livestock grazing should negatively affect plant diversity in semiarid environments such as the Southwest (Olf and Ritchie 1998, Cingolani et al. 2005). However, understory vegetation is also affected by the tree overstory (Arnold 1950, Moore and Deiter 1992, Naumburg and DeWald 1999), and the relative importance of grazing and overstory effects on the understory is unclear.

Qualitative assessments from photographs and early written accounts (Cooper 1960) suggest that understory vegetation was more abundant in Southwestern ponderosa pine forests historically than at present. This conclusion is consistent with historical reconstruction models (Covington and Moore 1994) and observed vegetation responses following contemporary thinning experiments (Moore et al. 2006). However, quantitative data about long-term changes in understory vegetation in this region are rare.

We used a series of long-term livestock grazing exclosures to quantify overstory and understory vegetation structure in 1941 and 2004. Our objectives were to (1) assess the effects of historical livestock grazing on overstory structure and age distribution, (2) assess the effects of recent livestock grazing and overstory on understory vegetation, and (3) quantify and explain changes in understory vegetation between 1941 and 2004.

MATERIALS AND METHODS

In 1912, R. R. Hill established livestock grazing exclosures at five sites within 25 km of Flagstaff, Arizona, USA (Arnold 1950). These sites (the "Hill plots") vary in soil type and span the elevational range of the ponderosa pine forest type in northern Arizona (Table 1). Four sites are located in Coconino National Forest, and one (Rogers Lake) in Northern Arizona University's Centennial Forest. At each site, an exclosure was built to exclude livestock (sheep and cattle) but not wild ungulates (Fig. 1). Each exclosure was paired with an adjacent area that continued to be grazed. Researchers described all sites as "overgrazed" when the exclosures were built (Talbot and Hill 1923). Sites were grazed by cattle and sheep since the 1870s, though grazing intensities have declined over time (Table 1).

Four sites were selectively harvested before the exclosures were built, and several sites received subse-



PLATE 1. (Top) 1941 and (bottom) 2005 photographs of the livestock enclosure at Fry Park, Arizona, USA. In each photo, the fence separates areas inside and outside the enclosure (left and right, respectively). Photo credits: 1941 photo, G. E. Glendening (USDA Forest Service photo 421138); 2005 photo, J D. Bakker.

quent silvicultural treatments (Table 1). Because these treatments were applied inside and outside the enclosures, they are considered part of the inter-site variability. The enclosures were actively maintained for at least five decades after establishment. The enclosure fences continue to be maintained at sites that are grazed by livestock, but have fallen into disrepair at two sites (Black Springs and Reese Tank) that are no longer grazed by livestock (Table 1). These sites were included in analyses of overstory vegetation in 2004 because our interest was in the long-term effects of historical livestock grazing practices, but were omitted from analyses of understory vegetation in 2004 because understory vegetation was assumed to be more responsive to recent livestock grazing practices. Half of the area outside the enclosure at Black Springs was destroyed by an interstate highway in the 1950s, so

2004 measurements were made on the other side of the enclosure.

Sampling occurred in 1941 and 2004. At the Fort Valley Experiment Station, precipitation from September 1940 to August 1941 totaled 83.4 cm, or 148% of the long-term mean (1909–2004; USDA Forest Service 2004). Precipitation from September 2003 to August 2004 totaled 35.6 cm, or 63% of the long-term mean.

Field methods

In 1941, G. Glendening subdivided each grazing treatment (i.e., inside or outside the enclosure) at each site into 10–20 strata to simplify sampling and distribute it across the entire area (Fig. 2). Strata were sampled using the line transect method (Canfield 1941) with 2–4 lines per stratum (Table 1, Fig. 2), for a total of 520 lines. The location of each line was selected by randomly

TABLE 1. Summary statistics and land-use history details for the Hill plots, five livestock exclosures in northern Arizona, USA.

Measure	Big Fill	Black Springs	Fry Park
Exclosure area (ha)	0.618	0.786	0.840
Mean elevation (m)	2070	2100	2170
Substrate†			
Parent material	limestone	limestone/sandstone	basalt/cinders
Soil	Typic Haploboroll	Mollic Eutroboralf	Typic Argiboroll
Soil texture	fine sandy loam	fine sandy loam	loam
Disturbance history‡			
Localized	PL 1946	PL ca. 1954	none
Generalized	SH 1896, 1919, 1947	SH 1902; PCT 1976, 1997	SH 1910
Type of livestock			
1939–1941	cattle§	cattle§	cattle
2002–2004	none since 2000	none since ca. 1960	cattle
Grazing intensity (AUM/ha)¶			
1939–1941	0.58	1.01	1.35
2002–2004	0	0	0.03
Number of undisturbed lines sampled, inside and outside exclosures			
1941	in, 80; out, 80	in, 40; out, 40	in, 80; out, 80
2004	in, 71; out, 80	in, 37; out, 36	in, 80; out, 78

† From Miller et al. (1995).

‡ Data obtained from the Fort Valley Archives and from Coconino National Forest (J. Rolf, *personal communication*). Codes: PB, prescribed burn; PCT, pre-commercial thinning; PL, power/phone line through site; RD, road through site; SH, selective overstory harvest.

§ Near sheep driveway historically.

¶ Animal unit months per ha; larger values indicate higher grazing intensity. The 1939–1941 data are from the Fort Valley Archives (U.S. Forest Service, Rocky Mountain Research Station, Flagstaff, Arizona), and the 2002–2004 data are from annual range inspections on file at the Coconino National Forest.

Data not available; classified as overgrazed by Merrick (1939).

choosing X, Y starting coordinates. Lines were 15.24 m (50 ft) long and oriented parallel to the long axis of the stratum. In 2004, we used the same starting coordinates where possible (the starting coordinates were recorded on the 1941 data sheets for 79% of lines), otherwise we generated new starting coordinates. The 1941 data were published in summary form by Arnold (1950), who focused on overstory–understory relationships.

Overstory vegetation was quantified as canopy cover (percentage of line directly beneath tree crowns) and tree density (number of trees within a 1.22 m (4 ft) wide belt centered on the line). In 1941, canopy cover and tree density were measured separately for mature trees (>25 years old; no minimum size) and regeneration of each species (Glendening 1941). In 2004, canopy cover and tree density were measured in total for each species because there were very few young trees.

