

## ARTICLE

# Long-term frequent fire and cattle grazing alter dry forest understory vegetation

Becky K. Kerns<sup>1</sup>  | Michelle A. Day<sup>2</sup><sup>1</sup>USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA<sup>2</sup>USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA**Correspondence**

Becky K. Kerns

Email: [becky.kerns@usda.gov](mailto:becky.kerns@usda.gov)**Funding information**

Joint Fire Science Program, Grant/Award Number: Project ID 12-1-01-10

**Handling Editor:** Sharon M. Hood**Abstract**

Understanding fire and large herbivore interactions in interior western forests is critical, owing to the extensive and widespread co-occurrence of these two disturbance types and multiple present and future implications for forest resilience, conservation and restoration. However, manipulative studies focused on interactions and outcomes associated with these two disturbances are rare in forested rangelands. We investigated understory vegetation response to 5-year spring and fall prescribed fire and domestic cattle grazing exclusion in ponderosa pine stands and reported long-term responses, almost two decades after the first entry fires. In fall burn areas open to cattle grazing, total understory cover prior to utilization was about 12% lower compared with fall burn areas where cattle were experimentally excluded. This response was not strongly driven by a particular palatable or unpalatable plant functional group. Fire and grazing are likely interacting in a numerically mediated process, as we found little evidence to support a functionally moderated pathway. Post-fire green-up may equalize forage to a certain extent and concentrate herbivores in the smaller burned areas within pastures, constraining a positive understory response to burning. Fall fire and grazing also increased annual forbs and resprouting shrubs. The effects of spring burning were relatively minor, and we found no interaction with grazing. The nonnative annual grass *Bromus tectorum* (cheatgrass) remains a problematic invader linked to fall burning but not grazing in stands that had higher propagule pressure when the experiment was initiated. At these sites, exotic grass was a major component of the vegetation by 2015, and invasion was also increasing in spring burn and unburned areas. Information from our study suggests that frequent fall fires and cattle grazing combined may reduce understory resilience in similar dry ponderosa pine forests. Consideration of longer fire return intervals, resting areas after fire, virtual fencing, or burning entire pastures may help to mitigate the effects noted in this study.

**KEYWORDS**cattle grazing, disturbance interactions, functional traits, *Pinus ponderosa*, planned fire, plant community, ponderosa pine, post-fire, prescribed fire, restoration, vegetation

## INTRODUCTION

Large mammalian herbivory and fire are two fundamental ecological processes that strongly influence ecosystem patterns and regulate function across the globe (Bond et al., 2005; He et al., 2019; Malhi et al., 2016; Smith et al., 2016). Herbivory is a chronic disturbance resulting in the selective removal of palatable plant parts throughout the grazing season, a process governed by a complex variety of factors (Courant & Fortin, 2010; Farnsworth & Illius, 1998; Fortin et al., 2015; Milchunas & Lauenroth, 1993; Senft et al., 1987). Large mammals can also indirectly alter plant communities through other mechanisms such as trampling, the addition of nutrients from urine, soil compaction and erosion, and changes in biotic processes (Hambäck & Beckerman, 2003; Heggenes et al., 2017; Sitters et al., 2017; Trlica & Rittenhouse, 1993). Fire is an episodic disturbance that can directly kill plants or damage above-ground and below-ground tissue and structures, and also indirectly alter biotic processes (e.g., competition, germination) and abiotic conditions (light environment, soil exposure, nutrient availability) (Bowman et al., 2009; DeBano et al., 1998; Holland et al., 2017; Lentile et al., 2007; Romme et al., 2011; Stephan et al., 2010). While fire and grazing share some similarities as consumers of plant material and top-down drivers that regulate ecosystem function, they are dissimilar processes (Spasojevic et al., 2010). For example, fire has no dietary preference, although flammability is key (Bond & Keeley, 2005; Cardoso et al., 2018).

Plant communities can vary in their resilience (the ability of a vegetation community to recover or adapt following disturbance; Falk et al., 2022) to disturbances such as fire and grazing. The dry coniferous forests of the western US that evolved with frequent fire (<30 years) are generally composed of plant species that are resistant or resilient to characteristic fire regimes, even responding positively to fire depending on their traits (Bowd et al., 2018; Brown & Smith, 2000; Falk et al., 2022; Keeley et al., 2011; Pausas & Keeley, 2014; Pyke et al., 2010; Stevens et al., 2020). Similarly, plant communities that evolved with large herbivores or megaherbivores (animals larger than 1000 kg as adults such as elephants, or bison; Cumming & Cumming, 2003; Owen-Smith, 1988) are generally resistant or resilient to characteristic grazing regimes, with various responses depending on species traits (Adler et al., 2004; Callaway et al., 2005; Cingolani et al., 2005; Copeland et al., 2023; Diaz et al., 2007; Mack & Thompson, 1982; Milchunas et al., 1988; Vesik & Westoby, 2001). However, unlike fire, western forests and rangelands have a less established evolutionary history (>500 to 10,000 years; Price et al., 2022) of large ungulates similar in size and behavior as cattle (*Bos*), which are

novel domestic large herbivores introduced by Europeans in the late 1500s to North America; however, populations were likely small outside of the Southwest until the mid-1800s (Bates et al., 2009; Beever, 2003; Borman, 2005; Copeland et al., 2023; Davies et al., 2009; Jones, 2000; Mack & Thompson, 1982; Milchunas et al., 1988). Sporadic populations of North American bison (*Bison bison*) did occur in western forests and rangelands, although densities are not well known in the Northwest (Martin et al., 2022). In contrast, the Great Plains ecoregion has a very well recognized evolutionary history of grazing with a high abundance of large herbivores, particularly North American bison, that provided a keystone role in shaping the structure and function of these rangeland ecosystems (Copeland et al., 2023; Mack & Thompson, 1982).

Integral synergistic relationships between large ungulates and fire have been identified in a range of ecosystems with an evolutionary history of both disturbance processes such as the mesic grasslands and savannas of North America and Africa (Archibald et al., 2005; Collins, 1987; Collins & Calabrese, 2012; Collins & Smith, 2006; Eby et al., 2014; Fuhlendorf & Engle, 2004). Such ecological disturbances are proposed to interact through modifications that are either (1) functionally moderated or (2) numerically mediated (Didham et al., 2007; Foster et al., 2015). Functionally moderated interactions can occur if burning changes the per-unit effect of herbivores on vegetation. For example, in the North American tallgrass prairie, burning increases highly palatable C4 dominant grasses that large herbivores preferentially utilize (Collins, 1987; Gibson & Hulbert, 1987; Veen et al., 2008). Preferential grazing will then decrease their dominance, increase resources for less competitive species, and increase species richness and plant diversity (Collins et al., 1998; Foster et al., 2015). However, frequent fire can also increase the dominance of unpalatable species, and post-fire herbivory can exacerbate this pattern leading to divergent outcomes difficult to reverse (Foster et al., 2015).

The second major disturbance interaction pathway, numerically mediated or interaction chains, can occur if burning alters or concentrates the local abundance of herbivores, in turn affecting vegetation. A classic example is an increased number of animals grazing in recently burned areas, which can serve as “magnets” for herbivores and concentrate impacts, but also increase vegetation heterogeneity at the landscape scale (Allred et al., 2011; Fuhlendorf et al., 2009; Fuhlendorf & Engle, 2004; McGranahan et al., 2012). Herds then follow spatially discrete fires and graze on succulent regrowth with less discrimination between palatable species. Therefore, fire can essentially equalize forage, a process distinct from fire or grazing alone (Archibald et al., 2005; Fuhlendorf et al., 2009; Fuhlendorf & Engle, 2001;

McNaughton, 1983; Vermeire et al., 2004). Patch burn grazing is a management tool that capitalizes on this type of interaction in grasslands, savannas, and shrublands to strategically place ungulates within underutilized portions of pastures or away from sensitive areas, or to create other ecosystem benefits (Fuhlendorf & Engle, 2001; Scasta et al., 2016; Vermeire et al., 2004).

The degree to which generalizations about fire and large herbivore interactions and processes are transferable to western US forested rangelands with an evolutionary history of frequent fire but with a less established co-evolutionary history of large ungulate herbivory is not well known. Cattle commonly use forested rangelands as they provide the necessary summer range (Huntsinger & Starrs, 2010). Livestock (domestic cattle, sheep) use occurs on about half of US Forest Service lands nationally, depending on the year (USDA Forest Service, 2023). Despite widespread cattle use in forests, grazing studies remain uncommon, particularly in the past 20 years. Yet the impact of cattle grazing on plant communities may be substantial, depending on a variety of factors (Copeland et al., 2023; Fleischner, 1994; Jones, 2000; Milchunas et al., 1998; Pekin et al., 2016; Souther et al., 2020; Wisdom et al., 2006). Livestock grazing in general combined with lack of fire and other land-use changes, has been blamed for many deleterious changes to plant communities and forest health (Belsky & Blumenthal, 1997; Beschta et al., 2012; Borman, 2005; Condon & Pyke, 2018; Keeley et al., 2003; Madany & West, 1983). However, some note that negative impacts are largely associated with earlier histories of unrestricted use or overgrazing in the late 1800s through the midcentury, and improved practices used today can actually increase plant community resilience in the face of climate change, reduce wildfire impacts and risks, and exotic grass invasion (Bates & Davies, 2014; Borman, 2005; Davies et al., 2010; Davies, Bates, et al., 2016; Davies, Boyd, et al., 2016; Diamond et al., 2009, 2012; Donovan et al., 2022; Foster et al., 2015; Hernández et al., 2021; Svejcar et al., 2014).

Better understanding of cattle grazing and fire interactions in dry forests is critical because growing wildfire risks have prompted increased use of intentional burning or prescribed fire to reduce fuel loads and wildfire impacts, and achieve other ecological restoration goals (McWethy et al., 2019; North et al., 2021; Prichard et al., 2021; Stephens et al., 2020; USDA, Forest Service, 2022). Despite widespread cattle grazing in forested rangelands, manipulative fire and grazing studies in the west outside of nonforested areas are rare (Pekin et al., 2015; Powell et al., 2018; Royo et al., 2010; Wisdom et al., 2006; Zimmerman & Neuenschwander, 1984). We investigated the understory vegetation response to cyclical fall and spring prescribed fire and cattle grazing exclusion in

ponderosa pine (*Pinus ponderosa*) forest stands and report long-term responses 12–18 years after the first entry fires. Our study was designed to consider both the isolated and interactive long-term effects of two acute disturbance regimes (spring and fall reburning) and a chronic disturbance (annual seasonal grazing). The two seasonal burn regimes used here reflect commonly used but less historically characteristic fire seasons, particularly spring burning (Agee, 1993; Kerns et al., 2006). Our overarching goals were to determine the understory plant response to frequent fire and cattle grazing and apply disturbance interaction concepts to aid in forest management and restoration decision-making. Specific research questions included: (1) Does cattle grazing alter the long-term understory response to frequent prescribed fire regimes in these forests? (2) Is there evidence for a functionally moderated or numerically mediated disturbance interaction pathway? (3) How do responses and disturbance interactions differ based on plant functional groups and associated traits?

Plants in dry forests of the west are largely adapted to frequent fire (<25-year fire return interval, Agee, 1993), thus it would be logical to suspect that the understory would be either resilient (demonstrated by no effect on plant cover or abundance) or respond positively to fire and increase in abundance or richness. Intentional or prescribed fire is often applied in dry forests with the explicit or implicit goal of increasing plant abundance and diversity (Strahan, Stoddard, et al., 2015; Webster & Halpern, 2010). However, the understory may be less resilient (demonstrated by a decrease in plant cover or abundance) to more novel disturbances such as cattle grazing and spring burning. Because these forests did not evolve with large ungulates, we suspected classical disturbance interaction pathways may not hold, similar to our short-term results (Kerns et al., 2011). If a fire and grazing interaction were detected, evidence for a functionally moderated process would include changes in plant functional group abundance or species richness via an interaction linked to forage preferences or avoidance (Foster et al., 2015). Last, we explore our results in the context of our earlier work reporting short-term responses as well as challenges surrounding forest restoration and resilience goals and management policies in the western United States.

## METHODS

### Study location, climate and vegetation

The study area is within the dry ponderosa pine forests (1570–1730 m) of the interior northwestern US, Blue Mountain Ecoregion (EPA Level III) in the state of

Oregon (Figure 1). The stands are part of a larger long-term experiment established in 1997 on the Malheur National Forest that has explored a range of questions about prescribed fire (Hatten et al., 2008; Kerns & Westlind, 2013; Smith et al., 2004; Thies et al., 2005). Stands were identified and delineated by forest managers in 1995 and thinned from below.

Precipitation falls mostly between October and April as rain and snow. Estimated mean annual cumulative precipitation (based on water year) for the three main sampling years (2009, 2012, 2015) were 44.1, 35.6, and 46.7 mm, respectively (Rock Springs SNOTEL Site, elevation 1612 m, 20 km northwest of the area sites, <https://wcc.sc.egov.usda.gov/nwcc/site>; accessed 3/10/2022). Slopes are moderate and bedrock and residuum are of igneous origin (basalt, andesite, rhyolite, tuffaceous interflow, altered tuffs, and breccia; Carlson, 1974), including some ash from pre-historical volcanic eruptions to the west (Powers & Wilcox, 1964). Soils are largely Mollisols, with inclusions of Inceptisols and Alfisols (Hatten et al., 2008).

