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## ARTICLE

# Ungulate herbivores as drivers of aspen recruitment and understory composition throughout arid montane landscapes

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## Abstract

Herbivory by wild and domestic ungulates can influence tree recruitment and understory forest communities throughout the world. Herbivore-driven declines in tree recruitment have been observed for quaking aspen (*Populus tremuloides*), a foundation species whose health and management is recognized as a critical priority throughout much of its range. Livestock fencing is commonly used to promote aspen regeneration, but its effectiveness is rarely assessed, especially across large spatial scales. Using a livestock-reduction experiment, we evaluated the effects of ungulate herbivory on aspen in the Great Basin and southern Cascades, an expansive and environmentally heterogeneous region where aspen faces the interacting threats of climate change, conifer encroachment, and herbivory. We found that livestock fencing only reduced the intensity of herbivore browsing on aspen when wild ungulate abundance was low and did not increase stem densities of aspen recruits. Contrary to expectations, wild ungulate abundance was a strong driver of browsing intensity on juvenile aspen within fenced, but not unfenced, aspen stands, and when the abundance of these herbivores was high, browsing intensity in fenced stands exceeded that in unfenced stands. The density of aspen recruits decreased with browsing intensity on juvenile aspen and with the density of both adult aspen and conifers, suggesting that both herbivory and intra- and interspecific competition are important drivers of recruitment. Fire history was also an important driver of recruitment, with stands that burned 10–20 years ago having the greatest density of aspen recruits. Finally, in the stand understory, we found that livestock fencing decreased forb cover, increased shrub species richness, and increased the cover of exotic annual grasses, a group dominated by *Bromus tectorum*. This latter finding suggests that livestock fencing may not be appropriate in areas where controlling the spread of this invader is a priority. In sum, our findings indicate that aspen recruitment is limited by browsing by both wild and domestic ungulates, is mediated by competition with neighboring trees and fire history, and will

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require management actions beyond livestock fencing, as this approach does not control browsing by wild ungulates.

#### KEYWORDS

fire history, Great Basin, livestock-reduction experiment, mammalian herbivory, plant community, *Populus tremuloides*, southern Cascades, wildlife

## INTRODUCTION

Herbivory by wild and domestic ungulates can be a major driver of forest health and regeneration for a wide range of tree species throughout the world (Bernes et al., 2018; Beschta & Ripple, 2009; Côté et al., 2004; Danell et al., 2003; Redick & Jacobs, 2020). Numerous studies have documented that browsing can cause reduced tree recruitment (Bradshaw & Waller, 2016; Faison et al., 2016), large-scale changes in forest demographics (Davis et al., 2011), and shifts in the structure and composition of understory plant communities (Martin et al., 2011; Tanentzap et al., 2011). In an era of unprecedented global change, ungulate browsing may have especially severe consequences for forests, as many tree species are already suffering declines due to a variety of anthropogenic stressors, including drought and high temperatures (Allen et al., 2010; Anderegg et al., 2015; van Mantgem et al., 2009), altered fire regimes (Cohen et al., 2016), and novel pests and pathogens (Kautz et al., 2017; Sturrock et al., 2011; Weed et al., 2013). The successful management of forests experiencing novel climatic and disturbance regimes will require a broader understanding of how the intensity and effects of ungulate herbivory vary across vast, heterogeneous landscapes and the extent to which actions to mitigate ungulate herbivory effectively promote the health and resilience of forests.

A growing number of studies have found that browsing by wild and domestic ungulates can limit the recruitment of quaking aspen, *Populus tremuloides* (Refsland & Cushman, 2021; Rhodes, Larsen, Maxwell, et al., 2018; Rogers & Mittanck, 2014; Seager et al., 2013), a tree species that influences a wide range of ecosystem services and has a vast distribution in North America (Rogers et al., 2020). Browsing on juvenile aspen removes both foliage and apical meristems, often preventing these trees from attaining sufficient height to escape ungulate herbivory and recruit into the forest overstory (Baker et al., 1997; Smith et al., 1972). Failure of juvenile aspen to recruit into the overstory can alter the population dynamics of stands, resulting in missing age/size classes and even the replacement of aspen with other tree species (Brown et al., 2006; Shinneman & McIlroy, 2019). In addition, extensive browsing of aspen by ungulates has the capacity to alter the vegetation composition of the

stand understory (Kay, 2001a; Kay & Bartos, 2000). Because it provides valuable habitat and food for diverse wildlife species, loss of or changes to understory vegetation can substantially reduce the value of aspen stands for these species (Augustine & McNaughton, 1998). Therefore, intense browsing not only places aspen stands at risk of long-term decline due to reduced recruitment but also compromises the immense habitat value provided by this foundation species.

In the more arid portions of its range, herbivore-driven declines in the recruitment of aspen may be exacerbated by stress-induced mortality due to drought (Michaelian et al., 2011), high temperatures (Luo & Chen, 2015), pests and pathogens (Morelli & Carr, 2011), and competition from encroaching conifers (Clement et al., 2019; Jones et al., 2005). These stressors may increase aspen's susceptibility to browsing by reducing the resources available to escape or defend against herbivory via compensatory growth (Baret & DesRochers, 2011; Carmona et al., 2011) and/or resistance mediated by defensive compounds (Donaldson et al., 2006; Rhodes, Anderson, & St. Clair, 2017). Because herbivory interacts with anthropogenic stressors (Bailey & Whitham, 2002; Smith et al., 2016; White et al., 2003), informed management of aspen populations requires evaluating its responses to herbivory within the context of these other stressors.

Researchers and land managers have addressed the impacts of ungulates on aspen by altering the grazing regimes of domestic ungulates (Jones et al., 2009), culling native herbivores (Houston, 1982; Olmsted, 1979), reintroducing apex predators to control native herbivore populations (Beschta et al., 2018; Ripple & Beschta, 2007), and erecting fences around aspen stands (Kay, 2001a; Kay & Bartos, 2000). In semiarid ecosystems used for livestock production, managers often erect fences designed to exclude only domestic ungulates, thereby reducing browsing intensity on aspen while preserving valuable habitat for wild ungulates (Kay & Bartos, 2000). Such livestock fences can have complex and unintended effects on the movements and behavior of wild ungulates. Specifically, wild ungulates may preferentially browse in areas where competition with domestic ungulates is minimized (Chirichella et al., 2014; Madhusudan, 2004) or may avoid crossing obstructions such as livestock fencing (Segar & Keane, 2020).

Although livestock fencing is commonly implemented across the more arid portions of aspen's range, the efficacy of this management practice in promoting recruitment is rarely assessed (but see Kay & Bartos, 2000; Kay, 2001b; Maxwell et al., 2019). Most research on the effects of fencing has focused on fences that were erected specifically for an experiment, and consequently often analyzes the effects of a relatively small number of fences occurring within a predetermined range of environmental conditions (e.g., Rhodes, Larsen, & St. Clair, 2018; Rogers & Gale, 2017; Walker et al., 2015). When fencing is used as a management practice, rather than in an experiment, fences are placed intentionally across a landscape to promote recruitment and occur throughout a variety of environmental conditions across large and heterogeneous landscapes. Analyzing fences erected in this context is useful for understanding (1) the extent to which management actions can generate real changes in aspen recruitment and (2) the extent to which the effects of management practices vary throughout heterogeneous landscapes. The intensity of herbivory on aspen can vary greatly due to spatial heterogeneity in climate, topography, and herbivore abundance and composition (Rhodes, Wan, et al., 2017), suggesting that the effects of livestock fencing on aspen stands will be equally variable. For example, fenced areas in arid landscapes that surround surface water are likely to be highly desirable for wild ungulates and may experience severe browsing pressure, even after domestic ungulates are excluded. In addition, site-level factors that influence accessibility to aspen, such as the percent slope or the cover of large woody debris (Kota & Bartos, 2010), may act as a proxy for fencing by reducing the ease with which herbivores can travel through and forage in an aspen stand. Furthermore, management practices that only mitigate ungulate herbivory without considering the co-occurring stressors of climate and conifer competition (see Calder et al., 2011; Maxwell et al., 2019) may not always improve aspen recruitment (Clement et al., 2019; Rogers & Gale, 2017). For example, aspen recruitment in conifer-dominated forests may be more effectively promoted by forest thinning or prescribed burning than fencing. Given the limited resources available for land management and the costly nature of installing and maintaining fencing, it is critical to understand the factors that predict a stand's response to ungulate herbivory and to identify locations where aspen recruitment may be effectively promoted by the construction of fencing.

Although aspen stands are widely recognized as biodiversity hotspots (Chong et al., 2001; Kuhn et al., 2011), in large part due to the understory environments they create, relatively little work has evaluated the effects of livestock and wild ungulates on aspen understory plant communities. These communities have distinctive compositions that differ greatly from those found in surrounding conifer

forests and provide invaluable habitat for an array of wild-life species (DeByle & Winokur, 1985). Given that cattle grazing has been shown to alter the composition of plant communities (Jones, 2000; Stahlheber & D'Antonio, 2013) and can both promote and suppress invasions by exotic plants (Dorrough et al., 2006; Skaer et al., 2013), it is important to investigate the influence of livestock fencing on the characteristics of understory aspen communities.

