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Interactive effects of fuels reduction and large herbivores on shrub assemblages in dry conifer forests of the interior west, USA

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A B S T R A C T

Deciduous shrubs are widely distributed throughout temperate and boreal conifer forests and influence a wide range of ecological processes and forest resources. In the interior western U.S., many deciduous shrubs are highly preferred forage by wild (elk, *Cervus canadensis*; deer, *Odocoileus* spp.) and domestic (cattle) ungulates which can influence shrub abundance, composition, structural characteristics, and related ecological processes and interactions. Stand disturbances and silvicultural practices can also affect shrub assemblages and managers in the interior western U.S. are increasingly implementing fuels reduction treatments such as stand thinning and prescribed fire to reduce fuel loads caused by more than a century of fire suppression. We evaluated the effects of ungulate herbivory and fuels reduction, alone and in concert, on deciduous shrub assemblages in coniferous dry forests of the interior west. We measured shrub richness, diversity, height, abundance and community composition in forest stands that underwent fuels reduction 15–17 years earlier, compared to untreated stands where no silvicultural treatments have occurred in over 50 years. Within each stand type, we also measured shrub assemblages in stands with and without ungulate herbivory. Shrub richness, diversity, frequency and height all declined in stands subjected to either fuels reduction treatments or herbivory; effects were most pronounced under the combined effect of fuels reduction and herbivory. Fuels reduction and herbivory also resulted in significant differences in shrub abundance and assemblage composition. Fuels reduction in dry forests with abundant ungulates may contribute to suppressed, more homogenous shrub communities. These effects may result in unintended impacts or alterations to important ecosystem processes and forest resources. Our results highlight the importance of considering responses of forest resources with low economic value, such as shrubs, in forest management activities.

1. Introduction

Deciduous woody species (shrubs) are a common and integral component of the understory of most conifer forests, and their abundance, richness and structure can influence a wide range of ecological processes and forest resources (Johnson and Clausnitzer, 1992; Moser and Witmer, 2000; Hagar, 2007a; Kleintjes Neff et al., 2007; Endress et al., 2012; Lilleeng et al., 2016). Deciduous shrubs and broadleaved trees make up a large proportion of plant diversity of temperate and boreal conifer forests, and their presence can influence soil fertility and nutrient cycling with the addition of high-quality litter to the soil as well as nitrogen fixation by some species (Hagar, 2007a). Shrubs also increase structural heterogeneity and complexity in the understory and lower canopy layers that promote high biodiversity (Niemi et al., 1998; Hagar, 2007a, 2007b; Rooney, 2001; Roberson et al., 2016). They support diverse food webs for insects, soil organisms, and wildlife including small mammals, birds, and bears by providing cover and food resources (e.g., leaves, roots, berries) that differ in composition from those provided by other vegetation (Berg, 2002; Hagar, 2007b; Briand et al., 2009). For wild and domestic ungulates such as elk, deer and cattle, shrubs are an important forage resource, particularly in late summer through winter, following senescence of herbaceous vegetation (Canon et al., 1987; Clark et al., 2013; Hegland and Rydgren, 2016).

Under certain conditions, ungulate herbivory can substantially reduce or eliminate the functional presence of highly preferred species, leaving behind fewer, less palatable shrubs on the landscape (Endress et al., 2012; Frerker et al., 2013; Endress et al., 2016; Lilleeng et al., 2016). Consequently, strong herbivore pressure is considered a major contributor to the decline of shrubs in temperate and boreal forests (Frerker et al., 2013; Endress et al., 2016; Hegland and Rydgren, 2016), resulting in changes to species composition and forest dynamics (Woodward et al.1994; Baker et al., 1997; White et al., 1998; Lilleeng et al., 2016; Kolstad et al., 2018). Ungulates may also affect the structural complexity of forest stands by altering shrub architecture and limiting heights below the browse line (height below which shrubs cannot escape heavy browsing pressure; Keigley et al., 2002), resulting in hedged or 'arrested' shrubs (Hester et al., 2000; Riggs et al., 2000; Beschta and Ripple, 2012; Endress et al., 2016). Herbivore-related suppression of the shrub layer can have cascading impacts on stand dynamics including: altered competitive interactions between plant

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species (Pastor et al., 1988; Randall and Walters, 2011); decreased reproductive potential and establishment of shrubs (Beschta and Ripple, 2008); modified understory shade and subsequent changes to understory herbaceous composition (Woodward et al., 1994); decreased structural complexity of the sub-canopy with related impacts to fauna (Hagar, 2007a) and invertebrates (Roberson et al., 2016; Lilleeng et al., 2018); and reduced fruit production that can have cascading effects across multiple trophic levels (Ripple et al., 2014). Growth of shrub species that are highly selected in the diets of ungulates can be suppressed to such a degree that even low herbivore densities may be sufficient to arrest growth below the browse line (Hester et al., 2000; Endress et al., 2016).

Fuels reduction treatments, including mechanical thinning and prescribed fire, can also affect shrub assemblages (Willms et al., 2017). Mechanical thinning and prescribed fire have generally been shown to reduce shrub abundance and cover in favor of herbaceous vegetation, at least in the short term (Curtis et al., 1998; Willms et al., 2017). Fuels reduction treatments, which usually involve combinations of stand thinning and prescribed fire, are common silvicultural practices in dry coniferous forests of the interior western U.S. Fuels reduction is one of the primary forest management goals of national forests in the western U.S., with plans for a significant increase in fuels reduction activities (e.g., Reinhardt et al., 2008; USDA Forest Service, 2018) because fuel loads in many dry conifer stands greatly exceed those of pre-European settlement, and constitute a major source of uncharacteristic stand-replacement fire events (Franklin and Agee, 2003; Hessburg et al., 2005). Despite the increase in fuels reduction efforts in recent years and plans to further increase their scale and scope, little is known about how such treatments affect shrub assemblage composition and structure.

Further complicating our understanding of shrub responses to forest management and herbivory is research indicating that these factors do not operate independently, but rather interact to further affect the shrub layer (Endress et al., 2012; Pekin et al., 2014; Endress et al., 2016). Fuels reduction generally includes clearing standing dead and downed wood, removing ladder fuels, burning after thinning, and increasing space between trees (Agee and Skinner, 2005). Elimination of such structures may suppress establishment, growth, and abundance of shrubs by removing physical barriers to ungulate access, such as standing dead and downed wood, that protect shrubs from ungulate browsing (Smit et al., 2006, 2012). Loss of structural components in the understory may also alter microsite conditions favorable to woody species establishment (Gray and Spies, 1997; Beschta and Ripple, 2007; Gómez-Aparicio et al., 2008). Moreover, disturbances such as prescribed fire and stand thinning can attract heavy use by large herbivores by increasing the quantity of highly preferred and nutritious vegetation following disturbance (Vavra et al., 2007). Therefore, a structurally-simplified understory combined with increased herbivore pressure may lead to drastically different shrub layer characteristics and dynamics, in turn affecting other ecological processes and forest resources. Research on this topic is limited, however, and most work has focused on particular shrub species (e.g. Endress et al., 2016) rather than community-level responses.

