



Impact of ungulate exclusion on understory succession in relation to forest management in the Intermountain Western United States

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Abstract

Questions: Do successional trajectories in plant diversity, heterogeneity and dominance respond differently to ungulate exclusion in unmanaged forests vs managed forests that are thinned and burned? Is vegetation in recently thinned and burned stands more sensitive to changes in the grazing regime?

Location: Northeast OR, USA.

Methods: We evaluated changes in plant community composition, diversity, heterogeneity and dominance under herbivory by multiple ungulates (cattle, elk, deer) vs ungulate exclusion at sites where trees were recently thinned and a prescribed burn was applied (managed), and in sites that were not thinned or burned in over 40 yr (unmanaged). Plant species diversity was calculated with the Simpsons index and richness as the total number of plant species. We estimated changes in plant community heterogeneity using a measure of taxonomic dissimilarity. Plant dominance was measured as the relative evenness among different plant functional groups (annual and perennial forbs and graminoids, and shrubs, subshrubs and trees).

Results: As expected, managed sites displayed more early succession species, such as annual forbs and annual graminoids, while unmanaged sites were dominated by late-succession species such as shrubs, subshrubs and trees. Species richness, particularly of annuals, was strongly reduced when ungulates were excluded from managed sites, and to a lesser extent from unmanaged sites for some perennial plant species. Species diversity decreased to a slightly greater extent with ungulate exclusion at managed sites. Species dominance was not influenced by ungulate exclusion. The effect of ungulate exclusion on plant heterogeneity also depended on forest management. Heterogeneity increased at managed sites and decreased in unmanaged sites with ungulate exclusion. Overall, the change in vegetation composition over time increased with the exclusion of ungulates, particularly at managed sites.

Conclusions: The strength and direction of specific vegetation and diversity responses to ungulate exclusion vary with forest management, and the influence of ungulate exclusion on plant succession is more pronounced in recently thinned and burned sites. Management of wild and domestic ungulates thus needs to account for forest management activities that alter vegetation seral stage and increase the sensitivity of vegetation to the ungulate grazing regime.

Introduction

Understanding the responses of plant communities to ungulate grazing is crucial for sustainable land management. While grazing effects on vegetation are complex and

variable (Olff & Ritchie 1998), large herbivores have been shown to strongly influence plant diversity patterns in Africa (Belsky 1992), North America (Rambo & Faeth 1999; Towne et al. 2005; Bakker et al. 2006; Veen et al. 2008), Europe (Enyedi et al. 2008) and Australia (Schultz

et al. 2011). Plant diversity responses to ungulate herbivory are often associated with variations in spatio-temporal heterogeneity of plant species composition (Bakker et al. 2003; Veen et al. 2008), which is indicative of changes in species colonization and extinction rates (Olff & Ritchie 1998). Ungulates are also known to impact species dynamics by reducing dominance and cover of certain plant species or life forms, such as shrubs and trees, which tend to crowd out species that are less dominant or smaller in stature (Belsky 1992; Collins et al. 2002; Pekin et al. 2014). Accordingly, plant community responses to grazing are a function of several interrelated ecological processes that include changes in plant species diversity, spatial heterogeneity and dominance.

Current ungulate grazing regimes coupled with climatic changes are thought to be contributing to the degradation of vegetation communities in the interior western United States (Beschta et al. 2013). However, vegetation responses to grazing often depend on a variety of pre-existing site conditions, such as soil fertility (Olff & Ritchie 1998), habitat productivity (Bakker et al. 2006; Deléglise et al. 2011; Schultz et al. 2011; Lezama et al. 2014), fuel removal (Pekin et al. 2014) and silvicultural practices (Reimoser & Gossow 1996; Tremblay et al. 2006). And in some circumstances, grazing by wild and domestic ungulates may increase the resiliency of vegetation communities of the western United States in response to climate change (Svejcar et al. 2014).

