



Grazing by wild and domestic ungulates reduces floral resources and native bee abundance in a multi-use landscape

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ABSTRACT

The breadth of management goals in large and complex landscapes encompasses biotic communities with diverse life histories. However, managing multiple communities may be challenging when resource requirements overlap, like forage for ungulates and floral resources for bees. For three years in a riparian forest in northeastern Oregon, USA, we manipulated the presence of wild deer and elk, domestic cattle, and the combination of wild and domestic ungulates, to understand the separate and cumulative influence of grazing by different functional feeding guilds on bloom and bee communities. While we found no effect of individual grazing treatments, of either wild or domestic ungulates on bloom and bee abundance or richness, there was a negative association between cumulative herbivore pressure of all ungulates and bloom and bee abundance. Additionally, bloom community composition differed by grazing treatment late in the growing season, primarily because several blooming species were annuals associated with cattle grazing. Using information on elk dietary preferences and bee-flower associations, we found that elk-preferred forbs are attractive to bees and occupy important positions in mutualist networks. Bees that specialize on these forbs may be at risk of decline if co-occurring elk selectively reduce floral resources. Management strategies, such as electronic fences, phenologically informed livestock grazing, targeted seed mixes, increased physical complexity in riparian areas, and/or improved ungulate forage allocation, could help maintain ecosystem services provided by ungulates, while preserving floral-rich habitats for bees.

1. Introduction

The breadth of management goals in large and complex landscapes has grown to encompass biotic communities that include species with diverse life histories. Throughout the world, wild ungulates like elk (*Cervus canadensis*) and deer (*Odocoileus* spp.) and domestic ungulates like cattle (*Bos taurus*) co-occur and are managed for food production, recreation, and the regulation of vegetation (Hobbs, 1996). These ungulates can manipulate vegetation communities by trampling and consuming biomass (Wisdom et al., 2006), impart a selective pressure that favors grazing-adapted species (Olff and Ritchie, 1998), modify the soil nutrient balance (Frank and Groffman, 1998), and ultimately alter the availability of resources for other biotic communities linked to plants

(Filazzola et al., 2020). Consequently, disentangling the individual and combined effects of wild and domestic ungulates on vegetation communities can inform management strategies to provision ecosystem services in ways that are consistent with multiple-use objectives.

Bees rely on flowering plants to provide nectar and pollen for their offspring and are essential for the delivery of pollination services, but the influence of ungulates on vegetation communities likely alters floral resource availability. Based on complex interactions between habitat type, disturbance intensity, ungulate species, and shared evolutionary histories, ungulate grazing can have a positive, neutral, or negative association with bee communities (e.g., diversity, richness, abundance) (Glenney et al., 2022; Thapa-Magar et al., 2022; Tonietto and Larkin, 2018). Consequently, understanding the pathways by which grazing

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influences bee communities is critical for the conservation of functional ecosystems. Furthermore, the association between ungulate grazing and bee communities is largely restricted to studies in grazing-adapted ecosystems, like grasslands (Glenny et al., 2022; Thapa-Magar et al., 2022). As a result, little is known about the association between ungulate grazing and bee communities for most vegetation types, including sensitive riparian areas. Grazing plans for cattle that incorporate the cumulative influence of wild ungulates could result in ungulate management that more effectively maintains biodiversity.

Functional differences between domestic and wild ungulates could result in an additive pressure from herbivores on vegetation and bee communities. Cattle are bulk grazers that remove more vegetation biomass as grass, have large body sizes that disturb soils through trampling, and are spatially restricted by fencing and human management (Findholt et al., 2004). By contrast, wild ungulates are more selective mixed feeders, adapting diets to match the seasonal availability of nutritious forage (Cook et al., 2016; Torstenson et al., 2006). These dynamic nutritional requirements lead to more diffuse disturbances across space and time (Schielz and Rubenstein, 2016). As a result, domestic and wild ungulates are a part of complementary functional feeding guilds that influence vegetation communities in multi-use ecosystems. However, the ecological effects of wild and domestic ungulates are typically studied in isolation, and the cumulative effects of co-occurring functional feeding guilds on bloom and bee communities remain unknown (DeBano et al., 2016; DeBano et al., 2025). Individuals from different functional feeding guilds potentially partition habitats across space and time and consume complementary forage, resulting in an additive herbivore pressure on vegetation communities (Schoenecker et al., 2022; Stewart et al., 2002). Studies that consider the influence of multiple functional ungulate guilds on bloom and bee communities can help develop holistic management strategies for biodiversity conservation in multi-use landscapes.

Herbivory from different functional feeding guilds may influence the strength of selective pressure on flowers and shift the floral community composition to alter resources available to bees. For instance, bulk feeding by cattle removes the grass overstory and increases light and space at the soil surface that can be invaded by ephemeral annuals (Bartuszevige and Endress, 2008; Eskelinen et al., 2022). By contrast, the preference of wild ungulates for woody deciduous shrubs (Averett, 2025; Endress and Averett, 2020) and perennial forbs (Knight, 2004) could result in targeted herbivore pressure on important flowering resources for pollinators (Mitchell et al., 2022). However, it remains unclear whether the flowering plants most susceptible to ungulate-induced changes are also key food resources for bees (DeBano et al., 2016). For instance, large, showy perennials that bloom consistently across years are often more attractive to bees (Fenster et al., 2004), but also more likely to be grazed by ungulates (Díaz et al., 2001). The response of bees to the individual and cumulative effects of grazing by wild and domestic ungulates likely depends on how floral communities are structured by ungulate disturbances.

To further quantify ungulate-native bee relationships, we conducted a three-year field experiment that manipulated the abundance of wild and domestic ungulates and observed the response of blooming plant and bee communities. We hypothesized that the combination of wild and domestic ungulates would decrease overall bloom and bee abundance and richness because ungulates from different functional feeding guilds have an additive effect on cumulative herbivore pressure. Additionally, we hypothesized that bloom and bee communities would differ depending on the grazing treatment because individuals from different functional feeding guilds would preferentially feed on different species and potentially strengthen selective pressures for grazing-adapted flower species and their visiting pollinators. Furthermore, extensive work within this system has identified preferred food items of elk (Cook et al., 2014), but less is known about the importance of these plant species for bees (Roof et al., 2018). To understand the extent of diet overlap between bees and elk, we observed bee-flower interactions, and

described the functional roles of elk-preferred and non-preferred flower species in mutualist interaction networks.

2. Methods

2.1. Study area

This study was conducted in a 2217-ha portion of the Meadow Creek drainage within the USDA Forest Service (USFS) Starkey Experimental Forest and Range (Starkey) as described by Averett et al. (2017), DeBano et al. (2025), and Mitchell et al. (2022). Starkey is a long-term research site established in the 1940s in northeastern Oregon, USA (1120 m; 45°13' N, 118°30' W) to support studies on the effects of management on wild and domestic ungulates, in tandem with interactions among these species and their effects on ecosystems (Rowland, 1997; Fig. 1). As a result, the movements, population dynamics, and interactions of ungulates across functional feeding guilds have been extensively studied across Starkey through radiotelemetry and trapping/handling of animals (Wisdom, 2005).