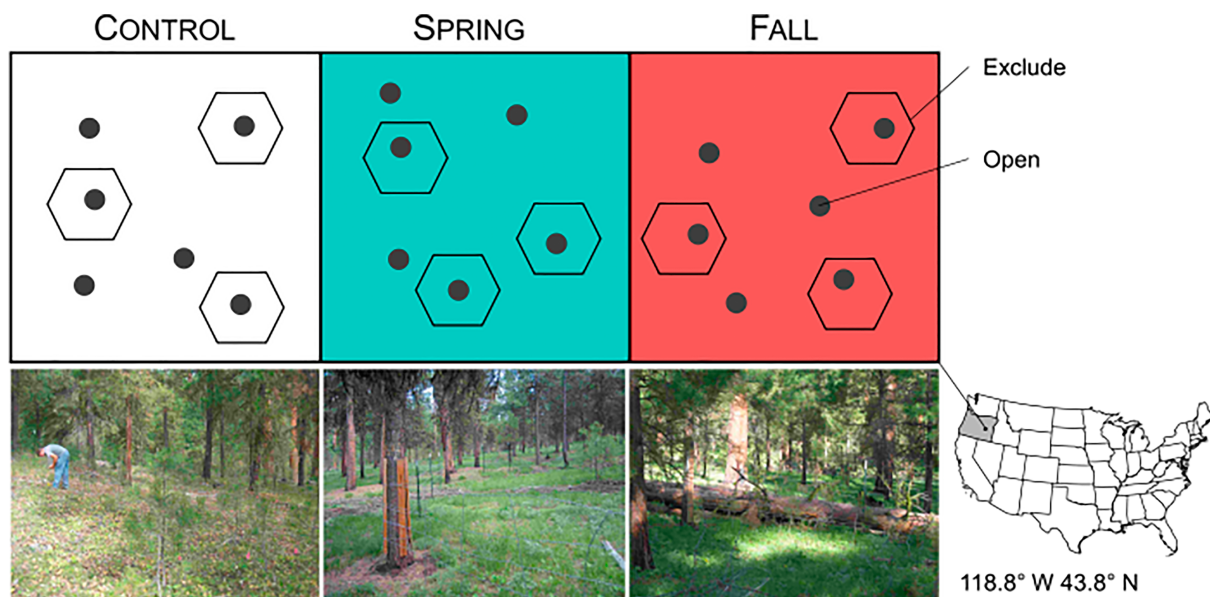
Overstory vegetation is dominated by mixed-aged ponderosa pine, but western juniper (*Juniperus occidentalis*) and mountain mahogany (*Cercocarpus ledifolius*) also occur. Ponderosa pine trees are approximately 100–120 years old with infrequent individuals over 200 years old (Emigrant Creek Ranger District, unpublished data). Understory species composition across the stands is highly variable (Figure 2; Appendix S1). One stand (Figure 2C) has a markedly higher plant cover, total C and N compared to the other three stands, indicating higher productivity (Kerns et al., 2011). Details on the plant functional groups in Figure 2 are described later in the *Data Analysis* section.

## Study design

This study is a split-plot randomized complete block with two factors: burning and grazing (Figure 1; Kerns et al., 2011). Each stand serves as a replicate block. Burning every 5 years is the whole plot treatment with three factor levels: control (no burn), spring, and fall. Each block was divided into three roughly equal units with boundaries (roads, firelines) established to control prescribed burns. Burning treatments were then randomly assigned. Grazing is the split-plot treatment with two levels: open to cattle grazing (open) and cattle excluded (excluded). For the open treatment, we utilized the three pre-existing systematically designed subplot centers set up in 1997 (Thies et al., 2005). We then constructed three fenced exclosures in 2002 before the first reburns but after the first entry burns within each reburn treatment. Exclosure plot centers were located along a random bearing at a minimum distance of 35 m from pre-existing plots. We replicated each of these treatment combinations across the four experimental blocks to give a total of 72 observations (a total of six experimental units with three subplots each, replicated four times).

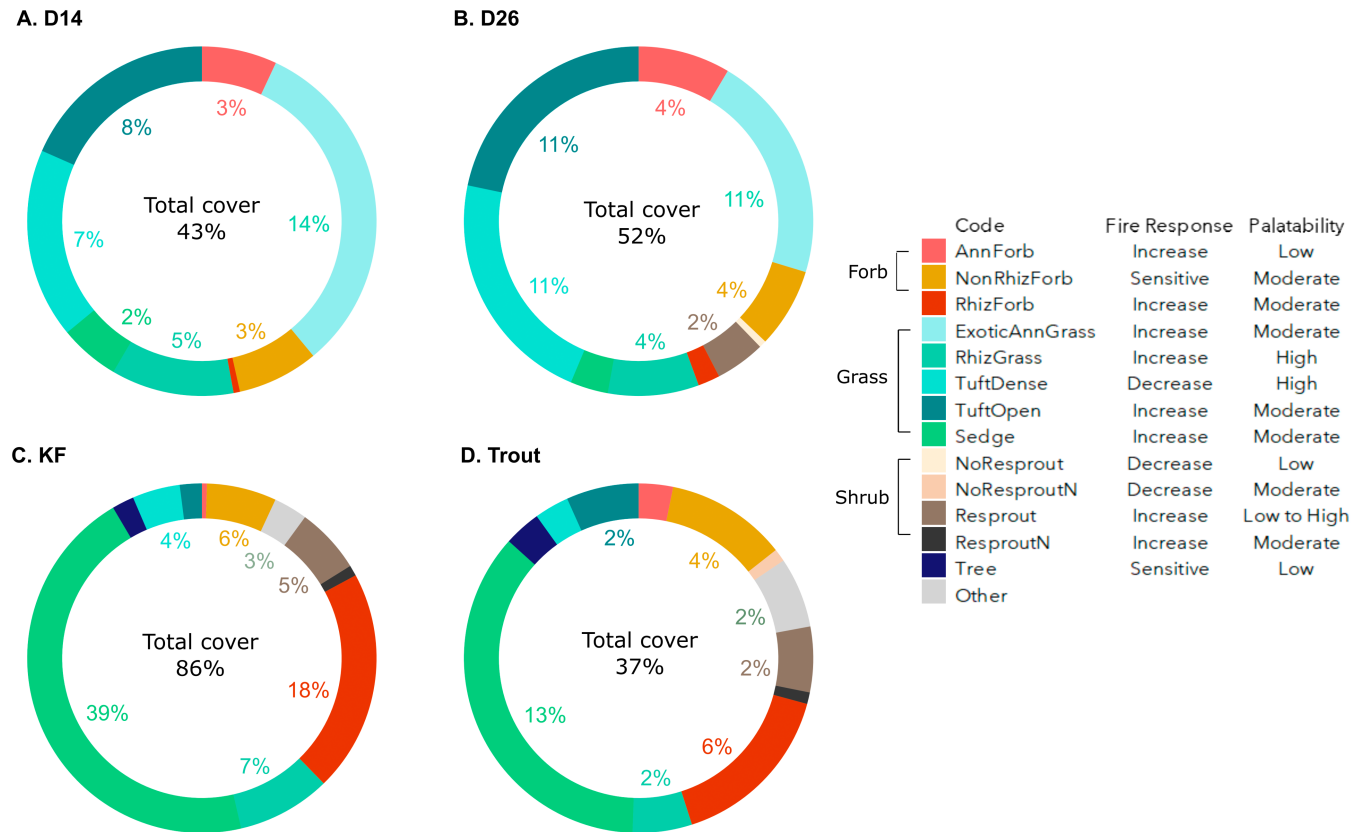
## Prescribed fire and grazing treatments

Fall fires were initiated in 1997 and spring fires in 1998 and then ignited every 5 years by hand-carried drip torches using a multiple-strip head-fire pattern. For the last reburns, operational limitations closed the burn window in 2012 and most (3) stands were subsequently



**FIGURE 1** Study area schematic showing the three randomly assigned burn treatments, 10-m radius open vegetation subplots, and fenced grazing exclosures within each treatment plot. Photograph credit: Control, Becky K. Kerns. Spring and Fall, Michelle A. Day.





**FIGURE 2** Species composition for the four stands based on the plant functional groups used for analysis, their potential fire response, and palatability class. Data are based on cover ( $\geq 2\%$ ) across all treatments. Two sites (A, B) are dominated by bunchgrasses (TuftDense, TuftOpen) and exotic annual grasses (ExoticAnnGrass). The other two sites (C, D) are dominated by sedges and rhizomatous forbs. Plant functional group descriptions, species traits, and species level details on the floristic diversity for each stand are provided in Appendix S1. Note that donut segment length is scaled to represent the proportion of that functional group to the total, but percentages represent the actual cover values within the stand due to the large differences in total cover among stands.

burned in the fall of 2013 and spring of 2014. Crews attempted to maintain flame lengths at approximately 60 cm during the burns. Detailed information regarding prescribed burn dates, fire conditions and fuels, and resultant effects on overstory structure and ground conditions have been described previously (Kerns et al., 2011; Kerns & Day, 2018; Thies et al., 2005, 2006; Westlind & Kerns, 2017).

Cattle grazing was operational in nature with a target utilization rate that did not to exceed 45%. We made no attempt to manage grazing at the plot scale, although we did quantify utilization in 2012 and 2015. Stocking, start day, and days of use were typical to prior years (Kerns et al., 2011). Two stands (Figure 2A,B) are located in a 3046-ha pasture grazed by cattle from mid-June through early August. From 2008 to 2014 AUMs ranged from 373 to 521, with 30–50 days of use, depending on the number and class of animals and annual moisture conditions. The two other stands (Figure 2C,D) are in one 2428-ha pasture grazed from early July to early August. From 2008 to 2014 AUMs

ranged from 460 to 592, with 25–50 days of use. It is estimated that the study area has been continuously grazed for the past 140+ years, although current stocking has been substantially reduced (Kerns et al., 2011). The fenced exclosures were designed to exclude cattle only. Extant native herbivores such as elk, deer, antelope, and smaller animals can access the exclosures, and exclosures are open when cattle are not present.

### Sampling

Utilization was measured nondestructively at the time of vegetation sampling prior to cattle reaching the study area, and later in the year after cattle use in 2012 and 2015 using herbaceous and browse utilization classes (based on key forage species, Appendix S1; BLM 1996) on a 10-m radius subplot. While the area was grazed each year, we strived to complete vegetation sampling prior to cattle utilization, although occasionally crews were late and minor utilization was noted.

We measured vegetation nondestructively in 2009 (three reburns, 2-year response), 2012 (three reburns, 5-year response), and 2015 (four reburns, 1–2-year response). To capture variation within each subplot, the current year's plant canopy cover for all species <1.4 m (understory) was visually estimated by species to the nearest percentage point on eight small (1-m<sup>2</sup>) nested quadrats using a marked (0.10 m) frame. Quadrats were arranged 5 and 6 m from the subplot center in each cardinal direction. To increase consistency in ocular estimates of plant cover, standardization exercises were performed periodically throughout each field season, and crew continuity was maintained all season and year-to-year when possible. We measured specific bunchgrass metrics for nine key forage species (Appendix S1; Table S3): density, number of flowering stems, maximum leaf height, and maximum flower stem height within each quadrat. Shrub cover, which is highly patchy in the study areas, was also recorded by species on the 10-m radius subplot. The presence of all species for richness analysis was also recorded on the 10-m radius subplot. Overstory tree cover was measured using a moosehorn densiometer at the subplot center, and 5 and 15 m from the center in each cardinal direction (total of nine points for each subplot) in 2009, and additional points were added in 2012 and 2015 to decrease variability.

## Data analysis

We assessed treatment effects using a repeated measures randomized block, split-plot ANOVA model and the Proc Mixed procedure in SAS 9.3 (SAS Institute; Cary NC). Random effects were stand and stand  $\times$  burn treatment. Fixed effects were year, burn, and grazing treatment. The covariance structure used was spatial power, and the degree of freedom method was Kenward–Roger. We used Fisher's Protected least significant difference (LSD) for multiple comparisons for the reburn treatment component, which has three factor levels.

Because of the high floristic diversity at the sites (over 200 species recorded; Appendix S1), plant cover response variables were created based on species growth form and trait-based pooled species groups referred to as functional groups (Figure 2; Appendix S1; Kerns & Day, 2018). Categories were more finely developed than in previous work (Kerns et al., 2011) as requested by local managers and to elucidate responses that might be undetectable with more general groups (Willms et al., 2017). Traits used are important for both fire and grazing resistance and resilience: growth form, duration, reproductive strategy, architecture, nutrient capture, and origin (Agee, 1993; Kerns & Day, 2018; Pyke et al., 2010). Richness metrics

were examined using broader classification, including: total, native perennial graminoid, native perennial forb, native annual form, exotic, and shrub.

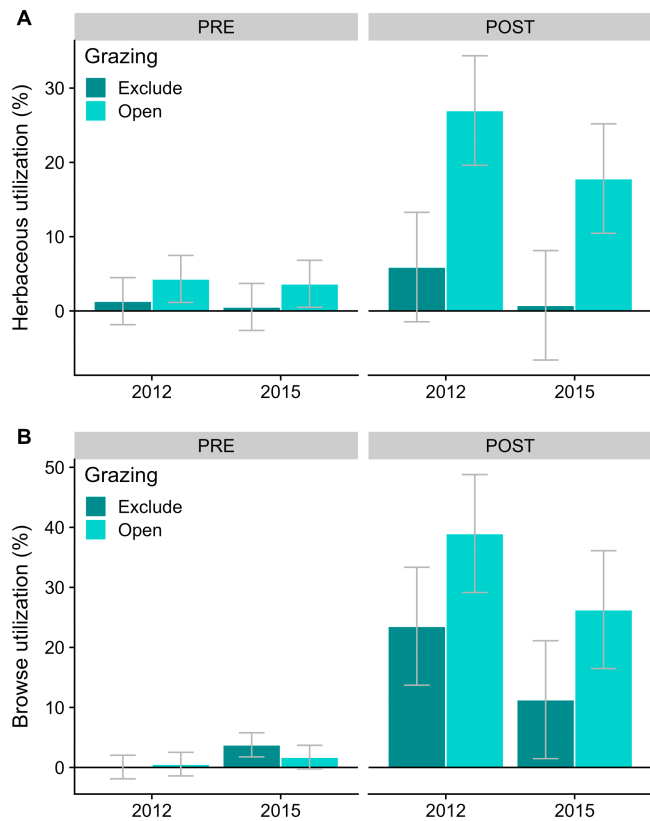
Plot-level means were generated for most variables using quadrat or subplot data as appropriate. Some variables were transformed to improve skewed distributions and heteroscedasticity based on an assessment of residuals. If a variable was transformed, back-transformed means associated with transformed data are presented. We present mean values and their variability (95% CI) by year graphically for most response variables, even if the year did not interact with burning or grazing. *P*-values are noted in the text when practical, and statistical output for all tests of main fixed effects are included in Appendix S2. *P*-values that support evidence of treatment differences (values near 0.10) for contrasts of interest are presented in the text, regardless of the main fixed effects test results. We interpret *p*-values as a continuous measure of the strength of evidence and avoid dichotomous statements regarding statistical significance. Values near 0.10 indicate some evidence of a treatment effect; smaller values ( $p \leq 0.05$ ) suggest stronger evidence, and larger values indicate weaker evidence, assuming the relative effect size is biologically meaningful (Matthews, 2021; Ramsey & Schafer, 2012; Wasserstein & Lazar, 2016).

