



# Long-term Protection from Heavy Livestock Grazing Affects Ponderosa Pine Understory Composition and Functional Traits☆☆☆



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## ABSTRACT

Making accurate predictions of plant community responses to grazing management is a major objective of rangeland ecology. Metrics such as species composition are site specific, whereas others such as functional groups and functional traits can be generalized across different rangeland types. We analyzed long-term (1912–1941) shifts in the understory community at five sites in a ponderosa pine (*Pinus ponderosa* P. & C. Lawson var. *scopulorum* Engelm.) forest when protected from heavy livestock grazing. We examined differences in total basal cover, species composition, species richness, functional group composition, and community-weighted mean (CWM) functional traits between heavily grazed and ungrazed areas in four time periods (1912, 1920, 1930, 1940). Total understory basal cover was greater in ungrazed than heavily grazed areas in 1920 but not in later time periods. Understory species composition diverged by 1930 and continued to differ in 1940. Functional group composition differed from 1920 onwards. In 1920 and 1930, C<sub>3</sub> graminoids declined more in relative abundance in heavily grazed than ungrazed areas. By 1940, forbs accounted for much more of the cover in heavily grazed than ungrazed areas. During the study period, CWM specific leaf area and foliar N<sub>mass</sub> declined by 8% and 11%, respectively, in ungrazed quadrats, while CWM leaf dry matter content increased 8%. Leaf traits, but not maximum height or seed mass, demonstrated consistent and predictable responses to protection from heavy grazing. Herbaceous understory species with leaf traits that allow for slower resource acquisition became more abundant in response to protection from heavy grazing. Our results indicate that managers should expect to observe more rapid changes in functional group composition and leaf functional traits than in species composition and species richness following protection from heavy livestock grazing.

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## Introduction

Grazing by domestic ungulates is one of the most widespread forms of land use world-wide (Díaz et al., 2006). Research on the impacts of grazing (here, referring specifically to livestock grazing) has largely focused on understanding shifts in species composition (Milchunas and Lauenroth, 1993). However, this approach may have hindered a broader understanding of the processes underlying

community-level responses to grazing because it does not allow for generalizations beyond a specific locality (Vesk and Westoby, 2001).

Given the degree to which land-use change impacts plant biodiversity (Chapin et al., 2000), understanding the functional consequences of grazing can improve management of rangelands. Identifying consistent shifts in plant functional strategies (as quantified by functional groups or plant traits) in response to grazing can improve regional and global models of vegetation dynamics (Díaz et al., 2006). While livestock grazing is one of the factors resulting in dramatic increases in tree density (Bakker and Moore, 2007) and shifts in plant community composition (Arnold, 1950; Cooper, 1960; Clary, 1975; Milchunas, 2006) across the Southwest US, relatively little attention has been given to functional responses following protection from heavy grazing (Arnold, 1955).

Plant functional classifications have received much attention from ecologists seeking predictable patterns in response to disturbance, particularly grazing (McIntyre et al., 1999). A classification

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based on life history strategies is common and has revealed a common pattern with increased grazing pressure favoring annual versus perennial plant species (Arnold, 1955; Milchunas and Lauenroth, 1993; McIntyre and Lavorel, 2001). Many classification schemes exist (Smith et al., 1997), including the well-established GFL classification of graminoids (G), nonleguminous forbs (F), and legumes (L) (Wright et al., 2006). Graminoids are often further refined by distinguishing between taxa with C<sub>3</sub> (cool season) and C<sub>4</sub> (warm season) photosynthetic pathways to reflect phenological differences and because utilization by grazers varies with grazing season (Smith, 1967).

A more recent alternative is to consider continuously distributed plant functional traits instead of categorical functional groups. Functional traits influence vegetation dynamics, community response to disturbance, and ecosystem function (Pakeman and Quested, 2004). Westoby (1998) proposed a leaf-height-seed (LHS) scheme that quantifies plant strategies by locating species in a three-dimensional trait space defined by specific leaf area (SLA), vegetative height, and seed mass. These traits play a central role in a plant's ability to capture resources, compete, and regenerate. The leaf economics spectrum represents a gradient of resource acquisition rates (Wright et al., 2004) and can be examined using a set of coordinated traits: SLA, leaf dry matter content (LDMC), and leaf nitrogen concentration (foliar N<sub>mass</sub>) (Laughlin et al., 2010). Leaves with high SLA have low LDMC and high foliar N<sub>mass</sub>; species with this set of coordinated traits tend to have high relative growth rates stemming from high net photosynthetic capacity (Reich et al., 1997; Wright et al., 2004). Maximum vegetative height at maturity primarily reflects a species' competitive ability. In ecosystems where light is limited, taller plants have the potential to realize faster growth rates due to their ability to intercept more light (Poorter et al., 2008). Seed mass reflects variation in a species' ability to disperse to and colonize sites. Seed mass also reflects a fundamental tradeoff between seed size and reproductive output. Larger-seeded species produce fewer seeds for a given reproductive effort; however, seedlings of these species have more reserves with which to establish in low-resource environments (Kitajima, 2002) and are better equipped to tolerate defoliation (Armstrong and Westoby, 1993).

Westoby (1999) related the LHS scheme to grazing response. He proposed that under heavy non-selective grazing, high SLA species should be at a competitive advantage due to faster regrowth. Taller species should decrease in abundance because they would receive more attention from livestock. Species that produce large quantities of small seeds should increase in abundance because heavy grazing would create many gaps in which seedling establishment could occur. These responses are based on the underlying concept that through the selective removal of plant material, grazing affects a plant's ability to capture resources, compete, and regenerate (Grime, 1977; Noy-Meir et al., 1989). As grazing intensity increases, selection is thought to favor less competitive species adapted to rapidly acquire resources under temporarily favorable conditions. Alternatively, by excluding grazing from the environment, competition for light and nutrients should increase.

Some prior work has examined the effects of grazing on plant traits. Vegetative height has long been a key functional trait thought to reflect a mechanism of grazing avoidance, with increased levels of grazing intensity consistently favoring shorter plants (Dyksterhuis, 1949; Arnold, 1955; Díaz et al., 2001; Díaz et al., 2006). Seed mass, SLA, foliar N<sub>mass</sub>, LDMC, and leaf toughness have been used to understand and predict the impact of grazing because these traits are thought to reflect a general trade-off in growth versus defense (Moles and Westoby, 2004; Adler et al., 2004; Cingolani et al., 2005; Louault et al., 2005; Laliberté et al., 2012; Wesuls et al., 2012; Moreno García et al., 2014). Some researchers suggest that

generalizations of grazing impacts described by plant traits may be difficult (Vesk and Westoby, 2001), whereas others suggest that plant species' responses to herbivory might be idiosyncratic with regard to LHS traits (Butterfield and Callaway, 2012). Nevertheless, Díaz et al. (2006) suggested reanalyzing existing species-based studies to evaluate trait-based responses to grazing.