In this study, we evaluated the impacts of ungulate herbivory and fuels reduction treatments, two common disturbances in dry conifer forests of the interior western U.S., on shrub structure and composition. Specifically, we sought to determine how ungulate herbivory and fuels reduction treatments alone, and in combination, affect species richness, diversity, height, abundance and composition of shrub communities. Increased knowledge of the effects of ungulate herbivory and fuels reduction on shrub assemblages – an ecologically important resource in dry conifer forests – will inform land managers, restoration practitioners, and researchers regarding the potential use and management of these important disturbances and management tools to reach specific objectives. We hypothesized that both herbivory and fuels treatment activities would alter shrub composition and reduce shrub abundance, richness, diversity, and height, with the most pronounced effects in stands both fuels treated and exposed to ungulate herbivory.

2. Methods

2.1. Study area

Research was conducted within the 10,000 ha Starkey Experimental Forest and Range (SEFR) in the Blue Mountain Ecological Province of northeast Oregon. Elevations range from 1200 m to 1500 m above sea level. Precipitation averaged 510 mm annually, most of which occurred as winter snow or spring rain (Rowland et al., 1997). Late summer (July-August) is a period of predictably high temperatures, typically > 30° C, and sparse precipitation, often totaling < 20 mm and defined as drought most years (Prism Climate Group, 2014; National Oceanic and Atmospheric Administration, 2019). This climate supports drier montane conifer forest types typical of those in the interior western United States. Our research specifically focused on coniferous forest stands classified as dry forest potential vegetation types (Burcsu et al., 2014) dominated by overstories of Douglas fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*). Stands also included Ponderosa pine (*Pinus ponderosa*), western larch (*Larix occidentalis*), Englemann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta)* with varying degrees of overstory subdominance (Franklin and Dyrness, 1988).

Approximately 500 cow-calf pairs graze SEFR from mid-June to mid-October annually, with an additional 200 mule deer and 350 elk that occupied SEFR from April-November for the last 25 years (Endress et al., 2016). Ungulate densities for cattle (7.15/km^2), mule deer (1.95/km^2), and elk (4.55/km^2) were similar to those outside of SEFR (Wisdom and Thomas, 1996).

In the 1980s, an outbreak of western spruce budworm (*Choristoneura freemani*) defoliated the majority of the conifer stands in SEFR, killing most adult grand fir and Douglas-fir individuals, resulting in large amounts of standing dead and coarse woody debris (Bull et al., 2005). Fuels reduction treatments were applied to randomly selected stands between 2000 and 2003 (Long et al., 2008a) to reduce the amount of fire-hazard debris and research effects on forest recovery. Treated stands were mechanically thinned with a feller-buncher to meet a goal of < 35 tons/ha. Objectives were to leave live, fire resistant large trees (> 51 cm at diameter breast height) and maintain ≥18.4 m^2/ha basal area of standing trees. After thinning, stands were broadcast burned with hand drip torches. A total of 681 ha of forest were treated; 1474 ha of similar forest, also affected by the spruce budworm infestation, were left untreated (Long et al., 2008b).

As part of fuels reduction research in SEFR, six ungulate exclosures (~7 ha each) were constructed one year after fuels reduction. Three were located in fuels reduction areas and the other three were placed in untreated stands. Exclosures have a 2.4m tall fence that excludes elk, deer, and cattle but allowed other wildlife passage. Each exclosure was divided into seven one-hectare subplots that were used for ungulate herbivory research to study effects of no, low, moderate, and high densities of elk and cattle for seven years (Endress et al., 2012; Clark et al., 2013; Pekin et al., 2014; Endress et al., 2016). Since the seven-year study was completed (2012), the exclosures have been maintained, and no other ungulate herbivory or treatments have occurred for the past five or six years (depending on the exclosure).

2.2. Data collection

We sampled two levels of fuels treatment: (1) forest stands that had no silvicultural treatments or disturbance events in over 50 years (untreated); and (2) treated stands that underwent fuels reduction 15–17 years ago (2000–2003). We further sampled two levels of ungulate herbivory, extant (exposed to herbivory) and excluded (herbivores excluded). Extant herbivory consisted of contributions from all free-ranging cattle, elk, and deer within SEFR during spring-fall.

Ungulate use of the study area is extremely low during winter because most wild ungulates migrate to the SEFR winter range in late fall-early winter each year (Rowland et al., 1997), and cattle are removed in mid-October. Excluded herbivory treatments consisted of the six upland exclosures not grazed by ungulates since 2012. This design resulted in four treatments (Ungulates + Fuels Treatment, No Ungulates + Fuels Treatment, No Ungulates + No Fuels Treatment, Ungulates + No Fuels Treatment) and allowed us to evaluate shrub responses to the main effects (herbivory, fuels treatments) and their interaction.

Using a proportion allocation sampling design (Krebs, 1989), we randomly placed sampling plots within fuels treated and untreated areas proportional to the total area of each treatment (70:30 untreated to treated ratio) under extant herbivory. This design resulted in 109 plots in untreated stands and 58 in treated stands under extant herbivory. Sample plots were ≥50 m apart and ≥10 m from the stand edge (to minimize edge effects). Because the ungulate exclosures were smaller (~7 ha each), we used an alternative sampling approach. In this case, we used a stratified random sampling approach to place 21 plots within each exclosure (three plots within each of the original 1 ha subplots; ≥15 m from each other and ≥10 m from the edge). While legacy effects of the previous research were not evident (Endress and Averett, unpublished data), our stratified random sampling approach within the exclosures minimized any potential confounding effects. This resulted in samples sizes of 63 fuels reduction and 63 untreated excluded plots. Outside of the exclosures (plots exposed to herbivory) the average distance between plots was 4.5 km (1st and 3rd quartiles being 2.8 km and 6.6 km); inside the exclosures (no herbivory) the average distance between plots was 4.7 km (1st and 3rd quartiles being 0.9 km and 7.5 km).

Plots were located using a Trimble GeoXT GPS unit and sampled during late summer of 2016 or 2017. Plots were circular with a 7-meter radius (154 m^2) and divided into four subplots (each being a quadrant of the circular plot). Within each subplot, shrub species presence/absence was recorded, and plot-level abundance estimates for each species were calculated as the frequency for a particular species (proportion of subplots occupied) in a plot. We categorized shrubs into three different growth forms based on a species maximum height observed at SEFR: subshrub (< 0.5 m), shrub (0.5–3.0 m), or large shrub (> 3.0 m). Subshrubs were excluded from height measurements. For shrubs and large shrubs, the height of the tallest individual stem of each species in each plot was measured.

We removed 25 plots located in untreated forest stands under extant herbivory following data collection but prior to analyses because they occurred on slopes > 20%, and the fuels reduction treatments implemented within SEFR only occurred on forest stands with slopes less than 20%. Slope can have a large effect on site conditions and subsequent community composition and structure (Holechek et al., 1989), and therefore inclusion of these steep plots could potentially confound results when comparing treated and untreated plots. This resulted in the following sample sizes for analysis: N = 84 Untreated + Ungulates, N = 58 Treated + Ungulates, N = 63 Untreated + Ungulates Excluded and N = 63 Treated + Ungulates Excluded.