Understory vegetation was measured using the line transect method (Canfield 1941), which deals differently with herbaceous and shrub species. Each time a herbaceous plant was encountered that was rooted directly beneath the line, its basal cover was measured as the distance it occupied along the line. Each time a shrub was encountered that hung over the line, its foliar cover was measured by projecting the plant canopy down onto the line. Distances were recorded to the nearest ~0.3 cm (0.01 ft) in 1941 and to the nearest 0.25 cm in 2004. Total species density (*sensu* Gotelli and

Colwell 2001) was calculated as the number of species (both herbaceous and shrub) recorded on a line. Herbaceous plant density was calculated as the number of herbaceous plants per line. Shrub density was not calculated because it is unknown how many times the

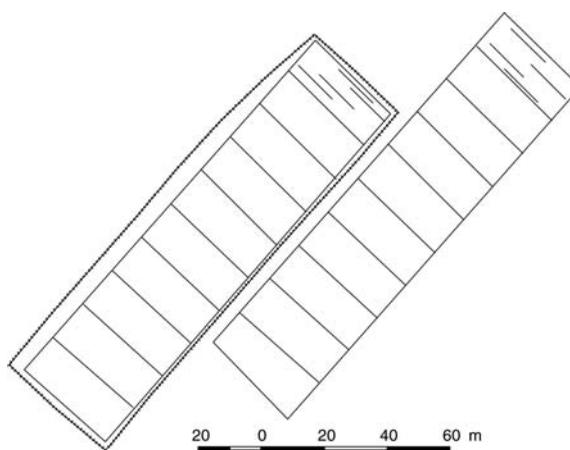


FIG. 2. Layout of the Rogers Lake site showing the fenced livestock exclosure (hatched lines) and strata (rectangles) inside and outside the exclosure. As illustrated for the topmost stratum in each grazing treatment, each stratum was sampled with four randomly selected 15.24-m (50-ft) lines. Other sites had a similar layout but differed in the number and size of strata.

TABLE 1. Extended.

Reese Tank	Rogers Lake
0.669 2490	0.574 2220
mixed igneous Mollic Eutroboralf sandy loam	basalt/cinders Typic Argiboroll loam
RD ca. 1978 SH 1940, 1978, 1989; PCT 1964; PB 1999 (west half)	none SH 1905
sheep none since ca. 1992	sheep sheep
0.17 0	# 0.18
in, 20; out, 20 in, 12; out, 6	in, 40; out, 40 in, 40; out, 40

canopy of each plant overlapped the line. The percent cover of each species on each line was calculated as the sum of the recorded distances for that species divided by the line length. Covers of herbaceous and shrub species were analyzed separately because they were measured using different methods. Herbaceous cover data were analyzed in total and separately for graminoid and forb life forms. Nomenclature is based on the USDA Natural Resources Conservation Service PLANTS database (USDA 2004).

In 2003–2004, the overstory vegetation was also measured within 4–7 20 × 20 m plots within each grazing treatment at each site. These plots were centered on permanent chart quadrats (J. D. Bakker and M. M. Moore, *unpublished data*) and therefore partially overlapped, so data were summarized for the total area sampled in each grazing treatment and site. In total, the species identity and diameter at breast height (dbh; measured 1.37 m above ground level) were measured for 1626 live trees taller than breast height, and the total basal area (square meters per hectare) was calculated for each grazing treatment and site. All live trees were also cored 40 cm above ground level and aged using standard dendrochronological methods (Stokes and Smiley 1968). Contemporary diameter and age distributions were obtained for each grazing treatment and site.

Analyses

Analyses of line transect data were restricted to lines outside of localized disturbances (powerline rights-of-way and roads) and prescribed burns; 520 lines from 1941 and 480 lines from 2004 met these criteria (Table 1). As described previously, understory analyses in 2004 were restricted to the three sites grazed by livestock in recent years (389 lines). Cover data were arcsine (square

root x) transformed and density data were $\log(x + 1)$ -transformed for analysis. We used $\alpha = 0.05$ throughout.

Results from multiple sites were combined using meta-analytic techniques. These techniques were developed to combine the results of multiple studies, which is conceptually and analytically similar to combining results from multiple sites (Gurevitch and Hedges 1999; a similar application is found in Yeo [2005]). Statistical details and formulae are provided in Appendix A. Briefly, we calculated the grazing or year effect size (d_{ij}) of site j in class i (year when testing grazing effects, grazing treatment when testing year effects) for each variable. Effect sizes from individual sites were combined using a mixed-effects model, which assumes random variation in effect size among and within sites (Gurevitch and Hedges 2001). Most meta-analyses included all five sites though, as described before, two sites were excluded from meta-analyses of understory effects in 2004. The cumulated effect size (i.e., the overall effect across sites; d_{i+}^*) was assessed for significance by converting it to a z statistic (Lipsey and Wilson 2001). Effect sizes were also converted into correlation coefficients (r_{ij}) that were combined to yield a common correlation coefficient across sites (r_{i+}).

Our first objective was to evaluate the effect of historical livestock grazing on overstory structure and age distributions. We used meta-analytic techniques to assess the significance of grazing treatments on canopy cover and tree density in 1941 and 2004. Kolmogorov-Smirnov tests (implemented in SPSS version 13.0; SPSS 2004) were used to compare diameter and age distributions from 2004 between grazing treatments. A paired t test was used to compare total basal area in 2004 between grazing treatments.

Our second objective was to assess the effects of recent livestock grazing and overstory vegetation on the understory vegetation. Overstory effects were quantified using multiple regression with tree canopy cover and tree density as independent variables and understory variables as dependent variables. Because our objective was to relate the understory to the overstory immediately around it, lines were considered the experimental units for these regressions. Grazing effects were assessed using two meta-analyses to combine the results from individual sites. One meta-analysis used the unadjusted understory data and the other the residuals after adjusting for overstory effects. By comparing the cumulated effect sizes and common correlation coefficients from the two analyses, we assessed the importance of grazing effects before and after accounting for overstory effects.