Both compositional and trait-based approaches provide valuable information regarding rangeland responses to grazing. Where a functional trait-based approach has the potential to be more generalizable across rangeland types, species and functional group data are easier to collect and provide important site-specific information. Combining both can allow for a more comprehensive understanding of the effects of grazing on vegetation structure and function.

In this study, we reanalyzed data from a unique long-term study to determine vegetation responses to continued heavy livestock grazing and recovery patterns when livestock were excluded for 30 yr. Permanent chart quadrats were established in 1912 in heavily grazed ponderosa pine–bunchgrass forests in northern Arizona. About half of the quadrats continued to experience heavy grazing while the others were protected from livestock grazing and are hereafter referred to as being ungrazed. A subset of the quadrats were used to document the influence of increasing pine regeneration on perennial grass cover (Arnold, 1950), but no studies have been published that used them to examine the effects of excluding heavy grazing over time. To isolate the effects of grazing during the study period, we statistically controlled for overstory dominance, soil texture, and elevation among quadrats and over time. To date, this is one of the few long-term studies examining changes in species composition due to grazing in the ponderosa pine type of the Southwest (Arnold, 1950; Milchunas, 2006; Loeser et al., 2007).

We formulated three hypotheses on the basis of our understanding of grazing management during the study period. First, we hypothesized that ungrazed and continuously grazed communities would diverge in species composition and in functional group composition, and that these changes would result primarily from recovery by perennial graminoids in ungrazed areas because these species would have been at a competitive disadvantage under the heavy levels of grazing common before protection (Talbot and Hill, 1923; Arnold, 1955). Second, we hypothesized that species richness would be higher in ungrazed areas because the duration and intensity of grazing would limit richness in grazed areas to those species able to tolerate or avoid grazing. Third, we hypothesized that functional traits would diverge between ungrazed and grazed communities. Specifically, we hypothesized that ungrazed communities would exhibit 1) lower mean SLA, lower foliar N<sub>mass</sub>, and higher mean LDMC because species with this set of coordinated traits would have a greater competitive advantage in less disturbed environments (Grime, 1977), 2) a higher mean vegetative height due to increased competition for light, and 3) greater seed mass because seedling establishment would be favored by species that produce larger seeds in low-light and lower-resource environments (Kitajima, 2002).

## Methods

### Study Area

Between 1870 and 1910, the Southwest experienced an unprecedented introduction of domesticated livestock as a result of Euro-American settlement of the region (Olberding et al., 2005; Milchunas, 2006). In 1914, national forests in Arizona issued grazing permits for 6 800 horses, 243 000 cattle, and 379 000 sheep (Hill, 1915). Although little information is available regarding specific stocking rates, it was widely recognized that the ponderosa pine–bunchgrass forests of northern Arizona were overstocked and grazing ranged



Fig. 1. Contrast in vegetation between ungrazed (left) and heavily grazed (right) areas at Fry Park. Photograph taken in 1935 by W. J. Cribbs.

from heavy to severe (Hill, 1918; Talbot and Hill, 1923; Arnold, 1950).

In 1912, Robert R. Hill initiated a study to examine the effect of grazing on the herbaceous understory species associated with the ponderosa pine–bunchgrass forests of northern Arizona. Five sites spanning a range of soil types and elevations within 25 km of Flagstaff, Arizona were selected as representative of the overgrazed rangeland common during this time period (Talbot and Hill, 1923; Arnold, 1950) (Table S1; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>). At each site, an ~0.7-ha enclosure was built to exclude domestic livestock (Fig. 1). Within each enclosure, five permanent 1 × 1 m quadrats were established. Adjacent to each enclosure, in areas where livestock grazing continued, five additional permanent quadrats were established. At each site, individual quadrats inside and outside the livestock enclosures were interspersed within different overstory canopy types (e.g., full shade, partial shade, no shade) (Talbot and Hill, 1923; Arnold, 1950). In total, 50 quadrats were established. Quadrats were sampled intermittently between 1912 and 1941. Due to the temporally unbalanced sampling of the quadrats (Fig. S1; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>), we partitioned the data into four time periods: 1912–1917 (termed 1912), 1920–1926 (1920), 1930–1933 (1930), and 1938–1941 (1940). For a given quadrat, all data from years within a given time period were averaged. A total of 185 quadrat–time period combinations were used in the analysis.

Before fencing the enclosures, all sites were heavily grazed by cattle and sheep for 40 yr (since 1870). In general, livestock were grazed continuously from May through October (Hill, 1915). All sites were considered heavily grazed to overgrazed when the enclosures were established (Talbot and Hill, 1923). Subsequent grazing intensity at each site was estimated on the basis of the degree of utilization of the dominant bunchgrasses (Merrick, 1939). For example, sites were considered overgrazed if these species were consumed to such a degree that their likelihood of continued persistence was reduced. Better livestock control resulted in lighter and more uniform

utilization at Reese Tank, though the other sites were considered heavily grazed to overgrazed at least through 1938 (Merrick, 1939) (Table S1; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>).

Data from the nearby USFS Fort Valley Experimental Forest show that between 1912 and 1941 annual precipitation ranged from 43.4 cm in 1939 to 81.4 cm in 1919 (WRRC 2012). Figure S1B (available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>) shows annual precipitation between 1912 and 1941 as a percent departure from the long term (1909–2012) average of 56.5 cm (WRCC, 2012).

