Ochoco Wild Horse

in Riparian Area,

outside Territory.

“Fargo”

1998 - 2020

OCHOCO WILD HORSE HERD MANAGEMENT PLAN
OBJECTIONS
Central Oregon Wild Horse Coalition

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Quantifying the grazing impacts associated with different herbivores on rangelands

S. D. ALBON

Macaulay Institute and

Search for more papers by this author

M. J. BREWER

Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen AB15 8QH, UK

Search for more papers by this author

S. O'BRIEN

Macaulay Institute and

Present address: Joint Nature Conservation Committee, Aberdeen AB10 1UZ, UK.

Search for more papers by this author

A. J. NOLAN

Macaulay Institute and

Search for more papers by this author

D. COPE

Macaulay Institute and

Present address: Defra, Sustainable Energy Policy Division, 123 Victoria Street, London SW1E 6DE, UK.

Search for more papers by this author

S. D. ALBON

Macaulay Institute and

Search for more papers by this author

M. J. BREWER

Biomathematics and Statistics Scotland, Craigiebuckler, Aberdeen AB15 8QH, UK

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THESIS

EFFECTS OF FERAL HORSE HERDS ON PLANT COMMMUNITIES ACROSS A PRECIPITATION GRADIENT

Submitted by

Lauren Baur

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

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Master's Committee:

Advisor: Melinda D. Smith

Kathryn A. Schoenecker
Paul Meiman

ABSTRACT

EFFECTS OF FERAL HORSE HERDS ON PLANT COMMMUNITIES ACROSS A PRECIPITATION GRADIENT

Feral horse herds in the western United States are managed with the goal of maintaining "a thriving natural ecological balance" with their environment. Because rangeland ecology is complex and grazers such as horses can have different effects under different environmental conditions, more data are needed to better inform Appropriate Management Levels and other management decisions. We used long-term grazing exclosures and fenceline contrasts to evaluate the impacts of feral horses on plant communities at five sites across the western United States. These sites ranged from 229 to 413 mm mean annual precipitation and represented four different ecosystems (Great Basin desert, Colorado Plateau, Rocky Mountain grassland and mixed grass prairie). We found that feral horses significantly reduced grass biomass and total biomass at alpha=0.1, but did not have a significant effect on plant community composition, species richness, diversity, evenness, or dominance. The effects of horses did not vary by site, indicating that different precipitation levels are not driving differences in grazing effects within the range encompassed by our sites. In other words, our results imply that while feral horses do reduce plant biomass, they are not causing plant community shifts, and their effects may not be as site-specific as has been assumed. Additional multi-site studies, preferably with standardized exclosures and larger sample sizes, would increase our understanding of feral horse grazing effects.

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Thanks to my supportive family and friends. To my committee, Melinda Smith, Kate Schoenecker, and Paul Meiman. Thanks to the US Geological Survey for funding, and to everyone from the Bureau of Land Management, National Park Service, US Geological Survey and US Forest Service who made this project possible, including: John Axtell, Bill Pickett, Jared Bybee, Jim Sparks, Mike Jensen, Stan Kitchen, Elizabeth Burghard, Bill Whitworth, Chad Sexton, and Martina Thornton. To Ken, the BLM range tech who set up my rain bucket at Clan Alpine. To my hardworking and intrepid field assistant Mariah Patton, and lab assistants Abby, Jennie and Claire. Thanks to Phil Turk for statistics help, and to Nate Lemoine for help with data analysis and figures. To Jesse Gray for fieldwork help and Jennifer Ackerfield for plant ID help. To everyone who took a look at some plant that was stumping me. To Mike Bynum, who taught me many of the plant ID skills I needed to do this project. To Jennifer Radcliffe for manuscript comments. To TJ Holmes at Spring Creek Basin for sharing her time, knowledge and positivity, and to her family for the food and conversation. And thanks to everyone else who made our fieldwork more pleasant including Carol and Steve, Dave and his family in Fallon, Ivan and Lloyd in Naturita, and Art and Nancy at Bighorn Canyon. Finally, thanks to CSU motorpool; sorry about all the wear and tear on that truck.

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INTRODUCTION

Feral horses are widespread in the western United States, and the nature of their ecological role has often been a source of controversy. While the effects of cattle grazing on western rangelands have been thoroughly studied (e.g. Kauffman and Krueger 1984, Belsky et al. 1999, Jones 2000), the impacts of feral horses have received less attention (Beever 2003, Nimmo and Miller 2007). The effect of feral horses on rangelands west of the Rocky Mountains is of particular importance given that a large majority of federally managed feral horse herds and herd management areas (HMAs) are found in that region, on land managed by the Bureau of Land Management (BLM). However, most studies of feral horse grazing effects in North America have been conducted in salt marshes of the East Coast (Wood et al. 1987, Turner 1987, Turner 1988, Furbish and Albano 1994, Seliskar 2003, De Stoppelaire et al. 2004) and the Pryor Mountain Wild Horse Range of northern Wyoming/Southern Montana (Detling 1998, Gerhardt 2000, Gerhardt and Detling 2000, Fahnestock and Detling 2000), with a limited number of studies conducted in the Great Basin (Beever and Brussard 2000, Beever et al. 2003, Beever et al. 2008, Davies et al. 2014) or other western rangelands. Thus, we still lack basic understanding of the effects of feral horse grazing on rangelands of the western US, despite the fact that this represents a critical knowledge gap for effective rangeland management.

When compared to other ungulates, feral horses are expected to differ in their effects on rangeland plant communities because of differences in their digestive anatomy, as well as their grazing behavior. Although horses and cattle share a high dietary overlap (Scasta 2014), horses have higher energy requirements than cattle (Hanley 1982, Duncan et al. 1990). As cecal digesters rather than ruminants, they digest their food less completely, and retain most forage for a shorter time in their digestive tract (Duncan et al. 1990). Therefore, horses need to eat more plant biomass per unit of body mass than cattle (Janis 1976, Holechek 1988, Duncan et al. 1990, Menard et al. 2002, Scasta 2014). On the other hand, unlike ruminants, equids can live on a high-cellulose diet (Gwynne and Bell 1968, Janis 1976), enabling them to survive and even thrive in habitat that would be considered low quality for other ungulates. Horses also differ from cattle in their grazing behavior. While cattle prefer to stay near water sources (Kauffman and Krueger 1984, Beever 2003), horses are able to range farther from water (Beever and Brussard 2000). Although Crane et al. (1997) found that feral horses in Wyoming spent proportionally more time in riparian habitat than in other habitat types, Ganskopp and Vavra (1986) did not observe such a preference among feral horses in Oregon. Horses also show a preference for higher elevation habitats (Ganskopp and Vavra 1986, Crane et al. 1997). This may mean horses cause less damage than cattle around water sources, but it also means that plants that might survive in high-elevation refuges when only cattle are present are more likely to be grazed when horses are present (Symanski 1994, Beever 2003, Beever and Aldridge 2011). Because of these differences, relying on studies of cattle grazing effects to inform management of feral horse herds and HMAs is not appropriate. Instead, improved information on the specific effects of feral horse grazing is needed.

While there have been some studies of the effects of feral horses on plants in rangelands of the Intermountain West (Beever and Brussard 2000, Beever et al. 2003, Beever et al. 2008, Davies et al. 2014), the number of sites that has been studied is small compared to the area where feral horses are found. However, grazing effects on plant communities can be locally specific and dependent on local environmental conditions (Milchunas et al. 1988, Menke and Bradford 1992, Hobbs 1996, Ostermann-Kelm et al. 2009, Beever and Aldridge 2011). For example, the magnitude and direction of grazing effects on plant diversity appears to be influenced by the productivity of a site, which is correlated with precipitation level (Milchunas et al. 1988, Milchunas and Lauenroth 1993, Frank 2005, Bakker et al. 2006, Lezama et al. 2014). In productive grasslands, grazing often increases plant diversity, while in less productive grasslands, grazing can reduce diversity (Bakker et al. 2006, Lezama et al 2014, Koerner et al. in prep). In addition, the magnitude of grazing effects tends to increase with increasing productivity

(Milchunas and Lauenroth 1993, Lezama et al. 2014). Thus, to more comprehensively understand the impacts of feral horse grazing in the western US, studies across a range of environmental conditions are required.

The purpose of this study was to assess the effects of feral horse grazing on plant communities at five sites that span a large portion of the geographic area where feral horses are found in the western US. These sites cover a range of precipitation from 229 to 413 mm/yr, and represent four different rangeland ecosystems (Great Basin desert, Colorado Plateau, Rocky Mountain grasslands, and mixed grass prairie). In an effort to capture long-term effects, the project was limited to sites with preexisting exclosures or fenceline contrasts. Because of previous studies showing such a relationship between grazing effects and productivity or precipitation, we hypothesized that horse grazing would increase plant species richness and diversity at wetter sites, and decrease them at drier sites. We also predicted that the magnitude of grazing effects would increase with increasing precipitation.

METHODS

Study sites

For this study, we selected five rangeland sites which had preexisting exclosures or fencelines separating areas grazed by feral horses from areas not grazed by feral horses (Figure 1). Length of treatment ranged from about 10 years at the Colorado site to 81 years at the Utah site (Table 1). The sites spanned a precipitation gradient from about 229 mm/yr in Nevada to 413 mm/yr in Colorado. Because most of our sites were remote and lacked long-term precipitation records, we defined this gradient based on interpolated mean annual precipitation data from the Terrestrial Precipitation Analysis package (TPA) (Lemoine et al. 2016).

The driest site, Clan Alpine Herd Management Area (abbreviated as CA), is located in Churchill County, NV. It has an approximate mean annual precipitation of 229 mm. All of our sampling plots at CA were located in the same Natural Resource Conservation Service soil map unit, the Old Camp-Singatse-Rock outcrop association, the largest component of which is the Loamy Slope 8-10 P.Z. (R027XY007NV) ecological site (NRCS 2016). In the area of the HMA where we sampled, the vegetation includes both riparian and nonriparian species, dominated by the invasive annual grass *Bromus tectorum* (L.), native saltgrass (*Distichlis spicata* (L.) Greene), and bluegrasses (*Poa* spp. L.), along with some shrubs including *Sarcobatus vermiculatus* (Hook.) Torr., and exotic forbs such as *Salsola* spp. L. and *Kochia* spp. Roth.

The second driest site was the Sulphur Herd Management Area (Sulphur) in Millard County, UT, also in the Great Basin, with a mean annual precipitation of 332 mm. Although National Resource Conservation Service soil data were not available for this site, soils in the area are gravelly loams, sandy loams, and loamy sands (Clary and Holmgren 1982). The site is dominated by black sagebrush (*Artemisia nova* A. Nelson), rabbitbrush (*Chrysothamnus* spp. Nutt) and snakeweed (*Gutierrezia sarothrae* (Pursh) Britton and Rusby). Native bunchgrasses like *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Elymus* *elymoides* (Raf.) Swezey, and *Achnatherum hymenoides* (Roem. & Schult.) Barkworth, as well as *Bromus tectorum*, are fairly prevalent.

The third site was the Pryor Mountain Wild Horse Range (PM) in Carbon County, MT/Big Horn County, WY. This site is in the Bighorn Mountains and has been described as "Rocky Mountain grassland" (Gerhardt and Detling 1998, Stohlgren et al. 1999), with mean annual precipitation of about 352 mm. Three of our exclosures at this site were located in the Silty-Limy (SiLy) RRU 46-S 10-14" p.z. (R046XS141MT), Silty (Si) RRU 58A-C 11-14" p.z. (R058AC040MT), and Loamy (Lo) 5-9" p.z. (R032XC020MT) ecological sites, while the fourth was located on limestone outcrop (NRCS 2016). The vegetation at Pryor Mountain is dominated by grasses like *Pseudoregneria spicata* (Pursh) Á. Löve and *Bouteloua gracilis* (Kunth) Lag. ex Griffiths, with the shrubs *Artemisia nova* and *Cercocarpus ledifolius* Nutt. also important in some locations.

The fourth site was Theodore Roosevelt National Park (THRO) in Billings County, ND. It is in the Great Plains region, with an average annual precipitation of 389 mm. Although this site was only the second wettest according the interpolated data, it was by far the most productive (see Figure 4). Our sampling plots were located in the park's South Unit, and covered several ecological sites and soil types, with plots farther east being on sandier soils, and those farther west on more clayey soils, with loamy soils also represented throughout (NRCS 2016). The park is mostly mixed grass prairie, with some area covered in badlands formations and woodlands. The park is dominated by native graminoids such as *Elymus elymoides, Carex inops* L.H. Bailey, and *Bouteloua curtipendula* (Michx.) Torr., though nonnative Kentucky bluegrass (*Poa pratensis* L.) is also abundant (Ashton and Prowatzke 2014).

The fifth and wettest site was Spring Creek Basin Herd Management Area (SCB), in San Miguel County, CO, on the Colorado Plateau. According to TPA, this site has an annual precipitation of 413 mm. Despite being the wettest site, SCB was less productive than THRO, probably due to differences in temperature/aridity and soil fertility. Our sampling at this site took place on Silty Saltdesert

(R035XY410CO), Basin Shale (R035XY408CO), and Clayey Saltdesert (R035XY403CO) ecological sites (NRCS 2016). The vegetation at SCB is characterized by shrubs including *Atriplex canescens* (Pursh) Nutt., *Sarcobatus vermiculatus* (Hook.) Torr, and *Krascheninnikovia lanata* (Pursh) A. Meeuse & A. Smit, as well as native perennial bunchgrasses like *Hilaria jamesii* (Torr.) Benth and *Sporobolus cryptandrus* (Torr.) A. Gray. *Bromus tectorum* is also common.

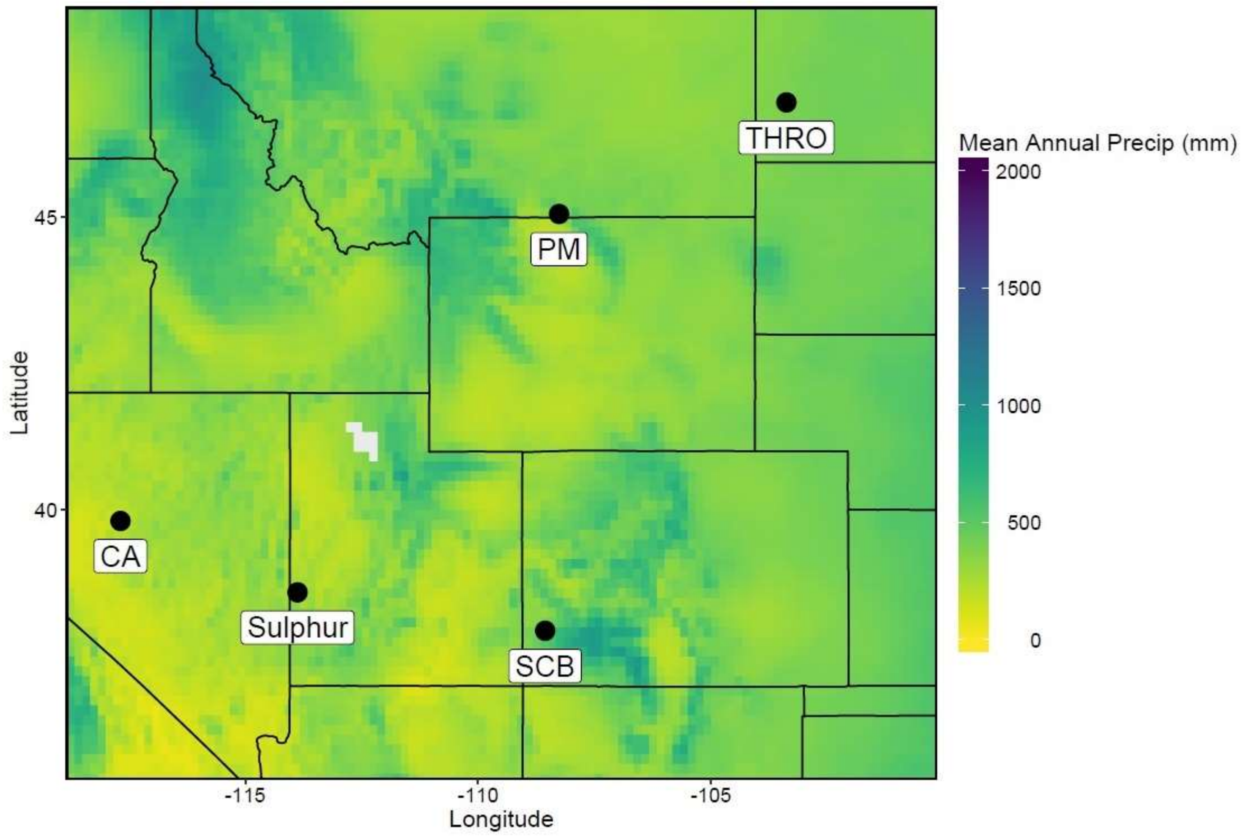

Figure 1: Map of vegetation sampling (site) locations and precipitation levels across the western USA, 2014-2015. CA=Clan Alpine Herd Management Area, Sulphur=Sulphur Herd Management Area, SCB=Spring Creek Basin Herd Management Area, PM=Pryor Mountain Wild Horse Range, THRO=Theodore Roosevelt National Park. See Table 1 for more information.

Table 1: Detailed study site descriptions indicating length of treatment, grazers present, and other environmental characteristics. HMAs are Herd Management Areas, administered by the Bureau of Land Management. The AML, or Appropriate Management Level, is the number of horses that the BLM has determined can be sustained on the HMA. Population estimates and AMLs are from blm.gov for Bureau of Land Management sites. Information for Theodore Roosevelt National Park is from personal communication with Bill Whitworth, Chief of Resource Management, and Chad Sexton, Geographic Information Systems Analyst. Dung counts for ungulates other than cattle, horses and bison are pooled because of the difficulty of accurately distinguishing between the feces of those animals in the field.