Using a livestock-reduction experiment, we evaluated the effects of browsing by domestic and wild ungulates on aspen recruitment and understory composition throughout an extensive and heterogeneous region on the arid, western margin of aspen's range. Specifically, we addressed the following research questions: (1) To what extent does intact livestock fencing reduce the abundance of domestic ungulates and alter the abundance of wild ungulates? (2) To what extent does livestock fencing reduce browsing intensity on suckers and juvenile aspen and promote increased aspen recruitment? (3) How do wild ungulate abundance, stand structure, and topoclimatic factors mediate the effectiveness of livestock fences in reducing browsing intensity and promoting increased aspen recruitment? And (4) How does livestock fencing alter the cover of native woody and herbaceous plants and exotic annual grasses within aspen stands? Addressing these questions is critical for understanding the influence of ungulate herbivores and other factors on the persistence of aspen stands and associated understory communities, which are known to provide valuable ecosystem services and wildlife habitat.

## METHODS

### Study system

Our study was conducted at 87 sites distributed throughout two ecoregions in western United States—the Great Basin in Nevada and the southern Cascades in California (Environmental Protection Agency, 2021; Appendix S1: Figure S1). Our sites in the southern Cascades ranged from 1562 to 2060 m elevation, received 447–808 mm mean annual precipitation (MAP), and experienced mean annual temperatures (MATs) of 4.9–7.1°C. Our sites in the Great Basin ranged from 1679 to 2560 m elevation, received 284–467 mm MAP, and experienced MATs of 3.5–8.1°C.

Quaking aspen is one of the few deciduous hardwood tree species found in the Great Basin and southern Cascades. It is fast-growing, is shade-intolerant, and regenerates both sexually via seed and asexually through the production of ramets from genets via root suckering (Mock et al., 2008). Although individual aspen trees are not particularly long-lived (generally <150 years; DeByle &

Winokur, 1985), aspen clones can persist for thousands of years (Kemperman & Barnes, 1976). Aspen commonly regenerates after fire and exists as both seral and relatively stable, persistent stands (Callahan et al., 2013; Shinneman et al., 2013). At our sites in the southern Cascades, aspen occurred as a minor component of coniferous forests dominated by *Pinus ponderosa*, *Pinus jeffreyi*, and *Abies concolor* or occurred along the margins of seasonally flooded montane meadows. By contrast, at our sites in the Great Basin, aspen occurred as pure stands scattered throughout sagebrush-steppe landscapes. Due to the region's aridity, ~50% of our aspen stands in the Great Basin were located in riparian areas surrounding streams and springs.

In both the Great Basin and southern Cascades, aspen stands in upland sites (amid sagebrush steppe and coniferous forest, respectively) had understory plant communities dominated by bunchgrass and shrubs (predominantly *Artemisia tridentata*, *Purshia tridentata*, *Ericameria nauseosa*, and *Symphoricarpos* spp.). By contrast, aspen stands in riparian or montane meadow sites had understories dominated by forbs, sedges, rushes, and riparian shrubs (predominantly *Salix* spp. and *Rosa woodsii*). At lower elevation upland sites in the Great Basin, the understories of aspen stands were often invaded by cheatgrass (*Bromus tectorum*), an invasive, non-native annual grass. In both regions, aspen stands ranged widely in structure, varying from dense, impenetrable thickets of small aspen to relatively open stands with a few widely spaced larger trees.

All of our sites were located within areas that are regularly used for livestock grazing. Cattle (*Bos taurus*) are the most common livestock species across our two regions, although multiple sites were grazed by sheep (*Ovis aries*) or a combination of sheep and cattle. In addition, several of our sites in the Great Basin were frequented by herds of feral horses (*Equus caballus*). Mule deer (*Odocoileus hemionus*) were ubiquitous throughout both regions, whereas Rocky Mountain elk (*Cervus canadensis nelsoni*) were abundant at our sites in the eastern Great Basin but absent from those in the western Great Basin and southern Cascades. Aspen stands provide important habitat for domestic, native, and feral ungulates, who all regularly feed on juvenile aspen and co-occurring understory vegetation (Beck & Peek, 2005; DeByle & Winokur, 1985; Kaye et al., 2005; White et al., 1998).

## Livestock-reduction experiment

We evaluated the effect of livestock fencing on aspen recruitment and understory plant communities using 51 existing livestock exclosures and 51 unfenced (control) aspen stands. All exclosures in the experiment were

established by the US Bureau of Land Management, US Forest Service, and Nevada Department of Wildlife between 1979 and 2011 (Appendix S1: Figure S1). Using preexisting exclosures established by land management agencies, we were able to sample a relatively large number of plots compared with most exclosure studies. However, this experimental design posed challenges, as not all exclosures in our study were regularly maintained. We developed a metric to differentiate between intact and compromised exclosures whereby livestock exclosures were only included in our study if (1) less than 5% of perimeter fencing was damaged and (2) the plot inside each fenced area (see below) contained less than five livestock dung piles. Of the 51 livestock exclosures initially included in our study, 15 were excluded because they failed to meet these criteria, yielding a final exclosure count of 36. We further verified the integrity of the 36 exclosures with detailed notes on the condition of the fence, the quantity and likely age of livestock dung throughout the exclosure, and the presence or absence of any livestock tracks. The 36 exclosures categorized as intact had minimal or no damage to the fence, with no easy points of entry for livestock, had no visible livestock tracks, and had less livestock dung (average of 1.2 piles per plot) than compromised exclosures (5.9 piles per plot) and controls (4.0 piles per plot). However, because even intact exclosures frequently had a few livestock dung piles in the plot, we considered these fenced areas to be "livestock reductions" rather than complete exclosures. Fenced areas varied in size from 0.05 to 10.1 ha and were constructed of barbed wire, wood, or welded pipe fencing that was typically less than 1.2 m tall to allow access to deer and elk.

Using aerial imagery and visual surveys, we identified 51 unfenced aspen stands to serve as controls. To ensure that the fenced and unfenced stands encompassed similar climate, topography, and herbivore guilds, wherever possible we selected control stands that were located within 500 m of a fenced area and occurred within a similar habitat type (Appendix S1: Figure S1). Table 1 summarizes the distribution and sample size of our fenced and unfenced plots across ecoregions, habitat types, and fire histories and reveals that the two groups were very similar with respect to mean elevation, temperature, and precipitation.

Within each of our focal fenced ( $n = 36$ ) and unfenced, control ( $n = 51$ ) aspen stands, we established one circular sampling plot (8-m radius) by entering the stand from a point nearest to a road or trail. We then proceeded at least 10 m into the aspen stand and dropped a sampling pin to mark the plot center. For stands that covered an area with a radius smaller than 10 m, we located plots at the center of the stand. Within each plot, we also established three circular subplots (2-m radius)

**TABLE 1** Ecoregions, habitat types, plot counts, and environmental variables for a field experiment designed to assess the effects of domesticated and wild ungulate herbivores on aspen regeneration.

Plot characteristics	Unfenced	Fenced
Ecoregion		
Great Basin	32	22
Southern Cascades	19	14
Habitat		
Upland	24	15
Riparian	19	10
Meadow	5	9
Snow pocket	3	2
Years since fire		
0–10	1	1
10–20	9	5
20–30	1	0
>30	40	30
Topoclimate		
Elevation (m)	2018.8 (41.5)	1928.9 (49.7)
Slope (%)	13.5 (2.0)	14.1 (2.0)
Mean annual temperature (°C)	5.2 (0.2)	5.5 (0.2)
Mean annual precipitation (mm)	497.3 (32.9)	517.1 (29.6)

Note: Values for the topoclimate characteristics are expressed as mean ( $\pm$ SE). Other values are sample sizes.

and three 8-m long transects that extended from the plot center to the edge along azimuths of 0°, 120°, and 240°, respectively.

The GPS location of each plot center was recorded within 2 m accuracy (Eos Arrow 100 GPS; Eos Positioning Systems, Inc., Terrebonne, QC, Canada) to allow for later extraction of topoclimatic variables. In addition, we recorded the elevation, slope, and aspect of each plot, as well as the presence of streams, springs, or other forms of surface water inside or within 10 m of the plot.

## Vegetation sampling

All plots were sampled between June and September 2020. Within each circular plot, we counted all adult trees (diameter at breast height [dbh]  $\geq$ 12.7 cm) by species. Within each subplot, we counted aspen suckers (stem height <1 m), juveniles (stem height 1–2 m), and recruits (stem height  $\geq$ 2 m and dbh <12.7 cm). For both aspen

suckers and juveniles, we recorded the number of stems that had clear evidence of ungulate browsing on apical meristems. We defined aspen stems taller than 2 m as “recruits” because their apical meristems were above the browse line for most ungulate species.

We used the point-intercept method to characterize the effects of livestock fencing on the composition of understory plant communities. Specifically, we recorded any of five functional groups—perennial grasses, exotic annual grasses, forbs, sedges and rushes, and shrubs—that intercepted the transect every 0.5 m along three 8-m transects/plot (16 points/transect; 48 points/plot). In addition, for each shrub encountered, we recorded its species. Each transect ran from the plot center to the plot edge and was located along azimuths of 0°, 120°, and 240°, respectively. Finally, we used a densiometer to quantify forest canopy cover every 2 m along each transect.

## Abundance of domestic and wild ungulates

We used trail cameras to estimate the abundance of wild and domestic ungulates at a subset of the plots in our livestock-reduction experiment. Specifically, we deployed low-glow infrared trail cameras (Spypoint Force Dark; Spypoint, Inc., Victoriaville, QC, Canada) at 60 plots (29 fenced plots and 31 unfenced plots). Each trail camera was placed within 2 m of the plot edge and pointed toward the center. Cameras at fenced plots were positioned such that they only detected ungulates within the fenced area. Of the 29 fenced plots at which we placed cameras, 11 fences were later determined to be compromised, so the final trail-camera dataset included 18 fenced plots and 31 unfenced plots. Cameras were deployed at plots between 8 July and 14 July 2020 and were retrieved between 31 August and 23 September 2020.

