



# Response of native versus exotic plant guilds to cattle and elk herbivory in forested rangeland

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## Keywords

Conditioned Correspondence Analysis; Conifer Forest Management; Grazing; Non-Native Species; Prescribed Burning; Stand Thinning; Ungulates

## Nomenclature

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## Abstract

**Questions:** Are exotic plant species favoured by non-native ungulate herbivores and disadvantaged by native herbivores in forested rangelands? Do the impacts of ungulates on exotic vs native plants depend on forest management activities such as prescribed fire and stand thinning?

**Location:** Northeastern Oregon, USA.

**Methods:** We recorded changes in richness and cover of different exotic and native plant life forms in experimental plots that were grazed only by cattle (a non-native herbivore), only by elk (a native herbivore) or not grazed by any ungulate over a 7-yr period at both managed (recently burned and thinned) and unmanaged (where no fire and thinning has occurred in >40 yr) forest stands.

**Results:** There was a general decrease in exotic plant species richness and cover across all treatments. However, the decrease in exotic richness, particularly of exotic annual forbs, was slightly lower in plots grazed by elk than in ungrazed plots at managed stands. Managed stands also displayed a larger increase in native annual forb richness and exotic graminoid richness, and a larger decrease in native perennial graminoid cover with cattle grazing than elk grazing. At unmanaged stands, cover of woody native plants such as shrubs, sub-shrubs and trees as well as native perennial forbs decreased or remained relatively constant with elk grazing while increasing strongly at plots that were ungrazed or grazed by cattle.

**Conclusions:** Cattle and elk have variable effects on different plant guilds at managed vs unmanaged forest stands. Overall, cattle grazing tends to have a larger impact on herbaceous plant guilds at managed stands, while elk grazing tends to have a larger impact on woody plant guilds at unmanaged stands. However, in contrast to findings from other ecosystems, grazing only has a minor impact on exotic plant dynamics in our study area, and cattle grazing does not favour exotic plants any more than grazing by elk or ungulate exclusion.

## Introduction

Ungulate herbivores play an important role in plant species dispersal and dynamics across the globe (Augustine & McNaughton 1998; Rooney & Waller 2003; Manier & Hobbs 2006; Bartuszevige & Endress 2008; Pekin et al. 2014). Results from experimental studies suggest that exotic herbivores favour the spread and establishment of exotic plants, whereas native herbivores favour native plant species (Parker et al. 2006). In the western United States, grazing by non-native ungulates, specifically cattle, has been shown to favour exotic over native plant species

(Kimball & Schiffman 2003). However, knowledge of ungulate impacts on exotic vs native plants are largely obtained from grasslands, and studies on the effect of cattle on exotic plant species dynamics in western forests are lacking (Vavra et al. 2007).

Ungulates alter the relative abundance of different plant species through both direct and indirect mechanisms (Hobbs 1996). For example, plant species preferred as forage by ungulates often decrease in abundance or become locally extirpated (Rooney & Waller 2003; Rooney 2008), which may in turn give a competitive advantage to unpalatable plant species (Díaz et al. 2007). Because of

differences in their feeding preferences (Augustine & McNaughton 1998) and in their seed dispersal ability (Bartuszevige & Endress 2008), native and non-native ungulates are likely to influence plant community composition differently (Parker et al. 2006). Furthermore, some plant species may be more resilient to grazing than other plant species, and display high regeneration rates even under heavy grazing (Augustine & McNaughton 1998). Consequently, the establishment and dominance of exotic plant species will depend on the extent to which species are preferred by different local ungulate herbivores, the individual responses of the species to herbivory and management of the ungulate populations.

Forest lands of the western US are grazed extensively by cattle as well as native wild ungulates, including elk and deer (Wisdom & Thomas 1996). Negative impacts of overgrazing by native ungulates such as deer are widely documented in forests of the eastern and midwestern US (Rooney & Waller 2003; Côté et al. 2004; Rooney 2008; Randall & Walters 2011). Some knowledge also exists regarding ungulate effects on forest vegetation communities in the western US (Hobbs 1996; Belsky & Blumenthal 1997; Endress et al. 2012; Pekin et al. 2014). However, the differences and similarities in the effects of wild vs domestic ungulates in the region are not well documented (Vavra et al. 2007) because single studies that include both domestic and wild ungulates are rare.