2.3. Data analysis

2.3.1. Effects on richness, diversity, height and frequency

We used generalized linear models (GLM) to test effects of fuels reduction and herbivory on species richness, diversity, and shrub layer height separately. Models for diversity and shrub layer height were fit with a normal distribution (link function = identity), while species richness data, which consisted of discrete counts, was fit with a negative binomial distribution (link function = log). We chose a negative binomial model because a Poisson regression model indicated evidence for over-dispersion in the data (the residual deviance divided by the degrees of freedom was > 1.0). All models included main effects and the interaction term (fuels reduction + ungulate herbivory). Richness was calculated by summing the total number of shrub species present within each plot. We used Shannon's Index to estimate diversity. Shrub height for each plot was calculated by averaging the maximum heights of all species present in the plot. Plot level height values were then log transformed to yield an approximately normal distribution. Statistical analyses were conducted in JMP Pro 13.0 (SAS Institute, Cary, NC, USA).

Effects of fuels reduction and herbivory on species abundance were analyzed using multiple logistic regression models (GLM; link function = logit) for the two most abundant species (one model for each species) within each of the three growth form categories: (1) bearberry (*Arctostaphylos uva-ursa* and birchleaf spirea (*Spiraea betulifolia*) for subshrubs (2) snowberry (*Symphoricarpos albus*) and rose (*Rosa* spp.) for small shrubs; and (3) serviceberry (*Amelanchier alnifolia*) and Scouler's willow (*Salix scouleriana*) for large shrubs. Species abundance (the proportion of subplots occupied per plot) was the response variable, and fuels reduction (Yes/No) and herbivory (Yes/No) were the predictors. Main effects and the two-way interaction were included in each model.

2.3.2. Effects on shrub community assemblages

We used global nonmetric multidimensional scaling (NMS; McCune and Grace, 2002) using PC-Ord 7 (McCune and Mefford, 2015) with a Sørensen (Bray-Curtis) distance measure to extract the dominant shrub assemblage compositional gradients. We used the NMS "slow and thorough" autopilot setting and penalty for ties in the distance matrix (Kruskal' strategy 2). Sørensen distance was used because we were interested in relative differences in species abundance between plots. We excluded rare species (occurring in < 10% of plots) to reduce extraneous noise associated with rarity and enhance any signal relating community composition to treatments (McCune and Grace, 2002). Outlier analysis identified ten plots as outliers (average Sørensen distance ranging from 2.2 to 5.2 standard deviations from the grand mean). Investigation of the outlier plots revealed that their species composition was consistent with true community variation in our sampling area and removal of the ten plots had little influence on the final ordination structure. Therefore, they were included in the analysis. Plots not occupied by shrubs were excluded from the analysis because calculation of Sørensen distance is not possible for sample units with zero values. Multivariate analyses were performed on a final matrix consisting of 250 plots by 15 species. The optimal dimensionality for the NMS ordination was evaluated in PC-Ord using a built in stress test that seeks to balance low stress with improving fit (McCune and Mefford, 2015). An additional dimension was considered for the final solution only if stress was reduced by 5 or more. Once the highest dimensionality was obtained where stress was reduced by at least 5, the final stress was evaluated using a randomization test where the final stress observed must be lower than 95% of the randomized runs. If the randomization criteria was not met, then a lower dimensional solution that meets the stress test criteria was selected (McCune and Mefford, 2015). NMS was run with a random starting configuration and a maximum of 500 iterations. Ordinations were rotated by orthogonal principal axes to load the greatest amount of variance on axis 1 while ensuring that axes 1 and 2 were independent of one another. A built-in randomization test was performed to determine if the final stress from the NMS ordination was lower than expected by chance.

To relate fuels reduction treatments, herbivory, and plot variables (slope, aspect, elevation) with shrub community variability, a second matrix containing these variables was overlaid onto the ordination space using joint plots. Pearson product-moment correlation coefficients (r) and Kendall's rank correlations (tau) between those variables and the ordination axes were calculated. Slope, aspect, and elevation were calculated for each plot from a 30m resolution digital elevation model (US Geological Survey 2006) in ArcGIS 10.3. Aspect values were folded from NE (minimum) to SW (maximum; McCune and Keon, 2002).

Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was used (McCune and Mefford, 2015) with a two-way factorial design to test for differences in shrub assemblage composition as a function of our experimental treatments (fuels reduction, herbivory, and their interaction). To evaluate the degree to which our data was spatially autocorrelated, we conducted a non-parametric partial Mantel test which tested the association between species composition and location while controlling for herbivory treatment, fuels reduction treatments, slope and aspect using PC-ORD 7.0 (McCune and Mefford, 2015).

Indicator species analysis (ISA; Mielke, 1984) was used (McCune and Mefford, 2015) to generate indicator values (IV), which identified species most indicative of different treatments. Indicator values are based on both relative frequency (proportion of plots in each group that contained the species of interest) and relative abundance (proportional abundance of a particular species in a group relative to its abundance in all groups) of species and represent the strength of tendencies for species to occur within specific groups. IVs range from zero (not an indicator) to 100 (perfect indicator, i.e., the species is only and always found in that group; McCune and Grace, 2002); Significance of IV's were determined by comparing observed values to results from 10,000 randomizations (McCune and Mefford, 2015).

3. Results

3.1. Richness, diversity, height and abundance

We identified 31 shrub species in our plots (S1). Both fuels reduction and herbivory significantly decreased shrub richness ($p < 0.001$; Fig. 1, Table 1). Untreated stands without herbivory averaged 9.5 species per plot (SD = 2.6), while untreated stands exposed to herbivores averaged 6.9 species per plot (SD = 3.3). Species richness in fuels treated stands was lower than in untreated stands; treated areas without herbivory averaged 8.0 species per plot (SD = 2.33) compared with fuels treated areas exposed to herbivory that averaged 4.5 species per plot (SD = 3.44). A significant interaction was found ($p = 0.019$; Fig. 1, Table 1), with effects most pronounced in fuels treated stands exposed to herbivores.

Shrub diversity declined significantly in response to both fuels treatment and ungulate herbivory ($p < 0.001$; Table 1). We found a significant fuels reduction treatment + herbivory interaction ($p = 0.012$), with plots exposed to both herbivory and fuels reduction being the least diverse (Table 1, Fig. 1). We also found a significant interaction between fuels treatments and herbivory on shrub layer height ($p = 0.016$; Table 1, Fig. 1). Height in untreated stands with no herbivory averaged 112 cm in height, in contrast to 68 cm in untreated stands exposed to ungulates. Further reductions in height occurred in fuels treated stands, with lowest mean height of the shrub layer in fuels treated stands exposed to herbivores (mean = 49 cm). By contrast, mean height of the shrub layer in fuels treated stands without herbivory was 106 cm.

Table 1
Results from generalized linear models for the effects of ungulate herbivory (yes/no) and fuels reduction treatments (yes/no), and their interactions on species richness, diversity (Shannon-Wiener), and mean shrub height (log transformed).