## RESULTS

### Utilization

Pre-cattle utilization results from 2012 to 2015 were collected at the time of vegetation sampling and provided information about extant early-season herbivory (Figure 3). There was little evidence for fire and grazing interactions and no evidence that burning impacted utilization at the experimental scale (Appendix S2). Pre-cattle utilization among all the treatments was very low (less than 4% utilization across all metrics), documenting the successful measurement of vegetation prior to utilization. We found evidence for very small effects owing to the grazing treatment. Native grazers utilized the excluded areas, but slightly less than open areas (Figure 3; Open-Excl  $p < 0.005$ ). There was some evidence for a small but opposite effect for browse utilization in unburned areas (Control: Open-Excl  $p = 0.06$ ), and for all treatments in 2015 (Graze  $\times$  year  $p = 0.11$ ; 2015 Open  $\times$  Excl  $p = 0.05$ ).

Post-cattle utilization results document patterns related to seasonal domestic cattle presence in addition to native ungulates during the growing season. Post-cattle utilization for both herbaceous and browse showed dramatic increases, and as expected we found strong evidence for increased utilization in areas open to cattle



**FIGURE 3** Pre- and post-cattle utilization results over time for herbaceous and browse vegetation in open areas (open) and those excluded from cattle use (exclude). Utilization shows a large increase in herbivory associated with seasonal cattle use (post) in open areas. Burn treatments are not shown as there was no evidence burning impacted utilization. Excluded areas allow access by native ungulates. Data are means and 95% confidence intervals.

(Herbaceous and Browse: Graze  $p < 0.01$ ; Figure 3). Burning did not impact utilization, and there was no evidence that fire and grazing interacted. Both herbaceous and browse utilization also increased in excluded areas, demonstrating consistent use of enclosures by native ungulates during peak growing season. While the post-cattle utilization differences are substantial, average utilization is largely within current management guidelines (less than 45% maximum utilization).

## Vegetation

### Overstory and total understory cover

Mean overstory tree canopy cover in fall burn areas was 29.8% (95 CI 22.4–37.3) about 10% lower in comparison with the spring (40.1%, 95 CI 32.6–47.5) and control (39.5%, 95 CI 32.1–47.0) treatments (Burn  $p = 0.10$ ; C-F  $p = 0.07$ , C-S  $p = 0.06$ ). Grazing did not impact overstory cover.

Total cumulative understory cover varied based on fire and grazing treatments (Burn  $\times$  Graze  $p = 0.05$ ; Figure 4; Appendix S2, Table S2). Across all years, areas reburned in the fall and where cattle were excluded had on average about 12% higher total cumulative cover (Fall: Open-Excl  $p = 0.02$ ) compared with the open areas. While there was no evidence for an interaction with year, the effect size was larger in 2009 (15%) 2 years after the third reburns.

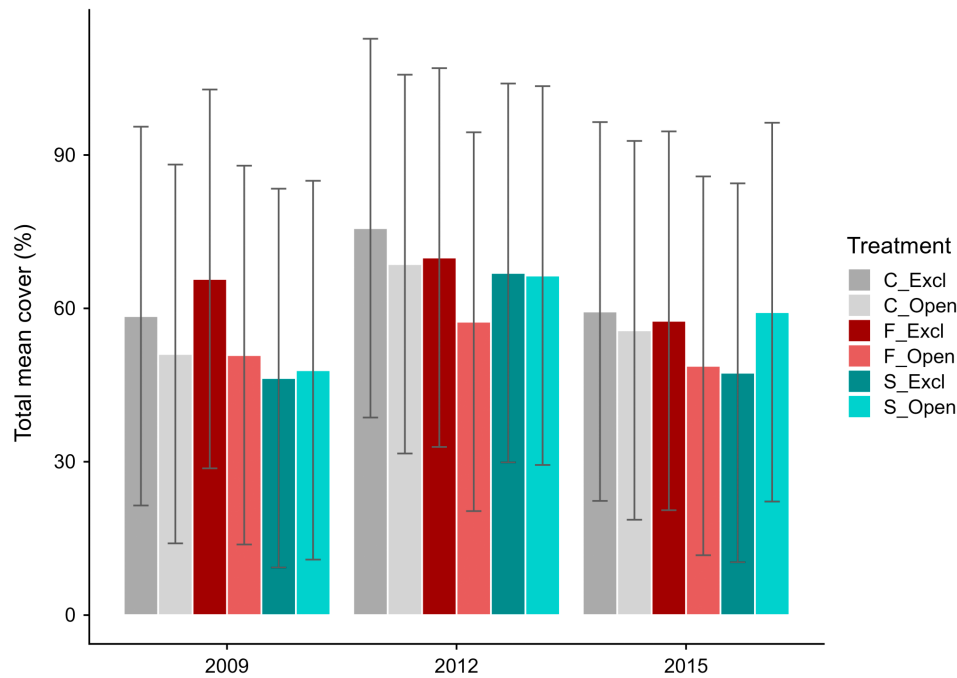
### Grasses and sedges

There was less evidence that native grass and sedge groups differentiated based on burning and grazing treatments (Figure 5). However, rhizomatous grass cover was about 6% higher in unburned areas where cattle were excluded (Control: Open-Excl  $p = 0.07$ ), although evidence for a fire and grazing interaction was lacking. We had no or very weak evidence grazing or burning altered exotic grass cover at the scale of the experiment (Graze  $p = 0.92$ ; Burn: C-F  $p = 0.13$ ). However, given the strong pattern of invasion associated with the stands (Figure 2) and its relevance for forest managers, we present stand-scale patterns by burn treatment for the cheatgrass-dominated exotic annual grass group (Figure 6).

There was evidence burning was important for several bunchgrass metrics. In excluded areas, the fall burn treatment had higher bunchgrass density compared to unburned controls (Figure 7; Excl: C-F  $p = 0.07$ ). In 2015, fall burn areas had about four more plants (based on one square meter) compared to controls on average, regardless of grazing treatment (C-F  $p = 0.03$ ). Grass flowering stalk density also differed owing to burn treatment and year (Figure 7; Burn  $\times$  Year  $p = 0.04$ ). In 2009, flowering stalk density in fall burn areas was over nine times higher compared with control and spring burn areas (C-F  $p = 0.01$ , F-S  $p = 0.01$ ). Very similar results were noted when flowering density was scaled to abundance. We found no evidence of a difference for bunchgrass or flowering stalk density owing to grazing treatments, but there was some evidence that grazing reduced grass leaf height slightly (1.4 cm, Graze  $p = 0.11$ ) prior to utilization, and that burning impacted leaf height based on year (Burn  $\times$  Year  $p \leq 0.01$ ). Fall burning increased leaf height in 2009 by about 3 cm (C-F  $p = 0.09$ ) and spring burning decreased leaf height by about 3.4 cm in 2012 (C-S  $p = 0.06$ ). We found no evidence of treatment differences for grass flowering stalk height.

### Forbs

Nonrhizomatous forb cover was higher overall in areas that were excluded from cattle grazing compared to open



**FIGURE 4** Total understory cover in the study area by treatment and year. Understory cover was lower for the fall burn treatment in areas open to grazing, particularly in 2009. Data are means and 95% confidence intervals. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring.

areas (Graze  $p = 0.10$ ). While there was no evidence of a fire and grazing interaction, this pattern was more evident in areas that were burned in the fall, where cover was almost twice as high in areas that were not grazed (Fall: Open-Excl  $p = 0.06$ , Figure 8). We found strong evidence for higher annual forb cover in areas that are open to grazing (Graze  $p < 0.01$ ), which was driven by values in 2009 (Graze  $\times$  Year  $p = 0.05$ ; 2009 Open-Excl  $p < 0.01$ ). Burning also increased annual forb cover depending on the year (Burn  $\times$  Year  $p = 0.07$ ). Differences again were driven by values in 2009 (C-F  $p = 0.02$ ; C-S  $p < 0.01$ ). Exotic forb cover, while very low in the study area, showed a strong increase in response to fall burning in 2009 only (C-F  $p = 0.04$ ), although there was little evidence for a global interaction with year.

## Shrubs

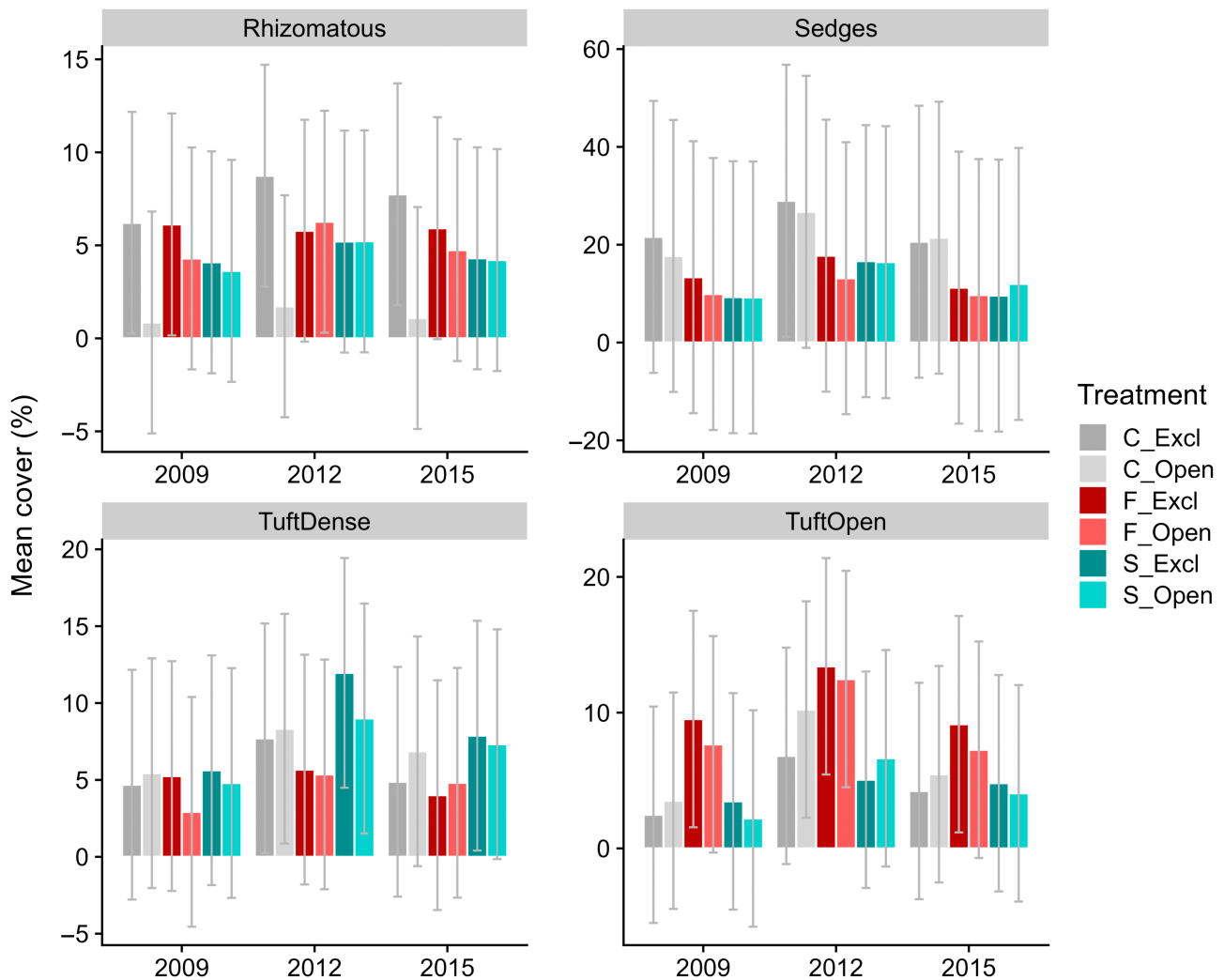
Shrubs are not a dominant component of the vegetation in these forests and their distribution is highly spatially variable, thus mean cover values at the plot scale for most groups are very low and these results should be interpreted cautiously. We found moderate to strong evidence that nonresprouting shrubs (nonnitrogen fixing) were sensitive to both burning and grazing and that burning and grazing interacted (Figure 9; Burn  $\times$  Graze  $p = 0.01$ ), but burning responses depended on year

(Burn  $\times$  Year  $p < 0.01$ ). Unburned controls had higher cover than both burn treatments in 2009 and 2012 (2009 C-F, C-S  $p = 0.08$ ; 2012 C-F  $p = 0.03$ , C-S  $p = 0.01$ ). The grazing response was driven by unburned and excluded areas that had high cover (Control: Open-Excl  $p < 0.01$ ), particularly in 2012 and 2015. We had strong evidence that burning increased cover of the resprouting nitrogen-fixing shrub *Ceanothus velutinous* and in particular fall burning (Burn  $p < 0.01$ ; C-F  $p < 0.01$ ; S-F  $p = 0.02$ ). However, cover values across the study are very low and differences are quite small. There was some evidence other resprouting shrubs (nonnitrogen fixing) increased in areas open to grazing by 2015, especially for fall burning (2015 Open-Excl  $p = 0.07$ ). There was some evidence that burn treatments reduced cover for nonresprouting nitrogen-fixing shrubs (Burn  $p = 0.11$ ), particularly in 2009 (C-F  $p = 0.01$ ) and 2012 (C-F and C-S,  $p = 0.09$ ).