Intermountain forests of the western US have been invaded by several herbaceous annual and perennial plant species of Eurasian origin, which in some cases were intentionally introduced and have become naturalized (Westbrooks 1998). Because many exotic plants of the western US are early seral species, they are favoured by major disturbances such as burning and stand thinning (Griffis et al. 2001), both of which are common forest management activities in the region (Agee & Skinner 2005). Accordingly, the effect of ungulates on exotic plant dynamics in western forests is likely to be strongly influenced by prescribed burning and stand thinning. We showed in a recent study that the impact of ungulate herbivory on understorey composition differs, depending on recent forest management activities, including thinning and burning (Pekin et al. 2015). Forests in the western US are often mechanically thinned to avoid stand-replacing fires (Vavra et al. 2004). Controlled burns are then implemented to further reduce fuel loads in the forest understorey (Bull et al. 2005). In the present study, we compare the impact of grazing by cattle to grazing by elk and ungulate exclusion (no grazing) on the changes in abundance and diversity of exotic and native plant species in managed (thinned and burned) and unmanaged forest sites in northeastern Oregon, US. In doing so, we seek to test the hypothesis that exotic plant species are favoured by cattle and disadvan-

tagged by elk, and to inform management regarding the role of cattle vs elk grazing in driving plant invasions in forested rangelands.