	Estimate	SE	p
Richness			
Fuels treated	−0.176	0.048	< 0.0001
Herbivory	−0.325	0.068	< 0.0001
Fuels treated * Herbivory	−0.254	0.109	0.0192
Diversity			
Fuels treated	−0.174	0.035	< 0.0001
Herbivory	−0.290	0.035	< 0.0001
Fuels treated * Herbivory	−0.088	0.035	0.012
Height			
Fuels treated	−0.257	0.023	< 0.0001
Herbivory	−0.141	0.023	< 0.0001
Fuels treated * Herbivory	−0.089	0.023	0.0157

Size class distributions of shrubs varied strongly among the treatments (Fig. 2). In particular, we found a greater proportion of large shrubs (e.g., *S. scouleriana*, *A. alnifolia*) > 2.5 m in height in plots where herbivores were excluded (Fig. 2): in untreated stands with ungulates excluded, 37.7% of large shrubs were > 2.5 m in height, while just 3.8% of shrubs were > 2.5 m in height in untreated stands exposed to herbivores. We found similar results in fuels treated sites: 26.7% of large shrubs were > 2.5 m in height with ungulate exclusion versus 10% with ungulates present.

Treatment effects on shrub abundance varied, but all species showed significant treatment effects (Tables 2 and 3, Fig. 3). Herbivory decreased the abundance of *A. uva-ursi* by 29–38%. The herbivory + fuels treatment interaction was significant, with declines greatest in fuels treated stands (p = 0.0129; Table 2, Fig. 3). Herbivory

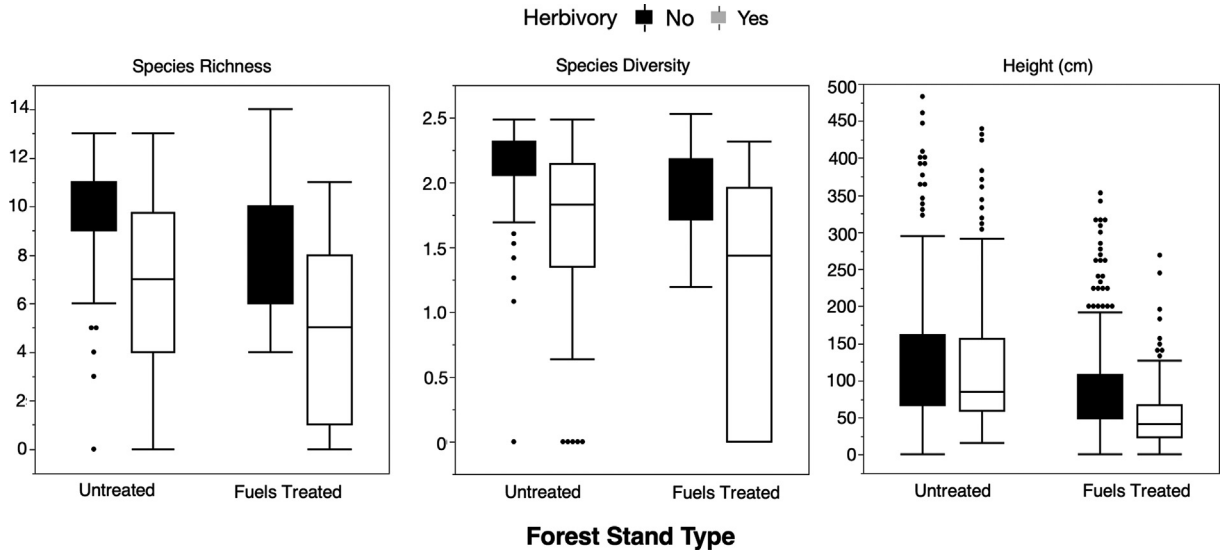

Fig. 1. Box plots: mean (±1.5 × interquartile range) of species richness, diversity (Shannon-Wiener Index H'), and shrub layer height across untreated and fuels treated plots (x-axis) with absence (black) or presence (gray) of ungulate herbivory.

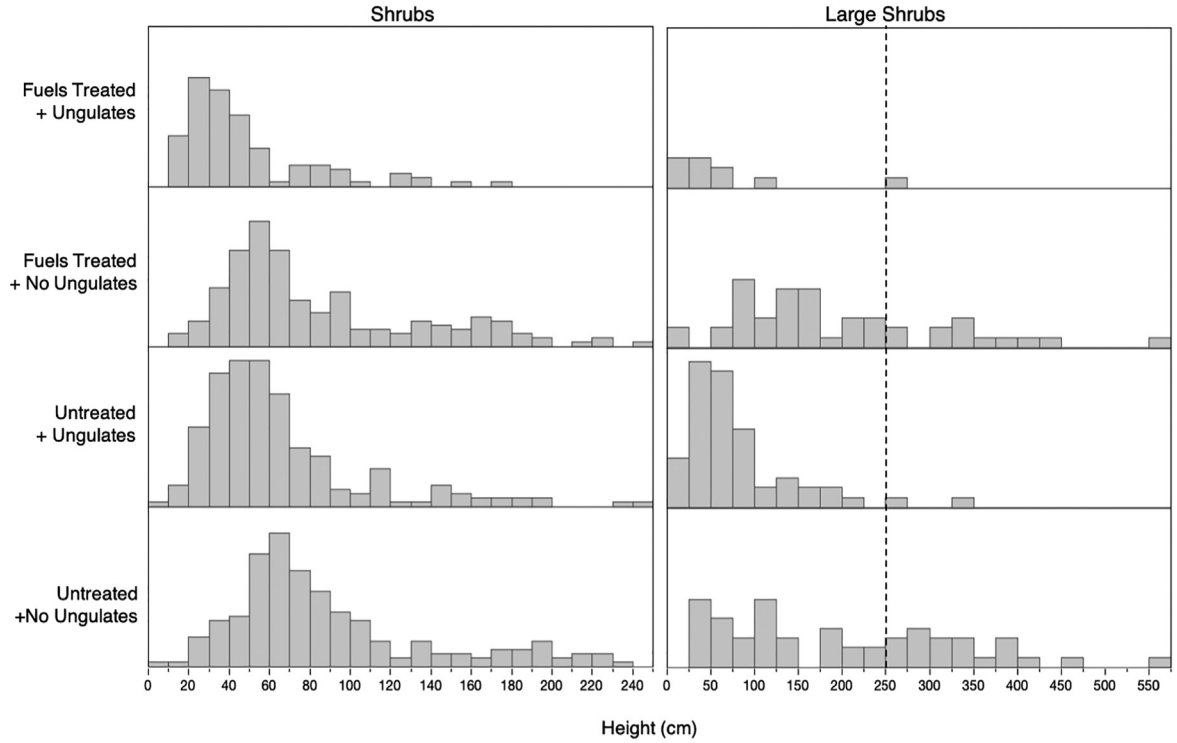

Fig. 2. Size class distributions of shrubs (0.5–3 m in height) and large shrubs (potential to grow > 3 m) within the four treatment combinations. The dashed line represents the browse line for ungulates (250 cm).

Table 2
Summary of logistic regression models of the effects of ungulate herbivory (yes/no) and fuels reduction treatments (yes/no) on shrub frequency for the two most common species in each shrub size class. *P* values < 0.05 are in bold.