Our third objective was to quantify and explain changes in understory vegetation between 1941 and 2004. Strata means (averaged across all undisturbed lines) were the experimental units for analyses of temporal dynamics because the starting coordinates used in 1941 were not available for all lines, and because lines may not have been precisely relocated. Strata that

TABLE 2. Mean tree canopy cover and density inside and outside five livestock exclosures in 1941 and 2004, and cumulated grazing effect sizes ($d_{++}^* \pm s_{++}^*$).

Year and tree status	Canopy cover (%)				Tree density (trees/ha)			
	In	Out	Effect size \pm SD	<i>P</i>	In	Out	Effect size \pm SD	<i>P</i>
1941								
Mature trees	6.3	5.5	0.01 \pm 0.19	0.481	98	58	0.17 \pm 0.13	0.089
Regeneration	5.9	1.7	0.60 \pm 0.18	<0.001	1318	576	0.47 \pm 0.39	0.118
Total	18.5	11.4	0.22 \pm 0.17	0.095	1422	655	0.41 \pm 0.40	0.153
2004 total	52.4	28.1	0.65 \pm 0.22	0.002	726	225	0.85 \pm 0.27	<0.001

Notes: Following the notation of Gurevitch and Hedges (2001), d_{++}^* is the effect size (standardized mean difference between groups, across sites, for mixed model), and s_{++}^* is the standard deviation associated with this effect size (see summary of meta-analytic techniques in Appendix A). Mature trees and regeneration were measured separately in 1941 but not in 2004. Data for the five sites are reported in Appendix B. Data were transformed for analysis but have been back-transformed for clarity of presentation. As a result, 1941 total values are not equal to the sum of the mature tree and regeneration values. Positive and negative effect sizes indicate larger responses inside and outside exclosures, respectively. *P* values indicate whether effect sizes are significantly different from zero (no difference between grazing treatments); values ≤ 0.05 are in boldface type.

were not measured in both years were omitted from analyses of temporal dynamics. We performed two meta-analyses, one with unadjusted understory data and one with the residuals after adjusting for overstory effects in each year. Separate analyses were conducted for each grazing treatment, and the between-class homogeneity statistic (Q_B) was used to test for differences between grazing treatments. Cumulated temporal effect sizes were reported separately for each grazing treatment if Q_B was statistically significant; otherwise, the grand cumulated temporal effect size (i.e., across both grazing treatments and all sites) was reported.

RESULTS

Grazing effects on overstory vegetation

Six tree species (alligator juniper [*Juniperus deppeana* Steud.], oneseed juniper [*J. monosperma* (Engelm.) Sarg.], pinyon pine [*Pinus edulis* Engelm.], limber pine [*P. flexilis* James], ponderosa pine, and gambel oak [*Quercus gambelii* Nutt.]) were present on the sites, but ponderosa pine comprised >99% of the overstory in both years. Therefore, comparisons were made for all trees rather than for individual species.

In 1941, canopy cover of mature trees did not differ between grazing treatments but canopy cover of regeneration was significantly higher inside than outside exclosures (Table 2). Regeneration and total tree densities did not differ overall (Table 2) because densities were significantly higher inside exclosures at three sites and outside the exclosure at one site (Appendix B). In 2004, total canopy cover was almost twice as high inside as outside exclosures and total tree density was more than three times greater inside exclosures.

Total basal area was 40% higher inside than outside exclosures in 2004 (in, 36.6 m²/ha; out, 26.0 m²/ha; $t_4 = 3.48$; $P = 0.025$). Trees were smaller inside exclosures (Fig. 3A), but age distributions did not differ between grazing treatments (Fig. 3B).

Overstory and grazing effects on understory vegetation

Total species density, herbaceous plant density, and herbaceous cover variables were negatively correlated with overstory vegetation in 1941 and 2004 (Table 3, Fig. 4). Shrub cover was not correlated with overstory vegetation in 1941 but slightly positively correlated with it in 2004. Correlations with overstory vegetation were stronger in 2004 than 1941 (Table 3, *r* values; Fig. 4, *F* values), but predicted values of response variables were smaller (Fig. 4, fit lines).

Total species density and herbaceous plant density did not differ between grazing treatments in 1941, but were significantly lower inside exclosures in 2004 (Figs. 5A, B and 6A, B, solid symbols; Appendix C). After accounting for overstory effects, neither variable differed between grazing treatments in either year (Fig. 6A, B, open symbols).

Shrub cover was low and did not differ between grazing treatments in either year (Figs. 5C and 6C). In 1941, graminoid cover was higher inside exclosures (Figs. 5E and 6E), but total herbaceous cover and forb cover did not differ between grazing treatments (Figs. 5D, F and 6D, F), even after accounting for overstory effects. In 2004, all three herbaceous cover variables were higher outside exclosures, though not after accounting for overstory effects.

Temporal dynamics of understory vegetation

Species density declined by 34% between 1941 and 2004, but did not differ between years once overstory effects were accounted for (Fig. 7A). Herbaceous plant density declined more inside than outside exclosures (61% vs. 13%; $Q_B = 5.19$, $P = 0.023$), but did not differ between grazing treatments or years after accounting for overstory effects (Fig. 7B).

Shrub cover declined by 69% between 1941 and 2004, but increased after overstory effects were accounted for (Fig. 7C). Herbaceous cover declined by 59% and forb cover by 82% between 1941 and 2004, but did not differ between years once overstory effects were accounted for (Fig. 7D, F). Graminoid cover declined by 69% inside

