Effects of past logging and grazing on understory plant communities in a montane Colorado forest

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Abstract Throughout *Pinus ponderosa–Pseudotsuga menziesii* forests of the southern Colorado Front Range, USA, intense logging and domestic grazing began at the time of Euro-American settlement in the late 1800s and continued until the early 1900s. We investigated the long-term impacts of these settlement-era activities on understory plant communities by comparing understory composition at a historically logged and grazed site to that of an environmentally similar site which was protected from past use. We found that species richness and cover within functional groups rarely differed between sites in either upland or riparian areas. Multivariate analyses revealed little difference in species composition between sites on uplands, though compositional differences were apparent in riparian

zones. Our findings suggest that settlement-era logging and grazing have had only minor long-term impacts on understories of upland Front Range *P. ponderosa–P. menziesii* forests, though they have had a greater long-term influence on riparian understories, where these activities were likely the most intense.

Keywords Community composition ·
Pinus ponderosa C. Lawson · Multivariate analyses ·
Pseudotsuga menziesii (Mirbel) Franco ·
Riparian areas · Species richness

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Introduction

Human activities have impacted nearly all of the world's ecosystems, and often these activities have adversely affected critical ecosystem components and processes (Vitousek et al. 1997). In *Pinus ponderosa* C. Lawson—dominated forests of the Rocky Mountains, USA, intense land use including logging, domestic grazing, and fire suppression began at the time of European-American settlement in the mid to late 1800s (Cooper 1960; Dillon et al. 2005; Veblen and Donnegan 2005). Researchers have recently begun to investigate how this past land use has altered forest overstories from the pre-settlement condition by examining early photographs, written descriptions, and scientific studies, and also by reconstructing historical stand conditions from living and remnant woody material (e.g., Brown and Cook

2006; Fulé et al. 1997; Kaufmann et al. 2001). Their findings suggest that past logging, grazing, and fire suppression have generally homogenized forest structure and increased stand density by removing the largest and oldest trees, encouraging tree establishment and growth, and decreasing tree mortality due to fire.

Past land use can also cause long-term departures from the pre-settlement condition in forest understories, though these changes are more difficult to assess because detailed information about the pre-settlement understory condition is often unavailable. Settlement-era photographs seldom focused on understory vegetation. Early reports and scientific papers describing the understory often list common species (e.g., Cooper 1960; Leiberg et al. 1904; Schneider 1911), but they rarely contain quantitative data. Annual growth rings and other 'natural records' are of limited use for reconstructing historical forest understories because most species are herbaceous and decompose quickly (Swetnam et al. 1999). Any preserved plant material that may remain on site (e.g., in soils, lake sediments, or packrat middens) is generally of limited spatial, temporal, and/or botanical resolution (but see Anderson et al. 2000 and citations therein; Kerns et al. 2003). Alternative approaches are therefore needed to provide detailed information about historical forest understories.

Areas that have been minimally disturbed by human activities can provide insight into the pre-settlement understory condition, and this approach has been implemented in several *P. ponderosa*—dominated ecosystems. In Utah, Madany and West (1983) compared an ungrazed relict site to a site that was grazed by livestock from the late nineteenth to the early twentieth century, and found that past grazing has reduced herbaceous plant cover and increased the cover of woody species over the long-term. In Arizona, Gildar et al. (2004) compared the understory community of a site with 120 years of fire suppression to sites where the historic fire regime has remained relatively intact, and found that plant community structure was related to fire history, but within-site variability was also an important driver. Similarly, Keeling et al. (2006) found evidence that fire suppression has altered *P. ponderosa–Pseudotsuga menziesi* (Mirbel) Franco understories of Idaho and Montana to some degree, though environmental
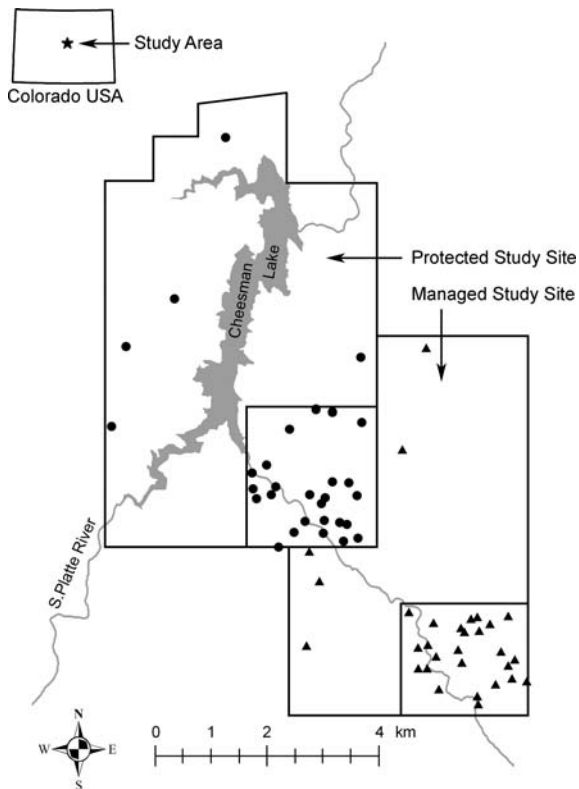
variability was a stronger force in shaping the understory community.