#### Environmental Variables

We incorporated percent sand, elevation, and overstory tree basal area as covariates in our analysis. These variables were measured as described in Bakker and Moore (2007) and Laughlin et al. (2011). Percent sand content and elevation were constant over time while tree basal area ( $\text{m}^2 \text{ha}^{-1}$ ) increased during the study period. To quantify this change in basal area, we reconstructed historical tree basal area on 20 × 20 m overstory plots centered on each quadrat in each time period. For trees that were alive during contemporary sampling, radial growth increments were measured on tree cores and a proportional reconstruction method (Bakker, 2005) was used to calculate historical tree diameters. For trees that were dead during contemporary sampling, a transition matrix decomposition model was used to estimate tree death date and then tree diameter was reconstructed at each time period using a stand reconstruction model (Bakker et al., 2008). Comparisons of reconstructed and historical data indicate that these methods are reliable within  $\pm 10\%$  (Huffman et al., 2001). Reconstructed tree densities and pine basal areas were significantly positively correlated ( $R^2 = 0.43$ ,  $P < 0.0001$ ). Reconstructed forest structure showed increases in pine basal areas on both grazed and ungrazed quadrats throughout the study period. Between 1912 and 1940, average pine basal area increased from 3.4 to 6.6  $\text{m}^2 \text{ha}^{-1}$  on grazed quadrats and from 4.3 to 7.2  $\text{m}^2 \text{ha}^{-1}$  on ungrazed quadrats.

The reconstruction model was performed in R version 2.11.0 (R Development Core Team, 2010) using code available in Bakker et al. (2008).

### Vegetation Data

From 1912–1941, trained botanists from the U.S. Forest Service compiled lists of all plant species present and mapped the basal cover of all understory vegetation on each quadrat. In general, graminoids were mapped as polygons and forbs were mapped as points. Digitized quadrat maps were used to calculate the area occupied by each herbaceous species. We assumed that each point represented a plant with 0.0025% basal cover, the approximate diameter of a typical forb stem on these plots (Laughlin et al., 2011). For each quadrat, we calculated the average basal cover by species in each time period. Due to the use of common names on historical datasheets, some species identifications were lumped at higher taxonomic levels (i.e., genus), but are referred to here as species for simplicity. A total of 69 species were used in our analyses, including 16 graminoids, 45 nonleguminous forbs, 6 legumes, and 2 shrubs (Table S3). Seven of the sixteen graminoids are C<sub>3</sub> species. In terms of lifespan, 2 of the graminoids (*Muhlenbergia minutissima* [Steud.] Swallen and *Bouteloua simplex* Lag.) are annuals, one (*Elymus elymoides* [Raf.] Swezey) is a short-lived perennial (Lauenroth and Adler, 2008), and the remainder are all thought to be long-lived perennials. Five of the nonleguminous forbs are considered annual-biennial, and the rest are perennials. All six legumes are perennials.

To quantify understory community dynamics in response to exclusion of heavy livestock grazing, we calculated several multivariate and univariate metrics for each quadrat in each time period. Community composition was examined on the basis of the average percent basal cover of each species and functional group composition based on the average percent basal cover of five functional groups (C<sub>3</sub> graminoids, C<sub>4</sub> graminoids, nonleguminous forbs, legumes, and shrubs).

Functional strategies were examined by focusing on five functional traits: SLA, LDMC, foliar N<sub>mass</sub>, seed mass, and maximum vegetative height. The mean value for each trait was obtained for each species as described in Laughlin et al. (2010). Where species were lumped at higher taxonomic levels, we used the average trait value for the combined species. We calculated the community-weighted mean (CWM) trait value for each trait. A quadrat's CWM trait value is the mean trait value across all species in a quadrat weighted by their relative abundance (Shipley et al., 2011):

$$\bar{T}_{jk} = \sum_{i=1}^s t_{ij} p_{ik}$$

where  $t_{ij}$  is the average value of trait  $j$  for species  $i$  and  $p_{ik}$  is the relative abundance of species  $i$  in quadrat  $k$ . Therefore  $\bar{T}_{jk}$  is an estimate of the value of trait  $j$  for the average individual in quadrat  $k$ .

### Data Analyses

Response metrics were analyzed for differences between grazing treatments after accounting for the environmental variables (percent sand, elevation, and tree basal area) as covariates. Each time period was analyzed separately. In each model, the effects of covariates and grazing were only investigated if the overall model was significant at  $\alpha = 0.05$ . A model with Type I (sequential) sums of squares was used so that the effect of grazing was examined after fitting the covariates to the data.

All analyses were conducted using distance-based linear models (DISTLM) in the PERMANOVA+ add-on (v. 1.0.3) to PRIMER (v.6.1.13). DISTLM (Anderson, 2001) relieves the assumption of normally distributed data and can be applied equivalently to univariate and multivariate ecological response variables. The appropriate sums of squares are calculated from a distance matrix that can be obtained using any distance measure (Anderson, 2001). Bray–Curtis dissimilarity was used as the distance measure for multivariate compositional metrics (community and functional group compositions) as recommended by Faith et al. (1987); these matrices were relativized by row totals to reflect relative basal cover before analyses. Euclidean dissimilarity was used as the distance measure for the multivariate analysis of CWM traits and for all univariate comparisons (total understory basal cover, species richness, basal cover of each functional group, and individual CWM traits). CWM traits were relativized by trait ranges before analysis so that all traits were expressed on the same scale.

### Results

In 1912, at the start of the experiment and following a period of intense livestock grazing, the grazing treatments did not differ in total understory basal cover or how that basal cover was distributed among species or functional groups. By 1920, total basal cover was significantly greater in ungrazed quadrats. Though this effect disappeared in later decades, when averaged over periods, total basal cover in ungrazed quadrats and grazed quadrats was  $16.8 \pm 0.25$  and  $14.2 \pm 0.58$  (mean  $\pm$  SE,  $n = 4$ ), respectively (Fig. 2A; Table S3; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>). Community composition did not differ until 1930 and 1940 (Table S2; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>). Species richness was consistently higher in ungrazed than