## Species richness

Mean total species richness was remarkably similar across all treatments (mean = 37 for all treatments; Appendix S2, Table S5). Differences in plant group richness were limited. Exotic richness in the study area remains low, with less than two species in most treatments. Repeated fire altered exotic richness





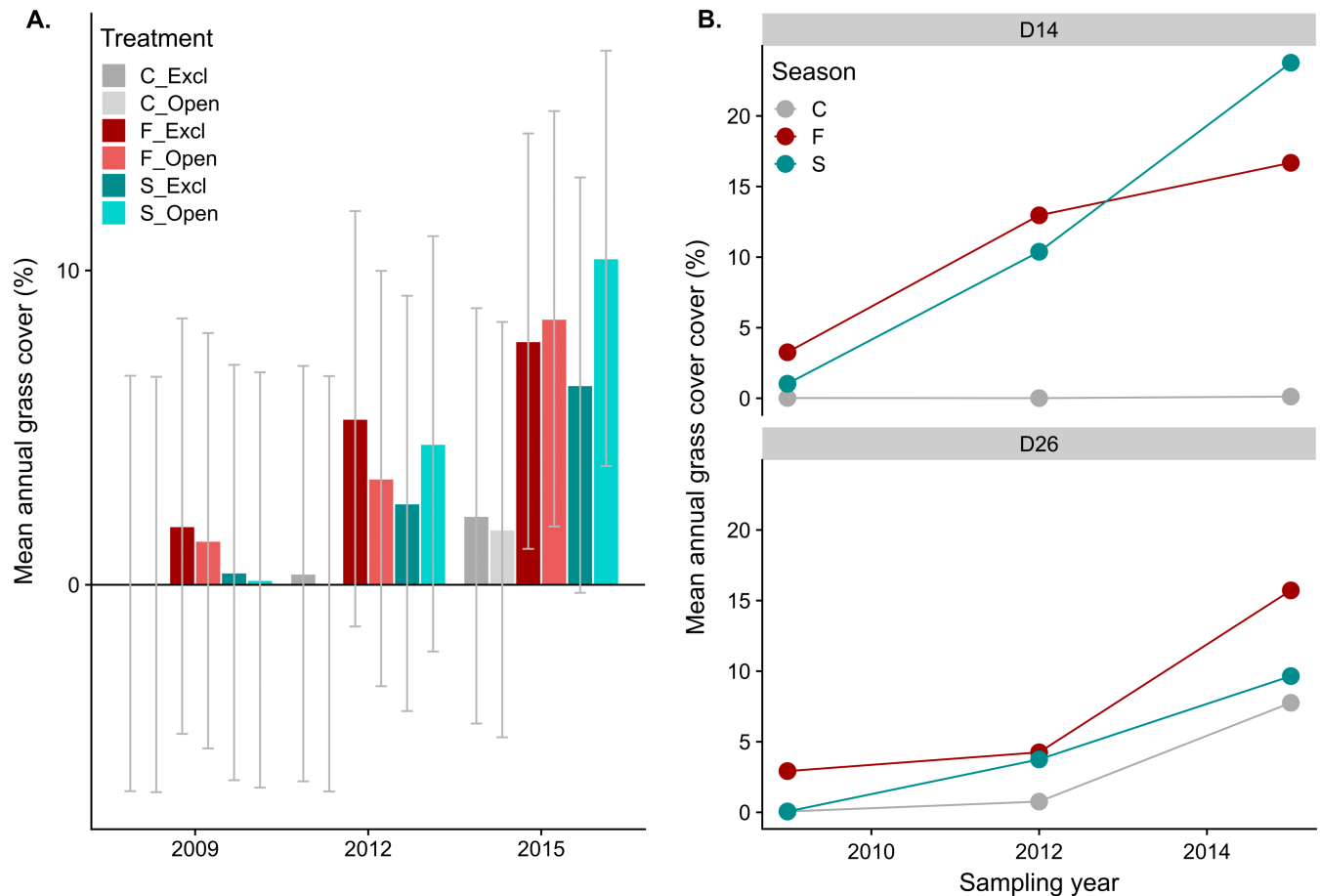
**FIGURE 5** Understory cover for grass and sedge functional groups by treatment and year. Most grasses and sedges did not strongly respond to fire and grazing treatments. Data are means and 95% confidence intervals. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring. See Appendix S1 for plant group definitions.

(Burn  $p = 0.03$ ), with more exotic species found in fall burn areas as compared to the control and spring (about one species), an effect due to the presence of the dominant exotic species *Bromus tectorum*. The only evidence that grazing altered richness was for annual forbs, where areas open to grazing had slightly more species (6.3 species, 95% CI 3.7–8.9 compared with 5.7 species, 95% CI 3.1–8.3) (Excl-Open  $p = 0.07$ ).

## DISCUSSION

We demonstrate that the understories in these forests were generally resilient to 18 years of frequent fall and spring prescribed fire, an outcome consistent with recent reviews from largely single fire studies that exclude livestock grazing (Abella & Springer, 2015;

Knapp et al., *in press*; Willms et al., 2017), and our prior work focused on prescribed fire regimes in grazed areas (Kerns & Day, 2018). However, a key finding was that cattle grazing altered the understory response to fall reburning. In fall burn areas open to cattle grazing, total understory cover was about 12% lower (prior to utilization) compared to areas where cattle were experimentally excluded, suggesting that these two disturbances combined may lower understory resilience in dry ponderosa pine forests. While a 12% reduction in total cover may seem small, our low productivity stands have total understory cover values ranging on average from 37% to 43% (Figure 2). Therefore, a 12% reduction in cover is about a one-third reduction in plant cover in these areas, which may have impacts on understory resilience. Fire and grazing are likely interacting in a numerically mediated manner as we found little



**FIGURE 6** Exotic annual grass cover by treatment and year. Exotic annual grass cover has increased through time in the study area (A). Data are means and 95% confidence intervals. Stand-scale patterns (B) show substantial increases in exotic grass cover in fall and spring burn areas at the bunchgrass-dominated sites (see Figure 2A,B for stand details), as well as the control at one site in 2015. Exotic annual grass cover was close to zero at the two other stands. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring.

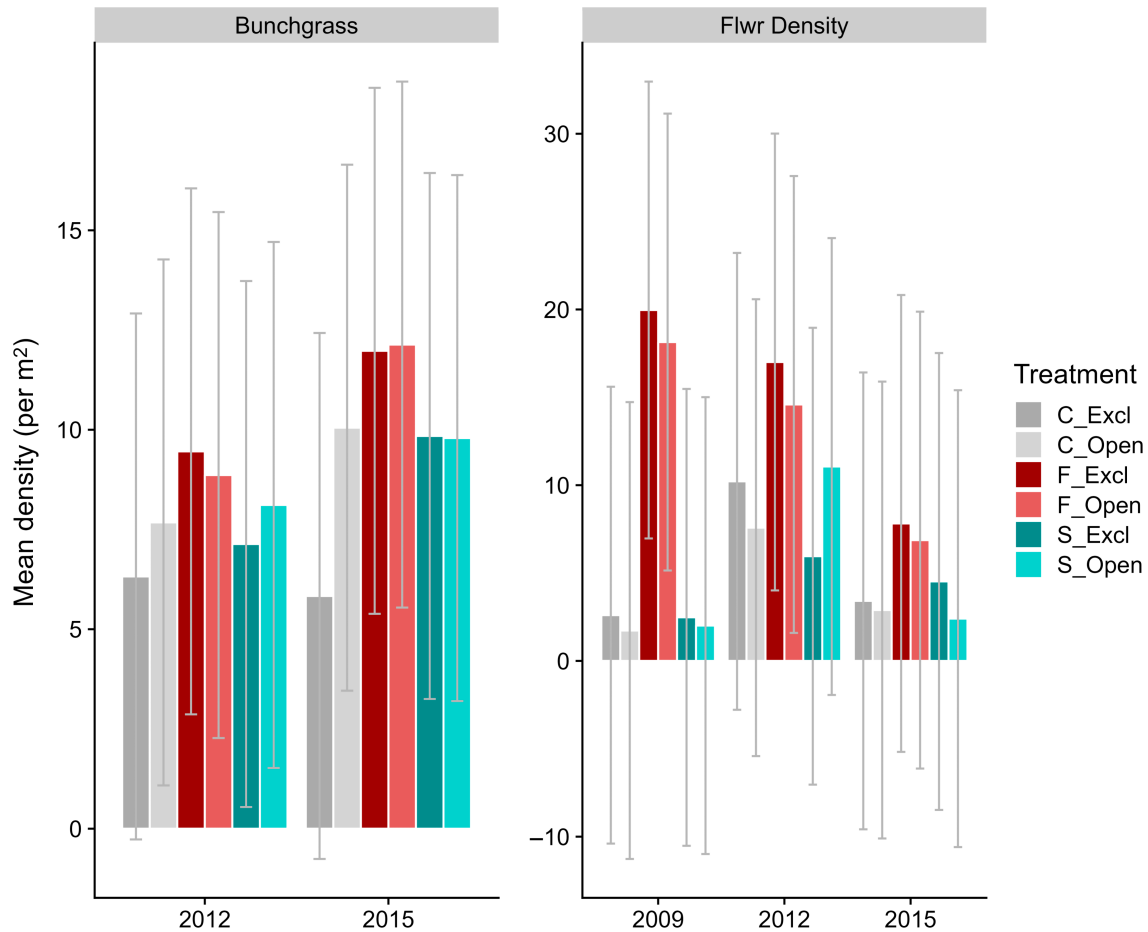
evidence for a functionally moderated interaction pathway. The more finely developed plant functional groups we examined often responded as expected to fire and grazing depending on their traits, yet responses were nuanced. Next, we dive into these results, highlighting and discussing key insights.

### Cattle herbivory drives growing season utilization

The utilization patterns we document are expected but important to highlight because they set the stage for interpreting our results. While we did not physically separate herbivores other than cattle, our data point to cattle as major drivers of utilization in the study area during the growing season. Herbaceous and browse utilization by cattle dwarfed early-season native herbivory. Elk, antelope (grazers), and deer (browsers) are the other

native ungulates in the study area. These results are consistent with expectations as native herbivores are not fenced into pastures and utilization generally tends to be diffuse.

Although we purposefully designed our study so that native ungulates could access the exclosures, pre-cattle utilization results revealed minor herbaceous avoidance and minor increased browse in unburned fenced exclosures. These effects were very small (<3%) particularly compared with post-cattle utilization patterns. Native ungulate utilization also rose substantially later in the growing season (Figure 3). These findings suggest that the impact of the fencing on wildlife had only minor effects on our results, although we caution that we could not directly measure the effect of wild ungulates with our study design. Minor wild herbivore avoidance of exclosures is not unsurprising, as animals needed to purposely jump into the areas to graze, although gates were open when cattle were not present. Divergent patterns



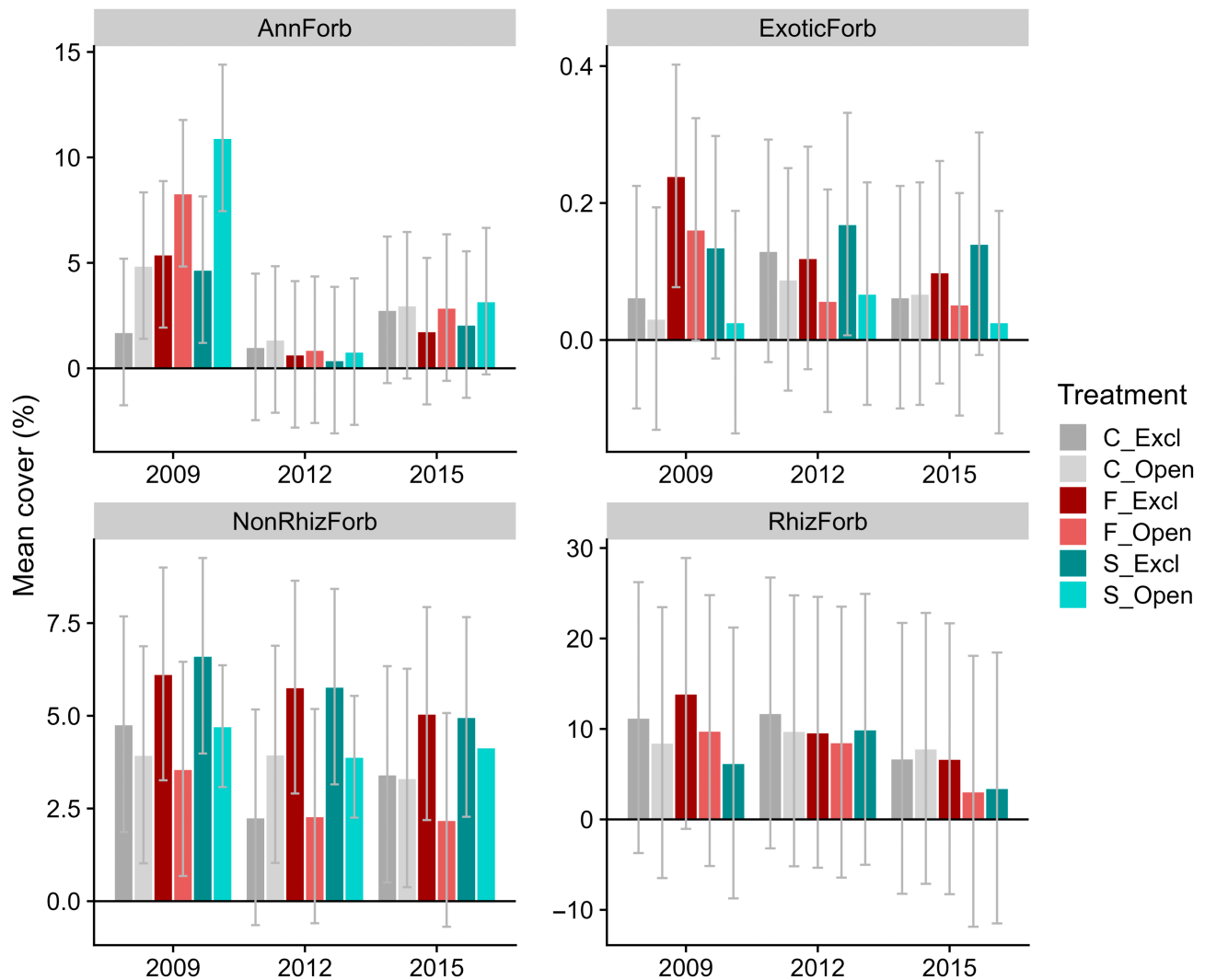
**FIGURE 7** Bunchgrass and flowering stalk density increases in response to fall burning, depending on year (see text). Data are means and 95% confidence intervals. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring.

for browse and herbaceous utilization are likely due to differences in species-specific foraging preferences and behavior (Stewart et al., 2003). Long-term protection of shrubs from both cattle grazing and fire may entice more native browsing through increased abundance, as shrub cover tended to be higher within exclosures, although strong evidence for this pattern was lacking.