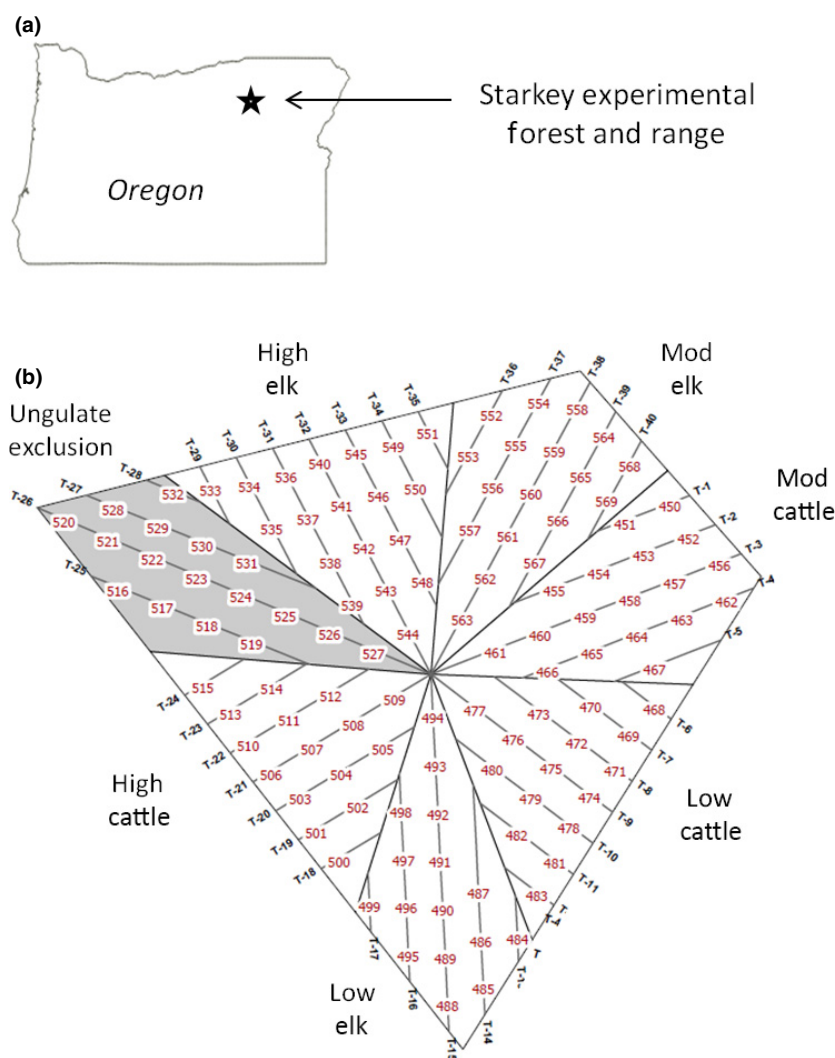
## Methods

### Study area

We conducted our study at the Starkey Experimental Forest and Range (SEFR) in the Blue Mountains Ecological Province (Fig. 1a; 45°12' N, 118°3' W, northeast Oregon). SEFR has a climate typical of montane forests of interior western North America (Rowland et al. 1997; Wisdom 2005). Elevations range from 1200 to 1500 m, and mean annual precipitation generally ranges from 600 to 700 mm (PRISM Climate Group 2012). Most precipitation occurs during winter as snow or during spring as rain, and there is an extended dry period during late summer–early autumn (Rowland et al. 1997). Forests in the region are generally dominated by Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*; Franklin & Dyrness 1973). In addition to Douglas-fir and grand fir, other canopy tree species present include several pine species (e.g. *Pinus ponderosa* and *P. contorta*), western larch (*Larix occidentalis*) and Englemann spruce (*Picea engelmannii*). Common understorey graminoids (i.e. grass and grass-like species) include fescue (*Festuca* spp.), sedge (*Carex* spp.), brome (*Bromus* spp.) and bluegrass (*Poa* spp.). Common shrubs include bearberry (*Arctostaphylos uva-ursi*), huckleberry (*Vaccinium* spp.), rose (*Rosa* spp.), snowberry (*Symphoricarpos albus*), shinyleaf spiraea (*Spiraea betulifolia lucida*) and twinflower (*Linnaea borealis*). Common forbs include lupine (*Lupinus* spp.), strawberry (*Fragaria* spp.) and yarrow (*Achillea millefolium*). Most of the woody vegetation in the region is native, and exotic species are restricted to annual and perennial forbs and graminoids. A list of all species recorded in the study sites is given in Appendix S1.

### Forest management

We utilized the variation in forest management at SEFR to ask questions regarding the effect of ungulates under the different management scenarios. We took advantage of recent management activities, in the form of fuel reduction treatments, which were conducted between 2000 and 2003 (Vavra et al. 2004; Bull et al. 2005). These included both thinning and prescribed burning, which are common management activities in western forests. The specific reasons and details of the burning and thinning process are described in detail in Vavra et al. (2004) and Bull et al. (2005). Briefly, forest stands were mechanically thinned with a feller-buncher to reduce fuel loadings to <35 t·ha<sup>-1</sup>, compatible with fuel loads considered unlikely to carry stand-replacement fires (Vavra



**Fig. 1.** (a) Location of Starkey Experimental Forest and Range in northeast Oregon and (b) an example of ungulate treatment and vegetation sampling design from Bally Camp.

et al. 2004). Controlled burns were implemented during the autumn of the same year, or on occasion, the following year due to time and logistical constraints (Bull et al. 2005). These management activities were implemented in a manner typical of fuel reduction treatments conducted across dry forests of the western US (Agee & Skinner 2005).

### Study site establishment

Five exclosures ranging in size from 5 to 7 ha were established at five mixed forest sites in the SEFR. Three of the five exclosures, Half Moon (HM), Louis Spring (LS) and Bally Camp (BC), were constructed on fuel-treated stands. The other two exclosures, Doug Prairie (DP) and Bee Dee (BD), were constructed where no fuel

reduction treatments or any other silvicultural treatments had been implemented in >40 yr. The untreated sites were similar in forest structure and composition to pre-treatment conditions of the fuel treated sites (Bull et al. 2005).

The exclosures were constructed in the year following fuel treatment, and included a fence that was 2.5 m in height that excluded all ungulates (cattle, elk and mule deer), but allowed other wildlife to pass. The size and shape of each exclosure were adjusted to site conditions, such as topography, slope, forest structure and the shape of the forest patch, to minimize site variation within and among exclosures. While the primary objective of this study was to assess differences in the response of the vegetation community to cattle vs elk herbivory, three levels of stocking density were included for cattle and elk in the treatments

to determine if any observed differences in ungulate effects varied with grazing intensity.

The ungulate exclosures were thus divided into seven equal-sized paddocks (ranging from 0.73 to 1.1 ha per paddock, depending on the exclosure) in which seven different levels of cattle and elk herbivory treatments were randomly assigned and implemented (Fig. 1b). The grazing treatment levels included low, moderate or high late summer browsing by elk or by cattle and one level of total ungulate exclusion.