Prior to statistical analysis, we standardized the trail-camera data from each plot as follows: (1) We multiplied the number of photographs of an ungulate species by the number of individuals of that species in each photograph; and then, (2) we divided this number by the total number of days that the trail camera was active. Juvenile individuals of any species accompanied by a mother were not included in photograph counts because juveniles receive most of their nutrition from milk rather than plant material.

## Historical fire occurrence

Spatial data on fire occurrences in Nevada over the last 50 years were downloaded from the geospatial services portal for the Bureau of Land Management (USDI

BLM, 2021), and spatial data on fire occurrences in California since 1878 were extracted from Data Basin (Conservation Biology Institute, 2021). These data layers contained fire perimeters for past fires of 4.05 and 20.23 ha or greater for timber fires and brush fires, respectively. We assigned plots to the following categories: 0–10, 10–20, 20–30, and >30 years since the last fire.

## Climate variables

We extracted 30-year normals (1960–1990) for MAT and MAP, annual range in temperature, and seasonality of temperature and precipitation for all plots using 4-km resolution data from WorldClim 1.4 (Hijmans et al., 2005). In addition, we used 4-km resolution data from TerraClim (Abatzoglou et al., 2018) to calculate derived climate variables, including winter (December–February) and spring (March–May) snow water equivalent (SWE), spring and summer (June–August) climate water deficit (CWD), minimum spring temperature, and maximum summer temperature. These variables were averaged over two time periods: (1) 30-year normals (1960–1990) and (2) the five-year period (2015–2019) immediately preceding field sampling. We calculated climate anomalies for each derived variable by subtracting the 2015–2019 average from the 30-year normals.

## Data analyses

We used one-way permutation ANOVA tests to compare camera counts in fenced versus unfenced aspen stands for five herbivore species: cattle, sheep, deer, elk, and feral horses. Permutation ANOVAs were used for these analyses because our response variables were all non-normally distributed. Camera counts for all species were log-transformed (base 10) due to extremely high variance in the data. One-way permutation ANOVAs were conducted in R (R Core Team, 2021) using the *RVAideMemoire* package (Hervé, 2020).

We used two-way permutation ANOVA tests to determine the effect of livestock fencing on ungulate browsing intensity and on the stem density of aspen recruits. Once again, permutation ANOVAs were selected for these tests because our response variables were non-normally distributed. For these ANOVAs, we quantified browsing intensity by dividing the number of stems in the sucker or juvenile size class that showed evidence of browsing by the total number of stems in the size class. In these ANOVAs, we also assessed whether browsing intensity and aspen recruit stem density varied between our two focal ecoregions (i.e., Great Basin and southern Cascades). We performed

similar two-way permutation ANOVAs to determine whether our two grouping factors and their interaction affected shrub species richness and the understory cover of each functional group. Each ANOVA was run in R with 10,000 permutations using the *lmPerm* package (Wheeler & Torchiano, 2016). Prior to performing permutation ANOVAs, we used nonparametric Levene's tests to check for heteroscedasticity in our response variables (*car* package; Fox & Weisberg, 2019).

We used nonmetric multidimensional scaling (NMDS) to visualize the effects of fencing and ecoregion on overall understory plant community composition and shrub species composition. To statistically test whether fenced and unfenced plots in the two ecoregions differed significantly in composition, we performed an analysis of similarity (ANOSIM). To determine whether the composition of plant communities was driven by topoclimatic variables, herbivore abundance, and/or stand structure, we fit vectors representing these predictors to our NMDS. For both the NMDS and the ANOSIM, we used Bray–Curtis distance measures. We developed our NMDS and conducted ANOSIM tests using the *vegan* package (Oksanen et al., 2020).

We used negative binomial generalized linear models (GLMs) to identify the best-performing predictors of browsing intensity on aspen, as well as the stem density of aspen recruits across our environmentally heterogeneous study region. We used the subset of plots ( $n = 49$ ) where wildlife cameras were deployed when modeling browsing intensity, whereas we used the full dataset ( $n = 87$ ) to model aspen recruit stem density. To account for spatial autocorrelation, we generated distance-based Moran's eigenvector maps (MEMs) using the *dbmem* function in the *adespatial* package in R (Dray et al., 2021). MEMs were calculated using haversine distances and principal coordinates analysis; therefore, all axes were orthogonal and no variable reduction was necessary. The generated MEMs were included as covariates in our GLMs. When included as covariates, MEMs have the effect of detrending spatial data, thereby helping to elucidate the relationship between the predictors of interest and the response variable. We tested the significance of five generated MEMs by incorporating each of them into our GLMs and retained MEMs only if they were statistically significant or reduced the corrected Akaike information criterion ( $AIC_c$ ) of a candidate GLM. We calculated Pearson's correlation coefficients among all predictor variables using the *psych* package (Revelle, 2020) and excluded any correlated predictors ( $\rho > 0.5$ ). We estimated the goodness of fit of each GLM by calculating a Cragg and Uhler pseudo- $R^2$  using the *pscl* package (Jackman, 2020).

To determine whether the drivers of browsing intensity on aspen were consistent across size classes, we

developed separate GLMs predicting browsing intensity for suckers (0–1 m stems) and juveniles (1–2 m stems). For these GLMs, our response variables were the number of browsed suckers and juveniles per plot, respectively. The log-transformed total number of suckers and juveniles was used as an offset. Plots containing no suckers or juveniles were omitted from the analysis ( $n = 45$  remaining plots for suckers and  $n = 37$  remaining plots for juveniles). For GLMs predicting browsing intensity, we tested the importance of variables of interest through stepwise addition of variables. Specifically, we first included the main effect of livestock fencing, followed by the interaction between livestock fencing and wild ungulate abundance. The latter was represented in each GLM by the inclusion of one of five possible variables: deer abundance, elk abundance, total wild ungulate abundance, and total wild ungulate abundance normalized by animal unit equivalent (AUE; deer = 0.19, elk = 0.7, and feral horses = 1.1), which is a commonly used metric to weight mammal species by their total expected forage intake (Natural Resources Conservation Service, 2003). We selected the GLM with the wild ungulate abundance variable that yielded the lowest  $AIC_c$ . We then added variables related to (1) stand structure and understory composition, (2) water availability, (3) topography, (4) climate, and (5) spatial variance (MEMs) to the GLM. Finally, to account for potential seasonal variation in browsing intensity (Rhodes, Larsen, Maxwell, et al., 2018), we included sampling date in the GLM. Variables were retained if they were statistically significant at  $\alpha = 0.05$  and/or reduced the  $AIC_c$  of the model. The best-performing candidate GLMs were selected by multiple model comparisons using the delta  $AIC_c$  ( $\Delta_i$ ) and the Akaike weight ( $\omega_i$ ), which were calculated as follows:

$$\Delta_i = AIC_{c_i} - AIC_{c_{\min}}, \quad (1)$$

$$\omega_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}, \quad (2)$$

where  $i$  is the candidate model,  $R$  is the whole set of models, and  $r = 1$  indicates that all model weights must add up to 1.

After developing models identifying predictors of browsing intensity, we used negative binomial GLMs to test the importance of (1) browsing on suckers and juvenile aspen, (2) fire history, (3) stand structure and understory composition, (4) topography, (5) climate, and (6) spatial variance (MEMs) in predicting the stem density of aspen recruits. Once again, we systematically added and deleted variables of interest and retained variables if they were statistically significant ( $\alpha = 0.05$ ) and/or reduced the  $AIC_c$  of the model.

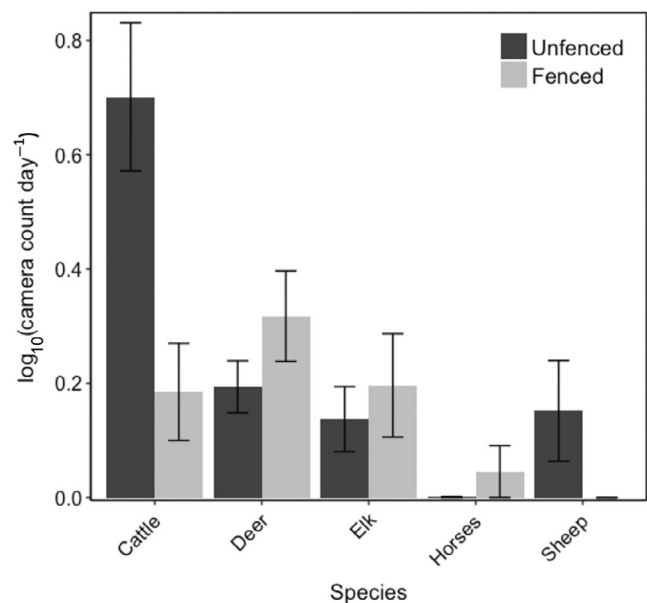
The best-performing candidate GLMs were again selected by multiple model comparisons using  $\Delta_i$ . All GLMs were developed in R using the *glmmTMB* package (Brooks et al., 2017), and  $AIC_c$  scores were calculated using the *wiqid* package (Meredith, 2020).