Climate at Starkey is typical for this region, with mean daily temperatures ranging from -1.5°C in January to 18°C in August, and strongly seasonal precipitation patterns, with moisture usually falling as snow in the winter and rain in the spring (average 569 mm per year) (1990–2020; PRISM Climate Group). Late summers are punctuated by prolonged dry spells, with increasing temperatures and summer droughts in recent years (Brown et al., 2022). Vegetation along Meadow Creek is typical of riparian areas in the region, with a mixture of deciduous shrubs (e.g., *Crataegus douglasii* Lindl., *Symphoricarpos albus* (L.) S.F., Blake, *Rosa woodsii* Lindl., *Alnus incana* (L.) Moench, *Salix* spp.) and conifers (e.g., *Pinus ponderosa* P. & C. Lawson, *Pseudotsuga menziesii* (Mirbel) Franco). Native herbaceous species (e.g., *Carex* spp.; *Veratrum californicum* Durand) co-occur with a non-native perennial grass (*Alopecurus pratensis* L.) that was previously introduced to support cattle grazing in the area. See Averett et al. (2017) and Rowland et al. (2025) for additional description of the study area.

The Meadow Creek riparian zone is used throughout the year by three co-occurring wild ungulate species - mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and elk (DeBano et al., 2025). Densities of elk in Starkey (~ 2.4 per km^2) fall within the range found on adjacent public lands. Deer densities (~ 0.52 per km^2 ; Merems et al. (2020)) were substantially lower compared to adjacent public lands during the years of study. Cattle grazing at Starkey has occurred since the early 1900s (Skovlin, 1991). However, cattle were excluded from Pasture 3 in 1991 (Case and Kauffman, 1997; Fig. 1)—and all of Meadow Creek—from 2013 to 2016 in preparation for a long-term riparian restoration experiment (Mitchell et al., 2023). Cattle were then reintroduced throughout Meadow Creek in 2017 (Mitchell et al., 2023; Rowland et al., 2025).

Cattle in Meadow Creek are managed under a deferred rotational grazing regime and moved between five pastures throughout the year (Rowland et al., 2025; Fig. 1). Beginning in 2017, cattle began grazing each year in Pasture 1 or Pasture 5 on ~ 15 June (Table S1). After cattle entered a pasture, observers monitored the riparian “greenline” weekly to ensure grazing thresholds established by the USFS for riparian areas in the Pacific Northwest had not been exceeded (see Mitchell et al. (2023) and Rowland et al. (2025) for details). Once one of these thresholds had been reached, cattle were moved to the next pasture in the rotation schedule. Although the exact date cattle entered a pasture differed depending on the year, all pastures had been grazed by August–September (Table S1).

2.2. Experimental design

Exclosures were built along the riparian corridor in Pastures 2, 3 and 5 to control access by ungulates to vegetation and establish four grazing treatments (Fig. 1). Specifically, 2.4-m fences excluded all ungulates

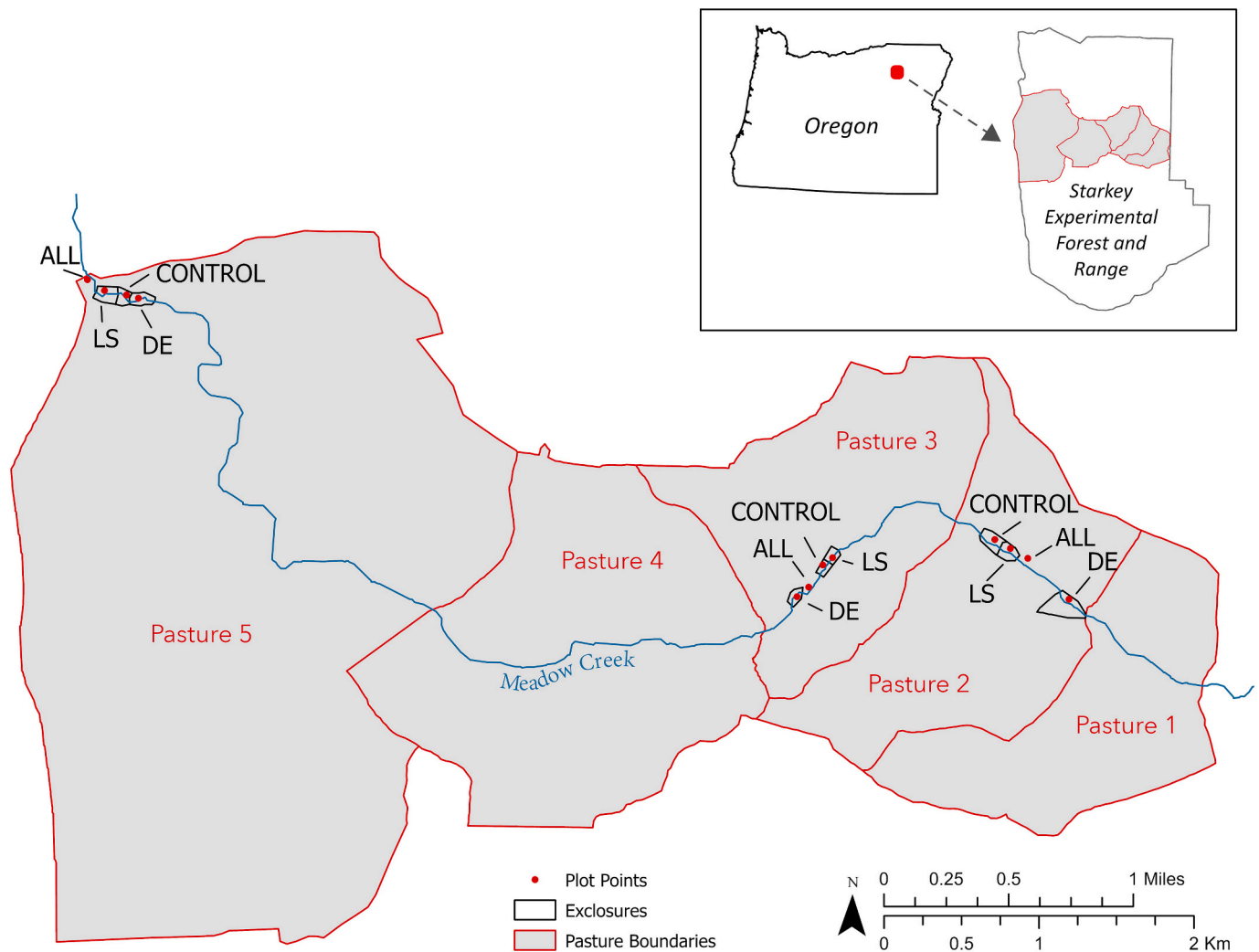


Fig. 1. The 2217-ha Meadow Creek study area in northeast Oregon (upper inset) was composed of five riparian pastures defined by livestock fences (red lines). Pasture sizes ranged from 1122 ha (Pasture 5) to 201 ha (Pasture 1). Within Pastures 2, 3, and 5, fenced exclosures were built to manipulate the assemblage of ungulates that can access sites (black lines) and establish four grazing treatments: (1) complete ungulate exclusion (CONTROL); (2) deer-elk only (DE); (3) livestock only (LS); and cattle, deer, and elk in the extant region outside the exclosures (ALL). Red points mark the center of the five transects located at each sampling site. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(CONTROL) and 1.5-m fences allowed deer and elk access but excluded cattle (deer-elk only; DE). For the livestock-only treatment (LS), 2.4-m fencing excluded all ungulates, but a small number of cow-calf pairs was placed in the LS exclosure for a subset of the days while the remainder of the herd grazed that pasture (Table S1). The average exclosure size (CONTROL, LS, and DE) was ~1.3 ha. The ALL treatment was the extant portion of the pasture, i.e., outside the exclosures but exposed to herbivory by deer, elk, and cattle when present. In total, we established 12 sampling sites (one site within each exclosure type and one ALL site in each pasture; Fig. 1). Mean distance between sampling site centers across pastures was 4143 m. Within pastures, mean distance between sites ranged from 151 m (Pasture 5) to 377 m (Pasture 2), which we deemed to be sufficient separation given recent estimates of the typical foraging distances of many bees (Kendall et al., 2022).