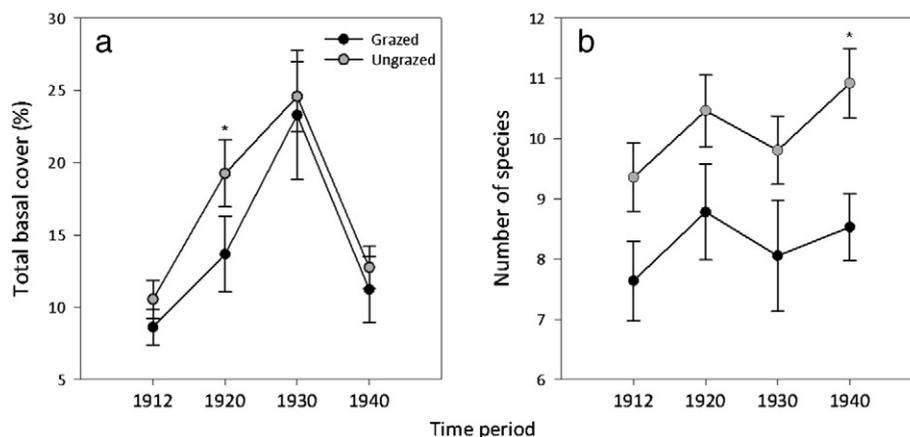
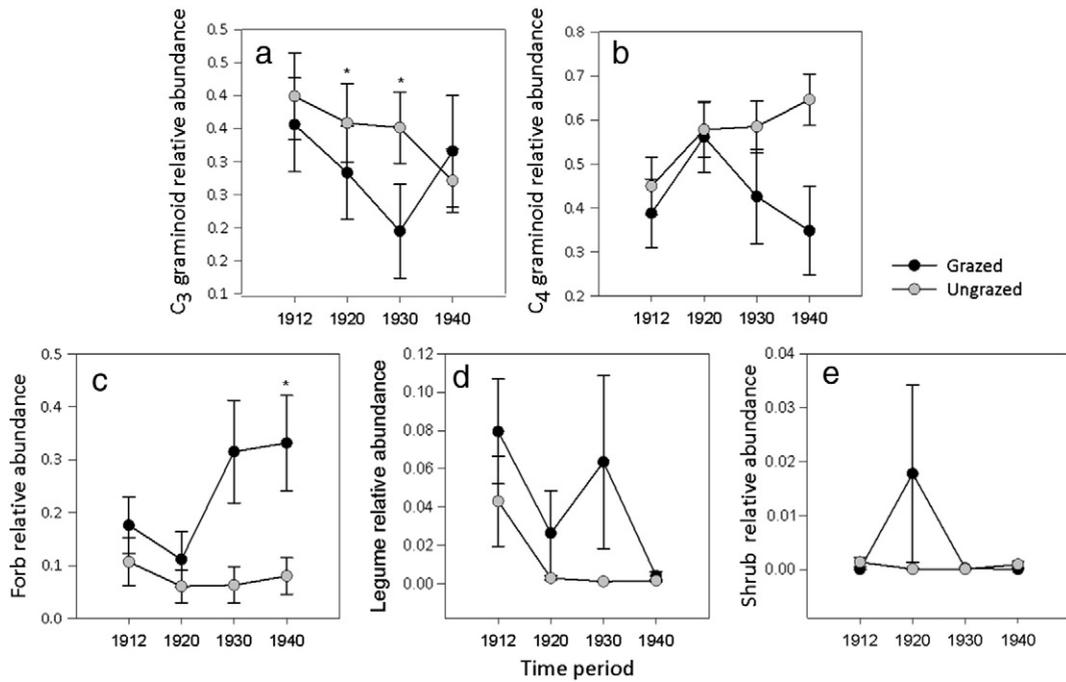


Fig. 2. Changes in average ( $\pm$  SE) (a) total cover and (b) species richness between grazed and ungrazed treatments in the 1912–1940 time periods. Asterisks indicate significant differences from DISTLM results ( $P < 0.05$ ; Table S2). Note that the scale of the y-axis differs between panels.



**Fig. 3.** Changes in average ( $\pm$  SE) relative abundance of (a) C<sub>3</sub> graminoids, (b) C<sub>4</sub> graminoids, (c) nonleguminous forbs, (d) legumes, and (e) shrubs between grazed and ungrazed treatments in the 1912–1940 time periods. Asterisks indicate significant differences from DISTLM results ( $P < 0.05$ ; Table 1). Note that the scale of the y-axis differs among panels.

**Table 1**

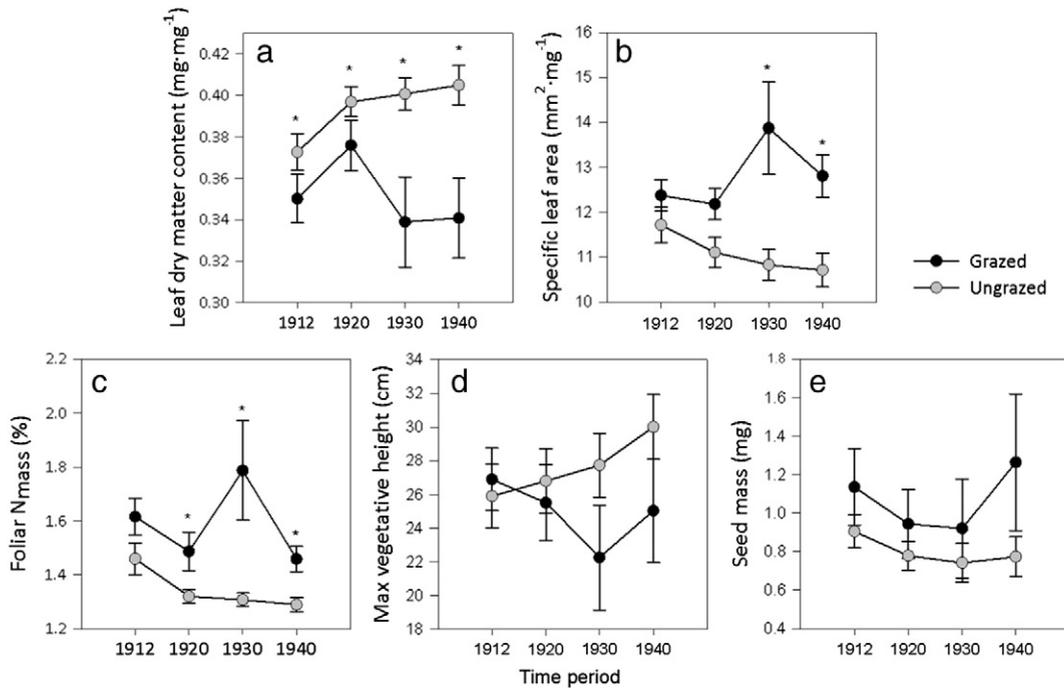
DISTLM results for functional group composition and for abundance of each functional group. “Covariates” refers to the combined effects of ponderosa pine basal area, percent sand, and elevation. “Grazing” refers to whether a quadrat is inside or outside the enclosures built in 1912. Each time period was analyzed separately. The overall  $R^2$  value is reported in all cases, but the results (pseudo- $F$  statistic,  $P$ -value, partial  $R^2$ ) for covariates and the grazing term are reported only if the overall model is significant ( $\alpha = 0.05$ ).  $P$ -values  $\leq 0.05$  are highlighted in bold. Models that were not significant are indicated by “NS.”