In montane forests of the southern Colorado Front Range, heavy logging and domestic grazing began in the late 1800s and continued until the early 1900s (Jack 1900; Veblen and Donnegan 2005). Our objective was to investigate the long-term impacts of these settlement-era activities by comparing the understory community within a logged and grazed *P. ponderosa–P. menziesii* forest to that of an environmentally similar site which was protected from past land use. Fire suppression has occurred in both study sites since European-American settlement, so its effects cannot be discerned here. Because logging and grazing were often more intense in riparian areas than on upland slopes (Jack 1900; Veblen and Donnegan 2005), and because large within-site variability may mask more subtle effects of past land use (e.g., Gildar et al. 2004), we also compared the two sites separately for each of five topographic categories (north, south, and east/west slopes; ridgetops; and riparian areas).

Methods

Study area

Our study area is in the southern Front Range Mountains of Colorado, USA, approximately 60 km southwest of Denver (Fig. 1). Forests here are dominated by *P. ponderosa* and *P. menziesii*, with *Juniperus scopulorum* Sarg., *Picea pungens* Engelm., and *Populus tremuloides* Michx. occurring intermittently. Precipitation averages 40 cm annually, most of which falls during the spring and summer (www.wrcc.dri.edu). January is the coldest month, with average highs of 7.3°C and average lows of −13.0°C; the warmest temperatures occur in July, when maximum daytime temperatures average 28.9°C (www.wrcc.dri.edu). Soils on upland slopes and ridgetops are gravelly coarse sandy loams derived from weathered Pike's Peak granite, and are highly erodible (USDA Forest Service 1992). In drainage bottoms, soils are also of granitic origin but are generally finer, more developed, and less susceptible to erosion. Elevations range from 2100 to 2500 m in the areas we sampled.

Fig. 1 Location of protected (●) and managed (▲) plots in the Colorado Front Range, USA

Fig. 2 Lopped and scattered tree branches lay on the ground after a settlement-era timber harvest near the managed study site. Photo courtesy of the Pike National Forest

This area has experienced a considerable amount of human activity since it was settled by European-Americans in the mid to late 1800s, with the heaviest use coming from settlement-era loggers and ranchers. Widespread, unregulated logging occurred from the 1880s to the 1900s when several local lumber mills were established, and nearly all merchantable timber was removed (Fig. 2; Delay 1989; Jack 1900). Unregulated grazing by domestic cattle also occurred from the 1880s to the 1900s, and many areas were severely overgrazed (DeLay 1989; Gary and Currie 1977; Jack 1900). Logging and grazing largely ceased in 1906 when the Pike National Forest was established, and since then only a limited amount of logging and grazing has occurred. Prospectors flooded the area in the early 1890s when rumors of gold discovery first surfaced, but precious metals were never found and mining activity ceased within the decade (DeLay 1989). In the 1930s, the Civilian Conservation Corps planted *P. ponderosa* trees in select locations to help reforest heavily logged and

grazed areas (DeLay 1989; Gary and Currie 1977). Since the 1930s, the region has been used mainly for recreation, and trails and campgrounds are abundant.