In ecosystems with woody vegetation, ungulate effects are thought to be especially pronounced in recently burned sites because these early-succession vegetation communities provide new growth that is often highly preferred as forage by ungulates (Wisdom et al. 2006). Accordingly, forest management activities that include burning and/or stand thinning may make vegetation communities more sensitive to changes in the grazing regime (Hobbs 1996). The importance of fire, ungulate herbivory and their interactions in rangelands is thus well recognized (Fuhlendorf et al. 2008). However, little is known regarding the role of ungulates in mediating changes in plant community heterogeneity, dominance and diversity following forest management activities that involve episodic disturbances such as prescribed fire and stand thinning.

Stand thinning and prescribed fire are common management activities in the western United States (Agee & Skinner 2005). Forests and woodlands of the interior western United States are also extensively grazed by wild ungulates such as elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*), as well as domestic livestock (Wisdom et al. 2006; Huntsinger et al. 2010). The impacts of domestic and wild ungulates on vegetation in the western United States is surrounded in controversy (Huntsinger et al. 2010; Beschta et al. 2014; Svejcar et al. 2014),

and remains largely un-elucidated, especially in forested lands. Studies from western sagebrush steppe in Colorado have shown that ungulate grazing has significant effects on plant species dominance but relatively minor effects on diversity (Hobbs et al. 1996; Manier & Hobbs 2006), and that the specific effects on the vegetation community vary with seral stage (Milchunas & Vandever 2014).

We sought to increase knowledge regarding how the removal of large ungulate herbivores from the landscape affects plant succession in the western United States, and how these effects vary with forest management activities. We thus assessed changes in plant community composition, heterogeneity, dominance and richness under extant ungulate herbivory (grazed) and ungulate exclusion (ungrazed) in recently thinned and burned (managed) sites vs sites where no silvicultural activity has been conducted in >40 yr (unmanaged). Because management directly affects seral conditions, the response of vegetation communities to grazing and associated changes in plant species diversity, heterogeneity and dominance may differ between managed and unmanaged sites. In particular, we hypothesized that the effect of ungulate exclusion on vegetation successional trajectories will be more pronounced at managed stands since these represent early seral vegetation communities that are both more preferred by ungulates as well as being potentially more sensitive to grazing.

Methods

Study area description

We conducted our study at the Starkey Experimental Forest and Range (referred to as Starkey from here onwards) in the Blue Mountains Ecological Province of northeast Oregon (Fig. 1), ca. 50 km southwest of La Grande, Oregon (45°12'N, 118°3'W). Conditions at Starkey are typical of seasonally arid montane forests of interior western North America (Rowland et al. 1997). These dry forests occur on millions of hectares of public lands, and are co-occupied by high densities of domestic and wild ungulates (Rowland et al. 1998). Elk, mule deer and domestic cattle (*Bos taurus*) co-occur at Starkey (Rowland et al. 1998), as is typical of forests and rangelands in the western United States. Approximately 500 cow-calf pairs of cattle have grazed Starkey during the past 25 yr from mid-June through mid-October of each year under a deferred rotation grazing system (Rowland et al. 1997). During this same period, ca. 200 mule deer and 350 elk grazed Starkey in the spring, summer and autumn (Apr through Nov) of each year (Rowland et al. 1997). The population densities of cattle (7.15 km⁻²), elk (4.55 km⁻²) and mule deer (1.95 km⁻²) at Starkey are typical of densities found on shared summer ranges in much of western North America (Wisdom & Thomas 1996). The utilization of upland forest