Source	Overall	Covariates		Grazing			
	$R^2$	$F$	$P$	$R^2$	$F$	$P$	$R^2$
Functional Group Composition (5 Functional Groups)							
1912	0.241	4.42	<b>&lt;0.01</b>	0.224	1.04	0.40	0.018
1920	0.281	4.35	<b>&lt;0.01</b>	0.204	4.92	<b>&lt;0.01</b>	0.077
1930	0.355	5.55	<b>&lt;0.01</b>	0.275	4.85	<b>&lt;0.01</b>	0.080
1940	0.292	3.54	<b>0.02</b>	0.215	3.79	<b>&lt;0.01</b>	0.077
C <sub>3</sub> Graminoids							
1912	0.198	4.06	<b>0.01</b>	0.129	3.88	0.05	0.069
1920	0.492	21.27	<b>&lt;0.01</b>	0.339	13.87	<b>&lt;0.01</b>	0.153
1930	0.357	9.59	<b>&lt;0.01</b>	0.199	9.61	<b>&lt;0.01</b>	0.158
1940	0.162	—	NS	—	—	NS	—
C <sub>4</sub> Graminoids							
1912	0.217	4.26	<b>0.01</b>	0.197	1.13	0.30	0.020
1920	0.198	3.87	<b>0.02</b>	0.180	1.03	0.30	0.018
1930	0.427	9.71	<b>&lt;0.01</b>	0.425	0.10	0.76	0.002
1940	0.232	3.97	<b>0.02</b>	0.146	3.90	0.08	0.086
Nonleguminous Forbs							
1912	0.032	—	NS	—	—	NS	—
1920	0.027	—	NS	—	—	NS	—
1930	0.100	—	NS	—	—	NS	—
1940	0.211	3.51	<b>0.03</b>	0.125	3.84	<b>0.04</b>	0.087
Legumes							
1912	0.092	—	NS	—	—	NS	—
1920	0.246	5.23	<b>&lt;0.01</b>	0.212	2.04	0.15	0.033
1930	0.109	—	NS	—	—	NS	—
1940	0.249	3.87	<b>0.02</b>	0.248	0.03	0.90	0.001
Shrubs							
1912	0.090	—	NS	—	—	NS	—
1920	0.044	—	NS	—	—	NS	—
1930	0.040	—	NS	—	—	NS	—
1940	0.115	—	NS	—	—	NS	—

grazed quadrats, though this difference was only statistically significant in 1940, suggesting that the treatments were gradually diverging (Fig. 2B; Table S2; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>). Changes in model significance (based on  $P$  values) suggest that overall differences in community composition between grazing treatments continued to increase into the 1940 time period. However, the low partial  $R^2$  values for the grazing term indicate that the compositional differences between grazing treatments were subtle (Table S2; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>).

Functional group composition responded more quickly than community composition; differences were already evident in 1920 (Fig. 3; Table 1). In 1920 and 1930, these differences were due to a lower abundance of C<sub>3</sub> graminoids in grazed than ungrazed quadrats (Fig. 3). However, we observed a decline in C<sub>3</sub> graminoid abundance in ungrazed quadrats throughout the study period as C<sub>4</sub> graminoid abundance increased. For example, the dominant C<sub>4</sub> graminoid, *Muhlenbergia montana* (Nutt.) Hitchcock, increased from 11.1% in 1912 to 31.3% in 1940 in ungrazed quadrats while *Festuca arizonica* Vasey, the dominant C<sub>3</sub> graminoid, declined from 16.4% to 11.8% between 1912 and 1940, respectively (Table S3; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>). In 1940, differences between treatments reflected an increased abundance of forbs in grazed quadrats (Fig. 3).

CWM traits responded significantly to grazing (Fig. 4; Table 2). Considering all traits together, differences between the grazing treatments were evident in 1930 and 1940. LDMC was lower in grazed than ungrazed quadrats already in 1912, but the difference between these grazing treatments increased throughout the study period; the amount of variation explained by the grazing treatment increased from 6% to 21% (Table 2). Between the 1912 and 1940 time periods, CWM LDMC increased on average 8% ( $0.03 \text{ mg mg}^{-1}$ ) in ungrazed quadrats. CWM foliar  $N_{\text{mass}}$  was lower in ungrazed than grazed quadrats from 1920 onwards, decreasing on average 11% ( $0.17\% N$ ) in ungrazed quadrats between the 1912 and 1940 time periods. CWM SLA was lower in ungrazed than grazed quadrats from 1930 onwards,



**Fig. 4.** Changes in average ( $\pm$  SE) community-weighted mean trait values of (a) LDMC, (b) SLA, (c) foliar N, (d) max vegetative height, and (e) seed mass between grazed and ungrazed treatments in the 1912–1940 time periods. Asterisks indicate significant differences from DISTLM results ( $P < 0.05$ ; Table 2). Note that the scale of the y-axis differs among panels.

**Table 2**

DISTLM results for community-weighted mean traits (CWMs; all five traits) and for each trait separately. “Covariates” refers to the combined effects of ponderosa pine basal area, percent sand, and elevation. “Grazing” refers to whether a quadrat is inside or outside the exclosures built in 1912. Each time period was analyzed separately. The overall  $R^2$  value is reported in all cases, but the results (pseudo- $F$  statistic,  $P$ -value, partial  $R^2$ ) for covariates and the grazing term are reported only if the overall model is significant ( $\alpha = 0.05$ ).  $P$ -values  $\leq 0.05$  are highlighted in bold. Models that were not significant are indicated by “NS.”