To estimate herbivore pressure at each site, we established a series of motion-activated trail cameras (Bushnell Trophy Camera HD with infrared flash; Bushnell, Overland Park, KS, USA) at 600-m intervals along the 13-km reach of Meadow Creek, and at 100-m intervals near exclosures. Cameras were mounted ~1 m above the ground on trees or T-posts, placed in open areas to maximize the field of view along the stream edge, and faced parallel to the stream. We used any camera located within a 600-m buffer of the mid-points of each grazed site (i.e.,

all treatments other than CONTROL), resulting in 48 total cameras (mean cameras per site = 4; SD $\pm$ 2.52). Each camera was programmed to take three consecutive photos after being triggered by movement (an ‘event’). We manually inspected each photo and recorded the ungulate species and number of individuals for each event. Only one photo was retained within one minute from the previous photo, to avoid counting events more than once.

We estimated cumulative herbivore pressure for each site by counting the number of ungulates, by species, detected with camera traps from 1 April through the end of bloom and bee sampling events in 2017, 2018, and 2019 (described below) (Table S2). Occasional interruptions in the activity of cameras (e.g., faulty batteries or memory cards and camera theft) resulted in sites with variable camera trapping intensities. To control for this variation, we divided the total number of ungulates detected by the total number of days cameras were active during that period. While we acknowledge that camera traps do not strictly reflect grazing or browsing pressure, the counts of herbivores recorded on camera trap areas is an effective proxy for “herbivore pressure” (DeBano et al., 2025; Weber et al., 2025).

2.3. Plant sampling

To quantify floral resources for bees, we identified and counted the number of blooming stems at every site from 2017 to 2019 using methods consistent with previous studies (e.g., DeBano et al., 2025; Roof et al., 2018). The number of blooming stems is considered a reasonable approximation of floral resources available to bees at a site (Cariveau et al., 2025). To capture the inter- and intra-annual changes in floral resources, a sampling event described the blooming plant community at each site in May, June, July, August, and September each year, with the exception of August in 2017 (Table S2). In each sampling event, we identified and counted all blooming stems that intersected five parallel, 20 × 0.3-m belt transects that were positioned perpendicular to the stream and separated by 15 m. The layout of transects was identical across all sites, resulting in equal areas sampled. Plants that were indistinguishable in the field were combined into a larger group, including *Trifolium repens* L. and *T. pratense* L. (*Trifolium* spp.); *Arnica sororia* Greene and *A. chamissonis* Less. (*Arnica* spp.); *Nocca fendleri* (A. Gray) Holub and *Thlaspi arvense* L. (*Thlaspi* spp.); and *Symphytotrichum spathulatum* (Lindl.) GL Nesom, *S. eatonii* (A. Gray) GL Nesom, and *Canadanthus modestus* (Lindl.) GL Nesom (*Symphytotrichum* complex). In addition, *Penstemon* stems (excluding *P. procerus* Douglas ex Graham) and one species of *Descuriana* were identified to genus only. Scientific names for plants follow USDA NRCS PLANTS Database naming conventions (<http://plants.usda.gov>).

2.4. Bee sampling

To link changes in blooming stems to bee communities, we collected bees at every site concurrently with plant sampling in May, June, July, and September each year (Table S2) following methods outlined by DeBano et al. (2025). Specifically, a UV-reflective blue, UV-reflective yellow, and white pan trap (236 ml, Highland Plastics, Mira Loma, CA 91752), filled with ~170 ml of soapy water, were placed on the ground at the center of each of the five transects where plants were sampled. Traps were placed in a triangular arrangement, separated by 0.5 m. We collected pan traps after two days and noted any disturbed traps. Concurrently, one vane trap with a fluorescent yellow collection bucket and fluorescent blue vanes (SpringStar, Woodinville, WA, 98072) was suspended 1.5 m from the ground in the center of the middle transect at each site.

To document bee-plant relationships, we netted bees from flowers at each site for at least 20 min during each sampling event on clear and calm days. We placed collected bees in vials, euthanized them with ethyl acetate, and recorded the flower species they were collected from. All bees were taken to the laboratory, washed, pinned, and subsequently identified using methods described in Kuhlman and Burrows (2017).

2.5. Statistical analyses

Within this region, plant and pollinator community composition is known to vary across the year as a result of species that exhibit different phenologies (DeBano et al., 2016; Kimoto et al., 2012; Mitchell et al., 2023). To account for this temporal variation, we analyzed bloom and bee assemblages separately for each month of the year. Most flowering plant species senesce by August and September, when only a few species are left blooming (Brown et al., 2022). Therefore, bloom and bee data in August and September were combined into a single 'Late summer' sampling event. All analyses were conducted in RStudio (version 2025.05.1 + 513), using a significance level of $\alpha < 0.05$.

2.5.1. The response of bloom and bee abundance and richness to herbivory

We calculated bloom and bee abundance and richness and herbivore pressure to understand how the individual and cumulative effects of ungulates in different functional feeding guilds altered bloom and bee communities. Bloom abundance was the total number of blooming stems

that intersected all transects at a site during a sampling event, and bloom richness was the number of blooming species detected in all transects at a site during a sampling event. Bee abundance was estimated separately for both trap types to account for pan traps that were disturbed by ungulates. For pan traps, the total number of specimens collected was divided by the number of intact pan traps and multiplied by 15 to estimate the number of individuals given a full set of traps ($n = 15$). Only 22 of 2160 total pan traps deployed were disturbed (1.1%). To estimate bee richness, we combined all specimens collected from pan and vane traps for each sampling event, and extrapolated bee species richness to an asymptote value using the *iNEXT()* function from the *iNEXT* package (Hsieh et al., 2016). The bloom and bee abundance and richness at a site were relativized to the control in the same month, year, and pasture using the log-response ratio (LRR) (Hedges et al., 1999). Cumulative grazing pressure was $\log + 0.01$ transformed to normalize data for linear modelling.