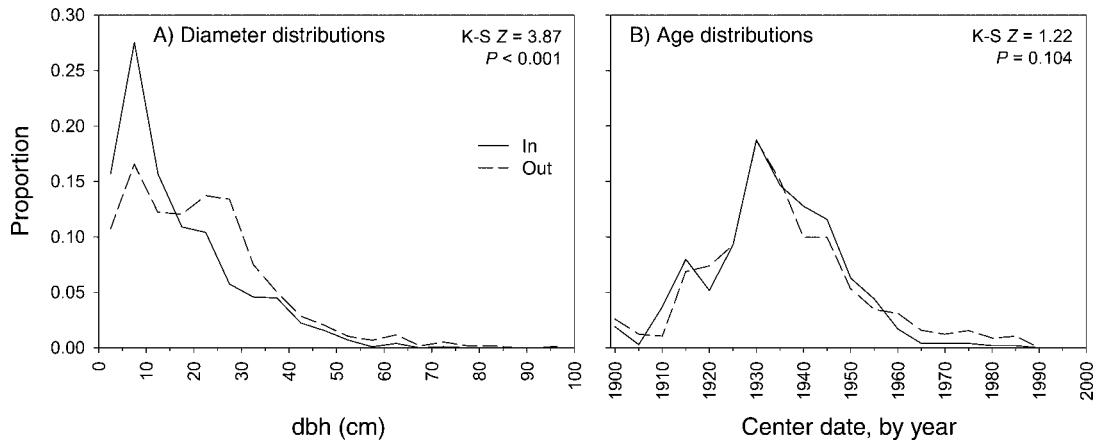


FIG. 3. Overstory (A) diameter and (B) age distributions inside and outside five livestock exclosures in 2004. Data are grouped into classes for presentation but were ungrouped for analysis with Kolmogorov-Smirnov (K-S) tests. Note that all ages are center dates at 40 cm above ground level; for the leftmost ("1900") date in panel (B), all dates prior to 1900 are included.

exclosures but only by 8% outside exclosures ($Q_B = 4.3$, $P = 0.038$). After accounting for overstory effects, however, graminoid cover did not differ between grazing treatments or years (Fig. 7E).

DISCUSSION

Grazing effects on overstory vegetation

Although these forests are dominated by a single tree species, the effects of livestock grazing on overstory dynamics are more complex than previously suggested (Belsky and Blumenthal 1997). In particular, historical livestock grazing had long-term legacy effects on the overstory: tree canopy cover and density were lower where livestock grazing continued than where it ceased in 1912. These effects were evident in 1941 and reported in early research about ponderosa pine regeneration (Westveld 1921, Pearson 1933, Arnold 1950), but were much more apparent by 2004. Similar grazing effects on woody plant density can be seen over larger areas of northern Arizona by comparing Grand Canyon National Park (GCNP) with surrounding lands. GCNP was heavily grazed by sheep and cattle from the late 1800s until it was fenced to exclude livestock grazing in the late 1930s. Contemporary tree densities are higher in GCNP (Grandview site; 955 trees/ha ≥ 2.5 cm dbh) than at an adjacent site that continued to be grazed (830 trees/ha ≥ 2.5 cm dbh, comprising 689 live trees/ha and 141 cut trees/ha; Fulé et al. 2002). However, reconstructed forest structure at the time of Euro-American settlement did not differ between sites (Fulé et al. 2002), indicating that contemporary differences in stand structure are due to subsequent land management practices (see also Menzel 1996). Lower woody plant densities have also been reported in other ecosystems in areas where grazing continued than where it ceased (Cheal 1993, Spooner et al. 2002, Mengistu et al. 2005; cf. Riggs et al. 2000).

We attribute the observed differences in pine regeneration to livestock rather than wild ungulates (Riggs et al. 2000) because wild ungulates had minimal effects in northern Arizona forests in the early 1900s. Merriam's elk (*Cervus elaphus merriami*) was hunted to extinction around 1900, and Rocky Mountain elk (*C. elaphus nelsoni*) was introduced in small numbers in 1913

TABLE 3. Correlation coefficients (r_{i+}) for overstory and grazing effects in 1941 and 2004.

Response variable, by year	Overstory	Grazing	
		Overall	Residuals
Species density			
1941	-0.22	0.10	0.13
2004	-0.38	-0.27	-0.09
Herbaceous plant density			
1941	-0.46	0.04	0.07
2004	-0.61	-0.43	-0.21
Shrub cover			
1941	0.05	0.00	0.00
2004	0.19	0.15	-0.01
Herbaceous cover			
1941	-0.48	-0.01	0.03
2004	-0.64	-0.44	-0.22
Graminoid cover			
1941	-0.34	0.31	0.29
2004	-0.61	-0.41	-0.18
Forb cover			
1941	-0.34	-0.27	-0.14
2004	-0.40	-0.29	-0.11

Notes: Grazing effects are reported based on the unadjusted data (overall) and on the residuals after accounting for overstory effects (Fig. 4). Data for the five sites are reported in Appendix C. Negative correlations with overstory indicate a decline in the response variable as the importance of the overstory increases; negative correlations with grazing indicate a response that was larger outside than inside exclosures. Statistically significant ($P \leq 0.05$) correlation coefficients are shown in bold. Meta-analytic techniques are summarized in Appendix A.