### Grazing and fall fire reduced total cover: Evidence for a numerically moderated interaction?

The difference we found in total understory cover between fall-burned grazed (open) and ungrazed treatments was due to a modest positive understory response to fall fire in excluded areas and a modest reduction in cover in areas open to grazing, resulting in an average 12% difference between the two treatments (across all years). It is likely that this interaction was only detected for fall burning because fall burns have more impact on

environmental conditions compared with spring burns. As noted here and in other work, fall burning reduces tree abundance and cover, litter cover and depth, and increases mineral soil and rock exposure, although major changes were largely associated with the initial entry fires (Kerns et al., 2011; Kerns & Day, 2018; Thies et al., 2005, 2006). While we do not see a large positive response to fall reburning, consistent with the subtle nature of plant responses to fire in the study area (Kerns & Day, 2018), a modest increase in understory cover and new growth after fire may draw in herbivores and concentrate post-fire grazing, characteristic of a numerically mediated disturbance interaction pathway (Didham et al., 2007; Foster et al., 2015). This type of interaction is also more likely to occur following smaller patch burns such as prescribed fires (Foster et al., 2015). Our burn treatments were embedded in large pastures (2400–3000 ha) that were not burned, which may exacerbate this effect. It is also well documented that herbivores will forage in recently burned areas with less discriminatory foraging behavior (Allred et al., 2011; Fuhlendorf et al., 2009;



**FIGURE 8** Understory cover for forb functional groups by treatment and year. Forbs show differential responses to fire, grazing, and time since fire. Data are means and 95% confidence intervals. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring. See Appendix S1 for plant group descriptions.

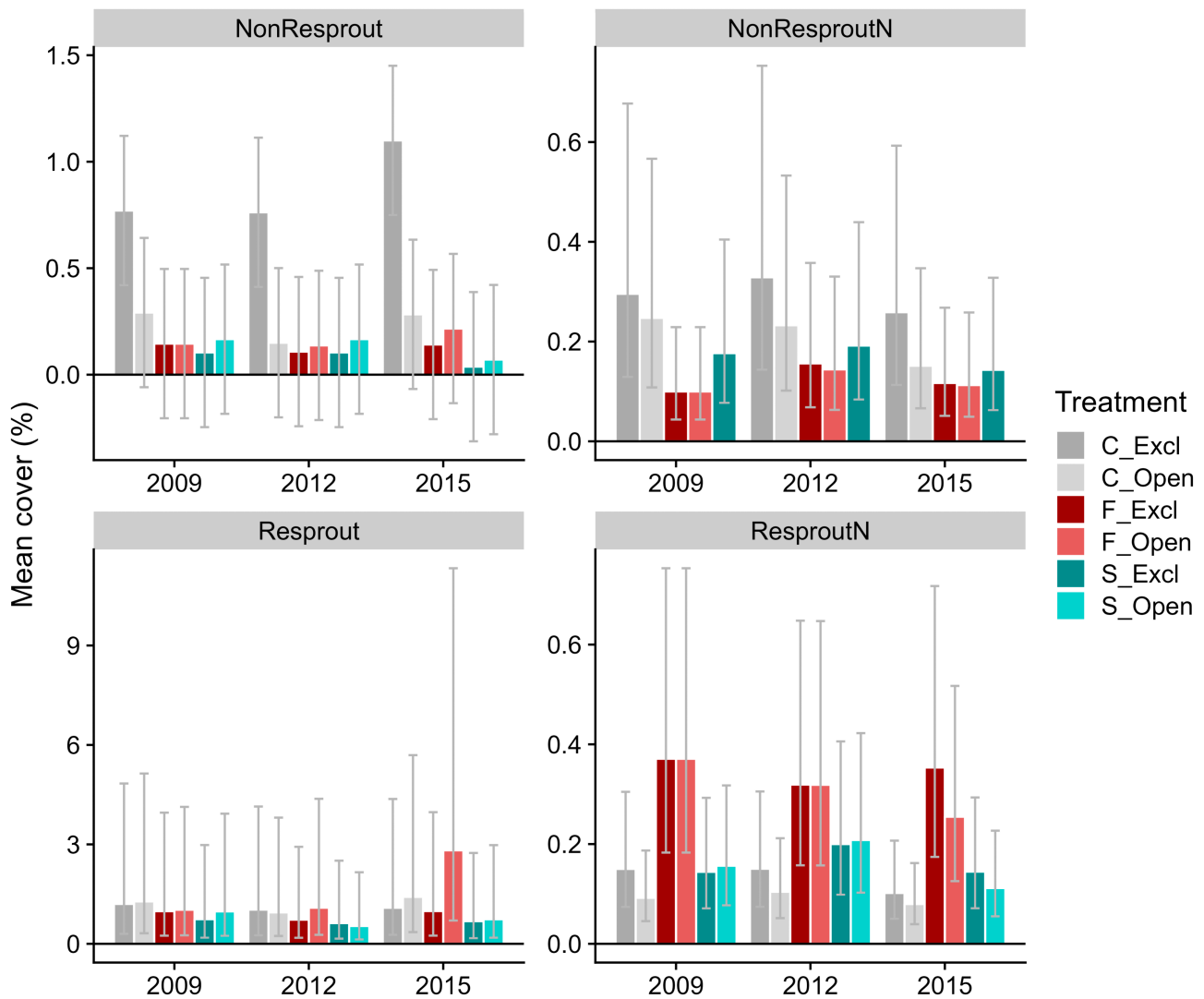
Fuhlendorf & Engle, 2004; McGranahan et al., 2012). Plant regrowth after fire can lack the chemical and physical properties of mature plants, rendering typically unpalatable plants highly palatable for short periods of time and equalizing forage (Augustine & McNaughton, 1998).

Short-term equalization of post-burn forage may explain why we found a fire and grazing interaction for total cover, rather than for plant groups known to be highly palatable (Figure 2) or for utilization as expected. Indeed, our total cover results were not strongly driven by any one plant group. Rather most herbaceous plant groups (except annual forbs) showed small but negative trends for the open grazing and fall burning combination for most years, although statistical evidence was not strong. Nevertheless, our total cover result would not manifest if patterns for the dominant cover groups (perennial grasses and forbs) were strongly divergent and

stochastic. However, we did not examine species-specific responses, and our sites had considerable floristic diversity, which could mask community-based effects.

Lack of grazing preference after fire has the potential to reduce negative impacts related to selective grazing that may occur without fire. We have some evidence that grazing in unburned areas reduced the cover of rhizomatous grasses, an effect not found in burned treatments. However, concentrated grazing after burning may also constrain the understory response for species more sensitive to defoliation, typical in regions with shorter or limited large ungulate grazing histories and where summer drought occurs (Milchunas et al., 1988; Milchunas & Lauenroth, 1993). Unpalatable species that are not typically selected may be even less tolerant of defoliation. Many sagebrush steppe rangelands with some similar bunchgrass species as dry forests demonstrate resilience to moderate post-fire grazing





**FIGURE 9** Understory cover for shrub functional groups by treatment and year. Shrubs demonstrate sensitivity to burning and grazing based on resprouting ability, although most effect sizes are very small owing to the low cover of these groups across the study area. Data are means and 95% confidence intervals. Treatment labels: C, Control; Excl, Cattle excluded; F, Fall; Open, Open to grazing; S, Spring. See Appendix S1 for plant group descriptions.

(Bates et al., 2009; Bates & Davies, 2014). However, these studies do not examine very frequent fires in forested plant communities as in this study.

### Graminoids and species richness: Evidence for a functional moderated interaction?

Our results for graminoid cover groups, key forage plants in the study area, were largely unremarkable, although surprisingly rhizomatous grasses (e.g., pinegrass or *Calamagrostis rubescens*) demonstrated sensitivity to grazing in unburned areas. For these highly palatable rhizomatous grasses, fire may increase resilience to grazing, potentially providing a pathway for a functionally

moderated interaction. As noted above, these grasses may be selectively grazed in unburned areas, and post-fire forage equalization may reduce negative impacts. For other important forage groups such as bunchgrasses, we note that some plants subjected to grazing can be shorter and more prostrate than ungrazed or lightly defoliated populations, and cover may not change or increase in response to grazing, although this is more typical for heavy grazing (McNaughton, 1979; Tomás et al., 2000). Concerns about this issue led to our collection of key forage bunchgrass density and other bunchgrass metrics in 2012 and 2015. We found that fall burning increased bunchgrass density and reproductive potential, the latter of which was independent of bunchgrass abundance. This amplified fire effect on bunchgrass vigor could

potentially lead to a functionally moderated interaction if these key forage species were preferentially grazed leading to changes in dominance and species richness (Collins et al., 1998; Foster et al., 2015). However, we have little evidence to support this type of interaction. First, we did not find a fall fire and grazing interaction for herbaceous utilization, which is based on key forage bunchgrass species. In addition, species richness results provide little evidence for the changes we might expect. Indeed, our total species results were profoundly similar among our treatments. We saw a very small increase in annual forb richness associated with grazing and increases in exotic (discussed below) and shrub richness with fire; but there was no evidence of fire and grazing interactions. Similar to burning, it is likely that grazing alters the relative abundance of plants at the community level without driving large impacts on species richness and composition (McGranahan et al., 2012; Milchunas et al., 1988).

### Fall fire and grazing increased annuals and resprouting shrubs but effects waned

Some plant groups responded as expected to fire and grazing treatments based on their traits (Figure 2) but nuances around the disturbances were important. Annual forbs and resprouting shrubs increased in response to fall fire and grazing, although the cover of these plant groups was relatively low across the study area. Both plant functional groups possess traits that either confer resilience to fire (short-lived, rapidly dispersed and reproduces from seed, location of buds, resprout ability), resistance to grazing (low palatability) or resilience to low- to moderate-intensity grazing if they are considered palatable owing to resprouting capacity (e.g., *Symphoricarpos* spp.). The annual forb response to fire and grazing is consistent with other studies documenting increases in this plant group in response to both fire and grazing independently, particularly heavy grazing for annual forbs (Bowd et al., 2018; Hayes & Holl, 2003; Pyke et al., 2010; Souther et al., 2020; Strahan, Laughlin, et al., 2015). Other plant groups did not respond strongly as expected, chiefly perennial rhizomatous grasses and forbs (but see our discussion above about rhizomatous grasses), and this may indicate that the fire return interval in this study is too frequent for these species to increase in response (Kerns & Day, 2018).

The response of annual forbs was also strongly tied to 2009, two growing seasons after the second reburns. Muting of post-fire annual forb flushing is understandable by 2012, as increases can be ephemeral. However,

the lack of a similar response in 2015 (1–2 growing seasons after burning) is curious and may be related to waning fire effects as noted at this site (Zald et al., 2020). Waning fire effects may also explain why the total cover result was more evident in 2009. The very frequent fire interval tested in this study is on the low end of the historical fire regime (e.g., intervals less than 10 years are not common for the area, see Kerns & Day, 2018) for the area and may lead to reductions in surface fuels that carry fire, limiting fire spread and the impact of fire (Westlind & Kerns, 2017). It is also possible the annual flush was not strongly evident in 2015 because most stands were burned just the year before, limiting a direct temporal post-fire comparison to 2009. Variation in precipitation may also be important, although 2012 recorded the highest annual precipitation among the three sampling years.

Waning fire effects for very frequent fire regimes may be potentially enhanced if a fire-grazing inhibitory disturbance loop develops (Burton et al., 2020). That is, if grazing is constraining understory recovery it may inhibit fire spread due to fuel discontinuity (Archibald et al., 2005; Davies et al., 2010, 2022; Scasta et al., 2016). However, increases in cheatgrass may increase fuel continuity (Brooks et al., 2004) and moderate this effect at our bunchgrass-dominated sites as discussed in the following section. As noted in other studies from these sites, longer burn intervals may produce a more desired future condition across a range of ecosystem responses (Kerns & Day, 2018; Westlind & Kerns, 2017).