To test for an association between the LRR of bloom and bee abundance and richness with herbivore pressure and grazing treatments, we used separate linear mixed effects models with cumulative herbivore pressure and grazing treatment as main and interactive effects using the *lmer()* function from the *lme4* package (Bates et al., 2014). The year was included as a random intercept to account for repeated sampling events within a year. To account for multiple measures of bee abundance for each sampling event (vane and pan traps), we nested the site within the year as another random intercept term. We used a Satterthwaite's *t*-test of the estimated marginal means to determine the magnitude and direction of the main effects on the response variables using the *summary()* function from the *lmerTest* package (Kuznetsova et al., 2017).

2.5.2. The response of bloom and bee composition to herbivory

To understand the influence of grazing treatments on bloom and bee community composition while controlling for the seasonality of communities, we analyzed communities separately for each month. We used a PERMANOVA with grazing treatment as a main effect to test if the community composition of blooms and bees was associated with the grazing treatment, and a blocking variable to account for sites sampled within the same pasture with the *adonis2()* function from the *vegan* package (Oksanen et al., 2007). To account for multiple tests, a Bonferroni correction was used to adjust the significance level to $\alpha = 0.0125$. Following a significant PERMANOVA, we used a pairwise PERMANOVA (*pairwiseAdonis*, *github/pmartinezabizu*) to identify communities that were different between treatments within a month, and an indicator species analysis to identify which species were most strongly associated with different grazing treatments within a month using the *multipatt()* function from the *indicspecies* package (Cáceres and Legendre, 2009).

To visualize the response of bloom and bee communities in each sampling event, we used the *metaMDS()* function in *vegan* to create non-metric multidimensional scaling (NMDS) plots (Oksanen et al., 2007). Specifically, we calculated Bray–Curtis dissimilarities for each sampling event and used an iterative process with several random starts to find a solution for point positions with the lowest stress value. The iterations stopped if a new lowest stress value was not found within 20 random starts.

2.5.3. Dietary overlap between elk and bees

Elk-preferred plant species have been identified through extensive foraging trials with captive elk in the Blue Mountains of northeastern Oregon (Cook et al., 2014). Such trials have provided fine-grained data on elk dietary preferences in relation to available forage (Cook et al., 2016; Cook et al., 2018). We used a simplified version of elk preference categories from DeBano et al. (2025) to divide plants into two groups: elk-preferred and non-preferred species. Here, we considered any plant species identified as 'strongly selected', 'selected', or 'neutral' in DeBano et al. (2025) as an elk-preferred plant and species identified as 'strongly avoided' or 'avoided' as non-preferred. We combined 'neutral'

plant species with the two ‘selected’ categories identified in DeBano et al. (2025) into one ‘elk-preferred’ category because neutral species are consumed in proportion to their availability (Cook et al., 2016) and are frequently documented in elk diets (DeBano et al., 2016).

To visualize the functional roles of blooming plants in mutualist networks, we plotted bee-flower interactions documented with our hand netting efforts for early (May and June) and late (July, August, and September) periods of the growing season with the *plotweb()* function in the bipartite package (Dormann et al., 2008). We also tested for an association between bee visitor richness and bloom abundance for elk-preferred and for non-preferred blooming plants. We summed bloom abundance for each species across all sampling events and years to better capture the full range of bee species likely to visit a blooming plant and compared that with the number of bee species visiting each blooming plant. We used a generalized linear model with a Poisson family distribution to model count data and log +1 transformed bloom abundance to ensure normality. Bloom abundance and elk-preference were included as main and interactive effects in the model. In addition, to identify bee genera with the highest dietary overlap with elk, we calculated the proportion of interactions with elk-preferred flower species for each bee genus.

3. Results

Cumulative herbivore pressure increased throughout the summer each year for sites grazed by ungulates (Fig. 2). Specifically, extant grazing by cattle, deer, and elk (ALL) had the greatest cumulative herbivore pressure each year, and livestock-only (LS) pressure was similar to the deer-elk only (DE) treatment. Due to the deferred rotational grazing scheme, cumulative herbivore pressure in LS and ALL sites increased most sharply late in the growing season (Table S1; Fig. 2).

We counted a total of 49,865 blooming stems from 114 flowering plant species (Table S3). *Draba verna* L. (10.7%), *Myosotis stricta* Link ex Roem. & Schult. (8.7%), and *Collinsia parviflora* Lindl. (7.2%) were the most abundant annuals. *Potentilla gracilis* Douglas ex. Hook. (6.6%),

Ranunculus uncinatus D. Don ex. G. Don (3.7%), and *Achillea millefolium* L. (3.6%) were the most abundant perennials, whereas *Ribes cereum* W. H. Brewer & S. Watson (1.2%), *C. douglasii* (0.23%), and *S. albus* (0.1%) were the most abundant shrubs. Among blooming plants visited by bees, there were a total of 17,042 blooming stems from elk-preferred, 16,675 from non-preferred, and 2509 from species with no data.

We collected 15,886 bees across all sampling events (vane traps $n = 3087$; pan traps $n = 10,749$; hand-net $n = 2050$). Across all sampling events and years, hand-netting resulted in approximately 68 person-hours of sampling effort in 145 sampling events. We collected 255 unique species of bees from 24 genera with all three sampling methods (pan trap $n = 206$; blue vane trap $n = 126$, hand-net $n = 161$; Table S4). *Lasioglossum* was the most frequently collected genus (34%), followed by *Halictus* (23%) and *Bombus* (14%).

3.1. Responses of bloom and bee abundance and richness to herbivory

While we found no statistically significant association between individual grazing treatments and bloom and bee abundance or richness (Fig. 3A,C; Table 1), there was a negative association between cumulative herbivore pressure by all ungulates and bloom and bee abundance (Fig. 3B, D; Table 1). As cumulative herbivore pressure doubled, bloom abundance declined by 18% and bee abundance declined by 5.6% (Table 1). There was no statistically significant effect of herbivore pressure on bloom or bee richness (Table 1).

3.2. The response of bloom and bee composition to herbivory

Although overall bloom community composition did not differ relative to grazing treatment in May or June (Fig. 4A,B; Table 2), it did in July and late summer (Aug. – Sept.) (Fig. 4C,D; Table 2). Pairwise bloom community composition differed between the CONTROL and LS treatments in July (F -stat $df=1$ 2.289, $SS = 0.66$, adjusted p -value = 0.03), but not in late summer after adjusting for multiple pairwise comparisons. The indicator species analysis identified 10 flowering species that