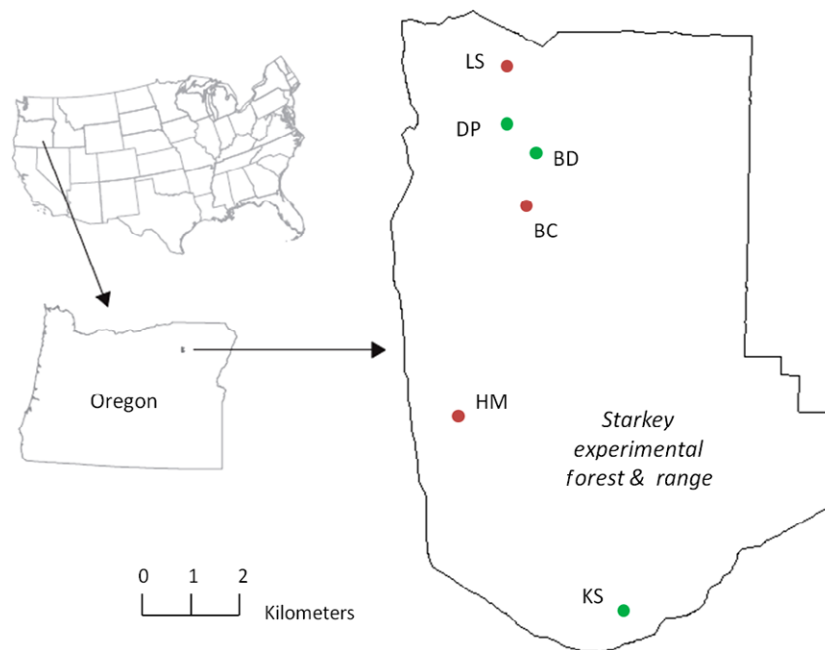


Fig. 1. Location of the six study sites within the Starkey Experimental Forest and Range. Sites LS, BC, HM (shown in red) have undergone thinning and fire and thus represent managed sites. Sites DP, BD, KS (shown in green) represent unmanaged sites that have not been burned or thinned in over 40 yr.

sites by cattle at Starkey generally are 40–50%, which is also typical for forested rangelands of the western United States (Holechek et al. 1998).

Elevations at Starkey range from 1200–1500 m a.s.l., and most precipitation occurs as winter snow or spring rain, with a predictable drought during late summer–early autumn (Rowland et al. 1997). The landscape is generally dominated by Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), interspersed with grasslands and meadows (Franklin & Dyrness 1973; Rowland et al. 1997). In addition to Douglas-fir and grand fir, other canopy tree species present in the landscape include ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*) and Englemann spruce (*Picea engelmannii*). Common understorey grasses and other graminoids include Idaho fescue (*Festuca idahoensis*), elk sedge (*Carex geyeri*), pinegrass (*Calamagrostis rubescens*), western fescue (*Festuca occidentalis*), Kentucky bluegrass (*Poa pratensis*) and annual bromes (*Bromus* spp.). Common forbs include lupine (*Lupinus* spp.), strawberry (*Fragaria* spp.), tall annual willowherb (*Epilobium paniculatum*) and western yarrow (*Achillea millefolium*). Common shrub and subshrub species include bearberry (*Arctostaphylos uva-ursi*), big huckleberry (*Vaccinium membranaceum*), rose (*Rosa* spp.), snowberry (*Symphoricarpos albus*), shinyleaf spiraea (*Spiraea betulifolia lucida*), currant (*Ribes* spp.), raspberry (*Rubus* spp.), Saskatoon serviceberry (*Amelanchier alnifolia*), snowbrush (*Ceanothus velutinus*), oceanspray (*Holodiscus discolor*), willow (*Salix* spp.), orange honey-

suckle (*Lonicera ciliosa*) and boxleaf myrtle (*Paxistima myrsinites*).

Forest management activities

Thinning and prescribed fire treatments were implemented at Starkey from 2000–2003 in sites ranging between 10 and 50 ha in size (Vavra et al. 2004). Sites were mechanically thinned with a feller-buncher to reduce fuel loadings to $<35 \text{ t} \cdot \text{ha}^{-1}$, compatible with fuel loads considered unlikely to carry stand replacement fires (Vavra et al. 2004, 2007), and broadcast burned following mechanical thinning. Controlled burns were implemented during the autumn of the same year, or on occasion, in the following year, due to time and logistical constraints. Prescribed burning was implemented in a manner typical of fuels reduction activities conducted by managers across dry forests of the western United States (Agee & Skinner 2005).