Site name	**State**	**Ecosystem**	**Mean annual precip (mm)**	**Elevation (m)**	**HMA/park size (hectares)**	**# of exclosures**	**Exclosure size**	**Exclosure or fence construction date**	**# of cages**	**AML**	**Estimated horse population**	**Mean number of dung piles per dung transect**		
												horse	**cattle or bison**	**other ungulates (deer, bighorn sheep, pronghorn, elk, domestic sheep)**
Clan Alpine (CA)	Nevada	Great Basin	229	~1400	122,307	2	~40x140m and ~20x140m, respectively	1990 and 1994	10 (9 survived)	612-979	724 in 2014, 700 in 2015	11	11.5	5
Sulphur	Utah	Great Basin	332	~1920	107,529	0 (5 transects with horses, 5 without horses)	N/A	1933	10	165-250	718 in 2014, 729 in 2015	9.8	0	26
Pryor Mountain (PM)	Montana	Rocky Mountain grassland	352	~1280-1520	13,430	4	Approximately 50 x 50m (slightly bigger)	1992 and 1994	20 (19 survived)	90-120	160 in 2014, 172 in 2015	3	0	2.25
Theodore Roosevelt (THRO)	North Dakota	Great Plains (mixed grass prairie)	389	~1760	18,680	0 (THRO1=3 transects with horses, 3 without horses; THRO2= 4 transects with horses, 4 without horses)	N/A	Park established in 1947; fence constructed between 1950 and 1956	10 (6 survived)	50-90	~100	20.5	6.5 inside park, 26.5 outside	0
Spring Creek Basin (SCB)	Colorado	Colorado Plateau	413	~1980	8,658	5	4 are 30 x 30ft (9.1 x 9.1 m), 1 is bigger, 32m long	2003 and 2004	25	35-65	57 in 2014, 61 in 2015	4.8	0.2 (One single piece of cow dung, more likely missed in initial sweep than deposited in 2015)	9.6

Experimental design

Because we were sampling preexisting exclosures and fencelines of different sizes, sampling layout varied somewhat between sites (Table 1). Three of the sites (CA, PM and SCB) had preexisting grazing exclosures, and data were collected inside and outside each exclosure. Clan Alpine differs from the other sites in that its exclosures were built to protect springs. In 2014 our sampling protocol at CA was similar to that of Beever and Brussard (2000); we located species composition transects inside exclosures at exclosed springs and in grazed areas at nearby springs without exclosures. In 2015 we added transects immediately outside the exclosures at the exclosed springs. Given these differences in sampling, CA species composition data were included in analysis for 2015, but not 2014. However, plant species richness, evenness, diversity and dominance were still calculated for 2014 (Supplementary Table 1).

Sulphur and THRO did not have grazing exclosures, but each site had a fenceline with horses confined to one side. Sulphur HMA is separated by a fenceline from the USDA Forest Service's Desert Experimental Range (DER); horses graze on the BLM side but not the DER side. At THRO, we sampled in the park's South Unit, where the horses are confined inside the park fence and mostly on the east side of the Little Missouri River which bisects the park. In 2014 we placed transects on either side of the river. In 2015 we added transects on either side of the park fence. We treated these two groups of transects as separate "sites" for analysis (THRO1 and THRO2).

Species composition sampling

To assess plant species composition, we recorded absolute percent cover of all plant species within square 1m x 1m quadrats, placed every 2 m along transects inside and outside the permanent exclosures or on either side of the fenceline. Most transects were 50 m long, but at Spring Creek Basin the exclosures were too small, so we used multiple shorter transects. Some larger exclosures had multiple 50-m transects inside to increase sampling. For each quadrat, we visually estimated aerial cover of each species separately to the nearest 1%. We also estimated the percent cover of biological soil crust, and of totally exposed ground covers including bare ground, rock, and litter where they exceeded a contiguous 1% of the quadrat. In 2015 we also noted all animal dung inside quadrats to confirm the identity of grazers that were present. Species composition data were collected at each site once in 2014 and twice in 2015 (early and late in the growing season); the larger of the two values for each species in 2015 was used in subsequent analyses.

Fecal transects

To assess the level of use of our sampling sites by herbivores, in 2015 we used dung transects consisting of two 50-m tapes placed 4 m apart running parallel to our species composition transects, outside exclosures, or on the side of the fence with horses, at each site except THRO1. One transect at Sulphur and two at THRO2 were also placed on the side of the fence without horses. During our first sampling trip of 2015, we cleared all large animal dung from the area between the tapes, recording the number of dung piles. We repeated this process on our second sampling trip to see how many dung piles had been added since the first trip. No statistical analyses were performed on these data; instead, we used average number of piles per transect as a general metric of herbivore presence (see Table 1).

Biomass sampling

We constructed small temporary exclosures (“cages”), each 1 x 1 x 1 m in size, and installed them outside permanent exclosures or in horse-grazed areas at each site in spring 2015. In late summer, we collected all aboveground herbaceous biomass inside 0.25 m^2 circular frames. For each cage, we clipped one frame inside the cage, one frame approximately 1-2 m outside the cage, and one inside the permanent exclosure. At the time the cages were placed, we determined where to place each outside frame by comparing the area up to ~2m away from the cage on each of its four sides, and choosing the side of each cage that had the most plant species in common with the area inside the cage. Since we were not collecting biomass from woody plants, we avoided placing the cages and their corresponding outside frames directly on top of shrubs. If multiple sides of the cage had the same species in common with the area inside the cage, the side that seemed to be most similar in biomass to the area inside the cage, based on a casual visual estimate at the time the cages were installed, was chosen. Frames inside the permanent exclosures were placed by randomly tossing them into the exclosure and clipping where they fell. Biomass was divided into three categories: grass (including other graminoids such as sedges), forbs, and litter. Biomass was field-dried and then dried in drying ovens in the lab for at least 24 hours at 60°C before weighing.

Statistical analysis

For species composition data, the experimental unit for analysis was the plot level. In most cases, each plot consisted of all quadrats inside or outside a single permanent exclosure. However, at Sulphur, each 50m transect was considered a plot, meaning the site had a total of five plots with horse grazing and five plots without. At THRO1, each plot consisted of three transects (meaning there was only one plot per treatment), and at THRO2, each plot consisted of two transects (two plots per treatment). (Transects were grouped into plots based on their proximity to each other. At Sulphur, the transects were roughly evenly spaced along the fenceline, while at THRO1 and THRO2, transects were more clustered due to topography.) Mean species richness, evenness, diversity ($e^{H'}$), and Berger-Parker dominance were calculated at the quadrat level and then averaged at the plot level to avoid bias caused by the fact that not all plots had an equal number of quadrats. For CA, these calculations were done using all available data for 2014, but grazed plots without corresponding ungrazed plots were dropped from the 2015 data. An alpha level of 0.1 was set for all analyses, and 2014 and 2015 data were analyzed separately.

The plot-level values of species richness, evenness, diversity ($e^{H'}$), and dominance were analyzed using a mixed linear model with PROC MIXED in SAS® version 9.4 (SAS Institute Inc., Cary, NC, USA). Factors were site and grazing (i.e., feral horses present or not), with the grazing treatment nested within site. A similar mixed linear model was used to analyze grass, forb and total herbaceous biomass (hereafter "total biomass") inside and outside permanent exclosures. In both models, effects of grazing treatment, site, and treatment by site interactions were assessed. Although data were collected on litter biomass, those data were not used in analyses.

As mentioned above, the layout used for species composition sampling at Clan Alpine differed from that used at other sites in that some grazed plots did not have corresponding ungrazed plots, meaning some data could not be used in the analyses to assess site or grazing effects. Because of this, CA was not included in statistical analysis for 2014. For 2015 sampling, new transects were added, and two grazed plots at CA without corresponding ungrazed plots were dropped from the analysis for 2015. At THRO the groups of transects established in 2014 and 2015, respectively, were designated as separate "sites" (THRO1 and THRO2) in the analyses.

To assess differences in plant community composition, community matrices were constructed, consisting of relativized mean percent cover per quadrat of each species in each plot. These community matrices were used to construct Bray-Curtis resemblance matrices. The resemblance matrices were analyzed using two-factor permanovas (Primer v6), with site and treatment (with vs. without horses) as factors, with treatment nested within site.

To assess short-term grazing effects/utilization (i.e., to compare biomass inside and outside temporary exclosures), t-tests were conducted in SAS with PROC TTEST. Biomass was averaged across all temporary exclosures and all corresponding grazed plots for each site, and those averages were used to calculate 2015 growing season offtake ((ungrazed-grazed)/ungrazed) for each site (McNaughton 1979, Bonham 1989).

RESULTS

Plant community response to feral horse grazing

In 2014 (Figure 2) and 2015 (Figure 3), richness, diversity ($e^{H'}$) and dominance, but not evenness, varied significantly by site at alpha=0.1. However, there were no significant grazing effects, and grazing by site interactions were not significant (Table 2). Two-factor permanovas showed that, as expected, plant community composition differed significantly among the five study sites (p=0.005 for both 2014 and 2015). However, plant community composition was not different between grazed vs. ungrazed plots (p=0.987 for 2014 and p=0.969 for 2015). Individual single-factor permanovas performed separately for each site in each year also failed to find any significant effect of grazing on community composition at any individual site (p>0.1, data not shown).

Long-term effects of feral horse grazing on biomass

Averaging across all treatments (inside permanent exclosures, inside temporary exclosures, and outside), THRO had by far the highest total biomass, followed by CA, SCB, PM and Sulphur (Figure 4). Total biomass and grass biomass differed significantly by site and with grazing. Forb biomass did not differ significantly between sites or with grazing (Table 3). Across sites, grazed areas had a mean of 52.9% less grass biomass and 40.3% less total biomass than areas experiencing long-term exclosure from wild horse grazing. (These percentages are calculated as percent removed; see Table 4.) CA was an outlier with 95.3% less grass biomass outside than inside permanent exclosures. However, interactions between site and grazing were not significant for total, grass, or forb biomass (Table 3).

Short-term grazing intensity and annual utilization

Percent offtake of total biomass in 2015 was highest at Pryor Mountain (26.3%) and lowest at THRO (1.9%; Table 5). At Sulphur, average biomass was higher outside than inside temporary exclosures by 52.7%. When offtake was divided into grasses and forbs, grass biomass was higher outside the temporary exclosures at 3 of 5 sites, but forb biomass was higher inside than outside at 4 of 5 sites (Table 5). However, only grass and total biomass at Sulphur showed significant differences in biomass inside vs. outside the temporary exclosures (Table 5). No other significant differences in grass, forb or total biomass inside vs. outside the temporary exclosures were observed at any site.

Table 2: Results of linear mixed-model analysis of variance for the effects of site and feral horse grazing on plant species richness, evenness, Shannon's diversity ($e^{H'}$) and Berger-Parker dominance. P-values ≤ 0.1 are in bold.

		Richness			Evenness			Diversity			Dominance		
		df	F	P	df	F	P	df	F	P	df	F	P
2014	Site	4, 6.27	21.91	**0.0008**	4, 24	1.28	0.3050	4, 9.78	12.04	**0.0008**	4, 24	3.33	**0.0265**
	Grazing	1, 20.9	0.01	0.9211	1, 24	0.38	0.5442	1, 19.8	0	0.9553	1, 24	0.29	0.5974
	Site*grazing	4, 20.9	1.59	0.2137	4, 24	1.92	0.1397	4, 19.8	1.66	0.1980	4, 24	1.99	0.1280
2015	Site	5, 26	25.01	**<0.0001**	5, 25.5	1.12	0.3727	5, 26	9.92	**<0.0001**	5, 14.1	2.40	**0.0903**
	Grazing	1, 26	0.18	0.6755	1, 25	1.17	0.2892	1, 26	0.33	0.5678	1, 22.7	1.66	0.2100
	Site*grazing	5, 26	0.79	0.5645	5, 25	0.88	0.5067	5, 26	1.01	0.4305	5, 22.7	1.01	0.4322

Table 3: Results of mixed-model analysis of variance for the effects of site and feral horse grazing on grass, forb, and total herbaceous biomass (comparing grazed areas with areas inside permanent exclosures). P-values ≤ 0.1 are in bold.

		Grass			Forbs			Total		
		df	F	P	df	F	P	df	F	P
2015	Site	4, 6.57	23.01	**0.0006**	4, 1	0.89	0.6520	4, 7.87	18.34	**0.0005**
	Grazing	1, 22.7	5.1	**0.0338**	1, 21.7	0.09	0.7634	1, 23.1	3.96	**0.0586**
	Site*grazing	4, 22.7	0.48	0.7481	4, 21.7	1.53	0.2298	4, 23.1	0.26	0.9005

Table 4: Long-term grazing effects on grass and total biomass inside vs. outside permanent exclosures at each site. Percent removed is calculated as ((biomass inside exclosures-biomass outside exclosures)/biomass inside exclosures).

	Log response ratio		Percent removed	
	Grass	Total	Grass	Total
CA	-3.05911	-0.58321	95.3%	44.2%
Sulphur	-0.68856	-1.16463	49.8%	68.8%
PM	-0.59923	-0.37607	45.0%	31.3%
THRO	-0.31058	-0.30964	26.7%	26.6%
SCB	-0.64418	-0.36088	47.5%	30.3%
Mean	-1.06033	-0.55889	52.9%	40.3%

Table 5: Comparison of biomass inside vs. outside temporary exclosures (“cages”) for each site in 2015. Percent offtake is ((biomass inside cages-biomass outside cages)/biomass inside cages)*100. P-values were determined by t-tests comparing mean biomass inside vs. outside cages for each site. P-values ≤ 0.1 are in bold.

	Total		Grass		Forbs	
	Percent offtake	P	Percent offtake	P	Percent offtake	P
CA	14.1%	0.6079	-4.0%	0.9755	15.0%	0.6262
Sulphur	-52.7%	**0.0939**	-59.9%	**0.0794**	72.5%	0.4067
PM	26.3%	0.4796	-3.3%	0.9313	53.1%	0.4041
THRO	1.9%	0.3335	13.9%	0.5652	93.2%	0.3084
SCB	16.7%	0.5963	28.1%	0.4308	-33.3%	0.5778

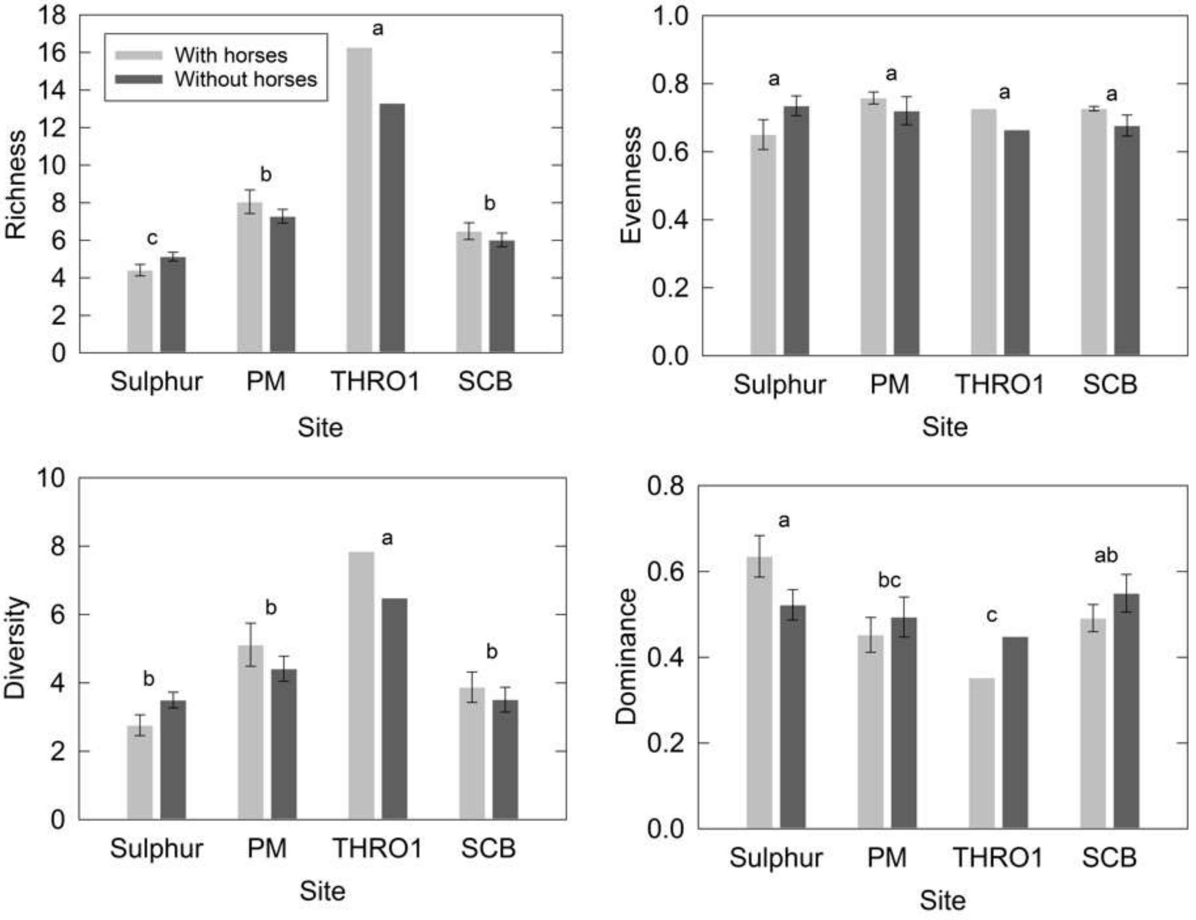

Figure 2: Effects of feral horse grazing on plant species richness, evenness, Shannon's diversity ($e^{H'}$), and Berger-Parker dominance per m^2 in 2014. Error bars represent standard error. Different lower case letters denote significant differences between sites at alpha=0.1. Sites are in order from driest (lowest precipitation) to wettest (highest precipitation).