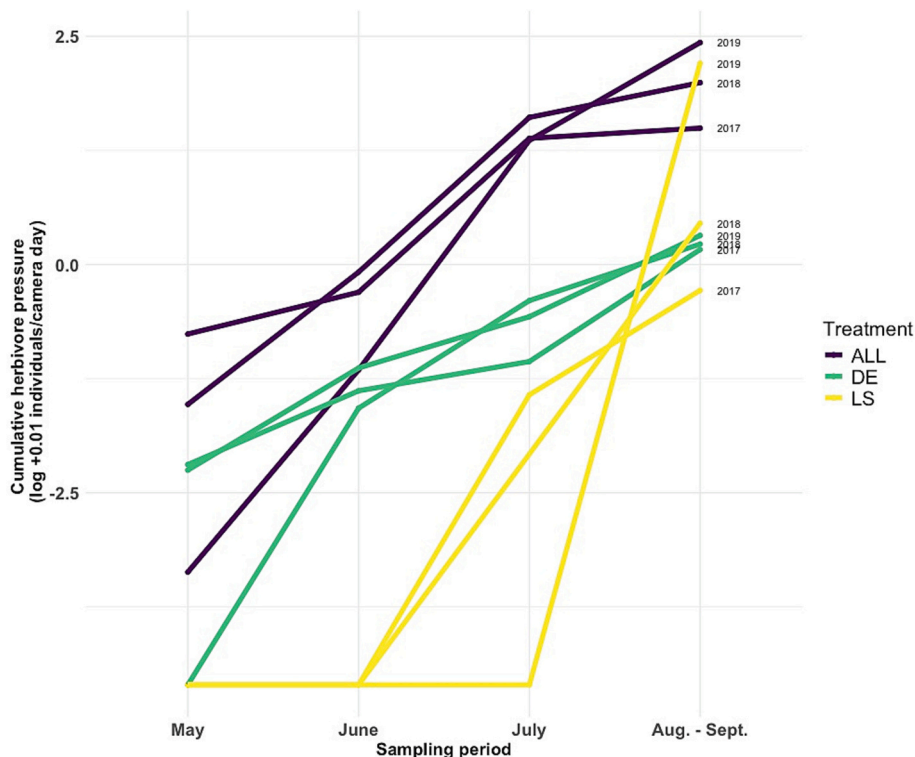


Fig. 2. The monthly cumulative herbivore pressure (log+0.01 transformed) derived from camera trapping data across all sampling events within a year, by treatment (ALL = extant grazing of deer, elk, and cattle; DE = deer and elk-only; LS = livestock-only). No ungulates were detected in the control treatment.

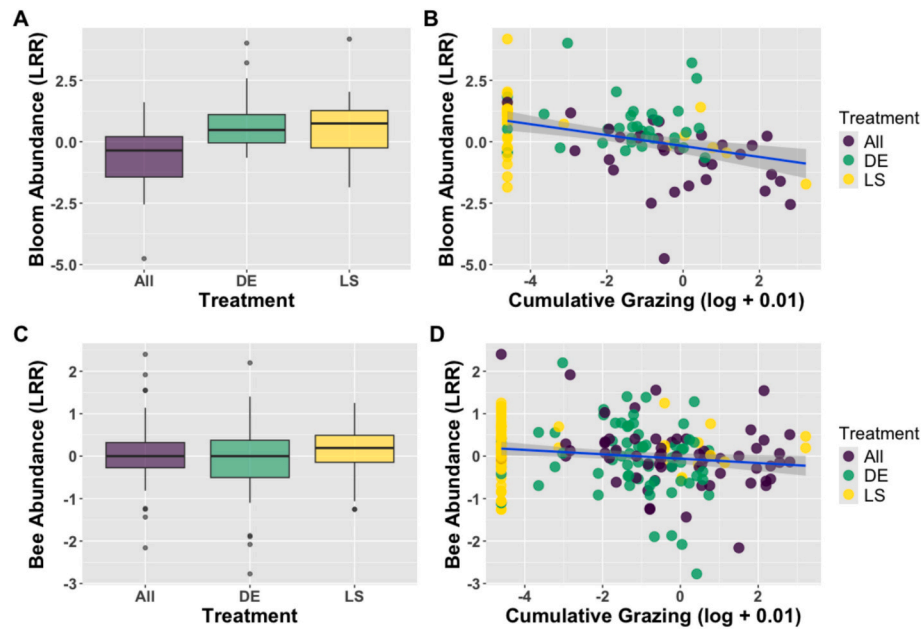


Fig. 3. The log-response ratio (LRR) of bloom abundance in response to (A) grazing treatments (ALL = extant grazing of deer, elk, and cattle; DE = deer-elk only; LS = livestock only) and (B) cumulative herbivore pressure (individuals/camera day) for each sampling event. The log-response ratio of bee abundance from blue vane traps and pan traps in response to (C) grazing treatments and (D) cumulative herbivore pressure for each sampling event. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Results from linear mixed effects models testing for an association between cumulative herbivore pressure and grazing treatment on bloom abundance and richness, and bee abundance and richness. Results with a p -value < 0.05 are in bold font.

	Covariate	Est	SE (+/-)	T-value	Df	p -value
Bloom abundance	Herbivore pressure	-0.218	0.099	-2.20	86.53	0.030
	DE	0.822	0.557	1.477	8.420	0.177
	LS	-0.352	0.578	-0.609	9.727	0.557
	All	-0.844	0.510	-1.655	5.957	0.149
	Herbivore pressure: DE	0.284	0.152	1.872	85.624	0.065
	Herbivore pressure: LS	-0.02	0.126	-0.128	86.132	0.898
Bloom richness	Herbivore pressure	0.044	0.042	1.050	85.822	0.297
	DE	0.414	0.307	1.350	7.211	0.218
	LS	0.176	0.313	0.560	7.868	0.591
	All	-0.250	0.292	-0.857	5.949	0.425
	Herbivore pressure: DE	-0.024	0.063	-0.391	85.313	0.696
	Herbivore pressure: LS	-0.036	0.0527	-0.687	85.595	0.494
Bee abundance	Herbivore pressure	-0.123	0.049	-2.419	190.94	0.016
	DE	-0.166	0.147	-1.133	11.522	0.280
	LS	0.117	0.187	0.625	28.037	0.536
	All	-0.013	0.131	-0.106	7.262	0.918
	Herbivore pressure: DE	0.040	0.073	0.559	189.927	0.578
	Herbivore pressure: LS	0.115	0.063	1.811	192.94	0.072
Bee richness	Herbivore pressure	-0.006	0.059	-0.335	96.00	0.920
	DE	0.126	0.133	0.949	96.00	0.345
	LS	0.0452	0.190	0.238	96.00	0.812
	All	0.117	0.104	1.123	96.00	0.264
	Herbivore pressure: DE	-0.004	0.088	-0.048	96.00	0.962
	Herbivore pressure: LS	-0.007	0.0757	-0.097	96.00	0.923

were significantly associated with grazing treatments across all sampling events (Fig. S2): *Sidalcea oregana* (Nutt. Ex Torr. & A. Gray) A. Gray and the *Symphyotrichum* spp. complex were associated with the CONTROL sites; *Eriogonum heracleoides* Nutt., *Epilobium brachycarpum* C. Presl., and *Navarretia intertexta* (Hook.) Benth. were associated with LS sites; *Monardella odoratissima* Benth., *Perideridia gairdneri* (Hook. & Arn.) Mathias, *Sedum stenopetalum* Pursh, and *Polygonum douglasii* Greene

were associated with DE sites. There were no indicator species associated with ALL sites. Bee community composition did not differ between grazing treatment in any month (Fig. S1; Table S5).