Ungulate exclosures

Ungulate exclosures were established from 2002–2004 at six Douglas-fir- and grand fir-dominated forested sites: Half Moon (HM), Louis Spring (LS), Bally Camp (BC), Doug Prairie (DP), Bee Dee (BD) and Kaenta Springs (KS) (Fig. 1). Three of the six exclosures (LS, BC, HM) were constructed on managed (thinned and burned) sites. The other three exclosures (DP, BD, KS) were constructed

where no fuel reduction treatments or any other forest management activity had been implemented in >40 yr. These unmanaged sites were similar in structure and composition to the pre-thinned and pre-burned condition of the managed sites (Bull et al. 2005).

The exclosures were established by constructing a 2.5-m high fence that excluded all ungulates (cattle, elk and mule deer), but allowed for other wildlife to pass under, over or through. The size and shape of each exclosure varied from 0.73 to 1.1 ha with site conditions, including topography, slope, forest structure and shape of the forest patch, to minimize site variation within and among exclosures.

Vegetation sampling

Permanent 1 m × 1 m plots were established in each ungulate exclosure and an adjacent area of approximately the same size that was exposed to grazing. Due to differences in size and layout, the number of plots per exclosure and adjacent area varied from 24 to 36. Plots were located systematically along transects spaced 15 m apart. Plot locations were determined using a real-time differential global positioning system placed in a geographic information system (GIS), and were permanently marked with stakes.

Within the sampling plots, we identified all plant species and estimated canopy cover using the arcsine square root class scale, a commonly used cover class scale (McCune et al. 2002): 0, 1–5, 5–25, 25–50, 50–75, 75–95, 95–99, 99–100%. We defined canopy cover as the percentage of the quadrat covered by the vertical projection of each species. We sampled in July, 2 yr after fuel reduction treatments, and again in July, 7 yr later (i.e. 9 yr following fuel treatment).

Different plant guilds or plant functional groups show variable responses to ungulate herbivory (Hayes & Holl 2003; Rooney & Waller 2003; Rooney 2008). We thus separately assessed the responses of different plant functional groups to our grazing treatments. Plant species were categorized into functional groups according to seven life forms and associated life-cycle traits: annual forb, perennial forb, annual graminoid, perennial graminoid, shrub, subshrub and tree. These groups reflect the morphological variation within our vegetation community; hence, the relative abundances of individuals within these groups are a good proxy for understorey structure and biomass distribution at Starkey.

Data analyses

We used non-metric multidimensional scaling to evaluate changes in community composition using the metaMDS function of the vegan package in R (R Foundation for

Statistical Computing, Vienna, AT). We plotted compositional trajectories for the mean of grazed and ungrazed plots for each sampling year (2 and 9 yr following fuel removal initiation) separately at managed and unmanaged sites. We calculated the mean species scores for all species within each functional group and plotted functional group means in the same ordination space.

Several studies have used dissimilarity measures to assess spatio-temporal heterogeneity in plant species composition (Bakker et al. 2006; Collins & Smith 2006; Veen et al. 2008). We used Bray-Curtis dissimilarity (Bray & Curtis 1957) as a measure of spatial heterogeneity across our study sites. The dissimilarity of each vegetation sampling plot to all other plots within an ungulate exclosure or an adjacent grazed area was calculated at each of the six sites and for each of the sampling years (2 and 9 yr following fuel removal initiation).

Plant dominance in forests is often mediated by increases in the biomass or cover of dominant life forms that are higher in stature than other life forms in the understorey (Pekin et al. 2012a,b). We thus assessed plant dominance as inverse to the evenness of the relative cover of the different plant functional groups (i.e. functional evenness) using Simpson's index (Simpson 1949). Plant species diversity was also measured using Simpson's index. We calculated the change in mean dissimilarity, dominance and species diversity of each plot by subtracting the year two value from the year nine value. We also calculated the mean change in species richness in a similar fashion by subtracting the total number of plant species, or species belonging to a particular functional group, in year two from their respective values in year nine.