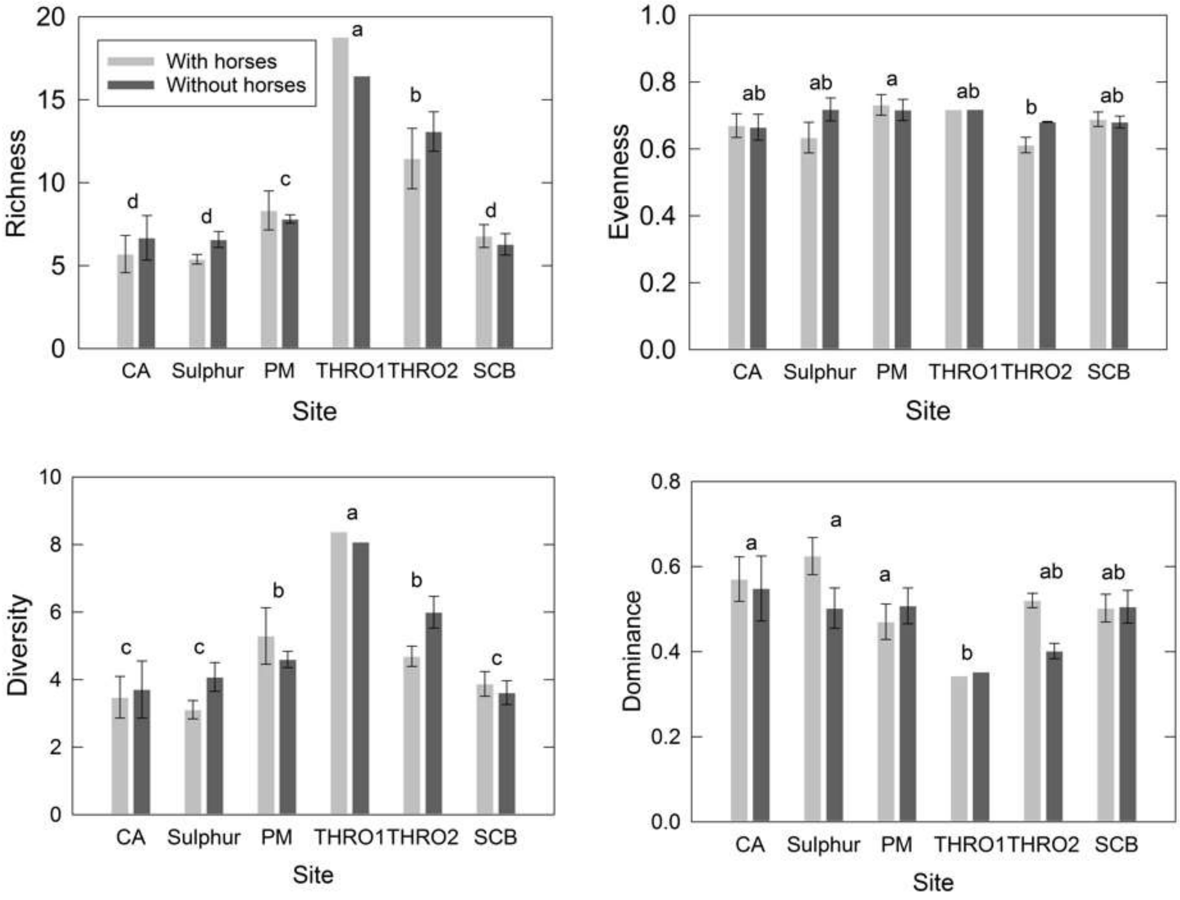

Figure 3: Effects of feral horse grazing on plant species richness, evenness, Shannon's diversity ($e^{H'}$), and Berger-Parker dominance per m^2 in 2015. Error bars represent standard error. Different lower case letters denote significant differences between sites at alpha=0.1. Sites are in order from driest (lowest precipitation) to wettest (highest precipitation).

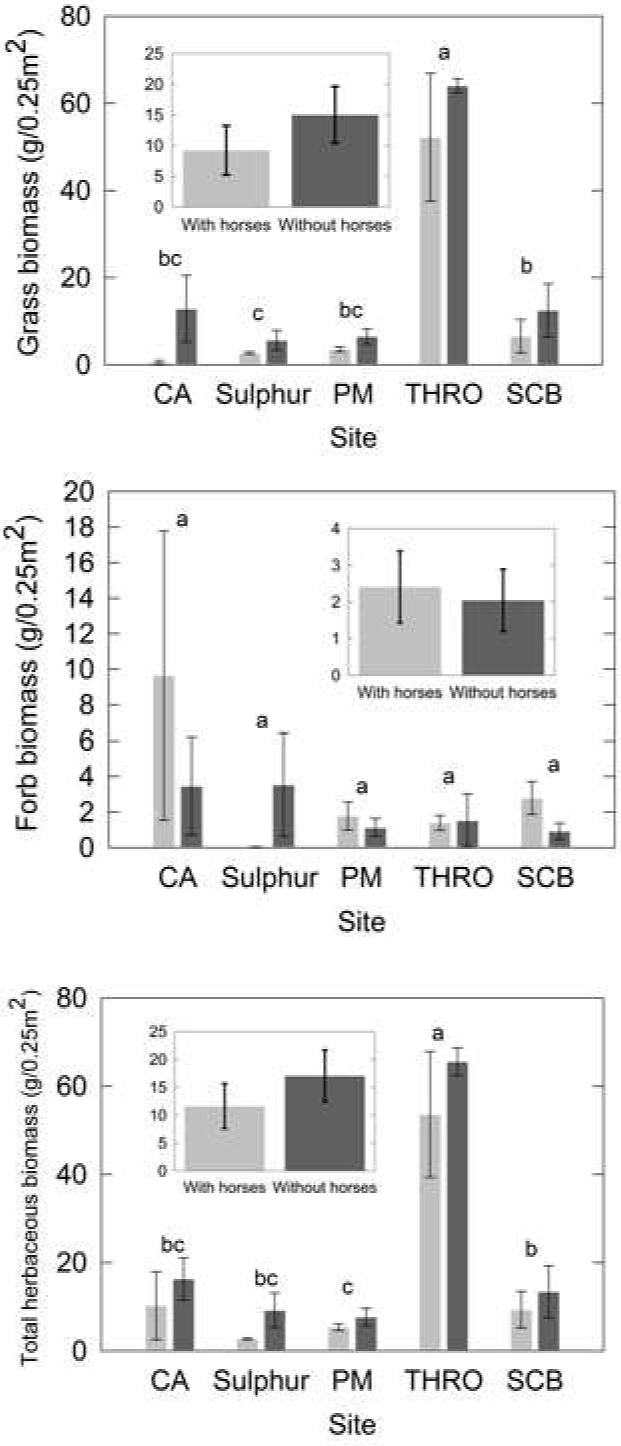

Figure 4: Long-term effects of feral horse grazing on grass, forb and total herbaceous biomass, measured in 2015. Error bars represent standard error. Different lower case letters denote significant differences between sites at alpha=0.1 (see Table 3). Sites are in order from driest to wettest. Insets show differences in biomass averaged across all sites.

DISCUSSION

We did not observe a significant effect of grazing by feral horses on any of several aspects of plant community structure (plant species richness, diversity, evenness or dominance) or plant community composition for the five rangeland sites spanning a 184-mm precipitation gradient. There was also no grazing by site interaction for any of these factors. Conversely, based on comparisons with long-term exclosed areas, feral horse grazing has significantly reduced grass biomass and total biomass at alpha=0.1, and this effect did not vary among sites. Thus, our hypothesis that grazing effects would vary by site, according to precipitation levels, was not supported.

Similar to our study, previous studies of feral horse impacts have usually found that horse grazing reduced overall aboveground plant biomass. This includes Villalobos and Zalba (2010) in grasslands in Argentina; and Wood et al. (1987), Turner (1987, in a study where clipping was used to simulate feral horse grazing), and Seliskar (2003) on east coast barrier islands. Wood et al. (1987) also observed lower grass biomass in areas grazed by feral horses. However, at Pryor Mountain, Gerhardt and Detling (2000) found no significant effect of horses on total biomass, and Fahnestock and Detling (1999a) found that grasses compensated for biomass removed by simulated horse grazing when water availability was adequate.

Studies looking at the effects of horses on plant species richness and diversity are more numerous, with more varied results. In Argentina, Villalobos and Zalba (2010) reported that horses reduced both richness and diversity. On Assateague Island, Seliskar (2003) found no effect on species richness. In the Sonoran Desert, Ostermann-Kelm et al. (2009) found increased plant diversity near horse trails compared with control plots far from trails. Among previous studies at Pryor Mountain, Gerhardt and Detling (2000) and Gerhardt (2000) found no effect on plant species richness, but Fahnestock and Detling (1999b) found that horses increased diversity in some cases. In the Great Basin, the presence of feral horses has usually been associated with lower plant species richness (Beever and Brussard 2000, Beever et al. 2008) and diversity (Davies et al. 2014). However, Beever et al. (2008) found increased species richness at some horse-occupied sites, while Davies et al. (2014) found no effect of horses on richness. Similar to our study, Beever et al. (2003) in the Great Basin and Detling (1998) at Pryor Mountain found that horse grazing was not a major influence on plant community composition.

One possible reason for the lack of significant effects on community composition and diversity is that our sites, like many arid and semi-arid rangelands, are non-equilibrium systems where plant communities and herbivore populations are not tightly coupled. Theoretically, this is the case because in systems with high precipitation variability, droughts keep herbivore populations below a level that would damage the vegetation (Behnke and Scoones 1993, Cowling 2000, Derry and Boone 2010, Von Wehrden et al. 2012). Because the BLM gathers and removes horses when their numbers exceed Appropriate Management Levels, these removals could be taking the place of drought-induced mortality events by periodically reducing populations.

Relatedly, arid and semi-arid systems often display nonlinear and even irreversible responses to grazing (Westoby et al. 1989, Friedel 1991, Laycock 1991, Joyce 1993). It is possible that grazing before the construction of the exclosures we sampled pushed the plant communities into an alternate stable state, after which removal of grazing was not enough to return the system to a previous state. In keeping with many previous horse grazing exclusion studies (e.g. Turner 1987, Rogers 1991, Detling 1998, Fahnestock and Detling 1999b, Beever and Brussard 2000, Fahnestock and Detling 2000, Seliskar 2003, De Stoppelaire et al. 2004, Davies et al. 2014), we have assumed that comparing plant communities inside and outside exclosures constitutes an observation of the effects of “horses” or of “grazing.” However, because vegetation recovery is rarely a simple reversal of grazing-induced changes, “effects of grazing” and “effects of protection from grazing” may not be equivalent (Fleischner 1994, Sarr 2002). Past or current grazing may have caused changes that are not detectable purely through the use of exclosures.

The productivity level of our sites may also have contributed to the lack of grazing effects that we observed. Assuming that there is a relationship between primary productivity and the effects of grazing on plant diversity, with grazing decreasing diversity at less-productive sites and increasing diversity at more-productive sites, this implies an intermediate range of productivity where no effect of grazing on plant diversity is observed. In a study by Frank (2005), the intercept where grazing effects switched from negative to positive (i.e., the point where the effect should be zero) was slightly below 100 g/m^2 net aboveground production. In another study by Bakker et al. (2006), this point was at approximately 225 g/m^2. Our sites may fall into such a range of intermediate productivity where grazing has no observable effect on plant diversity.

Another possibility is that the areas where we sampled were not receiving high enough grazing pressure to cause shifts in the plant community. Although only one of the sites, Sulphur, had a population that far exceeded its AML, two additional sites (THRO and PM) had horse populations slightly above the level recommended by their managing agencies. The BLM defines the upper AML as the “maximum number […]which […]avoids a deterioration of the range” (BLM 2010). However, whether AMLs accurately reflect such a threshold is questionable (NRC 2013), so it is possible that a herd could be above AML but still too small to cause plant community shifts. Additionally, horse density in the site as a whole may not directly correspond to horse use of the specific plots we sampled. Our dung transects showed that horses were present near our plots (see Table 1), and we observed horses while sampling at every site. Data comparing biomass inside and outside temporary exclosures in 2015 support the idea that grazing pressure was not very high, since there were no significant differences in biomass inside vs. outside the temporary exclosures. However, the fact that total and grass biomass was significantly higher inside the permanent exclosures vs. areas actively grazed (see Table 3), indicates that the areas have been under grazing pressure over the long term.

In other words, there are several possible explanations for the observed lack of grazing effects on plant community composition and diversity at these sites, and further research is needed to fully understand the role of these different influences.

It is also possible that plant community changes have occurred which our sampling did not detect. This study suffered from several limitations that restricted our power to detect grazing effects. Because our goal was to investigate long-term grazing effects across sites spanning a broad precipitation gradient in the western US, we were limited to sites with preexisting fencelines and exclosures, which were not standardized in number or dimensions. Given that there were often only a few existing exclosures or a single fenceline (or in the case of THRO1, a river) available for sampling at the study sites, sample sizes within each site were relatively small, potentially affecting our ability to detect a grazing effect. However, it is important to consider that other horse grazing exclusion studies have had similarly small sample sizes (e.g. Turner 1987, 1988; Rogers 1991; Furbish and Albano 1994; Detling 1998; Fahnestock and Detling 2000; Beever and Brussard 2000; De Stoppelaire et al. 2004).

The placement of exclosures around springs at CA may have biased species composition data at that site, due to the greater prevalence of riparian vegetation inside exclosures compared to outside. Similarly, the “grazed” and “ungrazed” plots at THRO1 were unusually far apart (about 11 km), introducing the possibility that differences were influenced by factors other than grazing. Additionally, our analysis was unable to account for differences in exclosure sizes and differences between exclosures and fencelines, despite the implications of such differences for edge effects, propagule dispersal, and access by native herbivores.

This study was also subject to other complications that often make studying feral horse effects difficult. Most places where feral horses are found have complex and sometimes poorly documented grazing histories, and are also occupied by other large herbivores such as cattle, whose effects can be difficult to separate from those of horses (Beever and Aldridge 2011, Beever and Herrick 2006). Three of our sites (PM, SCB and Sulphur) had no cattle present at the time of our study. (PM has had no livestock grazing since 1968 [Fahnestock and Detling 1999b]; SCB has had no cattle grazing since 2011 [TJ Holmes, personal communication]; and at Sulphur, no dung, tracks or any other signs of cattle were observed near our plots at any time during this study.) At CA, cattle were absent from the vicinity of the exclosures from 1983 to at least 2000 (Beever and Brussard 2000), but they were present during our study (personal observation). Our fecal transects suggest that roughly equal numbers of horses and cattle were present near the exclosures (see Table 1). Because of this, grazing effects at CA should be regarded as resulting from a combination of horse and cattle use. At THRO, bison were present inside the park fence (the area with horses), and there was a Forest Service cattle grazing allotment outside the fence (the area without horses). We hoped that because of the functional similarity between bison and cattle grazing (Knapp et al. 1999, Tastad 2013), we would be able to detect the additional impact of horses inside the fence; however, based on dung transects, cattle use of our transects outside the fence exceeded bison use of our transects inside the fence, potentially causing our data to underestimate the impact of horses. Similarly, domestic sheep graze both sides of the fence at Sulphur, and may have affected our results there, although there is limited dietary overlap between horses and domestic sheep (Hanley and Hanley 1982, Scasta 2014).

Native ungulates such as mule deer, pronghorn, bighorn sheep and/or elk also were present at all of our sites, but did not always frequent our specific plots (see Table 1). These other herbivores may also have influenced our results, especially at SCB and Sulphur where dung transects suggested higher use by native herbivores compared to our other sites. For example, effects on species composition caused by horses removing grasses may have been dampened by native browsers removing biomass from shrubs and forbs. We were also unable to quantify shrub biomass, meaning we may have been missing an important component of feral horse impacts, although shrubs typically make up only a small proportion of horse diets (Scasta 2014).

Because of these limitations in our study, and despite our attempts to cover as wide a precipitation gradient as possible, our data are not completely representative of the range of environments in which feral horses live. Thus, although we did not find significant interactions between site and grazing, it is premature to conclude that no relationship exists between precipitation levels (or other site-specific environmental factors) and magnitude of feral horse grazing effects. Additional data to address the effects of feral horses and connections between those effects and environmental conditions could be provided by future research.

FUTURE RESEARCH

This study was an attempt to ameliorate the scarcity of studies of feral horses in the majority of the geographic range where they occur in the US. However, our experimental design was limited by the availability of existing exclosures. Despite this limitation, our study highlights ways that feral horse research can be improved and expanded in the future. One way to better address the question of how feral horses affect vegetation would be a large scale, long-term study with standardized exclosures.

The National Research Council, in its 2013 report on the BLM Wild Horse and Burro Program, suggested designating and intensively studying "sentinel HMAs […] representative of diverse ecological settings." In keeping with this suggestion, a study could include sites in the Mojave Desert, throughout the Great Basin, in the Colorado Plateau, and in southwestern Wyoming to fully cover the geographic extent of feral horses on Bureau of Land Management lands. Because the Great Basin consists of mountain ranges separated by low valleys, and each mountain range can have a unique species composition (Berger 1986), it would be instructive to look at multiple mountain ranges as well as low elevations within in the Great Basin. The study should also include sites at a range of elevations, since in the Great Basin, elevation strongly affects temperature and precipitation (Berger 1986, Petersen 1994). Together with a wider geographic extent, this would enable investigation of a larger precipitation gradient to potentially detect relationships between precipitation and grazing effects.