3.3. Dietary overlap between elk and bees

We observed 137 bee species visiting elk-preferred, 41 bee species

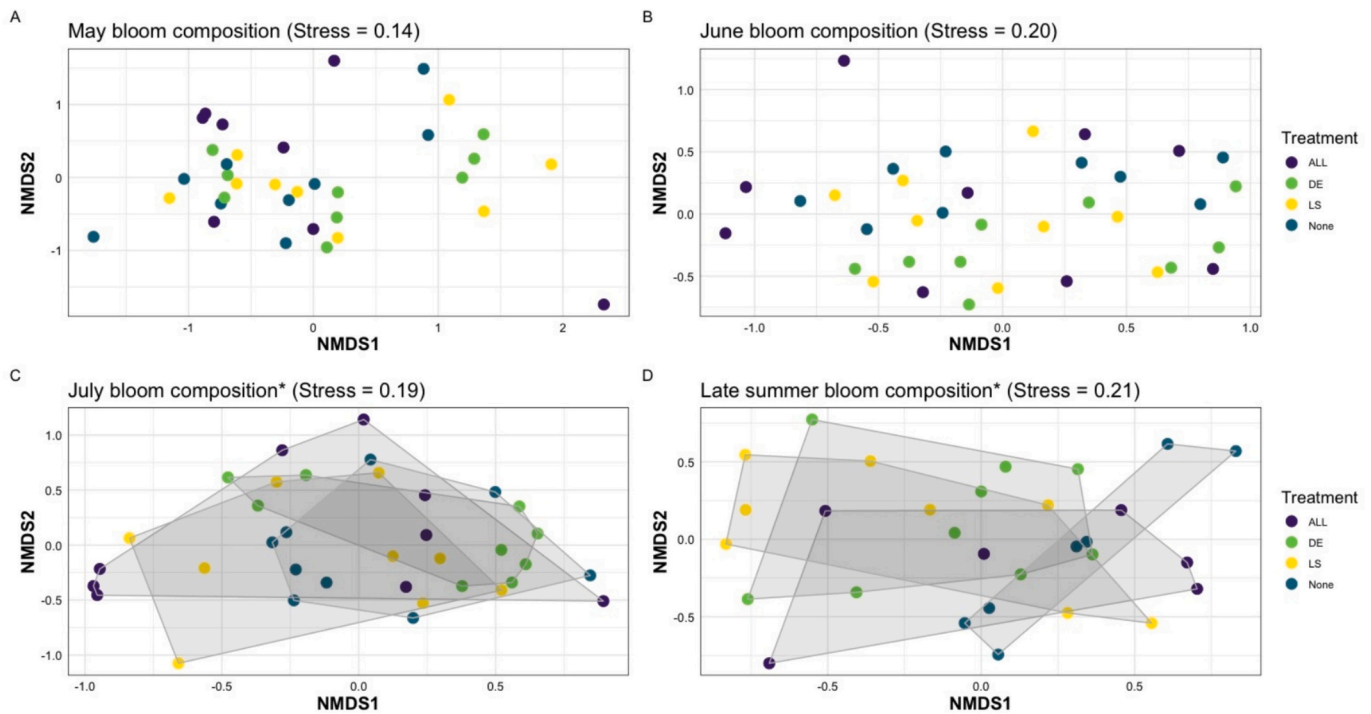


Fig. 4. Non-metric multidimensional scaling (NMDS) of bloom community composition during **A** May, **B** June, **C** July, and **D** late summer (Aug.-Sept.). Each point is the relative composition of the blooming plant community at a site, compared to all other sites during the same month. A significant association between grazing treatment and plant community composition within a sampling period (PERMANOVA, $p < 0.05$) is indicated by an asterisk, and points within a grazing treatment are surrounded by a convex hull (ALL = extant grazing of deer, elk, and cattle; DE = deer and elk-only; LS = livestock-only). The lowest stress value for a 2D-solution is reported.

Table 2

Results from separate PERMANOVAs on the effect of grazing treatment on blooming plant communities for each sampling event. Significant results (Bonferroni-corrected alpha < 0.0125) are in bold.

Month		DF	Sum Sq.	R ²	F-value	p-Value
May	Model	3	1.235	0.097	1.107	0.276
	Residuals	31	11.527	0.903		
	Total	34	12.762	1.000		
June	Model	3	1.384	0.114	1.366	0.016
	Residuals	32	10.80	0.886		
	Total	35	12.187	1.000		
July	Model	3	1.459	0.132	1.624	0.003
	Residuals	32	9.581	0.868		
	Total	35	11.039	1.000		
Late summer	Model	3	1.650	0.179	1.894	0.010
	Residuals	26	7.550	0.821		
	Total	29	9.201	1.000		

visiting non-elk preferred, and 35 bee species visiting both elk-preferred and non-preferred blooming plants. We observed 72.4% of interactions on elk-preferred, 9.1% of interactions on non-elk-preferred, and 18.5% of interactions on blooming plants with no elk preference data. Elk-preferred plants typically occupied more nested positions that are central to network structure in early and late-growing season networks (Fig. 5). A significant interaction between bloom abundance and elk preference categories showed that visitor richness was positively associated with bloom abundance for preferred plants, and negatively associated with bloom abundance for non-preferred plants (Fig. 6A; Table 3). *Diadasia*, *Agapostemon*, and *Anthophora* were the top three genera that visited elk-preferred bloom species (Fig. 6B).

4. Discussion

Ungulate species from multiple functional feeding guilds increase overall herbivore pressure on flower communities and can negatively influence bees. In this riparian system, we observed a negative response of bloom and bee abundance, but not richness, to cumulative herbivore pressure, indicating that intensive grazing reduces floral resources for bees. However, we did not observe differences in bloom or bee abundance or richness between grazing treatments, potentially because categorical treatments are not a reliable measure of herbivore intensity. For instance, unlike categorical treatments, the use of camera traps to measure herbivore pressure reflects actual numbers of individuals moving through sites. The cumulative herbivore pressure from individuals of different functional feeding guilds likely provided a more fine-scale measure of herbivory versus treatment types. Our results underscore the importance of monitoring herbivore pressure, and the composition of mixed ungulate herds, across the year to identify periods when floral resources important for bees may also be affected by herbivory or other disturbances.

The composition of late season blooming communities differed depending on the grazing treatment, potentially indicating that herbivores from functional feeding guilds strengthen selective pressures on different flower species. Cattle grazing creates opportunities for disturbance-adapted species to establish at sites by removing large amounts of grass, disturbing soils through trampling, and drying soils by increasing light availability and temperature at the ground level (Vavra et al., 2007). These mechanisms are supported by our findings from the indicator species analysis (ISA) because disturbance-adapted annuals like *E. brachycarpum* and *Navarretia intertexta* (Benth.) Hook. were relatively more abundant in the LS treatment late in the season. By contrast, the ISA revealed that perennials like *Sidalcea oregana* and *Symphyotrichum* spp. were relatively more abundant in the Control treatment, potentially because removing ungulates preserved plants that