Study sites

We established two adjacent ~30 km^2 study sites (Fig. 1), each with markedly different land use histories since European-American settlement (Brown et al. 1999; Kaufmann et al. 2000). The 'managed' site is located on the Pike National Forest, and land use history within the site is representative of the study area. Historical records and tree-ring data indicate that the managed site was intensively logged in the 1890s, but it does not appear to have been logged since (DeLay 1989; Jack 1900; Huckaby unpublished data). Though we do not have direct evidence of grazing, records indicate that several families homesteaded ranches in the immediate vicinity during the settlement era (DeLay 1989; Riddle and Kane 1991), and it is likely that the timing and intensity of domestic grazing here coincided with that of the region. Grazing has not occurred since the 1900s (Sheila Lamb, South Park Ranger District, personal communication). Prospecting activities were limited to a handful of small isolated test pits which were likely dug during the mining era (Riddle and Kane 1991). There are no records of tree planting and

tree ages do not correspond with known planting periods (Kaufmann et al. 2000; Huckaby unpublished data). The site has been lightly used for recreation for several decades. A four-wheel-drive road runs near the site's southern edge and through its southwest corner. There are no designated trails within the site, though it does contain closed logging roads which are accessible to hikers. A campground and a popular rock climbing area are nearby.

The 'protected' study site is located in the forest surrounding Cheesman Lake, a reservoir on the South Platte River. The reservoir and the surrounding forest have been owned and managed by the Denver Water Board since the 1890s. This site has been impacted only minimally by human activities. Prior to the 1890s, the site likely received very limited use from loggers, ranchers, or prospectors due to poor access (Riddle and Kane 1991). Some logging occurred during dam construction from 1894 to 1905, but was mostly below the current water line of the reservoir. After the dam was completed, a six-string fence was constructed around the property to exclude trespassing from loggers, prospectors, and domestic livestock. Cheesman Lake and the surrounding property have been closed to public recreation since 1905, except for shoreline fishing and limited hiking. There is no record of tree planting on the property.

All wildfires within the two sites have been suppressed since the early 1900s. Fire scars indicate that a handful of twentieth century wildfires burned in some plots (Brown et al. 1999), but were extinguished before they spread over more than a few hectares. However the 2002 Hayman Fire, which occurred after we completed our study, burned 55,800 ha including our sites. Portions of the managed site experienced light prescribed burning in 1987 and 1990.

We established 30 plots at the protected site and 30 at the managed site (Fig. 1). To minimize environmental differences between sites, 25 plots at each site were located within an intensively sampled 4-km^2 (2 km × 2 km) area. The 4-km^2 areas are similar in elevation, topography and soils, and are separated by a distance of only 1 km. Plots within the 4-km^2 areas were randomly located and equally distributed among five topographic categories: north-facing slopes, east-or-west-facing slopes, south-facing slopes, ridgetops, and riparian areas. Five additional plots per site were also randomly established across the remainder of the protected and managed sites, with one plot per

topographic category. All plots were located in forested areas. North, east/west, and south plots were situated in upland areas with slopes between 15 and 35%; the long axis of the plot was aligned down the fall line. Ridgetop plots were also in upland areas (slope <10%), with the long axis parallel to the ridge. Riparian plots were located above the banks of permanent streams, but could cross intermittent streams; plot aspect could vary, but slope had to be <15%. The long axis of riparian plots was parallel to the stream channel. Kaufmann et al. (2000) provide additional information about the study site selection process and plot establishment protocols.

Data collection

Field data were collected during June 1996 and June–July 1997. Although year-to-year variation in understory communities may occur due to differences in precipitation, monthly growing season (April–July) precipitation at Cheesman Lake did not differ between 1996 and 1997 (www.wrcc.dri.edu). Moreover, the variable 'year of sampling' was poorly correlated with understory composition in our ordination (results not shown).

We collected understory data in each plot using the modified-Whittaker sampling design (Stohlgren et al. 1995). In this design, the main plot is 1000 m^2, and contains one 100-m^2 subplot, two 10-m^2 subplots, and ten 1-m^2 subplots nested within it. We ocularly estimated vegetative cover for each species in the 1-m^2 subplots. Tree species were included in vegetative cover estimates only if they were less than breast height (1.4 m) tall. Species presence was recorded within the 10-m^2 subplots, the 100-m^2 subplot, and the 1000-m^2 plot. While phenological changes during the field season could not be avoided, we sampled the 60 plots in random order to minimize the effect of these changes on data quality.

Nomenclature follows the USDA Plants Database (2007), though varieties and subspecies were not distinguished. Of the 9,729 plant observations made during this study (e.g., an individual species in an individual subplot is one observation), 92.0% could be identified to genus and species, 5.9% could be identified to genus, and 2.1% could not be identified at all. Generic observations were generally due to a small number of genera for which we did not attempt to distinguish all individual species, either because

hybridization is common (e.g., *Rosa*), or because species are difficult to differentiate when sampled outside peak phenological development (e.g., *Carex*, *Chenopodium*). Generic observations were included in our analyses, while unidentified observations were excluded.