Moreover, given that feral horse grazing often occurs in tandem with cattle, sheep, and native ungulate grazing, there is a pressing need for studies that separate the effects of feral horses from those of other herbivores. A study targeting HMAs without cattle or bison, or in an HMA where grazers could be separated, would reduce the confounding effects of those grazers. Even better would be to find places that are inhabited by feral horses but have not historically experienced cattle grazing (if any such places exist). In general, the more detailed and reliable the record of past livestock grazing, the better. It would also be helpful to select locations where the horse population (past and current numbers and habitat use) is well documented. This would enable investigation of relationships between horse density/grazing intensity and grazing effects, a question which is critical to wild horse management.

As mentioned above, many feral horse exclosure studies have suffered from small sample sizes. In the case of this study, both small sample size and unbalanced data made analysis more difficult than it would have been if more exclosures of similar size had been available. A system of large exclosures with standardized dimensions, with multiple exclosures per site, would be extremely valuable for studying feral horse impacts. Despite the logistical difficulties involved, selecting exclosure locations randomly within each site would make the resulting data more representative of the study area as a whole, and prevent bias arising from exclosures being located near roads or springs. Clearly and permanently marked transects both inside and outside exclosures would facilitate long-term sampling of the same locations, allowing observation of changes over time as well as differences between grazed and ungrazed plant communities. Another advantage to long-term sampling of the same areas would be the ability to use allometric measurements to quantify changes in woody biomass.

Although our study focused on plant communities, previous research has shown that feral horses can also impact other ecosystem components such as soil (Beever et al. 2003, Beever and Herrick 2006, Ostermann-Kelm et al. 2009, Davies et al. 2014), invertebrates (Beever et al. 2003, Beever and Herrick 2006, Ostermann-Kelm et al. 2009), birds (Levin et al. 2002, Beever and Aldridge 2011), and small mammals (Beever and Brussard 2000, Beever et al. 2003). Even in locations where effects on plant diversity are not observed, grazing may be having other important impacts which merit further study.

Despite the challenges of studying feral horses' ecological effects, a large-scale, long-term study of carefully selected HMAs using large, standardized exclosures could go a long way toward addressing the questions and controversy surrounding this topic, and could contribute to optimal management of America's feral horses.

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APPENDIX: SUPPLEMENTARY TABLE

Supplementary Table 1: Diversity, richness evenness and dominance (with standard errors) per plot with and without horses for Clan Alpine in 2014.

Site	Treatment	Diversity	Diversity SE	Richness	Richness SE	Evenness	Evenness SE	Dominance	Dominance SE
CA	Without horses	3.200987432	0.173632556	4.82	0.46	0.708278	0.0366145	0.538904458	0.00728067
CA	With horses	2.176439341	0.747375628	2.84	1.28	0.536421	0.189395172	0.671912353	0.090523183

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Summary

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  Rangelands, produced by grazing herbivores, are important for a variety of agricultural, hunting, recreation and conservation objectives world-wide. Typically, there is little quantitative evidence regarding the magnitude of the grazing impact of different herbivores on rangeland habitats to inform their management.

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  We quantified the grazing and trampling impact of sheep, cattle, red deer *Cervus elaphus*, rabbits *Oryctolagus cuniculus*, mountain hares *Lepus timidus* and red grouse *Lagopus lagopus* on open-hill habitats in 11 areas of upland Scotland. The degradation of heather in upland Scotland *Calluna vulgaris*-dominated habitats, of conservation significance at a European scale, has been attributed, anecdotally, to increasing sheep and red deer populations.

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  Field indicators of habitat condition were used to generate a five-point scale of impact in vegetation polygons of seven habitats. The presence of each herbivore species was attributed on the basis of ‘signs’ of occupancy. A Bayesian regression model was used to analyse the association of herbivore species with grazing impact on plant communities, controlling for environmental attributes.

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  Overall the presence of sheep was associated with the largest increase (7/11 areas) in grazing and trampling impact of all herbivores. Cattle had the second largest impact but generally this was restricted to fewer areas and habitats than sheep. In contrast, impacts associated with wild herbivores tended to be small and only significant locally.

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  Although red deer presence was associated with a significantly lower impact than sheep, this impact increased with increasing deer density at both land-ownership and regional scales. For sheep there was little or no evidence of density dependence.

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  Synthesis and applications. The higher impact associated with sheep presence probably reflects their greater aggregation because of their limited ranging behaviour, exacerbated by sheep being herded in places convenient for land managers. Consequently, future reductions in sheep numbers as a result of reform of European Union farming policies may limit the extent of their impact, but not necessarily the local magnitude. However, reductions in sheep stocks may lead to increases in deer densities, with greater impact, particularly in heather-dominated habitats. Where habitat conservation is a priority this may well require a reduction in deer numbers.

Introduction

Across many parts of the world, vertebrate herbivores influence the structure, composition and functioning of ecosystems (Hobbs 1996; Augustine & McNaughton 1998). The rangelands that result from grazing and browsing are an important resource, managed for a variety of agricultural, forestry, hunting, recreation and conservation objectives (Gordon, Hester & Festa-Bianchet 2004). However, while there has been much progress in collaborative management in recent times, these multiple objectives can lead to conflicts, including habitat degradation as a result of over-grazing (Hallanaro & Usher 2005; Mysterud 2006). For example, in upland Scotland since the Second World War the extent of heather-dominated vegetation communities and semi-natural grasslands has declined markedly (Tudor & Mackey 1995), primarily because of afforestation and agricultural reclamation (Miles 1988). A direct consequence of these changes in land use has been increasing concentrations of stocks of sheep and red deer on the remaining habitat, highlighting concerns about grazing and trampling impacts, in particular to dwarf-shrub heath, blanket bog and montane plant communities (Sydes & Miller 1988; Staines, Balharry & Welch 1995). While there has been a growing awareness of the national and international importance of such habitats for the conservation of biodiversity (Thompson *et al.* 1995), there has been no previous attempt to quantify simultaneously the relative grazing impacts associated with different herbivore species using these rangelands (Clutton-Brock, Coulson & Milner 2004).

The total sheep stock in Scotland increased from 6·9 million (M) in 1945 to 8·6 M in 1965, before declining by about 12% to 7·5 M over the next decade (annual agricultural statistics, Department of Agriculture for Scotland and Department of Agriculture and Fisheries for Scotland, UK). The size of the national flock rose again after the UK joined the European Common Market in 1973. to peak at more than 9·4 M in the early 1990s, although in some parts of the country numbers did not exceed the 1965 peak (annual agricultural statistics, Scottish Office Agriculture and Fisheries Department and

Scottish Executive, UK). In upland Scotland most sheep are kept on enclosed, improved pastures at lower altitudes for much of the year. However, in summer the widespread practice is to allow sheep flocks free-range access to the semi-natural vegetation above the enclosed land. In some areas cattle may also be given access to the same unenclosed land, although they tend to roam less widely. Typically these open-hill rangelands are privately owned and often managed as sporting estates, with red deer being the main quarry species across the country (Wightman & Higgins 2001). In central and eastern Scotland, many estates are managed primarily for red grouse shooting. Here mountain hares may be sufficiently numerous to be hunted as well, but usually on a less systematic basis (Hewson 1976).

Estimates of red deer population sizes were not collected systematically in Scotland until 1960, following the establishment of the Red Deer Commission (now Deer Commission for Scotland). Analysis of repeat counts at landscape scales (deer subpopulations, 100–2000 km^2) suggest that from the mid-1960s red deer increased steadily to average 14 deer km^{-2} in 1986, 40% higher than in 1961 (Clutton-Brock & Albon 1989). In 1986, deer densities differed between areas of Scotland by an order of magnitude, with both the spatial and temporal variation in density correlating negatively with sheep stocks (Clutton-Brock & Albon 1989). Red deer numbers may still be growing but both the rate of this increase and their impact on the natural heritage are disputed (Hunt 2003; Clutton-Brock, Coulson & Milner 2004).

In this study, we quantified the grazing and trampling impacts associated with six different herbivore species on seven semi-natural, open-hill habitats, in 11 upland areas of Scotland. The five-point scale impact data we analysed were recorded at the vegetation polygon (patch) scale (down to 250 m^2) of the different habitats (Brewer *et al*. 2004). First, we described how the estimated grazing impact scores were associated with the presence/absence (not recorded present) of sheep, cattle, red deer, mountain hares, rabbits and red grouse recorded at the same patch scale as plant communities.

Secondly, we explored whether it is possible to detect differences in grazing impact associated with the presence of sheep vs. red deer. Given the two species have similar feeding niches (Milne *et al*. 1976) because of their similar body size and gut morphology, it would initially appear problematic to detect differences in grazing impact. However, Hofmann (1989) categorized sheep as ‘grazers’ and red deer as ‘intermediate feeders’ selecting a diet of browse and graze. Research investigating detailed foraging behaviour in heather–grass mosaics suggested that, compared with deer, sheep are more selective of grass species, but at grass–dwarf-shrub heath boundaries sheep have similar impacts on heather as deer, particularly where the patchwork is fine grained (Clarke, Welch & Gordon 1995; Hester *et al*. 1999). In general, however, red deer grazing impacts on heather are more diffuse (Palmer *et al*. 2003).

Thirdly, we investigated the relationships between estimated impact on vegetation and the stocking rates of sheep and counts of red deer for land management units (10–100 km^2) available for two areas of Scotland. Finally, we demonstrated that estimates of mean impact within habitats at the largest landscape scales (> 500 km^2) are related to the mean density of deer in these different areas across Scotland.

The implications of these results are discussed in terms of a more integrated approach to the management of herbivores on rangelands, recognizing the potential conflicts arising from contrasting objectives of different land managers. In addition, we discuss future research priorities to provide the evidence base for adaptive management targeted at more specific outcomes, in particular the enhancement of biodiversity.

Materials and methods

grazing and trampling impact assessment

Grazing and trampling impacts were assessed in 11 deer management group (DMG) areas between 1997 and 2003 (Fig. 1), following a standard method of surveying the impacts of grazing, browsing and trampling by larger herbivores in upland habitats (MacDonald *et al.* 1998). This approach provides a means of recording the state of habitats using descriptive classes, focusing on directly observable effects. The methodology uses a series of field indicators for each habitat type, including biomass removal, sward height and structure, selectivity of grazing, accumulation of plant litter, physical damage and dung.

Figure 1

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The name and location of the 11 deer management group (DMG) areas in which herbivore grazing and trampling impacts were surveyed (year of survey after the name) and the distribution of impact scores (L, light; L/M, light/moderate; M, moderate; M/H, moderate/heavy; H, heavy) for n= vegetation polygons sampled within each DMG. The percentage of vegetation polygons in each habitat is shown in Table 1.

For each field indicator, such as the proportion of long shoots of heather browsed and the extent of trampling damage, a number of alternative states were described, relating to light, moderate and heavy (L, M, H, respectively) impacts (see Table S1 in the supplementary material). The standard field survey sample area of upland habitat was 0·25 km^2 (25 ha). Each indicator was assessed separately, based on a number of point estimates, and an overall assessment, derived for a particular habitat type, was averaged across all indicators. As all three impact classes (L, M and H) could be observed within a part-polygon, a method of summarizing the impact across a habitat was devised that took into account the spatial heterogeneity. This was based on the percentage of the area occupied by each impact class (see Appendix S1 in the supplementary material) and had the effect of smoothing the three-class impact scale into a more continuous five-point scale by introducing intermediate classes (L/M and M/H). Where a number of discrete plant communities occurred within the sample area, they were all assessed separately.

The impact assessments were made for seven upland open-hill habitats based on the Land Cover Scotland 1988 (LCS88) data set (MLURI 1993). (i) Blanket bog, dominated by common cotton-grass *Eriophorum vaginatum* L., bog mosses *Sphagnum* spp. and heather. (ii) Dwarf-shrub heath, either dry heath, dominated by heather or blaeberry *Vaccinium myrtillus* L., or wet heath, dominated by cross-leaved heath *Erica tetralix* L. and deer-grass *Trichophorum cespitosum* L. Hereafter, these are both called Heath. (iii) Coarse grassland, characterized by species such as mat-grass *Nardus stricta* L., purple moor-grass *Molinia caerulea* L. and tufted hair-grass *Deschampsia cespitosa* L. (iv) Montane Grassland, wind-clipped grass/sedge/moss heath, with a range of species including stiff sedge *Carex bigelowii* L., blaeberry, woolly fringe moss *Racomitrium lanuginosum* L., and a variety of smooth grasses. (v) Montane heath, wind-clipped heath, dominated by heather. (vi) Smooth grassland, dominated by common bent *Agrostis capillaries* L. and sheep's-fescue *Festuca ovina* L. (bent-fescue grassland). (vii) Smooth grassland with bracken or rushes, dominated by bent-fescue grassland with bracken *Pteridium aquilinum* L. and/or rush *Juncus* spp.

Three of the 11 DMG (Table 1) were sampled on a 0·25-km^2 complete-coverage basis, where assessments were made for all the part-polygons of the main habitats present that occupied more than 10% of any 0·25-km^2 sample area (Brewer *et al*. 2004). In the other eight DMG, 0·25-km^2 sample squares were selected in a random stratified approach to provide data for management planning over extensive areas (200–1000 km^2) in a more rapid and cost-effective manner (Nolan *et al*. 2003). A geographical information system (GIS)-based computer model was used to select 0·25-km^2 sample areas of different habitats randomly, ensuring that the strata also took account of land-management units within and between estates. In practice this reduced field sampling to between 12% and 21% of the total area (Table 1).

Table 1. Summary survey details for each deer management group (DMG). In 1997 and 1998, surveys were done in smaller DMG in which all 0·25 km^2 were surveyed. From 1999 onwards, between 12% and 21% (median 17%) of the total area was surveyed. The percentage vegetation (BB, blanket bog; H, heath CG, coarse grassland; MG, montane grassland; MH, montane heath; SG, smooth grassland; SR, smooth grassland with bracken and/or rushes) is based on polygons and not on an area basis

DMG	**Year**	**Total area (km^2)**	**Sampling intensity (%)**	**Number vegetation polygon**	**% vegetation**						
					BB	**H**	**CG**	**MG**	**MH**	**SG**	**SR**
West Sutherland	2000	1136	14	836	39·6	41·3	7·2	2·7	3·1	5·3	0·9
Northern	1999	1318	12	1182	45·5	38·6	4·8	0·0	1·9	4·0	5·2
North Ross	2001	771	17	819	35·3	42·3	5·0	4·2	5·6	5·7	1·9
East Sutherland	2000	1006	17	972	44·8	38·9	4·3	0·2	2·2	6·5	3·2
Gairloch	1998	346	100	2651	33·7	53·8	0·7	2·2	7·2	1·9	0·5
Cairngorm–Speyside	1997	420	100	2041	28·5	48·2	4·8	2·9	10·1	4·8	0·6
South Ross	2000	1611	18	2072	27·9	39·2	10·2	6·6	6·4	6·8	2·9

DMG	Year	Total area	Sampling intensity (%)	Number vegetation	% vegetation						
					BB	H	CG	MG	MH	SG	SR
West Grampian	2002	710	21	969	26·5	41·2	10·5	4·5	6·8	8·6	2·0
Mid-West Association	2003	629	16	719	31·0	39·3	15·7	4·6	3·8	4·6	0·9
Angus Glens	1999	620	21	1067	14·9	42·8	13·9	3·8	2·5	12·1	9·9
South Loch Tay	1998	148	100	3437	18·6	33·5	24·7	3·1	4·8	11·9	3·5

Aspect, altitude and slope were determined for each part-polygon in ArcGIS 8·3 using a digital elevation model, reproduced from map data by permission of Ordnance Survey (© Crown copyright reference MLURI GD27237X 2006), with a resolution of 50 × 50 m. An index of topographic exposure (TOPEX) was calculated for each part-polygon as the sum of angle to the skyline in degrees, for the eight cardinal directions. Dominant soil type for each part-polygon was determined from an overlay of soil types from the 1 : 250 000 survey of the soils of Scotland (Macauley Institute for Soil Research 1984). The presence of burning was recorded in the field for each part-polygon of vegetation, assessed on a four-point scale of no-burning and the presence of small (< 2 ha), medium (2–5 ha) or large (> 5 ha) burns.

herbivore presence

Within each part-polygon, the presence/absence (not recorded present) of each species of herbivore was attributed on the basis of a range of ‘signs’ of occupancy, including visual sighting, evidence of recent animal presence (strands of wool, hair or feathers on vegetation, lying-up areas, animal tracks, trampling and thrashing of heather and burrows, etc.) and the presence of dung. While it was recognized that the identification of some species based on dung (notably deer/sheep) can be problematic, this was very rarely used as the sole criterion for differentiating animal presence. Surveyors carrying out the impact assessments were experienced in the identification of animal dung and calibrated their observations, aided by field guides describing animal species from tracks, signs and dung. As there may have been some ‘false negatives’, where a species recorded absent had been present but went undetected, we refer to ‘recorded’ presence and absence.

sheep and deer density estimates

After 2000, information on livestock management (numbers, grazing regime, etc.) was collected at the estate (separate landowner/management units) level. Specifically for sheep, we sought data on numbers and the period they were free-ranging on the open-hill. Given that some flocks were out all year and others for different periods of the summer, we calculated densities as total year equivalents divided by the area of the estate and the proportion of vegetation polygons in which sheep were recorded present, and expressed this as number km^{-2}. The most recent deer counts, between 0 and 3 years prior to the survey, were supplied by the Deer Commission for Scotland, divided by the unit land area, and expressed as number km^{-2}. For comparisons with sheep, we divided the density by the proportion of vegetation polygons occupied. As the distribution of habitat types differed between DMG (Table 1), we investigated deer density as an explanatory variable for the geographical variation between DMG in estimated mean impact scores within habitats.

statistical analysis

The ordered categorical (ordinal, five-point scale) response variable was modelled as described in Agresti (1984), where impact is a continuous entity on a five-point scale. Mathematically, this translates to a partitioning of the real number line by four cut-points that separate out the five response classes: light, light/moderate, moderate, moderate/heavy and heavy. This is preferable to simply assigning numerical values to the impact classes and treating this as a continuous response variable, or fitting a multinomial model that ignores the ordering of the classes.