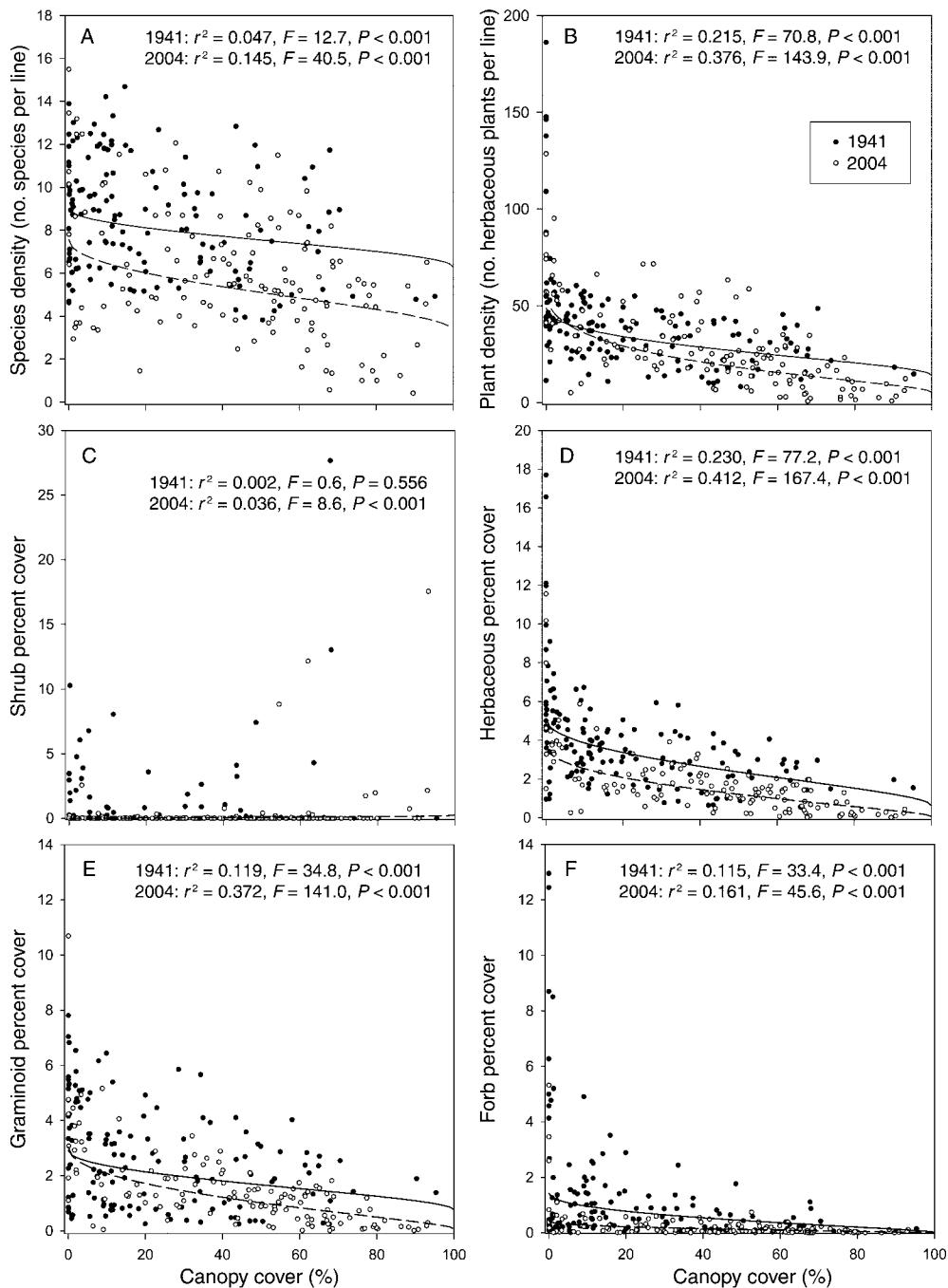


FIG. 4. Relationships between tree canopy cover and (A) species density (number of understory species, both herbaceous and shrub, per line), (B) herbaceous plant density (number of plants per line), (C) shrub cover, (D) herbaceous plant cover, (E) graminoid cover, and (F) forb cover in 1941 (solid lines, solid symbols) and 2004 (dashed lines, open symbols). Data are back-transformed to original units. Regressions were conducted using all lines from the five sites (520 in 1941, 389 in 2004; see *Methods* for details) but, to retain clarity of presentation, are summarized here as strata means (2–4 lines were sampled per stratum). The reported statistics refer to the multiple regression using tree canopy cover and density as independent variables, but response variables are plotted against canopy cover because it explained most of the variation in response variables. Note that y-axes differ in scale.

(Hoffmeister 1986). Also, grazing reports from Coconino National Forest indicate low populations of wild ungulates and high populations of livestock, particularly sheep during this period (e.g., Kneipp 1908).

There are several possible mechanisms by which livestock affected pine regeneration. The relative importance of these mechanisms is unclear, and deserves further research. First, protection from live-