### Browsing trials

We carried out the browsing treatments each year during August for 6 yr in a row at all sites. Browsing pressure for each treatment level was defined in terms of stocking densities, i.e. the number of days per ha that elk and cattle use the Douglas-fir and grand fir habitat types in the interior northwestern US, at levels typical of the range of grazing and browsing use established for cattle on summer ranges in Douglas-fir and grand fir habitat types on public lands like those at SEFR (Holechek et al. 1998). These stocking densities were calculated as low (eight elk and ten cattle days-ha<sup>-1</sup>), moderate (16 elk and 20 cattle days-ha<sup>-1</sup>) and high (32 elk and 30 cattle days-ha<sup>-1</sup>). For details on how stocking density was calculated for each ungulate, see Endress et al. (2012) and Pekin et al. (2014).

### Vegetation sampling

The 1-m<sup>2</sup> vegetation sampling plots were established in each paddock. Due to differences in paddock size and layout, the number of plots per paddock varied from 24 to 36, although the percentage of each paddock sampled remains similar. Plots were located 15 m apart along transect lines, with each transect line spaced 15 m apart from one another within each paddock. Within the sampling plots, we identified all plant species and estimated canopy cover using the arcsine square root class scale, a commonly used cover class scale (MjM Software, Glendale Beach, OR, US): 0, 1–5, 5–25, 25–50, 50–75, 75–95, 95–99, 99–100. Cover was defined as the percentage of the quadrat covered by the vertical projection of each species. Sampling was conducted 2 yr after fuel reduction treatments, and again 7 yr later (i.e. 9 yr following fuel treatment). Because the fuel reduction treatments were not all conducted in the same year, the vegetation sampling was conducted in July 2004/2011 or 2005/2012 depending on the site. All sampled plant species were categorized as native or exotic and according to life form (i.e. forb, graminoid, shrub, sub-shrub or tree) and associated life cycle (i.e. annual or perennial). See

Appendix S1 for full list of species and their classifications.

### Data analysis

The overall cover and richness (i.e. number of species) of individual exotic and native plant guilds were calculated for the two vegetation sampling time periods, i.e. pre-grazing (yr0) and 7 yr post-grazing treatment initiation (yr7). Differences in plant species composition between grazing treatments were also assessed through a constrained (or canonical) correspondence analysis (CCA; Legendre & Legendre 1998) using the *cca* function of the *vegan* package in R (R Foundation for Statistical Computing, Vienna, AT). A CCA allows for the detrending of the effect of some environmental variables on species composition so that the effect of a particular variable of interest is clearer in the final ordination. Much of the differences in species composition across our sites are likely to be explained by management, since forest thinning and fire strongly alter vegetation seral stage (Pekin et al. 2015). Accordingly, management-related differences in species composition are likely to overshadow any finer-scale effects of grazing. We thus removed (detrended) the effect of management to more accurately display changes in the vegetation community associated with the grazing treatments. Significance of the reduced CCA model was tested with a permutation test based on 500 permutations. Radar charts displaying the relative changes in the different native and exotic plant guilds across the plots were also made using the *radarchart* function in the R package *fmsb*.

Ungulate grazing effects on specific univariate vegetation responses were assessed with generalized linear mixed models (GLMM; Schall 1991) using the *glmmPQL* function of the R package *MASS* (Venables & Ripley 2002). The effect of browsing by elk and cattle was tested on the following response variables: change in overall native plant cover, exotic plant cover, native plant richness, exotic plant richness and richness and cover of the individual exotic and native plant guilds. The plot nesting design within individual treatment paddocks and the initial response value were included as random effects in case initial vegetation conditions may have biased the changes across individual paddocks. Ungulate grazing pressure and site management were included as random effects and also as covariates or fixed effects if they were significant ( $P \leq 0.05$ ) in the model. The differences between the effects of ungulate type (cattle vs elk) on the responses were tested using Tukey's HSD separately at managed and unmanaged sites.

## Results

### Plant composition across study sites

A total of 238 plant species were observed across our study sites (see Appendix S1 for a full species list). The vast majority of the observed species were perennials and forbs (Table 1). Native perennial forbs in particular were the most abundant plant guild, comprising 30% of overall understorey cover. Graminoids were the most common life form after forbs (Table 1) and were composed of more species than trees, shrubs and sub-shrubs combined (Table 1). Despite their low species number (Table 1), trees, shrubs and especially sub-shrubs comprised a relatively large proportion of overall vegetation cover.