A Bayesian regression analysis accounting for the ordinal response, similar to that of Brewer *et al.* (2004), was used to identify explanatory variables. The response impact class from the ith part-polygon (e.g. $i = 1, \dots, 2072$ for Cairngorm–Speyside) in grid square j ($j = 1, \dots, 1176$ for Cairngorm–Speyside) could thus be assigned an integer value between 1 and 5, called R_{ij}, that corresponded with the five classes listed above (in order). The impact class can be expressed in terms of a continuous latent variable, Y_{ij} (representing the underlying continuous grazing impact), taking values as follows:

$R_{ij} = k$ if

$Y_{ij} \in [a_{k-1}\ (a_k), k = 1, \dots, 5$

where a_k represents the cut-off points separating the classes, with $a_0 = -8$ and $a_5 = 8$. Further technical details of the statistical model can be found in the supplementary material. Unlike Brewer *et al.* (2004), variograms of the unstructured spatial effects suggested no need to account specifically for spatial autocorrelation.

The model included the following ecological and environmental variables as covariates. Herbivore factors: sheep, deer, cattle, hares, rabbits, grouse; with interactions sheep + deer, sheep + rabbits, deer + rabbits, hares + grouse (given the large number of potential interactions these were chosen as the most worthy of exploring). Habitat factors: vegetation community (seven levels). Interactions between herbivores and habitats. Other environmental factors, including: aspect (four levels, north, east, south and west); muirburn (four levels of burning); dominant soil categories (up to 21 levels). Environmental covariates: altitude; slope; TOPEX. Human-defined factors: estate/landownership unit.

Our model included this broad set of variables so that we could be more confident that estimated herbivore effects really were because of the herbivores and not unexplained ecological and environmental variables. OpenBUGS (Thomas 2004) was used to analyse the data fitting the above model. As there were a large number of explanatory variables, it was not always possible to fit all the terms, or all levels of all the factors, because certain combinations did not occur in the data sets for particular DMG. Thus some effects were not estimable; this was true of some of the interaction terms between herbivore presence and habitat where very small numbers of part-polygons recording presence (or absence) of the herbivore led to complicated patterns of aliasing. As a rule of thumb, the interaction term for a herbivore–habitat combination was not fitted if fewer than five part-polygons for that habitat were recorded as having the herbivore present (or absent). This was a particular problem for rabbits, where we were only able to estimate the grazing effects in five of 11 DMG. Also, in two of the DMG, North Ross and West Grampian, deer presence was recorded in nearly all part-polygons, and hence the effect of deer could not be estimated. Because the Bayesian approach was computer intensive, requiring many runs for different DMG and subsets of variables, we ran OpenBUGS on a Beowulf Linux cluster.

As the parameter estimates were on the logistic scale, and difficult to interpret, we found that a convenient way to represent the effects of the recorded presence compared with apparent absence of a herbivore species was the estimated change in the probability of observing an impact class of ‘Moderate’ or worse. For example, in the Northern (NO) DMG, the predicted impact of the presence of sheep on blanket bog was 0·42 (Fig. 3). This metric enabled a useful comparison in terms of comparing impact classes across DMG and habitat types, and was likely to be more useful than standard ‘proportional odds’ statements.

Figure 3

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The impact of the presence of deer (closed circles) and sheep (open circles) across the 11 DMG by habitat. The bars display 95% (2·5–97·5%) credible intervals. Where the mean is positive and the credible interval does not include zero, the probability of increasing impact with the presence of a particular herbivore is significant. If the credible interval touches zero then the significance is marginal. Where the credible interval includes zero, the overall impact is not significant because of the variance between polygons within habitats. The letters D and S beneath the bars denote that the herbivore by habitat interaction term was not estimable for that DMG and habitat for deer or sheep, respectively. The asterisks above the bars signify that there was a significant difference between the effects of sheep and deer for that DMG and habitat; these were all in the direction of sheep having a greater impact on vegetation than deer. It was not possible to estimate deer effects in North Ross (NR) or West Grampian (WG).

Results

herbivore species distribution

Deer were the herbivore most frequently recorded as present in vegetation polygons in all DMG (median 90·1%, interquartile range 81·3–96·6%), except South Loch Tay (74·0%), where evidence of sheep occurred in 96·3% of vegetation polygons (Table 2). Overall sheep were the second most frequently recorded herbivore (median 42·5%, interquartile range 26·6–55·5%). Evidence of deer and sheep using the same vegetation polygons was common (median 31%, interquartile range 22·9–55·3%)

but rarely were neither recorded (median 2·4%). Cattle were an order of magnitude less frequently recorded than sheep (median 2·9%), reflecting their comparatively low numbers.

Table 2. The percentage of vegetation polygons (sample size given in Table 1) in each deer management group (DMG) area in which different herbivores were recorded. For each DMG the first four columns total 100%

DMG	% with no deer or sheep	% sheep only	% deer only	% both deer and sheep	% cattle	% hares	% rabbits	% grouse
West Sutherland	5·7	3·9	67·6	22·7	1·8	1·1	0·5	8·1
Northern	5·0	12·1	39·9	43·0	3·8	22·0	2·4	37·5
North Ross	0·1	0	69·6	30·3	5·0	1·9	9·8	1·6
East Sutherland	2·1	4·2	55·4	38·3	3·4	3·1	4·9	20·4
Gairloch	3·2	15·5	50·2	31·0	8·7	4·1	1·2	27·5
South Ross	2·2	1·2	84·3	12·4	3·4	5·6	1·5	17·5
Cairngorm–Speyside	8·2	10·5	58·4	22·9	0·8	75·4	13·7	74·2
West Grampian	0·3	0·2	44·2	55·3	2·1	36·8	1·8	46·7
Mid-West Association	1·7	1·7	73·2	23·5	4·0	6·3	0·3	29·6
Angus	2·4	20·7	20·8	56·0	1·5	69·1	25·7	60·3
South Loch Tay	2·4	23·6	1·3	72·7	1·9	89·5	20·8	61·6

Among the smaller herbivores, evidence of grouse was most frequently recorded in vegetation polygons (median 29·6%). The wide interquartile range (17·5–60·3%) reflected changes in abundance across Scotland, as drier heather moor becomes more extensive and management intensifies from west to east. Hare presence (median 6·3%) appeared to have more of a bimodal distribution across DMG (around values of 3·1% and 69·1%, respectively). Like grouse, hares tended to be less frequently recorded in the west of Scotland and more frequently recorded in the central and east of Scotland. Rabbits were generally less common than hares in nine of the 11 DMG (median 2·4%), probably reflecting the fact that they prefer lower lying enclosed land with drier, mineral soils. Where Smooth grassland and heath habitats occurred close to these environments, as in some DMG in eastern Scotland, rabbit presence was recorded comparatively frequently (Table 2).

grazing and trampling impacts of different herbivore species

Averaged across all DMG, the highest predicted (median) impact was associated with the recorded presence of sheep (Fig. 2). The estimated impact of sheep was the highest of all herbivores in seven of the 11 DMG and significantly greater than zero in a further two (see Fig. S1 in the supplementary material). The second highest predicted impact was associated with the recorded presence of cattle

(Fig. 2), with the impact greater than that associated with sheep in two DMG and significantly greater than zero in a further two (see Fig. S1 in the supplementary material). The third highest predicted impact was associated with the recorded presence of rabbits (Fig. 2). However, these tended to be localized effects and generally were more discernible in DMG in eastern Scotland; in particular, they tended to be associated with Smooth grassland habitats (see Appendix S1 in the supplementary material). In Angus DMG, rabbit was the only herbivore associated with a significant predicted impact averaged across all habitats. For hares, the average predicted impact associated with their recorded presence was very small (Fig. 2). However, in one DMG, East Sutherland, hares did have a significant effect, though this was smaller than either sheep or cattle (see Fig. S1 in the supplementary material). Closer inspection of the herbivore–habitat interaction terms in the fitted models suggested that in some other DMG relatively heavy hare impacts were restricted to Heath.

Figure 2

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The median (with 5–95% ranges) grazing and trampling impacts associated with the recorded presence of each herbivore species, averaged across all DMG and all habitats. Results for individual DMG are given in Fig. S1 in the supplementary material.

In contrast, the average predicted impact associated with the recorded presence of red deer and red grouse tended to be negative (Fig. 2) Thus the vegetation polygons having signs of red deer presence had predicted impact scores lower than similar vegetation polygons without signs of their presence. However, in one DMG, Cairngorm–Speyside, the recorded presence of red deer did tend to increase the predicted impact, although this was smaller than either sheep or cattle (see Fig. S1 in the supplementary material). Closer inspection of the herbivore–habitat interaction terms in the fitted model for Cairngorm–Speyside suggested that red deer impacts were significant in five of seven habitats (Fig. 3).

comparing sheep and deer impacts by habitat

The presence of sheep tended to most frequently have a significant impact on Smooth grassland habitat across Scotland (10 of 11 DMG were significantly impacted), and least frequently on Blanket bog (five of 11 DMG) (Fig. 3). As described above, the presence of deer tended to be more diffuse. Overall there was a significant impact in only seven of 63 (11·1%) habitat–DMG combinations (two on Blanket bog but none on Coarse grassland) for deer compared with 58 of 77 (73·5%) for sheep (Fig. 3). A more detailed description is given in Appendix S2 in the supplementary material.

In 40 of 63 (63·5%) habitat–DMG combinations, where both red deer and sheep impacts could be estimated, the predicted impact of the recorded presence of sheep was significantly greater than the predicted impact of deer (Fig. 3). In contrast, in only one of all the 63 (1·6%) habitat–DMG combinations, Blanket bog in Cairngorm–Speyside, was the predicted impact of the recorded presence of deer significantly greater than sheep ($P = 0·045$; see Table S2 in the supplementary material).

sheep and deer impacts at local stocking densities

For East Sutherland and West Grampian, the only two DMG for which both sheep and deer density estimates were available at the estate scale, non-linear (asymptotic) regression revealed that the predicted impact associated with the presence of deer increased significantly with deer density, whereas the estimated impact associated with the presence of sheep tended not to vary with sheep density (Fig. 4). Thus, even at apparently low local densities, sheep had a pronounced impact compared with low densities of deer. However, in West Grampian, where predicted impacts were generally higher than in East Sutherland, at densities over 40 animals km^{-2} deer had similar impacts to sheep (Fig. 4b).

Figure 4

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The mean grazing and trampling impact scores associated with sheep (open circles) and deer (closed circles) estimated for different land management units (estates) within (a) East Sutherland DMG and (b) West Grampian DMG, plotted against the density of each herbivore on each estate. The fitted asymptotic regressions for sheep and deer are significantly different in both DMG.

deer impact and density at regional scales

The distribution of grazing and trampling impact scores differed significantly between the 11 DMG areas (χ^2 = 2928, d.f. = 40, P < 0·001). Impact scores tended to be lower in the DMG in the north and west of the Highlands and higher in the south and east of the Highlands (Fig. 1). In three habitats (Blanket bog, Heath and Coarse grassland), the fitted asymptotic regression indicated that deer population density explained a significant proportion of the variation in mean impact between DMG (r^2 = 0·5561, 0·6891 and 0·2845, respectively; Fig. 5a–c). However, on Smooth grassland with bracken and/or rushes (Fig. 5d) and three others not shown (Smooth grassland, Montane grassland, and Montane heath), deer density did not explain the variation in estimated impact.

Figure 5

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The estimated mean grazing and trampling impact scores within each of the 11 DMG plotted against the deer density from counts by the Deer Commission for Scotland, for (a) Blanket bog (y = 0·9042 ln(x) − 0·246), (b) Heath (y = 1·1003 ln(x) + 0·0502), (c) Coarse grassland (y = 0·6284 ln(x) + 0·505) and (d) Smooth grassland with rushes and/or bracken (y = 0·558 ln(x) + 1·7683).

Discussion

The rapid habitat assessment methods and subsequent analyses detected differences in the grazing and trampling impacts associated with different herbivore species at a variety of scales, ranging from land management/ownership units (10–100 km^2) to subregional (deer population) scales (500–2000 km^2) between areas of Scotland. At larger scales it was also possible to identify interactions between herbivores and habitats, not only for deer and sheep, which were very widely distributed across vegetation polygons, but also for those more locally restricted, as in the case of cattle, rabbits and mountain hares. The simple approach adopted here could be applied quite easily to other temperate and tropical multispecies grazing systems.

The evidence that the recorded presence of sheep was associated with higher grazing and trampling impacts than the other four mammalian herbivores was compelling. Sheep were associated with the highest impact across averaged habitats in seven out of 11 DMG, and increased the probability of observing a ‘moderate’ or greater impact in most habitats, not only those dominated by grasses but also on Heath. After sheep, the recorded presence of cattle was most commonly linked with increased impact on open-hill habitats, although their impact was localized, because cattle occurred in fewer habitats and a lower proportion of vegetation polygons within habitats. None the less, the estimated mean impact associated with cattle was slightly higher than sheep when averaged across habitats in three DMG.

In contrast to domestic stock, the recorded presence of red deer, mountain hares and rabbits had comparatively little impact on plant communities at the DMG scale; each species significantly increased the impact over all habitats in only one DMG (Cairngorm–Speyside, East Sutherland and Angus, respectively). However, in some other DMG the estimated grazing impact associated with the recorded presence of the wild mammalian herbivores was specific to particular habitat types, for example deer on Blanket bog and Montane heath in South Loch Tay, rabbits on Smooth grassland in both South Loch Tay and Cairngorm–Speyside, and hares on Heath in the Midwest.

distinguishing sheep and deer impacts

Although differences in diet selection and forage patch utilization by sheep and red deer are apparently subtle and vary with the grain of vegetation patch mosaics (Clarke, Welch & Gordon 1995; Hester & Baillie 1998; Hester *et al*. 1999; Palmer & Hester 2000; Palmer *et al*. 2003), the estimated impact associated with the recorded presence of sheep was repeatedly greater than the impact associated with deer. In no less than 40 of the 63 (63·5%) habitat–DMG area combinations where we could directly compare the two species because we had sufficient samples of recorded presence/not recorded present in habitats, the probability of sheep impact was significantly greater than deer impact. In only one habitat, Blanket bog, in one DMG area, Cairngorm–Speyside, did the estimated impact of deer grazing significantly exceed the estimated impact of sheep.

The success of our approach in distinguishing the magnitude of impacts associated with the presence of sheep vs. red deer probably reflects the fact that it assessed grazing impact at the extant scale of plant communities, thus recognizing that even 0·25-km^2 mapping units may be heterogeneous, with multiple patches of two or more habitats. Although the recorded presence/not recorded present (binary) data for herbivores may have included some false zeros, the assessment of large numbers of polygons in each DMG (median 1067) usually gave sufficient patches that had not been visited recently by one or more herbivore species, enabling us to estimate the independent effect of each herbivore species. Although in two DMG (North Ross and West Grampian), with relatively low numbers of vegetation polygons, it was not possible to estimate deer impacts because of their extremely high recorded presence (> 97%) this was not a problem in the other nine DMG. Otherwise, there were only problems of robust estimates of impact for extremely low recorded presence, particularly for rabbits, where in five DMG they were recorded in less than 2% of vegetation polygons.

Unfortunately, our methods did not estimate the relative degree of use by each herbivore, where it was recorded present in a vegetation polygon, and only latterly were landowners/managers questioned about their sheep management practices and stocking rates at estate scales. However, in the two DMG where we could investigate the relationship between estimated impact of sheep vs. red deer in relation to their respective densities simultaneously, we found little or no increase in impact associated with higher densities of sheep, but significant increases in deer impact as deer densities increased. In the West Grampian DMG, the estimated impacts of deer only reached those of sheep at about 50 head km^{-2}. However, in East Sutherland DMG, where impacts tended to be lower than West Grampian, sheep densities tended to be lower than deer densities (in 16 of 18 estates) even before taking into account that often sheep tended to be on the open-hill for only part of the year.

The apparent lack of a relationship between grazing impact associated with sheep and their density is puzzling. One possible explanation, which would be consistent with the lower recorded presence of sheep compared with deer in vegetation polygons (median 43% and 90%, respectively), is that sheep are more aggregated than red deer, so that as sheep numbers increase they occupy proportionally more range but the effective density per unit area remains similar. While sheep may be more socially gregarious, their aggregation is likely, at least in part, to be a simple consequence of the way sheep are managed, with flocks tending to be grazed in particular locations, often for restricted periods, dependent on their stocking density (Lawrence & Wood-Gush 1988). Although the ranging behaviour of both species has not been studied sympatrically, there is evidence that sheep do have smaller home ranges compared with deer (30 ha vs. > 100 ha, respectively; cf. Hewson & Wilson 1979; Clutton-Brock, Guinness & Albon 1982), and hence sheep may be more likely to remain at local, hillside scales (Lawrence & Wood-Gush 1988). An alternative, but not necessarily mutually exclusive explanation, could be that, in some areas, sheep densities had been reduced shortly before the surveys and there had been insufficient time for the vegetation to recover.