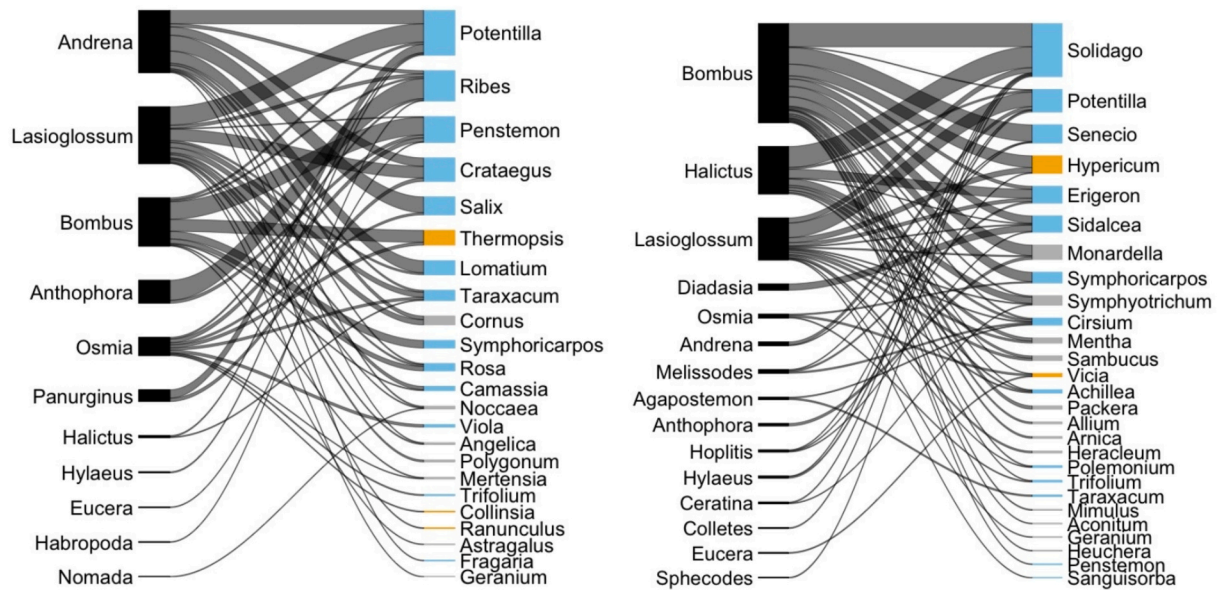


Fig. 5. Bipartite interaction networks depicting interactions between genera of bees (left side of each graph) and blooming plants (right side of each graph) that are elk-preferred (blue), non-preferred (yellow) and have no data (gray), with the early season (i.e., May and June) network on the left, and late season (i.e., July, August, and September) network on the right. Lines connecting plants and bees depict interactions, with line thickness representing the frequency with which an interaction was observed. Bee genera are ordered depending on the number of interactions observed. Singletons and doubletons were removed for legibility. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

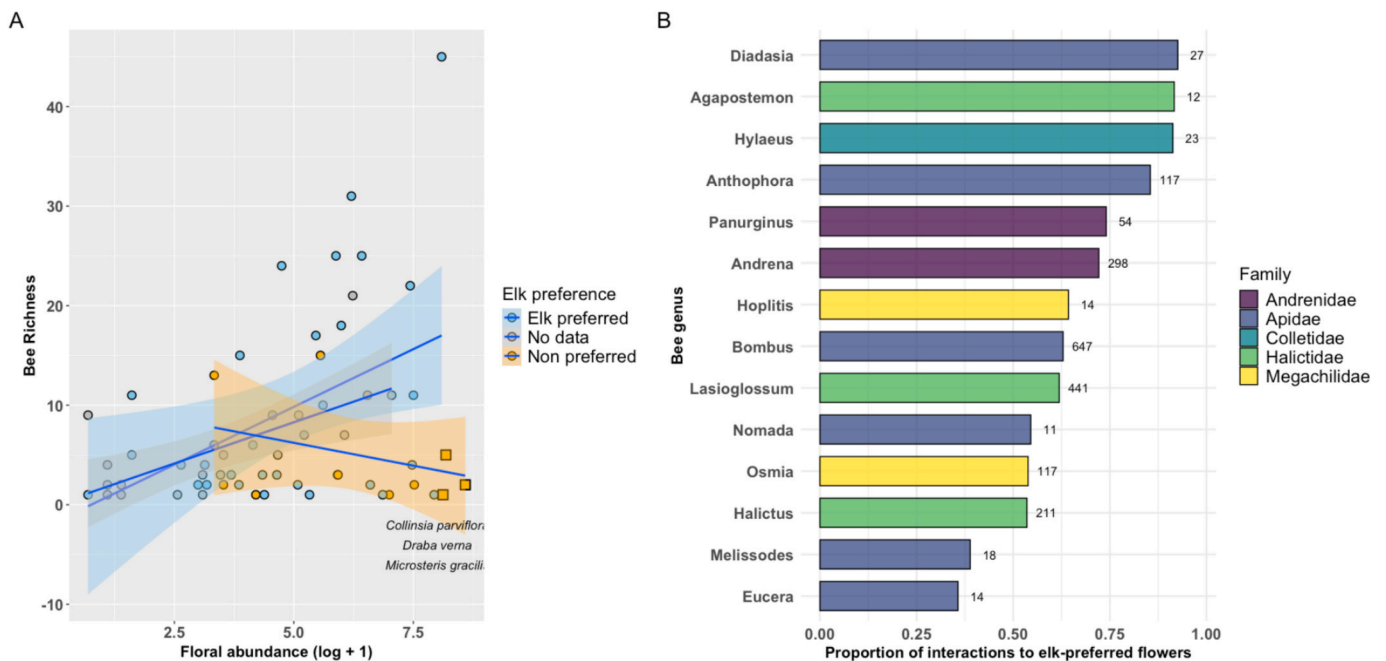


Fig. 6. **A** The relationship between abundance and visitor richness for blooming plants that are preferred, non-preferred, or have no data for dietary preference. Highlighted squares are annuals that are hyperabundant and receive few bee visitors. **B** The proportion of interactions for each bee genus that were observed on elk-preferred blooming plants. The number following each bar indicates the total number of interactions observed for that genus.

are targeted during foraging. Excluding all ungulates potentially preserves tall, herbaceous vegetation that shades the soil surface and maintains moist microclimates that are preferred by some perennial forbs. Interestingly, no flowering species were identified as indicators of the ALL treatment, which may reflect resource partitioning between ungulates from complementary functional feeding guilds. Non-overlapping grazing behaviors could select for plant assemblages reflective of the DE and LS treatments. Lastly, three of the four indicator species associated with the DE treatment (*Perideridia gairdneri* (Hook. &

Arn.) Mathias, *Sedum stenopetalum* Pursh, and *Polygonum douglasii* Greene) are avoided by elk. Dietary preferences of different ungulate species likely influence the strength of herbivory on blooming plant species.

The seasonal response of biotic communities to ungulate grazing potentially underscores how disturbance intensity changes across the growing season depending on the functional feeding guild (DeBano et al., 2025; Kimoto et al., 2012; Mitchell et al., 2023). Shifts in the bloom composition in July and late summer sampling events coincided

Table 3

Results from a generalized linear model testing for the interaction between total bloom abundance and elk preference on bee visitor richness. Results with a *p*-value <0.05 are in bold font.