	Estimate	SE	X^2	*p*
Subshurbs				
Arctostaphylus uva-ursi				
Fuels treated	0.4442	0.1316	12.15	**0.0005**
Herbivory	−0.9674	0.1355	59.12	**0.0001**
Fuels treated * Herbivory	0.3181	0.1315	6.19	**0.0129**
Spiraea betulifolia				
Fuels treated	−0.3535	0.1134	9.77	**0.0018**
Herbivory	−0.0080	0.1126	0.01	0.9433
Fuels treated * Herbivory	0.2150	0.1129	3.50	0.0614
Shrubs				
Symphoricarpos albus				
Fuels treated	−0.3143	0.1125	7.89	**0.005**
Herbivory	0.0198	0.1117	0.03	0.8595
Fuels treated * Herbivory	0.5401	0.1144	22.98	**0.0001**
Rosa spp.				
Fuels treated	−0.6874	0.1134	22.43	**0.0001**
Herbivory	−0.5232	0.1105	0.383	0.5356
Fuels treated * Herbivory	0.2044	0.1108	3.39	0.0655
Large shrubs				
Salix scouleriana				
Fuels treated	0.6875	0.2188	10.0	**0.0015**
Herbivory	−0.6597	0.2188	9.26	**0.0023**
Fuels treated * Herbivory	0.3756	0.2187	2.92	0.0876
Amelanchier alnifolia				
Fuels treated	−1.1212	0.1765	55.92	**0.0001**
Herbivory	−0.3240	0.1748	3.756	**0.0439**
Fuels treated * Herbivory	0.1472	0.1748	0.743	0.3888

had no effect on abundance of *S. betulifolia*, but *S. betulifolia* abundance was lower in fuels treated stands compared to untreated stands (p = 0.005; Tables 2 and 3). For *Rosa* spp., we found a weak interactive effect, with reduced abundance in fuels treated plots (Tables 2 and 3). A similar trend was found for snowberry (*S. albus*), with lower abundance in fuels treated plots exposed to herbivores. In the absence of herbivores, we found greater snowberry abundances in fuels treated plots. For the large shrub *A. alnifolia*, both herbivory and fuels treatment reduced shrub abundance, but no interaction was found (Table 2, Fig. 3). A statistically weak interaction term was found for *S. scouleriana* (p = 0.0876), and its abundance increased with fuels reduction in the absence of herbivory (Tables 2 & 3, Fig. 3).

3.2. Shrub assemblage responses

Fuels reduction (PERMANOVA, $F_{[2,44]} = 13.17$, $p < 0.001$) and herbivory ($F_{(2,44)} = 14.25$, $p < 0.001$) both impacted shrub assemblage composition. We found evidence for a weak interactive effect of fuels treatment and herbivory on composition ($p = 0.071$).

The NMS ordination yielded a three-dimensional stable solution that explained 86.7% of variation in the distance matrix (final stress = 14.69, randomization test, $p = 0.004$). Axis 1 explained 42% of variation and was positively associated with herbivory (Fig. 4). Slope, aspect, elevation and fuels treatments were poorly correlated with axis 1 (Fig. 4, Table 4). Ordered by decreasing strength, *Linnaea borealis* ($r = -0.75$), *Vaccinium scoparium* ($r = -0.66$), *Vaccinium membranaceum* ($r = -0.56$), *A. uva-ursi* (−0.53), and *Chimaphila umbellata* ($r = -0.43$) had the strongest negative correlations with axis 1, indicating negative associations between abundance of these species and plots subjected to ungulate herbivory (Table 4, Fig. 4). *Symphoricarpos albus* was the only species that was positively correlated with axis 1 ($r = 0.40$), indicating increased abundance in plots with ungulate herbivory (Table 4, Fig. 4).

Axis 2 explained 25% of variation and was positively associated with fuels treatment (r = 0.45; Fig. 3). Slope, aspect, elevation and herbivory treatments were poorly correlated with axis 2 (Fig. 4, Table 4). Species most positively correlated to axis 2, which indicated higher abundances in fuels treated areas, included *A. uva-ursi*

Table 3
Frequency (% of plots occupied) of common shrub species in sampled forest stands across four treatments: fuels treatment with and without ungulate herbivory and untreated plots with and without ungulate herbivory. The difference in frequency between no herbivory and herbivory treatments is also included.

	Fuels treated			Untreated		
	No herbivory	Herbivory	Difference	No Herbivory	Herbivory	Difference
Subshrubs						
Arctostaphylus uva-ursi	100	62.1	−37.9	92.1	63.1	−29
Chimaphila umbellata	33.3	8.6	−24.7	42.9	31	−11.9
Linnaea borealis	52.4	15.5	−36.9	90.5	38.1	−52.4
Mahonia repens	84.1	43.1	−41.0	84.1	71.4	−12.7
Paxistima myrsinites	27.0	13.8	−13.2	28.6	9.5	−19
Spiraea betulifolia	73.0	55.2	−17.8	77.8	81	3.2
Vaccinium membranaceum	34.9	27.6	−7.3	60.3	45.2	−15.1
Vaccinium scoparium	39.7	15.5	−24.2	74.6	28.6	−46
Shrubs						
Ceanothus velutinus	44.4	25.9	−18.6	17.5	2.4	−15.1
Symphoricarpus albus	88.9	63.8	−25.1	82.5	89.3	6.7
Ribes cereum	50.8	25.9	−24.9	47.6	28.6	−19
Ribes lacustre	4.8	6.9	2.1	49.2	22.6	−26.6
Rosa spp.	88.9	58.6	−30.3	88.9	84.5	−4.4
Large shrubs						
Amelanchier alnifolia	15.9	6.9	−9	54	48.8	−5.2
Salix scouleriana	41.3	8.6	−32.6	7.9	4.8	−3.2

(r = 0.50), *Ceanothus velutinus* (r = 0.40) and *Ribes cereum* (r = 0.20; Table 4). All other species were negatively correlated with axis 2, indicating decreasing abundances associated with fuel treatments. Axis 3 explained little variation in the distance matrix (r = 0.20) and had low correlations with the treatments or other measured variables (slope, elevation, aspect). Spatial proximity had little effect on species composition when accounting for treatments (herbivory, fuels reduction), slope and aspect (partial Mantel test; r = 0.07).

Nine shrub species showed significant affinities to untreated forest stands where ungulates have been excluded, including subshrubs (e.g., *L. borealis*, *V. scoparium*), shrubs (e.g., *Ribes lacustre*, *V. membranaceum*) and one large shrub (*A. alnifolia*; Table 5). Only one species, *S. albus*, showed an affinity to untreated stands exposed to ungulates. In fuels treatment stands, Indicator Species Analysis did not identify any species that showed an affinity to the treated + herbivory treatment, while *A. uva-ursi* (IV = 32.7), *S. scouleriana* (IV = 28.5) and *C. velutinus* (IV = 18.9) were all associated with fuels treated stands with ungulate exclusion.