We determined the growth form (forb, graminoid, shrub, and tree) and lifespan (short- or long-lived) of each species using the USDA Plants Database (2007), local botanical keys, and our knowledge of the species. Growth form and lifespan were determined for generic identifications only when the classification was appropriate for all species known to occur in montane Front Range forests. Short-lived species included annuals and biennials, as well as species considered to be biennial/perennial and annual/biennial/perennial (e.g., *Bahia dissecta* (A. Gray) Britton). Only true perennials were considered long-lived. We then integrated growth form and lifespan information for each species by further classifying it into one of four functional groups: short-lived forbs, long-lived forbs, graminoids, and woody plants. Short-lived graminoids were scarce and were not separated into their own category.

Environmental attribute data were collected for each plot (Table 1). These attributes can be broadly grouped as describing a plot's (1) disturbance history; (2) topography; (3) distance to roads and streams; (4) overstory structure; (5) forest floor; and (6) sampling year. Three of the disturbance history variables, the age of the oldest tree, the year of the last fire, and the year of the last stand-replacing fire, were determined from tree age and fire scar data collected by Brown et al. (1999) and Kaufmann et al. (2000). A fourth disturbance variable, land use history, indicated whether the plot was in the protected or managed site. Topographic variables included slope, elevation, and topographic category. Distance to the nearest stream and road (including former logging roads) was calculated from plot coordinates and GIS coverages obtained from the Pike National Forest. The overstory variables basal area and trees per hectare were calculated from diameter at breast height data collected for all live trees in a plot; only trees over 1.4 m tall were included in the calculation. Forest floor variables included the cover of duff, lichen, litter, moss, rock, soil, and wood, which were measured in the 1-m^2 subplots and averaged. Sampling year was 1996 or 1997.

Table 1 Environmental attributes measured in this study, and their ranges in protected and managed plots

Variable	Protected	Managed
Disturbance variables		
Land use history	1	2
Year of last fire	1587–1963	1851–1990
Year of last stand-replacing fire	1531–1851	1723–1851
Year of oldest tree germination	1522–1887	1617–1883
Topographic variables		
Topographic category	1–5	1–5
Slope (%)	0–36	0–35
Elevation (m)	2098–2346	2242–2494
Distance variables		
Distance to nearest stream (m)	14–809	0–432
Distance to nearest road (m)	37–2169	0–1040
Overstory variables		
Trees per ha	91–1176	184–2621
Tree basal area (m^2 per ha)	4.6–28.2	10.4–40.6
Forest floor variables		
Duff (%)	0–46	0–11
Lichen (%)	0–15	0–8
Litter (%)	20–92	32–76
Moss (%)	0–9	0–26
Rock (%)	0–32	0–18
Soil (%)	1–75	4–48
Wood (%)	0–11	0–19
Sampling variables		
Year measured	1996–1997	1996–1997

Univariate analyses

We used univariate multi-response permutation procedures (MRPP) to test for differences in functional group richness and cover between sites. MRPP is a nonparametric procedure for detecting differences among two or more groups that is not limited by assumptions of normally-distributed data or of homogeneous variances (McCune and Grace 2002; Mielke and Berry 2001). Richness within each functional group was calculated by tallying the number of short-lived forb, long-lived forb, graminoid, and woody species per 1000-m^2 plot. We calculated cover variables by averaging cover estimates for each species across the 1-m^2 subplots, then summing across a plot by functional group. We tested for functional group differences between sites using α of 0.05. We also tested for differences between sites by

topographic category; each of these tests was evaluated with a Bonferoni-adjusted α of 0.01 to maintain type I error (overall α of 0.05 divided by five topographic categories). We performed our analyses in Microsoft Excel using the procedure outlined in Mielke and Berry (2001) because univariate MRPP analyses cannot be easily conducted with most statistical packages.

Multivariate analyses

All multivariate analyses were conducted with PC-ORD version 5.0 (MjM Software Design, Glendon Beach, Oregon, USA) using the cover data for each species (averaged across the 1-m^2 subplots). We omitted all species whose cover was measured only in one or two plots following the recommendations of McCune and Grace (2002).

We conducted multivariate MRPP analyses using the Sørensen distance measure to test for differences in community composition between sites (McCune and Grace 2002). As with the univariate MRPP analyses, we tested for overall differences between sites ($\alpha = 0.05$), and also for differences between sites for each of the topographic categories ($\alpha = 0.01$).