Following the development of candidate GLMs, we used model averaging to avoid over- or underestimating the importance of predictor variables. Specifically, for candidate GLMs predicting both browsing intensity and recruitment, we calculated the full average of all models with  $\Delta_i < 2$ . GLMs were averaged using the *MuMin* package (Bartón, 2020).

## RESULTS

### Effects of livestock fencing on herbivore abundance

Across all camera-containing plots in both regions, the average daily camera count was 27.75 for cattle, 3.19 for sheep, 1.27 for deer, 1.55 for elk, and 0.12 for feral horses. Cattle were detected in 84% of unfenced plots and 28% of fenced plots. Livestock fencing significantly reduced cattle abundance ( $F_{1,47} = 7.99$ ,  $p = 0.007$ ; Figure 1), with the mean daily camera counts being 74% lower in fenced than in unfenced plots. Livestock fencing did not significantly affect the abundance of sheep ( $F_{1,47} = 1.71$ ,  $p = 0.206$ ), although these ungulates were not present in



**FIGURE 1** Mean ( $\pm$ SE) daily camera counts ( $\log_{10}$ [camera count  $\text{day}^{-1}$ ]) per plot for five herbivore species as a function of the presence or absence of livestock fencing in the Great Basin and southern Cascades.



any fenced plots and were observed in only 10% of unfenced plots. In addition, the abundance of deer, elk, and feral horses was not affected by livestock fencing ( $F_{1,47} = 2.13$ ,  $p = 0.152$ ;  $F_{1,47} = 0.34$ ,  $p = 0.577$ ;  $F_{1,47} = 1.66$ ,  $p = 0.37$ , respectively), with these three species present in 82%, 33%, and 4% of all plots in the experiment, respectively.

### Effects of livestock fencing on browsing intensity and aspen stem density

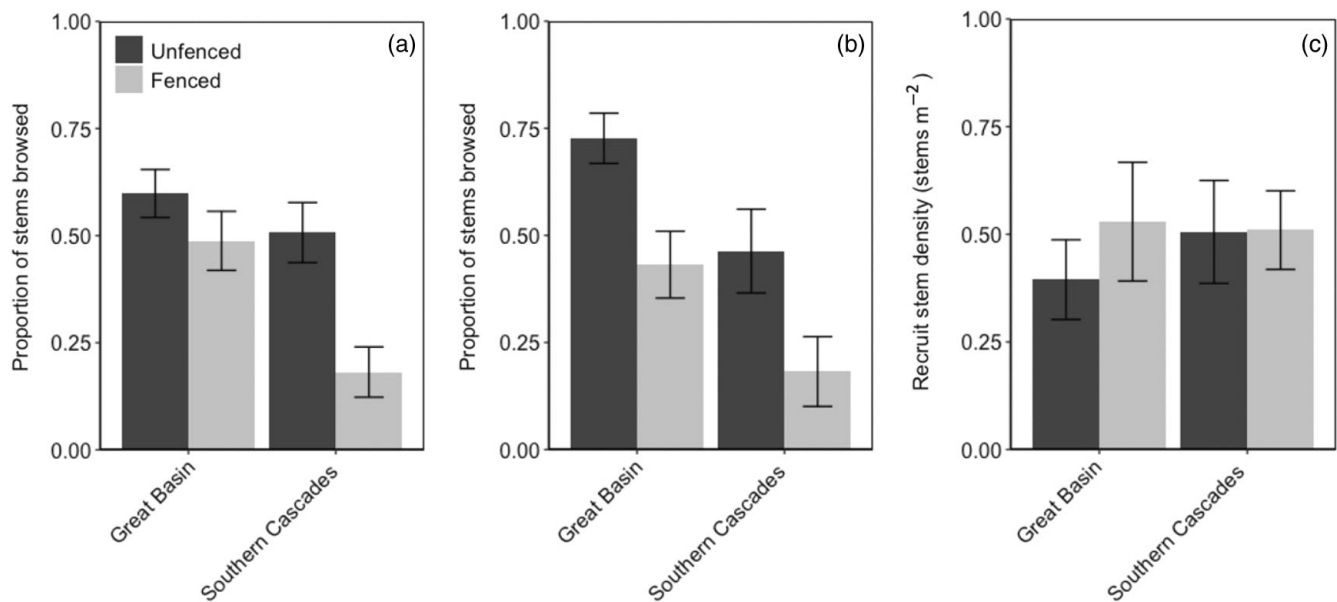
Overall browsing intensity on aspen suckers varied significantly by ecoregion ( $F_{1,78} = 8.36$ ,  $p = 0.005$ ; Figure 2a), with this smallest size class experiencing 33% higher browsing in the Great Basin than in the southern Cascades. Livestock fencing significantly reduced browsing intensity on suckers across both ecoregions ( $F_{1,78} = 10.06$ ,  $p = 0.002$ ), decreasing mean browse intensity by 36% relative to unfenced stands. The effect of fencing on the browsing of suckers did not vary by ecoregion ( $F_{1,78} = 2.45$ ,  $p = 0.122$ ). Browsing intensity on aspen juveniles also varied by ecoregion ( $F_{1,60} = 8.05$ ,  $p = 0.006$ ; Figure 2b), with browsing levels being 46% higher in the Great Basin than in the southern Cascades. Livestock fencing significantly reduced browsing intensity on juveniles ( $F_{1,60} = 10.16$ ,  $p = 0.002$ ), such that mean browse intensity was 48% lower in fenced than in unfenced stands. The effect of fencing on the browsing of juveniles did not vary by ecoregion ( $F_{1,60} = 0.01$ ,

$p = 0.940$ ). The stem density of aspen recruits was not affected by livestock fencing ( $F_{1,83} = 0.34$ ,  $p = 0.563$ ), ecoregion ( $F_{1,83} = 0.14$ ,  $p = 0.704$ ), or their interaction ( $F_{1,83} = 0.30$ ,  $p = 0.587$ ; Figure 2c).

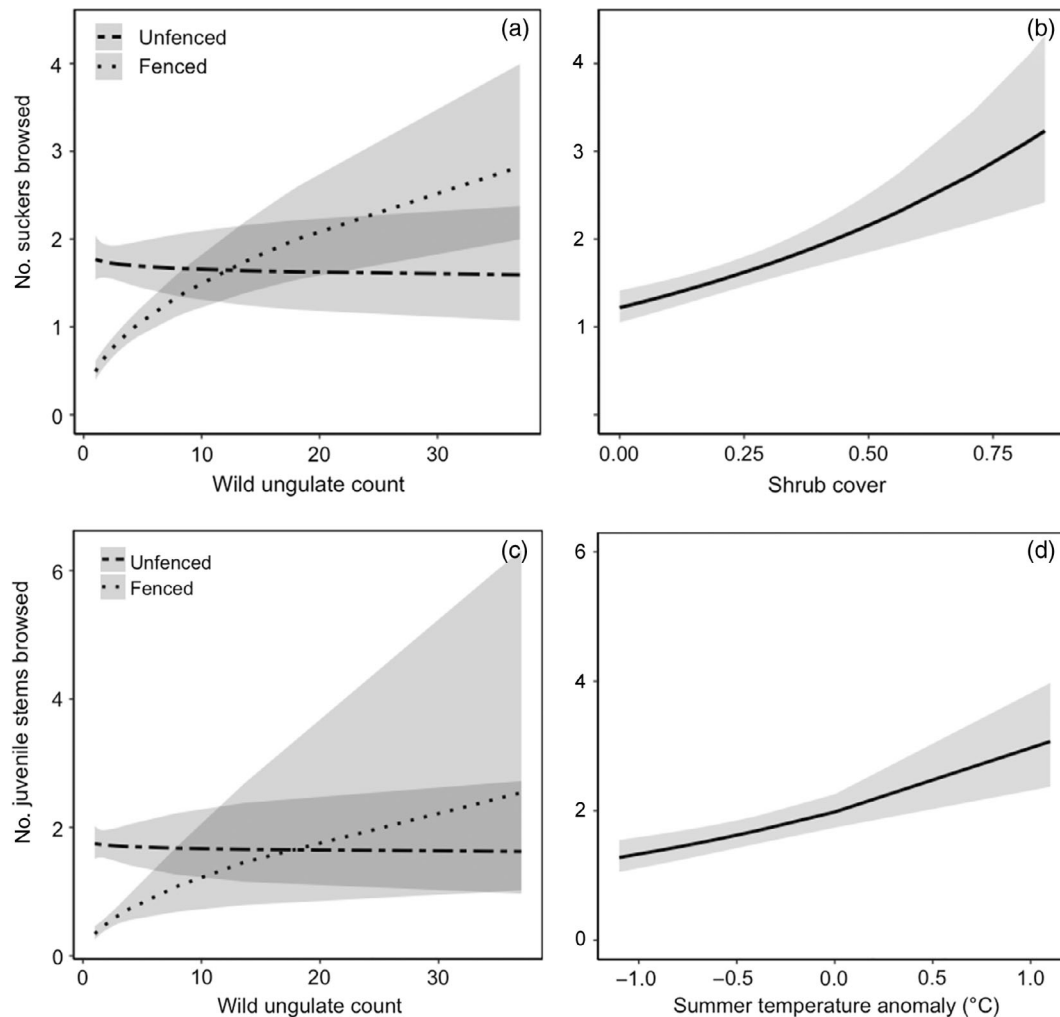
### Drivers of browsing intensity and aspen recruitment

Browsing intensity on aspen suckers was modeled by averaging four candidate models, each of which produced a  $\Delta_i < 2$  (Appendix S1: Table S1). In this averaged model, browsing intensity on aspen suckers increased with wild ungulate abundance in fenced, but not unfenced, plots, with each additional wild ungulate causing a 6% increase in the number of stems browsed (Figure 3a). Browsing intensity on aspen suckers was also positively associated with shrub cover (Figure 3b), the maximum summer temperature anomaly, and the plot sampling date (Table 2a), with plots sampled later in the summer having a greater proportion of browsed suckers. In addition, browsing intensity was associated with MEM1 (Table 2a), a Moran's eigenvector representing regionality (i.e., Great Basin vs. southern Cascades).