### Long-term spring reburning had limited impact

There has been considerable concern about spring burning in the management community, which is more historically novel and coincides with active plant growth. We found that the effects of spring burning were relatively minor, largely consistent with our findings and others and likely related to the low severity of the burn regime (Busse et al., 2000; Kerns et al., 2006, 2011; Kerns & Day, 2018; Knapp et al., 2009; Zald et al., 2020). Herbaceous plant groups were generally resilient to spring burning, although grasses were shorter in spring-burned areas, which might suggest some sensitivity. There was only limited evidence that spring fire and grazing operated synergistically. Nonresprouting shrubs demonstrated some sensitivity to both fall and spring burning, and the nonnitrogen fixing group was more sensitive to spring burning and grazing in general. However, the effect was small and only present in one post-fire year. Our data suggest that long-term frequent spring

burning outside the historical wildfire season is not strongly detrimental to the resilience of the forest understory. However, some species may be sensitive, and our plant functional group approach can obscure species-specific responses.

### Short- and long-term patterns differed

Our work looking at shorter term responses from these stands (Kerns et al., 2011) documented that cattle exclusion increased total plant cover, with an effect size similar to our findings here. However, we found no evidence of a fire and grazing interaction for total cover. We used finer scale plant groups in the current study; therefore comparisons for the other plant groups will not be made here. Differences in short- and long-term results for total cover may simply indicate that a fire and grazing interaction in these forests does not play out for many years, or that abiotic factors such as precipitation and drought may override or confound treatment responses. For example, inconsistencies among grazing studies in semi-arid regions may be due to interannual variability in precipitation that obscures grazing effects on plant communities (Fuhlendorf & Engle, 2001; Souther et al., 2020). While our study is long term, we lack annual data and thus are unable to decipher precipitation-related patterns.

A likely contributing factor to differences in short- and long-term results is the temporal variability associated with the sampling years used in each study and time since the fire. The current study was weighted to postburn years (1–2), and only included one 5-year recovery sampling date. Our prior study included 1 year of pretreatment data for the newly established grazing experiment, one postburn year (2004, 2 years after burning and 2 years after the study was established), and one 5-year recovery year (2007). Cattle preference, use, and grazing utilization in recently burned patches decline as time since fire increases (Allred et al., 2011; Powell et al., 2018). Thus, it may be more likely to detect a fire and grazing interaction 1–2 years after burning compared with 5 years after burning. The total cover data in this study partially support this interpretation, with a larger effect size in 2009 (~15%) and a smaller effect in 2012 (~12%). However, the effect size in the 1–2 post-burn year of 2015 was the smallest, in contrast to expectations. Like the discussion above regarding annual forb flushing, this may be because of waning fire effects by 2015 or because sampling occurred only 1 year after burning at most of the sites. Prescribed fire heterogeneity and resultant fire effects may also be important. While we strived to have similar prescriptions and conditions throughout the

almost two decades of burning in this study, spatial and temporal variability in fire effects may also drive responses.

Short-term results and other work in the area also found that fall burning exacerbated exotic species invasion (largely cheatgrass, Kerns et al., 2006, 2011; Kerns & Day, 2017b), a result not strongly evident in this study. However, results from these other studies are not directly comparable. The exotic species group used in Kerns et al. (2006, 2011) was broader and included all exotics, and data from Kerns and Day (2017b) incorporated a different set of experimental stands. In the present study, we document extremely high variability in annual grass cover among the stands used for the grazing experiment. Cheatgrass remains a problematic issue linked to fall burning at the sites with bunchgrass-dominated understories that harbored populations at the outset of the experiment; but invasion is also increasing in spring burn and even unburned areas. Propagule pressure is important for the continued persistence of an invader and invader extent, as demonstrated at this site and elsewhere (Colautti et al., 2006; Eschtruth & Battles, 2009; Kerns & Day, 2017b). In addition, biotic resistance may differ substantially at the sites. While higher community resistance to annual grass invasion has been noted in areas with abundant perennial bunchgrasses (Chambers et al., 2007; Davies, 2008; Lulow, 2006), neighboring species and resident biomass may have limited influence on invasion resistance in less productive vegetation types (Tortorelli et al., 2022). Interestingly, we continue to document no link between cheatgrass invasion and grazing, a result that conflicts with some historical observations and broad-scale studies (Condon & Pyke, 2018; Milchunas et al., 1988; Williamson et al., 2020) and studies documenting decreased invasion with grazing and fall fire and grazing at finer spatial scales (Davies et al., 2021; Porensky et al., 2020).

## CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Knowledge about fire and novel herbivore interactions in dry western forests is critical because of the widespread present and future co-occurrence of these two disturbance types and the implications for forest resilience and restoration. The sites used in this study display considerable floristic variability, which strengthens inference across a range of ponderosa pine stands. We found that total understory cover was lower in areas burned in the fall and open to grazing compared to fall burn areas where cattle were excluded. These results document patterns prior to current year utilization, but prior year

utilization also impacts present-year plant cover. Our evidence points to a grazing and fire numerically mediated interaction pathway, rather than a functionally moderated process related to species dominance and palatability. We found that total cover results were driven by consistent but modest trends across most herbaceous plant groups, rather than a few plant groups. We suggest that this pattern may be due to post-fire green-up and short-term forage equalization. There was also little evidence that species richness was affected strongly by fire and grazing. However, the broad floristic variability across these stands may obscure some community-based effects. Some plant groups, such as annual forbs and resprouting shrubs increased in response to fall fire and grazing. Long-term spring burning, a less historically characteristic burn season and frequent management concern, did not reduce understory resilience, although some species sensitivities may not be captured by our approach. The nonnative annual cheatgrass remains a problematic invader linked to fall burning but not grazing at stands with higher propagule pressure when the experiment was initiated. However, invasion was also increasing in spring burn and unburned areas at these sites.

While our burn treatments were operational in nature, they occurred within much larger unburned grazed pastures, resulting in patch burn grazing (PBG), which has noted ecological benefits in the mesic grasslands and savannas of North America and Africa and can increase diversity and vegetation heterogeneity at the landscape scale (Allred et al., 2011; Fuhlendorf et al., 2009; Fuhlendorf & Engle, 2004; McGranahan et al., 2012). We did not measure vegetation heterogeneity at the landscape scale, but some heterogeneity is likely given our results. However, we did not find an increase in species richness with PBG in this study, and we caution that the forested rangelands of the northwestern US have several notable differences compared to mesic grasslands and savannas. Our study area is characterized by a near complete lack of summer precipitation, and dominance of cool-season rather than warm-season grasses and there is a more limited (comparable to cattle) evolutionary grazing history. Additional research is needed to understand the potential ecological benefits of PBG in forested rangelands.

We caution that the combined impact of very frequent fire, cattle grazing, and annual grass invasion could erode the expected understory benefits of returning fire to these types of landscapes, particularly in the context of future global change drivers. Consideration of longer fire return intervals and resting areas (e.g., Bates & Davies, 2014) for 1–2 grazing seasons if very frequent fire regimes are used may help mitigate the effects noted in

this study. Burning larger portions of the landscape or entire pastures and use of virtual fencing (Boyd et al., 2022) could better distribute cattle and other ungulates and alleviate potential impacts owing to grazing concentration, although landscape-scale vegetation heterogeneity could be reduced with these approaches. However, we did not specifically test these suggested mitigations.

Manipulative fire and grazing studies in western forests are rare. Successfully balancing livestock production and forest rangeland conservation in the future will benefit from a more context-dependent, robust understanding that is informed by data on long-term outcomes across a variety of rangeland ecosystems (Copeland et al., 2023). Additional studies designed to elucidate both the individual and interactive effects of prescribed fire and grazing, patch scale burning, scale dependency, regime characteristics, and a more detailed understanding of interaction pathways would provide critical information to support management practices that promote forest resilience, particularly in the context of global change.

## ACKNOWLEDGMENTS

This study was largely funded by the Joint Fire Science Program (Project ID 12-1-01-10) and the National Fire Plan. We cannot list every individual who contributed to this project over the decades, but their efforts are recognized. Special thanks to Douglas Westlind for project oversight, Diana Jolles for early botanical work, Pat Cunningham, Ariel Muldoon, and Jim Baldwin for statistical consultation, Walter Thies and Christine Niwa for the initial efforts implementing the study, and the Malheur National Forest, Emigrant Creek Ranger District, for conducting periodic prescribed burns and other operational support.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Kerns & Day, 2017a) are available in the Forest Service Research Data Archive at <https://doi.org/10.2737/RDS-2017-0044>.

## ORCID

Becky K. Kerns  <https://orcid.org/0000-0003-4613-2191>

## REFERENCES

- Abella, S. R., and J. D. Springer. 2015. "Effects of Tree Cutting and Fire on Understory Vegetation in Mixed Conifer Forests." *Forest Ecology and Management* 335: 281–299.
- Adler, P. B., D. G. Milchunas, W. K. Lauenroth, O. E. Sala, and I. C. Burke. 2004. "Functional Traits of Graminoids in Semi-Arid



- Steppes: A Test of Grazing Histories." *Journal of Applied Ecology* 41: 653–663.
- Agee, J. K. 1993. *Ecology of Pacific Northwest Forests*. Washington: Island Press.
- Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. "Ungulate Preference for Burned Patches Reveals Strength of Fire–Grazing Interaction." *Ecology and Evolution* 1: 132–144.
- Archibald, S., W. J. Bond, W. D. Stock, and D. H. K. Fairbanks. 2005. "Shaping the Landscape: Fire–Grazer Interactions in an African Savanna." *Ecological Applications* 15: 96–109.
- Augustine, D. J., and S. J. McNaughton. 1998. "Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance." *Journal of Wildlife Management* 62: 1165–83.
- Bates, J. D., and K. W. Davies. 2014. "Cattle Grazing and Vegetation Succession on Burned Sagebrush Steppe." *Rangeland Ecology & Management* 67: 412–422.
- Bates, J. D., E. C. Rhodes, K. W. Davies, and R. Sharp. 2009. "Postfire Succession in Big Sagebrush Steppe with Livestock Grazing." *Rangeland Ecology & Management* 62: 98–110.
- Beever, E. 2003. "Management Implications of the Ecology of Free-Roaming Horses in Semi-Arid Ecosystems of the Western United States." *Wildlife Society Bulletin* 31: 887–895.
- Belsky, A. J., and D. M. Blumenthal. 1997. "Effects of Livestock Grazing on Stand Dynamics and Soils in Upland Forests of the Interior West." *Conservation Biology* 11: 315–327.
- Beschta, R. L., D. L. Donahue, D. A. DellaSala, J. J. Rhodes, J. R. Karr, M. H. O'Brien, T. L. Fleischner, and C. D. Williams. 2012. "Adapting to Climate Change on Western Public Lands: Addressing the Ecological Effects of Domestic, Wild, and Feral Ungulates." *Environmental Management* 51: 474–491.
- Bond, W. J., and J. E. Keeley. 2005. "Fire as a Global 'Herbivore': The Ecology and Evolution of Flammable Ecosystems." *Trends in Ecology & Evolution* 20: 387–394.
- Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. "The Global Distribution of Ecosystems in a World without Fire." *New Phytologist* 165: 525–537.
- Borman, M. M. 2005. "Forest Stand Dynamics and Livestock Grazing in Historical Context." *Conservation Biology* 19: 1658–62.
- Bowd, E. J., D. B. Lindenmayer, S. C. Banks, and D. P. Blair. 2018. "Logging and Fire Regimes Alter Plant Communities." *Ecological Applications* 28: 826–841.
- Bowman, D. M. J. S., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio, et al. 2009. "Fire in the Earth System." *Science* 324: 481–84.
- Boyd, C. S., R. O'Connor, J. Ranches, D. W. Bohnert, J. D. Bates, D. D. Johnson, K. W. Davies, T. Parker, and K. E. Doherty. 2022. "Virtual Fencing Effectively Excludes Cattle from Burned Sagebrush Steppe." *Rangeland Ecology & Management* 81: 55–62.
- Brooks, M. L., C. M. D'antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. "Effects of Invasive Alien Plants on Fire Regimes." *Bioscience* 54: 677–688.
- Brown, J. K., and J. K. Smith, eds. 2000. *Wildland Fire in Ecosystems: Effects of Fire on Flora*. Ogden: USDA Forest Service, Rocky Mountain Research Station.
- Burton, P. J., A. Jentsch, and L. R. Walker. 2020. "The Ecology of Disturbance Interactions." *Bioscience* 70: 854–870.
- Busse, M. D., S. A. Simon, and G. M. Riegel. 2000. "Tree-Growth and Understory Responses to Low-Severity Prescribed Burning in Thinned *Pinus ponderosa* Forest of Central Oregon." *Forest Science* 46: 258–268.
- Callaway, R. M., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. "Unpalatable Plants Protect Neighbors from Grazing and Increase Plant Community Diversity." *Ecology* 86: 1856–62.
- Cardoso, A. W., I. Oliveras, K. A. Abernethy, K. J. Jeffery, D. Lehmann, J. Edzang Ndong, I. McGregor, C. M. Belcher, W. J. Bond, and Y. S. Malhi. 2018. "Grass Species Flammability, Not Biomass, Drives Changes in Fire Behaviour at Tropical Forest-Savanna Transitions." *Frontiers in Forests and Global Change* 1: 6. <https://doi.org/10.3389/ffgc.2018.00006>.
- Carlson, G. 1974. *Soil Resource Inventory Basic Soil Information and Interpretive Tables: Malheur National Forest*. Portland: USDA Forest Service, Pacific Northwest Region.
- Chambers, J. C., B. A. Roundy, R. B. Blank, S. E. Meyer, and A. Whittaker. 2007. "What Makes Great Basin Sagebrush Ecosystems Invasible by *Bromus tectorum*?" *Ecological Monographs* 77: 117–145.
- Cingolani, A. M., I. Noy-Meir, and S. Díaz. 2005. "Grazing Effects on Rangeland Diversity: A Synthesis of Contemporary Models." *Ecological Applications* 15: 757–773.
- Colautti, R., I. Grigorovich, and H. MacIsaac. 2006. "Propagule pressure: a null model for biological invasions." *Biological Invasions* 8: 1023–37.
- Collins, S. L. 1987. "Interaction of Disturbances in Tallgrass Prairie: A Field Experiment." *Ecology* 68: 1243–50.
- Collins, S. L., and L. B. Calabrese. 2012. "Effects of Fire, Grazing and Topographic Variation on Vegetation Structure in Tallgrass Prairie." *Journal of Vegetation Science* 23: 563–575.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. "Modulation of Diversity by Grazing and Mowing in Native Tallgrass Prairie." *Science* 280: 745–47.
- Collins, S. L., and M. D. Smith. 2006. "Scale-Dependent Interaction of Fire and Grazing on Community Heterogeneity in Tallgrass Prairie." *Ecology* 87: 2058–67.
- Condon, L. A., and D. A. Pyke. 2018. "Fire and Grazing Influence Site Resistance to *Bromus tectorum* through their Effects on Shrub, Bunchgrass and Biocrust Communities in the Great Basin (USA)." *Ecosystems* 21: 1416–31.
- Copeland, S. M., D. L. Hoover, D. J. Augustine, J. D. Bates, C. S. Boyd, K. W. Davies, J. D. Derner, M. C. Duniway, L. M. Porensky, and L. T. Vermeire. 2023. "Variable Effects of Long-Term Livestock Grazing across the Western United States Suggest Diverse Approaches Are Needed to Meet Global Change Challenges." *Applied Vegetation Science* 26: e12719. <https://doi.org/10.1111/avsc.12719>.
- Courant, S., and D. Fortin. 2010. "Foraging Decisions of Bison for Rapid Energy Gains Can Explain the Relative Risk to Neighboring Plants in Complex Swards." *Ecology* 91: 1841–49.
- Cumming, D. H. M., and G. S. Cumming. 2003. "Ungulate Community structure and Ecological Processes: Body Size, Hoof Area and Trampling in African Savannas." *Oecologia* 134(4): 560–68. <https://doi.org/10.1007/s00442-002-1149-4>.