We ordinated the understory cover dataset using non-metric multi-dimensional scaling (NMS) to investigate relationships between community composition and our measured environmental factors. All ordinations used the Sørensen distance measure, 250 runs with real data, a maximum of 500 iterations per run, and a stability criterion of 0.00001. We first assessed the dimensionality of our data set by running preliminary ordinations with up to six axes and with random starting configurations. We concluded that a three-dimensional solution was optimal because additional axes provided only slight reductions in stress, a measure of 'badness-of-fit'; results of a Monte Carlo test with 250 randomizations indicated that stress for this solution was lower than expected by chance ($P = 0.004$). We then ran a final three-dimensional ordination using the best final configuration from the preliminary three-dimensional runs as our starting configuration. Correlation coefficients between each environmental variable and the three NMS axes were calculated, and environmental variables that were correlated with one or more axes ($|r| \geq 0.4$) were overlaid on the ordination as vectors.

The angle and length of the vector denotes the direction and strength of the relationship. If an NMS axis was correlated with multiple environmental variables, interrelationships among the axis scores and the environmental variables were further explored with multiple regressions in SAS 9.1 (SAS Institute Inc., Cary, North Carolina, USA). Nonsignificant variables were iteratively excluded from the regressions until only significant ($P < 0.05$) variables remained. The categorical variables land use history and topographic category were treated as ranked quantitative variables for these procedures. For land use history, we assigned a value of 1 to the protected plots and 2 to the managed plots. Topographic categories were assigned a value from 1 to 5 based on our a priori perception of water availability; riparian plots were assigned a value of 1 (most mesic), north plots 2, east/west plots 3, south plots 4, and ridgetop plots 5 (most xeric).

When multivariate MRPP indicated significant differences in community composition between sites, we conducted indicator species analyses (ISA) to determine if any species were representative of a particular site (McCune and Grace 2002). This procedure combines information about the frequency and abundance of a species in a group of plots relative to other groups to generate an indicator value (IV) for the species in each group. An IV of 0 denotes that the species is not present within a group while an IV of 100 denotes that the species is both exclusive to and always present in a group. For all analyses, we tested the significance of each IV using a Monte Carlo simulation with 5000 randomizations. A species was a significant indicator if IV ≥ 30 and $P < 0.05$.

Results

We identified 237 species within the 60 plots, with 152 species present in both sites. Thirty-two of the species were short-lived forbs, 119 were long-lived forbs, 44 were graminoids, and 33 were woody plants. Nine species, which were identified to genus only, could not be classified into functional groups due to variability within the genus. Dominant understory species included *Artemisia ludoviciana* Nutt., *Geranium caespitosum* James, *Mertensia lanceolata* (Pursh) DC., and *Muhlenbergia montana* (Nutt.)

Hitchc.; these species occurred on 90% or more of the plots at both sites. Only a handful of exotic species were found, with *Taraxacum officinale* F. H. Wigg and *Verbascum thapsus* L. being among the most common. A detailed analysis of exotics is reported in Fornwalt et al. (2003).

Univariate analyses

Few differences in functional group richness or cover were found between the two sites. Overall, the protected site had greater woody plant richness and cover than the managed site, though the two sites did not differ overall in the richness or cover of short-lived forbs, long-lived forbs, or graminoids (Table 2). When the two sites were compared by topographic categories, only woody cover differed, and this difference was limited to riparian areas (Table 2).

Multivariate analyses

Multivariate MRPP demonstrated that differences in species composition existed between the protected and managed sites overall ($P < 0.001$). Analyses by
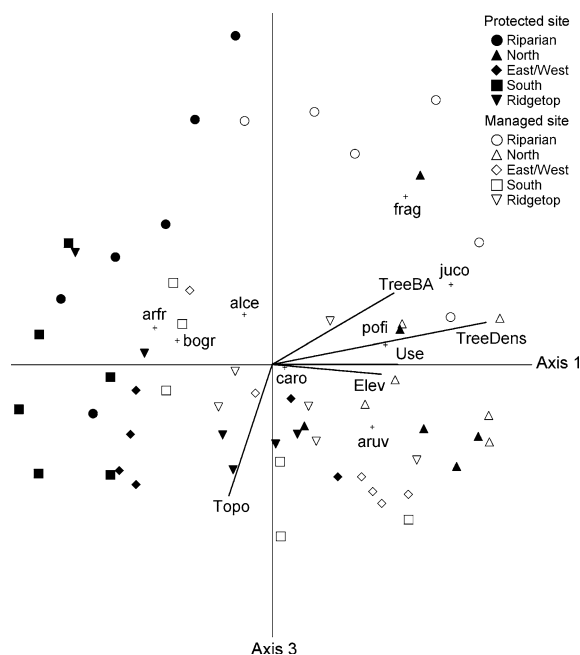
Table 2 Means and standard deviations for species richness and cover by functional groups