Exotics comprised a relatively small proportion of understorey species and cover (Table 1). Native perennial graminoids alone comprised 16% of total cover, while exotic perennial grasses and exotic perennial forbs comprised 4% and 5%, respectively. Annual grasses comprised <1% of understorey cover and were composed mostly of exotics, with only two native species. Because they were extremely scarce or non-existent, especially at unmanaged sites, native annual graminoids were not included as a separate group in the rest of the analyses.

### Multivariate changes in plant composition

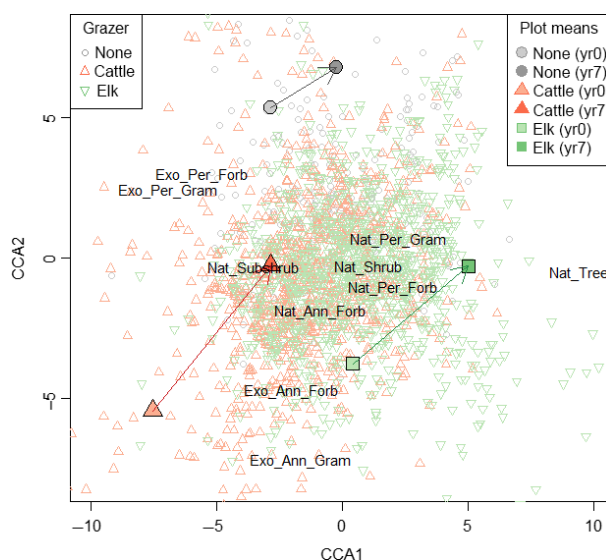
There were significant differences in plant species composition between the experimental paddocks before initiation of our grazing treatments (yr0; Fig. 2). Nonetheless, the direction of changes in cover of the plant guilds from the first (yr0) to the second (yr7) sampling period were relatively consistent. All trajectories (grazed and ungrazed) followed a similar successional gradient from their different starting points (Fig. 2). Generally, there was a movement away from exotics and towards native perennial species. Grazed plots in particular exhibited a move away from exotic annuals and ungrazed plots from exotic perennials, and both moved toward native perennial graminoids and forbs (Fig. 2).

### Effect of grazing and management on exotic and native plant guilds

The observed changes in exotic plant guilds were only significantly different between grazing treatments at managed sites (Table 2). While the decrease in exotic cover was similar between grazing treatments, the decrease in exotic species richness, particularly of annual forbs, was lower at plots grazed by elk (Table 2). In contrast, richness of exotic annual graminoids, which included only

**Table 1.** The total number of species, the proportion of total species, and the relative cover of vegetation observed in the study summarized by origin, life cycle and life form.

|            | Total species | Proportion of species (%) | Relative cover (%) |
|------------|---------------|---------------------------|--------------------|
| Origin     |               |                           |                    |
| Native     | 205           | 86                        | 89                 |
| Exotic     | 32            | 14                        | 11                 |
| Life cycle |               |                           |                    |
| Perennial  | 197           | 83                        | 93                 |
| Annual     | 40            | 17                        | 7                  |
| Life form  |               |                           |                    |
| Forb       | 160           | 68                        | 41                 |
| Graminoid  | 43            | 18                        | 20                 |
| Shrub      | 20            | 8                         | 9                  |
| Subshrub   | 6             | 3                         | 18                 |
| Tree       | 8             | 3                         | 12                 |



**Fig. 2.** Constrained Correspondence Analysis (CCA) showing the variation in plant species composition across ungrazed plots, and plots grazed by cattle and elk after the effect of site management has been removed. The constrained eigenvalues of CCA 1 and CCA 2 are 0.04 and 0.02 respectively. The relative locations of the plot means of each grazing treatments at the two sampling years (yr0 and yr7) are shown. The mean scores of species within specific exotic and native plant guilds are also indicated by the location of the guild name on the ordination.

three species (*Ventenata dubia*, *Apera interrupta* and *Bromus* sp.) decreased at plots grazed by elk while increasing at plots grazed by cattle, but neither grazing treatment was significantly different from the ungrazed treatment (Table 2).