Browsing intensity on juvenile aspen was modeled by averaging four candidate models, each of which produced a  $\Delta_i < 2$  (Appendix S1: Table S2). Like the model for aspen suckers, browsing intensity on juvenile aspen increased with wild ungulate abundance in fenced, but



**FIGURE 2** Mean ( $\pm$ SE) (a) proportion of aspen sucker (0–1 m tall) stems browsed, (b) proportion of aspen juvenile (1–2 m tall) stems browsed, and (c) density (stems  $m^{-2}$ ) of aspen recruits ( $\geq 2$  m tall and  $< 12.7$  cm dbh) as a function of the presence or absence of livestock fencing in the Great Basin and southern Cascades.



**FIGURE 3** Marginal-effects plots showing predictors of browsing intensity on aspen suckers (0–1 m tall) and juveniles (1–2 m tall). Panels show the predicted mean ( $\pm$ SE) count of browsed suckers per plot as a function of (a) fencing  $\times$  wild ungulate abundance and (b) shrub cover and the predicted mean ( $\pm$ SE) count of browsed juveniles per plot as a function of (c) fencing  $\times$  wild ungulate abundance and (d) maximum summer temperature anomaly.

not unfenced, plots, with each additional wild ungulate causing a 7% increase in the number of stems browsed (Figure 3c). Browsing intensity on juvenile aspen was also positively associated with the maximum summer temperature anomaly (Figure 3d) and perennial grass and shrub cover (Table 2b). A candidate model in which wild ungulate abundance was weighted using AUE performed nearly, as well as the best-performing model ( $\Delta_i = 1.91$ ,  $\omega_i = 0.060$ ), in which wild ungulate abundance was represented as the total number of individuals per day, with no correction for differing levels of forage intake by species. As a consequence, both total wild ungulate abundance and wild ungulate abundance weighted by AUE were present as predictors in the full averaged model. Candidate models in which total wild ungulate abundance was replaced by

either deer or elk abundance did not perform as well ( $\Delta_i = 3.82$ ,  $\omega_i = 0.023$ ;  $\Delta_i = 4.44$ ,  $\omega_i = 0.017$ , respectively; Appendix S1: Table S2).

The full averaged model of aspen recruit stem density was calculated from 10 candidate models, each of which produced a  $\Delta_i < 2$ . Recruit stem density was negatively associated with browsing intensity on juvenile aspen (Figure 4a) and the density of adult aspen and conifers (Figure 4b), and positively associated with the total number of juvenile aspen (Figure 4c). In addition, recruit stem density was highly contingent on time since fire, such that recruit stem density was greatest in plots that had experienced fire 10–20 years ago, intermediate in plots without recent fire (>20 years ago), and lowest in recently burned plots (<10 years ago; Figure 4d). Specifically,

**TABLE 2** Raw ( $\pm$ SE) and standardized parameter estimates for the full average of the best-performing negative binomial generalized linear models (GLMs) for (a) browsing intensity on aspen suckers (0–1 m tall), (b) browsing intensity on juvenile aspen (1–2 m tall), and (c) density (stems plot<sup>-1</sup>) of aspen recruits ( $\geq 2$  m tall and  $< 12.7$  cm dbh).

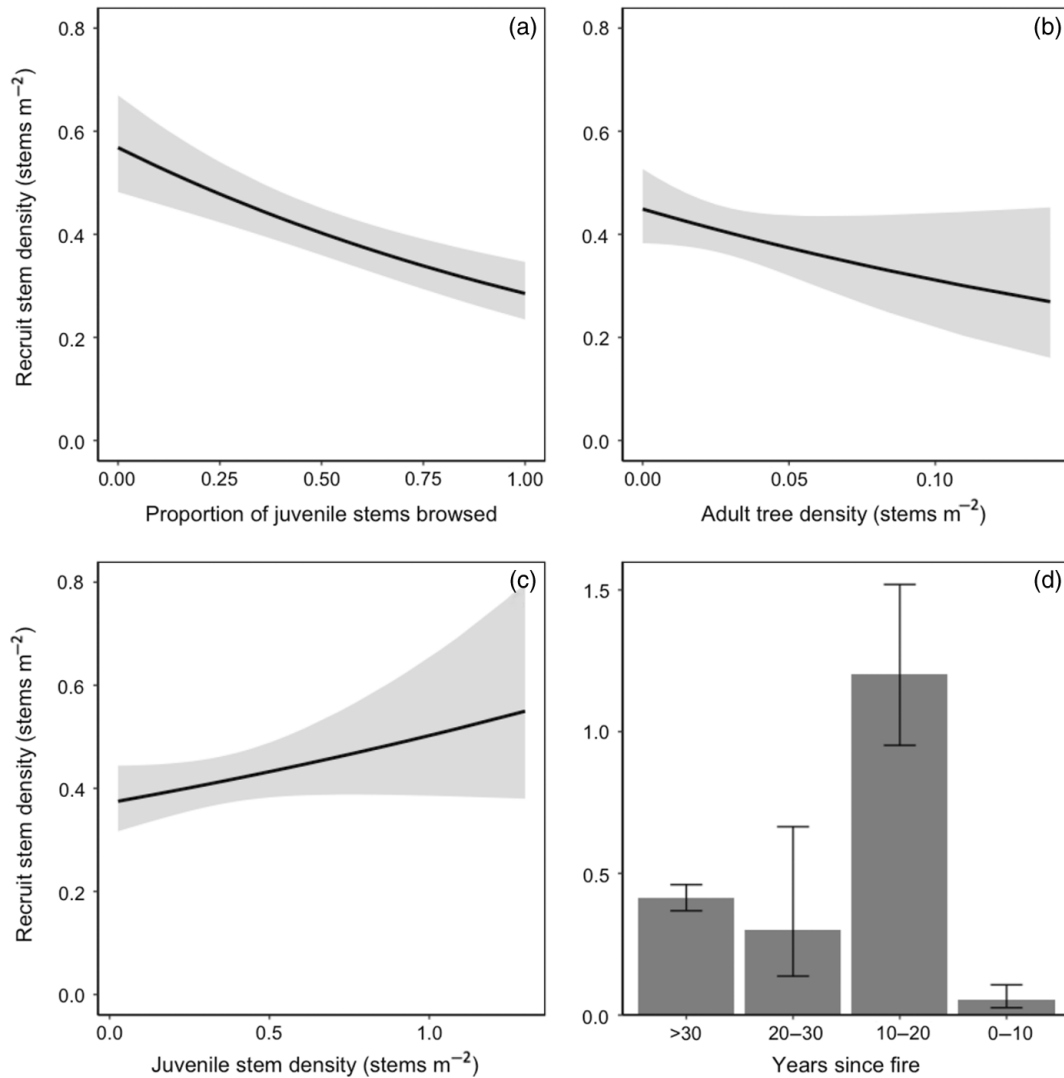
Response	Predictor	Standardized estimate	Estimate (SE)	<i>p</i> ( $> z $ )	<i>N</i>
(a) No. sucker stems browsed	Intercept	-0.451	-1.037 (0.275)	<0.001	4
	Livestock fencing	-0.886	-1.182 (0.263)	<0.001	4
	log(Wild ungulate abundance)	-0.027	-0.067 (0.306)	0.831	4
	Shrub cover	0.269	1.142 (0.442)	0.012	4
	Sampling date	0.15	0.005 (0.003)	0.152	3
	Fencing $\times$ log(Wild ungulate abundance)	0.476	1.182 (0.425)	0.007	4
	MEM1	0.018	0.166 (0.523)	0.755	1
	Max summer temp anomaly	0.016	0.021 (0.069)	0.762	1
(b) No. juvenile stems browsed	Intercept	-0.454	-0.478 (0.233)	0.047	4
	Livestock fencing	-1.265	-1.672 (0.319)	<0.001	4
	log(Wild ungulate abundance)	-0.027	-0.063 (0.376)	0.872	3
	Max summer temp anomaly	0.248	-0.403 (0.153)	0.011	4
	Perennial grass cover	0.189	0.340 (0.426)	0.432	2
	Fencing $\times$ log(Wild ungulate abundance)	0.571	1.354 (0.790)	0.093	3
	Shrub cover	0.167	0.111 (0.352)	0.758	1
	log(Wild ungulate abundance AU normalized)	0.053	0.026 (0.181)	0.888	1
(c) Recruit stem density	Fencing $\times$ log(Wild ungulate abundance AU normalized)	0.428	0.213 (0.590)	0.721	1
	Intercept	2.742	3.092 (0.248)	<0.001	10
	Proportion juveniles browsed	-0.275	-0.690 (0.280)	0.016	10
	Time since fire				10
	>30 years				
	20–30 years	-0.308	-0.308 (0.799)	0.706	
	10–20 years	1.072	1.072 (0.264)	<0.001	
	0–10 years	-2.055	-2.055 (0.714)	0.005	
	Adult tree density (all spp.)	-0.111	-0.018 (0.022)	0.414	5
	Juvenile stem density	0.09	0.008 (0.010)	0.429	6
	Adult aspen density	-0.025	-0.004 (0.011)	0.749	1
	Shrub cover	-0.016	-0.056 (0.194)	0.773	1
Surface water present	0.023	0.023 (0.111)	0.838	1	
Spring SWE anomaly	-0.008	-0.0002 (0.0008)	0.847	1	
Spring CWD	-0.006	-0.0002 (0.001)	0.868	1	

Note: *N* is the number of models in which each variable was present.