	Richness (1000 m^2)			Cover (%)		
	Protected	Managed	*P*-value	Protected	Managed	*P*-value
Short-lived forbs						
Overall	5.8 ± 3.2	5.0 ± 3.7	0.441	0.4 ± 0.6	0.5 ± 0.6	0.451
Riparian	9.0 ± 3.8	7.7 ± 4.7	0.494	1.2 ± 1.0	1.1 ± 0.8	0.844
North	3.0 ± 1.3	3.5 ± 2.3	0.610	0.0 ± 0.1	0.3 ± 0.3	0.080
East/West	6.5 ± 2.8	4.2 ± 3.6	0.281	0.2 ± 0.2	0.2 ± 0.2	0.896
South	4.8 ± 1.7	7.5 ± 2.3	0.061	0.2 ± 0.2	0.5 ± 0.5	0.093
Ridgetop	5.7 ± 2.9	2.3 ± 2.2	0.084	0.2 ± 0.2	0.3 ± 0.5	0.550
Long-lived forbs						
Overall	24.8 ± 7.2	26.2 ± 7.9	0.852	8.4 ± 6.9	8.2 ± 6.4	1.000
Riparian	34.0 ± 7.6	38.5 ± 7.6	0.268	17.0 ± 10.8	16.4 ± 9.1	0.844
North	25.5 ± 5.8	24.0 ± 4.6	0.896	7.6 ± 4.6	7.5 ± 5.0	1.000
East/West	23.3 ± 2.0	21.8 ± 4.5	0.191	6.2 ± 2.3	4.9 ± 3.1	0.429
South	17.7 ± 4.5	21.8 ± 3.4	0.188	3.7 ± 2.0	6.8 ± 3.5	0.132
Ridgetop	23.5 ± 3.7	24.8 ± 3.7	0.844	7.6 ± 2.2	5.6 ± 2.1	0.204
Graminoids						
Overall	9.3 ± 3.0	8.3 ± 3.1	0.188	7.9 ± 5.0	7.3 ± 5.8	0.727
Riparian	12.8 ± 3.9	13.0 ± 2.4	1.000	10.1 ± 7.4	10.3 ± 8.9	1.000
North	8.3 ± 2.8	6.8 ± 2.6	0.481	3.6 ± 1.1	4.9 ± 3.8	0.281
East/West	8.7 ± 1.2	6.3 ± 2.1	0.061	8.5 ± 2.8	6.5 ± 5.2	0.141
South	7.3 ± 1.4	7.3 ± 1.4	1.000	5.8 ± 3.3	5.4 ± 2.9	0.671
Ridgetop	9.5 ± 1.9	8.2 ± 1.0	0.307	11.5 ± 4.7	9.2 ± 6.2	0.351
Woody plants						
Overall	**7.2 ± 2.8**	**9.3 ± 4.2**	**0.015**	**6.9 ± 7.0**	**12.0 ± 8.2**	**0.010**
Riparian	10.3 ± 4.6	16.2 ± 4.3	0.041	**7.1 ± 6.9**	**22.4 ± 7.2**	**0.009**
North	7.8 ± 2.0	7.7 ± 1.6	1.000	12.8 ± 6.6	12.5 ± 9.4	0.671
East/West	6.0 ± 0.6	7.8 ± 1.9	0.041	4.7 ± 7.0	8.4 ± 4.6	0.169
South	5.5 ± 0.8	7.3 ± 2.4	0.091	1.5 ± 2.0	8.0 ± 6.7	0.018
Ridgetop	6.5 ± 1.4	7.7 ± 1.9	0.292	8.3 ± 7.2	8.7 ± 3.0	0.541

Differences in functional group richness and cover between the protected and managed sites are indicated in bold (for overall test, $\alpha = 0.05$; for topographic category tests, $\alpha = 0.01$ to adjust for multiple comparisons)

individual topographic categories revealed that differences were restricted to riparian areas ($P = 0.004$); community composition did not differ between the protected and managed sites for any of the four upland categories (north: $P = 0.119$; east/west: $P = 0.133$; south: $P = 0.013$; and ridgetop: $P = 0.225$).