There were significant differences between grazing treatments in the cover and richness of native plant guilds at both managed and unmanaged sites (Table 2). In unmanaged sites, overall native plant cover and cover

**Table 2.** Mean (standard error) change, over a 7 yr period, in richness (R) and cover (C) of native and exotic plant guilds across cattle grazed, elk grazed, and ungrazed plots at managed (prescribed burned and thinned) and unmanaged forest stands. Plant guilds with significant ( $P \leq 0.05$ ) differences in mean values among grazing treatment groups are shown in bold. Treatment groups with differing means (determined by Tukey's Honest Significant Difference test) are indicated by superscripts.

|                 | Managed                          |                                 |                                 | Unmanaged                       |                                 |                                 |
|-----------------|----------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
|                 | Cattle                           | Elk                             | None                            | Cattle                          | Elk                             | None                            |
| Native          |                                  |                                 |                                 |                                 |                                 |                                 |
| All species     |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 1.33 (0.21)                      | 0.92 (0.20)                     | 0.59 (0.38)                     | −2.73 (0.26)                    | −3.22 (0.23)                    | −2.37 (0.48)                    |
| C               | 14.15 (1.92)                     | 12.71 (2.17)                    | 15.59 (3.50)                    | <b>22.14<sup>a</sup> (3.48)</b> | <b>−0.85<sup>b</sup> (3.44)</b> | <b>31.52<sup>a</sup> (6.46)</b> |
| Perennial forb  |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.53 (0.12)                      | 0.46 (0.12)                     | 0.39 (0.22)                     | −1.51 (0.17)                    | −1.75 (0.16)                    | −0.98 (0.36)                    |
| C               | −0.24 (1.07)                     | −0.68 (1.05)                    | −2.83 (1.57)                    | <b>2.08<sup>a</sup> (1.63)</b>  | <b>−4.78<sup>b</sup> (1.62)</b> | <b>4.85<sup>a</sup> (3.54)</b>  |
| Perennial gram. |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.28 (0.07)                      | 0.30 (0.08)                     | 0.07 (0.13)                     | −0.67 (0.10)                    | −0.76 (0.09)                    | −0.71 (0.19)                    |
| C               | <b>0.34<sup>a</sup> (0.71)</b>   | <b>4.45<sup>b</sup> (0.90)</b>  | <b>4.01<sup>ab</sup> (1.17)</b> | 1.52 (1.02)                     | 4.93 (1.41)                     | 6.73 (2.59)                     |
| Annual forb     |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | <b>0.10<sup>a</sup> (0.08)</b>   | <b>−0.32<sup>b</sup> (0.09)</b> | <b>−0.21<sup>a</sup> (0.13)</b> | −0.65 (0.08)                    | −0.71 (0.08)                    | −0.88 (0.15)                    |
| C               | −2.09 (0.64)                     | −2.88 (0.82)                    | −1.53 (0.96)                    | −0.79 (0.09)                    | −0.88 (0.13)                    | −0.96 (0.16)                    |
| Shrub           |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.11 (0.03)                      | 0.09 (0.03)                     | 0.15 (0.05)                     | 0.14 (0.06)                     | 0.03 (0.06)                     | 0.15 (0.09)                     |
| C               | 5.14 (0.84)                      | 2.62 (0.65)                     | 3.79 (1.47)                     | <b>6.15<sup>a</sup> (1.06)</b>  | <b>2.20<sup>b</sup> (1.02)</b>  | <b>7.00<sup>ab</sup> (2.12)</b> |
| Subshrub        |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.08 (0.03)                      | 0.10 (0.03)                     | 0.00 (0.07)                     | −0.05 (0.06)                    | −0.04 (0.05)                    | 0.08 (0.10)                     |
| C               | 6.63 (1.04)                      | 3.76 (0.87)                     | 6.41 (1.86)                     | <b>8.54<sup>a</sup> (1.74)</b>  | <b>−0.64<sup>b</sup> (1.65)</b> | <b>10.27<sup>a</sup> (3.81)</b> |
| Tree            |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.24 (0.04)                      | 0.28 (0.04)                     | 0.18 (0.07)                     | 0.02 (0.04)                     | 0.03 (0.05)                     | −0.02 (0.08)                    |
| C               | 4.39 (0.73)                      | 5.45 (1.04)                     | 5.73 (1.47)                     | <b>4.65<sup>a</sup> (1.50)</b>  | <b>−1.68<sup>b</sup> (1.57)</b> | <b>3.63<sup>ab</sup> (2.42)</b> |
| Exotic          |                                  |                                 |                                 |                                 |                                 |                                 |
| All species     |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | <b>−1.10<sup>ab</sup> (0.10)</b> | <b>−0.95<sup>a</sup> (0.09)</b> | <b>−1.50<sup>b</sup> (0.14)</b> | −1.53 (0.11)                    | −1.58 (0.13)                    | −1.85 (0.23)                    |
| C               | −3.63 (0.71)                     | −2.96 (0.50)                    | −4.38 (1.27)                    | −11.20 (1.55)                   | −9.20 (1.22)                    | −11.40 (3.23)                   |
| Perennial forb  |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | −0.46 (0.06)                     | −0.45 (0.06)                    | −0.69 (0.09)                    | −1.00 (0.09)                    | −0.93 (0.08)                    | −1.19 (0.17)                    |
| C               | −1.89 (0.39)                     | −1.68 (0.26)                    | −2.65 (0.73)                    | −6.19 (1.24)                    | −5.47 (0.87)                    | −6.52 (2.20)                    |
| Perennial gram. |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | 0.18 (0.04)                      | 0.23 (0.04)                     | 0.13 (0.04)                     | −0.07 (0.06)                    | −0.18 (0.05)                    | −0.10 (0.11)                    |
| C               | 0.23 (0.51)                      | 0.02 (0.35)                     | −0.28 (0.80)                    | −4.57 (1.01)                    | −2.72 (0.76)                    | −3.87 (2.09)                    |
| Annual forb     |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | <b>−0.91<sup>a</sup> (0.05)</b>  | <b>−0.69<sup>b</sup> (0.05)</b> | <b>−0.96<sup>a</sup> (0.09)</b> | −0.45 (0.05)                    | −0.42 (0.06)                    | −0.54 (0.10)                    |
| C               | −1.74 (0.15)                     | −1.28 (0.16)                    | −1.63 (0.24)                    | −0.42 (0.24)                    | −0.97 (0.20)                    | −1.00 (0.20)                    |
| Annual gram.    |                                  |                                 |                                 |                                 |                                 |                                 |
| R               | <b>0.08<sup>a</sup> (0.03)</b>   | <b>−0.03<sup>b</sup> (0.02)</b> | <b>0.02<sup>ab</sup> (0.03)</b> | −0.02 (0.01)                    | −0.05 (0.02)                    | −0.02 (0.02)                    |
| C               | −0.24 (0.17)                     | −0.02 (0.23)                    | 0.19 (0.15)                     | −0.02 (0.01)                    | −0.05 (0.02)                    | −0.02 (0.02)                    |