- Davies, K. W. 2008. "Medusahead Dispersal and Establishment in Sagebrush Steppe Plant Communities." *Rangeland Ecology & Management* 61: 110–15.
- Davies, K. W., J. D. Bates, C. S. Boyd, and T. J. Svejcar. 2016. "Prefire Grazing by Cattle Increases Postfire Resistance to Exotic Annual Grass (*Bromus tectorum*) Invasion and Dominance for Decades." *Ecology and Evolution* 6: 3356–66.
- Davies, K. W., J. D. Bates, B. Perryman, and S. Arispe. 2021. "Fall–Winter Grazing after Fire in Annual Grass-Invaded Sagebrush Steppe Reduced Annuals and Increased a Native Bunchgrass." *Rangeland Ecology & Management* 77: 1–8.
- Davies, K. W., J. D. Bates, T. J. Svejcar, and C. S. Boyd. 2010. "Effects of Long-Term Livestock Grazing on Fuel Characteristics in Rangelands: An Example from the Sagebrush Steppe." *Rangeland Ecology & Management* 63: 662–69.
- Davies, K. W., C. S. Boyd, J. D. Bates, and A. Hulet. 2016. "Winter Grazing Can Reduce Wildfire Size, Intensity and Behaviour in a Shrub-Grassland." *International Journal of Wildland Fire* 25: 191–99.
- Davies, K. W., T. J. Svejcar, and J. D. Bates. 2009. "Interaction of Historical and Nonhistorical Disturbances Maintains Native Plant Communities." *Ecological Applications* 19: 1536–45.
- Davies, K. W., K. Wollstein, B. Dragt, and C. O'Connor. 2022. "Grazing Management to Reduce Wildfire Risk in Invasive Annual Grass Prone Sagebrush Communities." *Rangelands* 44: 194–99.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. *Fire Effects on Ecosystems*. New York: John Wiley & Sons.
- Diamond, J. M., C. A. Call, and N. Devoe. 2009. "Effects of Targeted Cattle Grazing on Fire Behavior of Cheatgrass-Dominated Rangeland in the Northern Great Basin, USA." *International Journal of Wildland Fire* 18: 944–950.
- Diamond, J. M., C. A. Call, and N. Devoe. 2012. "Effects of Targeted Grazing and Prescribed Burning on Community and Seed Dynamics of a Downy Brome (*Bromus tectorum*)-Dominated Landscape." *Invasive Plant Science and Management* 5: 259–269.
- Diaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. Casanoves, D. G. Milchunas, C. Skarpe, et al. 2007. "Plant Trait Responses to Grazing—A Global Synthesis." *Global Change Biology* 13: 313–341.
- Didham, R. K., J. M. Tylianakis, N. J. Gemmill, T. A. Rand, and R. M. Ewers. 2007. "Interactive Effects of Habitat Modification and Species Invasion on Native Species Decline." *Trends in Ecology and Evolution* 22: 489–496.
- Donovan, V. M., C. P. Roberts, D. T. Fogarty, D. A. Wedin, and D. Twidwell. 2022. "Targeted Grazing and Mechanical Thinning Enhance Forest Stand Resilience under a Narrow Range of Wildfire Scenarios." *Ecosphere* 13: e4061. <https://doi.org/10.1002/ecs2.4061>.
- Eby, S., D. E. Burkepile, R. W. Fynn, C. E. Burns, N. Govender, N. Hagenah, S. E. Koerner, K. J. Matchett, D. I. Thompson, and K. R. Wilcox. 2014. "Loss of a Large Grazer Impacts Savanna Grassland Plant Communities Similarly in North America and South Africa." *Oecologia* 175: 293–303.
- Eschtruth, A. K., and J. J. Battles. 2009. "Assessing the Relative Importance of Disturbance, Herbivory, Diversity, and Propagule Pressure in Exotic Plant Invasion." *Ecological Monographs* 79: 265–280.
- Falk, D. A., P. J. van Mantgem, J. E. Keeley, R. M. Gregg, C. H. Guiterman, A. J. Tepley, D. J. Young, and L. A. Marshall. 2022. "Mechanisms of Forest Resilience." *Forest Ecology and Management* 512: 120129.
- Farnsworth, K., and A. Illius. 1998. "Optimal Diet Choice for Large Herbivores: An Extended Contingency Model." *Functional Ecology* 12: 74–81.
- Fleischner, T. L. 1994. "Ecological Costs of Livestock Grazing in Western North America." *Conservation Biology* 8: 629–644.
- Fortin, D., J. A. Merkle, M. Sigaud, S. G. Cherry, S. Plante, A. Drolet, and M. Labrecque. 2015. "Temporal Dynamics in the Foraging Decisions of Large Herbivores." *Animal Production Science* 55: 376–383.
- Foster, C. N., P. S. Barton, C. F. Sato, C. I. MacGregor, and D. B. Lindenmayer. 2015. "Synergistic Interactions between Fire and Browsing Drive Plant Diversity in a Forest Understorey." *Journal of Vegetation Science* 26: 1112–23.
- Fuhlendorf, S. D., and D. M. Engle. 2001. "Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns: We Propose a Paradigm that Enhances Heterogeneity Instead of Homogeneity to Promote Biological Diversity and Wildlife Habitat on Rangelands Grazed by Livestock." *Bioscience* 51: 625–632.
- Fuhlendorf, S. D., and D. M. Engle. 2004. "Application of the Fire-Grazing Interaction to Restore a Shifting Mosaic on Tallgrass Prairie." *Journal of Applied Ecology* 41: 604–614.
- Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2009. "Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing." *Conservation Biology* 23: 588–598.
- Gibson, D. J., and L. C. Hulbert. 1987. "Effects of Fire, Topography and Year-to-Year Climatic Variation on Species Composition in Tallgrass Prairie." *Vegetatio* 72: 175–185.
- Hambäck, P. A., and A. P. Beckerman. 2003. "Herbivory and Plant Resource Competition: A Review of Two Interacting Interactions." *Oikos* 101: 26–37.
- Hatten, J., D. Zabowski, A. Ogden, and W. Thies. 2008. "Soil Organic Matter in a Ponderosa Pine Forest with Varying Seasons and Intervals of Prescribed Burn." *Forest Ecology and Management* 255: 2555–65.
- Hayes, G. F., and K. D. Holl. 2003. "Cattle Grazing Impacts on Annual Forbs and Vegetation Composition of Mesic Grasslands in California." *Conservation Biology* 17: 1694–1702.
- He, T., B. B. Lamont, and J. G. Pausas. 2019. "Fire as a Key Driver of Earth's Biodiversity." *Biological Reviews* 94: 1983–2010.
- Heggenes, J., A. Odland, T. Chevalier, J. Ahlberg, A. Berg, H. Larsson, and D. K. Bjerketvedt. 2017. "Herbivore Grazing—Or Trampling? Trampling Effects by a Large Ungulate in Cold High-Latitude Ecosystems." *Ecology and Evolution* 7: 6423–31.
- Hernández, E., E. A. Shaw, L. Aoyama, A. Brambila, C. Niederer, S. B. Weiss, and L. M. Hallett. 2021. "Fire Versus Grazing as Tools to Restore Serpentine Grasslands under Global Change." *Restoration Ecology* 29: e13353. <https://doi.org/10.1111/rec.13353>.
- Holland, G. J., M. F. Clarke, and A. F. Bennett. 2017. "Prescribed Burning Consumes Key Forest Structural Components: Implications for Landscape Heterogeneity." *Ecological Applications* 27: 845–858.

- Huntsinger, L., and P. Starrs. 2010. "Rangeland Grazing in North American Commercial Ranching." In *Range and Animal Sciences and Resources Management*, Vol. 1, edited by V. R. Squires, 60–91. Oxford, UK: Eolss Publishers Co Ltd.
- Jones, A. 2000. "Effect of Cattle Grazing on North American Arid Ecosystems: A Quantitative Review." *Western North American Naturalist* 60: 155–164.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. "Fire and Grazing Impacts on Plant Diversity and Alien Plant Invasions in the Southern Sierra Nevada." *Ecological Applications* 13: 1355–74.
- Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. "Fire as an Evolutionary Pressure Shaping Plant Traits." *Trends in Plant Science* 16: 406–411.
- Kerns, B. K., M. Buonopane, W. G. Thies, and C. Niwa. 2011. "Reintroducing Fire into a Ponderosa Pine Forest with and without Cattle Grazing: Understory Vegetation Response." *Ecosphere* 2: 1–23.
- Kerns, B. K., and M. A. Day. 2017b. "The Importance of Disturbance by Fire and Other Abiotic and Biotic Factors in Driving Cheatgrass Invasion Varies Based on Invasion Stage." *Biological Invasions* 19: 1853–62.
- Kerns, B. K., and M. A. Day. 2018. "Prescribed Fire Regimes Subtly Alter Ponderosa Pine Forest Plant Community Structure." *Ecosphere* 9: e02529. <https://doi.org/10.1002/ecs2.2529>.
- Kerns, B. K., W. G. Thies, and C. G. Niwa. 2006. "Season and Severity of Prescribed Burn in Ponderosa Pine Forests: Implications for Understory Native and Exotic Plants." *Ecoscience* 13: 44–55.
- Kerns, B. K., and D. J. Westlind. 2013. "Effect of Season and Interval of Prescribed Burn on Ponderosa Pine Butterfly Defoliation Patterns." *Canadian Journal of Forest Research* 43: 979–983.
- Kerns, B. K., and M. A. Day. 2017a. *Season and Interval of Burning and Cattle Exclusion in the Southern Blue Mountains, Oregon: Understory Vegetation Attributes*. Fort Collins: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2017-0044>.
- Knapp, E. E., B. L. Estes, and C. N. Skinner. 2009. *Ecological Effects of Prescribed Fire Season: A Literature Review and Synthesis for Managers*. General Technical Report PSW-GTR-224. Albany: USDA Forest Service, Pacific Southwest Research Station.
- Knapp, E. E., S. Sawyer, S. Hood, B. K. Kerns, F. K. Lake, J. Miesel, M. P. North, D. W. Peterson, J. W. Wagenbrenner, and P. R. Robichaud. in press. "Chapter 6: Effects of Prescribed Fire: Western Forests."
- Lentile, L. B., P. Morgan, A. T. Hudak, M. J. Bobbitt, S. A. Lewis, A. M. Smith, and P. R. Robichaud. 2007. "Post-Fire Burn Severity and Vegetation Response Following Eight Large Wildfires across the Western United States." *Fire Ecology* 3: 91–108.
- Lulow, M. E. 2006. "Invasion by Non-native Annual Grasses: The Importance of Species Biomass, Composition, and Time among California Native Grasses of the Central Valley." *Restoration Ecology* 14: 616–626.
- Mack, R. N., and J. N. Thompson. 1982. "Evolution in Steppe with Few Large, Hooved Mammals." *The American Naturalist* 119: 757–773.
- Madany, M. H., and N. E. West. 1983. "Livestock Grazing-Fire Regime Interactions within Montane Forests of Zion National Park, Utah." *Ecology* 64: 661–67.
- Malhi, Y., C. E. G. Doughty, F. A. Mauro, J.-C. S. Smith, and J. W. Terborgh. 2016. "Megafauna and Ecosystem Function from the Pleistocene to the Anthropocene." *Proceedings of the National Academy of Sciences* 113: 838–846.
- Martin, J. M., R. A. Short, G. E. Plumb, L. Markewicz, D. H. Van Vuren, B. Wehus-Tow, E. Otarola-Castillo, and M. E. Hill, Jr. 2022. "Integrated Evidence-Based Extent of Occurrence for North American Bison (*Bison bison*) since 1500 CE and before." *Ecology* 104: e3864.
- Matthews, R. 2021. "The p-Value Statement, Five Years on." *Significance* 18: 16–19.
- McGranahan, D. A., D. M. Engle, S. D. Fuhlendorf, S. J. Winter, J. R. Miller, and D. M. Debinski. 2012. "Spatial Heterogeneity across Five Rangelands Managed with Pyric-Herbivory." *Journal of Applied Ecology* 49: 903–910.
- McNaughton, S. 1979. "Grassland-Herbivore Dynamics." In *Serengeti: Dynamics of an Ecosystem*, 46–81. Chicago, IL: University of Chicago.
- McNaughton, S. J. 1983. "Serengeti Grassland Ecology: The Role of Composite Environmental Factors and Contingency in Community Organization." *Ecological Monographs* 53: 291–320.
- McWethy, D. B., T. Schoennagel, P. E. Higuera, M. Krawchuk, B. J. Harvey, E. C. Metcalf, C. Schultz, et al. 2019. "Rethinking Resilience to Wildfire." *Nature Sustainability* 2: 797–804.
- Milchunas, D. G., and W. K. Lauenroth. 1993. "Quantitative Effects of Grazing on Vegetation and Soils over a Global Range of Environments." *Ecological Monographs* 63: 327–366.
- Milchunas, D. G., W. K. Lauenroth, and I. C. Burke. 1998. "Livestock Grazing: Animal and Plant Biodiversity of Shortgrass Steppe and the Relationship to Ecosystem Function." *Oikos* 83: 65–74.
- Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. "A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure." *The American Naturalist* 132: 87–106.
- North, M. P., R. A. York, B. M. Collins, M. D. Hurteau, G. M. Jones, E. E. Knapp, L. Kobziar, et al. 2021. "Pyrosilviculture Needed for Landscape Resilience of Dry Western United States Forests." *Journal of Forestry* 119: 520–544.
- Owen-Smith, R. N. 1988. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University Press.
- Pausas, J. G., and J. E. Keeley. 2014. "Evolutionary Ecology of Resprouting and Seeding in Fire-Prone Ecosystems." *New Phytologist* 204: 55–65.
- Pekin, B. K., B. A. Endress, M. J. Wisdom, B. J. Naylor, and C. G. Parks. 2015. "Impact of Ungulate Exclusion on Understorey Succession in Relation to Forest Management in the Intermountain Western United States." *Applied Vegetation Science* 18: 252–260.
- Pekin, B. K., M. J. Wisdom, C. G. Parks, B. A. Endress, and B. J. Naylor. 2016. "Response of Native Versus Exotic Plant Guilds to Cattle and Elk Herbivory to Forested Rangeland." *Applied Vegetation Science* 19: 31–39.
- Porensky, L. M., R. McGee, and D. W. Pellatz. 2020. "Long-Term Grazing Removal Increased Invasion and Reduced Native