Herbivory reduced the abundance of most shrub species in both fuels treated and control plots, affecting highly abundant generalist species (e.g., *A. uva-ursi* and *L. borealis*) as well as less frequently sampled species such as *S. scouleriana* and *R. lacustre* (Tables 3–5). Among the shrub layer groups, subshrubs were affected most (Tables 3 and 4). *Mahonia repens, A. uva-ursi, L. borealis,* and *V. scoparium* abundances were lowest with herbivory (Table 3). *Linnaea borealis* was found in nearly every untreated plot without herbivory (occurred in 91% of plots), but was much less frequent in untreated plots with herbivory (38%) and with fuels treatment (16% with herbivory and 52% without herbivory; Table 3). Disturbance-dependent species including *S. scouleriana, C. velutinus,* and *A. uva-ursi* were more frequent in areas with fuels reduction, but only in the absence of herbivory (Tables 3 and 4).

4. Discussion

Our results illustrate the effects of fuels treatments and ungulate herbivory on shrub assemblages in dry coniferous forest vegetation types that commonly occur in the interior western U.S. We found support for our hypotheses that species richness, diversity, frequency and height of most shrubs were substantially reduced in fuels treated areas with and without herbivory. Effects were strongest under the combined effects of fuels treatments and herbivory, resulting in large differences in composition of shrub assemblages among treatment combinations.

4.1. Untreated forest stands

The substantially lower shrub height, richness, diversity and abundance within untreated forest stands exposed to herbivory by cattle, elk, and deer highlight the importance of ungulates in regulating shrub assemblages and influencing forest understory conditions. This top-down regulation by ungulates resulted in simplified shrub assemblages and reduced shrub richness and diversity. All but one species declined in abundance within untreated stands exposed to herbivory. The large number (nine) of shrub species that showed an affinity to untreated stands without ungulates highlights their role in regulating shrub assemblage composition. Effects were fairly consistent across shrub size classes, from subshrubs (e.g. *L. borealis*) to large shrubs (*A. alnifolia*).

Reductions in shrub height and/or abundance were not just restricted to species preferred by ungulates for forage. While declines were noted for preferred browse species such as serviceberry (*A. alnifolia*) and twinflower (*L. borealis*), declines were also observed in less preferred species (e.g. *M. repens*) (Hayes and Garrison, 1960; Riggs et al., 2000). It is possible that chronically high browse pressure by ungulates over many years in our study area has reduced the abundance of more preferred species to such a degree that ungulates targeted less preferred species (Frerker et al., 2013). Ungulate trampling has also been shown to affect shrub assemblages elsewhere (Rauzi and Smith, 1973; Singer and Schoenecker, 2003) and may also help explain these findings. The majority of species showing declines in response to herbivory were subshrubs. The short-statured, often prostrate form of many of these species makes them particularly susceptible to trampling. Subshrub species (e.g. *L. borealis, Paxistima myrsinites*) showed some of the strongest negative responses (in terms of abundance) to the presence of herbivores, but many less preferred and unpalatable species (e.g. *M. repens, C. umbellata*) also showed similar negative responses. Alternatively, selective herbivory may have altered competitive interactions among understory plant species that negatively affected subshrub growth and abundance. Research is needed to further evaluate direct effects of ungulates on subshrub abundance through consumption or trampling versus indirect effects by altering competitive interactions among shrub species.

Only one species, snowberry (*S. albus*), responded positively to herbivory within untreated stands. Snowberry abundance increased despite its importance as a browse species for cattle, elk, and deer

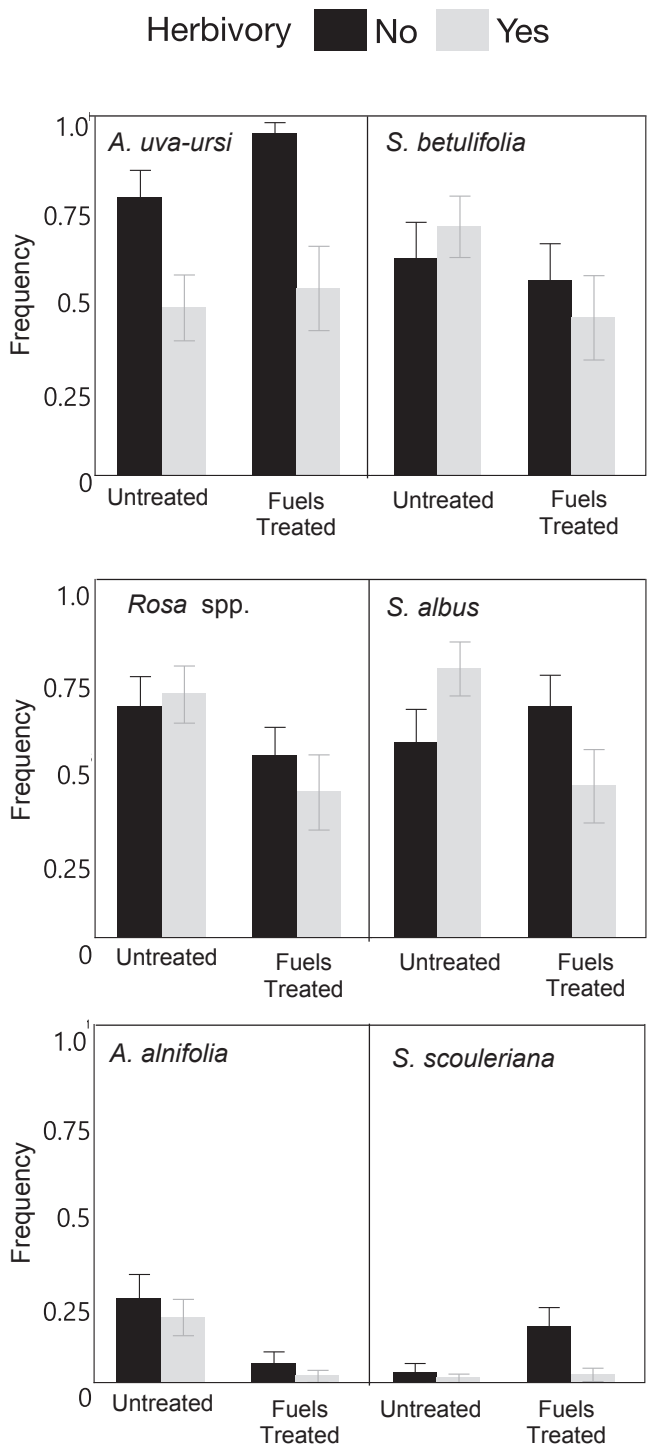

Fig. 3. Mean abundance (± SE) of the two most abundant subshrubs (*Arctostaphylos uva-ursi*, *Spiraea betulifolia*), shrubs (*Rosa* spp., *Symphoricarpos albus*) and large shrubs (*Amelanchier alnifolia*, *Salix scouleriana*) under the four herbivory-fuels reduction treatment combinations.

(Johnson, 1993; Clark et al., 2013). Snowberry is a clonal species, able to regenerate via rhizomes, and is considered resilient to browse by ungulates (Coates and Haeussler, 1986). The ability to rapidly regenerate in combination with the large declines in other shrub species, which may act as competitors for resources and space, may explain the increased abundance of snowberry in untreated forest stands exposed to herbivores.