of native shrubs, sub-shrubs and trees increased strongly at ungrazed plots and plots grazed by cattle, and decreased or increased to a much lesser extent at plots grazed by elk (Table 2). In contrast, cover of native perennial graminoids decreased less, and richness of annual forbs was maintained to a greater extent at plots grazed by cattle than by elk (Table 2). Grazing pressure did not have a significant effect on changes in exotic and native plant richness or cover ( $P > 0.05$ ) and was thus only included as a random effect in the final models.

## Discussion

It has been suggested that exotic plant species are disadvantaged by native herbivores since they did not evolve under predation by them, and are favoured by exotic or non-native herbivores that share their place of origin (Keane & Crawley 2002). The vast majority of the exotic plants in our study area are from Eurasia, which is also the origin of domestic cattle and the wild ancestor (*Bos primigenius*). Accordingly, we might expect exotic plant species in our study to benefit either from the exclusion of elk or

grazing by cattle. However, neither of these expectations was supported by our results, which contradicts general trends observed across a variety of ecosystems dominated by ungulate and non-ungulate herbivores (Parker et al. 2006). There was a temporal trend away from exotics and toward natives across all of our sites, suggesting that exotics are being crowded out as the sites progress toward later successional stages. Fire and stand thinning enable exotic plants to spread in western forests (Griffis et al. 2001). It is thus expected that many exotics will decrease in abundance and become locally extinct over time as late seral vegetation, nearly all of which is native in this system, takes hold. These findings demonstrate that exotic plant dynamics in our study area are largely driven by vegetation succession and any effect of ungulates on these dynamics are relatively minor.