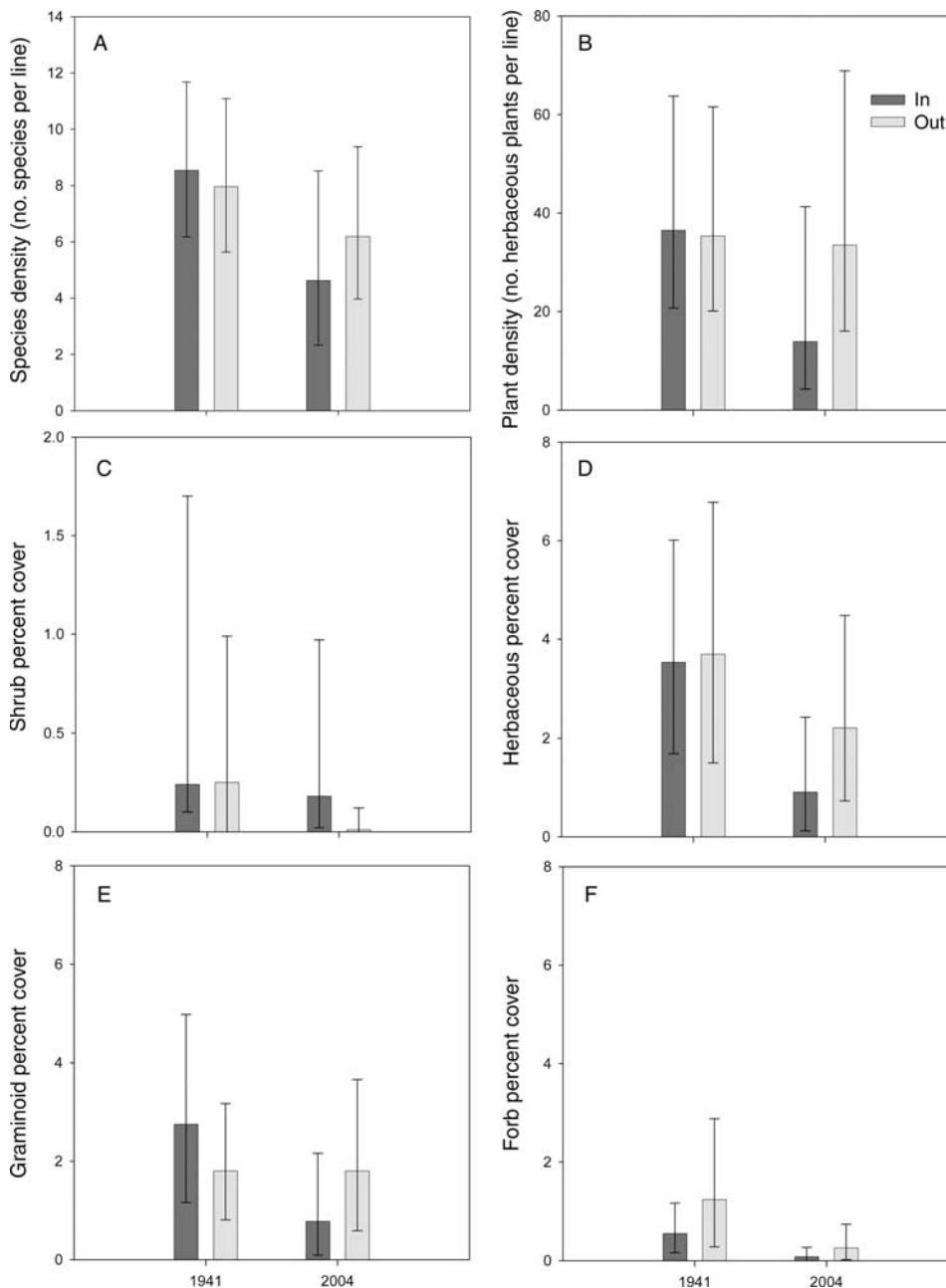


FIG. 5. (A) Species density (as defined in Fig. 4), (B) herbaceous plant density, (C) shrub cover, (D) herbaceous plant cover, (E) graminoid cover, and (F) forb cover inside and outside livestock enclosures in 1941 and 2004. All values are means \pm SD. Note that y-axes differ in scale. Data are not adjusted for overstory effects (Fig. 4) but are weighted by the degrees of freedom at each site and are back-transformed to original units. Grazing effect sizes are shown in Fig. 6, and temporal effect sizes in Fig. 7. Data for the five sites are reported in Appendix C.

stock would have increased the survival and height growth (Karl and Doescher 1998) of seedlings already present when the enclosures were built in 1912. For example, 57 young pine trees (~ 90 trees/ha) were present inside the Big Fill enclosure in 1912; of these, five had died by 1914 (Hill 1917) and “practically all” survived to 1921 (Hill 1921). In contrast, most young pine trees outside the enclosure were dead by 1914 (Hill

1917) and only two remained alive in 1921 (Hill 1921). Similarly, Pearson (1933) noted that regeneration in 1918 was “noticeably better” inside than outside other enclosures in northern Arizona, “due more to the growth of old seedlings than appearance of new ones” (Southwestern Forest and Range Experiment Station 1937:11). Second, germination and establishment may have been enhanced within the enclosures. The

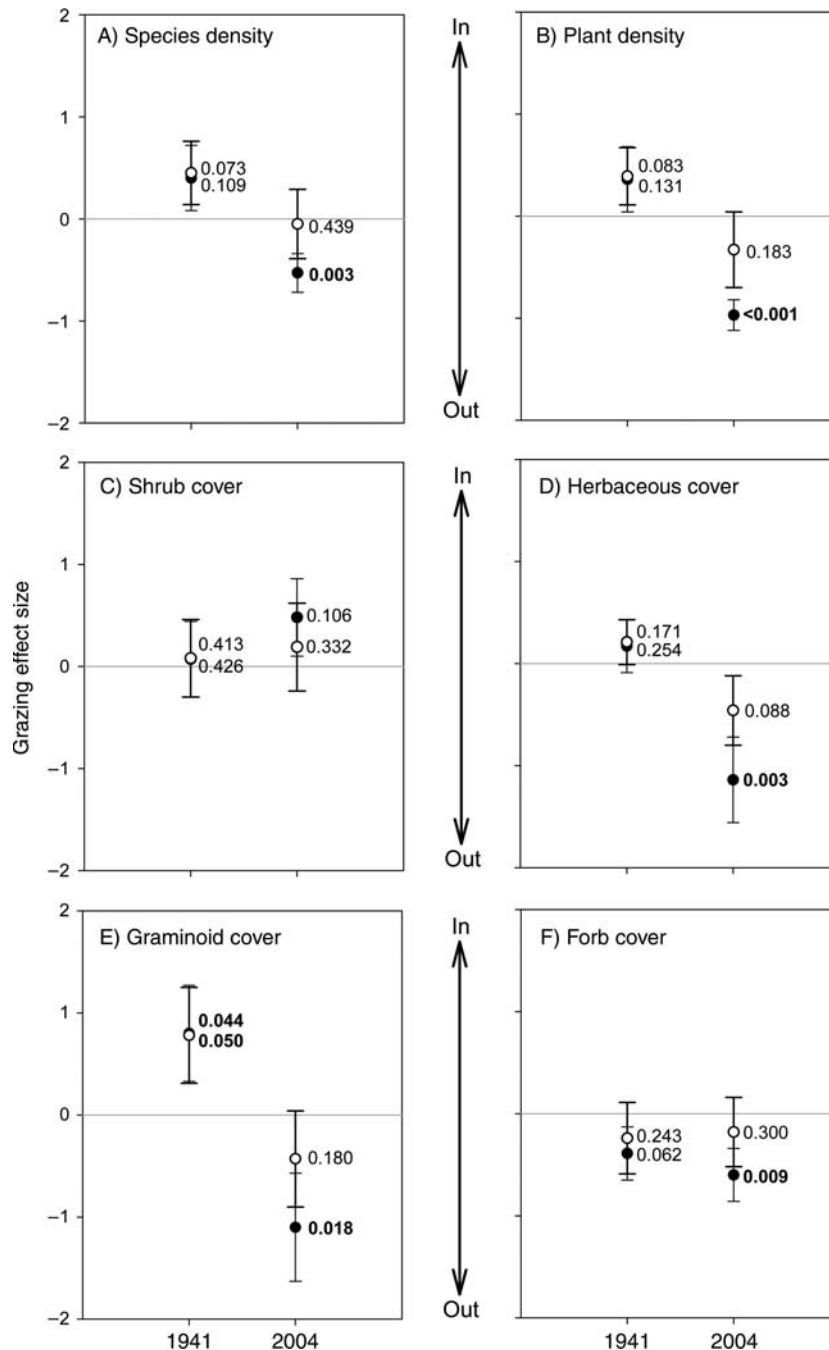


FIG. 6. Cumulated grazing effect size (mean \pm SD) for (A) species density (as defined in Fig. 4), (B) herbaceous plant density, (C) shrub cover, (D) herbaceous plant cover, (E) graminoid cover, and (F) forb cover in 1941 and 2004. Positive and negative effect sizes indicate larger responses inside and outside enclosures, respectively, and the horizontal line at zero indicates no difference between grazing treatments. Solid symbols indicate effect sizes using unadjusted data, and open symbols indicate effect sizes calculated from residuals after accounting for overstorey effects (Fig. 4). The *P* value reported beside each data point indicates whether that effect size is significantly different from zero; *P* values ≤ 0.05 are in bold. Effect sizes are in standard deviation units and are interpreted as follows: 0.2 is small, 0.5 is medium, 0.8 is large, and >1 is very large (Gurevitch and Hedges 2001). Meta-analytic techniques are summarized in Appendix A.