Although our models included terms representing the interactions between herbivores, these were fitted with an expected additive effect of increased impact associated with pairs of species with similar diet and habitat use. However, we did not expect to find lower recorded impacts on vegetation polygons containing signs of herbivore presence than on similar habitats without signs of that herbivore, as in the case of red deer in five of the seven habitats in East Sutherland. Although herbivores can drive vegetation state transition and influence productivity (van der Wal 2006), we have no evidence in this case that deer were having a beneficial effect within habitats. Nor was there any evidence that they avoided sheep more in this DMG than others (55% deer-only polygons in East Sutherland was the median across DMG). While it could be a chance effect, given the complexity of the fitted model, it is possible that deer sought out patches within habitats that were particularly productive because of edaphic conditions, and in effect the DMG appeared lightly grazed.

management implications

Our results have important implications for managers of rangelands in Scotland. First, our models offer the potential to produce interpolated maps of predicted grazing and trampling impacts, as a function of herbivore presence/absence, vegetation and other biotic and abiotic measures (Brewer *et al.* 2004). However, the maps would not predict impacts relative to changes in number or density of herbivores other than deer, as the impact associated with the presence of sheep was not related to their density, and for the other herbivore species density was not estimated. For red deer, we can predict the probable average impact of either reducing or increasing numbers across habitats at the estate scale (10–100 km^2) and within habitats at the regional scale (500–2000 km^2).

Secondly, our results can help conservation managers anticipate the possible effects of changes in grazing pressure on the natural heritage (Thompson *et al.* 1995). It is likely that the total sheep stock will continue to decline, because recent reform of the Common Agricultural Policy (CAP) has moved into a post-productionist phase where good environmental stewardship is rewarded. Where sheep are removed from an area, the reduction in grazing and trampling pressure should halt further degradation of heather-dominated communities (Armstrong & Milne 1995). However, as red deer also prefer to forage in grass patches, they may fill the ‘vacuum’ left by the removal of sheep, hindering recolonization by heather (Hope *et al.* 1996). Unfortunately, understanding of the extent to which red deer will change their foraging and ranging behaviour when sheep are removed is largely anecdotal (but see Clutton-Brock & Albon 1992). Addressing this knowledge gap is important, particularly given that the numbers of red deer are likely to continue to grow because of higher recruitment associated with increasingly mild winters and earlier onset of spring (Albon & Clutton-Brock 1988). In Heath habitats, deer densities above about 15 deer km^{-2} were associated with impacts of moderate or higher (Fig. 5), thus pro-active deer management to constrain the rate of deer population growth may be necessary if the priority is to halt the loss of heather.

Thirdly, there is an opportunity to reconsider the issue of whether heavy herbivore impact, leading to alternative plant communities, is an undesirable outcome rather than a dynamic process between alternative stables states (van der Wal 2006). Light or light/moderate grazing will maintain heather-dominated habitats but grass-dominated ones require moderate or greater levels of grazing. The debate is really about how herbivores are managed to create or maintain landscapes with different ecological properties and visual characteristics: the shape of which will depend on land managers aims in meeting either public and/or private objectives.

future research

While our approach was capable of distinguishing the grazing impact of different herbivores on open-hill habitats, this was scaled in terms of the relative condition of the dominant species within a vegetation community, and not in terms of the implications for habitat condition, plant diversity/species richness or wider biodiversity consequences. The implications of different grazing and trampling impact classes will vary between communities. For example, moderate grazing impact may actually increase species richness, by reducing the cover of dominant species and enhancing the competitive ability of other species (Clutton-Brock & Ball 1987; Gordon 1988; Welch & Scott 1995; Virtanen, Edwards & Crawley 2002). Furthermore, changes in physical habitat structure associated with cattle grazing may have cascading effects beyond the plant species composition, including increased invertebrate abundance benefiting insectivorous birds, and higher abundance of voles, compared with similar levels of grazing with sheep only (Evans *et al*. 2006). However, there are concerns that the facilitation of small selective herbivores, such as voles, by larger species, such as cattle, may reduce plant diversity because the smaller herbivores prefer rare, palatable species (Olff & Ritchie 1998).

Unfortunately the evidence from individual studies around the world indicates that the magnitude and direction of the effects of different herbivores varies over spatial and temporal scales. Such complex interactions present a challenge to land managers and conservationists alike, and have led to the emergence of new conceptual frameworks describing the influence of herbivores on plant diversity across gradients of soil fertility and rainfall (Van de Koppel *et al*. 1996; Olff & Ritchie 1998). These should be tested at a range of scales, in order to provide further insights into the adaptive management of herbivore–habitat interactions to enhance biodiversity (Gordon, Hester & Festa-Bianchet 2004).

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Supporting Information

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Aboveground and belowground mammalian herbivores regulate the demography of deciduous woody species in conifer forests

Bryan A. Endress,[1],† Bridgett J. Naylor,[2] Burak K. Pekin,[3] and Michael J. Wisdom[2]

[1]*Eastern Oregon Agriculture and Natural Resource Program, Department of Animal and Rangeland Sciences, Oregon State University, La Grande, Oregon 98750 USA*
[2]*USDA Forest Service, Pacific Northwest Research Station, La Grande, Oregon 98750 USA*
[3]*Eurasia Institute of Earth Sciences, Istanbul Technical University, Istanbul 34469 Turkey*

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Abstract. Mammalian herbivory can have profound impacts on plant population and community dynamics. However, our understanding of specific herbivore effects remains limited, even in regions with high densities of domestic and wild herbivores, such as the semiarid conifer forests of western North America. We conducted a seven-year manipulative experiment to evaluate the effects of herbivory by two common ungulates, *Cervus elaphus* (Rocky Mountain elk) and cattle *Bos taurus* (domestic cattle) on growth and survival of two woody deciduous species, *Populus trichocarpa* (cottonwood) and *Salix scouleriana* (Scouler's willow) in postfire early-successional forest stands. Additionally, we monitored belowground herbivory by *Thomomys talpoides* (pocket gopher) and explored effects of both aboveground and belowground herbivory on plant vital rates. Three, approximately 7 ha exclosures were constructed, and each was divided into 1-ha plots. Seven herbivory treatments were then randomly assigned to the plots: three levels of herbivory (low, moderate, and high) for both cattle and elk, and one complete ungulate exclusion treatment. Treatments were implemented for seven years. Results showed that cattle and elk substantially reduced height and growth of both cottonwood and willow. Elk had a larger effect on growth and subsequent plant height than cattle, especially for cottonwood, and elk effects occurred even at low herbivore densities. Pocket gophers had a strong effect on survival of both plant species while herbivory by ungulates did not. However, we documented significant interaction effects of aboveground and belowground herbivory on survival. Our study is one of the first to evaluate top-down regulation by multiple herbivore species at varying densities. Results suggest that traditional exclosure studies that treat herbivory as a binary factor (either present or absent) may not be sufficient to characterize top-down regulation on plant demography. Rather, the strength of top-down regulation varies depending on a number of factors including herbivore species, herbivore density, interactions among multiple herbivore species, and varying tolerance levels of different plant species to herbivory.

Key words: cattle; elk; grazing; North America; Oregon; plant population dynamics; plant–herbivore interactions; *Populus trichocarpa; Salix scouleriana;* trophic cascades; ungulate herbivory.

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† **E-mail:** bryan.endress@oregonstate.edu

Introduction

Mammalian herbivory can have profound effects on plant community structure, composition, and dynamics as well as the distribution, abundance, and demography of individual species (Augustine and McNaughton 1998, Endress et al. 2004, Beguin et al. 2011, Sankaran et al. 2013). A diverse array of mammals have been shown to affect plant population and community dynamics, ranging from large herbivores such as elephants, deer, and moose to small-bodied species such as hares, pocket gophers, and voles (Cantor and Whitham 1989, McInnes et al. 1992, Fritz et al. 2002, Côté et al. 2004, Howe et al. 2006, Lyly et al. 2014). While the strength of top-down regulation of vegetation by mammalian herbivores varies with environmental conditions (Oksanen et al. 1981, Gough et al. 2012, McLaughlin and Zavaleta 2013, Young et al. 2013), herbivory effects have been reported across multiple ecosystems, biomes, and continents (Gill 1992, Oksanen and Moen 1994, Asquith et al. 1997, Rooney and Waller 2003, Bakker et al. 2006).

Despite numerous studies, our understanding of specific mammalian herbivore effects on plant populations and communities remains limited for a number of reasons. First, most studies exclude herbivores from the ecosystem (often via exclosures) and then compare vegetation changes inside and outside of the exclosures (e.g., McNaughton 1985, Manson et al. 2001, Howe et al. 2006, Sankaran et al. 2013). While this approach is an important first step in documenting top-down regulation, traditional exclosure studies often report pooled effects among different herbivores (e.g., Sankaran et al. 2013, Pekin et al. 2014*a*). As most ecosystems contain multiple herbivores, it is difficult to separate species-specific effects or determine the relative contribution of different herbivores to the observed effects. Moreover, regardless of the number of herbivore species within the system, traditional exclosure studies treat herbivory as a binary factor (either present or absent) and compare effects of complete herbivore exclusion to an often unknown or unreported density of herbivores in the surrounding area. This makes it difficult to evaluate how results from the experiment relate to the broader landscape where herbivore densities vary in space and time. Further complicating our understanding is that herbivory often interacts with other factors such as fire, drought, insect outbreaks, and other land use activities that occur within the same ecosystem (Weisberg and Bugmann 2003, Eschtruth and Battles 2008, Endress et al. 2012, Pekin et al. 2015).

Research that explores how different herbivore species at varying densities influence the direction and strength of top-down regulation would advance our understanding of how, when, and to what degree mammalian herbivores affect plant individuals, populations, and communities. It would also increase our ability to develop management strategies that account for herbivores role in affecting vegetation dynamics. Addressing these questions is challenging and requires long-term manipulative experiments, which have been advocated for some time (Wisdom et al. 2006, Turkington 2009), but for which only a handful have been conducted (e.g., Goheen et al. 2013, Lyly et al. 2014, Pekin et al. 2014*b*). Results from these studies indicate that top-down regulation on vegetation is a product of multiple herbivore species differentially affecting plant species and often interacting with other ecological factors. This highlights the need for researchers to incorporate multiple species, densities, and interactions with other ecological factors into herbivory studies to advance our understanding of top-down regulation.

In the semiarid coniferous forests of western North America, ungulates are important regulators of plant population and community dynamics (Riggs et al. 2000, Wisdom et al. 2006, Endress et al. 2012). Yet, despite high densities of wild and domestic ungulates throughout ecosystems of the region, few studies have examined the role of mammals in influencing conifer forest dynamics (Wisdom et al. 2006). It has been hypothesized that ungulate herbivory coupled with episodic disturbances such as fire, insect outbreaks, or timber harvest is a key driver influencing trajectories of forest succession (Wisdom et al. 2006, Vavra et al. 2007). Endress et al. (2012) found when ungulates were excluded from early-successional postfire stands, recruitment of deciduous woody species including black cottonwood (*Populus trichocarpa* Torr. and A. Gray ex Hook), willow (*Salix* spp.) and aspen (*Populus tremuloides* Michx.) was four times greater than in adjacent areas that were exposed to herbivory by *Bos taurus* (domestic cattle), *Odocoileus hemionus* (mule deer), and *Cervus elephus* (Rocky Mountain elk). Additionally, ungulates suppressed plant growth as individuals that established in ungulate-excluded areas were significantly taller, with some species more than three times greater in height than individuals in areas exposed to herbivores. These findings further suggest strong herbivore effects on certain deciduous woody species by ungulates following disturbance events. However, results were pooled effects from multiple ungulates and compared complete herbivore exclusion to background herbivore density levels. We still know little about the relative importance of the different herbivores species and how the strength of top-down regulation varies with herbivore density. Additionally, ungulates are not the only mammalian herbivores in these landscapes, and previous research suggests that root herbivory by pocket gophers (*Thomomys talpoides*) may also affect deciduous woody species establishment and survival (Bryant and Skovlin 1982, Cantor and Whitham 1989). Belowground herbivory is an overlooked aspect of mammalian herbivore studies despite their presence in many ecosystems and the recognition that root herbivory can result in large impacts on plant demographic performance (Zvereva and Kozlov 2012, Stephens et al. 2013).

Here, we report on a large-scale, seven-year experiment in the semiarid coniferous forests of western North America that examines the effects of different ungulate herbivore species (elk, cattle) at varying densities on the growth and survival of two deciduous woody species. To compare the relative importance of different ungulate herbivores, we experimentally manipulated densities of cattle and elk in early succession postfire forest stands following fuel reduction treatments (stand thinning followed by prescribed fire) and evaluated the growth and survival of cottonwood and Scouler's willow (*Salix scouleriana* Barratt ex. Hook.), two deciduous woody species that recruit prolifically following fire and whose abundance and size appears to be strongly regulated by ungulate herbivores (Endress et al. 2012). Demographic performance of individuals was then used to evaluate how different herbivore species and densities influenced the strength of top-down regulation. We also monitored belowground herbivory by pocket gophers during the study to explore the effects of both aboveground and belowground herbivory on plant vital rates. We hypothesized that elk, considered "mixed feeders" that both graze herbaceous species and browse woody species (Hobbs et al. 1981, Cook 2002), would exert more pressure on cottonwood and willow than cattle, which are primarily grazers who prefer herbaceous species (Clark et al. 2013), resulting in greater effects by elk on the survival and growth of the two plant species. Moreover, we hypothesized that for both ungulates, increasing herbivore density would increase pressure on plant populations and have greater impacts on individual plant demographic performance.

METHODS

Study area and species description

Research was conducted in mixed conifer forest stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) and *Abies grandis* (Douglas ex D. Don) Lindl. (grand fir) within the Starkey Experimental Forest and Range (hereafter "Starkey") in the Blue Mountains Ecological Province of northeast Oregon. Elevations range from 1200 to 1500 m above sea level with approximately 400 mm annual precipitation, most of which occurs as winter snow or spring rain, with a predictable drought from late summer to early fall (Rowland et al. 1997). Forests are typical of those found throughout interior western North America (Wisdom 2005). Understories were a diverse mix of grass and grass-like species, forbs, and deciduous woody shrubs (Pekin et al. 2014*a, b,* 2015).

During the past 25 years, approximately 500 cow–calf pairs of cattle have grazed Starkey from mid-June through mid-October. During this same period, approximately 200 mule deer and 350 elk have grazed/browsed during spring, summer, and fall (April through November) of each year (Rowland et al. 1997, Wisdom 2005). 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 on summer ranges in western North America (Wisdom and Thomas 1996).

Both Scouler's willow and cottonwood are solitary, non-clonal species with the ability to stump sprout from the root crown following disturbance. Scouler's willow is a common understory shrub in conifer forest throughout western North America and recruits readily following fire (Anderson 2001). Cottonwood is often associated with floodplains and riparian areas (Steinberg 2001); however, it can frequently occur at low abundances in early-successional conifer forest stands (Moeur 1992, Endress et al. 2012). Within Starkey, high abundances of both species were reported following stand thinning and prescribed fire when cattle, elk, and deer were excluded from the sites (Endress et al. 2012). Additionally, in post-fire stands exposed to ungulates, cottonwood and Scouler's willow individuals were significantly less abundant and heavily browsed, resulting in suppressed plant heights.

Silvicultural treatments and exclosure design

Three large ungulate exclosures, Half Moon (7.3 ha), Bally Camp (6.8 ha), and Louis Spring (7.3 ha), were constructed following fuel reduction treatments across Starkey as part of a comprehensive research effort to examine forest management—ungulate herbivory interactions (Endress et al. 2012, Clark et al. 2013, Pekin et al. 2014*a, b,* 2015). Fuel reduction treatments were designed to reduce extremely high fuel loads (>150 tons/ha) that developed from an outbreak of western spruce budworm (*Choristoneura occidentalis*) that killed the majority of grand fir and Douglas fir trees in the overstory in the 1980s–1990s (Vavra et al. 2004*a, b*, Bull et al. 2005). Stands were mechanically thinned to reduced fuel loads to <35 tons/ha, and following thinning, sites were broadcast burned. Treatments were designed and implemented in a manner typical of fuel reduction activities across coniferous forests in the western United States (Agee and Skinner 2005). Stand thinning for the three sites occurred during summer 2001, and both Bally Camp and Louis Spring were broadcast burned in the fall of the same year (2001). Half Moon was not burned until the summer 2002 to meet desired conditions for prescribed burning compatible with burn conditions at the other exclosures.

The exclosures were established following fuel treatments by constructing an eight-foot high fence that excluded all ungulates (cattle, elk, and mule deer), but allowed for other wildlife to pass under, over, or through. The exclosures were constructed in the year following the fuel treatments: 2002 for Bally Camp and Louis Spring, and 2003 for Half Moon. The size and shape of each exclosure varied depending on site conditions (topography, slope, forest structure, and the shape of the forest patch) to minimize variation within exclosures. Each exclosure was then divided into seven, roughly equal-sized and shaped plots (ranging from 0.95 to 1.02 ha/plot), and seven levels of cattle and elk herbivory were randomly assigned to the plots. The levels included low, moderate, and high late summer browsing by elk or by cattle and one level of total ungulate exclusion.

Ungulate herbivory treatments

Herbivory treatments began three years following exclosure construction (Bally Camp and Louis Spring: 2005, Half Moon: 2006) and were conducted annually for seven years. Herbivory levels for each treatment level (low, moderate, and high) were defined in terms of the number of days per ha, or stocking density, that elk and cattle use Douglas fir and grand fir forests in the interior northwestern United States, broken down into three levels of forage utilization: high—45% utilization; moderate—30% utilization; and low—15% utilization. These levels typify the range of use established for cattle on summer ranges in Douglas fir and grand fir habitat types on public lands like those at Starkey (Holechek et al. 1998). Public land grazing policies typically do not allow a level of forage utilization by cattle that exceed the high treatment level, nor is it common that utilization levels by cattle on public lands occur below our established low treatment level (Holechek et al. 1998). Consequently, our levels of forage utilization encompass the broad range of levels that typically occur on public grazing allotments in the western United States.