The three-dimensional NMS ordination represented 79.1% of the total variation in the understory cover distance matrix, with axes one, two, and three explaining 30.1, 16.1, and 32.8% of the variation, respectively (Fig. 3; final stress = 15.77; instability <0.00001). Protected plots separated from managed plots along axis one, with moderate overlap. Plots also separated along axis three by topographic category, with the riparian plots distributed in the top half of the ordination diagram and upland plots in

Table 3 Environmental variables and their correlation with the three NMS ordination axes

Variable	Correlation (r)		
	Axis 1	Axis 2	Axis 3
Land use history	**0.500**	−0.097	0.010
Topographic category	−0.294	−0.328	**−0.510**
Elevation (m)	**0.466**	−0.364	−0.139
Trees per ha	**0.652**	0.037	0.290
Tree basal area (m^2 per ha)	**0.492**	−0.008	0.376

Only variables with $|r| \geq 0.4$ for one or more axes are shown (values are in bold)

the bottom half. Axis one was correlated with the environmental variables land use history, elevation, trees per hectare, and tree basal area, while axis three was correlated with topographic category; axis two was not correlated with any environmental variables ($|r| \geq 0.4$; Fig. 3; Table 3). When interrelationships between axes one and the four correlated environmental variables were further explored with multiple regression, land use history and trees per hectare were significant in the final model, but elevation and tree basal area were not ($P = 0.001$, $P < 0.001$, $P = 0.519$, and $P = 0.341$, respectively). Land use history and trees per hectare were correlated to each other to some degree ($r = 0.317$), though each was also correlated to axis one when the other was explicitly controlled for using partial correlations (land use: $r = 0.408$; trees per acre: $r = 0.601$).

The ISA identified three indicator species for the protected site and six for the managed site (Table 4). Species indicative of the protected site included *Allium cernuum* Roth, *Artemisia frigida* Willd., and *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, while species associated with the managed site included *Arctostaphylos uva-ursi* (L.) Spreng., *Carex rossii* Boott, *Fragaria* sp. L., *Juniperus communis* L., and *Potentilla fissa* Nutt. ISA for individual topographic categories was only conducted for riparian areas because multivariate MRPP indicated that composition was similar between sites for the four upland categories. Riparian areas in the protected site were identified by *Schizachyrium scoparium* (Michx.) Nash (IV at protected site = 77; IV at managed site = 1; $P = 0.015$), while the managed site was identified by *Fragaria* sp. L. (IV at protected site = 2; IV at managed site = 94; $P = 0.005$).

Fig. 3 Axes one versus three of an NMS ordination of species cover in protected and managed plots. Environmental variables that were correlated with the ordination axes ($|r| \geq 0.4$) are overlaid as vectors (Table 3). Environmental variables include: TreeBA = tree basal area; TreeDens = trees per hectare; Use = land use history (protected or managed); Elev = elevation; Topo = topographic category. Species indicative of the protected and managed sites are also shown (Table 4): alce = *Allium cernuum*; arfr = *Artemisia frigida*; bogr = *Bouteloua gracilis*; aruv = *Arctostaphylos uva-ursi*; caro = *Carex rossii*; frag = *Fragaria* sp.; juco = *Juniperus communis*; pofi = *Potentilla fissa*

Table 4 Indicator species of protected and managed study sites

Species	IV protected	IV managed	*P*-value
Protected site			
Allium cernuum Roth	34	6	0.040
Artemisia frigida Willd.	37	8	0.043
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	68	10	<0.001
Managed site			
Arctostaphylos uva-ursi (L.) Spreng.	16	56	0.004
Carex rossii Boott	27	63	0.002
Fragaria L.	1	30	0.030
Juniperus communis L.	0	33	0.001
Potentilla fissa Nutt.	3	48	<0.001

Only species with an indicator value (IV) ≥30 and a Monte Carlo *P*-value <0.05 were considered indicators of a particular site

Discussion

Given this area's intensive settlement-era use, we expected to find major differences in understory communities between protected and managed sites. We did not. Rather, our overall comparisons between protected and managed sites provide only modest indications that heavy logging and grazing from the late 1800s to the early 1900s have caused long-term changes to forest understories. Differences in functional group richness and cover between sites were few, and while multivariate MRPP and NMS ordination suggest that community composition differed somewhat between sites, the relatively short list of indicator species implies that the abundance of most species was similar (Fig. 3; Tables 2, 4).