Source	Overall			Covariates			Grazing		
	$R^2$	$F$	$P$	$R^2$	$F$	$P$	$R^2$	$F$	$P$
CWMs (5 Traits)									
1912	0.371	8.30	<0.01	0.348	1.63	0.15	0.023		
1920	0.295	5.71	<0.01	0.262	2.15	0.09	0.033		
1930	0.360	5.53	<0.01	0.272	5.37	<0.01	0.088		
1940	0.367	4.81	<0.01	0.261	5.81	<0.01	0.105		
LDMC									
1912	0.335	6.12	<0.01	0.271	4.29	<b>0.05</b>	0.064		
1920	0.449	10.00	<0.01	0.360	7.41	<0.01	0.089		
1930	0.543	11.52	<0.01	0.405	11.79	<0.01	0.138		
1940	0.516	7.32	<0.01	0.304	15.32	<0.01	0.212		
SLA									
1912	0.058	—	NS	—	—	NS	—		
1920	0.169	—	NS	—	—	NS	—		
1930	0.248	1.08	0.37	0.063	9.63	<0.01	0.186		
1940	0.337	1.54	0.22	0.087	13.18	<0.01	0.250		
Foliar $N_{\text{mass}}$ (%)									
1912	0.152	—	NS	—	—	NS	—		
1920	0.339	4.48	<0.01	0.193	10.11	<0.01	0.145		
1930	0.310	2.70	0.06	0.143	9.40	<0.01	0.166		
1940	0.442	4.74	<0.01	0.227	13.49	<0.01	0.215		
Vegetative height									
1912	0.303	6.51	<0.01	0.303	0.02	0.87	0.001		
1920	0.255	4.95	<0.01	0.240	0.93	0.34	0.015		
1930	0.323	5.40	<0.01	0.281	2.43	0.13	0.042		
1940	0.280	3.75	<b>0.02</b>	0.231	2.34	0.13	0.049		
Seed mass									
1912	0.293	5.33	<0.01	0.251	2.70	0.10	0.042		
1920	0.184	2.86	<b>0.05</b>	0.152	1.76	0.20	0.031		
1930	0.141	—	NS	—	—	NS	—		
1940	0.209	—	NS	—	—	NS	—		

decreasing on average 8% ( $1.0 \text{ mm}^2 \text{ mg}^{-1}$ ) in ungrazed quadrats between the 1912 and 1940 time periods. Although CWM height increased 16% in ungrazed quadrats between 1912 and 1940, no differences between grazing treatments were detected. Similarly, CWM plant seed mass was unaffected by grazing treatment.

## Discussion

Protection from continuous (May through October) heavy live-stock grazing resulted in changes in species composition, functional group composition, and functional traits in the understory flora of this ponderosa pine–bunchgrass ecosystem. Our results suggest that the herbaceous plant community responds within 1–2 decades of protection from heavy grazing by altering its functional group composition and some CWM functional traits; changes in species composition and species richness were not evident until after 2–3 decades. By combining a trait-based approach with analyses of community composition and functional group composition, we gained a more comprehensive understanding of how these understory plant communities respond when protected from continuous heavy live-stock grazing.

### Functional Traits

SLA, foliar  $N_{\text{mass}}$ , and LDMC represent aboveground traits associated with tradeoffs between resource acquisition and conservation and between growth and defense (Westoby, 1998; Díaz et al., 2001). Westoby (1999) proposed that under heavy nonselective grazing, high SLA should be favored, whereas low SLA should be favored at moderate to low stocking rates. Our results support this hypothesis: Protection from heavy grazing led to a shift toward more conservative leaf traits (low SLA, low foliar  $N_{\text{mass}}$ , and high LDMC). Other research in grasslands around the world has shown similar patterns (Cingolani et al., 2005; Louault et al., 2005; Wesuls et al., 2012; Moreno García et al., 2014). A community-level shift in ungrazed communities toward reduced acquisition and increased conservation

of nutrients and dry mass would suggest a greater accumulation of litter due to slower rates of decomposition (Garnier et al., 2004; Kazakou et al., 2006; Laughlin et al., 2010). Therefore changes in livestock grazing pressure can alter ecosystem functioning because community-level litter quality influences the below-ground decomposer subsystem (Wardle and Bardgett, 2004).

Because traits were weighted by relative abundance, changes in traits reflect changes in the dominant species, particularly  $C_4$  graminoids. Most of the graminoids in our system can be characterized as long-lived perennial species that allocate a relatively small proportion of their energy to reproduction and produce litter with lower rates of decomposition (Bazzaz et al., 1987; Laughlin et al., 2010). Species aligned with this strategy are at a competitive advantage when protected from heavy grazing because they are able to reduce resource availability. Conversely, species with the opposite strategy (high SLA, high foliar  $N_{mass}$ , and low LDMC) are at a competitive advantage in heavily grazed areas because they can more rapidly acquire nutrients and regrow after disturbance. In grasslands of Argentina and Israel, grazing-resistant species have higher SLA than grazing-susceptible species (Díaz et al., 2001).

Westoby (1999) proposed that taller species should decrease with increasing grazing pressure. We found a tendency for vegetative height to be greater in communities protected from heavy grazing, though this difference was not statistically significant. Although a number of studies have shown an increase in taller plants with a decrease in grazing pressure (Dyksterhuis, 1949; Noy-Meir et al., 1989; Díaz et al., 2006; Golodets et al., 2009), our results are in line with Wesuls et al. (2012) who found no significant grazing response for vegetative height. This can be attributed in part to the dominance in both areas by  $C_3$  and  $C_4$  graminoids, which differed minimally in maximum vegetative height (Table S4; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>).

With regard to seed mass, our results agree with work by Garnier et al. (2007), who found seed mass showed no consistent response following a reduction in land-use intensity across 11 sites in Europe. Species that produce larger quantities of smaller seeds should have higher establishment success in gaps created by heavy grazing (Westoby, 1999), but we found that CWM seed mass tended to be higher in heavily grazed quadrats. This can be attributed in part to heavier-seeded forbs (e.g., *Hymenoxys richardsonii* [Hook.] Cockerell, *Phlox* spp. [L.]); legumes (e.g., *Trifolium longipes* Nutt.); and grasses (e.g., *Sporobolus interruptus*, *Elymus elymoides*) (Tables S3–S5; available online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>), which responded positively to heavy grazing over time. Higher average seed mass in heavily grazed quadrats could also reflect the ability of larger seeded species to better tolerate defoliation (Armstrong and Westoby, 1993).

#### Species Richness and Composition

We found limited support for our hypothesis that communities protected from heavy grazing would have a higher number of species because only those species that were able to tolerate or avoid grazing would occupy grazed quadrats. Areas protected from heavy livestock grazing tended to have greater species richness throughout the study period, though this difference was not statistically significant until the 1940 time period. It is possible this delayed response is due to slow recruitment of additional species into the study areas after heavy grazing. The slower response in terms of richness than abundance of specific functional groups is similar to the pattern observed in restored ponderosa pine forests, where richness did not differ for a decade (Laughlin et al., 2008), whereas standing crops responded in just a few years (Moore et al., 2006).