Because our samples were nested within six separate sites, we tested for treatment effects using generalized linear mixed models (GLMM; (Schall 1991)) with the glmmPQL function of the MASS package (Venables & Ripley 2002) in R. The GLMMs included a random effect defining nesting of plots within individual sites. We tested the effect of ungulate exclusion on the response variables plant species diversity, taxonomic dissimilarity, dominance and species richness (overall and for each functional group).

Results

Variation in plant life-form composition

We identified 163 plant species across all sites. Nearly half (87) were perennial forbs, followed by a large number of perennial graminoid (33) and annual forb (26) species. We also identified 16 shrub, six tree, six subshrub and five annual grass species.

On average, 12 to 18 species co-occurred within a 1 m × 1 m plot (Table 1), and plant community

Table 1. Mean $\pm$ SE of richness (number of species) of (1 m $\times$ 1 m) plots in managed (thinned and burned) and unmanaged sites with extant ungulate herbivory (grazed) and ungulate exclusion (ungrazed). Mean values are shown for all species combined and for different functional groups at 2 and 9 yr (year 2 and year 9) following forest management activities (i.e. stand thinning and prescribed fire).

	Managed Sites				Unmanaged Sites			
	Ungrazed		Grazed		Ungrazed		Grazed	
	Year 2	Year 9	Year 2	Year 9	Year 2	Year 9	Year 2	Year 9
All Species	13.6 $\pm$ 0.3	12.6 $\pm$ 0.4	12.7 $\pm$ 0.4	14.1 $\pm$ 0.5	16.7 $\pm$ 0.4	12.9 $\pm$ 0.3	17.9 $\pm$ 0.5	15.1 $\pm$ 0.4
Perennial Forbs	6.0 $\pm$ 0.19	5.7 $\pm$ 0.24	4.7 $\pm$ 0.26	5.7 $\pm$ 0.31	8.2 $\pm$ 0.34	6.4 $\pm$ 0.31	8.1 $\pm$ 0.32	6.9 $\pm$ 0.28
Annual Forbs	3.1 $\pm$ 0.17	2.0 $\pm$ 0.15	3.3 $\pm$ 0.18	2.7 $\pm$ 0.24	1.2 $\pm$ 0.15	0.2 $\pm$ 0.05	1.7 $\pm$ 0.16	0.6 $\pm$ 0.09
Perennial Graminoids	2.5 $\pm$ 0.12	2.6 $\pm$ 0.13	2.6 $\pm$ 0.15	2.9 $\pm$ 0.13	3.4 $\pm$ 0.14	2.6 $\pm$ 0.12	3.6 $\pm$ 0.13	3.1 $\pm$ 0.13
Annual Graminoids	0.07 $\pm$ 0.02	0.09 $\pm$ 0.02	0.29 $\pm$ 0.07	0.36 $\pm$ 0.06	0.03 $\pm$ 0.02	0.00 $\pm$ 0.00	0.04 $\pm$ 0.02	0.00 $\pm$ 0.00
Shrubs	0.58 $\pm$ 0.07	0.73 $\pm$ 0.08	0.63 $\pm$ 0.08	0.77 $\pm$ 0.08	1.14 $\pm$ 0.12	1.15 $\pm$ 0.11	1.40 $\pm$ 0.13	1.33 $\pm$ 0.12
Subshrubs	0.83 $\pm$ 0.09	0.83 $\pm$ 0.08	0.61 $\pm$ 0.07	0.82 $\pm$ 0.08	1.62 $\pm$ 0.11	1.62 $\pm$ 0.11	1.80 $\pm$ 0.12	1.77 $\pm$ 0.10
Trees	0.47 $\pm$ 0.08	0.65 $\pm$ 0.08	0.48 $\pm$ 0.08	0.72 $\pm$ 0.09	0.93 $\pm$ 0.11	0.89 $\pm$ 0.10	0.83 $\pm$ 0.09	1.10 $\pm$ 0.09