Abbreviations: CWD, climate water deficit; GLM, generalized linear models; MEM, Moran's eigenvector maps; SWE, snow water equivalent; temp, temperature.

plots that burned 10–20 years ago had nearly three times more aspen recruits than plots that had not recently burned, while plots that experienced fire 0–10 years ago had nearly 90% fewer aspen recruits than plots that had not recently burned. Recruit stem

density was also positively associated with nearby (<10 m) surface water presence and negatively associated with shrub cover, spring SWE anomaly, and spring CWD, although the effect size of each of these variables was small (Table 2c).



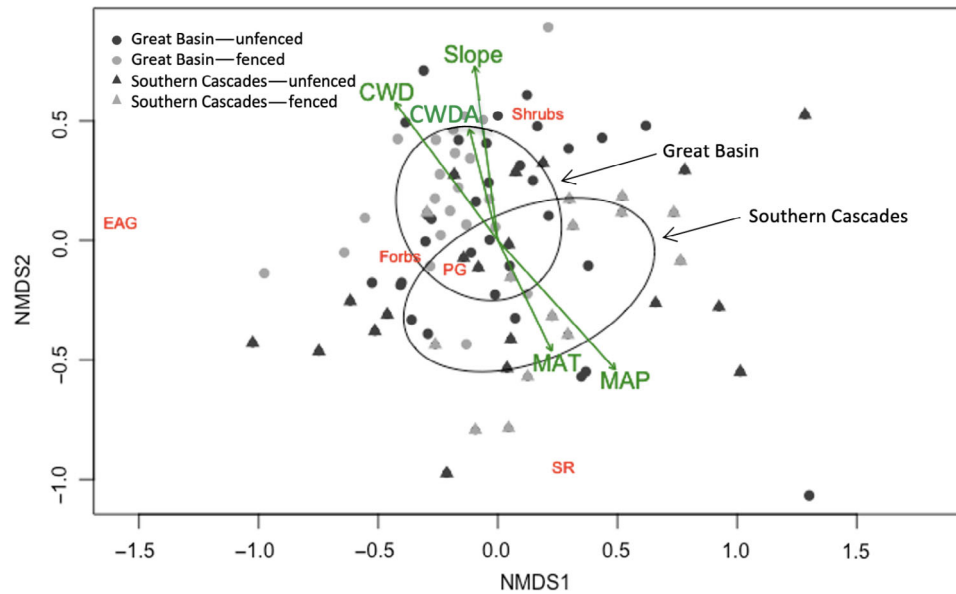
**FIGURE 4** Marginal-effects plots showing predictors of aspen recruit ( $\geq 2$  m tall and  $< 12.7$  cm dbh) density (stems  $m^{-2}$ ). Panels show the predicted mean ( $\pm$ SE) density of aspen recruits per plot as a function of (a) browsing intensity on juvenile stems, (b) total adult tree density (stems  $m^{-2}$ ) for all species in the plot, (c) juvenile aspen density (stems  $m^{-2}$ ), and (d) years since fire.

### Effects of livestock fencing on understory community composition

The composition of the understory plant community did not differ between fenced and unfenced aspen stands ( $p = 0.619$ ,  $R = -0.01$ ). However, community composition did differ significantly between the Great Basin and southern Cascades ( $p < 0.001$ ,  $R = 0.236$ ; Figure 5). In addition, community composition was significantly associated with five topoclimatic variables: MAT ( $p = 0.013$ ,  $R^2 = 0.10$ ), MAP ( $p = 0.001$ ,  $R^2 = 0.20$ ), spring CWD ( $p = 0.001$ ,  $R^2 = 0.19$ ), summer CWD anomaly ( $p = 0.028$ ,  $R^2 = 0.09$ ), and percent slope ( $p = 0.001$ ,  $R^2 = 0.20$ ; Figure 5).

Livestock fencing alone was not significantly associated with the proportional cover of the five understory plant groups: forbs ( $F_{1,83} = 3.01$ ,  $p = 0.087$ ; Figure 6a),

shrubs ( $F_{1,83} = 1.75$ ,  $p = 0.189$ ; Figure 6b), perennial grasses ( $F_{1,83} = 2.53$ ,  $p = 0.116$ ; Figure 6c), sedges and rushes ( $F_{1,83} = 1.86$ ,  $p = 0.176$ ; Figure 6d), and exotic annual grasses ( $F_{1,83} = 3.22$ ,  $p = 0.076$ ; Figure 6e). However, the interaction between livestock fencing and ecoregion was significant for the cover of forbs ( $F_{1,83} = 5.35$ ,  $p = 0.023$ ) and exotic annual grasses ( $F_{1,83} = 3.97$ ,  $p = 0.049$ ). Fencing reduced mean forb cover by 44% in the southern Cascades, whereas it had no effect in the Great Basin (Figure 6a). In addition, livestock fencing increased the mean cover of exotic annual grasses nearly 10-fold in the Great Basin but had no effect in the southern Cascades (Figure 6e). By contrast, there was no significant interaction between fencing and ecoregion for shrubs ( $F_{1,83} = 0.93$ ,  $p = 0.337$ ), perennial grasses ( $F_{1,83} = 0.07$ ,  $p = 0.794$ ), or sedges and rushes ( $F_{1,83} = 0.70$ ,  $p = 0.405$ ).



**FIGURE 5** Nonmetric multidimensional scaling (NMDS) visualizing the composition of the understory plant community for five functional groups: forbs, sedges and rushes (SR), shrubs, perennial grasses (PG), and exotic annual grasses (EAG), as a function of presence or absence of livestock fencing in the Great Basin and southern Cascades and five predictors of understory plant community composition: spring climatic water deficit (CWD), summer climate water deficit anomaly (CWDA), mean annual temperature (MAT), mean annual precipitation (MAP), and slope.

Shrub species richness was significantly greater in the Great Basin than in the southern Cascades ( $F_{1,83} = 24.75$ ,  $p < 0.001$ ; Figure 6f). Although the main effect of livestock fencing on shrub species richness was not significant ( $F_{1,83} = 1.54$ ,  $p = 0.218$ ), there was a significant interaction between fencing and ecoregion, such that shrub richness was greater in fenced than in unfenced plots in the Great Basin but not in the southern Cascades ( $F_{1,83} = 5.98$ ,  $p = 0.017$ ).

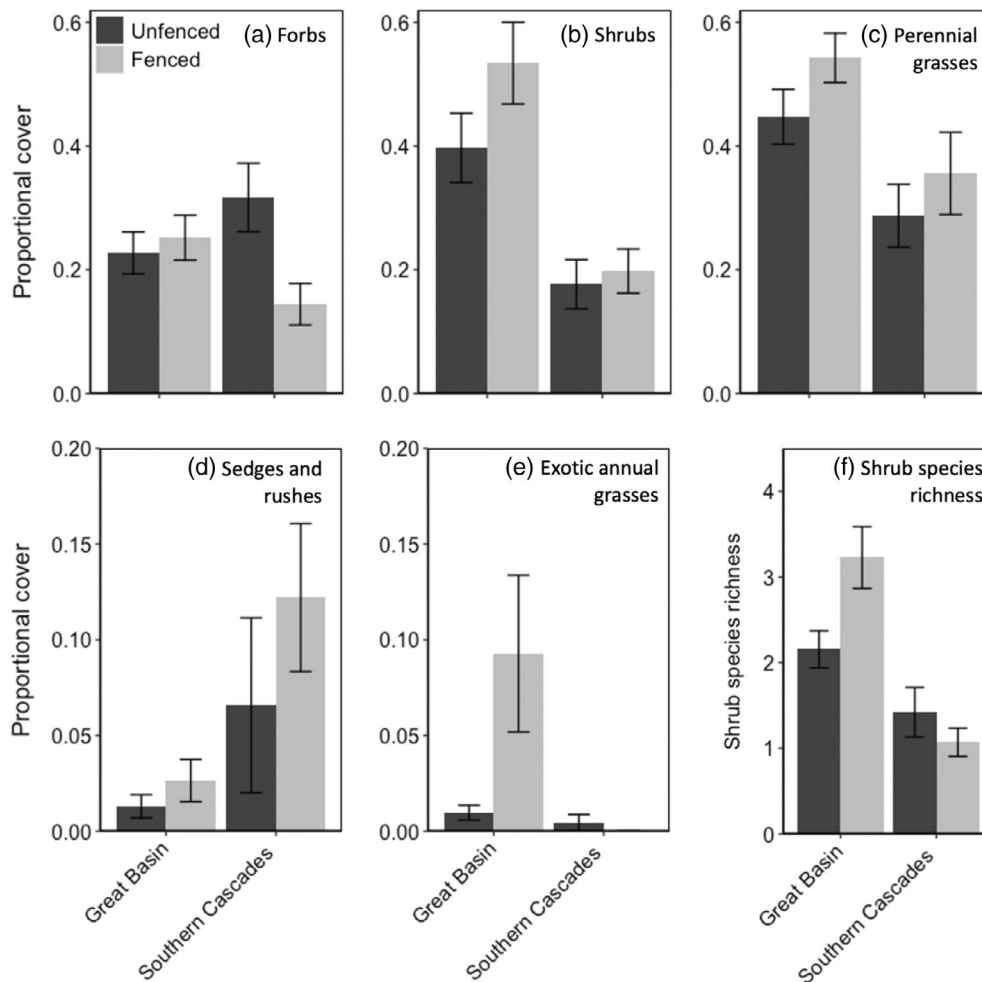
The overall composition of the shrub community varied between fenced and unfenced plots ( $p = 0.038$ ,  $R = 0.05$ ) and between the Great Basin and southern Cascades ( $p < 0.001$ ,  $R = 0.14$ ; Figure 7). Shrub species composition was also associated with the summer CWD ( $p = 0.026$ ,  $R^2 = 0.09$ ) and the annual range in temperature ( $p = 0.021$ ,  $R^2 = 0.09$ ; Figure 7). Specifically, sites with a higher summer CWD and annual range in temperature were associated with greater cover of *Symphoricarpos* spp., while riparian shrubs such as *R. woodsii*, *Prunus emarginata*, and *Salix* spp. were associated with a lower CWD and annual range in temperature.