Species composition and diversity also responded to protection, but more slowly than functional group or CWM traits. On the basis of Arnold's (1955) life form stages, Clary (1975) suggested that 100 yr may be required for full recovery from a denuded stage to a bunchgrass stage under reduced grazing pressure. Pearson (1942) found that clipping to 2 in for 10 yr had little impact on overall grass cover. Lacking direct evidence for understory reference conditions, it is difficult to know what it means for these herbaceous understory communities to "fully recover." Although this system is assumed not to have evolved with grazing (Milchunas, 2006), both the semiarid environment and presence of species that can withstand grazing (i.e., *Bouteloua gracilis* and *Sporobolus interruptus* [blue grama and black dropseed, respectively]); short-statured, sod-forming  $C_4$  graminoids) are thought to confer a degree of grazing resistance (Milchunas et al., 1988) and can help to explain the subtle compositional and functional trait differences found between treatments.

#### Influence of Covariates

The effects of excluding heavy grazing were determined after accounting for environmental controls, which were generally strong. Elevation, soil physical (texture) properties, and tree basal area are good predictors of herbaceous understory community composition (Bakker and Moore, 2007; Laughlin and Abella, 2007) and trait distributions (Shiple et al., 2011; Laughlin et al., 2011). On the basis of  $R^2$  values, the importance of excluding heavy grazing increased with time for CWM traits while the influence of covariates remained constant. However, this was not generally the case for community or functional group composition, where the influence of grazing remained relatively constant while the importance of covariates tended to increase. Given that elevation and soils were constant, the changing importance of the covariates must reflect the increase in tree basal area throughout the study period.

Total basal cover declined substantially from 1930–1940 and did so in both grazed and ungrazed quadrats. Typically, we would attribute this response to the pulse of ponderosa pine regeneration (increase basal area) in northern Arizona in the 1930s and 1940s (Arnold, 1950; and see Fig. 1). However, it should be noted that Arnold (1950) showed a similar decrease in graminoid basal cover on a subset of quadrats that were not influenced by pine regeneration from 1912–1941. Other factors that were not analyzed in this study may also have contributed to this decline in graminoid cover in 1940.

#### Management Implications

Anticipating plant community responses to disturbance and land-use change is a primary objective of rangeland ecology. The results from this study provide an important long-term perspective on plant community responses to protection from heavy grazing and provide insight into the speed at which managers will be able to detect changes in plant communities following a change in management. Our results indicate that managers should expect to observe more rapid changes in functional group composition than in species composition and species richness following protection from continuous heavy grazing.

Our results also indicate that managers can anticipate changes in leaf functional traits within plant communities following a change in grazing management. Species with low SLA, low foliar  $N_{mass}$ , and high LDMC will become increasingly more abundant in sites protected from heavy grazing. These species can be characterized as slow-growing perennial species that allocate a relatively small proportion of their energy to reproduction and produce litter that decomposes slowly (Reich et al., 1997; Wright et al., 2004). These findings contribute to a growing body of evidence that there are

consistent shifts in community-level leaf traits under a variety of grazing regimens around the world (Louault et al., 2005; Laliberté et al., 2012; Wesuls et al., 2012; Moreno García et al., 2014). Species with low SLA are at a competitive advantage when protected from heavy grazing because they are able to reduce resource availability. Conversely, under heavy grazing, species with high SLA are at a competitive advantage in grazed areas because they can more rapidly acquire nutrients and regrow after disturbance. Consistent trait-based responses indicate that these results are generalizable across species and ecosystems. Managers can utilize these results by anticipating similar community-level responses to protection from heavy grazing across a variety of rangeland types. Although our findings support a more generalizable understanding of plant community response to grazing on the basis of functional trait differences, our inferences are limited to rangelands where grazing intensity is heavy. More research is needed within contrasting grazing regimens to develop a more comprehensive understanding of trait-based responses to grazing.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2015.03.008>.