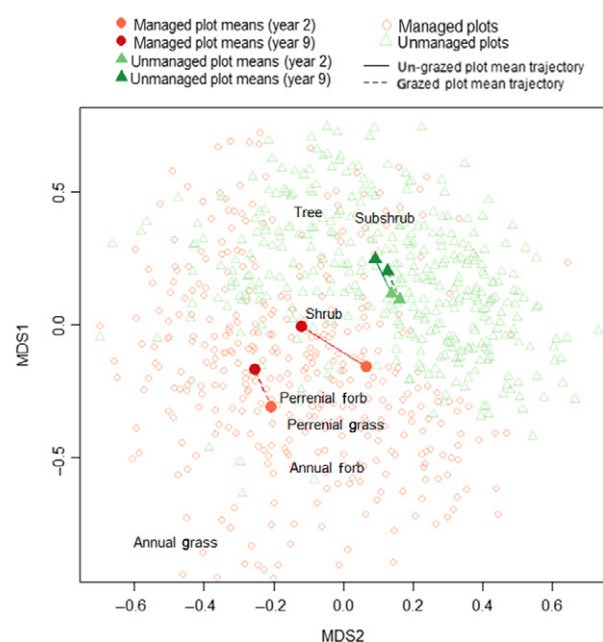


Fig. 2. Non-metric multidimensional scaling showing plant community composition under extant ungulate herbivory (grazed) and ungulate exclusion (ungrazed) across plots within managed (red circles) and unmanaged (green triangles) forest sites. The change, over a 7-yr period, in plot mean and SE are shown for each treatment group. Functional group locations represent the mean species scores for all species within each group.

composition differed strongly between managed and unmanaged sites (Fig. 2). Unmanaged sites, particularly those that were grazed, displayed the highest species richness, especially of woody life forms such as shrubs, subshrubs and trees (Table 1). Despite being more strongly dominated by shrubs, subshrubs and trees (Fig. 2), plots within unmanaged sites also generally had a higher number of perennial forbs (Table 1). In contrast, annual forbs and

grasses were much more common in managed sites (Table 1, Fig. 2), and were rarely observed in unmanaged sites (Table 1).

Grazed and ungrazed plots were compositionally more different from each other at managed sites than at unmanaged sites (Fig. 2). Ungrazed plots also displayed larger change in composition over the 7-yr period than grazed plots, especially at managed sites (Fig. 2). Ungrazed plots in managed sites were also compositionally more similar to plots in unmanaged sites than grazed plots in managed sites (Fig. 2), especially for annual forb and graminoid cover, which were much lower in grazed plots than in ungrazed plots in managed sites (Table 1).

Plant diversity, heterogeneity and dominance responses to ungulate exclusion

At managed sites, the mean plant species richness of grazed plots increased while that of ungrazed plots decreased (Fig. 3) resulting in a decrease in species richness with ungulate exclusion (Table 2). Although mean species richness of both grazed and ungrazed plots decreased over time at unmanaged sites (Fig. 3), richness decreased to a greater extent in ungrazed plots relative to grazed plots (Fig. 3, Table 2). Plant species diversity was reduced over time at all sites (Fig. 3); however, the decrease in species diversity was also slightly higher under ungulate exclusion at managed but not at unmanaged sites (Fig. 3, Table 2).

The effect of ungulate exclusion on taxonomic dissimilarity was reversed between managed and unmanaged sites (Fig. 3, Table 2). At managed sites, taxonomic dissimilarity increased at ungrazed plots and decreased at grazed plots (Fig. 3, Table 2). In contrast, ungulate exclusion decreased taxonomic dissimilarity at unmanaged sites relative to grazing (Table 2), which showed a sharp increase in taxonomic dissimilarity over time (Fig. 3). The change in