## DISCUSSION

Our study evaluated the drivers of aspen recruitment across the Great Basin and southern Cascades, an environmentally heterogeneous region where aspen health

and persistence have been threatened by drought, high temperatures, competition from conifers, and ungulate herbivory. In addition, we evaluated the effects of livestock fencing, a commonly implemented management practice in the western United States, on browsing intensity, aspen recruitment, and understory plant composition. We found that the effect of fencing was strongly dependent on wild ungulate abundance, such that fencing reduced browsing intensity on aspen when wild ungulate abundance was low but increased browsing intensity when wild ungulate abundance was high. Aspen recruitment was not affected by livestock fencing but was associated with browsing intensity on juvenile aspen, as well as adult tree density and fire history. To the best of our knowledge, this was the first region-wide study to assess the effectiveness of livestock fencing in the Great Basin and southern Cascades and one of only a few studies to evaluate the importance of multiple drivers of aspen recruitment and persistence in these regions (see Margolis & Farris, 2014; Shinneman & McIlroy, 2019). Our findings will aid land managers in selecting appropriate management practices to promote aspen persistence across this relatively understudied region and will inform conservation efforts for a number of tree species for which recruitment is limited by ungulate herbivory.

A key finding of our study was that the effect of livestock fencing was highly dependent on wild ungulate abundance (Figure 3a,c). Specifically, livestock fencing

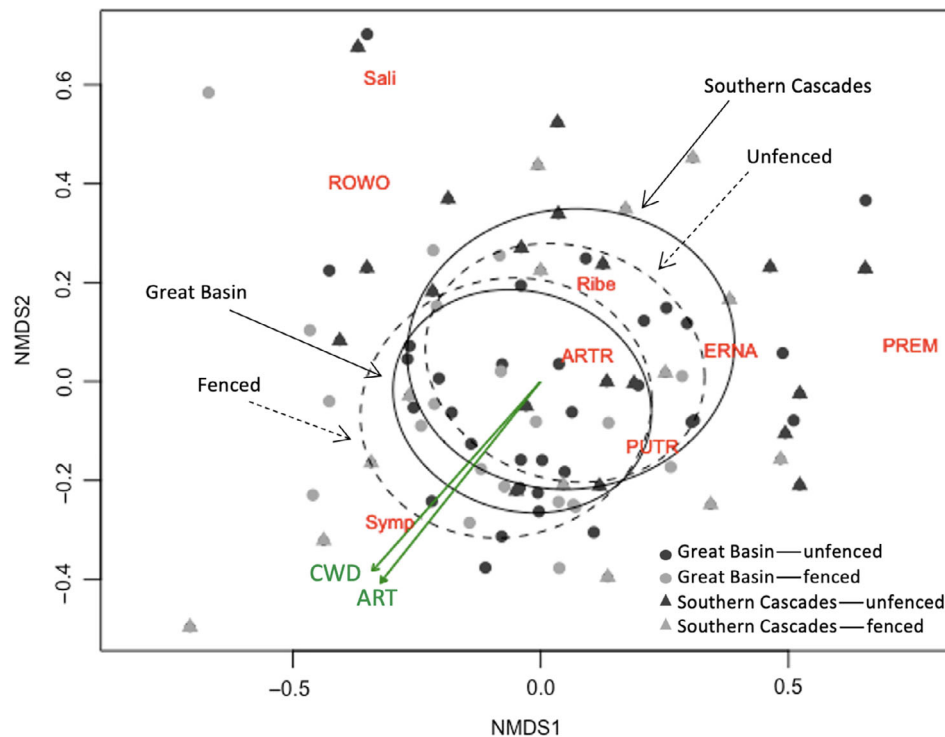


**FIGURE 6** Mean ( $\pm$ SE) proportional cover of (a) forbs, (b) sedges and rushes, (c) shrubs, (d) perennial grasses, (e) exotic annual grasses, and (f) shrub species richness as a function of the presence or absence of livestock fencing in the Great Basin and southern Cascades.

effectively reduced browsing intensity but only when wild ungulate abundance was low. Counterintuitively, browsing intensity was *greater* in fenced than in unfenced stands when wild ungulate abundance was high. This suggests that wild ungulates (i.e., deer, elk, and feral horses) preferentially forage in areas where they do not have to interact with livestock, a finding supported by Madhusudan (2004) and Chirichella et al. (2014), who found that the presence of livestock can cause competition for food between wild and domestic ungulates and can drive the displacement of wild ungulates to sites where livestock are absent or less abundant. However, we found that the camera counts of wild ungulates were not greater in fenced than in unfenced sites (Figure 1), suggesting that fenced areas are associated only with behavioral changes in wild ungulates (e.g., more time spent feeding vs. resting or traveling; Brown et al., 2010; Mattiello et al., 2002; Schieltz & Rubenstein, 2016). Our finding that wild ungulate

abundance mediates the effectiveness of livestock fencing is supported by Kay and Bartos (2000) and Rolf (2001), who also found that the effectiveness of livestock fencing in promoting aspen recruitment was reduced under high wild ungulate abundance.

Although wild ungulates were strong drivers of browsing intensity on aspen within fenced stands, we found that these herbivores were not drivers of browsing intensity in unfenced stands (Figure 3a,c). Our data suggest that browsing intensity may be more strongly driven by domestic ungulates in livestock-accessible stands. Kay (2001b) cited cattle as important drivers of browsing intensity on aspen in Nevada and observed that aspen recruits were abundant in sites surrounded by livestock fencing and relatively rare in unfenced sites. Notably, Kay (2001b) reported little evidence of aspen persistence outside of fenced sites, whereas we found that recruit stem densities were not significantly different in fenced versus unfenced stands (Figure 2c). Our findings are



**FIGURE 7** Nonmetric multidimensional scaling (NMDS) visualizing shrub community composition of the eight most common shrubs species in study plots: *Artemisia tridentata* (ARTR), *Ericameria nauseosa* (ERNA), *Prunus emarginatus* (PREM), *Purshia tridentata* (PUTR), *Ribes* spp. (Ribe), *Rosa woodsii* (ROWO), *Salix* spp. (Sali), and *Symphoricarpos* spp. (Symp), as a function of presence or absence of livestock fencing in the Great Basin and southern Cascades and the two predictors of shrub community composition: summer climate water deficit (CWD) and annual range in temperature (ART).

in closer agreement with those of Shinneman and McIlroy (2019), who observed both aspen persistence and decline across a large array of study plots in the northern Great Basin.

We found that browsing intensity on suckers and juveniles was positively associated with the cover of shrubs (Figure 3b) and perennial grasses, respectively (Table 2b). Grasses are preferred forage for cattle, elk, and feral horses, and their presence in the stand understory may attract these grazers and mixed feeders. Similarly, shrub cover may attract browsers such as deer. These hypotheses are supported by Kay and Bartos (2000), who found that, in aspen stands in Utah, livestock exhibited a dietary preference for grasses while deer exhibited a dietary preference for shrubs.

We also found that browsing intensity on both suckers and juvenile aspen increased with the maximum summer temperature anomaly (Table 2a,b, Figure 3d). We hypothesize that the maximum summer temperature anomaly may be a proxy for another variable that is more directly related to browsing intensity on aspen. For example, this metric was loosely correlated with shrub cover ( $r = 0.47$ ) and with the total number of herbivore species present at a plot ( $r = 0.40$ ). Although not a significant

predictor in our models, co-occurrence of multiple herbivore species has been associated with higher browsing intensity on aspen in a number of studies (Rhodes, Larsen, Maxwell, et al., 2018; Rhodes, Larsen, & St. Clair, 2018; Walker et al., 2015). Although our data do not provide a clear explanation for the effect of increasing summer temperatures on browsing intensity, changing temperature regimes have been shown to drive altered movement and behavior of wildlife, which could contribute to new patterns in the intensity of ungulate herbivory and novel effects on preferred forage species such as aspen (Malpeli et al., 2020). Increasing summer temperatures may also make aspen stands increasingly desirable sites for ungulates, who use the trees for shade in addition to food.