4.2. Fuels reduction stands

We documented the individual and combined effects of fuels reduction and herbivory, each of which reduced species richness, diversity, frequency, and height of the shrub community. Fuels reduction resulted in a sparse shrub layer. The combined effect of fuels treatments and herbivory had the greatest impacts. Shrubs were shorter and less abundant in fuels treated stands regardless of herbivory, and species composition differed substantially between fuels treated and untreated stands, which is particularly notable given the long period of 15–17 years following treatment application. These long-term effects indicate that shrub layer recovery following fuels treatments is slow, and stands either require a much longer recovery period following treatment, or that fuels reduction alters the successional trajectory of these stands. With either scenario, the reduced shrub abundance and height may reduce the availability of late season forage for domestic and wild ungulates, affect wildlife habitat, and has the potential to alter a range of ecological patterns and processes in these forest stands. Other ecological effects may occur in ways not easily recognized. For example, it has been hypothesized that the abundance of shrubs may affect conifer seedling recruitment, and that observed high density of conifer seedlings following fuels treatments may partially be due to the lack of competition from shrubs and other understory vegetation when herbivory pressure is high (Wisdom et al., 2006).

Episodic disturbance such as fuels treatments can facilitate the recruitment of shrub species (Irwin and Peek, 1983). Indeed, several species within SEFR recruit readily following fire, such as *Populus balsamifera*, *S. scouleriana*, *A. uva-ursi*, and *C. velutinus*. These species had their highest frequencies in fuels treated plots when ungulates were excluded, but were substantially suppressed in abundance and height when exposed to ungulates. The large difference in abundance of these species among herbivory treatments following fuels reduction is likely because these species are highly preferred by ungulates and relatively rare across SEFR (Vavra et al., 2007; Endress et al., 2012; Endress et al., 2016). Moreover, fuels reduction treatments also eliminate understory structural elements such as downed logs, coarse woody debris, and conifer saplings that can act as physical barriers to protect some shrub species from ungulate herbivory (Beschta and Ripple, 2007; Smit et al., 2012; Hall Defrees, 2017). These structural elements may also provide favorable microsites that support shrub establishment (Gray and Spies, 1997; Gómez-Aparicio et al., 2008). Loss of such structural elements may have made recruiting shrubs more accessible to ungulate herbivory as well as influenced site conditions for shrub recruitment in our study area.

4.3. Ungulate herbivores in forest ecosystems

Our findings are consistent with a myriad of research on the effects of ungulate herbivory on deciduous woody species across temperate and boreal forests (Rooney, 2001; Côté et al., 2004; Kribel et al., 2011; Rooney, 2009; Bernes et al., 2018). These studies have documented changes in stand composition due to the suppression of existing shrubs and a lack of regeneration due to herbivory, thereby altering forest stand structure, diversity, and species composition. While analyses of community-level effects of herbivory have not been well studied in forests of the interior western U.S., our findings are consistent with previous studies in dry forests in the region that focused on individual species responses to ungulates (Riggs et al., 2000; Vavra et al., 2007; Endress et al., 2012; 2016).

High levels of ungulate herbivory that result in a sparse, species-poor shrub layer have implications for a number of ecological processes and other forest resources. For example, high levels of browse may contribute to reductions in important late-season forage resources for both wild and domestic ungulates whose diets converge on shrubs following the senescence of herbaceous vegetation. Late summer is a critical period for lactating female ungulates that depend on shrubs as a

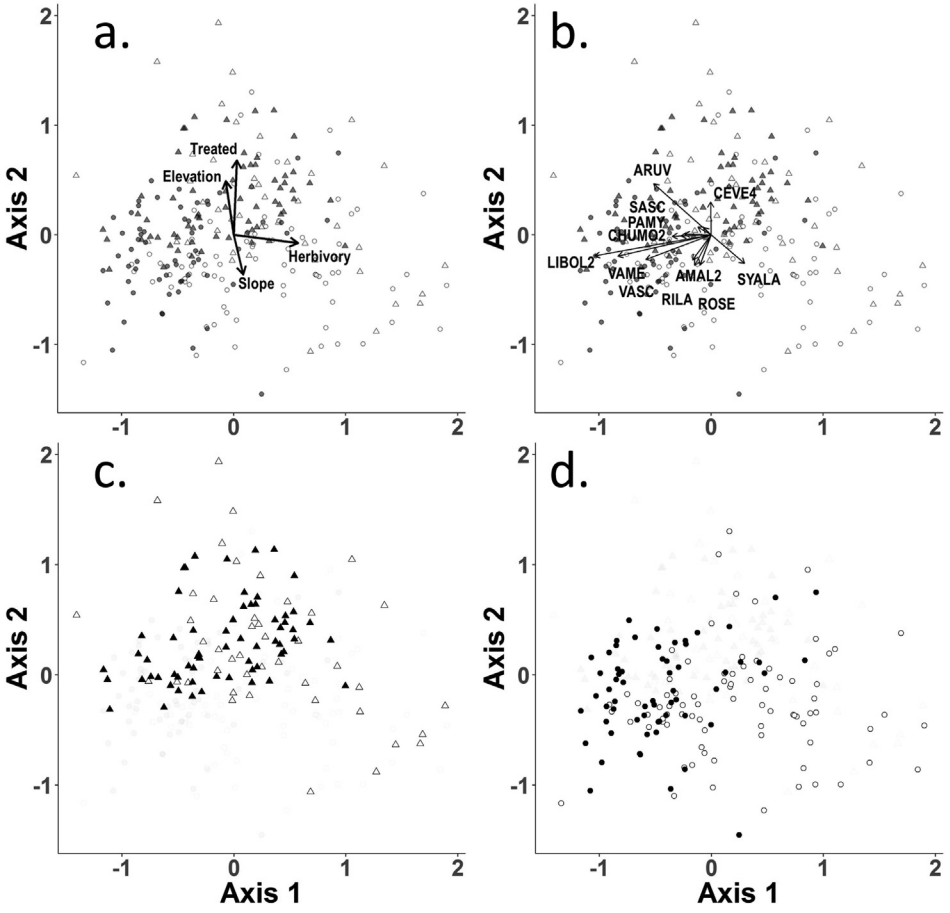

Fig. 4. (a) Ordination joint plot with experimental (herbivory, treated) and environmental variables (slope, aspect) overlaid; (b) ordination joint plot with species abundances overlaid. Vectors show direction and magnitude (length) of linear correlations between ordination axes and environmental/species abundance variables. Triangles indicate fuels treated plots, circles indicate plots with no fuels treatment. Black symbols are plots with no herbivory, and white symbols are plots exposed to herbivory. Species codes are as follows: AMAL2, *Amelanchier alnifolia;* ARUV, *Arctostaphylos uva-ursi*; CEVE4, *Ceanothus velutinus;* CHUMO2, *Chimaphila umbellata;* LIBOL2, *Linnaea borealis;* MARE11, *Mahonia repens;* PAMY, *Paxistima myrsinites;* RICEC2, *Ribes cereum;* RILA, *Ribes lacustre;* ROSE, *Rosa* spp.; SASC, *Salix scouleriana*; SYALA, *Symphoricarpos albus*; VAME, *Vaccinium membranaceum;* and VASC, *Vaccinium scoparium.* (c) ordination showing distribution of fuels treated plots with and without ungulate herbivory in species space; (d) ordination showing distribution of non-fuels treated plots with and without ungulate herbivory.