- Plant Abundance and Diversity in a Sagebrush Grassland.” *Global Ecology and Conservation* 24: e01267. <https://doi.org/10.1016/j.gecco.2020.e01267>.
- Powell, J., B. Martin, V. J. Dreitz, and B. W. Allred. 2018. “Grazing Preferences and Vegetation Feedbacks of the Fire-Grazing Interaction in the Northern Great Plains.” *Rangeland Ecology & Management* 71: 45–52.
- Powers, H. A., and R. E. Wilcox. 1964. “Volcanic Ash from Mount Mazama (Crater Lake) and from Glacier Peak.” *Science* 144: 1334–36.
- Price, J. N., J. Sitters, T. Ohlert, P. M. Tognetti, C. S. Brown, E. W. Seabloom, E. T. Borer, et al. 2022. “Evolutionary History of Grazing and Resources Determine Herbivore Exclusion Effects on Plant Diversity.” *Nature Ecology and Evolution* 6: 1290–98.
- Prichard, S. J., P. F. Hessburg, R. K. Hagmann, N. A. Povak, S. Z. Dobrowski, M. D. Hurteau, V. R. Kane, R. E. Keane, L. N. Kobziar, and C. A. Kolden. 2021. “Adapting Western North American Forests to Climate Change and Wildfires: 10 Common Questions.” *Ecological Applications* 31: e02433. <https://doi.org/10.1002/eap.2433>.
- Pyke, D. A., M. L. Brooks, and C. D’Antonio. 2010. “Fire as a Restoration Tool: A Decision Framework for Predicting the Control or Enhancement of Plants Using Fire.” *Restoration Ecology* 18: 27–284.
- Ramsey, F., and D. Schafer. 2012. *The Statistical Sleuth: A Course in Methods of Data Analysis*, 2nd ed. Pacific Grove: Wadsworth Group.
- Romme, W. H., M. S. Boyce, R. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. “Twenty Years after the 1988 Yellowstone Fires: Lessons about Disturbance and Ecosystems.” *Ecosystems* 14: 1196–1215.
- Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. “Pervasive Interactions between Ungulate Browsers and Disturbance Regimes Promote Temperate Forest Herbaceous Diversity.” *Ecology* 91: 93–105.
- Scasta, J. D., C. Duchardt, D. M. Engle, J. R. Miller, D. M. Debinski, and R. N. Harr. 2016. “Constraints to Restoring Fire and Grazing Ecological Processes to Optimize Grassland Vegetation Structural Diversity.” *Ecological Engineering* 95: 865–875.
- Senft, R., M. Coughenour, D. Bailey, L. Rittenhouse, O. Sala, and D. Swift. 1987. “Large Herbivore Foraging and Ecological Hierarchies.” *Bioscience* 37: 789–799.
- Sitters, J., E. S. Bakker, M. P. Veldhuis, G. Veen, H. Olde Venterink, and M. J. Vanni. 2017. “The Stoichiometry of Nutrient Release by Terrestrial Herbivores and its Ecosystem Consequences.” *Frontiers in Earth Science* 5: 32. <https://doi.org/10.3389/feart.2017.00032>.
- Smith, F. A., C. E. Doughty, Y. Malhi, J. C. Svenning, and J. Terborgh. 2016. “Megafauna in the Earth System.” *Ecography* 39: 99–108.
- Smith, J. E., D. McKay, C. G. Niwa, W. G. Thies, G. Brenner, and J. W. Spatafora. 2004. “Short-Term Effects of Seasonal Prescribed Burning on the Ectomycorrhizal Fungal Community and Fine Root Biomass in Ponderosa Pine Stands in the Blue Mountains of Oregon.” *Canadian Journal of Forest Research* 34: 2477–91.
- Souther, S., M. Loeser, T. E. Crews, and T. Sisk. 2020. “Drought Exacerbates Negative Consequences of High-Intensity Cattle Grazing in a Semiarid Grassland.” *Ecological Applications* 30: e02048. <https://doi.org/10.1002/eap.2048>.
- Spasojevic, M. J., R. J. Aicher, G. R. Koch, E. S. Marquardt, N. Mirotchnick, T. G. Troxler, and S. L. Collins. 2010. “Fire and Grazing in a Mesic Tallgrass Prairie: Impacts on Plant Species and Functional Traits.” *Ecology* 91: 1651–59.
- Stephan, K., M. Miller, and M. B. Dickinson. 2010. “First-Order Fire Effects on Herbs and Shrubs: Present Knowledge and Process Modeling Needs.” *Fire Ecology* 6: 95–114.
- Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. Peery, C. A. Schultz, and S. Thompson. 2020. “Fire and Climate Change: Conserving Seasonally Dry Forests Is Still Possible.” *Frontiers in Ecology and the Environment* 18: 354–360.
- Stevens, J. T., M. M. Kling, D. W. Schwilk, J. M. Varner, and J. M. Kane. 2020. “Biogeography of Fire Regimes in Western U.S. Conifer Forests: A Trait-Based Approach.” *Global Ecology and Biogeography* 29: 944–955.
- Stewart, K. M., R. T. Bowyer, J. Kie, B. L. Dick, and M. Ben-David. 2003. “Niche Partitioning among Mule Deer, Elk, and Cattle: Do Stable Isotopes Reflect Dietary Niche?” *Ecoscience* 10: 297–302.
- Strahan, R. T., D. C. Laughlin, J. D. Bakker, and M. M. Moore. 2015. “Long-Term Protection from Heavy Livestock Grazing Affects Ponderosa Pine Understory Composition and Functional Traits.” *Rangeland Ecology & Management* 68: 257–265.
- Strahan, R. T., M. T. Stoddard, J. D. Springer, and D. W. Huffman. 2015. “Increasing Weight of Evidence that Thinning and Burning Treatments Help Restore Understory Plant Communities in Ponderosa Pine Forests.” *Forest Ecology and Management* 353: 208–220.
- Svejcar, T., C. Boyd, K. Davies, M. Madsen, J. Bates, R. Sheley, C. Marlow, D. Bohnert, M. Borman, and R. Mata-González. 2014. “Western Land Managers Will Need all Available Tools for Adapting to Climate Change, Including Grazing: A Critique of Beschta Et al.” *Environmental Management* 53: 1035–38.
- Thies, W. G., D. J. Westlind, and M. Loewen. 2005. “Season of Prescribed Burn in Ponderosa Pine Forests in Eastern Oregon: Impact of Pine Mortality.” *International Journal of Wildland Fire* 14: 223–231.
- Thies, W. G., D. J. Westlind, M. Loewen, and G. Brenner. 2006. “Prediction of Delayed Mortality of Fire-Damaged Ponderosa Pine Following Prescribed Fires in Eastern Oregon, USA.” *International Journal of Wildland Fire* 15: 19–29.
- Tomás, M. A., A. D. Carrera, and M. Poverene. 2000. “Is there any Genetic Differentiation among Populations of *Piptochaetium napostaense* (Speg.) Hack (Poaceae) with Different Grazing Histories?” *Plant Ecology* 147: 227–235.
- Tortorelli, C. M., B. K. Kerns, and M. A. Krawchuk. 2022. “Community Invasion Resistance Is Influenced by Interactions between Plant Traits and Site Productivity.” *Ecology* 103: e3697.
- Trlica, M. J., and L. R. Rittenhouse. 1993. “Grazing and Plant Performance.” *Ecological Applications* 3: 21–23.
- USDA, Forest Service. 2022. “Confronting the Wildfire Crisis: A Strategy for Protecting Communities and Improving Resilience in America’s Forests.” FS-1187a. [https://www.fs.usda.gov/sites/default/files/fs\\_media/fs\\_document/Confronting-the-Wildfire-Crisis.pdf](https://www.fs.usda.gov/sites/default/files/fs_media/fs_document/Confronting-the-Wildfire-Crisis.pdf).
- USDA Forest Service. 2023. “Grazing Statistical Summary Reports.” <https://www.fs.usda.gov/rangeland-management/reports/index.shtml>.



- Veen, G. F. C., J. M. Blair, M. D. Smith, and S. L. Collins. 2008. "Influence of Grazing and Fire Frequency on Small-Scale Plant Community Structure and Resource Variability in Native Tallgrass Prairie." *Oikos* 117: 859–866.
- Vermeire, L. T., R. B. Mitchell, S. D. Fuhlendorf, and R. L. Gillen. 2004. "Patch Burning Effects on Grazing Distribution." *Journal of Range Management* 57: 248–252.
- Vesk, P. A., and M. Westoby. 2001. "Predicting Plant species' Responses to Grazing." *Journal of Applied Ecology* 38: 897–909.
- Wasserstein, R. L., and N. A. Lazar. 2016. "The ASA Statement on *p*-Values: Context, Process, and Purpose." *The American Statistician* 70: 129–133.
- Webster, K. M., and C. B. Halpern. 2010. "Long-Term Vegetation Responses to Reintroduction and Repeated Use of Fire in Mixed-Conifer Forests of the Sierra Nevada." *Ecosphere* 1: 1–27.
- Westlind, D., and B. Kerns. 2017. "Long-Term Effects of Burn Season and Frequency on Ponderosa Pine Forest Fuels and Seedlings." *Fire Ecology* 13: 42–61.
- Williamson, M. A., E. Fleishman, R. C. Mac Nally, J. C. Chambers, B. A. Bradley, D. S. Dobkin, D. I. Board, et al. 2020. "Fire, Livestock Grazing, Topography, and Precipitation Affect Occurrence and Prevalence of Cheatgrass (*Bromus tectorum*) in the Central Great Basin, USA." *Biological Invasions* 22: 663–680.
- Willms, J., A. Bartuszevige, D. W. Schwilk, and P. L. Kennedy. 2017. "The Effects of Thinning and Burning on Understory Vegetation in North America: A Meta-Analysis." *Forest Ecology and Management* 392: 184–194.
- Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. "Understanding Ungulate Herbivory-Episodic Disturbance Effects on Vegetation Dynamics: Knowledge Gaps and Management Needs." *Wildlife Society Bulletin* 34: 283–292.
- Zald, H. S., B. K. Kerns, and M. A. Day. 2020. "Limited Effects of Long-Term Repeated Season and Interval of Prescribed Burning on Understory Vegetation Compositional Trajectories and Indicator Species in Ponderosa Pine Forests of Northeastern Oregon, USA." *Forests* 11: 834.
- Zimmerman, G. T., and L. F. Neuenschwander. 1984. "Livestock Grazing Influences on Community Structure, Fire Intensity, and Fire Frequency within the Douglas Fir/Ninebark Habitat Type." *Journal of Range Management* 37: 104–110.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Kerns, Becky K., and Michelle A. Day. 2024. "Long-Term Frequent Fire and Cattle Grazing Alter Dry Forest Understory Vegetation." *Ecological Applications* e2972. <https://doi.org/10.1002/eap.2972>