Stocking density (SD) for cattle and elk was then calculated using standard forage allocation procedures based on the specified level of forage utilization (FU, expressed as a proportion), the available forage for each ungulate (AF, kg/ha), and the average daily forage intake of each ungulate (DFI, $\text{kg}\cdot\text{ha}^{-1}\cdot\text{d}^{-1}$) as $\text{SD} = (\text{FU} \times \text{AF})/\text{DFI}$. Using this formula, stocking densities were determined as follows: for elk (low, moderate, and high): 8, 16, and 32 d/ha respectively; for cattle (low, moderate, and high): 10, 20, and 30 d/ha, respectively. Use of this algorithm to establish stocking densities of domestic ungulates, and wild ungulate equivalencies, is a conventional method based on standard forage allocation procedures used on public grazing allotments throughout the western United States (Holechek et al. 1998) and encompass the range of cattle and elk densities that typically occur on public ranges during summer in the western United States.

The calculated stocking densities were then refined so that the final number of cattle days per ha and elk days per ha for each treatment level corresponded to what was logistically feasible to implement with the tractable animals. Moreover, the number of animals must be compatible with each ungulate's group behavior for foraging and the need to complete the trials in as few days as possible to minimize changes in forage availability and phenology. As a result, we used four elk and six to eight cattle per trial to most efficiently approximate the calculated stocking densities. The diets of elk and cattle tend to converge during late summer in grand fir and Douglas fir forests (Findholt et al. 2004) when both ungulates typically increase selection for nutritious deciduous shrubs because grasses and forbs senesce and are of low quality following the onset of summer drought (Cook et al. 2004). We thus carried out the browsing treatments each year during August because we hypothesized that browsing would have the greatest effect on deciduous woody species during this time (Vavra et al. 2004*a*).

Demography of cottonwood and willow

We conducted a census to identify, count, and permanently tag cottonwood and willow individuals within the exclosures before implementing the herbivory treatments. Plots were systematically searched on three separate occasions between May and July 2005 (Louis Spring, Bally Camp) and 2006 (Half Moon). When encountered, all individuals were given a unique ID number and tag, and their location georeferenced with a Global Positioning System (GPS) unit (Trimble Pathfinder ProXRS; Trimble, Austin, Texas, USA). In July, before initiating the herbivory trials, we revisited all individuals and measured their heights. We remeasured tagged individuals annually each summer over the seven years of the study. During each sampling event, we recorded plant survival and height. When we encountered newly recruited plants during sampling, they were tagged, measured, and growth and survival tracked throughout the duration of the study.

At the beginning of our study, we observed considerable pocket gopher activity at the base of willow and cottonwood individuals, often killing individuals by chewing through the entire stem just below the soil surface (Fig. 1a, b). To incorporate pocket gopher effects into our study, we recording the presence of recently created soil mounds directly at the base of individuals (1 = yes; 0 = no) during our measurements. Additionally, we verified the cause of plant mortality by excavating individuals that died during the study and examining for gopher damage near the root crown (Fig. 1b). Monitoring and measuring subterranean herbivore effects on plants using mounds presence and density is a frequent and standard approach when destructive or more formal experimental measurements are not possible (e.g., Cantor and Whitham 1989, Cox and Hunt 1994, Campos et al. 2001, Lara et al. 2007).

For individuals exposed to ungulate herbivory treatments (all individuals except those in the complete ungulate exclusion treatment), we also resampled individuals immediately following implementation of herbivory treatments (late August or early September of each year) and recorded if the plant had been browsed in the most recent herbivory trial (1 = yes, 0 = no), and their height remeasured. Over the course of the study, we tracked the fate of 946 cottonwood individuals and 1290 willow individuals. This resulted in the following sample sizes: for cottonwood—low elk (n = 113), moderate elk (n = 51), high elk (n = 130), low cattle (n = 186), moderate cattle (n = 109), high cattle (n = 87), and ungulates excluded (n = 270) and for willow—low elk (n = 163), moderate elk (n = 109), high elk (n = 243), low cattle (n = 127), moderate cattle (n = 145), high cattle (n = 252), and ungulates excluded (n = 251).

Data analyses

To evaluate herbivory intensity on willow and cottonwood populations exposed to the herbivory treatment levels, we calculated "browse pressure" for each species for each year of the experiment. This was calculated as the proportion of individual plants in the population that were browsed. We used logistic regression within a mixed modeling framework (Schall 1991) to test whether the proportion of plants browsed (browse pressure) differed among ungulates (cattle, elk) and densities (low, moderate, and high). We used the function glmmPQL of the MASS package (Venables and Ripley 2002) in R (R Core Team 2012). Because the proportion of browsed plants was calculated annually over seven years,

Fig. 1. (a) Pocket gopher mound at the base of a wilting cottonwood (*Populus trichocarpa*) seedling; (b) evidence of pocket gopher herbivory near root crown of a Scouler's willow (*Salix scouleriana*); (c) cattle grazing one of the experimental plots; and (d) an elk browsing *S. scouleriana* during the experiment.

we included sampling year as a random effect along with study site. Ungulate density (low, moderate, or high) and type (cattle or elk) were included as fixed effects. We ran three separate analyses. The first analysis included a fixed variable indicating the species (willow or cottonwood) to test for differences in browse pressure among the two plant species. We then ran the model separately for cottonwood and willow species to specifically evaluate effects of stocking densities and ungulate type by plant species. Interactions between effects were initially tested and left in the models if significant ($P < 0.05$).

We evaluated treatment effects on survival rates of plants over the seven-year study using Cox proportional hazards regression analyses

(Andersen and Gill 1982) with the R function coxph in the survival package (Therneau and Grambsch 2000). Independent variables included in the models were ungulate type (elk and cattle), ungulate density (none, low, moderate, and high), and the intensity of belowground herbivory (none, low, moderate, and high). Levels of belowground herbivory were determined by calculating the percentage of years that we observed active pocket gopher activity directly at the base of each individual. We grouped percentages into four intensity levels: low (0–24%) moderate (25–49%), high (50–74%), and very high (≥75%). Interaction effects among independent variables were initially tested, and both independent variables and interaction effects were dropped from the final model if not significant ($P > 0.05$).

We evaluated the effect of ungulate browsing on plant height using Poisson regression within a mixed modeling framework using the MASS function glmmPQL. Fixed independent variables included ungulate type and density, initial plant height, and belowground herbivory. Sampling year and site were included as random factors in the models. Models for willow and cottonwood were run separately.

RESULTS

Browse pressure

When the experiment began, densities of cottonwood and willow were similar. Cottonwood densities averaged 34 individuals per hectare (SE = 4.9), while willow densities averaged 31 individuals per hectare (SE = 6.2). Over time, willow densities remained fairly constant while cottonwood densities declined rapidly, resulting in a mean cottonwood density of 13.4 individuals per hectare (SE = 2.8) at the end of the study (Fig. 2). The proportion of plants browsed during the study differed significantly depending on plant species (cottonwood vs. willow), ungulate type (elk vs. cattle), and ungulate density (low, moderate, and high). Browse pressure was significantly greater for willow than cottonwood ($t = 5.049$, $P < 0.001$), and elk browsed a significantly greater proportion of plants (cottonwood and willow combined) than cattle ($t = 5.003$,

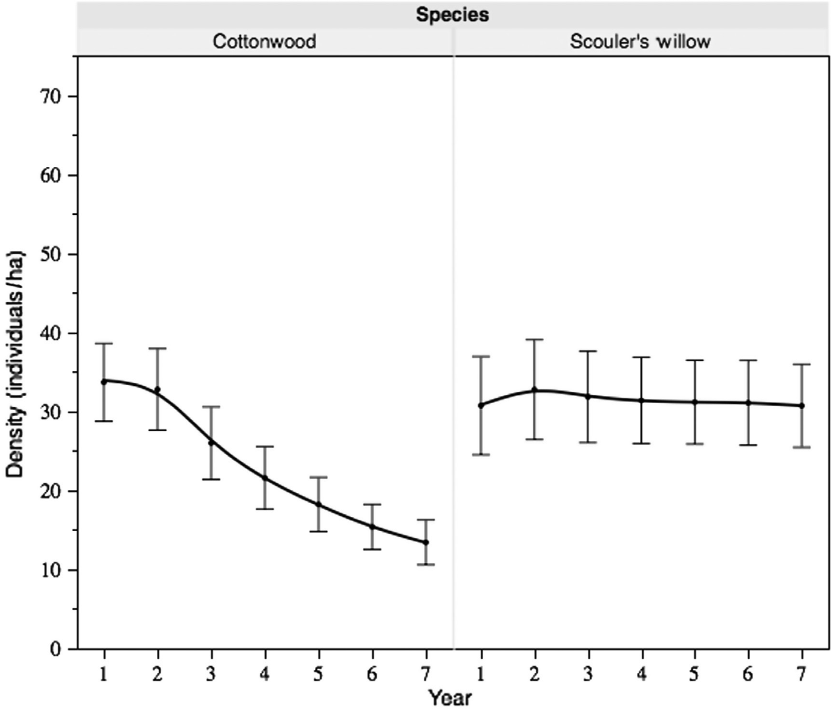

Fig. 2. Mean density (±SE) of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) across the herbivory treatments over the seven-year experiment.

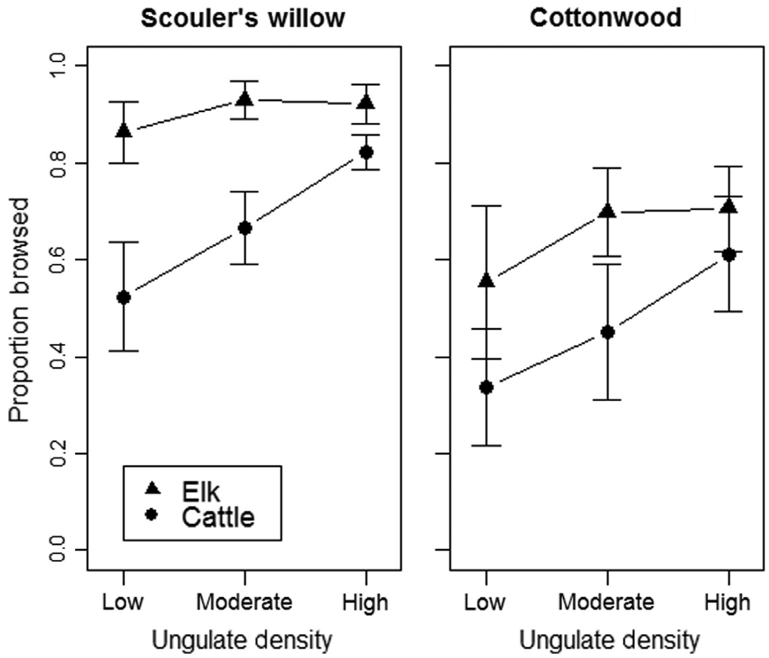

Fig. 3. The average proportion (±95% confidence intervals) of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals browsed per year by cattle (*Bos taurus*) and Rocky Mountain elk (*Cervus elephus*) over a seven-year period.

$P < 0.001$). Additionally, regardless of the ungulate species, increasing stocking density resulted in a greater proportion of browsed plants ($t = 6.311$, $P < 0.001$).

For cottonwood, regardless of the ungulate species (cattle or elk), as herbivore density increased, so did browse pressure (Fig. 3, Table 1). However, elk browsed a greater proportion of individuals than cattle (Fig. 3, Table 1). Mean percentage of individuals browsed per year for the cattle treatment ranged from 34% (SE = 5.8) in the low-density treatment to 61% (SE = 5.7) in the high-density treatment. For elk, browse pressure ranged from 55% (SE = 7.4) in the low-density treatment to 71% (SE = 4.2) in the high-density treatment.

Table 1. The effect of ungulate species (elk or cattle) and density on the proportion of browsed willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) based on logistic regression.

Parameters	Effect	Estimate	SE	*P*
Scouler's willow	Density	0.603	0.109	<0.001
	Species	1.593	0.192	<0.001
Cottonwood	Density	0.506	0.108	<0.001
	Species	0.835	0.173	<0.001

Similar results were found for willow (Fig. 3, Table 1). Browse pressure by elk was high ranging from 86% (SE = 3.0) at the low stocking density to 92% (SE = 2.0) in the high-density treatment. Browse pressure by cattle was lower and increased as density increased, ranging from 34% (SE = 5.8; low treatment) to 61% (SE = 4.2; high treatment).

Effects on survival

Survival rates differed considerably between the two plant species: 87.7% of willow individuals survived over the seven-year experiment, while cottonwood survival was 22.6%. This resulted in significant differences in survival probabilities between cottonwood and willow ($z = -11.410$, $P < 0.001$). Despite considerable browse pressure by both cattle and elk across stocking densities, we found no significant effect of ungulate herbivory on survival of either plant species. However, we found a significant effect of belowground herbivory on survival probabilities ($z = 10.185$, $P < 0.001$), with increased mortality

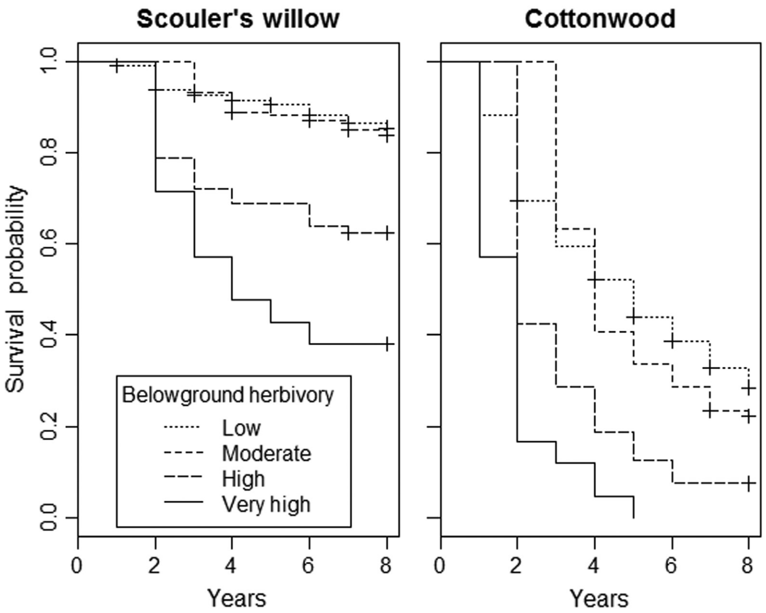

Fig. 4. Survival probability of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals over a seven-year period under variable belowground herbivory intensities by *Thomomys talpoides* (pocket gopher).

associated with increased belowground herbivory. A significant plant species by belowground herbivory interaction was found (z = 1.8461, P = 0.065) as survival decreased more rapidly for cottonwood than willow (Fig. 4).

For willow, survival probabilities and 95% CI were quite high at low (0.86, CI: 0.83–0.89) and moderate (0.84, CI: 0.79–0.89) levels of belowground herbivory and then dropped under high (0.62, CI: 0.51–0.77) and very high (0.38, CI: 0.22–0.66) intensity levels (Fig. 4, Table 2). Cottonwood showed a similar pattern, but survival rates were much more affected by belowground herbivory (Fig. 4, Table 2). At low belowground herbivory intensities, the probability of survival was 0.30 (CI: 0.25–0.34) and declined rapidly thereafter; no cottonwood individuals exposed to very high levels of belowground herbivory were alive after four years (Fig. 4).

Effects on height

Both aboveground and belowground herbivory affected the growth and size of cottonwood and willow (Figs. 5 and 6, Table 3). For willow, individuals in the complete ungulate exclusion treatment grew nearly 80 cm during the study from 72 cm (SE = 3) to 151 cm (SE = 7) and were significantly taller than willows in any of the

Table 2. The effect of belowground herbivory on Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) survival probability based on Cox proportional hazards regression.

Parameters	Belowground herbivory	Coef	Exp(coef)	SE(coef)	*z*	*P*(>|*z*|)
Scouler's willow	Moderate	0.1478	1.1593	0.2343	0.6309	0.528
	High	1.0908	2.9767	0.2601	4.1938	<0.001
	Very high	1.8988	6.6779	0.3043	6.2389	<0.001
Cottonwood	Moderate	0.1236	1.1316	0.1083	1.1412	0.254
	High	0.8510	2.3420	0.1080	7.8760	<0.001
	Very high	1.4345	4.1975	0.1492	9.6125	<0.001

Note: Model tests whether effects of shown herbivory groups (moderate, high, and very high) differ from the low belowground herbivory group.