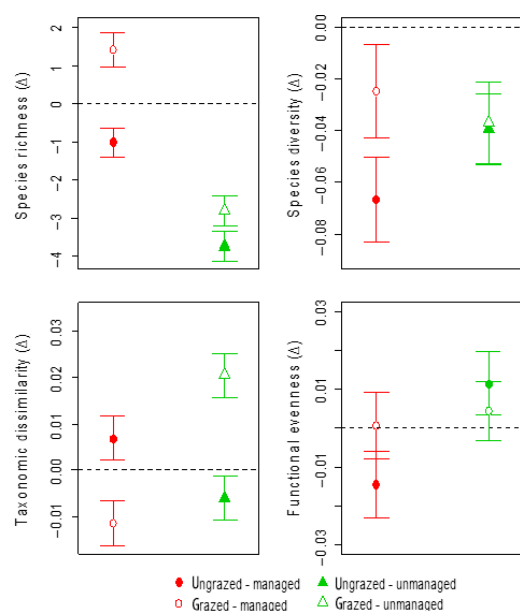


Fig. 3. The change (Δ) in mean plant species richness, diversity, heterogeneity (taxonomic dissimilarity) and dominance (functional evenness) across plots (1 m $\times$ 1 m) over a 7-yr period with extant ungulate herbivory (grazed) and ungulate exclusion (ungrazed). Mean values and SE of means (indicated by error bars) are shown separately for managed and unmanaged sites.

Table 2. Generalized linear mixed model results showing the effect of ungulate exclusion on the change (Δ) in plant species richness, diversity, heterogeneity (measured as taxonomic dissimilarity) and dominance (measured as functional evenness). The coefficients, estimate (*Est.*) and SE, and the *P*-value are given for each model.

Response (Δ)	Managed Sites			Unmanaged Sites		
	<i>Est.</i>	SE	<i>P</i>	<i>Est.</i>	SE	<i>P</i>
Species Richness	−2.41	0.55	<0.001	−1.06	0.54	0.052
Species Diversity	−0.04	0.02	0.088	0.01	0.02	0.910
Taxonomic Dissimilarity	0.02	0.01	0.008	−0.03	0.01	<0.001
Functional Evenness	−0.01	0.01	0.224	0.01	0.01	0.520

plant dominance (measured as functional evenness) over time did not vary significantly between grazed and ungrazed plots at managed or unmanaged sites (Fig. 3, Table 2).

Discussion

Our findings demonstrate how the effects of grazing exclusion on vegetation dynamics differ depending on forest management, and suggest that vegetation in recently thinned and burned sites is more sensitive to changes in the grazing regime. Our findings also agree with studies from around the globe showing that plot-level plant diversity decreases when large herbivores are completely

excluded from the landscape (Belsky 1992; Rambo & Faeth 1999; Towne et al. 2005; Bakker et al. 2006; Enyedi et al. 2008; Schultz et al. 2011). These findings together suggest that ungulates have an important role in plant successional dynamics and in maintaining plant diversity, particularly following episodic disturbance events associated with forest management activities.

It has been suggested that ungulate herbivores increase plant diversity in more mesic rangelands while decreasing plant diversity in drier rangelands (Olff & Ritchie 1998; Bakker et al. 2006). However, Manier & Hobbs (2006) did not find significant differences in plant species richness and diversity between rangelands with extant ungulate grazing and where ungulates were excluded for over 40 yrs in western Colorado. Moreover, Rambo & Faeth (1999) demonstrated that short-term ungulate exclusion results in decreased plant species richness in semi-arid rangelands in Arizona. Our current, as well as previous, findings from Starkey (Pekin et al. 2014), which is a seasonally arid forest environment, further demonstrate that plant diversity in forested rangelands of the western United States is not negatively impacted, and may even be increased, by ungulate grazing, at least at the intensities that naturally occur at Starkey.