## References

- Adler, P.B., Milchunas, D., Lauenroth, W.K., Sala, O.E., Burke, I.C., 2004. Functional traits of graminoids in semi-arid steppes: a test of grazing histories. *Journal of Applied Ecology* 41, 653–663.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- R: a language and environment for statistical computing [computer program]. R Foundation for Statistical Computing, Vienna, Austria.
- Armstrong, D.P., Westoby, M., 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74, 1092–1100.
- Arnold, J.F., 1950. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. *Journal of Forestry* 48, 118–126.
- Arnold, J.F., 1955. Plant life-form classification and its use in evaluating range conditions and trend. *Journal of Range Management* 8, 176–181.
- Bakker, J.D., 2005. A new, proportional method for reconstructing historical tree diameters. *Canadian Journal of Forest Research* 35, 2515–2520.
- Bakker, J.D., Moore, M.M., 2007. Controls on vegetation structure in southwestern ponderosa pine forests, 1941 and 2004. *Ecology* 88, 2305–2319.
- Bakker, J.D., Sánchez Meador, A.J., Fulé, P.Z., Huffman, D.W., Moore, M.M., 2008. "Growing trees backwards": description of a stand reconstruction model. In: Olberding, S.D., Moore, M.M., tech coordinators. (Eds.), *Fort Valley Experimental Forest: a century of research 1908–2008*. Proceedings RMRS-P-53CD. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA, pp. 136–147.
- Bazzaz, F.A., Chiariello, N.R., Coley, P.D., Pitelka, L.F., 1987. Allocating resources to reproduction and defense. *American Institute of Biological Sciences* 37, 58–67.
- Butterfield, B.J., Callaway, R.M., 2012. A functional comparative approach to facilitation and its context dependence. *Functional Ecology* 27, 907–917.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Cingolani, A.M., Posse, G., Collantes, M.B., 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology* 42, 50–59.
- Clary, W.P., 1975. Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge. Res. Pap. RM-158. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA (35 p.).
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecological Monographs* 30, 129–164.
- Díaz, S., Noy-Meir, I., Cabido, M., 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38, 497–508.
- Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., Campbell, B.D., 2006. Plant trait responses to grazing—a global synthesis. *Global Change Biology* 12, 1–29.
- Dyksterhuis, E.J., 1949. Condition and management of range land based on quantitative ecology. *Journal of Range Management* 2, 104–115.
- Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68.
- Garnier, E., Cortez, J., Billés, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Ericksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Queded, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thébaud, A., Vile, D., Zarovali, M.P., 2007. Assessing the effects of land use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany* 99, 967–985.
- Golodets, C., Sternberg, M., Kigel, J., 2009. A community-level test of the leaf-height-seed ecology strategy scheme in relation to grazing conditions. *Journal of Vegetation Science* 20, 392–402.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111, 1169–1194.
- Hill, R.R., 1915. Effects of grazing upon reproduction on the Coconino National Forest. Progress report. US Forest Service, Fort Valley Experimental Forest Archives, Flagstaff, AZ, USA.
- Hill, R.R., 1918. Can an over-grazed range come back? Progress report. US Forest Service, Fort Valley Experimental Forest Archives, Flagstaff, AZ, USA.
- Huffman, D.W., Moore, M.M., Covington, W.W., Crouse, J.E., Fulé, P.Z., 2001. Ponderosa pine forest reconstruction: comparisons with historical data. In: Vance, R.K., Edminster, C.B., Covington, W.W., Blake (comps.), J.A. (Eds.), *Ponderosa pine ecosystems restoration and conservation: steps toward stewardship*. US Forest Service RMRS-P-22, Washington, DC, USA, pp. 3–8.
- Kazakou, E., Vile, D., Shipley, B., Gallets, C., Garnier, E., 2006. Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. *Functional Ecology* 20, 21–30.
- Kitajima, K., 2002. Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Functional Ecology* 16, 433–444.
- Laliberté, E., Shipley, B., Norton, D.A., Scott, D., 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology* 100, 662–677.
- Lauenroth, W.K., Adler, P.B., 2008. Demography of perennial grassland plants: survival, life expectancy and life span. *Journal of Ecology* 96, 1023–1032.
- Laughlin, D.C., Abella, S.R., 2007. Abiotic and biotic factors explain independent gradients of community composition in ponderosa pine forests. *Ecological Modelling* 205, 231–240.
- Laughlin, D.C., Bakker, J.D., Daniels, M.L., Moore, M.M., Casey, C.A., Springer, J.D., 2008. Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem. *Plant Ecology* 197, 139–151.
- Laughlin, D.C., Leppert, J.J., Moore, M.M., Sieg, C.H., 2010. A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology* 24, 493–501.
- Laughlin, D.C., Moore, M.M., Fulé, P.Z., 2011. A century of increasing pine density and associated shifts in understory plant strategies. *Ecology* 92, 556–561.
- Loeser, M.R.R., Sisk, T.D., Crews, T.E., 2007. Impact of grazing intensity during drought in an Arizona grassland. *Conservation Biology* 21, 87–97.
- Louault, F., Pillar, V.D., Aufrère, J., Garnier, E., Soussana, J.-F., 2005. Plant traits and functional types in response to reduced disturbance in a semi-natural grassland. *Journal of Vegetation Science* 16, 151–160.
- McIntyre, S., Lavorel, S., 2001. Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology* 89, 209–226.
- McIntyre, S., Díaz, S., Lavorel, S., Cramer, W., 1999. Plant functional types and disturbance dynamics—introduction. *Journal of Vegetation Science* 10, 603–730.
- Merrick, G.D., 1939. Revegetation of deteriorated range land in northern Arizona. (thesis) Duke University, Durham, North Carolina, USA (37 p.).
- Milchunas, D.G., 2006. Responses of plant communities to grazing in the southwestern United States. General Technical Report RMRS-GTR-169. U.S.

- Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63, 327–366.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132, 87–106.
- Moles, A.T., Westoby, M., 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92, 372–383.
- Moore, M.M., Casey, C.A., Bakker, J.D., Springer, J.D., Fulé, P.Z., Covington, W.W., Laughlin, D.C., 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecology & Management* 59, 135–144.
- Moreno García, C.A., Schellberg, J., Ewert, F., Brüser, K., Canales-Prati, P., Linstädter, A., Oomen, R.J., Ruppert, J.C., Perelman, S.B., 2014. Response of community-aggregated plant functional traits along grazing gradients: insights from African semi-arid grasslands. *Applied Vegetation Science* 17, 470–481.
- Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77, 290–310.
- Olberding, S.D., Mitchell, J.E., Moore, M.M., 2005. “Doing the best we could with what we had”: USFS range research in the Southwest. *Rangelands* 27, 29–36.
- Pakeman, R.J., Quisted, H.M., 2004. Sampling plant functional traits: what proportion of the species need to be measured? *Applied Vegetation Science* 10, 91–96.
- Pearson, G.A., 1942. Herbaceous vegetation a factor in natural regeneration of ponderosa pine in the southwest. *Ecological Monographs* 13, 315–338.
- Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* 89, 1908–1920.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. *PNAS* 94, 13730–13734.
- Shipley, B., Laughlin, D.C., Sonnier, G., Oftinowski, R., 2011. A strong test of a maximum entropy model of trait-based community assembly. *Ecology* 92, 507–517.
- Smith, D.R., 1967. Effects of cattle grazing on a ponderosa pine-bunchgrass range in Colorado. *Tech. Bull. No. 1371*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, USA (60 p.).
- Smith, T.M., Shugart, H.H., Woodward, F.I. (Eds.), 1997. Plant functional types: their relevance to ecosystem properties and global change. International geosphere-biosphere programme book series. Cambridge University Press, Cambridge, England.
- Talbot, M.W., Hill, R.R., 1923. Progress report on the range study plots on the Coconino National Forest comprising a description of project and digest of data. US Forest Service, Fort Valley Experimental Forest Archives, Flagstaff, AZ, USA.
- USDA Natural Resources Conservation Service, 2014. The PLANTS, database. Available at: <http://plants.usda.gov>. Accessed [18 August 2014].
- Vesk, P.A., Westoby, M., 2001. Predicting plant species' response to grazing. *Journal of Applied Ecology* 38, 897–909.
- Wardle, D.A., Bardgett, R.D., 2004. Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Frontiers in Ecology and the Environment* 2, 145–153.
- Western Regional Climate Center (WRCC), 2012. Recent climate in the West. Available at: <http://www.wrcc.dri.edu/>. Accessed [17 July 2012].
- Westoby, M., 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199, 213–227.
- Westoby, M., 1999. The LHS strategy scheme in relation to grazing and fire. In: Eldridge, D., Freudenberger, D. (Eds.), *Proceedings of the VI International Rangelands Congress, Australia*. Volume 2. International Rangeland Congress, St Ives, AU, pp. 893–896.
- Wesul, D., Oldeland, J., Dray, S., 2012. Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *Journal of Vegetation Science* 23, 98–113.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.
- Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B., Tilman, D., 2006. Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* 9, 111–120.