increased herbaceous vegetation within the enclosures would have protected seedlings from frost-heaving (Haasis 1923), although it would also compete for water and nitrogen (Elliott and White 1987). Third,

seedling establishment outside enclosures may have been reduced by livestock trampling and/or browsing. Conifer seedlings are particularly susceptible to this type of damage in the first few years after germination

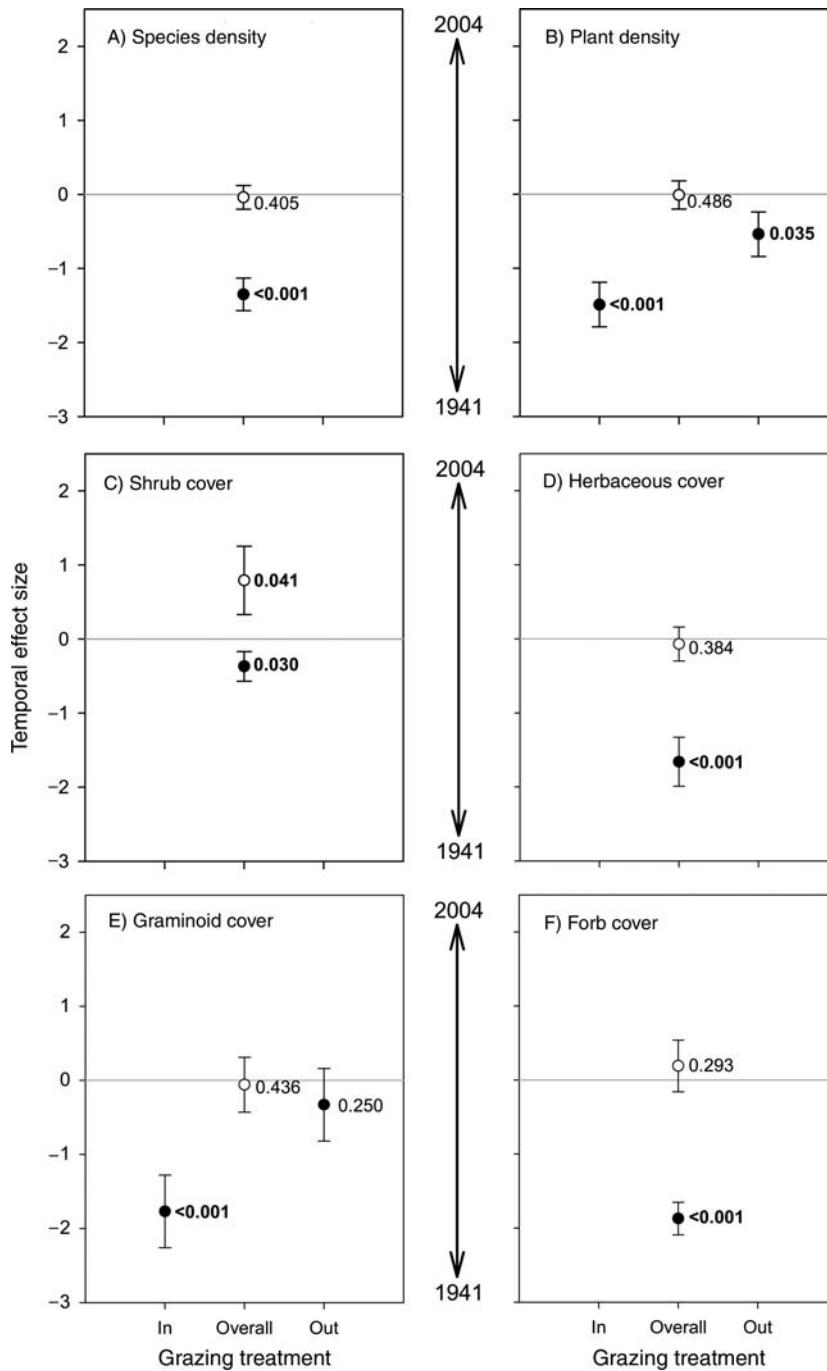


FIG. 7. Cumulated temporal effect size (mean ± SD) for (A) species density (as defined in Fig. 4), (B) herbaceous plant density, (C) shrub cover, (D) herbaceous plant cover, (E) graminoid cover, and (F) forb cover. Positive and negative effect sizes indicate larger responses in 2004 and 1941, respectively. Overall temporal effect sizes are reported (averaged across grazing treatments) unless the between-class homogeneity statistic (Q_B) indicated that effect sizes differed between treatments. Graph layout and effect size interpretations are as in Fig. 6.

(Eissenstat et al. 1982, Jiménez et al. 2005), particularly when subject to heavy grazing pressure (Pearson et al. 1971, Allen and Bartolome 1989). Early scientists in the Southwest clearly felt this was an important mechanism, and attributed lower regeneration densities

outside exclosures to damage by livestock, primarily sheep (Hill 1917, Westveld 1921, Pearson 1933).

While our results demonstrate that historical livestock grazing was a key disturbance event influencing overstory vegetation development on these sites, it was

not the only factor. Ponderosa pine regeneration patterns in the Southwest are the result of interactions between multiple factors, including historical livestock grazing, fire history, climatic conditions, and pine seed production (Meagher 1950). If these factors had not coincided, the results may have been very different (Paine et al. 1998). Silvicultural practices can also affect regeneration patterns by removing mature trees that are seed sources while creating openings and scarified sites in which seedlings can establish (Schubert 1974). Mean regeneration and mature tree densities were positively correlated in 1941 ($r^2 = 0.483$; $P = 0.0258$; $n = 10$ site \times grazing treatment combinations), suggesting that pine regeneration may have been limited in part by seed production. However, logging-related site scarification was not necessary for seedling establishment: regeneration densities were much higher at Reese Tank, which did not receive its first overstory harvest until 1940, than at the other sites, which were selectively harvested before the exclosures were built (Appendix B). Site disturbance from logging is of secondary importance with respect to pine regeneration compared to factors such as climate and seed production (Meagher 1950).