Our observations regarding the influence of ungulates on plant species heterogeneity (reflected in taxonomic dissimilarity) are also similar to those from other rangelands. The largest increase in plant heterogeneity observed in our study was in grazed plots at unmanaged sites. In Midwestern grasslands, a larger increase in plant heterogeneity was also observed under grazing by bison compared to where no ungulate grazing took place (Veen et al. 2008). Veen et al. (2008) attributed the increase in heterogeneity with grazing in these grasslands to reduced plant dominance, and studies from other Midwestern grasslands have shown that grazing effects on plant diversity are controlled by interspecific competition (Bakker et al. 2003). While many of the species lost from our plots under ungulate exclusion were small herbaceous species such as forbs, which are likely to be sensitive to direct competition from woody plant life forms for resources such as water, nutrients and light (Pekin et al. 2011, 2012a,b), we did not observe a significant effect of grazing on dominance among different plant functional groups in our current study. This may be due to differences in plant responses to herbivory or differences in resource competition among plant species in grasslands vs forests. Vegetation communities in forests are composed of a variety of woody and herbaceous plant guilds that are more structurally complex than grasslands and therefore may display greater resilience to herbivory.

Furthermore, grazing had the opposite effect on plant heterogeneity in managed vs unmanaged forest sites at Starkey. Collins & Smith (2006) found that the effect of

grazing on plant heterogeneity differs with the frequency of fires in the Midwestern United States. It has been suggested that variable forage selection by herbivores and pre-existing vegetation patterns both determine the effect of grazers on plant heterogeneity (Adler et al. 2001). While we do not know the relative strength of forage selection at managed vs unmanaged sites, most of the compositional differences (at the beginning and end of the study) across our plots were explained through forest management. The effect of ungulates on composition was relatively small. Thus, the reversal in the effect of grazing on trajectories of plant heterogeneity at managed vs unmanaged sites may be due to differences in initial vegetation patterns induced by the stand thinning and burning, which may, in turn, have been affected by ungulate forage selection.

Our previous study from Starkey demonstrated that ungulate effects on shrub dynamics and diversity are more pronounced in the absence of forest management (Pekin et al. 2014). In our current study, however, the diversity (specifically species richness) of the forest understorey, which is mostly composed of herbaceous plant species, differed only slightly between grazed and ungrazed plots at unmanaged sites, and the reduction in plant diversity with ungulate exclusion was much more pronounced in managed sites. Furthermore, overall plant species composition (indicated by the multidimensional scaling) was similar between grazed and ungrazed plots at unmanaged sites, whereas species composition and successional trajectories differed strongly between grazed and ungrazed plots in managed sites. Specifically, grazing slowed successional change of the vegetation community in managed sites much more than at unmanaged sites. A recent study on grassland steppe vegetation dynamics in Colorado also showed that ungulate grazing slows down vegetation succession only in early seral plant communities (Milchunas & Vandever 2014). These findings together suggest that the influence of ungulates on plant species dynamics in forested rangelands is relatively minor at later stages of succession, and provide support for the hypothesis that grazing has a more pronounced impact on early seral vegetation associated with fires or prescribed burning (Hobbs 1996). This may be due to either a higher sensitivity of early seral vegetation to changes in the grazing regime or increased grazing intensity in extant plots that were recently thinned and burned. Indeed, utilization of managed areas by the ungulates may have been higher since early seral vegetation is likely to be more palatable to ungulates (Wisdom et al. 2006).

It has been suggested that the persistence of high numbers of wild and domestic ungulates in the landscape poses an ever increasing threat to the sustainability of ecosystems in the interior western United States (Beschta et al.

2013). While its need and effectiveness has been recently criticized (Svejcar et al. 2014), there is a call for the reduction or elimination of ungulates from public grazing lands to allow vegetation communities to adapt to on-going climatic changes (Beschta et al. 2014). Our study demonstrates that changes in the strength and direction of plant community responses to ungulate exclusion in forested rangelands depend on management history. Furthermore, ungulates are likely to have an important role in maintaining plant diversity in western rangelands following management activities that favour early seral vegetation such as stand thinning and burning. Accordingly, any attempts to reduce or remove wild or domestic ungulates from western forests should carefully consider co-occurring forest management activities and associated vegetation seral stage, because alterations in the grazing regime may have larger and unintended consequences for the vegetation community where these activities prevail.

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