Exotic grasses have previously been shown to gain a competitive advantage from cattle grazing in California (Kimball & Schiffman 2003) as other vegetation is preferred by cattle during the summer and autumn when exotic annuals, such as cheat grass (*Bromus tectorum*), are less palatable (Holechek et al. 1982). While there was a slight increase in richness of exotic annual graminoids along with native annual forbs under cattle grazing relative to elk grazing at our managed sites, suggesting that cattle grazing may favour these guilds relative to elk grazing, annual grasses were not favoured by cattle grazing any more than by grazing exclusion. This finding, along with the very low abundance of annual grasses in our study, suggests that cattle have a minor if not a negligible role in facilitating exotic grass invasion in our study area.

In contrast to California grasslands, overall exotic plant richness was slightly favoured by elk grazing rather than cattle grazing in our study. This was due mainly to the maintenance of exotic annual forbs at plots grazed by elk, which decreased more strongly at ungrazed plots and plots grazed by cattle. The maintenance of these species under elk grazing coincided with a loss of native annual forb richness, whereas the increase in exotic annual graminoids and native annual forbs under cattle grazing coincided with suppression of native perennial graminoid cover. These results suggest that cattle grazing may to some extent facilitate co-existence of both exotic and native annuals with perennials by decreasing competition from native perennial graminoids. Whereas elk grazing may facilitate co-existence of exotic annual forbs with other annual and perennial species, possibly by freeing niche space through the loss of native annuals.

No differences in exotic plant guilds were observed among the grazing treatments at unmanaged sites in spite of strong suppression of vegetation cover by elk grazing. Stohlgren et al. (1999) also found no difference in exotic plant species richness between ungrazed plots and plots

grazed by a variety of native and non-native ungulates, such as bison and wild horses, across several western US states. These plots were located at mid- to high elevation and were dominated by steppe vegetation, which includes shrubs and grasses much like the understory in our forest study sites. However, Stohlgren et al. (1999) did not include any early seral vegetation communities, presumably because prescribed fire and other management activities are not as common in these non-forested ecosystems. The consistency between our findings and the Stohlgren et al. (1999) study suggests that exotic plant dynamics in mid- to late succession vegetation communities may be less sensitive to ungulate grazing than the same communities immediately following episodic disturbances such as burning or thinning.

The fact that the influence of ungulate grazing on exotic plant dynamics was only evident at managed sites can be explained by the fact that annuals were more abundant in these early seral vegetation communities. Perennials are generally favoured over annuals in the absence of grazing (Díaz et al. 2007). Because there was a general decrease in cover of annuals over our 7-yr study period, the role of cattle and elk in maintaining these exotic annual species was more evident at managed sites, where they had recently colonized and were being competitively excluded by other plant guilds with succession. As many of these exotic annuals will become locally extinct as the stands progress towards a late seral stage, the influence of ungulates on exotic species dynamics will become less significant. In fact, unmanaged sites were already virtually free of annual graminoids by the end of our study, suggesting that the effect of grazing on the establishment and dominance of exotic annuals in our region is likely to be inconsequential. However, we did not have any exotic shrubs or sub-shrubs in our study area, and the dynamics of these species may be impacted more strongly by ungulate grazing in areas where they persist, especially since trajectories of woody vegetation cover are strongly impacted by grazing in this ecosystem. Exotic plant invasions in western rangelands may also be driven by other local environmental characteristics such as soil type, disturbance (fire, etc.) and climate (Stohlgren et al. 1999).

In summary, we found that trajectories of vegetation composition were largely driven through management that alters the seral stage of the vegetation community. While cattle and elk grazing had variable effects on the diversity of some plant guilds, differences in their effects on exotic plant guilds were minor and confined to recently disturbed, i.e. thinned and burned, sites. Finally, cattle grazing did not have a substantially different effect on overall exotic plant species dynamics than elk grazing or grazing exclusion.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Taxonomic species and family, origin, life cycle, and life form of all plants sampled in the study.