Overstory and grazing effects on understory vegetation

Grazing exclosure studies (e.g., Potter and Krenetsky 1967, Zimmerman and Neuenschwander 1984, Rambo and Faeth 1999) can provide insight into plant communities following the cessation of grazing. In forested ecosystems, it is essential that overstory–understory relationships (e.g., Arnold 1950, Moore and Deiter 1992, Nemati and Goetz 1995) be explicitly accounted for when examining the factors controlling understory vegetation. Other studies of grazing effects in ponderosa pine forests have considered overstory effects to be part of the variability between grazing treatments (e.g., Potter and Krenetsky 1967), or intentionally sampled non-treed openings (e.g., Rambo and Faeth 1999). However, failure to account for overstory effects would have substantially altered our conclusions.

A few studies have assessed the relative importance of overstory and other factors with respect to understory vegetation. Livestock preferentially graze openings rather than stands of dense timber, so vegetation responses to grazing also differ between vegetation types (Smith 1967). Logging can benefit the understory by reducing the tree canopy, unless too much logging slash accumulates (Arnold 1953). Some studies have suggested that cover of grazing sensitive grasses and overstory abundance are positively correlated in grazed areas because livestock are less likely to graze beneath the overstory (Arnold 1950, McPherson and Wright 1990), though there was no indication of a positive correlation between overstory vegetation and graminoid cover in this study. Correlations between overstory and understory variables were not as strong in this study as in other studies (Clary 1969, Mitchell and Bartling 1991,

Moore and Deiter 1992, Nemati and Goetz 1995), possibly due to differences in how variables were measured.

The herbaceous plant basal cover measurements in this study are within the range of values reported from other studies using the line intercept method (Arnold 1953, Potter and Krenetsky 1967, Anderson and Inouye 2001, Rowlands and Brian 2001). Grazing effects were smaller than overstory effects; graminoid cover was the only variable that differed between grazing treatments after accounting for overstory effects. The effects of livestock grazing on herbaceous cover varied between years. In 1941, grazing had no effect on total herbaceous cover due to the counteracting responses of graminoids and forbs as has been reported by others (Harris et al. 2003). In 2004, graminoids and forbs responded to grazing in the same manner, and total herbaceous cover tended to be higher in grazed areas. In comparison, others have reported no difference between grazing treatments (Stohlgren et al. 1999, Guenther et al. 2004) or higher herbaceous cover in ungrazed areas (Rummell 1951, Schmutz et al. 1967, Smith 1967, Allen and Bartolome 1989). Costello and Turner (1941) reported that 15 of 22 sites in ponderosa pine forests had higher plant cover in ungrazed areas. However, it is unknown whether the overstory differed between grazing treatments in many of these studies.

Total species density tended to be higher inside exclosures in 1941 but did not differ between grazing treatments in 2004. Other studies have reported no difference in species richness between grazed and ungrazed areas (Guenther et al. 2004) or lower richness in ungrazed areas (Rambo and Faeth 1999, Stohlgren et al. 1999). These comparisons are complicated, however, by the fact that diversity is scale-dependent and because the effects of grazing on diversity can vary with environmental conditions (Harrison et al. 2003, Pykälä 2004) and among years (Loeser et al. 2005).

Temporal dynamics of understory vegetation

Most understory variables exhibited similar temporal dynamics in both grazing treatments, declining dramatically between 1941 and 2004. The year 1941 was much wetter than 2004, suggesting that climatic differences could confound the interpretation of temporal changes on these sites. However, plant cover and precipitation may not be directly correlated due to interspecific differences in response to precipitation and to stochastic variation in precipitation patterns (Anderson and Inouye 2001). Also, the trends exhibited in these data are broadly similar to those recorded on permanent chart quadrats measured a few years earlier (1938, 2002–2003; J. D. Bakker and M. M. Moore, *unpublished data*). Furthermore, most of the temporal dynamics on these sites were explained by the increased dominance of the overstory; variables did not differ between years once differences in overstory abundance were accounted for. Our results indicate that estimates of overstory abun-

dance must be included when modeling understory variables at different points in time. Such information can be obtained from permanent plots (Moore et al. 2004) or via reconstruction techniques (Bakker 2005).

CONCLUSIONS

This study demonstrates that historical livestock grazing practices are an aspect of land-use history that can affect ecosystem development. Because historical livestock grazing practices can have significant long-term effects, grazing history must be considered when extrapolating results from one site to another. Relict sites that have never been grazed by livestock often exhibit lower tree densities than nearby grazed areas (Schmutz et al. 1967, Madany and West 1983; cf. Harris et al. 2003, Guenther et al. 2004), but caution should be used when interpreting results from these sites. Areas that were historically grazed but later protected from grazing (e.g., Moore et al. 2004) are more appropriate as guides to potential vegetation development.

Our study provides the first quantitative, long-term analysis of factors controlling understory vegetation structure in Southwestern ponderosa pine forests, and of how this vegetation changed between 1941 and 2004. Conditions in 1941 are obviously not “reference conditions” or “presettlement” (Moore et al. 1999); between 1912 and 1941, grass cover declined by 25% beneath pine canopies, but almost doubled in open areas (Arnold 1950). Nonetheless, changes between 1941 and 2004 provide insight into the trajectory of change that has occurred in recent decades. The understory vegetation was more strongly controlled by the ponderosa pine overstory than by recent livestock grazing or by temporal dynamics, indicating that overstory effects must be accounted for when examining understory responses in this ecosystem.

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APPENDIX A

Summary of meta-analytical techniques applied in this paper (*Ecological Archives* E088-139-A1).

APPENDIX B

Tables summarizing the canopy cover and tree density inside and outside livestock exclosures at five sites in northern Arizona in 1941 and 2004 (*Ecological Archives* E088-139-A2).

APPENDIX C

Understory variables measured inside and outside livestock exclosures at five sites in northern Arizona in 1941 and 2004 (*Ecological Archives* E088-139-A3).