Covariate	Est	SE (+/-)	Z-value	p-Value
Bloom abundance	0.261	0.033	7.840	<0.001
Elk-preference _{No Data}	-0.261	0.033	-0.940	0.347
Elk-preference _{Non-preferred}	1.797	0.476	3.775	0.001
Bloom abundance: Elk-preference _{No Data}	0.030	0.062	0.486	0.627
_{Data} Bloom abundance: Elk-preference _{Non-preferred}	-0.436	0.080	-5.449	<0.001

with the period of sharply increasing cumulative grazing pressure due to the introduction of cattle in June. Cattle were rotated across the five pastures to minimize grazing time and disturbance to vegetation communities in any one location, resulting in some sites that were not grazed until late in the year when bloom diversity was lower. Rotational grazing schemes for cattle help reduce cumulative herbivore pressure and co-manage ungulates in ways that are consistent with preserving floral resources for bees (Davis et al., 2014; Enri et al., 2017; Mitchell et al., 2023). By contrast, wild ungulates move seasonally across the landscape to track plant phenology and maximize foraging efficiency (Middleton et al., 2018). Bees in riparian areas may consequently compete with wild ungulates for flowering shrubs early in the year (Endress and Averett, 2020; Mitchell et al., 2022) and then with cattle for flowering forbs late in the year when individuals congregate around water and forb diversity is naturally lower (Glenny et al., 2023b; Havens and Vitt, 2016). Establishing ungulate resistant shrubs like *Crataegus* spp. or *Ribes* spp. in riparian corridors could aid in reducing competition for floral resources early in the year.

Elk-preferred forbs occupied important functional positions in mutualist networks and provided floral resources for specialist bees. We found a positive association between floral abundance and visitor richness for elk-preferred flowers, indicating perennial forbs are both nutritious for elk and attractive to bees. The nutrients that are stored in the roots of perennial plants are diverted to aboveground biomass each year, which can be consumed by elk. These energy reserves are also diverted into plant height, floral displays, and other pollination syndromes (Fenster et al., 2004). As a result, elk-preferred flowers may also be attractive to pollinators and visited at an equal or greater proportion to their abundance (Vázquez et al., 2007). Annuals like *D. verna*, *C. parviflora*, and *M. gracilis* were among the most abundant flowers that received little bee visitation and were not sought by elk. Annuals in this system are opportunistic and ephemeral, which leads to many blooming stems with small inflorescences that are close to the ground. The floral display of annuals may consequently remain undetected by bees and provide little nutrition for elk.

The functional role of flowers in visitation networks can help guide conservation efforts to support bees that are the most vulnerable to elk herbivory. Elk-preferred flowers like *P. gracilis*, *Solidago missouriensis* Nutt., and *Taraxacum officinale* F.H. Wigg., occupied nested positions in networks and were visited by a range of generalist and specialist bees. Elk herbivory may consequently disturb plants that are associated with the stability and resilience of mutualist communities (Bascompte et al., 2006; Rezende et al., 2007). Elk-preferred plants were also visited by the most generalist bee genera, e.g. bumble bees (*Bombus* spp.) and sweat bees (*Lasioglossum* spp.). Generalists may be more resilient to elk herbivory because they have broad diets and can switch to alternative resources if elk or other grazers reduce bloom abundance of some species (Valdovinos et al., 2013). Instead, conservation efforts geared towards pollinators in areas of high elk density may be better focused on bees that specialize on elk-preferred flowers. For instance, >90% of *Diadasia* spp. interactions were with *Sidalcea oregana*. While elk herbivory disproportionately influences attractive flowers in key functional roles,

the asymmetric structure of mutualist networks potentially buffers bee communities from herbivore disturbance.

4.1. Management recommendations

Data are too deficient for most bees to incorporate species-specific goals into land management plans, but grazing regimes can be modified in ways that are consistent with bee diversity and conservation. For example, the abundance of wild ungulates, in addition to livestock, can be considered during the planning process for forage allocation in grazing plans. Grazing plans could also consider the timing of grazing and wild and domestic ungulate densities in relation to seasonal dynamics of the native bee community (Mitchell et al., 2023). These planning processes, which direct public lands grazing in the US, provide the mechanisms for co-management of deer, elk, and cattle through guidance in how forage is allocated and cattle stocking rates are set. Considerations of management objectives for native bees in allotment management planning is part of the larger process of multiple use management on public range allotments (Black et al., 2011).

The combination of seed mixes dominated by forbs, rest and rotation grazing schedules, and virtual fences (Musinska et al., 2025) to restrict cattle movement into specific locales can support native bees by conserving vegetation communities with large and attractive floral displays. Perennials and deciduous shrubs bloom each year and are available during resource bottlenecks when other vegetation (e.g., grasses and annual forbs) consumed by herbivores is greening up or senescing (Brown et al., 2022; Collins and Urness, 1983; Spitzer et al., 2020). Perennials that bloom late in the season in semi-arid landscapes provide food resources for bees and ungulates during a time when fewer flowers are available and many plants have passed their peak nutritional value. Seeding targeted areas with mixes that have a high abundance of *Symphyotrichum* spp. and *Solidago* spp., or similar species, would increase the availability of plants as both forage for ungulates (Holechek, 1984) and floral resources for bees (Glenny et al., 2023b; Havens and Vitt, 2016). The use of virtual fencing is another promising approach to reduce cattle herbivory and cumulative herbivore pressure in riparian areas while still allowing grazing in less-sensitive habitats (Bainbridge, 2025; Campbell et al., 2020).

Bee diversity is also linked to landscape heterogeneity that is linked to ecological processes beyond ungulate management. While we did not detect an influence of grazing treatment or cumulative herbivore pressure on bee richness, communities with more individuals are likely to include rare species (Gotelli and Colwell, 2001). Additionally, bee community composition at local scales may be more strongly influenced by nesting resources (Glenny et al., 2023a), or the surrounding landscape context (Elwell et al., 2016), than floral displays. Despite a lack of knowledge about the conservation status of most bee species, providing structures to increase the physical diversity of local communities can help support the full range of resources required by most bee species in grazed systems.

5. Conclusion

Ungulates from different functional feeding guilds are valued for the range of ecosystem services provided to communities worldwide but potentially have cumulative effects linked to vegetation that may be inconsistent with biodiversity conservation (Beckett et al., 2022; DeBano et al., 2025; Garcia et al., 2025; Glenny et al., 2022; Thapa-Magar et al., 2022). Functional feeding guilds that collectively lead to diffuse and heterogeneous herbivore pressure across a landscape are likely to improve conservation outcomes for blooming plants and bees. Land managers may consider virtual fences, temporally structured grazing regimes, and specialized seed mixes to manipulate the additive herbivory pressure from different feeding guilds and preserve floral resources for bees. Concurrently, state wildlife agencies charged with managing wild ungulate populations can work with public lands

managers to develop population management plans that consider cumulative herbivore pressure in relation to species of concern, including pollinators. Adaptive management strategies of ungulates are necessary to provision ecosystem services in ways that are consistent with bee conservation.

CRedit authorship contribution statement

Will Glenny: Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Sandra J. DeBano:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mary M. Rowland:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Scott R. Mitchell:** Writing – review & editing, Methodology, Investigation, Data curation. **Skyler Burrows:** Writing – review & editing, Data curation. **Michael J. Wisdom:** Writing – review & editing. **Joshua P. Averett:** Writing – review & editing. **Bridgett Naylor:** Visualization.

Declaration of competing interest

The authors have nothing to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111952>.

Data availability

Data will be made available on request.

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