Although livestock fencing reduced browsing intensity on aspen suckers (Figure 2a) and juveniles (Figure 2b), this reduction did not translate into an increased stem density of aspen recruits in fenced plots (Figure 2c). We hypothesize at least three explanations for this finding. First, the fences may not have been present long enough to promote increased stem densities of aspen recruits. Of the livestock fences that had a recorded construction date, nearly all were constructed less than

20 years ago (2003–2010). Second, livestock fencing may not have decreased browsing intensity enough to promote increased stem densities of aspen recruits, particularly given that fencing was associated with increases in browsing intensity in sites where wild ungulates were abundant. Third, factors other than herbivory may be more dominant drivers of recruitment in the two study regions. We found that fire disturbance and intra- and interspecific competition between juvenile aspen and adult trees in the canopy were important predictors of aspen recruit density (Table 2c). Specifically, aspen recruit density was greater in plots that had a lower density of adult trees of all species (Figure 4b), supporting past studies that found aspen juveniles are shade-intolerant and highly susceptible to intra- and interspecific competition (Jones et al., 2005; Kweon & Comeau, 2019). Similarly, recruit stem density was significantly greater in plots that had burned 10–20 years ago than in those that had not experienced fire within the last 20 years (Figure 4d). This suggests that recent fires provided desirable conditions for aspen recruitment, such as enhanced light regimes due to canopy gaps, increased sites for germination, and/or greater stimulation of suckering (Brewen et al., 2021; Keyser et al., 2005). By contrast, plots that had burned within the last 10 years lacked high densities of recruits. In northeastern California, Margolis and Farris (2014) found that 10 years did not provide sufficient time for aspen stems to grow to recruit size, particularly when stems were exposed to repeated ungulate herbivory.

Because recruit stem density was negatively associated with browsing intensity on juvenile aspen (Figure 4a), aspen recruitment may respond positively to fencing treatments that provide a greater reduction in browsing intensity on juvenile aspen, such as fencing designed to exclude both wild and domestic ungulates. For example, Rhodes, Larsen, Maxwell, et al. (2018) and Rhodes, Larsen, and St. Clair (2018) found that fencing, which excluded both wild and domestic ungulate herbivores, provided greater benefits to aspen recruitment than livestock fencing alone. Although recruit stem density was associated with browsing intensity on aspen juveniles, it was not associated with browsing intensity on aspen suckers (Appendix S1: Table S3). On average, plots had high densities of aspen suckers (0.86 stems  $m^{-2}$ ) relative to juveniles (0.24 stems  $m^{-2}$ ) and recruits (0.47 stems  $m^{-2}$ ), suggesting that the survival rate of aspen suckers is low and that other environmental filters (e.g., drought, disease, competition with understory vegetation) in addition to herbivory likely contribute to the loss of suckers. In addition, browsing on juveniles may cause a compensatory response in which stands produce large numbers of suckers (Rhodes et al., 2019). This

would produce inflated sucker counts and underestimates in browsing intensity (as browsing intensity is calculated as browsed suckers divided by total suckers), which may make browsing on this smallest size class a poor estimate of the intensity of herbivory relative to browsing on juveniles.

Recruit stem density was positively associated with the total number of juvenile aspen in the plot (Figure 4c). As these juvenile stems form the size class just below recruits, they are a good representation of the available number of stems that may become recruits in the future. Collectively, our data suggest that the survival of these juvenile stems to the recruit size class will benefit from management actions that both reduce the intensity of ungulate herbivory and decrease the intra- and interspecific competition experienced by juvenile aspen. Management actions that use disturbance to moderate the intra- and interspecific competition experienced by juvenile aspen have already been shown to successfully promote aspen recruitment in several ecosystems. In the northern Great Basin, both prescribed burning and mechanical treatment of juniper successfully increased aspen cover and stem density (Bates & Davies, 2018), and in the southern Cascades, conifer thinning increased aspen stem density (Jones et al., 2005). In northern Arizona, Clement et al. (2019) found that prescribed fire and conifer thinning were an even more important predictor of aspen recruitment than ungulate herbivory, whereas in Utah, Rogers and Gale (2017) found that ungulate fencing combined with conifer reductions promoted aspen recruitment significantly better than either manipulation alone. Also in Utah, Wan, Rhodes, and St. Clair (2014) found that aspen regeneration was 2.3–3.1 times greater in areas experiencing moderate to high fire severity than in those experiencing low-severity burns. Across 25 fires in Utah, Wan, Olson, et al. (2014) also reported that aspen regeneration and recruitment increased with increasing fire size and severity.

In addition to its effect on aspen, we found that livestock fencing altered the cover of forbs (Figure 6a) and invasive annual grasses (Figure 6e) in aspen understories. In the southern Cascades, fencing reduced forb cover by nearly 50%. Because cattle exhibit a dietary preference for grasses, their grazing may promote increased cover of forbs by reducing competition with grasses. Kay and Bartos (2000) found that cattle grazing reduced grass cover in aspen stands and indirect, positive effects of cattle grazing on forb cover have been widely observed in California's Mediterranean grasslands (Stahlheber & D'Antonio, 2013). In contrast to our results for the southern Cascades, livestock fencing in the Great Basin did not decrease forb cover. These different responses to fencing may be due to regional variation in soils, climate, species



composition, or herbivore guilds. For example, in the Great Basin, elk and feral horses may drive increases in forb cover similar to those observed in unfenced plots in the southern Cascades by selectively feeding on grasses.

Throughout the past century, disturbance caused by livestock grazing has been implicated in the spread of many exotic species (Dorrough et al., 2006; McIntyre & Lavorel, 1994). However, more recently, grazing has been proposed as a tool for controlling the spread of several exotic species, including cheatgrass (*B. tectorum*; Diamond et al., 2012; Mosley & Roselle, 2006; Perryman et al., 2020), an invasive exotic grass whose spread has driven reduced biological and structural diversity of sagebrush-steppe ecosystems and increased the frequency and intensity of wildfires (D'Antonio & Vitousek, 1992; Knapp, 1996). We found that the cover of exotic annual grasses (primarily cheatgrass) was nearly 10 times greater in fenced plots than in unfenced plots at our Great Basin study sites. Cattle may reduce the dominance of cheatgrass in our Great Basin study plots both by feeding on cheatgrass and by disrupting the buildup of litter, which has been shown to promote increased establishment of cheatgrass (Evans & Young, 1970; Jones et al., 2015). However, our findings should be interpreted with caution. Variance between the fenced and unfenced plots was uneven, so results from our permutation ANOVA may not be completely reliable. In addition, our study plots comprise a relatively high-elevation margin of cheatgrass's full range in the western United States. So, while our findings do not support facilitation of cheatgrass invasion by livestock in arid montane landscapes (Williamson et al., 2020), they do not necessarily reflect the relationship between grazing and cheatgrass throughout the entire range of this invader.

In addition to altering the cover of forbs and exotic annual grasses, livestock fencing affected the composition of shrub species (Figure 7). NMDS data indicated that fenced plots were clustered closely with *Symphoricarpos* spp., a group of deciduous, low-stature, upland shrubs dominated by *Symphoricarpos oreophilus*. By contrast, the upland shrubs *E. nauseosa* and *Ribes* spp. (a group dominated by *Ribes cereum*) were more closely associated with unfenced plots, while *A. tridentata* and *P. tridentata* were clustered closely with both fenced and unfenced plots. Although we hypothesized that fenced areas might protect populations of highly palatable shrubs species, our data did not support this as *P. tridentata*, which provides the highest forage value to ungulates of these five upland shrub groups (Mozingo, 1987), was common in both fenced and unfenced plots. Riparian shrubs that provide excellent forage value to ungulates, such as *P. emarginata* and *Salix* spp., were relatively rare and fell well outside of the centroids for both fenced and

unfenced plots. As riparian plots only comprised 33% of our study plots, these groups were likely more strongly associated with unusually wet locations rather than a particular fencing treatment.

In summary, our study has assessed the drivers of browsing intensity on aspen and drivers of aspen recruitment across an expansive and environmentally heterogeneous region along the arid margin of aspen's range. We found that aspen recruitment was driven by browsing intensity, fire history, and intra- and interspecific competition, while browsing intensity on aspen was driven by livestock fencing, wild ungulate abundance, and forage availability in the stand understory. Our study also found that livestock fencing can have consequences on the understory composition of aspen stands by reducing forb cover and increasing exotic annual grass cover. Collectively, our results suggest that management practices that reduce herbivory, introduce targeted disturbance (e.g., prescribed fire), and reduce intra- and interspecific competition (e.g., thinning) will be beneficial in promoting increased aspen recruitment. Although livestock fencing reduced the browsing intensity experienced by juvenile aspen, our results suggest that livestock fencing did not provide a large enough decrease in ungulate herbivory to promote increased aspen recruitment and/or was overshadowed by other drivers of recruitment unrelated to herbivory (e.g., disturbance and competition). Because the effects of fencing were strongly influenced by wild ungulate populations, restricting access to aspen stands by wild ungulates via wildlife fencing may be a valuable tool for promoting aspen recruitment in areas where these herbivores are abundant. In addition, moderating wild ungulate populations through hunting, culling, or reintroducing apex predators may be valuable for promoting aspen recruitment and long-term persistence of quaking aspen in the Great Basin and southern Cascades.

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## CONFLICT OF INTEREST


The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Cushman et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.m63xsj44w>.

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## SUPPORTING INFORMATION

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

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