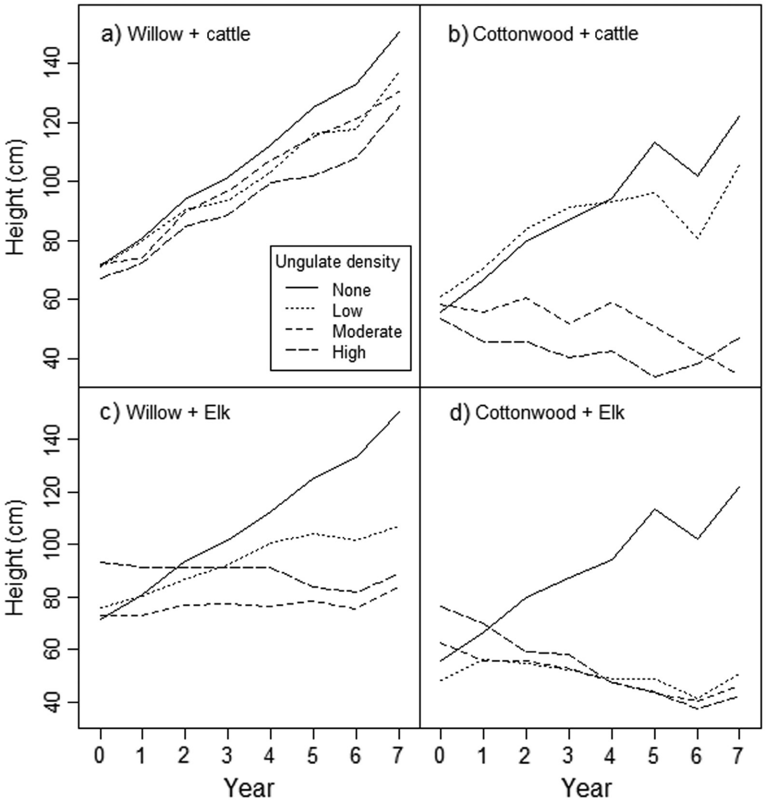

Fig. 5. Mean height of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals within different cattle (*Bos taurus*) and Rocky Mountain elk (*Cervus elephus*) browsing treatment plots over seven years. Year 0 represents the pretreatment height for individuals within browsing treatment plots.

ungulate herbivory treatments. Herbivory by elk had a greater impact on height than cattle and as stocking density increased, effects on height were more pronounced. While willow individuals in the cattle treatments were significantly smaller than those in the ungulate exclusion treatment, willows in all cattle treatments grew over the seven years, with mean height increases ranging from 59 to 66 cm. This was not the case for the elk treatments; not only were growth rates much lower, but also the mean height of individuals in the high elk treatment at the end of the study (mean = 90 cm; SE = 8.7) was shorter than the initial mean height prior to the herbivory treatment of 93 cm (SE = 5.4). Belowground herbivory by pocket gophers also had a significant negative effect on willow height (Fig. 6), and a significant interaction between cattle and belowground herbivory was found (Table 3).

The effect of herbivory (above and below) on cottonwood height was even more pronounced (Figs. 5 and 6). On average, individuals in the ungulate exclusion treatment grew 66 cm over the seven years. This was not the case in any of the herbivory treatments. In fact, only the low cattle treatment showed any meaningful increase in height during the study; cottonwood in all other cattle and elk treatments were either similar or shorter at the end of the study than at the beginning, regardless of stocking density (changes in height ranging −34 to 3 cm). Cottonwood was also highly sensitive to belowground herbivory by pocket gophers, with large declines in plant height accompanying very high level of gopher herbivory.

DISCUSSION

Our study is one of the first to evaluate top-down regulation of plant species by multiple herbivore species across a range of herbivore densities. We found that herbivore species,

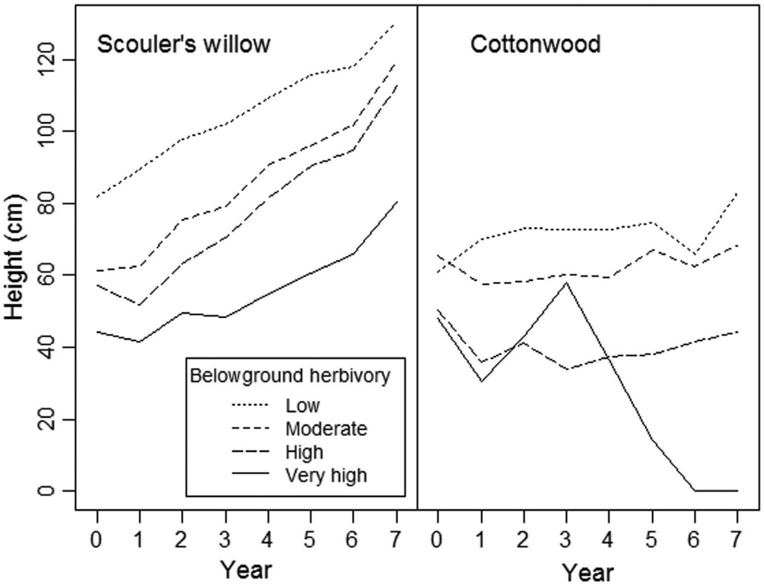

Fig. 6. Mean height of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals under different levels of pocket gopher (*Thomomys talpoides*) pressure over a seven-year period. Year 0 represents the pretreatment height for individuals within browsing treatment plots. No cottonwoods were alive in years 6 and 7, and mean heights are shown as zero values.

herbivore density, and plant species all influenced the strength of top-down regulation and that the effect of herbivore abundance on plant demographic performance and populations depended on the herbivore species, differential herbivore preference for specific plant species, and the ability of plant species to tolerate herbivory. We also found that top-down regulation of cottonwood and willow was not driven solely by large ungulates; belowground was also a strong driver of demographic performance, and significant aboveground–belowground herbivory effects were found.

Ungulate species

Results showed that herbivory by cattle and elk significantly reduced growth of the two plant species, with elk having a larger effect than cattle. This result supported our hypothesis regarding differences in foraging ecology between the two

Table 3. The effect of aboveground and belowground herbivory on height of Scouler's willow (*Salix scouleriana*) and cottonwood (*Populus trichocarpa*) individuals after 84 months based on Poisson regression.

Parameters	Herbivory	Estimate	SE	*P*
Scouler's willow	Cattle	−0.13	0.033	<0.001
	Elk	−0.301	0.041	<0.001
	Gopher	−0.123	0.021	<0.001
	Initial plant height	0.009	0	<0.001
	Cattle × gopher	0.09	0.023	<0.001
	Elk × gopher	0.028	0.031	0.38
Cottonwood	Cattle	−0.183	0.065	0.005
	Elk	−0.452	0.078	<0.001
	Gopher	−0.08	0.037	0.033
	Initial plant height	0.008	0	<0.001
	Cattle × gopher	−0.024	0.047	0.61
	Elk × gopher	−0.043	0.061	0.485

ungulate species. Cattle are "bulk grazers," with a diet composed largely of fibrous grasses and grass-like species even during late summer as grasses senesce with summer drought in dry forests (Clark et al. 2013). By contrast, elk are "intermediate grazers," with a broader diet of grasses, forbs, and shrubs in these same dry forests, and more pronounced switch to a shrub diet in late summer with senescence of grasses and forbs (Findholt et al. 2004). These differences in diet selection and foraging ecology between cattle and elk likely explain differences in browse pressure between the two herbivores and the subsequent effects on plant growth documented in our experiment. Elk had much greater impact on plant growth than cattle, suppressing growth of both willow and cottonwood across herbivore density treatments. Cattle also reduced plant growth, but effects were not as strong or as consistent.

We found no cattle or elk herbivory effect on plant survival rates or probabilities. However, this result must be interpreted with caution, as our experiment likely underestimated ungulate effects on survival. Due to the logistics of implementing the experiment, cottonwood and willow populations were not exposed to herbivory for three years after completion of the ungulate exclosures, providing time for plants to establish and grow in the absence of ungulate herbivory. This likely allowed willow and cottonwood to tolerate higher levels of herbivory than if they had been exposed to herbivores immediately after stand thinning and prescribed fire. Thus, it would be inappropriate to conclude that cattle and elk have no effect on survival rates based solely on this experiment given the time lag between the construction of the exclosures and the initiation of the herbivory treatments.

We hypothesized that elk would exert more pressure on deciduous woody plant species than cattle given that *Salix* spp. and *Populus* spp. are preferred forage species for elk (Cook 2002). Pekin et al. (2015) recently showed that elk reduced woody plant cover in the forest understory significantly more than cattle. Despite cattle's preference for herbaceous forage, browse pressure on cottonwood and willow by cattle was still moderate, ranging from 34% to 61%, which resulted in modest impacts on plant growth. Direct impacts of cattle on upland woody plant demography in the region have not received much attention, likely because cattle are primarily grazers of herbaceous species and deciduous woody species represent a very small proportion of their diet (Clark et al. 2013). Our study indicates that in addition to wild ungulates, cattle can also regulate woody species growth and size, despite their strong preference and selection for herbaceous vegetation. Thus, predicting herbivore impacts on plant population and community dynamics based on herbivore diet composition may miss important herbivore effects.

Role of ungulate abundance

One novel aspect of our research was the evaluation of herbivore impacts along an ungulate density gradient. Results showed that the importance of herbivore abundance on top-down regulation varied by ungulate and plant species. Herbivore pressure and effects by cattle on both willow and cottonwood increased as cattle densities increased. This was not the case for elk, where the effect of ungulate density depended on the plant species. Increasing elk density increased browse pressure on cottonwood populations. However, effects on growth of cottonwood were similar regardless of elk density, and any level of elk herbivory resulted in suppressing the species' growth.

Elk effects on willow showed a different pattern. In this case, browse pressure was similar regardless of elk density (ranging from 86% to 92%), with effects on growth increasing slightly with elk density. These results suggest that for elk, willow is a highly preferred browse species, with high levels of browse pressure even at low elk abundances, yet willow appears much more tolerant of herbivory than cottonwood, the latter exhibiting larger suppression effects on growth at lower browse pressures. Thus, when evaluating herbivore effects on plant populations, it is important to consider not only herbivore species and density, but also herbivore forage preference and each plant species' tolerance to herbivory. These issues have been largely ignored in studies evaluating the importance of top-down regulation by mammalian herbivores. Our results highlight the challenges in identifying and interpreting the strength and direction of top-down regulation of vegetation by herbivores when using traditional ungulate exclusion approaches that evaluate herbivory solely as a binary factor or when studies ignore factors such as foraging behavior and preference.

Evaluating herbivore effects across a range of herbivore densities provides opportunities to identify herbivory thresholds where top-down effects are expressed. For example, cottonwood appears tolerant of cattle herbivory at low cattle densities, with minimal impacts on growth; increasing cattle abundances results in large effects. On the other hand, any level of elk herbivory suppressed cottonwood growth, indicating a much lower herbivore threshold density for top-down regulation of plant demography. These findings indicate the need for a more thorough understanding of the role of herbivore abundance in regulating individual plant performance, plant population, and plant community dynamics.

The heavy browse pressure by elk and corresponding impacts to growth, even at lower densities, suggests that in the case of upland coniferous forests, increasing the abundance of top predators (e.g., wolves, cougars) may not result in large increases in the recruitment and abundance deciduous woody species that have been reported in some riparian ecosystems of western North America (e.g., Ripple and Larsen 2000, Ripple and Beschta 2004, 2007, Beschta 2005). Several reasons may explain the difference. First, our results showed that even in the low-density elk treatment, elk were able to suppress plant growth, particularly for cottonwood, where effects were nearly identical to the moderate- and high-density elk treatments. Additionally, the slow growth rates of cottonwood and willow measured in our study may weaken the importance of trophic cascades in this instance. Annual growth rates of cottonwood in the complete ungulate exclusion treatment averaged 9 cm/yr, which is half the growth rate reported in an adjacent riparian area by J. P. Averett (*unpublished data*). Assuming constant growth rates through time, it will take twice as long for cottonwoods in upland forests to grow above the browse line than in riparian zones, substantially increasing the probability of being browsed and suppressed by herbivores. Thus, it remains unclear what level of predator pressure would be required to reduce elk pressure on plant populations, either through altering elk distribution patterns, reducing densities, or both, to such a degree that cottonwood and willow would be able to escape herbivory and grow above the browse line (~2.5 m), particularly given the slow growth rates of willow and cottonwood in the uplands and high browse pressure. Finally, and perhaps most importantly, results indicate that pocket gophers, not ungulates, are a major regulator of cottonwood and willow abundance and size. Given that gophers are not a key prey species for large predators, the role of other smaller predators may be more important for deciduous woody plant dynamics in upland forests than large predators.

Belowground herbivory

The role of gophers in affecting vital rates of willow and cottonwood was an unexpected finding. Thus, more research should focus on the role of belowground herbivores in regulating willow and cottonwood. Cantor and Whitham (1989) reported that pocket gophers significantly reduced growth and survival in a related species, quaking aspen (*P. tremuloides*). Our approach was sufficient to identify pocket gopher-caused mortality, but our estimates of belowground herbivory intensity were imprecise and likely an underestimate. While gopher mounds directly at the base of individual plants are indicative of belowground herbivory (Fig. 1a), we could not account for root herbivory away from the stem or in instances where a mound did not form. However, the clear trends in increased mortality and decreased growth along our belowground herbivory intensity gradient suggest that our approach and interpretation were appropriate. Cantor and Whitham (1989) suggested that belowground herbivores feeding on roots are likely more important than aboveground herbivores that consume leaves and branches because of the effects of root herbivory on a plant's water balance. Results from the growing body of research on belowground invertebrate herbivory also indicate that plants respond to root herbivory much differently than to aboveground herbivory and that plants have a lower tolerance to root herbivory than aboveground defoliation (Zvereva and Kozlov 2012, Stephens et al. 2013, Johnson et al. 2016). Our results appear to support these findings and show that small mammal herbivory on root systems may be a primary force regulating the abundance and population dynamics of these two plant species. Manipulative experiments that control for both aboveground and belowground herbivores are needed to better understand herbivore impacts alone and in concert on plant demography.

Our results are similar to Lyly et al. (2014) in boreal forests, who found that while deer reduced growth of deciduous woody species, small mammals (voles and hares) had the largest effect on their survival. Herbivory by small mammals has been recognized as an important ecological process regulating plant populations and communities (Van der Wal et al. 2000, Howe et al. 2006, Smit et al. 2010, Gough et al. 2012, Goheen et al. 2013, McLaughlin and Zavaleta 2013, Rebollo and García-Salgado 2013), although most mammalian-focused herbivory research has focused on large-bodied species with some suggesting that larger mammalian herbivores are stronger regulators than smaller species (Bakker et al. 2006). Our findings and those by others (e.g., Goheen et al. 2013, McLaughlin and Zavaleta 2013, Rueda et al. 2013, Lyly et al. 2014) suggest that the strength of effect of mammalian herbivores in regulating vegetation is not related to body size. Rather, the entire herbivore community must be considered when evaluating herbivore impacts.

Plant species

Our experiment to evaluate effects of herbivores on two plant species provided insight on how differential herbivore preference, combined with differential tolerance levels to herbivory between plant species, affected the strength of top-down regulation. Both willow and cottonwood were browsed by the two ungulates but pressure on willow was considerably greater. However, herbivore effects were stronger on cottonwood, indicating this willow species is more resilient to ungulate herbivory than cottonwood. Responses to belowground herbivory were similar, with willow having higher survival and growth rates than cottonwood. These findings may help explain why Scouler's willow is common and widely distributed in upland conifer forests in the interior Pacific Northwest (Johnson 1998). By contrast, cottonwood is associated with more mesic forests or riparian ecosystems (Burns and Honkala 1990) and not as common in upland forests as willow. It is possible that our upland sites were near soil moisture tolerance limits of cottonwood given the 20% survival rate of cottonwoods in the ungulate exclusion treatment and the lower growth rates of cottonwoods relative to those found in nearby riparian areas (J. P. Averett, *unpublished data*).

Our results further suggest that willow and cottonwood may respond to herbivore density levels in different ways, likely along environmental and productivity gradients as shown for other plant species (Gough et al. 2012, Goheen et al. 2013, McLaughlin and Zavaleta 2013, Young et al. 2013). Thus, plant responses to herbivory that we documented may vary more widely across the landscape not only in response to herbivore species and abundance, but also with environmental gradients. This underscores the complexity of predicting the strength and direction of top-down regulation of vegetation by herbivores.

Implications for forest dynamics

The implications of top-down regulation of deciduous woody species by herbivores for long-term forest dynamics remain unclear. Based on our findings, in cases where ungulate herbivores are absent or exert very low browse pressure on deciduous woody species, low densities of cottonwood and willow will likely recruit to the canopy and change the overstory from one dominated exclusively by conifers to one that also includes a deciduous tree component. Densities of conifer seedlings in these postfire stands reach >1500 seedlings per hectare (B. A. Endress, *unpublished data*), much greater than densities of cottonwood and willow (Fig. 2). However, these two species are not the only deciduous woody species present with the potential to grow above the browse line and potentially influence forest structure, composition, and dynamics. A number of additional deciduous woody species including *Acer glabrum*, *Amelanchier alnifolia*, *P. tremuloides*, *Prunus virginiana*, *Sambucus* spp., and *Sorbus scopulina* are found in these forests, many of which are also browsed by ungulates (Dayton 1931, Johnson 1988, Riggs et al. 2000, Endress et al. 2012). If these species respond similarly to herbivory as cottonwood and willow in our study, under low ungulate browse pressure scenarios, a deciduous woody layer 3–10 m in height may develop and increase the structural complexity and diversity of these conifer dominated forest stands. Long-term monitoring is required to better understand whether and to what degree this occurs.

CONCLUSION

Our research identified four key factors that influence the strength of herbivory as a top-down regulator of plant structure and demographic performance: (1) herbivore species, (2) herbivore abundance, (3) herbivore diet selection, and (4) the ability of plant species to tolerate herbivory. Our research further demonstrated the importance of moving beyond traditional herbivory research that (1) only evaluates pooled herbivore effects and (2) considers herbivory solely as a binary variable (i.e., ungulate presences versus absence). Our results demonstrate the need for increased understanding of the importance and strength of herbivore effects both theoretically and in practice by incorporating multiple species across a range of herbivore densities. This would be particularly helpful to inform effective management of ecosystems that contain multiple herbivores that vary in abundance. This would substantially advance our knowledge of herbivory effects and mechanistic processes of regulation, particularly if new research evaluates responses along a wide spectrum of environmental gradients. Unfortunately, such research designs are both expensive and logistically challenging, particularly related to varying ungulate species and densities in a controlled manner across environmental conditions over long periods. These challenges largely explain the large knowledge gaps regarding herbivores as top-down regulators of plant dynamics, and why mammal herbivory research continues to focus on binary exclusion experiments.

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