Though overall compositional differences between the protected and managed sites were not overwhelming, they nonetheless may be due to both direct and indirect impacts of past land use. For example, grazing often directly reduces the abundance of palatable species while allowing unpalatable species to increase (Smith 1967). Our list of indicator species for the protected and managed sites is consistent with this finding. *Artemisia frigida* and *Bouteloua gracilis*, indicators of the protected site, are palatable to livestock but can decline under continuous heavy grazing, while indicators of the managed site, especially *Arctostaphylos uva-ursi* and *Juniperus communis*, are not typically grazed by cattle (Table 4; USDA Forest Service 2007). Logging and grazing can also encourage overstory tree regeneration and growth, and therefore they may indirectly alter understory composition over the long-term by favoring

shade-tolerant understory species (Belsky and Blumenthal 1997 and citations therein; see Bakker and Moore 2007 for an exception). Indeed, the managed site tended to have greater overstory tree density than the protected site (Fig. 3; Table 1; Kaufmann et al. 2000); furthermore, the species indicative of the protected site are relatively shade-intolerant species that thrive in open Front Range forests, while some indicators of the managed site generally occur in shadier environments (Table 4; Powell 1987; USDA Forest Service 2007).

When we compared the protected and managed sites by topographic category, we found that the degree of understory community change due to past logging and grazing varied greatly with topography. We found little to no evidence of long-term logging and grazing impacts in upland areas; functional group richness and cover were similar between the protected and managed sites (Table 2), and differences in community composition between sites were not detected in the multivariate MRPP analyses. However, there was more evidence of past logging and grazing impacts in riparian areas (Fig. 3; Table 2). Given the history of human use in Front Range riparian areas, it is not surprising that we found greater understory differences in these locations than in their upland counterparts. Throughout the Rocky Mountains, riparian areas were generally more heavily grazed by livestock than uplands (Belsky and Blumenthal 1997), and Jack (1900) and Gary and Currie (1977) both noted heavy grazing damage along streams only a few kilometers from our sites. Unfortunately, early written documents never indicate whether riparian zones were more thoroughly

logged than upland slopes, though this is probable since they tend to support a greater number of large trees (Kaufmann et al. 2000). We do know that logs were not floated down streams and rivers near our sites, a practice that occurred elsewhere in the region (Delay 1989; Jack 1900). Early settlers also preferred riparian areas for setting up camps and homesteads; the remains of one such dwelling can be found in one of our managed riparian plots.

Taken as a whole, the results presented here suggest that Front Range understory communities are generally resilient to past logging and grazing impacts over the long-term. However, this does not mean that rampant land use is justified in Front Range forests; rather, these results highlight the fact that many of the native understory species are highly adapted to a range of disturbances and growing environments. Grazing is part of the Front Range's natural disturbance regime, though grazing by wildlife was probably never as intense as livestock grazing (Veblen and Donnegan 2005). The majority of species also exhibit regeneration strategies that promote survival or rapid re-establishment after disturbance, such as sprouting, seed banking, and long-distance seed dispersal (Fornwalt unpublished data). Finally, though many of these species prefer open, high-light environments, some can tolerate shady forests as well (USDA Forest Service 2007).

A weakness of our study is the fact that our study sites are unreplicated. Unfortunately, this was unavoidable because the area surrounding Cheesman Lake contained only one of the known *P. ponderosa–P. menziesii* forests in the Front Range that had not been subjected to logging and grazing, and even it was lost as a research resource in the 2002 Hayman Fire. Though the protected and managed sites do differ slightly in elevation, the elevational effect probably is minimal because the elevational ranges at the sites overlap substantially, and elevation was not significant in the regression analyses. Moreover, the two sites are adjacent to one another, separated only by a fence, and both are situated in the middle of the elevational range for the *P. ponderosa–P. menziesii* vegetation type. Despite this inescapable constraint on our study design, our results lead us to conclude that settlement-era logging and grazing have had only modest influences on understories of Front Range *P. ponderosa–P. menziesii* forests, and this influence is largely restricted to riparian areas. Additional site-specific comparisons of this kind are needed to determine how applicable our conclusions may be to other *P. ponderosa*—dominated landscapes in the Rocky Mountains.

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