Table 4
Shrub species and environmental correlations (*r* and Kendall's tau) with Axis 1 and Axis 2 of the NMS ordination. Axis 1 was mostly highly correlated to herbivory ($r = 0.42$) and Axis 2 is most correlated with fuels reduction treatment ($r = 0.45$). Correlations ≥ 0.4 are in bold. The negative (−) indicates a negative correlation between species/environmental variables and Axis 1 and Axis 2.

Species	Axis 1		Axis 2	
	r	*tau*	*r*	*tau*
Subshrubs				
Arctostaphylus uva-ursi	**−0.53**	−0.32	**0.50**	0.35
Chimaphila umbellata	**−0.43**	−0.38	−0.08	−0.06
Linnaea borealis	**−0.75**	**−0.65**	−0.32	−0.25
Mahonia repens	−0.36	−0.25	0.06	0.10
Paxistima myrsinites	−0.38	−0.30	−0.06	−0.04
Spiraea betulifolia	−0.08	−0.00	0.16	0.10
Vaccinium membranaceum	**−0.56**	**−0.49**	−0.35	−0.29
Vaccinium scoparium	**−0.66**	**−0.58**	−0.32	−0.27
Shrubs				
Ceanothus velutinus	−0.05	−0.04	**0.40**	0.37
Ribes cereum	−0.25	−0.22	0.20	0.11
Rosa spp.	−0.23	−0.20	−0.38	−0.36
Symphoricarpus albus	**0.40**	0.31	−0.37	−0.26
Large shrubs				
Amelanchier alnifolia	−0.30	−0.26	−0.35	−0.29
Salix scouleriana	−0.19	−0.19	0.19	0.15
Environmental variables				
Herbivory	**0.42**	0.34	−0.15	−0.18
Fuels treated	0.09	0.09	**0.45**	0.39
Aspect	0.07	0.05	−0.14	−0.10
Elevation	−0.15	−0.05	0.39	0.25
Slope	0.16	0.10	−0.33	−0.24

Table 5
Indicator Species Analysis showing species frequency (percent of plots present) and abundance (mean proportion of subplots occupied) within each of the four treatment combinations and indicator values and p-values for species with the strongest IV's for each treatment.

	Frequency	Abundance	IV	*p*
Fuels Treated + No Herbivory				
Arctostaphylos uva-ursi	100	95.2	32.7	0.0002
Salix scouleriana	41.3	15.5	28.5	0.0002
Ceanothus velutinus	44.4	22.6	18.9	0.002
Fuels Treated + Herbivory				
None				
Untreated + No Herbivory				
Linnaea borealis	90.1	78.6	46.1	0.0002
Vaccinium scoparium	74.6	54.8	37.8	0.0002
Ribes lacustre	49.2	22.6	30.5	0.0002
Mahonia repens	84.2	67.5	27.6	0.005
Amelanchier alnifolia	54.0	23.4	26.1	0.0002
Vaccinium membranaceum	60.3	40.1	22.4	0.0062
Ribes cereum	47.6	22.6	17.0	0.086
Chimaphila umbellata	42.9	21.8	15.5	0.0494
Paxistima myrsinites	28.6	23.0	11.4	0.0668
Untreated + Herbivory				
Symphoricarpus albus	89.5	75.0	28.5	0.004

primary food source following senescence of grasses and forbs (Findholt et al., 2004). Reductions in the shrub layer can also reduce available habitat for a host of wildlife (Hagar, 2007a, 2007b), and many of the shrub species that responded negatively to the individual and combined effects of herbivory and fuels reduction treatments (e.g. *A. alnifolia*, *V. membranaceum*, and *V. scoparium*) are pollinated by insects and/or produce nutritious fleshy fruits consumed by small mammals, birds,

and other wildlife. The reduction and or elimination of these species from stands reduces available floral and fruit resources that may alter food web interactions. Additionally, where large ungulate densities are high, declines in shrub community richness, diversity and abundance in upland forests may further exacerbate pressure on deciduous woody species in adjacent, high priority conservation habitats, such as riparian areas and lowland meadows, which may already be exposed to high levels of herbivory (Kay, 1994; Averett et al., 2017).

It must be noted that while we found clear and strong impacts of fuels reduction and herbivory on the shrub layer, responses may vary across stands depending on site conditions, productivity, precipitation, ungulate densities, and the method of fuels reduction. Shrub layer composition, growth rates, recruitment, development (e.g., potential for growth to overcompensate for browsing effects), and response to herbivory will vary depending on environmental conditions in addition to ungulate diet selection and browse pressure which varies in space and time depending on plant community composition, forage availability and ungulate density and distribution (Hofmann, 1989; Endress et al., 2016). For example, shrub assemblages on more productive or mesic sites may have increased capacity to withstand high levels of ungulate herbivory, while drier forest or more marginal forest stands may have lower resistance and resiliency to herbivory. In general, we expect that the effects of herbivory and fuels reduction treatments on shrub assemblages will be greater in drier, less productive forest stands because of less favorable conditions for shrub establishment and recovery. Moreover, this research assessed ungulate herbivory as a binary response (yes/no). In reality, herbivore density varies both spatially and temporally, and across dry forests of the interior west, U.S.; there are few, if any, forests that are not exposed to some level of wild or domestic herbivory. Our findings highlight herbivore impacts on shrub assemblages, yet future research should focus on understanding how effects vary along a gradient of herbivore pressure. In addition, future research understanding how herbivory and fuels reduction influence shrub assemblages across the spectrum of dry, moist, and wet forest types would greatly inform our understanding on herbivore effects across forest types. Similarly, shrub responses may vary with different methods of fuels reduction. In our case, we evaluated the combination of mechanical treatments and broadcast burning, which is just one of many techniques to reduce forest fuels. Other approaches will likely affect the magnitude of fuels reduction impacts on deciduous woody plants.

5. Conclusion

Ungulate herbivory and fuels reduction treatments are common disturbances in dry forests of the interior western U.S. Impacts of these disturbances on the understory shrub community and associated ecological processes and values are rarely considered. Our study is one of the first to evaluate community-level responses of shrub assemblages to fuels reduction treatments and ungulate herbivory in dry coniferous forest types. Findings revealed that ungulate herbivory and fuels reduction activities, alone and in concert, can results in long-term substantial shifts in shrub diversity, composition and structure, and that the individual and joint effects of fuels reduction and ungulate herbivory should be important considerations for management actions in dry conifer forests if compositionally and structurally diverse shrub communities are desired.

CRediT authorship contribution statement

Dallas Hall Defrees: Conceptualization, Investigation, Methodology, Writing - original draft. **Joshua P. Averett:** Data curation, Methodology, Writing - review & editing. **Michael J. Wisdom:** Conceptualization, Writing - review & editing. **Bryan A. Endress:** Conceptualization, Investigation, Project administration, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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